

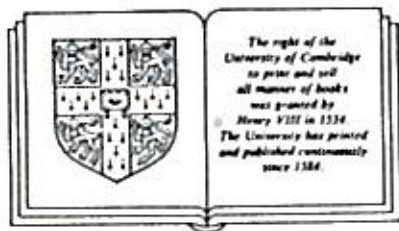
# Efficiency and economy in animal physiology

*Edited by*

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## An evolutionary perspective on the concept of efficiency: how does function evolve?

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### 10.1 ABSTRACT

The concept of efficiency is an explicit and useful vehicle for comparing the functioning of organisms and their component parts, and as such is an invaluable comparative yardstick that enables us (1) to assess function quantitatively, (2) to compare dissimilar taxa and physiological systems, and (3) to analyze the evolution of physiological systems. Efficiency is defined as the ratio of work output to chemical energy input. Efficiency should not be confused with the concepts of performance or effectiveness which measure the ability of organisms to execute behaviors. In many cases performance is a more appropriate measure of function at the organ or whole organism level than efficiency where appropriate inputs and outputs may be hard to define.

From an evolutionary perspective, efficiencies should be measured relative to an outgroup clade, not merely in comparison to the most easily obtainable species. Three major questions in the evolution of function are posed and a general phylogenetic method for investigating these questions is considered. First, how well integrated are organisms: to what extent is the functioning of subsystems at various levels of organization within organisms matched? Secondly, is there a tradeoff between efficiency and the ability to regulate function in organisms? Thirdly, does evolution optimize efficiency, and what are the evolutionary consequences of changes in efficiency? There is a tendency to believe that changes in efficiency may be causally related to evolutionary 'success', but considerable caution is needed in assigning historical importance to a presumed change in efficiency: historical hypotheses of functional sig-

nificance are difficult to test. The integration of quantitative analyses of organismal function with comparative and phylogenetic analyses will contribute to our understanding of how physiological systems evolve.

## 10.2 INTRODUCTION

The major theme of this paper is that an historical approach to the analysis of efficiency in organisms has the potential for clarifying many issues of importance to physiologists. For the most part, investigators who have used the concept of efficiency to evaluate animal structure and function have focused on proximal questions: how efficient are locomotor muscles, how efficient are particular biochemical reactions, how efficient are different species at moving from point A to point B etc. (e.g., Hildebrand, 1974; Milic-Emili and Petit, 1960; Taylor, 1980; Vogel, 1988)? As is well illustrated by many of the papers in this volume, the efficiency of both whole animals and parts of animals can be measured, and such measurements can tell us a great deal about the function of specific physiological systems. In addition, it seems to have been accepted by physiologists that measuring efficiency is a useful way to evaluate animal function.

Despite an increasing use of the concept of efficiency to study physiological systems, there are still many key questions that might fruitfully be addressed by integrating historical and phylogenetic analyses with physiological studies of efficiency. With remarkably few exceptions, there is little intellectual cross-fertilization between investigators who are interested in phylogenetic patterns to organismal design and those who study the function of specific physiological systems. And yet such interactions may prove to be an area in which considerable progress might be made on several key questions of interest to both historical and functional biologists. Thus, I feel that we need to foster an integration of quantitative analyses of organismal function with comparative and phylogenetic analyses to better understand how physiological systems evolve. The three goals of this paper are: (1) to discuss the definition of efficiency and related concepts that might be useful for evaluating organismal function, (2) to define specific issues in the study of animal function (focusing on the concept of efficiency) that might profit from an historical analysis, and (3) to discuss methodologies for analyzing historical patterns to physiological function.

### 10.2.1 The definition of efficiency

One tenet of this paper is that the concept of efficiency is a useful and explicit vehicle for comparing the function of organisms and their component parts. As noted by Blake (Chapter 2), investigators have used the concept of efficiency in different ways and have often measured it differently. Here I would like to define how the concept of efficiency will be used in this paper and emphasize how efficiency differs from the concepts of 'performance' and 'effectiveness'.

When the efficiency of any specific subsystem in an organism is measured the most common definition of efficiency is as the ratio of work output to work input or to chemical energy input (usually multiplied by 100 to give a value in percent), and this is the definition I will use here (Blum, 1970; Hildebrand, 1974; Vogel, 1988). With this definition it is easy to understand how efficiency could be measured at several different levels of biological organization. For example, in a study of muscle function during locomotion, the efficiency of sarcomere shortening could be studied by measuring the ratio of the work done by sarcomere shortening to the quantity of ATP used. Or, the efficiency of whole animal locomotion could be calculated as the ratio of the work done in moving a unit mass a unit distance to the energy used in converting stored fats or carbohydrates to ATP. In this example, the intermediate levels of the muscle fiber, whole muscle, and musculoskeletal system are bypassed in favor of measuring efficiency at two disparate levels.

This example illustrates a potential problem in extending the concept of efficiency beyond the analysis of a specific subsystem within an organism: as many levels of organization are spanned in a measure of efficiency, it becomes increasingly difficult to determine what the relevant inputs and outputs to the efficiency ratio are. Should the denominator of the efficiency ratio be ATP used, oxygen consumed, carbohydrate metabolized or raw foodstuffs needed? Depending on the problems of measuring these quantities and the assumptions that go into the measurement, different determinations of efficiency could be obtained.

While the concept of efficiency is attractive for the analysis of animal function, a key use of the concept of efficiency in comparative analyses is that it provides the ability to compare the function of organisms that may vary widely in size and shape and that may possess few homologous morphological features in common. For example, in aquatic locomotion the concept of Froude Efficiency ( $E_f$ ) is defined as the ratio of useful power produced during locomotion to the useful power plus the power



lost to the fluid (O'Dor and Webber, 1986; Trueman, 1980). Measuring  $E_f$  allows us to compare the locomotor hydrodynamics of fish (a rainbow trout has an  $E_f$  in the range of 0.61 to 0.81) to that of a squid (with an  $E_f$  of 0.2 to 0.3; Alexander, 1977; O'Dor and Webber, 1986). The difference in Froude Efficiency between these taxa appears to be largely due to the pulsatile nature of squid locomotion in contrast to swimming by trout in which force is being nearly continuously applied to the fluid. By using a common currency such as Froude Efficiency to measure animal function, we gain the ability to make comparisons that would otherwise be both difficult and qualitative. The ability to compare divergent taxa quantitatively is not a trivial advantage of a general concept like efficiency. It is vital for comparative and historical analyses of organismal function that quantitative comparative analyses be feasible.

The concept of efficiency should not be confused with the notion of performance, the ability to execute a behavior (Arnold, 1983; Emerson and Diehl, 1980; Garland *et al.*, 1988; Reilly and Lauder, 1988; Wainwright, 1987). In many cases performance is a more appropriate measure of function at the whole organism level than efficiency, where appropriate inputs and outputs may be very hard to define. Reasonable performance measures might include the percent of time that a prey escapes from a predator, the number of prey captured per feeding attempt, maximum burst speed, or the distance moved in a fixed time interval. Performance measures the ability of an animal to execute a particular behavioral test or the effectiveness of an animal at accomplishing a task. Performance *per se* does not measure the energetic expenditure or the efficiency of a behavior under the definition used in this paper.

Measures of performance may also be applied to specific organs or physiological systems. For example, the strength of skeletal elements might be compared by measuring the ratio of strength to skeletal mass. The specific strength of bones may vary within an organism and between taxa, and provides a measure of skeletal effectiveness at supporting loads. Measurements of specific strength reflect skeletal performance or effectiveness, not efficiency.

### 10.2.2 *Major questions in the evolution of function*

In the last twenty years major changes have occurred in the way comparative and phylogenetic analyses are conducted (Brooks, 1984; Brooks and Wiley, 1988; Eldredge and Cracraft, 1980; Ridley, 1983; Wiley,

1981). The vast majority of such research has been concerned with phylogenetic patterns of structure and the transformation of morphology. Relatively little attention has been given to how function evolves and to historical changes in organismal function. Furthermore, many hypotheses about physiological function may be tested with a comparative and historical approach, and yet only a very few investigators have succeeded in integrating physiological and historical analyses (e.g. Huey and Bennett, 1987).

Since the area of the evolution of function has received so little attention, there are many important questions that could be addressed, but as yet few answers. Here I would like to focus on three issues that are particularly relevant to the concept of efficiency, and use the analysis of efficiency to consider methodologies for investigating historical changes in organismal function.

*(1) How well integrated are organisms: to what extent is the functioning of subsystems at various levels of organization within organisms matched?* The issue of how well integrated organisms are is one of the oldest in biology. The nineteenth century morphologist Cuvier clearly expressed the view that organisms are highly integrated and that all parts are intercorrelated and must function as a coordinated whole. Cuvier states that ... all the organs of an animal form a single system, the parts of which hang together, and act and re-act upon one another; and no modifications can appear in one part without bringing about corresponding modifications in all the rest (Russell, 1982, p. 35). Indeed, Cuvier's view of the high degree of functional integration in complex morphological systems might even be seen as an indirect intellectual antecedent to the concept of 'symmorphosis' proposed by Weibel and Taylor (1981). Weibel (1984, p. 60), for example, in a discussion of the respiratory system, notes that 'in a functional system as complex as the one we are considering there is important interaction and cross-influence from one part to the other.' The concept of 'symmorphosis' suggests that structures at several levels of organization will be closely matched to their functional roles, and that there is a high degree of integration among levels. The issue of organismal integration is an important one in analyses of the evolution of function as the extent to which functions and structures are highly integrated might be expected to reflect the degree to which evolutionary changes may occur independently at different levels of design.

The question of how tightly linked changes at different levels of orga-



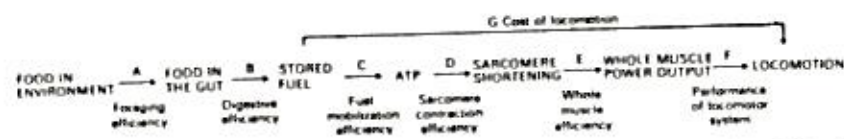


Fig. 10.1. Schematic diagram of a series of steps in the transformation of food in the environment to locomotor activity by an organism. The efficiencies of five processes (A to E) are shown. Step F represents measurement of locomotor performance and step G indicates measurement of the cost of locomotion (e.g., Daniel and Webb, 1987). A key question in the evolution of function is the extent of congruent change in phylogeny among the efficiencies at each link in this functional chain.

nization are is one that can be approached empirically in an historical context. If, for example, we wished to study the efficiency of locomotion, we might define a series of physiological processes or steps from the acquisition of food in the environment to movement across the ground (Fig. 10.1). The efficiency of each step in the chain can be measured to obtain a picture of the efficiency with which food is transformed to stored fuel, ATP is converted into length changes in sarcomeres, sarcomere contraction is converted into muscle length changes, etc. (Fig. 10.1: steps A to G).

In order to ask a question about the evolution of efficiency and the nature of the relationship among efficiencies at these different levels of organization, we need to measure efficiencies at several levels in several species. The analysis of one species alone does not tell us anything about the transformation of function in an historical sense. In addition, data from several species, even when analyzed in a traditional allometric fashion, also fail to inform us about patterns of historical change as allometric analyses assume that all points (species) are independent when in fact they are not (Felsenstein, 1985). This critical point is discussed in more detail below. First, let us consider the efficiencies of several different functions in several species.

If we had data on the efficiencies of energy conversion at levels C, D, E, and G (Fig. 10.1) from several species (Fig. 10.2: species a to n), then we could map the distribution of each efficiency onto a phylogeny to examine how evolutionary changes at each level have occurred (Fig. 10.2). The central idea in the historical analysis of function is the examination of congruent change among variables on a phylogeny. The phylogeny provides the historical context while the extent of congruent change provides the measure of evolutionary association. If, for exam-

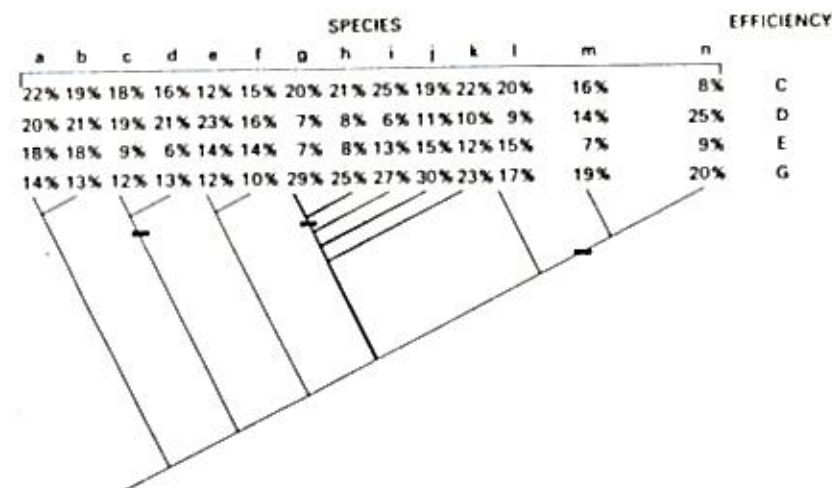


Fig. 10.2. Diagram of a cladogram representing the phylogeny of a group of species (a to n). Above each species the value of efficiency for each of three links in the chain shown in Fig. 10.1 is given as well as a measurement of the cost of locomotion. Note that the clade drawn in thick lines shares high values for the cost of locomotion and fuel mobilization efficiency, but low efficiencies of sarcomere contraction. The black bars on the stems leading to species c and d, g and h, and m and n represent the occurrence of these species in a novel habitat. No other species on this diagram are found in that habitat.

ple, changes in values of efficiency C (Figs. 10.1 and 10.2) always occur with changes in values of efficiency D or E, then we can say that, in the historical sense, these two levels of functional design are linked and have changed in concert. From the distribution of efficiencies in Fig. 10.2, one can see that one clade (shown in thick lines) is characterized by a higher cost of locomotion (G), a higher fuel mobilization efficiency (C), but a lower efficiency of sarcomere contraction (D) relative to other (outgroup) clades (such as c, d, e, and f; Fig. 10.2). This pattern indicates that there is no necessary positive physiological coupling between the cost of locomotion and sarcomere contraction efficiency. Since clade n in Fig. 10.2 exhibits both low fuel mobilization efficiency (C) and high sarcomere contraction efficiency (D) we can refute the hypothesis suggested by species g to l that these two efficiencies are necessarily inversely related.

Such a hierarchical analysis may provide insight into the causal basis of differences among species in behavior. If, for example, a clade in



Fig. 10.2 were found to have a relatively high cost of locomotion (and was therefore less efficient than other related clades) but was found also to have a high whole muscle efficiency (link E in Fig. 10.1), then one might wish to examine in detail the next link in the chain (i.e., link F in Fig. 10.1) for a possible explanation for this discrepancy. Perhaps those species with high costs of locomotion and high whole muscle efficiencies have an arrangement of the muscles and bones (such as shorter lever arms, less muscle mass, etc.) that produces the observed reduced performance.

In order to appreciate just how important a phylogeny is in interpreting the pattern of association between two physiological variables (such as those shown in Fig. 10.2), consider one alternative method of analyzing such data. If each species is treated as an independent data point and the data analyzed by correlation and linear regression analyses, one would estimate that the Pearson product-moment correlation (between the cost of locomotion (G) and efficiency D (Figs. 10.1, 10.2)) for these species to be -0.731 with a probability of 0.003. This would indicate a highly significant relationship between these two measures of physiological function. However, a scatterplot of these efficiencies shows that this relationship is determined largely by the species in one clade (Fig. 10.2: species g to k). Without this clade included (or with the mean value for the clade used), the correlation drops to -0.131 and is not significantly different from zero. The phylogeny illustrates how one could be misled using a traditional allometric analysis: by assuming that all the species (including g to k) are independent, the regression degrees of freedom are greatly inflated. In fact, as the phylogeny of Fig. 10.2 illustrates, species g to k should be treated as one point since high values for G and low values for D evolved once in the ancestor of that clade.

Several methods have been proposed in the literature for quantitatively analyzing data such as those presented in Fig. 10.2, and these will not be considered in detail here (see, for example, Cheverud *et al.*, 1985; Felsenstein, 1985; Huey and Bennett, 1987; Losos, in press; Martins and Garland, in preparation; Swofford, 1984;). The general goal of these numerical analytical techniques is to allow reconstruction of states at the nodes on the phylogeny, and to provide a quantitative assessment of the extent of congruence among characters. As yet I know of no examples using the concept of efficiency where such a phylogenetic analysis has been attempted. The key message from a simple example such as that shown in Fig. 10.2 is that the related questions of organismal integration and functional evolution are empirical ones: via a

combined phylogenetic and physiological analysis, considerable insight may be gained into the evolution of function.

Two subsidiary questions to the issue of organismal integration may also be addressed within a phylogenetic context. Firstly, do energetically demanding environments produce a close match of efficiencies at different levels of organization? For example, one might imagine that locomotion in a dense medium (such as water) might cause an increase in efficiency at each step in the chain of processes leading to work being done on the environment (as in Fig. 10.1). One way to ask such a question would be to add to Fig. 10.2 a measure of environmental demands on each species. One would then like to know the extent of historical congruence between changes in environment and changes in efficiency at each level. For example, three pairs of species in Fig. 10.2 exhibit low values of whole muscle efficiency (Fig. 10.2: species c, d; g, h; m, n). If it could be demonstrated that each pair of species also shares some aspect of the environment (indicated by the black bars in Fig. 10.2), then one would have demonstrated an historical correlation between the invasion of the novel environment and the presence of low whole muscle efficiency.

As an aside it is also important to note that the species exhibiting low whole muscle efficiency in Fig. 10.2 show only three independent evolutionary acquisitions of the novel habitat and muscle function. Although a total of six species are involved, only three independent historical origins have occurred. The use of six separate points in a graph showing a correlation between environment and muscle efficiency would be incorrect; there are three 'historical degrees of freedom'.

Secondly, does independence of efficiencies at different levels permit (in the historical sense) diversity of functions? In other words, is it true that the less tightly integrated two links in a chain such as that shown in Fig. 10.1 are, the greater the extent of divergence between the functions controlled by the those levels? Does a reduction in the level of integration permit independent specialization of function at each level, even though the overall efficiency of function across several levels may be less?

This question could be examined by comparing two clades that differ in the historical pattern of change in efficiencies. For example, consider one clade in which an historical analysis (such as that of Fig. 10.2) reveals that changes in the efficiencies of whole muscles in the limbs (link E in Fig. 10.1) are always associated with changes in sarcomere contraction efficiencies (link D in Fig. 10.1). This finding would suggest that there is a functionally important link that is not broken phylogenetically



between these two levels. In contrast, a second clade of species (when subjected to a similar historical analysis) may exhibit considerable independence of change in links D and E. Is it true that this second clade exhibits, for example, a greater locomotor repertoire than species in the first clade?

The issue of the tradeoff between the tight integration of function among levels and flexibility of design has received little attention, but may be an important question in analyses of the evolution of function.

*(2) Is there a tradeoff between efficiency and the ability to regulate function in organisms?* The idea that there is a possible tradeoff of high efficiency at some particular level of design for other aspects of physiological function (such as power) has been discussed extensively in the literature (Gnaiger, 1987). However, to my knowledge there have been no attempts to test the historical hypothesis that regulatory ability and efficiency may make mutually conflicting demands on functional systems. From an evolutionary perspective this hypothesis could be tested by examining the level of congruence between some measure of regulatory ability (perhaps response to a perturbation) and efficiency at a particular level (such as whole muscle efficiency; level E in Fig. 10.1). The ability of an animal to modulate the activity of a particular biochemical pathway may be inversely proportional to the efficiency with which that pathway operates because of functional constraints imposed by the demands of high-efficiency output. While the analysis of biochemical efficiencies is widespread, I am not aware of any attempts to consider such a tradeoff from an historical perspective.

*(3) Does evolution optimize efficiency, and what are the evolutionary consequences of changes in efficiency?* There are many functional biologists who believe that evolution does optimize efficiency (or structures, functions, and behaviors) but the evidence from evolutionary biology does not support this position. Townsend and Calow (1981, p. 7) claim that 'We believe it can safely be assumed that natural selection will tend to produce organisms which are *maximally* effective at ... foraging, defending themselves, storing fat, growing, etc.' (italics mine), and Alexander (1982: p.1) states that 'Evolution by natural selection is a process of optimization.'

Such views of evolution stand in contrast to numerous analyses of both the process of evolution itself, the genetic basis of evolutionary change, and results from morphological and paleontological research

(e.g., Cheverud, 1984; Gould, 1977, 1980a, b; Lewontin, 1974; Raup, 1972; Stearns, 1983). In particular, Lewontin (1983, p. 368) in his commentary entitled 'Elementary errors about evolution' states that 'it is simply factually incorrect to describe evolution as always being an adaptive or optimizing process.' Lewontin (1983) notes that (1) random events may result in the fixation of even deleterious genes in a population, (2) the environment is nearly always fluctuating (and is thus in a non-equilibrium state) which will cause features of organisms to be in a state of flux, and (3) genetic linkages among traits and pleiotrophic effects will cause selection on one character to cause a correlated response in other characters. Any of these three situations could produce structures, functions, or behaviors that are not close to some pre-defined optimal value. These observations, coupled with the fact that only very rarely have models of organismal function been successful in predicting performance without a proliferation of constraints and assumptions leads one to conclude that it must certainly be the exception rather than the rule when organismal design conforms to a previously defined optimal value. In addition, it is critical to realize that statements about natural selection and its role in shaping organismal design are nearly always assumptions invoked to justify the use of an optimality model, not a demonstrated fact (Cracraft, 1981).

Given that it is the rule, rather than the exception, that structures have multiple functions, and that both structures and functions are used by organisms to perform multiple biological roles (in the sense of Bock and von Wahlert, 1965; Gans, 1988) it is perhaps more useful to investigate patterns of functional interaction and how such patterns have changed than to take the procrustian approach of fitting organismal function into preconceived notions of how animals should be built.

I view the question of evolutionary increases in efficiency as an empirical one and urge that a priori assumptions about optimality or the nature of evolutionary change in physiology do not limit attempts to discover actual historical sequences of transformation. The analysis of efficiency within a phylogenetic context (e.g., Fig. 10.2) may show that, on average, the efficiency of some particular physiological system has increased over time. On the other hand, the efficiency of the same system may have decreased in other clades. Changes in efficiency that may be observed are certainly in no way a necessary product of the evolutionary process.

One notion that has achieved some currency in past discussions of the evolution of function is the idea that increases in efficiency are some-



how responsible for the evolutionary 'success' of groups of animals. One example of this approach is the analysis of the evolution of locomotor function in ray-finned fishes. The transformation of the shape of the tail in ray-finned fishes is a textbook example of structural and functional change that is presented in nearly every comparative anatomy and paleontology text (e.g. Romer, 1966; Romer and Parsons, 1986; Carroll, 1988). Early ray-finned fishes possess a heterocercal tail in which the notochord extends into a dorsal lobe which is larger than the ventral lobe. When the tail is swept from side to side, the asymmetrical tail generates an epibatic (lift) force tending to cause the body to rotate about its center of mass. Lift forces to compensate for this rotation must be generated by other fins so that the fish can swim in a straight line. Teleost fishes are characterized by a novel (homocercal) tail structure in which the dorsal and ventral lobes are nearly equal in size (Gosline, 1971; Lauder, 1989; Marshall, 1971) and homocercal tend not to generate moments about the center of mass. The transformation from the primitive heterocercal condition to a derived homocercal tail has been taken to reflect an increase in locomotor efficiency that has had an important part in the origin of the 25,000 species of teleost fishes (Gosline, 1971; Lund, 1967). As summarized by Affleck (1950, p. 365), 'Because the fin of a homocercal tail swings about a vertical axis it is more efficient as part of the propulsive unit than the fins of a heterocercal tail'. Leaving aside the question of whether the efficiencies of the two types of tail have been actually measured, it may be proposed that an increase in efficiency of tail function at one phylogenetic level may lead to increased speciation and diversification in clades that possess the more efficient structure or function. The logical structure of such an argument has been considered in detail elsewhere (Lauder, 1981, 1982; Lauder and Liem, 1990) but it is critical to note that at each phylogenetic level there will be many characters that are uniquely associated with any given clade. In fish phylogeny, there are other characters that arise concordantly with the transformation of the tail. How are we to argue that the change in the tail alone (just one out of many changes) is causally related to speciation in ray-finned fishes. It is an easy error to assume that the origin of a feature or an increase in efficiency at one phylogenetic level is causally related to the subsequent history of a group, but our ability to test the historical effects of one such unique event is extremely limited (Lauder, 1981; Lauder and Liem, 1990), and such hypotheses often reflect our desire to see causal historical relationships where only a correlation has been demonstrated.

### 10.3 CONCLUSIONS

Historical analysis and hypothesis testing has only recently begun to achieve widespread attention, and the influx of historical analytical techniques and concepts into physiological analysis is still in its infancy. However, there is much to be gained by attempting a marriage of the disciplines of physiology and historical biology. The benefits of such cross-fertilization in other areas are clearly evident (for example, the liaison between neurobiology and ethology to produce the area of neuroethology has generated many new insights into organismal function). In physiology, we have only begun to understand the most general patterns to the evolution of function. Many questions have yet to be defined. In some systems, so few species have been studied that an historical or comparative analysis is just not possible. However, the concept of efficiency, used by so many workers on so many different physiological systems, offers us a potentially valuable avenue to begin to ask key questions about the evolution of function. The notion of efficiency, when precisely defined and applied, is an invaluable comparative yardstick that enables us to assess function quantitatively and to compare dissimilar taxa and physiological systems. Such comparisons form the foundation of any attempt to study the evolution of function.

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