NEW DIRECTIONS IN ECOLOGICAL PHYSIOLOGY

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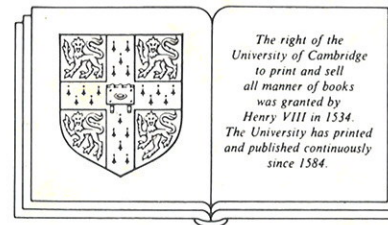
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The analysis of physiological diversity: the prospects for pattern documentation and general questions in ecological physiology

MARTIN E. FEDER

Introduction

Ecological physiology historically has emphasized the demonstration of pattern rather than the testing of hypotheses. Initially these demonstrations focused on extreme environments (e.g., patterns of physiological adaptation in deserts, high elevations, and cold environments), major taxa (e.g., responses to cold in insects vs. fishes vs. mammals), and the limits of physiological performance. More recently, a focus on less extreme environments and on animals undergoing routine behaviors has burgeoned alongside the initial foci. As outlined in the preceding chapters, the collective elaboration of pattern in ecophysiological attributes has been both a productive and a scientifically successful enterprise in its own right. Moreover, it has established a firm foundation for the effective proposition and testing of general hypotheses.

The discussion of goals for ecological physiology accordingly has usually focused on whether patterns are sufficiently documented rather than what major questions should be answered (but see Prosser, 1975, 1986b). Clearly, the documentation of ecophysiological pattern is still incomplete. Many unexamined species and populations remain to be reconciled with already recognized patterns, and perhaps novel patterns remain to be recognized. The future demonstration of pattern in ecophysiology, however, is justifiable only if the scientific advances it promises are commensurate with the effort expended in the process. The purpose of the first part of this essay is to consider whether the documentation of pattern in ecological physiology has reached the point of diminishing returns, and whether further case studies of physiological adaptation to the environment will really more firmly establish the conclusions upon which these patterns bear. My analysis suggests that the further elaboration of pattern in ecophysiological attributes is not a sufficient agenda for the future, although it will continue as a natural consequence of any ecophysiological investigation. Therefore, the field should also emphasize the proposition and solution of general questions, some of which are outlined in the second part of this essay.

The status of pattern documentation

What questions have historically justified the demonstration of pattern in ecophysiological attributes? Will elaboration of these patterns; study of additional attributes, species, and environments; or the discovery of novel patterns yield more robust answers to these questions?

1. *Do physiological characteristics vary among organisms, or are physiological characteristics similar in different organisms?*
2. *Is the variation in physiological attributes random, or does it show pattern?*

A first important documentation is that variation in physiological attributes is near universal. Ecological physiologists have recognized that many (if not all) physiological functions (e.g., metabolic rate, enzyme-substrate affinity, lethal temperature) vary among populations of a species, species of a genus, genera of a family, and so on (e.g., Table 3.1) (Prosser, 1955, 1973, 1986a), although physiological variation within populations is less well characterized (Prosser, 1955; Chapter 7). A second important documentation is that variation in physiological attributes is not random, but evidences pattern, structure, or regularity (e.g., see Figure 3.1). We do not see all possible combinations of physiological characteristics or unbounded variation in physiological attributes.

These findings are now second nature to ecological physiologists. That these conclusions are taken for granted does not minimize their significance. Diversity in physiological attributes is not a necessary outcome of evolution. It could be, as is somewhat more the case at the cellular level, that all organisms are similar in physiological attributes, with interindividual, interpopulational, and interspecific differences manifested solely in terms of gross behavior, population structure, and so forth. It could be, just as all animals contain carbon and water, that the inner workings of all animals are the same as in the laboratory rat. The finding of physiological diversity tells us something nonobvious but fundamental about the nature of life.

Recognition of pattern in physiological diversity is significant for several reasons. First, it is a necessary condition for the emergence of a "nomothetic" ecological physiology, that is, a field concerned with the lawlike properties reflected in repeated events, as opposed to the idiographic description of unique unrepeated events (Gould, 1980c). Second, the occurrence of pattern makes the field tractable. One need not study every species or higher taxon individually to understand its ecophysiological attributes; a smaller number of carefully chosen exemplars will suffice. Third, the recognition of pattern enables distinction between those explanations with which pattern is consistent and those explanations of which pattern is exclusive. At least in
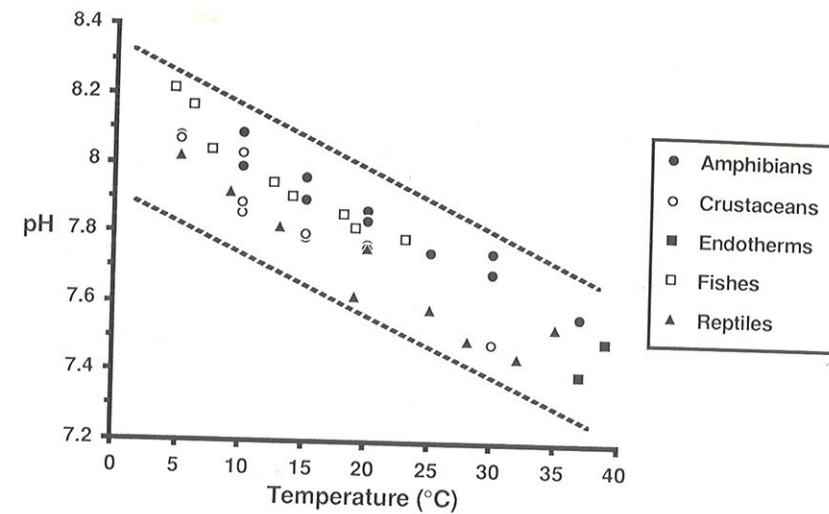
TABLE 3.1 An example of variation in a physiological characteristic, the hydrogen ion concentration in the blood

Blood [H⁺] (nmol/L)[a]	Species	Reference [b]
6.03	*Salmo* (rainbow trout)	75
6.76	*Salmo* (rainbow trout)	75
8.13	*Rana* (bullfrog)	46
8.13	*Cryptobranchus* (salamander)	c
8.32	*Rana* (bullfrog)	46
8.51	*Carcinus* (crab)	48
9.12	*Salmo* (rainbow trout)	75
9.33	*Callinectes* (crab)	48
9.55	*Chelydra* (snapping turtle)	46
10.23	*Bufo* (toad)	46
10.96	*Rana* (bullfrog)	46
11.22	*Salmo* (rainbow trout)	75
12.02	*Pseudemys* (red-eared turtle)	60
12.30	*Scyliorhinus* (dogfish shark)	41
12.59	*Cryptobranchus* (salamander)	c
12.88	*Uca* (fiddler crab)	48
13.49	*Rana* (bullfrog)	46
13.80	*Carcinus* (crab)	48
13.80	*Scyliorhinus* (dogfish shark)	41
14.45	*Bufo* (toad)	46
15.14	*Pseudemys* (red-eared turtle)	60
15.14	*Salmo* (rainbow trout)	75
15.85	*Callinectes* (crab)	48
16.22	*Carcinus* (crab)	48
16.22	*Scyliorhinus* (dogfish shark)	41
16.98	*Carcinus* (crab)	48
16.98	*Callinectes* (crab)	48
17.38	*Chelydra* (snapping turtle)	46
17.38	*Uca* (fiddler crab)	48
17.78	*Rana* (bullfrog)	46
17.78	*Cryptobranchus* (salamander)	c
20.42	*Bufo* (toad)	46
23.99	*Pseudemys* (red-eared turtle)	60
25.70	*Pseudemys* (red-eared turtle)	60
26.92	*Bufo* (toad)	46
28.84	*Chelydra* (snapping turtle)	46
31.62	*Pseudemys* (red-eared turtle)	60
31.62	*Gallus* (chicken)	46
32.36	*Uca* (fiddler crab)	48
35.48	*Pseudemys* (red-eared turtle)	60
39.81	*Homo* (humans)	47

[a]As do most physiological characteristics, the hydrogen ion concentration in the blood varies considerably. The data are arranged from the lowest to the highest concentrations of hydrogen ions, without respect to phylogenetic affinity. Variation is evident among individuals of the same species, among species, and among higher taxa. Overall, variation is approximately sixfold.

[b]References correspond to reference numbers in Reeves (1977).

[c]Moalli, Meyers, Ultsch, and Jackson (1981).

FIGURE 3.1 An example of pattern in physiological diversity. When the data of Table 3.1 are expressed as pH and then plotted as a function of the body temperature at which the measurements were made, a regular pattern emerges: pH falls as body temperature increases. This pattern is evident in numerous phylogenetic groups. The similarity between the slope of this relationship and the slope of the relationship between the pN of water (i.e., the pH at which pH = pOH) and temperature suggests that animals regulate their blood pH at a constant "relative alkalinity" (Rahn, 1967), perhaps to maintain a constant protein net charge state (Reeves, 1977). One insight to emerge from this analysis is that ectotherms do not lack the ability to regulate blood pH (as was previously thought), but are able to regulate blood pH at whatever level their current body temperature dictates.

theory, we have a means by which to determine the "general gas laws" by which species are governed (Schopf, 1979). Finally, the patterns that have been recognized point out several important general questions, which are discussed in the latter portion of this chapter.

Having granted that physiological diversity and pattern in physiological diversity are significant findings that have justified ecophysiological analysis in the past, is either sufficiently inconclusive to merit more substantiation? With the exception of variation within populations (Chapter 7), the answer is obviously no.

3. Is the pattern of physiological diversity consistent with the effects of natural selection?

A third (if not the central) contribution of ecological physiology is its relating variation in physiological characters within populations, species, or higher taxonomic levels, to the environments in which organisms live. In a synthetic sense, what is being demonstrated is that the physiology of organisms is in "equilibrium" (Lewontin, 1969; Eldredge and Gould, 1972) with their environment.[1] The physiological characteristics of individuals in a population are adequate to support maintenance, growth, and reproduction in the particular environment in which the population occurs. Thus, as environments vary from place to place, the physiological characteristics of their inhabitants vary correspondingly (e.g., Figures 3.2 and 3.3). As Dobzhansky (1951) put it: "The enormous diversity of organisms may be envisaged as correlated with the immense variety of environments and of ecological niches which exist on earth."

The demonstration of equilibrium between physiological and environmental variables has long held the highest of priorities for ecological physiologists; indeed, the field has invested much of its energies into assembling the best possible case for equilibrium. The resultant advances have been conceptual, technical, and empirical. We have, for example, realized that physiology-environment correlations should be sought at the molecular and cellular levels as well as at higher levels (Prosser, 1986a; Chapter 5), that "behavior" and "morphology" should be considered coequal with "physiology" in our analyses (Bartholomew, 1958; Gans, 1986; Chapters 1 and 2), that microclimate may be more meaningful than gross climate in characterizing physiology-environment correlations (Bartholomew, 1958), that organisms from extreme environments may exhibit very obvious physiology-environment correlations (Chapter 2), that function of a part in the context of a whole organism may yield different insights than function of a part in isolation in an experimental preparation (Chapter 1 in Gans, 1974; Huey and Stevenson, 1979), and so on. The issue at hand, however, is whether additional documentation of "equilibrium" will advance the field conceptually. First, let us consider the conceptual advances that documentation of equilibrium has afforded.

Gould (1980a) has characterized the seminal contribution of George Gaylord Simpson to the biological sciences as the demonstration that the fossil record is consistent with the major features of evolutionary theory. Lest this seem trivial, imagine if Simpson had found that the fossil record were inconsistent with evolutionary theory! In much the same sense, the documentation of equilibrium between physiological attributes and environmental variables is of fundamental importance because it is consistent with how Darwinian natural selection ought to work: natural selection, acting in diverse local environments, is expected to result in changes in physiological variables that enhance the Darwinian fitness of each physiological variant in the particular environment in which it finds itself. In evolutionary time, the cumulative
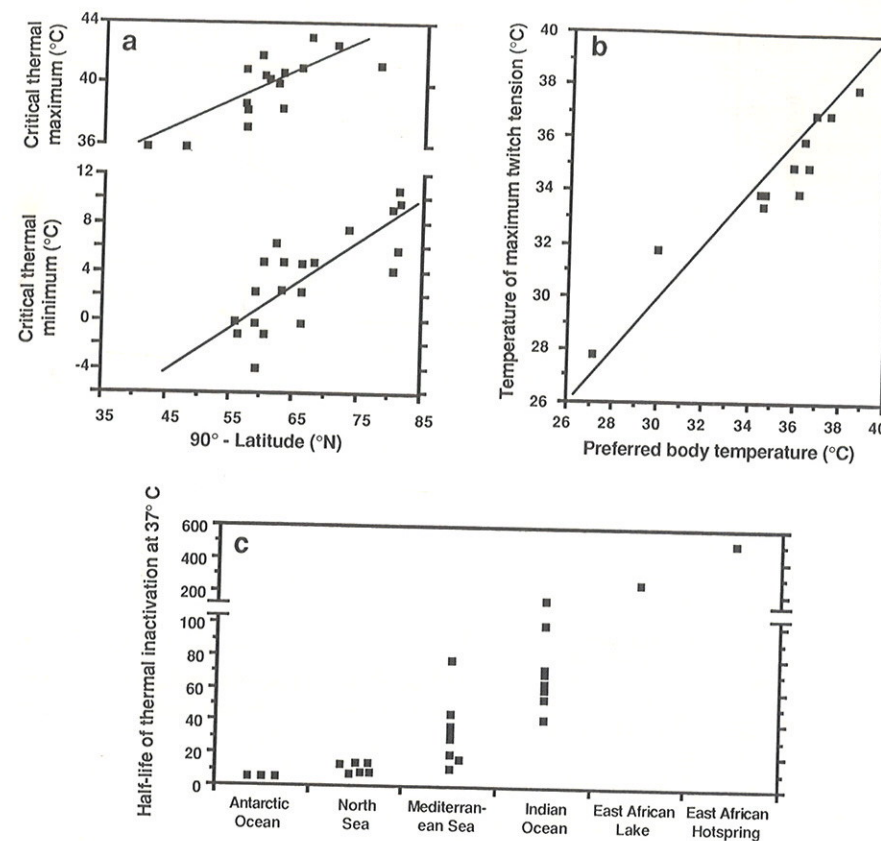
FIGURE 3.2 Three examples of "equilibrium" between different physiological characteristics of species and an environmental variable, temperature. (a) Indices of thermal tolerance, the critical thermal maximum and the critical thermal minimum, are correlated with latitude in amphibian species. Tropical species are able to tolerate warmer temperatures than are temperate species, whereas temperate species are able to tolerate cooler temperatures than are tropical species. (From Snyder and Weathers, 1975.) (b) The temperature at which skeletal muscle develops maximum isometric twitch tension is positively correlated with the preferred body temperature in lizard species. (From Licht, Dawson, and Shoemaker, 1969.) (c) The time required for exposure to a warm temperature (37 °C) to inactivate myofibrillar ATPase is positively correlated with the thermal environments of fish species. (From Johnston and Walesby, 1977.)
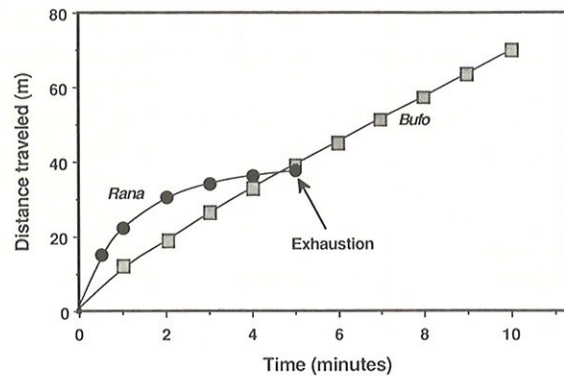
	Bufo [Toad]	Rana [Frog]	Reference
ATP generated during intense activity [μmoles ATP/(g mass · min)]			
Aerobic	3.7	1.8	b
Anaerobic	4.0	13.7	b
Aerobic [% of total]	48%	12%	
Blood oxygen capactiy (Vol %)	15.0	10.5	c
Blood volume (% of body mass)	15.7	7.0	c
Ventricle mass (% of body mass)	0.311	0.118	c
Enzyme activity [μmoles product/(g muscle·min)]			
Citrate synthase	20	7	d
Lactate dehydrogenase	75	108	d
Phosphofructokinase	0.69	1.21	a
Contractile properties of skeletal muscle			
Contraction time (msec)	71	54	d
Maximum rate of tension rise [kN/(m^2·msec)]	3.13	4.25	d

FIGURE 3.3 An example of "equilibrium" between the physiological characteristics of species and the ways in which they exploit their environment. Toads (*Bufo*) respond to threat or stimulation with relatively slow and steady movement or static defense; frogs (*Rana*) respond with intense activity, including powerful leaps (Bennett, 1974). Toads may forage widely for mates or prey, traveling up to 40 m in an hour (Wells and Taigen, 1984); frogs are more sedentary, often sitting and waiting for food to come to them. This difference is reflected in laboratory measurements of locomotor performance (shown in graph from Putnam and Bennett, 1981): *Rana* exhaust in five minutes whereas *Bufo* do not fatigue. Physiological characteristics that favor sustained activity and aerobic metabolism have greater values in *Bufo* than in *Rana*. Physiological characteristics that favor rapid or intense activity have greater values in *Rana* than in *Bufo*. [Sources: a, Bennett (1974); b, Bennett (1980); c, Hillman (1976); d, Putnam and Bennett (1983).]

result of this natural selection should be equilibrium between physiological and environmental variables. Insofar as the major empirical finding of ecological physiology is not inconsistent with this prediction, ecological physiology "supports" natural selection. Indeed, the phrases "not inconsistent" and "supports" are too weak, given the variety and intricacy of cases in which "physiology" and "environment" are correlated.

Consistency of ecophysiological patterns with Darwinian theory was not always as obvious as it seems today. The New Synthesis, which explicitly set forth the ways in which the biology of populations could be used to examine the predictions of Darwinian theory, emerged in the 1930's and 1940's. Most of the now-senior practitioners of ecological physiology were at relatively early stages of their professional careers at this time (Chapter 2). For example, George Bartholomew (Chapter 2) recollects discussion of the then-new New Synthesis while an undergraduate, a time at which the concept of a cline was novel and geographic variation in physiological characteristics relatively unexplored. Importantly, the extent to which analyses of physiological diversity could shed light on evolutionary mechanisms, and vice versa, was unknown. Thus, at the time a general exploration of ecophysiological variation represented a significant and fundamental expansion of knowledge with important implications for both physiology and evolutionary biology. Moreover, a physiological approach to adaptation appeared to offer special promise in that the functional consequences associated with variation in organismal characteristics could be observed directly. The question of consistency with natural selection was thus a more than adequate justification for past documentations of "equilibrium." Is it an adequate justification for the future?

Ecological physiologists have assembled an enormous number of case studies that establish "equilibrium" beyond any reasonable doubt. Bartholomew (Chapter 2) has outlined some of the variants of this pattern: related species that achieve different physiological solutions in dissimilar environments, unrelated species that achieve common physiological solutions to similar problems or in similar environments, and so on. This is a significant achievement, but also a significant problem: the field is a victim of its own success. It can continue to document physiology-environment correlations with as yet unexamined variables or in as yet unexamined species, but further studies will not appreciably augment the overwhelming mass of evidence already assembled to demonstrate "equilibrium." We know in advance what the outcome of additional studies will be: some feature of organismal function will be correlated with some environmental variable. If the documentation of equilibrium is a foregone conclusion, it is time to emphasize other issues.

4. Does variation in physiological characteristics provide useful insights into the phylogenetic relationships of animals?

Ecological physiology, it is sometimes claimed, may offer us key insights into the phylogenetic relationships of organisms by furnishing useful systematic characters (Ross, 1981). Ross (1981) questions this claim because of the high frequency of convergence evident in ecophysiological attributes. Similar variation in physiological characters in distinct taxa (i.e., convergence) will yield the appearance of phylogenetic affinity where none exists. Clearly, all physiological characters do not show convergence, and therefore could be of use in constructing phylogenies. Difficulties of convergence aside, the literature of systematics suggests that physiological characters have seldom, if ever, been of real value in resolving phylogenies; indeed, most phylogenies are now so well established that even contradictory physiological characters are unlikely to prompt their revision (Ross, 1981). Thus, the likely provision of systematic insight is an insufficient justification for the continued documentation of ecophysiological patterns in the future.

5. Does the analysis of physiological diversity disclose general principles of adaptation?

Natural selection, acting upon unrelated organisms facing similar environmental challenges, sometimes has resulted in similar modifications of physiological characteristics. This modification is not random or unstructured, but itself follows certain rules or patterns that may be defined as "general principles" of ecological physiology. For example, one nonuniversal but recurrent feature of organisms is countercurrent exchange; another is the pH-temperature relationship depicted in Figure 3.1; a third is the energetic consequences of hovering flight (Chapter 2). A final justification for the continued documentation of ecophysiological patterns is that it will disclose such "general principles" of physiological adaptation, which are held to have inherent value as unique and important contributions to the body of scientific knowledge.

A major difficulty of general principles of ecophysiology is that their definition is so inclusive. The minimum conditions that must be satisfied to establish a general principle are two fold: the physiological attribute it concerns (1) must have been derived independently in at least two lineages; and (2) must be recognizable as shared by these lineages. Thus, it is difficult to name a physiological attribute that does not reflect or define a general principle. Unlike mechanics, in which a small number of laws suffice to describe diverse phenomena, the general principles of ecological physiology are as numerous as instances of convergence in ecophysiological traits. Although describing all "general principles of ecological physiology" may provide considerable grist for the mills of more mechanistic physiologists, it is a never-ending process with a probable low yield of conceptual advances for our understanding of the process of physiological adaptation and its consequences.

Conclusion

Darwin (quoted in Medawar, 1969) belittled unbounded inductivism by likening it to going into a gravel pit, counting the pebbles, and describing their colors. Although Darwin's point is well taken, it is also true that wholesale inspection of pebbles will sometimes reveal diamonds or gold nuggets. In the final analysis, the effort expended and the likelihood of reward will jointly determine whether the inspection of pebbles is a worthwhile activity; consulting a geologist beforehand may increase the likelihood of reward and is therefore justifiable. Ecological physiologists need to consult one another as to whether the likelihood of future scientific reward justifies the continued description of adaptive patterns, which strategies bring large rewards most rapidly, and how limited resources should be apportioned among alternative investigative strategies.

Opinions are mixed as to whether the mine of ecophysiological patterns is played out and whether mining is a rewarding industry. At one pole, Carl Gans (1978) has argued that "all animals are interesting," that in the hands of a competent scientist even the most mundane of species can reveal important insights, and that therefore any unexamined species is an appropriate subject for investigation. At the other, Robert Platt (1964) has held that a field advances most quickly by the structured proposition and solution of general questions that transcend particular cases, and that studies not addressing such questions directly are wasted effort. While he agrees that the field should focus on general questions, George Bartholomew (1982, 1986, personal communication) feels that general answers are seldom forthcoming and that the best that can be expected is "a variety of different and highly specific answers to any given general biological question" (1986, p. 328). Each of these viewpoints is meritorious. Nonetheless, the research traditions of ecological physiology are such that Platt's approach has been relatively unexploited, which is why I wish to advocate it here.

Traditional pattern documentation, which has made numerous valuable contributions to our understanding of life, may be approaching the point of diminishing returns because the objectives that justify its continuance either have been met or cannot be met. By contrast, unsolved general questions abound concerning the nature of adaptation. A focus on these general questions may do much to invigorate the field. To this end, I have attempted to identify some questions from evolutionary organismal biology that may have particular relevance for ecological physiology and may serve as a complement to the elaboration of ecophysiological pattern. These questions uniformly predate modern ecological physiology in general and this essay in particular; Simpson (1953), for example, outlined many of the same questions, as did Darwin before him. Ecological physiology as a field has seldom addressed these questions directly, however. Because ecological physiologists already have immense knowledge of ecophysiological diversity and are able

to quantify organismal function, they may be in a unique position to make substantive contributions to the solution of these general questions.

General issues for the future

The physiological systems that ecological physiologists study have numerous components and intricate regulatory mechanisms. All components and controls must work together adequately for organisms to grow and reproduce. Complexity is the first of three interrelated issues embodied in the questions that follow. If general conclusions in ecological physiology are to be realistic, they must account for complexity and its evolution. The challenge, for example, is not only to explain how a particular enzyme facilitates speed in a particular species, but to explain how natural processes have yielded a coadapted complex of traits involving multiple systems, which as a group facilitate locomotion. Such processes obviously involve the transformation of numerous interacting physiological components from a primitive to a derived state. Can we realistically endorse classical microevolutionary processes as a sufficient explanation of physiology-environment equilibrium (Eldredge, 1985)?[2] Can a reductionist approach suffice to explain the evolution of complexity?

Insofar as "physiological adaptations" are complex and involve interacting systems, a second general issue is the constraint of each interacting component on the form and function of all others. Constraints can take several forms: acute conflicts between interacting components of physiological systems (Chapter 15); mechanical or structural constraints (Gould and Lewontin, 1979); linkage of physiological characteristics to ongoing processes of growth, development, and reproduction (Chapters 10 and 16); and genetic linkage that may prevent the independent evolution of physiological traits (Chapter 9). As a result of such constraints, the physiological characteristics of animals may be more appropriate for ancestral environments than extant ones, or may be prevented from approaching "optimal" function (Chapter 4). A general question concerns the extent to which constraint limits equilibrium between physiological variables and environmental ones, or retards the rate of equilibration between "physiology" and "environment."

Ecological physiologists usually attribute physiological diversity to the equilibration of organism and environment. A major implication of constraint, of course, is that not all variation in physiological characteristics is due to adaptation to the environment; some is surely due to other factors, which in turn may have either strong or negligible links to the environment. This implication does not obviate ecological physiology, but necessitates the elevation of phylogeny, history, ontogeny, and size to full equality with environment as potential explanations for physiological diversity. We need to know how important each of these additional variables has been in the deter-

mination of physiological diversity before we can accurately attribute physiological variation to adaptation. What follows are several specific questions or issues that touch upon these general issues of complexity, constraint, and attribution.

Equilibrium: testing the key assumptions

The consistency of equilibrium with its usual explanation, adaptation to the environment via natural selection, implies only that the data do not preclude the explanation; that is, the explanation is a plausible one (Gould, 1980c). Consistency does not imply that the data require such explanation or that alternative explanations can be excluded, nor does it demonstrate that physiological diversity has arisen through natural selection or even that the necessary conditions have been met for the origin of physiological diversity through natural selection. Ecological physiologists know far more about the potential results of natural selection than about how (and if) it actually modifies physiological features. A reasonable starting point for addressing these concerns would be to examine the key assumptions upon which rest the implied evolution of physiological characteristics. The assumptions are as follows:

For evolution of physiological traits to occur by natural selection, physiological traits must vary among individuals within populations and this interindividual variation in physiology must be heritable. Are these conditions met?

Although we know much about physiological variation among species, higher taxa, and (to a lesser extent) populations within species (but see Chapter 5), we know comparatively little about physiological variation among individuals within populations (Chapter 7). A key assumption underlying the implied evolutionary origin of physiological diversity is unsubstantiated.

Through electrophoresis and other techniques, population geneticists have revealed an unexpected degree of diversity in protein and gene structure in natural populations. Why not simply assume that physiological traits are similarly diverse? Most of the traits discovered through modern biochemical techniques have not yet been assigned any particular function. Indeed, a whole school of evolutionary theory has grown up about the assumption that most enzyme polymorphisms are selectively neutral (Chapters 5 and 8). If many or most traits are selectively neutral, then the amount of variability in these traits will be related to stochastic factors (e.g., the mutation rate) and have little bearing on "equilibrium." We know that this is not always the case. For example, we know that alternative forms of hemoglobin profoundly affect organismal function (Chapter 5), and hence hemoglobin phenotypes are not as variable as they might otherwise be. We need to charac-

terize physiological variation in enough populations to know whether in general it is large and random (which might indicate the absence of stabilizing selection), small (which might indicate stabilizing selection, limited genetic variability for physiological traits, "constraint," or some other explanation), or nonexistent (which would have profound implications for the origin of physiological diversity). Chapter 7 considers progress in this area.

Few would be surprised by findings of physiological diversity within populations, and the general description of this diversity may be just a matter of time. By contrast, the genetic basis (or, more specifically, the heritability) of the traits that ecological physiologists typically think about may prove more elusive. For obvious reasons, we know most about relatively simple traits encoded for by a small number of genes with a limited number of alleles; the further we depart from this condition, the less we understand. The traits ecological physiologists think about are, unfortunately, often complex. The expression of complex traits may represent the control of numerous genes (Chapters 5 and 8) or relatively few (e.g., Alberch, 1980,[2] and Chapter 9). The interaction of environmental factors with gene expression, especially during development, may play a major role in expression of complex traits (Alberch, 1980). The sorting out of these possibilities, and an understanding of the relative importance of each alternative means of expression of complex traits remain tasks for the future. To accomplish these tasks, we must know the mechanisms by which simple changes in DNA base-pair sequences are translated into complex organismal traits. Such knowledge exceeds the grasp of modern molecular biologists (at least for the moment), and yet we are faced with extrapolating this knowledge to the characters of interest to us as they appear in natural populations. Characterization of heritability, fortunately, requires "only" the breeding of the animals of interest or knowledge of their pedigrees. Some (but not enough) heritabilities have been determined for complex traits of interest to ecophysiologists in both wild and domestic species (Arnold, 1986). However, heritability is but a partial answer to a larger question.

Is variation in physiological characters related to variation in fitness?

Physiological variation must affect fitness for evolution to occur by natural selection. Given their focus on adaptation, ecological physiologists have assembled relatively few data bearing on whether variation in physiological traits within natural populations actually affects fitness (Arnold, 1983; see also Arnold's concluding remarks in Chapter 17). We typically do not know, for example, whether an animal with a greater than average metabolic rate or a lower than average cost of transport contributes more offspring to its population than an average conspecific.

The available data are mixed in their support of a close linkage between physiological variation and Darwinian fitness. Several exemplary efforts have

demonstrated the fitness consequences of allelic variation at loci coding for metabolic enzymes (Koehn, 1984; Watt, Carter, and Donohue, 1986; see also Chapters 5 and 8). These studies are of special interest in light of arguments that much isozyme variation is selectively neutral (Chapter 5). However, the traits these studies examine are not the complex, multi-component "adaptations" or performance traits (e.g., salt glands, the fish gill, sprint speed, maximum oxygen consumption) of interest to many ecophysiologists. More studies have failed than have succeeded in demonstrating a relationship between variation in such complex physiological characters and fitness. For example, relationships are not evident between sprint speed and survivorship in juvenile lizards (Raymound Huey, personal communication); between metabolism, calling, and courtship success in toads (Wells and Taigen, 1984); or between either metabolism or locomotor performance and foraging success within a toad population (B. Michael Walton, personal communication).

Do no such relationships exist, or are our analytical procedures inadequate to resolve them? In his recent review of selection in natural populations, Endler (1986) cited direct demonstrations of selection for 314 different traits in 141 species. Thus, demonstration of relationships between variation in complex physiological traits of animals and their Darwinian fitness (if any relationships exist) is possible. It may, however, be very difficult. Endler (1986) enumerates ten classes of reasons for failing to detect selection when it is present, and seven classes of reasons for mistaken detection of selection when none is present in natural populations. This enumeration specifies two general problems for the demonstration of physiology-fitness relationships.

First, programmatic demonstrations may well require larger sample sizes, more extensive fieldwork, more regular sampling, longer-term studies, and greater background knowledge of natural history than most physiologists are willing to provide or granting agencies are willing to support. As Endler (1986, p. 98) has stated: "There are no shortcuts in demonstrating natural selection." Indeed, many of the investigations listed above may have failed to detect physiology-fitness relationships because of inadequate sampling. The stringent requirements for characterizing such relationships raises an important point: if the failure to demonstrate a relationship between variation in complex physiological traits and fitness can always be attributed to inadequate methodology as opposed to obvious alternative explanations (e.g., that of no relationship), then the search for such relationships becomes a self-fulfilling prophecy rather than a scientific enterprise.

Second, variation in the complex physiological trait of interest must be large in relation to the breadth of the physiology-fitness function (Figure 3.4). Many ecophysiologists, I think, infer from demonstrations of physiology-environment equilibrium that the physiological traits they study are under strong stabilizing selection such that any variation in these traits is tanta-
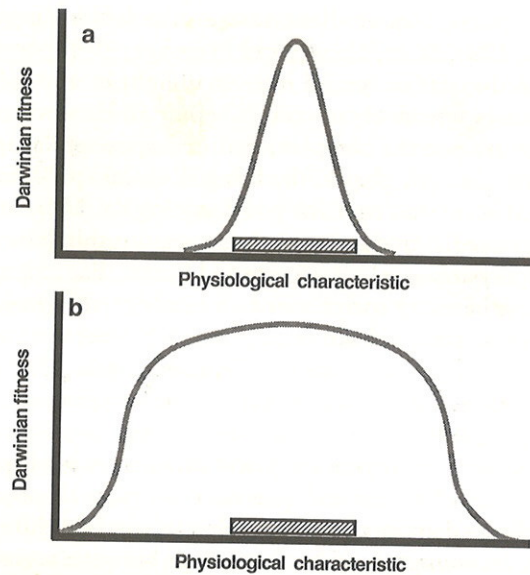
FIGURE 3.4 Two possible extreme forms of the relationship between physiological variation and fitness. For a given amount of variation in a physiological attribute (indicated by the horizontal bar), stabilizing selection would be strong in (a) ("peak" model) and weak in (b) ("plateau" model). An open question for ecological physiologists is how the actual relationships between physiological variation and fitness are distributed between the two extremes shown.

mount to a decrease in fitness (Figure 3.4a). Too high a hemoglobin oxygen affinity for a given elevation or too low a gill surface area for a given body size, for example, would compromise fitness according to this logic. If, however, interindividual variation is either minor or negligible with respect to the breadth of the physiology-fitness function (Figure 3.4b), detection of a relationship between physiological variation and fitness will be difficult or impossible. Because we have so little knowledge of the actual shape of the physiology-fitness relationship for complex traits, we cannot predict how serious this problem may be.

Given these problems, it may make sense for ecological physiologists to avail themselves of natural populations whose demography and natural history are already understood in detail (e.g., Clutton-Brock, Guinness, and Albon, 1982), and only then to perform physiological studies on characteristics of likely importance during actual differential mortality or reproduction in the field. In addition, ecological physiologists should be alert for unusual situations in which differential mortality or differential reproduction

is clearly in evidence (e.g., Lande and Arnold, 1983). Such instances may not be representative ones, but they may be productive. Ecological physiology badly needs more studies of whether variations in physiology among individuals are correlated with fitness.

Do the physiological characteristics that promote Darwinian fitness of individuals within a population also promote the persistence of species through evolutionary time?

Ecophysiologists often ascribe the persistence of species and higher taxa in evolutionary time to the various physiological (and other) adaptations in the individual organisms that comprise the species. However, the nexus of recent interests in mass extinctions, macroevolution, punctuated equilibria, and clade selection suggests that features other than adaptations in the traditional ecophysiological sense may be important in determining the evolutionary persistence of species and higher taxa, as follows (Stanley, 1979; Gould, 1982; Vrba and Eldredge, 1984; Jablonski, 1986): the persistence of a taxon will be related to the difference between the speciation rate and the extinction rate. Characteristics that promote speciation include physiological (and other) adaptations in the traditional sense; but also include a population structure of small isolated populations, a low capacity for dispersal, extinction of major competitors, and heterogeneity of a taxon's habitat through evolutionary time. The latter two "characteristics" are functions of biotic, abiotic, geological, and stochastic processes unrelated to the taxon's adaptations. In addition to traditional adaptation, geographic range may affect extinction rate. All else being equal, widespread taxa are less likely to become extinct, apparently because the chance of some populations not being affected by a given extinction event is maximized (Figure 3.5). From study of Cretaceous marine bivalves and gastropods, Jablonski (1986) has suggested that during catastrophic mass extinctions, these rules change (p. 132):

Many traits of individuals and species that had enhanced the survival and proliferation of species and clades during background times become ineffective during mass extinctions, and other traits that were not closely correlated with survivorship differences become influential.

In other words, the present array of physiological types may have little to do with the long-term adaptation of their ancestors to ancestral environments, and may reflect mainly that their ancestors by chance were at the right place at the right time during mass extinctions.

These suppositions have not been examined exhaustively and are strenuously disputed by some evolutionary biologists, in part because relevant data are difficult to assemble from the fossil record. Because of their familiarity with extreme environments (Chapter 2), ecological physiologists may be in a unique position to assess the relative importance of adaptedness in the tra-
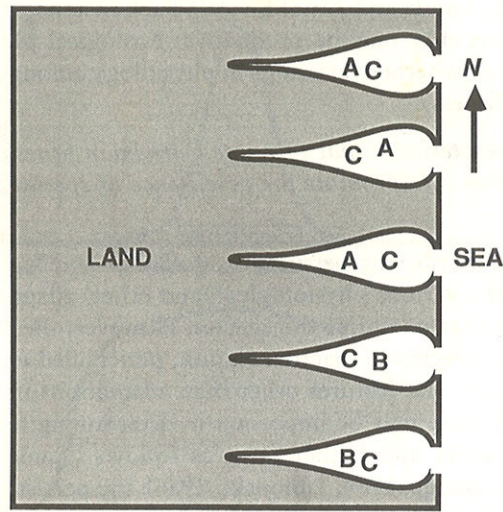
FIGURE 3.5 A hypothetical example of "species selection" by differential extinction rates. Suppose three species of flying insects whose aquatic larvae are intolerant of seawater are distributed in estuaries along a north-south transect as shown. Suppose occasional storm fronts moving from east to west inundate the estuaries with seawater. Storms affecting the southernmost two estuaries are likely to exterminate all populations of species B but only some populations of species C. Storms affecting the northernmost three estuaries are likely to exterminate all populations of species A but only some populations of species C. All else equal, species C is likely to persist longer than the other species through the years. The physiological attributes that engender the persistence of C are those promoting dispersal of adults, not those promoting salinity tolerance of larvae.

ditional sense versus the other characteristics enumerated above in determining species' persistence in the face of local extinctions. Are species with otherwise equivalent physiologies but different geographic ranges and population sizes differentially prone to extinction? To what extent are physiological features that promote dispersal or hinder gene flow key to a taxon's survivorship? Can one quantify extinction rates in extant populations by comparing the performance of species in replicates of transient environments (e.g., drying vernal ponds) or habitat islands (e.g., mountain tops or rare host plants) (e.g., see Smith, 1983)? The implications of these suppositions, if proven, for ecological physiology are enormous: physiological adaptation in the traditional sense may be of secondary importance in promoting the persistence of species and higher taxa. The implication of physiological findings for the hypotheses of "species selection" may be equally large.

Peaks or plateaus: How is variation in physiological attributes related to variation in fitness?

Assuming that physiological variation and fitness are related, many ecological physiologists discuss physiological adaptations as if attributes of an organism typically represent the result of natural selection for the "correct" solution to pressing problems posed by the environment, such that deviation from the "correct physiology" in any particular environment will have dire consequences for fitness. This is typified in Figure 3.4a: either too high or too low a level of a physiological attribute will reduce fitness in a given environment or situation. A sharp peak is certainly implicit in textbook discussions that stress the importance of spectacular adaptations (e.g., salt glands, countercurrent exchangers, unusual metabolic pathways), which presume that animals lacking such adaptations would soon succumb to their environments. A sharp peak is also implicit in the numerous ecophysiological studies demonstrating a close correlation between the physiological attributes of animals and the environments from which they come (e.g., hemoglobin P_{50} vs. altitude, water vapor conductance vs. numerous biotic and abiotic variables in bird eggs, preferred body temperature vs. thermal performance optimum in lizards); animals often appear not to express too high or too low a P_{50}, water vapor conductance, thermal tolerance range, thermal optimum, etc. for the specific circumstances in which they find themselves.

An alternative view (Figure 3.4b) is that, within limits, variation in any given physiological attribute is relatively unimportant in its consequences for fitness; only very large deviations from the "correct" physiology (or gross environmental change) should reduce fitness. As long as gross limits are not exceeded, fitness should be unaffected if an Arctic fox's coat were 10% less insulative than normal, if a lizard were to regulate its body temperature with 5 °C less precision, and so on. Thus, according to this view, the shape of the fitness function is a plateau and not a peak. Why might this be so? In real environments, stochastic variation in abiotic factors, in motivation, and in the distribution and abundance of predators, prey, or potential mates may be so large as to confound the importance of any particular "physiological adaptation" in a given instance. Real animals have multiple redundant safety systems; other components (e.g., behavior; see Chapter 2) can often compensate for deleterious variation in any particular physiological component. Physiological traits may be maintained when not essential (or maintained in excess) either because selection for their removal is slight or because their expression is linked to or constrained by the need to express some essential characteristic (Chapter 9).

A question for ecological physiologists is how actual physiology-fitness relationships are distributed between the extremes represented by the peak model and the plateau model. If most relationships more closely resemble the

plateau model than the peak model, then natural selection should maintain not a close match, but only a loose correlation between physiological characteristics and environmental ones. As the environments of populations change, selection might permit physiological evolution to lag well behind environmental change. Dissimilarity in physiological attributes could not be equated with dissimilarity in fitness.

How is this question to be answered? Although direct characterization of physiology-fitness relationships in the field would be preferable, the difficulties with this procedure are numerous, as outlined above and by Endler (1986). The few direct characterizations that have been attempted for complex physiological or performance characters thus far support the plateau model better than its alternative. The fineness or the coarseness of the equilibria between physiological and environmental variables constitutes a less direct examination of these alternatives. The data, however, need to be examined carefully for bias; demonstrations of poor relationships or no relationships may seldom be published (but see McNab, 1971). A largely unexploited tactic in animal ecological physiology for distinguishing between these alternatives is the field experiment; application of this tactic to plants has already yielded significant insights (e.g., Clausen, Keck, and Hiesey, 1940). One variant is to alter a physiological characteristic experimentally, release the experimental subjects, and observe if and by how much fitness is affected. Another is to alter *environmental* variables in the field (e.g., by moving animals to novel environments), follow free-ranging experimental subjects, and observe by how much fitness changes and how rapidly a new equilibrium is achieved between physiological and environmental characteristics (e.g., Berven, 1982). According to the "peak model," even small changes in physiological characteristics or environmental variables should cause large changes in fitness; according to the "plateau model," only large changes in physiological or environmental variables should cause changes in fitness. For example, Silberglied, Aiello, and Windsor (1980) removed presumptive protective coloration from the wings of butterflies, released and recaptured the insects, and surprisingly found that the absence of protective coloration did not affect the vulnerability of insects to natural predators. Closer approximations of fitness are essential. We may already know, for example, that an inability to regulate body temperature precisely causes a 10% decrement in locomotor speed in a foraging lizard; we need to know whether the 10% decrement in speed translates into a negligible change, a 10% change, or a 100% change in fitness (Huey, 1982).

The historical trajectory of physiological complexity

The evolution of any complex physiological adaptation involves the historical transformation of numerous interacting components from a primitive to
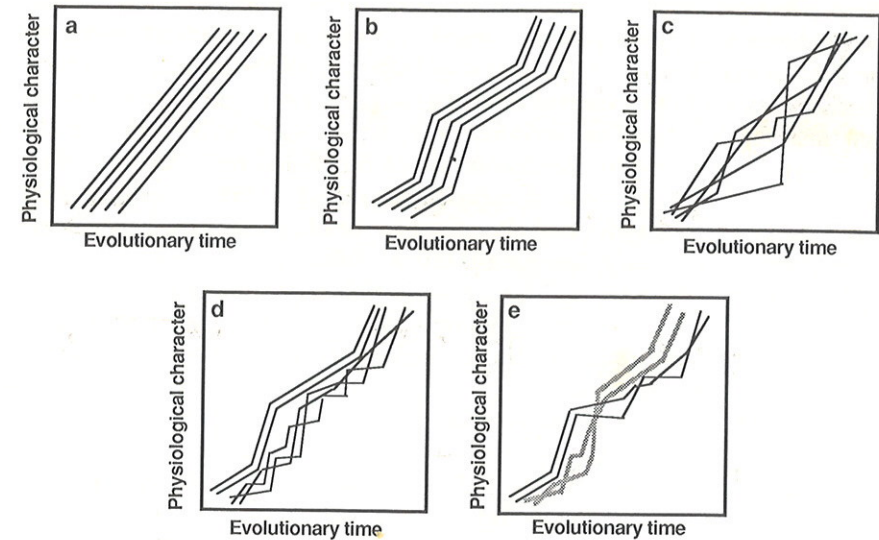
FIGURE 3.6 Possible patterns of change in the components of a complex physiological trait through evolutionary time. All component traits might change in parallel, at a constant rate (a) or at a variable rate (b). Each component trait might change at its own rate, with extreme variations prevented by selection (c). Some component traits may be rate-limiting, with others free to vary as long as they do not depart drastically from the rate-limiting components (d). If so, some components may be rate-limiting early in an evolutionary transformation [solid lines in (e)], whereas others may be rate-limiting later in a transformation [shaded lines in (e)].

a derived state. The patterns of such transformations are of interest because they may inform us of both the mechanisms of the transformation and the constraints upon them (Simpson, 1953; Lauder, 1981, 1982).

Consider the tranformation from a salivary gland of an ancestral reptile to a salt gland, from a reptilian kidney to a mammalian one, from the unshelled egg of an amphibian or fish to the shelled egg of a reptile or bird, or from the respiratory system of an inactive mammal species to that of an active mammal species. Transformation could occur in at least five ways (Figure 3.6): (a) parallel and gradual evolution of component traits; (b) parallel but punctuated evolution of component traits; (c) independent evolution of component traits; (d) rate of evolution limited by a single component or set of components; (e) rate of evolution limited first by some components and then by others.

Parallelism among the evolutionary trajectories of the components of a complex trait should bear some relationship to the control of expression of

these components. If, for example, expression of each of a series of components shares a common genetic control, a common biochemical precursor, or a common developmental pathway (Alberch, 1980; Lauder, 1981), the components might be expected to change at similar rates through evolutionary time. Lauder (1981) has proposed that major coordinated changes in the phenotype may occur by the dissolution of functional links between components or the duplication of components (Lauder, 1981). Such changes would be consistent with rapid alterations in the phenotypic trajectory interspersed with periods of relative stasis (Figure 3.6b).

By contrast, "independent" (i.e., nonparallel) evolutionary trajectories of components of a complex trait (Figure 3.6c) might reflect (1) the absence of common control of expression of the components and (2) selection. Complex traits presumably play some functional role in their primitive state and while evolving as well as in their derived form. Variation in the components of a complex trait thus should be constrained during evolution by the need to maintain the coordinated function of the complex trait. If common control of expression of the components is absent, then each component should exhibit some variation independent of the other components' variation; however, selection should operate against any animal in which an important component varies so much that function of the complex trait is compromised. Additionally, if components differ in their importance to the function of the complex traits, less important components may be less constrained and more important components may be more constrained in their evolutionary trajectory (Figure 3.6d and e).

Distinction among these models is possible by tracing the evolutionary trajectories of components of complex traits in independently derived lineages of organisms (Lauder, 1982). In many ways, transformational analysis may be a simpler task for paleontologists than for ecological physiologists. Paleontologists can measure directly the rate of change of components as expressed in the fossil record, whereas ecological physiologists are limited to inferring trajectories from their end points. This is, however, not an impossible task for ecological physiologists, particularly if the analysis is conducted in a phylogenetic context [see Lauder (1981, 1982) and Chapter 4]. Although few ecological physiologists have attempted to distinguish among these models of evolutionary trajectory directly, many have an excellent intuitive "feel" for patterns and mechanisms of variation within individuals. For example, the ever-expanding literature on acclimation clearly documents the large extent to which components of an organism can vary independently of one another, and the control of acclimation (i.e., central vs. local) is an emerging theme in this area. The controversy regarding "symmorphosis" (Chapter 14) essentially concerns the extent to which selection maintains parity among components of a functional complex during evolutionary time. Distinction

among these and other models of evolutionary trajectories is thus a significant problem that is already within the purview of ecological physiology, but has seldom been recognized as such.

The relative importance of adaptive and nonadaptive mechanisms in generating or constraining physiological diversity

Ecological physiologists often invoke only the cumulative effects of natural selection to explain the physiological diversity of organisms (Gould and Lewontin, 1979; Gould, 1980c). However, as discussed above, mechanisms other than "typical" natural selection may account for some fraction of physiological diversity. These mechanisms are nonadaptive in that selection for increased fitness is not involved in their action. Thus, an important question is, What is the relative importance of natural selection and various nonadaptive mechanisms in producing physiological evolution?

A second question concerns the limits of physiological diversity. We see repeated instances of well-defined physiological types, generally recognized along taxonomic lines: a mammalian physiology, an insect physiology, an elasmobranch physiology, and so on. Although we can recognize obvious physiological variants within each major group, we do not see all possible combinations of physiological traits: no moist-skinned terrestrial animals (e.g., slugs or amphibians) that routinely are endothermic, for example, and no healthy mammals with sharklike concentrations of urea in their blood. To paraphrase Gould (1980b), vast regions of potential physiology are unoccupied, whereas others are swarming with minor variations on common physiological themes. Why is this so (Simpson, 1953; Gould, 1980b; Wake, 1982), and what is the relative importance of natural selection and nonadaptive mechanisms in determining the commonness or rarity of physiological types?

Natural selection, of course, can almost always be invoked to explain both the amount and the limits of physiological diversity (Gould and Lewontin, 1979): physiological characteristics are so diverse because organisms evolved in so many diverse environments. The stochastic nature of natural selection is likely to promote multiple solutions to any given environmental challenge (Bartholomew, 1986; Chapter 2), thereby amplifying physiological diversity. The unexploited regions of physiological space are vacant because they represent unworkable solutions to environmental challenges (e.g., a terrestrial endotherm with the skin of an amphibian would either incur an intolerable level of water loss or expend energy uneconomically in behavioral hydroregulation). However, nonadaptive mechanisms may also account for physiological diversity and may be as consistent with patterns of physiological diversity as are adaptive explanations:

1. Phylogenetic inertia (Wilson, 1975; Ridley, 1983). Whether due to limited genetic variability, difficulty in simultaneously modifying the various components of a complex trait, a "plateau-shaped" fitness function, or simply the slow pace of natural selection, physiological characteristics may change very slowly in the face of environmental change or not change at all. If so, then some physiological space may be empty because selection and other evolutionary processes have not yet hit upon the improbable combinations of physiological characteristics necessary to occupy such empty regions. In theory, a marine mammal that osmoregulates in the manner of a shark is not impossible, but its evolution would entail numerous physiological adjustments whose joint probability is vanishingly small. Also, as a population begins to exploit a new environment, it will doubtless retain many characteristics it had in its previous environment. Although retained features may improve fitness in the new environment, they would not have originated in response to selection by the new environment (Gould and Vrba, 1982).

2. Genetic correlation. As detailed in Chapter 9, natural selection on one trait may lead to correlated changes in all other traits to which it is genetically linked. This phenomenon may cause nonadaptive (or even maladaptive) changes in physiological traits, or may promote changes that fortuitously enable an animal to occupy a new environment or exploit its current environment better. If this process is important and widespread, then physiological space may be filled as it is largely due to physiological traits that have been "hitchhiking" on other (potentially nonphysiological) traits, which were the actual object of selection. For example, Kingsolver and Koehl (1985) have proposed that the evolution of increased body size (and a correlated response in the size of wings that served as thermoregulatory structures) led to wings large enough to support flight in insects.

3. Developmental constraints. Canalization during development may not allow enough unbounded phenotypic variation for evolution to occur in any direction of change; instead, evolution may likely proceed only along a relatively small number of paths specified by "developmental constraints" (Alberch, 1980). Although this viewpoint remains a controversial one, it suggests that some vacant regions of physiological space may be unoccupied because developmental constraints preclude evolution in those directions and that some well-occupied regions of physiological space might represent evolution that has been canalized by developmental constraints.

4. Constraints and chance. At any point in evolution, natural selection may act along several paths dictated by the variation in an evolving population (Wright, 1932; Bock, 1959). In some cases, only one "choice" is feasible (e.g., only increased thermal tolerance, and not decreased thermal tolerance, will improve the survivorship of a sessile organism faced with stead-

ily increasing environmental temperatures), but in many cases several options are equally viable in terms of their immediate utility. The choice between equally viable options is largely a matter of chance. For example, in suspension-feeding brachiopods, in which the lophophore is the food entrapment organ, the evolution of increased lophophore size occurred along two coequal pathways (LaBarbera, 1986). In "plectolophes," lophophore size increased by expansion of its median portion; in "spirolophes," the lophophore formed a spiral and its size increased by expansion of its margins. As far as can be determined, both alternatives were equally advantageous at their origin.

Because selection is a response to the immediate utility of a trait rather than a trait's long-term consequences, chance "choice" of a pathway early in evolution may pose unforeseen opportunities or constraints later in evolution. For example, in salamanders the loss of lungs may have allowed the loss of tongue elements used in breathing, which in turn may have allowed the development of a projectile tongue and hence novel modes of foraging (Roth and Wake, 1985). As brachiopods evolved larger body sizes, the allometry of "plectolophe" lophophores proved inadequate to support function; lineages of plectolophe brachiopods were constrained to small size (LaBarbera, 1986). Comparable phenomena may result from extinction, which, like selection, is in part a stochastic process (Jablonski, 1986; also see above). We do not know to what extent diversity (or lack thereof) may stem from a species being poorly or well adapted, or may simply represent the luck of the draw.

How are we to assess the relative importance of natural selection and these alternative mechanisms in determining physiological diversity? First, we must eschew an exclusive focus on natural selection as the mechanism generating physiological diversity, and view selection as one of several potential mechanisms that may have been at work in any given case. Second, we must incorporate adaptation, phylogenetic inertia, correlated responses to selection, developmental constraints, chance, and other potential mechanisms as formal and coequal variables in our analysis. This will require different kinds of data sets and different sorts of analyses. In essence, what is needed is a way of examining the effects of one potential mechanism of physiological diversity while the effects of all others are either held constant or removed from the analysis. Both statistical techniques (e.g., partial correlation analysis, path analysis, multivariate analysis of variance, canonical correlation analysis) and "comparative techniques" (Ridley, 1983; Clutton-Brock and Harvey, 1984; Huey and Bennett, 1986; see also Chapter 4) are available to achieve this end. To examine the importance of constraint (developmental, mechanical, on one component by another, etc.), we need analyses of contingency. In how many instances have physiological characteristics evolved independently of one another? How frequently have two or more traits evolved only in the

presence of one another? To what extent is the expression of one physiological trait necessary, sufficient, both necessary and sufficient, or neither necessary nor sufficient for the expression of a second trait?

What are the general consequences of physiological diversity for the ecological and evolutionary properties of animals?

Ecological physiologists may never be able to predict which physiological specializations will evolve in response to a given environmental challenge (Bartholomew, 1986). Once a specialization is in place, however, can we determine what its subsequent consequences are likely to be for a species's ability to exploit various environments and to persist in evolutionary time (Pough, 1978)?

A common theme in ecological physiology concerns how the evolution of physiological innovations enables species or higher taxa to invade previously unoccupied "adaptive zones" (Simpson, 1953; see also Mayr, 1960; Liem, 1973; and Lauder, 1981): new environments, vacant niches, or new ways of exploiting already occupied environments. For example, some ecological physiologists view the evolution of aerial respiration as entrée to terrestriality, the evolution of the cleidoic egg as a key to the amniotes' invasion of xeric environments, and the evolution of salt glands as allowing those birds and reptiles that possess such glands to exploit saline environments. In abstract terms, ecophysiologists' recognition of key innovations in physiological evolution implies that *general* ecological and environmental consequences attend physiological characteristics. Much as a single electron in the outermost shell of an atom will confer certain chemical properties regardless of the identity of the element in question, these *general* consequences of physiological characteristics are, by implication, more or less independent of the particular species in which the physiological characteristics occur. The admission of "general ecological-evolutionary consequences of physiological traits" has several important implications. First, it suggests that independent evolutions of a physiological characteristic can be viewed as independent trials of a natural experiment (Ridley, 1983); that the presence of a given physiological characteristic ought to have regular and repeatable consequences; and that the historical and phylogenetic idiosyncrasies of individual species cannot wholly confound recognition of general consequences. Much as ensembles of gas molecules behave in accordance with the general gas laws, ensembles of species ought to behave in ecological and evolutionary time according to their physiological characteristics, although individual molecules or species can and do behave eccentrically (Schopf, 1979; Gould, 1980b, pp. 112–116; Ridley, 1983, pp. 40–43). Second, if species can be expected to behave in lawlike fashion according to their physiological characteristics, ecological physiologists can pose hypotheses concerning general

ecological-evolutionary consequences of physiological characteristics and can falsify these hypotheses with established methodologies and statistics (Lauder, 1981; Ridley, 1983; Clutton-Brock and Harvey, 1984). Given this perspective, the emergent questions are: Can we recognize general behavioral, ecological, and evolutionary consequences of major physiological characteristics; that is, consequences that are independent of the species in which the physiological trait is expressed? If so, what are these general consequences of major physiological characteristics?

There is a tension between this perspective and another mode of ecophysiological study, which considers each species an irreducible adaptive case unto itself that can only be compared to (but never equated with) other unique species. This tension is in part a matter of intellectual preference (inductivism vs. other modes of investigation, the idiographic vs. the nomothetic approach; see Gould, 1980c), and in part a legitimate disagreement about the prospects for recognizing general consequences in light of several biological issues (Bartholomew, 1986; Chapter 2):

1. Each species has its own unique evolutionary history with its own set of selection pressures and its own stochastic responses in evolutionary time. Accordingly, detection of general consequences, necessarily by examination of multiple species, may be impossible or unlikely.
2. Natural selection can yield multiple solutions to any given environmental challenge. Not only one physiological innovation, but scores or hundreds of possible innovations may give entrée to a new adaptive zone. The importance of any one physiological characteristic as an evolutionary breakthrough diminishes accordingly, and the prospects for recognizing the general consequences of any particular feature against the background of alternative solutions may be dim.
3. Key physiological innovations may come to bear on fitness only during instances of intense selection (e.g., broad-scale extinctions). Between incidents of intense selection, more or less any suite of physiological characters might suffice. If intense selection is rare, the identification of key innovations and their consequences may be impossible in practice.

These challenges may ultimately defeat most attempts at ecophysiological generalization. Yet, even if general ecological-evolutionary consequences of physiological attributes cannot be recognized, this failure would be of profound interest.

Recent awareness of general consequences and their implications has highlighted several tactics for their detection:

1. Establish the independence of repeated trials in natural experiments (Lauder, 1981; Ridley, 1983; Chapter 4). One way to avoid problems of nonindependence is to include phylogeny as an explicit factor in analyses of

physiological diversity; Chapter 4 discusses how this can be done. Another is to examine taxa that are as distantly related as possible. For example, in plants, insects, fishes, birds, mammals, and possibly dinosaurs, endothermy is associated with high rates of growth and sustained activity; only in birds and mammals is endothermy usually associated with routine thermoregulation. This observation suggests that a general consequence of endothermy is the capability for sustained high rates of growth or activity, a conclusion that would be confounded had the analysis been limited to birds and mammals (Bennett and Ruben, 1979).

2. Search for and focus upon instances in which putative "general consequences" are not supported by the data. An excellent example is Kramer's (e.g., 1983) work on the general consequences of aerial gas exchange for aquatic vertebrates. This work began on a field expedition to document adaptations for aerial respiration in fishes, when Kramer noticed that the majority of fish species in hypoxic Amazonian swamps did not breathe air despite a potentially large selection pressure to do so. He subsequently began descriptive and experimental work to test explicitly the presumed general benefits of aerial respiration. Similarly, my own work on cutaneous gas exchange began when I learned that tropical plethodontid salamanders both attain large body sizes and experience high body temperatures, conditions from which they were thought to be excluded by the inadequacies of cutaneous gas exchange. Subsequent work has discounted many a priori expectations regarding cutaneous gas exchange (Feder and Burggren, 1985).

3. Distinguish among multiple competing explanations of general consequence, one of which is that no general consequences exist, rather than defend or refute a single hypothesis (Platt, 1964; for physiological examples, see Kramer, 1983, and Feder, 1984). Defense of a single hypothesis is too often self-fulfilling, and the textbooks of ecological physiology are replete with "general consequences" that have been subjected to repeated substantiation but never falsification. Perhaps it is time to declare open season on such "general consequences."

Toward a nomothetic ecological physiology

An increased emphasis on the solution of general questions in ecological physiology has the potential to invigorate the field in many ways. Numerous ecological physiologists perceive a lack of direction in the field, or perceive their work as adding minor entries to a vast encyclopedia of adaptations whose broad outlines are already well established. For these people, general questions can serve as a novel and exciting focus. Numerous workers outside of the field perceive ecological physiology as a curiosity or an anachronism. To paraphrase a comment directed at a sister field (Gould, 1980c, p. 101):

"The flowering of ecological physiology has yielded a panoply of elegant individual examples and few principles beyond the unenlightening conclusion that animals work well." Answering the questions posed herein clearly has the potential to alter such perceptions, and, as detailed throughout this volume, has done so already. We have direct evidence that such invigoration is possible from the field of paleobiology. Only seventeen years ago, paleontology was characterized as a moribund field whose major objective was the encyclopedic accumulation of fossils and the description of their relationships to one another (Gould, 1980c). Today, paleobiology is a thriving field whose general questions (e.g., punctuated equilibria vs. gradualism; periodicity and importance of extinction; macroevolution vs. microevolution) are regularly debated in the journals *Science* and *Nature*. What achieved this transformation was an emphasis on general questions (Gould, 1980c), brought about in no small part by a volume on which this one was patterned (Schopf, 1972) and the founding of the journal *Paleobiology* (Gould, 1980c). This is not to say that the fostering of a nomothetic ecological physiology is a trivial matter. But how might it be achieved?

To establish a focus on general questions alongside the traditional focus on ecophysiological patterns, we need an increased awareness of general questions, and of their significance, and debate on both the general questions themselves and the most expeditious means of answering them. This chapter was written in hopes of stimulating such debate and awareness. The general questions it includes are not the only ones or even novel ones, but they can serve as points of departure for discussion. Another means of increasing awareness of general questions is to implement Platt's (1964, p. 352) procedure on a daily basis:

It consists of asking in your own mind, on hearing any scientific explanation or theory put forward, "But, sir, what experiment could *dis*prove your hypothesis?"; or, on hearing a scientific experiment described, "But, sir, what hypothesis does your experiment *dis*prove?"

A focus on general questions will also require officers of scientific societies, journal editors, and symposium conveners to encourage the nontraditional, often theoretical discourse that general questions will entail. A focus on general questions cannot succeed, however, by excluding the traditional foci on ecophysiological patterns, natural history, and case studies of unusual species or populations. These traditional endeavors both complement and potentiate the solution of general questions, for general questions can be neither framed nor solved rigorously without accurate information on the natural history and systematics of their subjects (Gans, 1978; Bartholomew, 1986; Feder and Lauder, 1986; Greene, 1986; Chapter 4).

Shortly before I began this essay, I received a set of the journal *Physiological Zoology* dating back to 1956. As I scanned the titles of papers in chron-

ological order, it became obvious that, technical advances aside, many of the 1956 papers would not have been out of place in the 1986 volume, and vice versa. This is an interesting statement about the rate of conceptual progress in ecological physiology. However, I think the prospects of a similar occurrence thirty years hence are minimal. The field must change or it will disappear. On the negative side, ecological physiology is under increasing financial pressure and its academic positions are at risk due to both general budgetary constraints and competition with disciplines with seemingly greater biomedical relevance, particularly molecular biology. On the positive side, this is a time of considerable conceptual ferment in organismal biology. Many of the developments considered in this volume are quite recent and are yet to be assimilated into ecological physiology. Bridges are being built to conceptual advances in both molecular biology and evolutionary biology. That this volume appeared speaks to a growing and active concern about the degree of conceptual progress in ecological physiology. Thus, prospects for a nomothetic ecological physiology are clearly visible. However, these prospects require active support if they are to flourish, and it is up to us to develop them.

Acknowledgments

Notes

1. Throughout this chapter, the word "environment" is used with very broad meaning (cf. Ridley, 1983). It may refer to the ensemble of abiotic and biotic factors that an animal encounters where it lives, a species's niche, or a species's way of life (e.g., herbivory vs. insectivory, wide foraging vs. sit-and-wait predation, semelparity vs. iteroparity).
2. Throughout this section, reviews and examples have been cited to lead the interested reader into the primary literature, not to credit the priority of ideas.

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