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Does comparative respiratory physiology have a role in evolutionary biology (and vice versa)?

Rationale for this chapter

This comprehensive volume draws together timely contributions from comparative respiratory physiologists studying diverse organisms by using a variety of techniques and methodologies. Yet all have addressed a central issue in comparative respiratory physiology: adaptations of animals that allow them to survive, if not thrive, in a wide range of environments that threaten respiratory homeostasis. Most authors have taken a truly comparative approach, in which no single organism is isolated for study, but rather broad taxonomic groups are investigated. By taking this approach, each author has successfully revealed not only respiratory adaptations unique to particular taxa, but also adaptations common to a diverse range of organisms. Thus, we are slowly but surely identifying 'universal' versus 'exceptional' respiratory adaptations.

In listening to the symposium presentations, and in reading the resulting papers, I quickly discovered that the word '*adaptation*' has been used numerous times by each author. When we discuss respiratory adaptations we are, of course, looking at the most recent product of a sequence of evolutionary changes from ancestral animals. I suspect that virtually every author in this volume (and I venture most authors of journal articles on comparative respiratory physiology) has, during the conception, execution or analysis of their experiments, thought about the evolutionary processes leading to the respiratory adaptations they study. Indeed, as will be emphasized below, understanding the evolution of physiological processes is one of the chief goals of comparative physiology. Yet the word '*evolution*' is but rarely mentioned in this volume, and there are few explicit references to actual evolutionary changes in physiological systems.

The purpose of this essay is to encourage comparative respiratory physiologists to: (i) continue to expand the scope of their studies to examine the actual evolutionary processes leading to respiratory adaptations (in addition to examining the adaptations in a strictly physiological context); and (ii) approach questions of physiological evolution by using the numerous tools of contemporary evolutionary biology that have proven so useful to comparative anatomists and systematists.

Studying physiological evolution

To observe that most authors in this volume have not explored the evolutionary implications of their findings is certainly not to offer criticism. To the contrary, because we know so little about many of the fascinating physiological systems that are being discussed in this volume, a detailed discussion of evolutionary processes would be highly speculative at best, and the authors are to be complimented on successfully restricting the potentially broad scope of their subjects. Yet, as the field of respiratory physiology matures, and as we come to know more of physiological mechanisms and the respiratory adaptations that they represent, we will turn increasingly to examining *how these respiratory mechanisms and adaptations evolved*. That is, we shall begin to integrate comparative respiratory physiology and evolutionary biology.

The degree of success with which we shall achieve this integration will depend to some extent upon how thoroughly we adopt the tools of modern evolutionary biology. As physiologists, we all know instances in which anatomists have incorrectly predicted physiology on the basis of anatomy, of how ecologists have incorrectly implied physiological mechanisms on the basis of whole animal energetics, etc. The intent has always been sincere, but in these instances the anatomist or ecologist has been unwilling to learn about physiology before venturing, however fleetingly, into a new field. The same lesson can be directed at us. Accordingly, we as physiologists must be willing to learn the tools of evolutionary biology if we are to analyse physiological evolution.

What are these tools? It is beyond the scope of this essay to define them in detail; such tools deserve more than the passing mention that could be afforded here and have been discussed repeatedly (mostly outside the physiological literature) (Lauder, 1982; Cracraft, 1983; Felsenstein, 1985; Futuyma, 1987; Huey & Bennett, 1987; Patterson, 1987; Huey, 1987; Coddington, 1988; Herring, 1988). Let it suffice to present two examples of useful tools of modern evolutionary biology. First, there are new *statistical procedures designed for interspecific comparisons*. One might reasonably ask ‘what is different about interspecific comparisons?’ As Huey (1987) has recently discussed in detail, species are not statistically independent sampling units, but rather are linked together by often strong phylogenetic affinities. If closely related species are automatically assumed to be statistically independent units, as almost invariably is the case in physiological studies, we risk an exaggerated Type I statistical error by using an artificially inflated degree of freedom in our calculations. Statistical tools to deal with lack of independence between species (e.g. nested analysis of variance; variance partitioning) have been proposed (Crook, 1965; Ridley, 1983; Clutton-Brock & Harvey, 1984; Mace *et al.*, 1981; Stearns, 1983, 1984; Cheverud *et al.*, 1985; Dunham & Miles, 1985; Felsenstein, 1985). Unfortunately, this potential problem in comparative studies is rarely recognized by comparative physiologists (but see Huey, 1987; Huey & Bennett, 1987).

A second example of a useful tool to be borrowed from evolutionary biologists is *cladistic analysis*. This approach uses the presence of shared, derived characters to establish systematic relationships between species (Hennig, 1979; Wiley, 1981). Traditional cladistic analysis has relied extensively upon anatomical characters that are qualitative in nature (e.g. presence or absence of a structure, rather than its size). While many cladists would argue that quantitative physiological characters do not lend themselves well to cladistic analyses, systematic inferences drawn from qualitative physiological characters (e.g. endothermy, formation of hypertonic urine, haemocyanin modulation by lactate) are just as viable for cladistic analysis as are skeletal articulations or protein patterns in gel electrophoresis (see Burggren & Bemis, 1990). In any event, most comparative physiologists will use the concepts inherent in cladistic methods to predict patterns of physiological evolution within already established phylogenies, rather than to construct new phylogenies (though we may be able to contribute to them).

I wish to emphasize that, while I advocate that physiologists study the evolution of respiratory adaptations using the tools of modern evolutionary biology, I am not simply airing my personal opinion that we should do so. Rather, we must realize that many contemporary evolutionary biologists[1] appear to have a general and broad disrespect for how comparative physiologists have regarded and continue to regard evolutionary processes, and for the utility of any resulting information in understanding the evolution of a species (see discussion in Burggren & Bemis, 1990). To overstate the case bluntly, *no one outside of comparative physiology is listening to what we say about evolution*!

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[1] By 'evolutionary biologist' I mean the great number of those biologists who consider ecology, systematics, behaviour, physiology or other disciplines as tools for studying evolution, rather than as an end in themselves.

CAMBRIDGE
Cambridge University Press
978-0-521-36602-1 - Physiological Strategies for Gas Exchange and Metabolism
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To help understand the current nature of the interaction (or lack of interaction) between comparative physiology (including comparative *respiratory* physiology) and evolutionary biology, let us examine the 'evolution' of the goals of comparative respiratory physiology.

Goals of comparative respiratory physiology

During the late 1800s and early 1900s, concomitant with major advances and refinements in theories and techniques, many innovative new approaches to comparative respiratory physiology were being established, led by Paul Bert and then August Krogh. Measurement of whole animals' metabolic rates remained a staple of respiratory physiology during the first half of this century (and well beyond), but experimental techniques were also being developed to permit the investigation of blood O_2 and CO_2 transport and acid–base balance, as just two examples. Attention began to be turned towards respiratory adaptations of unusual animals in unusual environments, an approach championed by August Krogh (see Krebs, 1975) and later used to great effectiveness by Lawrence Irving and Per Scholander, among many others.

These early 'modern' studies were guided by two related goals of comparative respiratory physiology: (i) to understand how respiratory systems function; and (ii) to understand the physiological processes allowing animals to exchange and transport gases in extreme environments. The first goal was a common one shared by comparative physiologists and more clinically related physiologists alike. The second goal essentially involved the study of respiratory adaptations. Of course, these goals remain at the centre of most contemporary studies in comparative respiratory physiology.

The goals of comparative physiology (including comparative *respiratory* physiology) have been explicitly stated and re-examined numerous times in recent years (see chapters in Greenberg *et al.*, 1975; see also Ross, 1981; Greenberg, 1985; Randall, 1986; Downer, 1986; Feder *et al.*, 1987). In fact, no biological field of which I am aware seems to subject itself to such intense, regular (and healthy!) self-scrutiny. Less common, however, have been pragmatic statements of how to achieve the goals of comparative physiology most effectively (Huey, 1987). A survey of the early literature in respiratory physiology indicates that the prevailing attitude of the first half of this century was that the goal of understanding respiratory adaptations could best be achieved by making metabolic and respiratory measurements on a wide variety of animals, often exotic species from exotic places. As a result of this approach, comparative respiratory physio-

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logists can base new experiments on an extremely large and diverse collection of data on respiratory adaptations in animals. Yet, to understand completely respiratory adaptations to the environment, it is an implicit but fundamental requirement that we understand *how such adaptations evolved*, not just how they currently operate in living animals. Presumably, most comparative physiologists regard this as a truism. Yet, with the tremendous advantage of hindsight, the 'encyclopaedic' categorization of the myriad respiratory adaptations of animals, only infrequently guided by testable hypotheses constructed *a priori*, has largely failed to achieve the fundamental goal of understanding how physiological processes actually evolved, as distinct from how extant animals are adapted to their environment. This criticism applies not just to comparative respiratory physiology, of course, but to all of comparative physiology (see Greenberg *et al.*, 1975; Ross, 1981; numerous chapters in Feder *et al.*, 1987).

The view that our in-depth studies have not revealed to us in equal depth how physiological processes have evolved is somewhat controversial, and will not be endorsed by comparative respiratory physiologists following highly traditional paths. It therefore is illuminating to ask 'what has been the overall contribution of comparative respiratory physiologists to evolutionary biology?' To answer this question, we should see how biologists outside of our discipline regard our studies on respiratory adaptations. After all, our studies will be entirely self-serving if we can't make generalizations useful to other biologists. Up until the past few years, I had naively assumed that comparative physiologists were indeed studying evolutionary problems by using reasonable paradigms applied to reasonable theory. Thus, I was disturbed to discover recently that many (if not most) contemporary evolutionary biologists hold the view that there is little or no merit in studying physiology if one's goal is to learn how animals evolve (for detailed discussion see Burggren & Bemis, 1990). In fact, recent books on evolutionary biology (Mayre & Provine, 1980; Futuyma, 1987) typically do not even list the word 'physiology' in otherwise extensive indexes. As C. Ladd Prosser (1986) (under)states, 'evolutionists pay little attention to physiology'.

Why are 'evolutionary' studies in comparative physiology (respiratory physiology included) so broadly and readily ignored by evolutionary biologists outside of our field? A complete answer is beyond the scope of this introductory chapter, because it involves a critique of how physiologists have traditionally studied animal adaptations and evolutionary processes (see Huey, 1987; Bennett, 1987; Burggren & Bemis, 1990, for reviews of this subject). Suffice it to say that the views of our colleagues in evolution-

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ary biology have been shaped by the sad fact that traditional comparative physiology is performed outside of a framework of modern evolutionary biology, often embracing theories, positions or approaches that contemporary morphologists, evolutionary biologists and geneticists have long abandoned (cf. Mayr & Provine, 1980; Bennett, 1987; Huey, 1987). Too many comparative investigations that purport to investigate the evolution of respiratory adaptations do not test a specific hypothesis that has been formulated on the basis of rigorous evolutionary theory and sound systematics. While Carl Gans (1970) warned us of this problem in his classic paper '*Respiration in early tetrapods – the frog is a red herring*', it would seem that as a group comparative physiologists have not been overly receptive to the suggestion that they make forays into evolutionary biology and systematics. Again, to paraphrase C. Ladd Prosser (1986), 'most physiologists have a only a superficial knowledge of evolution.'

To develop a specific example of how comparative physiologists can err in studies with evolutionary overtones, the present author singles out one of his own early papers for criticism (primarily because this study is a good example of a bad evolutionary study, but also to disarm those who would suggest that he is quick to criticize others). Burggren (1976) conducted a study examining the relationship between ventilation patterns and heart rate in two chelonians: the freshwater turtle *Pseudemys scripta* and the terrestrial tortoise *Testudo graeca*. The intent was to contrast the effects of terrestrial and aquatic life on cardiorespiratory function. Sidestepping the issue of the physiological merits of the study, *from the perspective of a study in evolutionary biology* the author committed significant trangressions. First, Burggren (1976) made a rather popular, simple assumption: that the physiological differences between an aquatic and a terrestrial species would reflect only adaptations to the aquatic and terrestrial habitat. Unfortunately, this common assumption ignores the fact that *Testudo* and *Pseudemys* are phylogenetically distinct members of lineages which have been evolving separately for millions of years. Many of the observed differences may have little or nothing to do with aquatic or terrestrial habits. No attempt was made to determine whether the observed breathing patterns, ventilation tachycardia, atropine sensitivity of heart rate, beta-adrenergic excitation of the heart, etc. were (i) shared primitive features common to other Chelonia, (ii) shared derived features common to only these Chelonia, or (iii) unique to the genus *Testudo* or *Pseudemys*. As a result, the evolutionary meaning (as distinct from the physiological meaning) of any of the differences Burggren (1976) found is ambiguous. In fact, the physiological differences between these two chelonian genera might be

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due solely to *the phylogenetic distance between them* and not to physiological adaptations to different environments, a possibility that cannot be refuted owing to the design of Burggren's study (or most other comparative respiratory studies purporting to differentiate between aquatic and terrestrial species).

A far more appropriate way to have tested the hypothesis that habitat affects physiology would have been to compare three or more closely related species that occupy different habitats. The more closely related the species (preferably within the same genus), the more confidence we can have that the adaptations we find are related to specific environmental differences. The power of this approach, which really is just the standard comparative method applied rigorously in the context of an animal's phylogenetic history, has been beautifully demonstrated by Huey (1987) in his discussion of the comparative method in physiology. Figure 1, modified and expanded from Huey's (1987) paper, indicates that ignoring phylogeny when comparing physiological data from just two species (especially distantly related species) can lead to quite erroneous conclusions about the effect of environment on a physiological response or adaptation.

Returning to Burggren's (1976) study of cardiorespiratory adaptations in chelonians, the results from chelonians were compared with other 'reptiles' such as alligators. The 'reptiles' are a paraphyletic taxonomic grouping: i.e. a taxonomic group, more convenient than accurate, that does not include all of the descendants of a single common ancestor and whose members do not uniquely share derived characters (Figure 2). This contrasts with a monophyletic group (e.g. the Lepidosaurs: sphenodonts, lizards and snakes), which all share derived characters that are not found in any other tetrapod taxa. By placing birds and crocodilians in separate taxonomic groups, even though crocodilians are much more closely related to birds than to turtles, we emphasize differences between birds and crocodilians rather than similarities. From a strictly phylogenetic perspective, there is no reason to expect greater similarities in physiology between turtles and alligators than between turtles and birds. Now, we know after decades of *empirical* experimentation that reasonable and interesting comparisons can be made between alligators and turtles. These comparisons are valid because both groups, for example, are ectotherms, exhibit intermittent breathing, and have central cardiovascular shunts, but *not* because of a spurious close phylogenetic relationship suggested by the word 'reptile'!

The appropriateness of using the word 'reptile' (or 'great apes' or 'annelids') may seem like a simple semantic argument. Yet, when we begin

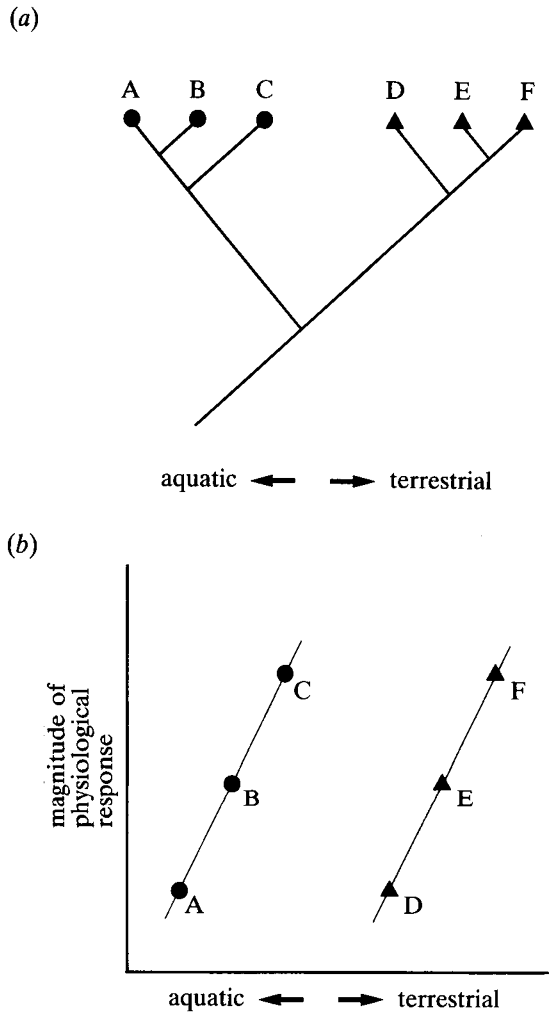
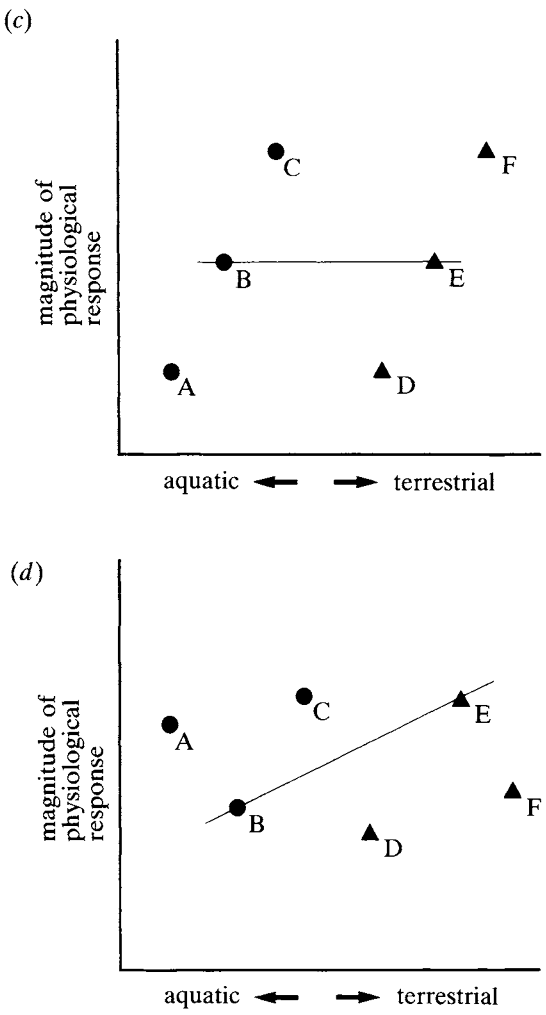


Figure 1. (*a*) A cladogram of six hypothetical animal species. Superimposed on this phylogenetic analysis is an indication of the environment these animals live in, ranging from completely aquatic to fully terrestrial. Parts (*b*), (*c*) and (*d*) show possible regressions of physiological characteristics of the animals against environment. Part (*b*) shows that correlations between environment and physiology are clearly evident when phylogeny is taken into account and several species are examined. Separate analysis of the two taxonomic groups indicates a very pro-

to investigate new taxa or make new comparisons where we don't have the benefit of empirically derived knowledge, we should be particularly careful to avoid structuring our comparisons around paraphyletic groups. If we fail to plan our experiments according to sound phylogenetics (i.e. if we do no studies on monophyletic taxa), comparative physiologists may be led to



Caption to fig. 1. (cont.)
nounced effect of environment. (*c*) The regression when comparing only species B and E (a common approach in comparative physiology). The erroneous conclusion from this regression is that environment has no effect on physiological characteristics. Part (*d*) shows an alternative situation in which there is no effect of environment, but analysis of only two distantly related species erroneously suggests that there is. (Modified and expanded from Huey, 1987.)

erroneous interpretations of the evolution of physiological processes. Just as unfortunately, we may miss the most interesting of the *predictive* possibilities of our work, because predictions about evolutionary processes can only make sense in the light of phylogeny.

To give one brief example of the power of using rigorous phylogenetic

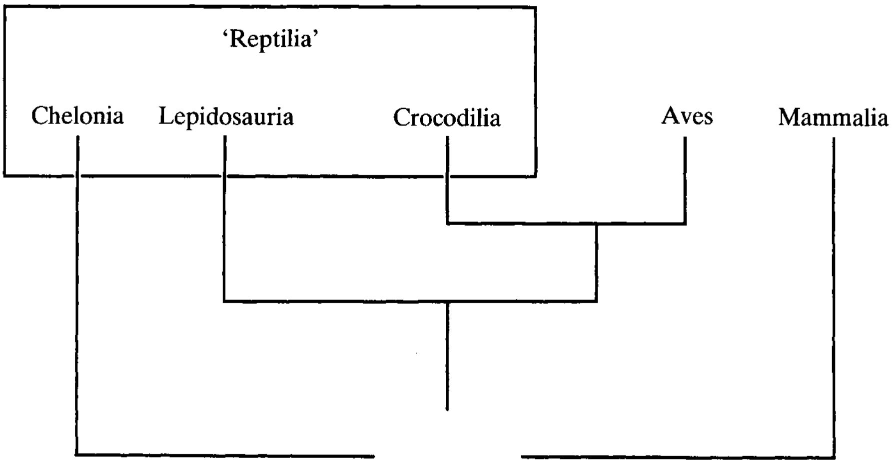


Figure 2. As shown in this conventional phylogeny of the living amniote vertebrates, the 'Reptilia' are a paraphyletic taxonomic group. For example, the Crocodilia are included with the Chelonia, even though these two taxa are very distantly related. Note that for clarity numerous fossil groups have been excluded from the Reptilia. Also, since it is not the purpose of this figure to debate the origins of the amniotes, the relationship between stem reptiles, thecodonts and therapsids has purposely been left undefined.

approaches to physiological studies, consider the unpublished findings of R. Huey, F. van Berkum, A.F. Bennett & P.E. Hertz (discussed in Huey, 1987) on the thermal dependence of sprint speed in lizards. The authors' operating hypothesis was that lizards that are normally active over a broad range of body temperature should also sprint effectively through a broad range of body temperatures: that is, they should be 'thermal generalists'. This hypothesis predicts that species with a high standard deviation of field body temperatures should also be able to sprint well over a wide range of body temperatures. Huey and co-workers carefully considered the phylogenetic relationships of the species they used and, quite appropriately, they initially analysed patterns within groups of closely related lizards (genera and families) rather than lumping both close and distant relatives in a single grouping. Taking this approach, dictated by sound systematics, they found that, indeed, thermal generalists (i.e. those that sprinted well over a wide range of body temperatures) were typically active over a wide range of body temperatures in nature. However, to illustrate the pitfalls of ignoring phylogeny, the authors purposely then used an approach all too common to comparative physiological studies, and lumped together for comparison data on sprint speeds from twenty distantly related lizard