1 The accomplishments of ecological physiology

ALBERT F. BENNETT

Introduction

Strange animals living in unusual situations have always fascinated humans. We are particularly interested in and impressed by animals with functional capacities that exceed our own, such as Arctic mammals and small birds that can exist in bitter cold, desert animals that can survive intense heat or forego drinking water, hibernators that can become torpid for weeks, divers that can stay under water for hours, or animals that can lift and carry many times their own mass. Our natural curiosity leads us to ask how they can do that, or to paraphrase the title of a book by Knut Schmidt-Nielsen (1972), How do these animals work? The primary task and subject of the field known as ecological physiology (or physiological ecology or environmental physiology) is to understand how animals are designed with reference to their natural environments and evolutionary histories.

To place the field in perspective, this chapter reviews very briefly where it originated and where it has been, what its major accomplishments are, and where it finds itself today. This is a short and personal essay on those topics.

Ecological physiology arose from a blending of the traditions of comparative physiology and natural history (Chapter 2). The former traces its traditions to laboratory physiology in the latter half of the nineteenth and early twentieth centuries. It has developed a large and impressive data base on the physiological capabilities of numerous different kinds of animals, often concentrating on those that best exemplify some physiological process (Krogh, 1929). It subscribes to a rigorous protocol of experimental design and analysis. The field of natural history, also already well-developed in the nineteenth century, contributed a knowledge of animals, sometimes very unusual animals, and their habits under natural conditions in the field. The merger of these two areas resulted in experimental scientists undertaking research on nontraditional animals and referring the results of that research to the behavior and functional responses of species under natural conditions.

Animal ecological physiology began to assume a separate existence and prominence in the late 1940's with the seminal contributions of George Bartholomew, Knut Schmidt-Nielsen, and Per Scholander. These and other investigators and their students were responsible for an explosion of knowledge during the past forty years. Ecological physiology is now a firmly established area of biological investigation with hundreds of practitioners. The center of activity of the field has always been the United States, but it is also well represented in Canada, Europe, Australia, and Africa. It forms an important component in numerous scientific societies, including the American Physiological Society, the American Society of Zoologists, the Ecological Society of America, and the Society for Experimental Biology. Ecological physiologists also play prominent roles in scientific societies associated with particular animal taxa, especially those concerned with mammals, birds, reptiles, and amphibians. Papers in this area are published in numerous scientific journals, including the *American Journal of Physiology*, *Comparative Biochemistry and Physiology*, the *Journal of Comparative Physiology*, the *Journal of Experimental Biology*, the *Journal of Experimental Zoology*, the *Journal of Thermal Biology*, *Physiological Zoology*, *Respiration Physiology*, various taxonomic journals (e.g., *Condor*, *Copeia*), ecological journals (e.g., *Ecology*, *Oecologia*), as well as more general scientific publications. Its research is supported by two different programs of the National Science Foundation: Population Biology and Physiological Ecology in the Division of Biological Systems and Resources, and Regulatory Biology in the Division of Cellular Biosciences. The field has grown and matured rapidly and has assumed an important and well-defined place in modern biological studies.

The insights of ecological physiology

I would like to enumerate briefly what I consider to be major insights and accomplishments to emerge from this field. Any such designation is bound to be hazardous and eclectic. However, I have tried to select themes that have been particularly well developed in ecological physiology and have implications far beyond that particular area of biological investigation.

Energy availability and utilization are important constraints on animal function.

The measurement of energy intake and utilization by animals has been a major area of study within ecological physiology. This area can assume such a prominence that it is sometimes regarded as the principal subject and accomplishment of the entire field (e.g., Townsend and Calow, 1981). Through energetics, ecological physiology finds its strongest links with ecology and behavior. In these fields, energy exchange assumes a major role in many hypotheses (e.g., life history strategy and foraging theory). Most often, ecological physiology has provided the methodology and data to test such hypotheses empirically. It consistently asks how much processes or activities cost and proceeds to make the appropriate determinations. The field has been successful in energetic studies primarily because of its insistence on quantification of energy exchange.

Energy availability has often been found to impose constraints on animals. These constraints may arise either because of the relatively large amount of energy required in comparison to that available from the environment, or because of limitations of the physiological processing capacities of the animal. Some physiological processes and behaviors, such as endothermy in the cold and sustained flight, are so expensive that they require nearly all of an animals's energy intake or are beyond that which can be taken from the environment. Other constraints on energy use may reflect internal limitations of physiological rate processes. The ability to undertake sustainable behaviors, for instance, is limited by the capacity for oxygen transport and utilization. In ectothermic animals, maximal oxygen consumption may be low and may be even further diminished at low body temperatures. Ecological physiology often undertakes studies to measure the capacity of functional processes in order to define the limits within which function is permitted.

Body temperature regulation is expensive in time and energy. Its alternative, temperature conformity, entails variability in all physiological processes.

Interest in thermoregulation and its consequences has been an immense area of ecological physiology. A large set of empirical observations on the thermal biology of animals has been assembled. In addition, sophisticated biophysical models have been constructed to predict thermal exchange. This research has led to an appreciation of the considerable complexity of thermal environments and the importance of microclimates rather than macroclimates in determining thermal balance. One of the major lessons of ecological physiology is that the influence of temperature on energy exchange and behavior in natural environments is liable to be large and cannot be neglected.

Physiologists have known for more than 200 years that rate processes are very sensitive to temperature. But it remained for ecological physiologists to elaborate the consequences of temperature conformity and thermoregulation for nearly all aspects of animal life. If rate processes are temperature dependent, then exposure to cold depresses many different time-dependent phenomena, including metabolic, growth, and behavioral capacities. Some organisms accept this dependence; others go to extraordinary lengths with behavioral and physiological adjustments to overcome the effects of low and/or variable body temperatures. Many undergo long-term physiological adaptation (acclimation, acclimatization) to their thermal regime. Others regulate temperature behaviorally, expending a large amount of effort and limiting activity times to certain portions of the day or night. Still others regulate temperature metabolically by varying heat production. For mammals, birds, and some insects, this thermoregulation is extraordinarily expensive. It represents by far the largest component of their energy budgets and diverts energy from other important processes such as growth and reproduction.

Body size affects nearly every biological variable.

Comparative studies on hundreds of different species found their natural comparative base in the examination of the effects of size on biological variation. The original summaries by Kleiber (1932) and Benedict (1938) concerning the effect of size on basal metabolic rate have now been supplemented with observations on nearly all physiological and many ecological variables, including such factors as heart rate, glomerular filtration rate, territory size, and life-span. These have been summarized by Peters (1983), Schmidt-Nielsen (1984), and Calder (1984).

Most functions do not depend on animal size in a simple linear manner. If one animal is twice the mass of another, it does not require twice as much food, water, or space in which to obtain them. Rather, nearly all physiological and ecological factors can be described as exponential functions of body mass. Metabolic rate, for instance, scales with mass to the 0.75 power, a relationship that has profound consequences for energy requirements and thermoregulation. Ecological physiology has generated an enormous series of predictive equations that can be used to estimate the magnitude of almost any function in many animals, given only the taxon and the animal's mass. The scaling of different morphological and physiological variables has proved to be a fruitful area for examination of their functional bases and general design criteria of animals (e.g., Taylor and Weibel, 1981). Further, allometric equations can be used as a basis for examination of the physiological and/or ecological causes of deviations from general relationships. Many groups of desert-adapted mammals and birds, for instance, have a lower metabolic rate than would be anticipated on the basis of their size. Both the ecological consequences and physiological underpinnings of such deviations have been important as documentation of environmental adaptation.

Behavior is an important component of functional adjustment to the environment.

A basic strength of laboratory physiology is its ability to isolate and control experimental variables. However, an important variable that is often lost in laboratory investigations is behavioral response. A principal contribution of ecological physiology has been the appreciation that behavior is often the primary and sometimes the crucial means by which an animal copes with an environmental challenge. This appreciation has reemphasized the necessity of validating conclusions based on laboratory experiments with field observations on animals.

For many animals, behavioral discretion is often the better part of regulatory valor. Animals can exist in a variety of very challenging environments, thermally, energetically, osmotically. Sometimes they cope with them by conforming to the environmental variable or by regulating the variable internally, often at great energetic expense. But often ecological physiologists have found that a third option is used: animals may avoid those environmental challenges, either behaviorally or physiologically, by effectively removing themselves from certain challenging aspects of the environment. This avoidance may lead to a variety of adaptive patterns, even within restricted taxa, to a common environmental challenge (Chapter 2). Animals that hibernate or become torpid avoid acute or chronic energetic or thermal stress. Animals that migrate avoid the problems of continuous residence in seasonally inhospitable environments. Just because an animal lives in a particular environment does not mean that it experiences the full force of that environment, particularly as perceived by a human. Ecological physiologists have found that avoidance is a common response and again one that can be evaluated only by observations on animals in natural environments.

The organism is a compromise. The result of natural selection is adequacy and not perfection.

This view is discussed in detail in Chapter 2. More than many other field of biology, ecological physiology has appreciated the limitations imposed on animals by their environments, their resources, and their phylogenetic history. Not all possibilities are open to animals, and they sometimes have to make the best of bad situations.

Animals are *adapted to their environments.*

A considerable amount of effort in the field has gone into the documentation of the correspondence between physiological capacity and natural environment. The issue at question has never been the tautological demonstration that animals can occur where they do. Rather the problem has been how animals are able to occupy different niches and environments, whether they possess adaptive specializations in their form and functional capacities or whether there is a much less specific match between animal and environment. Studies in ecological physiology have provided many textbook examples of adaptation, for example, the kidney of a kangaroo rat, the nasal gland of a sea bird, the pelage of an Arctic fox. As a whole, this body of information, including less spectacular but nevertheless crucial adjustments, provides overwhelming documentation of the fact of adaptation of species to occupy specific environments. We now take this conclusion for granted because of the mass of documentary evidence provided by this and other areas of organismal biology.

The state of the art

Ecological physiology is no longer a new or even a young field of biological science. It has lost the shine of first discovery and has confronted limitations that were not apparent in its initial promise. In short, it has grown from its adolescence to its maturity, a sobering and unexciting experience for everyone. To a large extent, it has been a victim of its own successes.

Ecological physiologists set out to describe how animals function in their natural environments and how they adapted to them evolutionarily. They have been extraordinarily successful in doing precisely that. They have characterized the physical challenges imposed by nearly every environment on earth, from the deep sea to high altitudes, from humid tropical forests to hot deserts to cold polar regions. They have outlined, sometimes in minute detail, the interplay between organism and environment in a number of different animal taxa. The field has been successful because of its enormous background of information on the physiological responses of many different kinds of animals, its technical excellence and precision, its empirical basis, and its appreciation of the importance of observations on animals in natural environments. It has accomplished many of the goals that it originally set out to meet. In this, it has done better than many other areas of biology.

However, up to this time, the field has progressed largely by exploiting adaptations of novel animals to novel environmental situations. These will be progressively harder to come by, and certain areas of the field already seem to be engaged in collecting further examples of phenomena that are already well understood. The surprises, the unusual and unexpected examples, will be slower in coming in the future than they have been in the past. When they do appear, new phenomena are rapidly and thoroughly explored, but they do not form the basis of fundamentally new approaches or ways of looking at things. Witness, for example, the discovery of thermal vent communities in the deep sea. These proved to be populated with animals of previously unknown phyla, with metabolic patterns and physiologies previously undescribed. Yet, in spite of their novelty, their inaccessibility, and their discovery only in the mid-1970's, we already know much about their physiology, about how they make a living and extract energy from a seemingly unpromising environment. Even the discovery of totally new animals in a completely new environment did not produce any qualitative change in the field.

Our future does not lie in the discovery of new animals or new environments. Perhaps these await us in space, and our progeny can renew this exploratory phase of our science. There are certainly still many opportunities for ecological physiologists to investigate new animals on earth, particularly invertebrates and especially insects. But I reiterate my belief that the discovery of new adaptive patterns will be infrequent. Considerable progress will be made, as it always is, on the heels of advances in instrumentation and technique. In particular, improvements in computer technology, telemetry instrumentation, and applied statistics will greatly improve our ability to ask questions and get answers. But these again are refinements of current paradigms.

It is time to begin searching for new directions for studies in ecological physiology. This is not to say that traditional approaches are complete or trivial or should be abandoned. It is not to say that we know all there is to know about physiological adaptation in a majority or even in a significant fraction of the total number of animal species. But it is to say that the broad outlines of physiological adaptation have already been sketched and that past accomplishments do not form a totally adequate agenda for future work. Unless we are to be content with fitting more examples into well-worn analytical paradigms, we must expand our horizons to new questions and new sorts of studies.

If we are content to continue only in traditional approaches, we run the risk of becoming outmoded. Consider, for example, the field of comparative anatomy. It was a vigorous discipline up to thirty years ago. It was a classical area of biology, a staple of every undergraduate biology curriculum, a cornerstone of evidence for evolutionary thought. Yet rather suddenly it became irrelevant to modern biological thought and ceased to be an active area of investigation. Its extinction did not result from their running out of animals to describe: the anatomy of most species of animals is still uninvestigated. Comparative anatomy passed from the scene because it succeeded in its descriptive mission and did not develop new insights, because it was producing new information quantitatively but not qualitatively. Fortunately, anatomical studies have become reoriented and reorganized as the field of functional morphology. The near demise of comparative anatomy is a cautionary tale for ecological physiology.

This book describes some potential new techniques and new directions in ecological physiology. They are not meant to be exclusive or to supplant existing approaches totally. They are suggestions of possible ways in which the field may wish to proceed in the future. I am impressed with the diversity and vitality of these approaches: ecological physiology is not wanting for new ideas. Our future will be at least as interesting as our past.

Acknowledgments

I thank W. Burggren, M. Feder, and R. Huey for helpful comments on the manuscripts. Financial support was provided by NSF Grants BSR 86-00066, BSR 86-07794, and DCB 85-02218.

References

Benedict, F. G. (1938) *Vital Energetics: A Study in Comparative Basal Metabolism.* Washington, D.C.: Carnegie Institute of Washington.

Calder, W. A., III. (1984) *Size, Function, and Life History*. Cambridge, Mass.: Harvard University Press.

Kleiber, M. (1932) Body size and metabolism. *Hilgardia* 6:315-353.

Krogh, A. (1929) Progress of physiology. *Am. J. Physiol.* 90:243-251.

Peters, R. H. (1983) *The Ecological Implications of Body Size.* Cambridge University Press.

Schmidt-Nielsen, K. (1972) *How Animals Work.* Cambridge University Press.

Schmidt-Nielsen, K. (1984) *Scaling: Why Is Animal Size So Important?* Cambridge University Press.

Taylor, C. R., and Weibel, E. R. (1981) Design of the mammalian respiratory system. I. Problem and strategy. *Respir. Physiol.* 44:1-10.

Townsend, C. R., and Calow, P. (1981) *Physiological Ecology: An Evolutionary Approach to Resource Use.* Sunderland, Mass.: Sinauer.