Vertebrate Ecophysiology

An Introduction to its Principles and Applications

Ecophysiology attempts to clarify the rôle and importance of physiological processes, such as digestion, excretion and respiration, in the ecological relations of species in their natural habitats. The basic principles and methods that are central to any ecophysiological study are outlined and discussed, including animal capture, blood collection, and the measurement of plasma components and hormone concentrations. Attention is paid to animal welfare and ethical considerations, and the question of stress and how to identify its presence in animals in their natural environment is approached through a series of case studies. Examples are given from a wide range of vertebrates living in deserts, cold climates and oceans, and recent findings on the physiological adaptations of Antarctic birds and mammals are a highlight of the book. This textbook will provide an introduction to the study of ecophysiology for advanced undergraduates and postgraduate students, as well as for researchers in ecology, biodiversity and conservation.

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To Felicity, for sharing and enriching my life

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Don Bradshaw

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Introduction

Ecophysiology is a relatively new discipline and seeks to clarify the rôle and importance of physiological processes in the ecological relations of species in their natural habitat. It has its antecedents in the fields now known as 'environmental physiology' and 'physiological ecology', both of which developed strongly in the United States in the 1950s and 1960s. Ecophysiology differs principally from both of these in its emphasis on studying animals unrestrained in their natural environment, rather than in laboratory situations where animals are forcibly constrained and often exposed to stressors that may not be obvious, even to the experimenter.

Ecologists often have little training, or interest, in the study of basic physiological processes (such as digestion, respiration, excretion, etc.) and many would dispute that the primary ecological processes structuring populations – those of birth, growth, food acquisition, recruitment, reproduction and death – require any understanding of the physiological processes and mechanisms occurring in the individual animal. Indeed, Andrewartha and Birch (1954), in their seminal text on population ecology, went even further and argued that evolution had nothing to do with ecology! One only needs to cite Theodosius Dobzhanky's oft quoted aphorism that 'Nothing makes any sense in biology except in the light of evolution' to realise that this was an extreme view no longer shared by either ecologists or evolutionary biologists (Dobzhansky, 1953).

Another major factor distinguishing ecophysiological studies is the emphasis placed on genetics. Animals vary from one to another; the study of individual variation and its evolutionary significance is only now starting to be appreciated (see, for example, Bennett, 1987). The importance of the genetic

structuring of the physiological responses of individual animals within a population is very important and this is an area traditionally ignored in physiological studies. Ecophysiology attempts to integrate individual responses (which are rarely uniform) within the context of a single population or species.

Although animals are usually studied singly in the laboratory (which facilitates the elucidation of significant mechanisms) they rarely exist alone in nature and occur in populations that are more or less isolated in space and time. Many populations are polymorphic in nature, and much of this variety and its underlying genetic variability is lost when animals are transferred to the laboratory and exposed to markedly different and uniform conditions of climate and nutrition. This inherent variation found within natural populations is held to be an essential component of the adaptive responses of organisms to environmental pressures and one of the major foci of ecophysiological studies.

Variation is intrinsically difficult to study (our minds function by association through similarity) and this is immediately evident when one considers normal laboratory procedures. Animals are studied in groups that are thought to be large enough to encompass the individual variability found within a given population, and responses are then averaged and compared by using statistical tests, which embody a typological concept (the Gaussian distribution). Typically, animals that behave 'aberrantly' (i.e. fall more than two standard deviations from the 'norm') are excluded from the analysis rather than being made the subject of further analysis to determine the reasons for their discrete behaviour. As Block and Vannier (1994) point out in their interesting paper '. . . the ecophysiological approach must take into account polymorphism in individual responses, which are largely responsible for the adaptive capacity of any given population. In this respect, ecophysiological study yields information which is fundamental for an understanding of the mechanisms underlying adaptive strategies.'

In classical physiology, of course, this process of elimination of variability goes even further by relying on stocks of laboratory species that have been selected over long periods of time and display greatly reduced genetic variability – to the extent that skin transplants are possible between some strains of rats. Clearly, this is a necessary adjunct to the study of mechanism, where the aim is to produce a stable and reproducible preparation, but this begs the question of whether this variation is equally a nuisance to the animal in the pursuit of its normal existence and what rôle, if any, such variation plays at the level of the population.

In this book the basic principles and methods that are central to any ecophysiological study will be outlined and discussed, using concrete examples from the published literature. The very important question of stress, and how

to recognise its presence – and then measure its intensity and effect on the vital processes of an animal – will also be addressed. So too will be the question of homeostasis, which is a fundamental organising paradigm in biology and one of central importance in ecophysiology. Are animals in their natural environment maintaining their internal state within limits that permit normal activity, or do they display perturbations, which if prolonged, will lead to a loss of condition and perhaps to pathological states?

Answers to some of these questions will be illustrated by considering, firstly, a wide range of vertebrate animals that inhabit deserts: reptiles, burrowing frogs, Australian kangaroos and wallabies, desert rodents in the Sahara and North America, and desert-inhabiting birds. Although less is known of their ecophysiology, the final chapter will consider marine birds and mammals, such as the albatrosses, penguins, seals and whales, where recent research is revealing fascinating details about the physiological adaptations and compromises that they make in order to survive in challenging environments, such as the Antarctic.

The book is meant as an introduction to the study of ecophysiology that will assist advanced undergraduate and postgraduate students, as well as researchers in ecology, biodiversity and conservation. Primarily, I hope that it will be of interest and assistance to young researchers interested in studying animals in their natural habitat. Writing the book would not have been possible without the assistance of many of my colleagues and former students, foremost amongst these being: Professeur Maurice Fontaine, the late Hubert and Marie-Charlotte Saint Girons, François Lachiver, Claude Grenot, Roland Vernet, Xavier Bonnet, Pierre Jouventin, Henri Weimerskirch, Yvon Le Maho, Patrick Duncan and Barbara Demeneix in France; Ken Nagy, Joe Williams, Dan Costa and Rudy Ortiz in the United States; Phil Withers, Don Edward, Nick Gales, Brian Clay, Terry Miller, Julie McAllister, Stephen Ambrose, Keith Morris, Chris Dickman, Ian Rooke, Ron Wooller, Bob McNeice, Darren Murphy, Juliet King, Dorian Moro, Mitch Ladyman, Stewart Ford, Ernie Stead-Richardson and Jessica Oates in Australia. My sincere thanks go to Danielle Philippe for her invaluable assistance in carrying out the many arduous tasks involved in acquiring and checking references and permissions for the book and in proofreading the index. Thanks also to Mark Gargaklis for the Schnabel spreadsheet in Appendix I. Acknowledgement is also made to WAPET for support received when working on Barrow Island and to the Australian Research Committee for continued funding of my research on Australian animals over many years.