BIOLOGY OF THE REPTILIA

BIOLOGY OF THE REPTILIA

Edited by

CARL GANS

The University of Michigan,
Ann Arbor, Michigan, U.S.A.

VOLUME 12

PHYSIOLOGY C

Physiological Ecology

Coeditor for this volume

F. HARVEY POUGH

Cornell University,
Ithaca, New York, U.S.A.

1982

ACADEMIC PRESS

A Subsidiary of Harcourt Brace Jovanovich, Publishers
LONDON NEW YORK
PARIS SAN DIEGO SAN FRANCISCO SÃO PAULO
SYDNEY TOKYO TORONTO

ACADEMIC PRESS INC. (LONDON) LTD.
24/28 Oval Road
London NW1 7DX

United States Edition published by
ACADEMIC PRESS INC.
111 Fifth Avenue
New York, New York 10003

British Library Cataloguing in Publication Data

Biology of the Reptilia.
Vol. 12
1. Reptiles
I. Gans, Carl II. Pough, F.H.
597.9 QL641 68–9113

ISBN 0-12-274612-0
LCCCN 68 9113

Printed in Great Britain at the Alden Press, Oxford

BIOLOGY OF THE REPTILIA

Contributors to Volume 12

ROGER A. AVERY, *Department of Zoology, University of Bristol, Bristol BS8 1UG, U.K.*

GEORGE A. BARTHOLOMEW, *Department of Biology, University of California, Los Angeles, California 90024, U.S.A.*

BRUCE T. FIRTH, *Department of Zoology, The University of Adelaide, Adelaide, S.A., Australia*

CARL GANS, *Division of Biological Sciences, The University of Michigan, Ann Arbor, Michigan 48109, U.S.A.*

RAYMOND B. HUEY, *Department of Zoology, NJ-15, University of Washington, Seattle, Washington 98195, U.S.A.*

HARVEY B. LILLYWHITE, *Division of Biological Sciences, University of Kansas, Lawrence, Kansas 66044, U.S.A.*

PAUL F. A. MADERSON, *Department of Biology, Brooklyn College, Brooklyn, New York 11210, U.S.A.*

WILLIAM J. MAUTZ, *Laboratory of Nuclear Medicine and Radiation Biology, University of California, Los Angeles, California 90024, U.S.A.*

JOHN E. MINNICH, *Department of Zoology, University of Wisconsin at Milwaukee, Milwaukee, Wisconsin 53201, U.S.A.*

KENNETH A. NAGY, *Department of Biology, Laboratory of Biomedical and Environmental Sciences, University of California, Los Angeles, California 90024, U.S.A.*

F. HARVEY POUGH, *Section of Ecology and Systematics, Cornell University, Ithaca, N.Y. 14850, U.S.A.*

C. RICHARD TRACY, *Department of Zoology and Entomology, Colorado State University, Fort Collins, Colorado 80523, U.S.A.*

J. SCOTT TURNER, *Department of Zoology and Entomology, Colorado State University, Fort Collins, Colorado 80523, U.S.A.*

Preface

The area of physiological ecology represents a new development and one of the success stories of the last 25 years. Not only is it a new area, but the physiological ecology of reptiles, rather than following patterns set by studies on other groups, was fundamental in founding the area and has since included the key developments in the field. For this reason it was obvious from the beginning that physiological ecology needed to be included within the framework of the *Biology of the Reptilia* and I am delighted to have had the energetic assistance of Dr. F. Harvey Pough in assembling and editing these volumes.

Inevitably the topic includes more than can be provided here. For that matter, our knowledge of some areas of the field can be seen still to be in the anecdotal stage. Nevertheless, we have desisted from including treatment only of the most mature areas; clearly a statement that there are many potentially interesting aspects for which we as yet lack quantitative analyses may serve as a stimulus and a guide to future work.

On the other hand there are some areas, notably the utilization of thermal and water resources about which we not only have an enormous amount of literature but also some level of disagreement on how to proceed or interpret the data. Consequently, we have chosen to reflect this by selecting authors whose work is characterized by particular viewpoints and approaches to the topic.

It is my pleasure to thank Mr. Dennis M. Harris and Dr. George A. Zug for their painstaking reading of the manuscripts and proofs and for assisting us in making sure that the nomenclature was as uniform and as up to date as possible. We also are in the debt of many colleagues who read individual manuscripts of this set and shared their views as well as special insights, and provided aid with references to published and unpublished work. Beyond those acknowledged in the individual chapters it is a pleasure to acknowledge R. M. Andrews, R. A. Avery, G. A. Bartholomew, C. A. Beuchat, C. M. Bogert, S. D. Bradshaw, W. H. Dantzler, C. O. da C. Diefenbach, D. Duvall, W. A. Dunson, L. D. Garrick, P. T. Gregory, J. E. Heath, H. Heatwole, R. B. Huey, V. H. Hutchison, L. O. Larsen, H. B. Lillywhite, R. A. Marlow, W. J. Mautz, J. E. Minnich, K. A. Nagy, E. R. Pianka, W. P. Porter, H. Rahn, R. Ruibal, H. Saint Girons, R. S. Seymour, V. H.

Shoemaker, T. L. Taigen, C. R. Tracy, J. S. Turner, G. J. W. Webb, W. R. Welch, J. Wright, and A. Zucker. The University of Michigan and Cornell University assisted with the considerable bills for postage and copying.

January 1982 Carl Gans

Contents

4. Field Studies of Body Temperatures and Thermoregulation
R. A. Avery

5. Physiological Control of Body Temperature
George A. Bartholomew

Part 2

Water Relations

10. Patterns of Evaporative Water Loss
William J. Mautz

CHAPTER 1

Physiological Ecology: Its Debt to Reptilian Studies, Its Value to Students of Reptiles

CARL GANS

Division of Biological Sciences, The University of Michigan, Ann Arbor, U.S.A.

and

F. HARVEY POUGH

Section of Ecology and Systematics, Cornell University, Ithaca, U.S.A.

I. Introduction

The traditional approach of comparative biologists to the study of reptiles was motivated by the desire to fill gaps in our knowledge. Unfortunately, the initially greater amount of information about the physiology of amphibians and mammals suggested that reptiles be viewed as showing conditions of structure, behavior or physiology that were by definition "transitional" between those seen in amphibians and fishes on the one hand and those seen in mammals and birds on the other. One of the important advances in vertebrate biology during the twentieth century has been the growing realization that this evolutionary stepping stone concept of Recent classes is inappropriate. Instead, each grade of tetrapods appears to represent a distinctive approach to terrestrial life.* The study of the physiological ecology of animals specifically addresses several major aspects of these distinct approaches and the physiological ecology of reptiles has proved to be an especially fruitful field. Consequently, concepts and techniques deriving from reptilian studies have been extended and applied in the study of other organisms. Not only this, but reptiles continue to present the clearest and best documented examples of many topics in physiological ecology.

What, then, is physiological ecology and why has it been historically so

*Here we explicitly deal with Recent reptiles. Inference about the physiology or physiological ecology of extinct reptiles is beyond the scope of this series, although such inference must draw heavily on observations of Recent reptiles.

closely associated with the study of reptiles? Physiological ecology may best be viewed as a philosophical approach to the study of organismic adaptation and diversity rather than as a specific paradigm. Consequently, it can be distinguished from the older disciplines, not so much by the measurements it makes as by the context in which it phrases its questions. Physiological ecologists ask how organisms deal with aspects of their environments, but do not restrict themselves to the artificial divisions among levels of biological organization that are unfortunately necessary for some teaching and for much research in biology. For these reasons, physiological ecology differs fundamentally from general and comparative physiology. General physiology presumably deals with major principles, such as Starling's Law of the Heart. These principles are assumed to have broad application but, above all, they are pertinent to mammals. Comparative physiology, in contrast, asks how one process, be it oxygen transport or electroreception, is handled by diverse organisms, by fishes and by humans, by amoebae and octopuses. It also asks how it is handled in diverse environments in forests and marine situations, in deserts and the arctic.

Physiological ecology extends experiments and interpretation farther into the realm of environmental analysis. In asking how organisms deal with their environment, physiological ecology measures the same structures and processes that are the traditional subject of physiological study. However, it also draws heavily upon ecology and evolutionary biology. These are fields in which definitions are subject to debate, precise quantification is difficult or impossible, and confidence that a phenomenon is understood may last only one seasonal cycle. Repeated experience with the pitfalls of explaining and predicting has led physiological ecologists to appreciate the endless diversity of natural systems. It has also engendered an unwillingness to limit explanations to the "either/or" dichotomies that underlie the methodology of traditional experimental science. In practice, physiological ecology should avoid dividing animals into morphological, behavioral, physiological, and ecological compartments. Function, not phylogeny, forms the basis for primary comparisons in physiological ecology.

II. Why Studies of Reptiles Led the Way

In retrospect, it is obvious that the abundance of lizards in desert habitats and the conspicuousness of their thermoregulatory behavior provided the milieu for early studies of the dynamic interchange between animals and their physical environments. Physiology moved out of the laboratory when field-oriented biologists noted that reptiles in the wild (a) were not "cold-blooded" and (b) did not conform to the paradigms developed by such classical physiologists as F. G. Benedict (1932) on animals restrained in the laboratory. That is, the body temperature of freely moving reptiles was not equal to the temperature of the air surrounding them; nor did the body temperatures of such reptiles necessarily track the fluctuations of environmental temperature. The surprising part of this discovery was that lizards regulate their body temperature within narrow limits by means of a complex suite of mechanisms that range from movement to color change. These observations were made, apparently simultaneously, by workers in the deserts of central Asia (Sergeyev, 1939) and of North America (Bogert, 1939; Cowles, 1939). Once students started measuring actual body temperatures and comparing them with the daily temperature extremes of these deserts, it became obvious that the local reptiles did not conform.

For a time, the discovery that the activity temperatures of most species of reptiles were species-specific and differed from those of other species (Cowles and Bogert, 1944), coupled with the observation that such temperatures could be easily measured, led to ever-expanding numbers of lizard watchers. (These workers, noose-bearing fishing pole in one hand and Schultheis thermometer in the other, were later referred to as the "noose 'em and goose 'em" school.) Other investigators began to study mechanisms of thermoregulation, examining for instance the effect of changing integumentary absorptivity, capillary shunts, and the influence of such integumentary modifications as feathers and hair (Cowles, 1958, clothed some lizards in fur coats). The facile explanation that every observed temperature resulted from thermoregulation was soon called into question; witness the demonstration (Heath, 1964) that by some criteria then in use, even beer cans appeared to thermoregulate.

Students began to document the complexity of behavioral thermoregulatory mechanisms; these involved not only shuttling between thermal source and thermal sink, but also diverse postural adjustments (Heath, 1965; Muth, 1977). Whole cycles of studies dealt with the establishment of set points or control limits for the different behaviors (Bartholomew, this volume). An extension of field studies to mountains and subtropical habitats showed that the body temperatures maintained during activity by congeneric species of lizards are quite similar even in widely different habitats, whereas unrelated species of lizards have very different body temperatures when both live in the same habitat (Bogert, 1949a, 1949b, 1981; Brattstrom, 1965). In the half century since these pioneering studies of reptilian thermoregulation, a full cycle has been completed; reptiles that do not thermoregulate are now subjects of great interest (Avery and Huey, this volume).

The terminology of thermoregulation used by comparative physiologists in the 1940s could not accommodate the complications introduced by the