BIOLOGY OF THE REPTILIA

Edited by

CARL GANS

The University of Michigan
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Coeditor for this volume

DONALD W. TINKLE

Museum of Zoology, The University of Michigan
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Contributors to Volume 7

GORDON M. BURGHARDT, *Department of Psychology, University of Tennessee, Knoxville, Tennessee 37916, U.S.A.*

CHARLES C. CARPENTER, *Department of Zoology, University of Oklahoma, Norman, Oklahoma 73069, U.S.A.*

GARY W. FERGUSON, *Department of Biology, Texas Christian University, Fort Worth, Texas 76129, U.S.A.*

HAROLD HEATWOLE, *Department of Zoology, University of New England, Armidale, New South Wales 2351, Australia*

ERIC R. PIANKA, *Department of Zoology, The University of Texas at Austin, Austin, Texas 78712, U.S.A.*

THOMAS W. SCHOENER, *Department of Zoology, University of Washington, Seattle, Washington 97185, U.S.A.*

J. A. STAMPS, *Department of Zoology, University of California, Davis, California 95616, U.S.A.*

FREDERICK B. TURNER, *Laboratory of Nuclear Medicine and Radiation Biology, University of California, Los Angeles, California 90024, U.S.A.*

Preface

This is an exciting period in herpetology. Our progress may be illustrated in terms of the old story of the six blind men attempting to characterize an elephant by touch. We may not yet understand our animal fully, but we are recognizing that it cannot be understood by individual approaches alone, that we need to use tools from numerous biological specializations as well as an evolutionary framework within which to organize the results. The present volume probably makes this most obvious because of the range of topics it spans. It is the first dealing with questions about the nature of an individual reptile as an organism and about reptilian sensory responses to a variety of social cues; about how and what reptiles may learn; about the way reptilian species organize space and resources; and about the way they interact with members of the same species and, in some cases, with members of other species as well.

In dealing with these topics, we see a variety of approaches. Some summarize an enormous number of facts from the literature and from personal experiments; others compare reptilian data with those derivable from better studied groups. In each case synthesis of the present conceptual level appears the most critical component. It is necessary now to make value judgments of what has gone before, to discuss and to criticize. This should not mean disrespect for colleagues who carried out tedious research often under conditions of hardship. It does mean that research approaches that could not be improved upon decades ago may not be satisfactory now, and that there may be improved ways of structuring experiments and observation so as to achieve maximum utility in analysis.

The present assemblage of chapters may tell us more about the levels of our ignorance than document the levels of our knowledge. Each of the authors indicates the level beyond which the conclusions rely upon extrapolation from data that are either anecdotal or were otherwise derived during studies directed to different aims. It has been necessary to winnow facts from an enormous mass of random observations; it is hoped that future reports will increasingly be able to discuss phenomena on the basis of experiments designed to test them.

Another generalization that may be derived from these studies is their emphasis on a few groups. Diurnal lizards occupying deserts and forests, a few turtles, and recently some crocodilians, are the donors of much of the information that follows. Several authors emphasize the bias this incorporates

toward the importance of visual cues to the detriment of olfaction, chemical cues, temperature sensing, hearing, and vibration reception. Even though the contributors realize the uncertainty of the world they describe, they as yet lack data to evaluate the missing portions of the system. Almost half, if not most, species of reptiles are nocturnal and at least partially crepuscular if not fossorial. They remain to be dealt with.

Finally, this volume documents that the contact between our metaphorical blind men is still most tentative. Reference is made to structural and physiological adaptation in behavior, to functional morphology, and to populational and behavioral concepts in physiology. However, we still have a long way to go in tying such aspects together. Field experiment and museum analysis of diversity, laboratory experiment and ecological model are parts of the whole. They and other approaches will have to be applied to each problem and considered in each analysis before we can understand how reptiles interact with other organisms and aspects of their environment.

In compiling this volume, the editors must express their appreciation to our collaborator, Bill Milstead, whose death unfortunately kept him from helping us see it to completion.

We have again utilized the aid of Drs H. Wermuth and G. Zug in modernizing the many names used. This relieves the reader of the need to read with a checklist at hand. Comparison should be simplified because all experiments with a particular species are apt to appear under a single name. At least two kinds of uncertainty remain. There is first of all the question whether the animals were identified properly initially. Secondly we are at a loss as to how to deal with a few problematical groups, for instance the skinks variously termed *Leiolopisma*, *Lygosoma*, *Scincella* and *Sphenomorphus*. Still the difficulty here reflects mainly biological problems and the index hence calls attention to the difficulty so that the reader has the option of considering such problems further or of bypassing them.

Drs S. J. Arnold, G. M. Burghardt, H. W. Campbell, C. C. Carpenter, R. H. Chabreck, D. Crews, C. J. Cole, O. Cuellar, G. W. Ferguson, H. S. Fitch, J. P. Hailman, N. G. Hairston, T. A. Jenssen, G. Naulleau, W. S. Parker, E. Pianka, D. Platt, A. S. Rand, J. Roughgarden, M. Rosenzweig, R. Ruibal, T. W. Schoener, O. W. Sexton, A. C. Smith, J. Stamps, T. M. Uzzell, M. B. Vinegar, J. A. Wiens, H. Wermuth, E. E. Williams, J. Wright and R. G. Zweifel assisted us in reviewing individual manuscripts. Ms Linda Hilton provided editorial assistance. Drs Heinz Wermuth and George Zug critically read the manuscripts for usage and accuracy of the Latin names employed. National Science Foundation Grant GN815 provided for some financial assistance during the planning stages, and the Department of Zoology (now Division of Biological Sciences) and the Museum of Zoology of The University of Michigan assisted with the considerable bills for postage. Dr Paul E. Feaver prepared the index.

March, 1976 Carl Gans

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CHAPTER 1

Reptilian Species Diversity

ERIC R. PIANKA
Department of Zoology, The University of Texas at Austin

I. Introduction

Although species diversity has recently been termed a "non concept" (Hurlbert, 1971), it is an extremely useful notion that can be defined as the *effective number of species present* (Hill, 1973), either in a community, a portion of a community, or over a broader geographic area. Diversity can be quantified in a wide variety of ways, but its basic components are simply the actual number of species and their relative importances, usually measured by relative abundances (see also next section "Components of Diversity"). Many different indices of diversity have been proposed and used, and an extensive literature on species diversity has accumulated (for a sampling, see Woodwell and Smith, 1969; Krebs, 1972; MacArthur, 1965, 1972; Whittaker, 1972; Ricklefs, 1973; Pianka, 1966a; Schoener, 1974).

The ways in which species within ecological communities partition available resources among themselves is a major determinant of the diversity of coexisting species (Schoener, 1974). Moreover, the niche relationships of the component species in a competitive community strongly influence many aspects of community structure and function.

Here I attempt to review the present status of knowledge on species diversity of reptiles and I briefly compare aspects of reptilian species diversity with those in some other taxa, especially birds and mammals. Species diversity has received considerably greater attention in lizards than it has in other groups of reptiles. Much of my review therefore concerns lizard communities. Indeed, as I am the only one who has undertaken detailed ecological investigations of *entire* saurofaunas (Pianka, 1967, 1969a, 1971, 1973, 1974b, 1975), I discuss largely my own work, which has been restricted to deserts. I do, however, treat other studies where appropriate. In what follows, I draw freely from this body of my own data on desert lizard "communities" ("assemblages" would probably be a preferable

term—Pianka, 1973). To provide the reader with a background, I therefore briefly describe these desert-lizard systems.

Over the past decade, I have gathered data on the diets, times of activity, and microhabitats of over 15 000 individual lizards of 91 species on some 28 different desert study sites at similar latitudes on three continents. These areas vary widely in total number of lizard species: ten areas in western North America support from four to ten species, another ten sites in the Kalahari desert of southern Africa support from 11 to 17 species, while eight Australian study areas support from 15 to 39 sympatric species of lizards. Microhabitat and time of activity were recorded for most active lizards, and stomach contents were analyzed for those that could be collected. Many of these data have been published (Pianka, 1966a, 1967, 1968, 1969a, 1969b, 1970, 1971, 1973, 1974b, 1975; Pianka and Huey 1971; Pianka and Pianka, 1970, 1976; Pianka and Parker, 1972, 1975; Parker and Pianka, 1973, 1974, 1975, 1976; Huey and Pianka, 1974; Huey, Pianka, Egan, and Coons, 1974), and a number of other papers are in preparation.

II. Components of Diversity

Analyses of species diversity typically proceed through recognition of various components of diversity. However, diversity can be broken down into its components in a large number of different ways, all of which can provide potent insights into the factors underlying patterns of diversity. To set a theoretical framework for the remainder of this review, I next outline briefly various such approaches to diversity.

A. Number of Species and Their Relative Importance

As indicated above, the two fundamental factors determining the *effective* number of species present are simply (1) the total number of species actually present and (2) their relative importance; the latter may be estimated by relative abundance, biomass, or productivity (Dickman, 1968; Whittaker, 1970, 1972). The former component, number of species, is variously referred to as "species richness" and/or "species density," whereas the latter component is usually termed "equitability" and/or "evenness." Thus, two communities with the same number of species can differ in species diversity if one community has fewer very rare species than the other. Various indices of diversity weight these two components rather differently (Hill, 1973), and some indices all but ignore one component or the other. This may be justified to some extent; however, in birds at least, relative abundance contributes relatively little to species diversity as estimated