Lizard Ecology

Studies of a Model Organism

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Preface

PROGRESS IN SCIENCE is achieved by an understanding of the past as well as of the present. An awareness of historical trends leading to contemporary generalizations inevitably deepens one's appreciation of the nature and limits of those generalizations.

This book addresses the current status of studies on lizard ecology but has a historical basis traceable to the publication in 1967 of a volume edited by the late W. W. Milstead, *Lizard Ecology: A Symposium* (Columbia: University of Missouri Press). That volume, which was based on a symposium held in 1965, demonstrated to a broad audience that lizards are often model organisms for ecological studies: many species are abundant, easily observed, low in mobility, easy to capture, and hardy in captivity. Moreover, several key papers provided an intellectual standard and a framework that have helped to guide and stimulate subsequent research.

During the past 15 years studies of lizard ecology have advanced so dramatically that a new critical synthesis of the field is required. In response, we organized this book to summarize advances in several areas of active research on lizards and to evaluate progress made during those 15 years. Most of the chapters were originally presented in December 1980 at a symposium held during the annual meetings of the American Society of Zoologists in Seattle, Washington.

The authors have diverse backgrounds and approaches, and they include younger as well as established researchers. Authors were selected by the editors and by three participants in the 1965 symposium, William R. Dawson, Rodolfo Ruibal, and Donald W. Tinkle.

We dedicate this book to the memory of three great lizard ecologists: Raymond B. Cowles, William W. Milstead, and Donald W. Tinkle. Cowles's insights on behavioral thermoregulation of ectotherms have had a fundamental impact on physiological ecology—indeed, Cowles and Bogert's 1944 paper is a landmark in lizard ecology. Milstead's pioneering research on competition in *Cnemidophorus* came in the early 1960s, a time when studies on competition were not yet a dominant theme in population ecology, and he organized and edited the 1967 volume. Tinkle's monumental studies on life-history phenomena and his advocacy of long-term studies have left a lasting imprint on population biology and ecology. Don Tinkle planned to contribute to this book his analysis of a 10-year study of a lizard population, but his tragic death in early 1980 deprived us of this contribution.

Each chapter of this book was critically reviewed by at least two extramural reviewers. We sincerely thank the following colleagues as well as several anonymous reviewers for their efforts: George A. Bartholomew, James P. Collins, Robert K. Colwell, Justin D. Congdon, David Duvall, Paul W. Ewald, Joseph Felsenstein, John H. Gillespie, Neil Greenberg, Paul E. Hertz, Robert Holt, A. Ross Kiester, Armand Kuris, Polley A. McClure, Timothy C. Moermond, F. Harvey Pough, Stuart L. Pimm, A. Stanley Rand, James N. M. Smith, James R. Spotila, Stephen C. Stearns, Christopher H. Stinson, Donald R. Strong, Jr., Laurie J. Vitt, R. Haven Wiley, and John W. Wright.

Kathryn Rahn was a great help with editorial matters. We wish to acknowledge George A. Bartholomew (President, American Society of Zoologists [A.S.Z.]), Malcolm S. Gordon (Chairperson, Division of Ecology, A.S.Z.), Alan J. Kohn (Local Meeting Chairman, A.S.Z.), and especially Mary Wiley (Business Manager, A.S.Z.) for their untiring support of the symposium. We also thank the Ecological Society of America (Robert T. Paine, President) for cosponsorship. A grant from the National Science Foundation (D. W. Kaufman, Associate Program Director) provided financial assistance.

R.B.H.
E.R.P.
T.W.S.

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Contents

Introduction

SINCE THE 1960s studies of the ecology of lizards have developed considerably in both number and importance, have added new dimensions, and are increasingly theoretical, experimental, and synthetic. Current research projects are not only generating new and better examples of established ecological phenomena but also developing novel or more general theories of ecology, physiology, and behavior. Some studies of these "low-energy" animals are challenging long-held precepts that were derived largely from studies of "high-energy" species such as birds. Thus, research on lizards is playing an increasingly creative role and is helping to establish a new and more general paradigm for ecology.

This book considers advances in several areas of active research on lizard ecology. Our principal objectives are to describe some current developments (empirical, theoretical, methodological), to promote debate and integration among areas, to evaluate recent progress, and to discuss when possible how ecological studies of lizards complement those of other animals. We are neither advocating a single approach to ecological studies nor surveying the entire field.

The book covers three broad topics. The first part, on physiological ecology, discusses the ecological and behavioral significance of activity metabolism, the dynamics of energy flow, how the biophysical environment influences activity and distribution, and how malaria affects physiology and ecology. A second part, on behavioral ecology, contains an analysis of the adaptive zone and behavior of lizards and examines the significance of chemoreception, the establishment and maintenance of territories, the interactions among sexual selection and territoriality, and the psychobiology of parthenogenesis. The third part, on population and community ecology, evaluates patterns of life history, the relationship between niche overlap and interspecific competition, whether temporal differences in activity reduce dietary overlap, the effects of sympatry on patterns of body size, the predictability of adaptive radiations, and the integration of coevolutionary theory with biogeography. Each part begins with an overview that provides historical background. The book concludes with a chapter by an avian ecologist critically assessing current studies of lizards. This volume is thus designed to address where we are, where we have come from, and where we should be going.

Changing Perspectives

Prior to the late 1950s, natural history dominated the focus of most ecological research on lizards. The pioneering work of R. B. Cowles, H. S. Fitch, G. K. Noble, A. M. Sergeyev, and R. C. Stebbins, among others, laid a solid foundation for the field.

Research became increasingly comparative during the late 1950s and early 1960s. Blair (1960) dynamically portrayed the population ecology of the rusty lizard (*Sceloporus olivaceus*). Milstead (1961) pioneered analyses of interspecific competition in lizards. Collette (1961), Ruibal (1961), and Rand (1964) documented an unexpected degree of interspecific diversity in the ecologies of *Anolis* lizards in the Caribbean. This diversity quickly attracted the attention of numerous scientists interested in evolutionary, physiological, behavioral, and community ecology.

This burst of research during the early sixties inspired Milstead's volume (1967). Several papers from that volume have had lasting impact. Tinkle's analysis of temporal variation in the population dynamics of *Uta stansburiana* (Tinkle, 1967) set a high standard for long-term studies, inspiring a generation of students and leading to some of the first empirical analyses of life-history patterns in vertebrates (Tinkle, 1969; Tinkle, Wilbur, and Tilley, 1970; Turner, 1977; Chapter 11 below). Rand's and Ruibal's chapters in Milstead on social and territorial behavior of West Indian *Anolis* (Rand, 1967; Ruibal, 1967) and Carpenter's intensive analysis of iguanid displays (Carpenter, 1967) presaged important work on communication, social behavior, and reproduction in lizards (Rand and Williams, 1971; Jenssen, 1977; Rand and Rand, 1976; Stamps, 1977a,b, and Chapter 9 below; Crews, 1979, and Chapter 10 below; Chapters 7 and 8 below). Norris's chapter on color adaptation and thermal relations (Norris, 1967) represented an early application of the biophysical principles and procedures that are playing increasingly important roles in population ecology and physiological ecology (Chapter 3 below). Dawson's synthesis of thermal physiology (Dawson, 1967) provided a physiological basis for interpreting behavioral temperature regulation by lizards—a subject that continues to be a central feature in many ecological studies (Dawson, 1975; Heatwole, 1976; Huey and Slatkin, 1976; Avery, 1982; Huey, 1982; Chapters 1 and 3 below).

Developments since 1967

Energetics and Activity. Demonstrations that lizards have strikingly lower energetic requirements (Bennett and Nagy, 1977; Turner, Medica, and Kowalewsky, 1976; Nagy, 1981, and Chapter 2 below) and endurance capacities (Moberly, 1968; Bennett, 1978, and Chapter 1 below) than do birds and mammals have led to an awareness of fundamental ecological and behavioral distinctions between ectotherms and endotherms (Case, 1978; Regal, 1978, and Chapter 5 below; Bennett, 1980, and Chapter 1 below; Pough, 1980) and have led to new ideas of the evolution of endothermy (Bennett and Ruben, 1979). Research on the physiological effects of malarial parasites on lizards (Schall, Chapter 4 below) is constructing links between physiological ecology, parasitology, and population biology.

Temperature Regulation. Our understanding of the mechanisms and the physiological significance of temperature regulation has increased enormously (Dawson, 1975; Avery, 1982; Bartholomew, 1982). Field research on thermoconformity in *Anolis* (Ruibal, 1961; Rand, 1964; Hertz, 1974) has led to some of the first theoretical models of the ecology of temperature regulation for ectotherms (Huey and Slatkin, 1976; Huey, 1982). Complex biophysical models of heat and mass flux, now greatly expanded, are being applied to diverse and complex ecological problems (Porter et al., 1973; Roughgarden, Porter, and Heckel, 1981; Tracy, 1982; Chapter 3 below). Discoveries revealing the medical and adaptive significance of fever have relied heavily on experiments with lizards (Kluger, 1979).

Social Behavior. Research on comparative analyses of display patterns (Carpenter, 1967) quickly led to more general studies of reproductive isolation and communication (Gorman, 1969; Rand and Williams, 1971; Ferguson, 1971; Carpenter and Ferguson, 1977; Crews and Williams, 1977; Jenssen, 1977; Kiester, 1977). Lizards were found to be ideal subjects on which to test ideas concerning sexual selection, mating strategies, and the differential behavior of males and females (Andrews, 1971; Stamps 1977a,b, and Chapter 9 below; Trivers, 1972). Interdisciplinary linkages were forged (1) between social behavior and physiology, particularly endocrinology (Crews, 1975; Crews and Williams, 1977; Greenberg and McLean, 1978; Chapters 8 and 10 below), and (2) between social behavior and population biology, especially as concerned spacing systems (Kiester and Slatkin, 1974; Simon, 1975; Stamps, 1977a,b; Stamps and Tanaka, 1981; Schoener and Schoener, 1982a; Chapters 7 to 9 below).

Foraging. Field observations of lizards helped to inspire early models of optimal foraging behavior (MacArthur and Pianka, 1966; Schoener, 1969, 1971). Recent field and experimental studies (Schoener, Huey, and Pianka, 1978; Huey and Pianka, 1981; Stamps, Tanaka, and Krishnan, 1981; Chapters 5 and 12 below) extend and modify certain aspects of these models. Other studies examine interactions among foraging, habitat structure, and risk of predation (Vitt and Congdon, 1978; Moermond, 1979b).

Reproductive Strategies. Studies of geographic and temporal variation in life-history determinants are now almost routine and form a basis for many comparative and theoretical analyses of life-history evolution (Tinkle, Wilbur, and Tilley, 1970; Hirshfield and Tinkle, 1975; Pianka and Parker, 1975; Turner, 1977; Ballinger, 1978; Vitt and Congdon, 1978; Andrews, 1979; Chapters 2 and 11 below).

Interspecific Interactions. Except for Milstead's research, few studies of lizards considered the possible role of competition until the mid-1960s. Intensive observational studies (Rand, 1964; Schoener, 1968, 1975; Schoener and Gorman, 1968; Sexton and Heatwole, 1968; Pianka, 1969; Jenssen, 1973; Huey and Pianka, 1974; Roughgarden, 1974; Schoener, 1974a; Lister, 1976; Roughgarden and Fuentes, 1977; Case, 1979; Huey, 1979; Moermond, 1979a; Chapters 12 to 14 below) as well as experimental work (Nevo et al., 1972; Dunham, 1980; Smith, 1981; Roughgarden, Rummel, and Pacala, 1982; Pacala and Roughgarden, 1982; Chapter 16 below) not only are providing definitive examples of resource partitioning as it relates to environmental availability and potential competitors but also are inspiring development of complex competition models (Roughgarden, 1972, 1979; Schoener, 1974b, 1977; Chapters 14 and 16 below). Although direct observation of predation on lizards is infrequent, indirect measures have suggested predation rates may differ between types of places, such as islands versus mainlands, and between kinds of lizards, such as males versus females (Vitt, Congdon, and Dickson, 1977; Andrews, 1979; Schoener, 1979; Schall and Pianka, 1980; Schoener and Schoener, 1980).

Community Ecology. At the time of the Milstead symposium, studies of community ecology were limited. MacArthur's insights on species diversity helped inspire considerable work on this topic in lizards (Pianka, 1967, 1973, 1974, 1975, 1977; Sage, 1973; Case, 1975; Fuentes, 1976; Inger and Colwell, 1977; Schall and Pianka, 1978). A unique development has been the attempt to deduce the evolutionary and ecological history of radiations of *Anolis* (Williams, 1972, and Chapter 15 below). Current experimental studies are testing many general hypotheses on community structure (Roughgarden, Rummel, and Pacala, 1982; Pacala and Roughgarden, 1982; Chapter 16 below).

Island Biogeography. MacArthur and Wilson's theories of island biogeography and ecology received some of their first tests and challenges from research with lizards (Grant, 1967; Williams, 1969; Case, 1975), and *Anolis* lizards have become prime subjects for experimental biogeography (Schoener and Schoener, 1982b).

The years since Milstead (1967) have been exceedingly productive for all areas of lizard ecology. As Fig. I.1 illustrates, while the number of new studies per year in some areas (sociobehavioral, community) is now

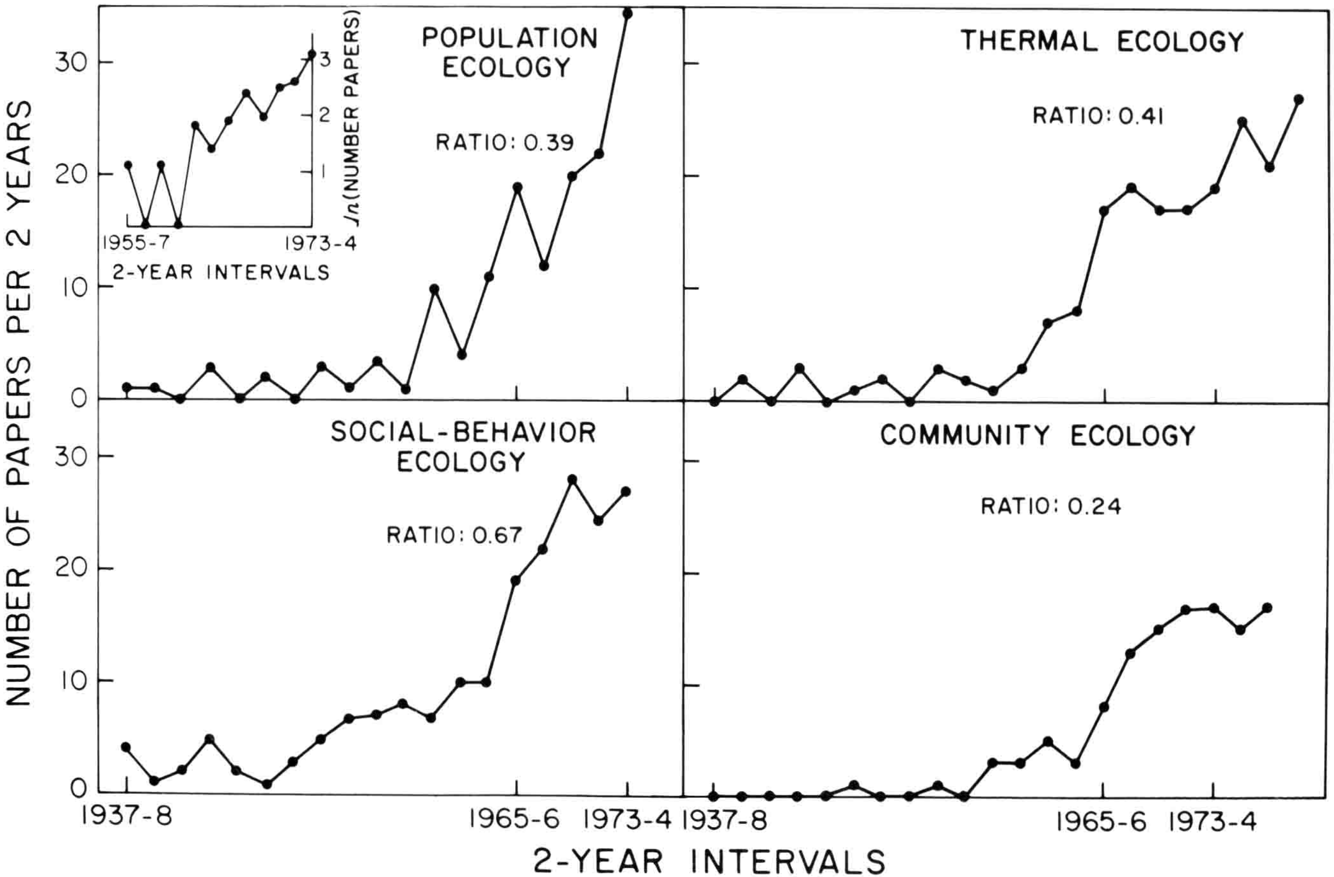

Figure I.1 Number of lizard ecology papers published per 2-year period. Ratio gives number of pre-1965 papers divided by number of post-1965 papers. Insert, top left, shows plot on a semilog scale. (Compiled from Turner, 1977; Pianka, 1977; Stamps, 1977a; Schoener, 1977; Avery, 1982; Huey, 1982; and Scott, 1982.)

beginning to level off, in one (population ecology—see insert) growth is still exponential. Indeed, the cumulative number of papers in the latter field is growing exponentially with $r \simeq 0.14$, a rate substantially higher than average for major scientific disciplines (Price, 1963). Clearly, for many types of ecological studies lizards are model organisms—moreover, they now challenge birds as the paradigmatic organism of ecology.

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PART I
PHYSIOLOGICAL ECOLOGY

PHYSIOLOGICAL ECOLOGY of animals occupies common ground between comparative physiology and ecology, and it has contributions to make to each field. Topics that appear prominent in this area include, according to my view, the following.

Energetics. An analysis of the capture and expenditure of free energy by animals is important not only to the understanding of their autecology but to the assessment of the dynamics of populations and communities as well. Such analysis provides us with a means for estimating in a universal currency the costs of particular activities and, in some cases, their benefits. Nagy (Chapter 2) skillfully applies a battery of techniques including one involving use of doubly labeled water to determine the energy budget of *Uta stansburiana.* His useful analysis documents lizards as "low-energy machines" (see Chapter 1). The provision of data on *U. stansburiana* is especially fortunate because of the prominent place this species occupies in lizard demography (see Turner, 1977). Bennett (Chapter 1) provides another view of energetics emphasizing metabolic support of activity. The limited aerobic powers of many lizards could force a heavy dependence on anaerobic metabolism during vigorous activity. Such a dependence would have profound biochemical and behavioral consequences (see below). Bennett's chapter reminds us that the pathways through which energy is made available may rival in ecological importance considerations of power input and total energy utilization. His work also shows us the substantial progress that has been made in characterizing the activity physiology of lizards since the beginning provided by Bartholomew and Tucker (1963, 1964), Bartholomew, Tucker, and Lee (1965), and Moberly (1966, 1968a, 1968b).

Effect of Physical and Biotic Factors. When coupled with adequate studies of the animals in nature, laboratory investigation of the physiological effects of physical factors upon these organisms has provided insight concerning patterns of adaptation to harsh environments, mechanisms of acclimatization, control of reproductive timing, and so on. Bennett illustrates the importance of these effects in his analysis of the thermal dependence of oxygen transport in lizards (Chapter 1). This dependence is an important determinant of a lizard's potential for activity.

Biotic factors undoubtedly play an important role in conditioning physiological response, yet we know relatively little about the details of their actions in wild populations of most organisms. The involvement of such things as nutritional state, parasite burden, and social interactions in affecting the physiological state and ultimately the fitness of organisms remains an important item on the agenda for physiological ecology. For this reason Schall's work (Chapter 4) on the effects of malarial parasites on the western fence lizard (*Sceloporus occidentalis*) is particularly welcome. It shows just how crucial biotic factors can be in the biology of free-living lizards. In addition to having ecological importance, Schall's study is valuable in providing a broadened framework for parasitological studies.

Distributional Limits. Except in the most obvious cases, knowledge of the manner in which myriad biotic and physical factors act in imposing limitations on the distribution of organisms is not well understood. This topic has been of interest to physiological ecologists since their early efforts at "tolerance physiology." Porter and Tracy (Chapter 3) show us how adequate information on the physiology and ecology of a lizard such as the desert iguana (*Dipsosaurus dorsalis*) can be used to explore situations in which physical factors appear limiting.

Model Species. Physiological ecology deals primarily with wild animals beyond the realms of agriculture, medicine, or anthropology. It therefore allows contact with a wide assortment of species which may depart conspicuously in physiological characteristics from more conventional laboratory subjects. This sometimes makes these species especially promising material for investigating the distribution and underlying mechanisms of particular physiological processes. Such has been the case with *D. dorsalis,* one of the subjects serving to establish the presence of febrile responses in ectothermic vertebrates (see Kluger, 1979). The lizards employed in Bennett's studies of activity physiology (Chapter 1) may be very useful subjects for investigations dealing with the mechanisms by which vertebrates cope with metabolic acidosis. The *Sceloporus* studies by Schall (Chapter 4) should also be valuable for further assessment of host-parasite interactions in natural populations.

Behavioral Interpretations. Behavior contributes importantly to maintenance of homeostasis in various animals. One aspect of this relates to these animals' positioning themselves in suitable microclimates. Appreciation of the significance of such behavior often depends upon analysis of the flow of energy and material between the animals and their environment, as well as upon an understanding of physiological requirements. Porter and Tracy (Chapter 3) provide helpful examples of this flow, for example, in showing just how movements of a land iguana (*Conolophus*) through its home range on Isla Sante Fe in the Galapagos affect thermal economy.

Bennett's analysis (Chapter 1) of activity metabolism in lizards gives us an opportunity to interpret behavior through understanding of functional capacities. It is much easier to appreciate the predilection of many of these animals for sit-and-wait patterns of predation or low-speed patrol when one is aware of their low aerobic capacities (Regal 1978, and Chapter 5 below).

Evolutionary Interpretations. Using results on contemporary species to develop inferences concerning evolution of physiological functions has considerable risk attached to it. Nevertheless, such information does allow fruitful speculation about certain topics and identification of key evolutionary steps. The characterization of reptiles and other ectothermic tetrapods as low-energy machines (Pough, 1980; Bennett, Chapter 1) emphasizes anew the importance of enhancement of aerobic power in the evolution of endothermy and ultimately homeothermy. Bennett also notes that the limitations on aerobic input effectively bar many lizards from exploiting niches requiring sustained vigorous activity. This has important implications not only for foraging and predator avoidance but also for the feasibility of terrestrial migrations. In the present context, we can better appreciate the evolutionary possibilities of lizards if we understand the functional substrate represented in a saurian grade of organization (Bennett, Chapter 1; Regal, Chapter 5).

William R. Dawson