A Chronological Bibliography, the History and Status of Studies of Herpetological Communities, and Suggestions for Future Research

by

Norman J. Scott, Jr.

U.S. Fish and Wildlife Service
Museum of Southwestern Biology
University of New Mexico
Albuquerque, New Mexico 87131

and

Howard W. Campbell[1]

U.S. Fish and Wildlife Service
Denver Wildlife Research Center
Gainesville, Florida 32601

Abstract

The Chronological Bibliography of Herpetological Community Studies is used to prepare an historic resumé of the field. The taxonomic and geographic distributions of the studies are described, and the contributions of studies of special themes and habitats are identified. Community studies are derived from classical natural history investigations with input from many other disciplines. The clearest recent trend is the sophisticated mathematical analysis of community structure exemplified by the works of Pianka, Inger, and Schoener. Energy flow studies have begun to appear, and the inevitable controversies have sprung up. Another recent development is the large amount of pertinent research being sponsored by a multitude of governmental agencies. The symposium contributions summarized reflect the current state of the art of herpetological community studies. Suggestions for the future include the need for a rigorous examination of our operating assumptions, such as the role of competition, the amount and availability of the resource bases, and the ecological reality of arbitrary communities. The role of sociality needs to be examined in a community context. New field and analytical techniques need to be developed, and long-term studies should receive high priority. Herpetologists working on government projects should take the responsibility for publishing their findings in scientific journals. Detailed prior planning is seen as the most important factor in determining the success of a herpetological community study.

Though research on herpetological communities has expanded greatly in recent years, it still claims only a small proportion of the herpetological literature. For instance, 246 herpetological titles were published in the 1978 volumes of *Copeia*, *Ecology*, *Herpetologica*, and the *Journal of Herpetology*. Of these, only eight (3%) were sufficiently community oriented to include in the Chronological Bibliography of Herpetological Community Studies following this paper. Since all noncaptive reptiles and amphibians live in communities where they interact with other organisms, the opportunities for community research are virtually limitless. This paper is intended to analyze past community studies, to determine their strengths and weaknesses, and to make suggestions for the future that will encourage further research into an area rich in investigative opportunities.

[1]Deceased: Died at Gainesville, Florida, on 10 December 1981.

In order to see where we are going, it is instructive to see where we have been. Accordingly, the first part of this paper reviews the historical development of herpetological community studies and defines the major driving forces and trends within the field. The raw data for this review are the contents of the bibliography. After the historical summary, the current status of herpetological community studies is defined based on a resumé of the papers in this volume and the current literature. Finally, the perceived trends in these studies are defined, and recommendations are made in which progress can be made in the most productive directions.

The Chronological Bibliography of Herpetological Community Studies was compiled by following the community criteria laid down in the Preface; that is, the studies that are listed involve three or more reptile or amphibian species living in the same area. There should also be enough ecological or behavioral information to enable species comparisons, and their interactions (or lack thereof) may be deduced. The rather extensive literature on mimicry was omitted, largely because most of the material is still very theoretical and speculative, and field tests are lacking. We have not seen all of the studies listed in the bibliography, and several citations were included on the basis of information provided by other authors. We have tried to make the bibliography as complete as possible, but new references are continually coming to our attention. Foreign studies are particularly likely to have been overlooked. It is complete enough, however, to provide an accurate basis for the historical resumé.

History of Studies of Herpetological Communities

Historical Resumé

The origins of studies of herpetological communities are not very remote, although their roots are deeply buried in the explorations of the early collectors and naturalists. Nothing published in the 19th century was community oriented, and interest in the ecological relationships of sympatric reptiles and amphibians grew slowly in the early 1900's. The development of the study of herpetological communities parallels that of the study of ecology itself, with perhaps a 10- to 15-year lag in most subject areas.

As befitting an infant discipline, early studies were descriptive. Picado's (1913) description of Costa Rican bromeliad faunas included reptiles and amphibians, and his holistic approach could well be emulated by present and future workers. Wright's *Life Histories of the Anura of Ithaca* (1914) was an early example of what could be done by an astute observer collecting data at one site over a period of years, and this type of detailed description of the long-term average phenology of the frog fauna has been rarely duplicated for other areas. During the 1920's, similar studies appeared; interestingly enough, all dealt with snakes: Klauber (1924) in southern California, Brimley (1925) in North Carolina, and Loveridge (1927) in Massachusetts. These studies were mainly concerned with documenting activity and, to some extent, habitat preferences.

The same themes were present in the 1930's. Conant (1938) wrote of reptilian activity patterns in Ohio, and Klauber (1939) contributed a study on snakes. Habitat preferences began to be emphasized: Mosauer (1935) described the fauna and its adaptations in a sand dune area, Humphrey (1936) documented altitudinal distributions of Arizona rattlesnakes, and Dunn (1937) produced a paper amplifying Picado's (1913) original observations on bromeliad herpetofaunas. During this same decade, the work of Uhler et al. (1939) on snake food habits foreshadowed the proliferation of similar studies so important in modern community analyses.

The 1940's saw the emergence of the modern type of descriptive study that integrates most of the important aspects of the biology of the organisms—their demography, abundance, habitat preferences, food habits, activity patterns, and enemies. Fitch (1949), who continues to be one of the most active researchers in the field (this volume), produced an excellent integrated study on California snakes, and Hairston's (1949) report on the ecology of Appalachian salamanders is another fine example. An important development during this period was the initial attempts to quantify animal abundances and other important ecological variables. Quantitative descriptions of populations, their food habits, and their habitat preferences are the raw materials for modern community analyses.

The next decade and a half (1950–65) was

Table 1. *Number of papers dealing with each taxonomic and geographic segment of the herpetofaunal community.* Some papers fit into more than one category and may be tabulated several times.

Region and taxon	Africa	Asia[a]	Australia	Central America[b]	South America	Europe	Totals
Tropics							
Reptiles and amphibians	10	8	1	16	6	–	41
Lizards	7	2	1	35[c]	1	–	46
Snakes	6	2	8	2	2	–	20
Turtles	–	–	–	–	3	–	3
Crocodilians	–	–	–	–	4	–	4
Frogs	6	6	–	8	5	–	25
Salamanders	–	–	–	1	–	–	1
Totals	29	18	10	62	21	–	–
Temperate Zone							
Reptiles and amphibians	–	–	2	19	2	1	24
Lizards	12	–	9	40	5	1	67
Snakes	4	–	2	43	–	–	49
Turtles	–	–	–	2	–	–	2
Frogs	3	1	2	20	1	–	27
Salamanders	–	–	–	13	–	–	13
Totals	19	1	15	137	8	2	–

[a]Includes the East Indies.

[b]Includes the West Indies.

[c]Includes 27 studies restricted to the genus *Anolis*.

largely a period of consolidation and amplification of the trends already established. Habitat preferences continued to be a favorite topic; guts (mostly snake) were analyzed, and other biological characteristics of sympatric species were examined. Increasingly more emphasis was placed on species interactions, and competitive exclusion became a key phrase and focus of analysis (Hairston 1951; Fouquette 1954; Milstead 1957*a*, 1957*b*, 1957*c*, 1965; Pianka 1965). As in other areas of ecology at the time, competition was assumed to be an organizing force in reptile and amphibian communities; however, no one tested the assumption.

In the mid-1960's, community studies had matured to the point where comparisons between communities were being made. The early studies of Brown and Alcala (1961) in the Philippines, Heatwole and Sexton (1966) in Panamá, and Pianka (1965) in the North American deserts are the first models of a field that has burgeoned in the last 10 years. Pianka has continued to be highly productive both in theoretical community comparisons and in natural history studies. At the same time, Barbault (1967) began detailed community studies that would ultimately provide the greatest wealth of quantitative information on entire herpetological communities available today.

Taxonomic and Geographic Distribution of Studies

A tabulation of the taxonomic distribution of the studies in the bibliography (Table 1) reveals that there have been only a few on crocodilians and turtles. The former group is never very speciose in any one area, and crocodilian "communities" are scarce; however, it is surprising that turtles have not received more attention. They are abundant and easily caught in many places, and multispecies aggregations are common. Lizards are often common, diurnal, and conspicuous, and they have been the subject of the majority of studies in both temperate and tropical habitats. Twenty-seven of the total of 33 tropical lizard studies have been carried out on the genus *Anolis* in the West Indies.

Our list of the geographic distribution of the studies in the bibliography is probably biased toward studies in Australia, Africa, and the New World; even so, relatively few community studies have been done in Asia and Europe. The great majority of temperate zone work has been done in North America, and a large proportion of the tropical studies have been done in Central America, including the West Indies. The efforts of a few very prolific workers are largely responsible for several of the totals: Barbault in tropical Africa, Inger in tropical Asia, Schoener in West Antillean *Anolis*, and Pianka in temperate Africa and in Australia.

Special Study Themes

Several ecological and taxonomic systems have received a disproportionate share of attention. The system represented by the genus *Anolis* in the West Indies mentioned above is one of the best examples. Under the guidance of Ernest Williams at Harvard University, many outstanding theoreticians, systematists, ecologists, and behaviorists have developed an impressive body of data and theory that will provide material for integrative studies of evolution and ecology for many years to come.

Other taxonomically-based systems that have been exploited are the North American natricine snakes (Fitch 1941; Hebrard 1951; Carpenter 1952; Fouquette 1954; Fleharty 1967; Burghardt 1968; Hebrard and Mushinsky 1976, 1978; Mushinsky and Hebrard 1977*a*, 1977*b*; Kofron 1978), whiptail lizards (*Cnemidophorus* and *Ameiva*; Milstead 1957*a*, 1957*b*, 1957*c*, 1965, 1972, 1977; Medica 1967; Asplund 1968*b*; Hillman 1969; Schall 1973, 1977; Scudday and Dixon 1973; Scudday 1977; Mitchell 1979; Cuellar 1979), sea snakes (Shuntov 1971; Voris 1974; Dunson 1975; Heatwole 1975*a*, 1975*b*; Limpus 1975; McCosker 1975; Minton and Heatwole 1975; Dunson and Minton 1978; Redfield et al. 1978) and rattlesnakes (Humphrey 1936; Damman 1961; Pough 1966; Klauber 1972). All of these groups, except the rattlesnakes, are largely diurnal forms that are often abundant and have enough species in a genus so that several similar forms may occur in a given spot.

Other faunas that have contributed the raw materials for a large number of papers are desert reptiles (54 papers) and calling and successional studies of frog ponds (21 papers). Again, the attractive combination seems to be an abundance of animals in a habitat where they are easily observed and collected.

Food habits studies are basic to the understanding of any animal community. The bibliography includes 19 titles which are primarily descriptions of the food habits of coexisting species. Almost half of these are studies of snakes, whereas most of the other studies are divided between lizards and amphibians.

Special Habitats

Several specific kinds of habitat have been singled out for special study. The common thread drawing these studies together is that they deal with habitats that either concentrate animals or that have naturally high populations. For instance, bromeliads concentrate both amphibians and reptiles, especially in the dry season (Picado 1913; Dunn 1937; Smith 1941; Neill 1951), and their faunas are rather easily characterized. Similarly, Funderburg and Lee (1968) and Lee (1968, 1969) investigated the herpetological associates of Floridian pocket gophers (*Geomys*), other mammals, and cabbage palms.

Islands have been a favorite laboratory for evolutionary studies since Darwin and Wallace, and they are beginning to be recognized as good places to study community interactions. An attractive feature of most archipelagos is that similar biotic communities tend to be repeated under a similar climate, but the biogeographic history of each island produces a distinct combination of species. Thus, each island can be viewed as a separate evolutionary "experiment." The *Anolis* students mentioned above have exploited the insular features of their fauna to such a degree that there are few comparable mainland studies. Other workers who have successfully used island systems are Soulé (1966), Case (1975, 1978); Dunham et al. (1978); Case et al. (1979); and Bennett and Gorman (1979).

In the early 1950's, a noteworthy subset of herpetological communities spawned a diverse literature. Anchored by Woodbury and his students in Utah, studies of hibernating aggregations of reptiles (most often snakes) became popular. The Utah dens have produced several of the few long-term community studies, and the availability of large numbers of research animals has provided opportunities for detailed insight into the biology of the snakes involved. The paper by Brown and Parker in this volume is the latest in these studies, and its conclusions hold little promise for the future of this important study system that has produced so many articles (Woodbury and Hansen 1950; Woodbury 1951; Woodbury and Parker 1956; Hirth 1966; Hirth and King 1968; King 1968; Hirth et al. 1969; Parker and Brown 1973). Other workers that have studied hibernating aggregations of reptiles and amphibians are Neill (1948), Carpenter (1953), Storm (1955), Cooper (1956), and Drda (1968).

Natural History Studies

Modern community studies, even highly theoretical works, have evolved from origins in classical descriptive natural history. Whereas early workers were content to describe communities, many recent studies probe the questions of "how" communities function and "why" communities are structured as they are. Quantitative instead of just qualitative approaches are becoming more common, and new field and analytical techniques are constantly being developed.

Probably the best known herpetological community is that of the University of Kansas Natural History Reservation. For more than 30 years, Henry Fitch and his students have studied the herpetofauna of this tract of land. Much of the information was published as a series of autecological monographs, but recently the data are being analyzed for community patterns (Henderson 1974; Fitch, this volume). There still remains a wealth of information for further integration.

Natural history studies make up the bulk of the bibliography, and the list of recent contributors is long. Outstanding individual records include Rand (1961, 1962, 1964, 1967; Rand and Humphrey 1968; Myers and Rand 1969; Rand and Williams 1969); Heyer (1967, 1973, 1974, 1976*a*, 1976*b*; Dixon and Heyer 1968; Heyer and Bellin 1973); Heatwole and Sexton (Sexton et al. 1964; Heatwole 1966, 1975*a*, 1975*b*, 1976; Heatwole and Sexton 1966; Test et al. 1966; Sexton and Heatwole 1968; Minton and Heatwole 1975); Duellman (1960, 1965, 1967, 1978); Dixon (Dixon and Medica 1966; Dixon and Heyer 1968; Scudday and Dixon 1973; Dixon and Soini 1975, 1977; Staton and Dixon 1977; Henderson et al. 1978, 1979); Milstead (Milstead et al. 1950; Milstead 1953, 1957*b*, 1960, 1965, 1972; Milstead and Tinkle 1969); and Hebrard and Mushinsky (Hebrard and Mushinsky 1976, 1978; Mushinsky and Hebrard 1977*a*, 1977*b*).

The most productive group in the quantitative exploration of herpetological communities has been Robert Barbault and his collaborators, Claude Grenot and Roland Vernet, of the Laboratoire de Zoologie of the Ecole Normale Supérieure in Paris. Publishing since 1967, Barbault has authored or coauthored more titles (19) in the bibliography than any other author. Starting in Africa, he quantified the populations, biomass, habitat use, activity cycles, and trophic structure of the reptile and amphibian communities of the Ivory Coast savannahs (Barbault 1967, 1970, 1971, 1972, 1973, 1974*a*, 1974*b*, 1974*c*, 1974*d*, 1975*a*, 1975*b*, 1976*a*, 1976*b*, 1976*c*, 1976*d*). Transferring his experience to México, he continued the same types of studies in Chihuahua (Barbault 1977; Barbault and Grenot 1977; Grenot et al. 1978; Barbault et al. 1978). Grenot and Vernet also investigated North African herpetofaunas (Grenot and Vernet 1972*a*, 1972*b*; Vernet and Grenot 1972*a*, 1972*b*). In recent publications, Barbault and Grenot processed their data using niche overlap theory, and their analyses tend to converge on those of Pianka (Grenot et al. 1978; Barbault et al. 1978). This wealth of material is little known in North America and has not been incorporated into recent reviews (Pianka 1977; Schoener 1977).

Three recent authors have made outstanding contributions by cataloging and analyzing some of the most complex herpetological communities known. Dixon and Soini (1975, 1977) and Duellman (1978) worked intensively for many years on the Amazonian slopes of Peru and Ecuador. Both sets of studies stem from similar sorts of backgrounds: strong systematic training and experience, blended with a natural history approach to the interpretation of communities. These works should provide copious raw material for developing hypotheses on the structure and function of tropical communities.

Other Disciplines

Many other herpetological disciplines such as systematics, physiology, and autecology have contributed to the development of community studies. The debt to alpha taxonomy is obvious but often overlooked. Many ecologists are unaware of the taxonomic problems in their study area and often do not wish to become involved in their solution. At a minimum, every ecological study should deposit properly prepared voucher specimens in a public museum. Neglect of the nuts and bolts of classical taxonomic herpetology can lead to confusion and imprecision in community studies.

Often a wide gulf exists between laboratory physiologists and field ecologists. The few people that have made an attempt to bridge the gap have provided valuable insight into community function that could not be gained in any other way. Clark (1967), Sexton and Heatwole (1968), and Pough et al. (1977) investigated habitat selection and water loss in snake, lizard, and frog communities; Ruibal (1961) and Schall (1977) looked at thermal adaptations in lizards; and Burghardt (1968) studied innate food habits in a water snake community. Fleharty (1967), in the most complete laboratory analysis of a community to date, studied food habits, water loss, specific gravity, and oxygen consumption in garter snakes. The common feature of these studies is that laboratory and field studies were integrated to provide a unique understanding of the communities involved.

Autecological studies have been, and will continue to be, the basis for most of what we know about the ecology of reptiles and amphibians, and there is much in these studies that can be used in community syntheses. However, it is important to remember that a community has properties greater than the sum of the parts, and single species orientations can be misleading in a holistic analysis.

Recent Studies

The greatest number of papers in the "Modern Period," dating from the mid to late 1960's, still deals with "natural history" subjects such as population size and fluctuation, behavior, and food and habitat preferences. These are becoming more and more useful in gauging community interactions for several reasons: past experience has indicated which ecological variables are most likely to yield useful information, comparative studies are much more common, and techniques of studying communities have become more sophisticated. In spite of these developments, the most distinctive trend in recent herpetological literature is the application of theoretical, mathematical approaches to community analysis. These studies will be examined in detail below. Other recent developments in the literature are the studies of energy flows through reptile and amphibian populations, three recent controversies that remain undecided, and the accumulation of a vast body of knowledge buried in government reports.

Theoretical Studies

As studies of herpetological communities became more quantitative in the 1960's, theoretical analyses became possible. Species and the communities they formed were viewed as active agents in dynamic evolutionary systems. Words like "competition" and the "niche" became common, and differential equations proliferated. The concept of strategies, such as reproductive or feeding strategy, was developed, and resource partitioning analyses were extended beyond mere food habits studies. Space, structural features of the habitat, and the time of day or year were also seen as vital resources.

The earliest papers with significant theoretical analyses include Hairston (1951) on Appalachian salamanders, Fouquette (1954) using garter snake food habits, Milstead's series (1957*a*, 1957*b*, 1957*c*) on Trans-Pecos whiptails, and Colette (1961) analyzing the correlation between *Anolis* ecology and morphology. Since then, theoretical considerations have been a large part of many papers, and the development of techniques of analysis have been a major effort for many authors. Three of these workers stand out, both because of their prolific output and the ingenuity, depth, and novelty of their community analyses.

Eric Pianka (1965, 1966), borrowing techniques from the avian community studies of Robert MacArthur, was a leader in applying quantitative techniques to the testing of hypotheses of community structure. He has continued to develop and refine his analyses, and his comparative approach, using widely dispersed diurnal desert lizard systems, has contributed to the robust nature of his conclusions (Pianka 1969*a*, 1971, 1973, 1975; Pianka et al. 1979). Pianka's emphases have been on the detection of the effects of interspecific interactions, primarily competition, on structure within communities, and the elucidation of geographic patterns of lizard diversity. His approach has been fruitful and, as a result, more is known about ecological characteristics of diurnal desert lizard communities than for any other group of reptiles or amphibians (Pianka 1975, 1977). Although concerns for the structural dynamics of entire lizard communities has dominated his work, Pianka has not neglected the natural history of small segments of communities or even single species (Pianka 1969*b*; Pianka and Pianka 1976; Huey and Pianka 1977; Pianka and Huey 1978; and several other papers outside of the scope of this bibliography). Without this solid natural history base, Pianka's more esoteric theoretical conclusions would be much less acceptable to the general herpetological scientific community.

During the same period, Tom Schoener was adapting a system for measuring structural habitat developed by Rand (1964) to quantify niche characteristics in communities of West Indian *Anolis*. Schoener's earliest studies dealt with single species interactions, but he soon used the same techniques to describe patterns and consequences of resource use by multispecies communities. Patterns analyzed have included animal size relations (Schoener 1969, 1970*b*) and food and habitat use (Schoener 1968, 1970*a*, 1974*a*, 1974*b*, 1975; Schoener and Gorman 1968; Schoener and Schoener 1971*a*, 1971*b*).

Robert Inger and his collaborators have applied innovative analytical techniques to large bodies of community data from the Asian tropics and subtropics (Lloyd et al. 1968; Inger and Colwell 1977; Inger 1980). The questions he deals with (habitat use, species packing) are similar to those studied by Pianka, but the approaches are rather different. Much of the difference derives from problems of scale; Pianka treated 4 to 29 sympatric lizard species in his studies, but Inger treated more than 100 species of reptiles and amphibians. Inger has also contributed to our knowledge of the ways that small segments of faunas interact (Inger and Greenberg 1966*a*, 1966*b*; Inger 1969), and Inger and Greenberg (1966*a*) conducted one of the few field experiments on amphibians.

In addition to the prolific workers cited above, a number of other herpetologists have contributed creative analyses to the further development of our theoretical body of knowledge. They are too numerous to list here, but a few deserve mention for the amount and quality of their work: Crump (1971, 1974, this volume), Wilbur (1972; Wilbur and Collins 1973), Heyer (1973, 1974, 1976*b*; Heyer and Berven 1973), Hurtubia (1973; Hurtubia and di Castri 1973), Fuentes (1976), Moermond (1974, 1979), Huey (Huey and Webster 1976; Huey and Pianka 1977; Pianka and Huey 1978; Huey 1979; Pianka et al. 1979), and Case (1975, 1978; Case et al. 1979).

Energy Flow Studies

Strangely enough, herpetological communities have largely escaped the analyses based on energy flows to which other vertebrates were subjected during the era of the International Biological Program when funding for system-oriented ecological research was most easily obtained. Perhaps the thought was that, even at high densities, reptile and amphibian metabolism was so low compared with mammals and birds that their role in community energetics was negligible. Two recent studies indicate that this generality is probably untenable. Burton and Likens (1975*a*, 1975*b*) showed that salamanders in a New Hampshire forest constitute as much of the animal biomass as any other group of vertebrates, and that energy flow through the salamanders is about 20% of that through the birds in the same ecosystem. Bennett and Gorman (1979), working on the arid West Indian island of Bonaire, concluded that lizards were major consumers, and their daily energy requirements exceeded those of small mammal faunas in temperate zone systems. Clearly the assumption that reptiles and amphibians can safely be ignored in analyses of ecosystem energetics needs reexamination, especially in tropical systems.

Controversy

Any field of human endeavor ultimately generates controversy, but the study of herpetological communities seems to be, with few exceptions, relatively free from disagreement. This situation is partly good in that it has allowed a free and objective interchange of ideas without the barriers that are artificially erected when differences of opinion become polarized. On the other hand, we believe that the theoretical underpinnings of much of our work has not been adequately examined, and many operating assumptions are accepted without sufficient review. We will return to this idea in the section on suggestions for the future. There are three theoretical areas with opposing views in the papers of the bibliography. One has very little associated data, and the other two have data that are interpreted in two different ways.

The first is the explanation by Janzen (1976) for an apparent lack of reptiles in Africa when compared with tropical America. Using sweeping correlations, Janzen concluded that the community of scavengers supported by the grazing herbivores in Africa also suppressed the reptile populations. Kreulen (1979) took issue and responded with other correlative observations. Janzen's (1979) reply contained no new information but suggested some tests for his hypothesis.

The second controversy has developed over explanations of the sizes of individuals of the lizard genus *Uta* on islands in the Sea of Cortez. Soulé (1966) concluded that the size of utas on islands was determined by the competitive pressure from other iguanid species present. With the collection of more data and further analysis, Dunham et al. (1978) found other variables, such as number of perennial plant species, to be equally well correlated and suggested caution in evaluating correlative data with the *a priori* assumption that competition is the community organizer. The latter authors suggested several ways to remedy the problems that they see in many similar studies.

The third area of controversy lies in differing interpretations of the effects of competition in larval amphibian communities (Heatwole, this volume). Wilbur (1972) and Wilbur and Collins (1973), on the basis of extensive experimentation with *Rana* and *Ambystoma* larvae, concluded that competition was one of the major organizers of many tadpole communities. Heyer (1976*b*) disagreed, and based on his own studies from Thailand, Panamá, and the eastern United States, concluded that predation and random factors were usually responsible for observed tadpole community structure, and that interspecific competition was not.

These controversies seem to be rather different, but there is a common thread running through them all: the relative importance of predation and competition as organizers in herpetological communities. Janzen's (1976) hypothesis that predation is a major determinant is based on little data and much speculation, and is obviously intended to be heuristic, but the practical means of testing it are not clear. Soulé's (1966) conclusion that *Uta* size depended on competition was tested, and serious doubt was cast on it. Wilbur (1972) and Wilbur and Collins (1973) pinpointed several areas where they believe competition is operating, but Heyer (1976*b*) saw only predation pressure or random effects. At least one side in each of these arguments believes that one of the most powerful tools for generating definitive data is community experimentation (Wilbur and Collins 1973; Tinkle and Gibbons 1977; Janzen 1979).

Governmental Reports

Governments at all levels have suddenly become aware of the presence of a large number of animal species that have been ignored in previous planning. Now land and pesticide use, waste disposal, resource development, and a multitude of other governmental activities require a complete vertebrate inventory or environmental impact statement before the project can be carried out. The preparation of these inventories or statements include the gathering of a great amount of potentially useful information on reptile and amphibian communities. Most of the information is buried in reports with limited distribution which are collectively referred to as "gray literature." We have not attempted to examine this literature here, but we believe it should not be ignored in the future. Part of the problem with using it is in determining its reliability, since it is often not reviewed by competent biologists, and voucher specimens are seldom prepared.

Review of the Symposium

The contents of the symposium largely reflect the current status of research into herpetological communities. Heatwole reviews our current knowledge of community structure to set the stage for the rest of the volume. Crump examines the role of life history strategies as they may affect amphibian communities. Her paper provides several predictions for future research. After the reviews, Wiest describes in detail the anuran succession in a series of Texas ponds, and Jones examines niche relations in West Indian frogs.

Three papers on resource partitioning in snakes follow. The first two are the most recent in a long series of studies on well-known systems. Brown and Parker continue the Utah den series, but recent events appear to indicate that this distinguished series of studies will soon be terminated. Fitch summarizes the food habits of the snakes of the University of Kansas Natural History Reservation. The third paper, by Reynolds and Scott, examines a mammal-eating snake community in Chihuahua, México.

Creusere and Whitford initiate the section on lizard communities. Their paper clearly documents the large amount of individual variation in activity patterns; their work underscores the need to look at individual strategies and not to generalize from observations on total populations. Mautz describes an interesting Mexican cave saurofauna, and Bury provides biomass estimates for a series of Mojave Desert lizard and tortoise faunas.

Scott analyzes an African forest herpetofauna and compares it to previous studies in Asia and Central America.

Three papers describe the attributes of herpetofaunas living on sandy substrates. Werner synthesizes work in the Sinai Desert, Campbell and Christman document faunal succession on sandy sites in Florida, and Smith describes resource partitioning in the most highly adapted sand-swimming segment of the same fauna.

The next three papers describe field techniques for community study that have been proven in extensive studies. Lillywhite used tracking methods to study California snakes, Campbell and Christman used various trapping and collecting methods to gather data on Florida faunas, and Vogt and Hine did the same in Wisconsin.

The mix of papers in the symposium seems to be a fair representation of the current state of herpetofaunal community studies. Many of the subject areas prominent in the historical review are present here: frog pond succession, hypothesis-generating theory, food habits, resource partitioning, special habitats, and mathematical analyses.

Suggestions for the Future

The literature review and the symposium contributions point to several clear recommendations for future work. For instance, the general unavailability and unawareness of Barbault's work in North America underscores the need for much more effective reprint exchange and translation services than we have at present. Recent tendencies to cut back or eliminate foreign language requirements in graduate curricula have certainly contributed to the problem. More personal contacts between workers in different countries would also help.

Another specific area that needs work is the extension of the studies of insular populations of *Anolis* to mainland sites. The West Indian anoles are known in great and voluminous detail, and generalities derived from their study are being extrapolated to many other systems and have threatened to become dogma. However, since these island populations are unusual in many respects, we should be wary of extending the ecological and evolutionary conclusions to mainland forms. From what little that is known, mainland *Anolis* are probably not subject to the same degrees of competitive and predatory pressures as the island ones.

One of the basic assumptions underlying the great majority of resource partitioning studies is that competitive exclusion between species is responsible for the community patterns. Unfortunately, very few attempts have been made to show that competition really exists, and fewer yet have good evidence for its presence. There is a good possibility that competition is an important interaction between island anoles but not between mainland species. Competition is easy to assume and makes a convenient focus for partitioning studies, but we should realize that the best correlations in the world do not prove the importance of competition as a force that structures communities.

One of the few ways to get a better idea of the real importance of competition are experimental studies done in the field. Only two community-level experimental studies have been published so far (Inger and Greenberg 1966*a*; Cuellar 1979), and more work along these lines will be needed before we will be able to say whether our assumption has been correct. In the final analysis, interspecific competition will probably prove to be a major determinant of the structure of some communities, whereas it can be ignored in others.

Another neglected aspect of resource partitioning studies is the determination of resource abundance and availability. Theoretically, for exploitative competition to occur, two species must be using a common, limited resource base. The demonstration of these conditions in a given study would greatly strengthen the assumption of the importance of competition. Perhaps more interaction with quantitatively-oriented entomologists and other biologists will help alleviate the problems of sampling food resources.

Related to the problem of the assumption of competition is the arbitrary nature of herpetological communities. Most workers have not attempted to define their version of the community in ecologically meaningful terms. They have dealt with a convenient subset of the animals present, assuming that the interactions between these species are important in determining structure. Pianka (1973, 1977) is one of the few workers in the area to recognize the potential problems. Detailed study of the relations between herpetological species with no concern for other faunal components of the community could be very misleading. For instance, large spiders, scorpions, and centipedes could conceivably be the most important competitors with forest litter reptiles and amphibians, and an analysis of resource partitioning would be grossly inaccurate without including them. Perhaps a clearer picture would emerge if herpetologists thought in terms of "the reptile and amphibian components of the community" instead of the current usage. Pianka (1973) and Heatwole (this volume) would use the word assemblage in the same context.

Another technique that has been underexploited by researchers is the combined field and laboratory study. The few mentioned above have shed a great deal of light on the adaptations of reptiles and amphibians to their environment, and when a comparative approach is followed, many of the proximate causes for observed community patterns become clear.

Comparing the structure of different communities is a useful technique for detecting global patterns. Pianka has been the leader in developing this method, but the contrasts need not be intercontinental to be useful. Comparisons between a variety of local communities, such as Campbell and Christman's Florida sandhill paper in this volume, can serve to focus attention on faunal patterns that would otherwise be missed. In order to make comparisons between two sites, the data need to be compatible. This is one of the strongest arguments for developing and standardizing techniques that have broad applications in a variety of communities.

The importance of social factors in structuring herpetological communities is almost unknown. Surely the intense territoriality shown by many lizards, frogs, and crocodilians leaves its imprint on the local assemblage. The demographic consequences of high and low population densities have not been investigated. How sensitive are frog choruses, tadpole aggregations, synchronous sea turtle nestings, and other mass activities to low population levels? Most social phenomena in reptiles and amphibians are still poorly known, and their inclusion in an integrated model of community dynamics is a long way in the future.

The development of field techniques for the study of herpetological communities seems to have lagged behind the data gathering in recent years. Papers describing trapping, marking, and census methods were common in the literature of the 1940's and 1950's, but their frequency has dropped in recent years. With field herpetology becoming more and more quantitative, it is necessary to pay more attention to our field methods. Comparisons between techniques are needed, such as Campbell, Christman, Vogt, Hine, and Lillywhite have done in this volume, and methods need to be evaluated over a wide range of habitats. Studies designed for maximum efficiency and utility will then use those methods that give results that can be compared with temperate forest studies because the study techniques have been compatible.

New analytical techniques also need to be developed. Quantitative analyses of community data should be a tool leading to biological understanding and not a goal in itself. If the biological significance of a quantitative procedure is not evident, it should not be used. The checkered history of the information theory parameters, H and H′, is a good example. These diversity measurements are useful for quantifying niche features such as food habits or the use of structural features of the habitat. However, when H′ is calculated as a community parameter based on the distribution of individuals among species, its meaning becomes obscure. The community H′ has generated much more heat than light, and correlations with some sort of community "stability" or "maturity" seem to be spurious. To say that one community has a higher H′ than another carries very little information, and what little there is could be better expressed in more intuitive ways.

Long-term studies are much needed. Almost all of our ideas about herpetological communities derive from short-term "snapshots" of the system. Reptile and amphibian populations vary considerably from year to year; relative species densities fluctuate and some species disappear to be replaced by others. Clearly, conclusions based on one instant in this dynamic system are bound to be misleading. Long-term studies are not easily supported and are often neither cost nor time efficient if volume of publications is the currency of the trade. However, if we are ever going to be able to say with confidence that we understand the functioning of a herpetological community, it will have to be after the community has been studied for many years.

Future studies will inevitably be more concerned with the effects of humans on herpetological communities. There have been a few studies in the past that have dealt with subjects such as urban herpetofaunas, and we foresee a proliferation of these in the future. As humans have an ever greater impact on the environment, we will want to focus on such questions as the community impacts of pesticides and the effects of habitat simplification. Another subject of increasing concern is the evaluation of the results of "island" size on diverse herpetological communities now that it is clear that in the near future there will be no longer any large blocks of continuous natural habitat in many parts of the world.

Herpetologists funded by governmental agencies should shoulder greater responsibilities, taking great pains to see that the data are accurately gathered and that the realities of funding and deadlines are not allowed to compromise the quality of the data and the report. Funding agencies should be made aware of the levels of money and time necessary to do a proper job. If enough funds are not available, a more limited study should be designed. A major characteristic of many governmental surveys is the attempt to cover vast areas of geography, numbers of taxa, and kinds of habitats by using superficial techniques designed only to satisfy a bureaucratic end. A professional herpetologist trapped into this kind of situation is not likely to derive satisfaction from the results. A second responsibility of those directing governmentally-funded studies is to see that the results are published in a reviewed journal. As mentioned above, the huge volume of gray literature embodied by in-house reports is almost unusable. If the data are worth gathering, they are worth reporting. A third obligation of any biologist, but especially those working on governmental projects, is to deposit adequate series of voucher specimens in an established public museum. This serves to protect both the worker and the government. Government contract officers need to be educated to this necessity and should be prepared to pay their fair share of the costs of specimen preparation and curation. Unfortunately, most agencies are still parasitizing the museums they use, although many curators now have established charges for their services.

Many other recommendations could be made concerning how to increase the effectiveness of community studies, but perhaps the most important one refers to study design. The most sophisticated studies are those that are well planned from the beginning. Pianka, Schoener, and Inger knew what they wanted to measure before they went into the field, and they had a fairly good idea of what questions they were trying to answer. When it came time to analyze the data, they had the necessary measurements. Before a field person devotes a substantial amount of time and other resources to a study, they should as clearly as possible outline the questions they wish to ask and the data they need to answer them. In this way, many descriptive studies could be turned into much more useful examinations of community structure and function.

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