

HERPETOLOGICAL COMMUNITIES

A Symposium of the Society for the
Study of Amphibians and Reptiles and
the Herpetologists' League, August 1977

Edited by
Norman J. Scott, Jr.

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Dedicated to the Memory
of
Howard W. "Duke" Campbell, Wildlife Biologist,
Denver Wildlife Research Center, Gainesville, Florida.

Preface

The idea that organisms occur in communities of species whose interactions produce distinct community characteristics is relatively new. Before 1960, most ecological investigations of reptiles and amphibians were aimed at the production of autecological studies of single species or simple lists of species present. Since then, the study of communities or community segments has become more popular, but work of this type still accounts for only a small part of the herpetological literature. The present volume originated as a symposium at the Lawrence, Kansas, meetings of the Herpetologists' League and the Society for the Study of Amphibians and Reptiles on 9-10 August 1977. The purpose of the symposium was to provide a vehicle whereby reviews and original research articles dealing with herpetological communities could be incorporated into a single source. The diversity of ideas, study systems, techniques, and approaches will, I hope, stimulate workers to look at their own herpetological paradigm with an eye towards more integrative analyses of community structure and function.

For the purposes of the symposium, a herpetological community was defined as three or more reptile or amphibian species interacting (or potentially interacting) in the same habitat. This definition allowed the inclusion of very simple communities, such as Mautz's cave lizards, but eliminated studies based on single species or on isolated, two-species interactions. The rationale for this definition is that specific community characteristics begin to appear as the higher order effects of several species interacting, whereas autecological or pair-wise studies can be (and often are) carried out without gaining much insight into community-level dynamics.

This volume is organized into subject matter sections. Two review papers are followed by eight studies of amphibian, snake, and lizard communities, four studies of entire assemblages from tropical and sandy soil habitats, and three papers dealing with field techniques for the study of herpetofaunal communities. The final paper gives a historical resumé of herpetological community studies, a summary of the papers included in the volume, and recommendations for the future. This paper is followed by a chronological bibliography of herpetofaunal community studies.

Many people helped in the preparation of this volume. Each contribution was reviewed several times and reviewers are acknowledged in the individual papers. I am especially grateful to R. E. Robino, Denver Wildlife Research Center, Albuquerque, who was instrumental in editing the manuscripts for final submission and who shared the entire process from beginning to end. I also thank Roy W. McDiarmid, Denver Wildlife Research Center, Washington, D.C., who read and commented on the entire manuscript and provided much needed support during the editing process. I thank the authors for their cooperation, both in revising their own papers and reviewing the contributions of others, and for their patience during the long lag between submission and publication. A few of the papers have been recently revised but many have not been brought up-to-date since 1977.

Norman J. Scott, Jr.

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REVIEWS

A Review of Structuring in Herpetofaunal Assemblages

by

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Abstract

The structuring of herpetofaunal assemblages in terms of numbers of species and individuals, equitability, biomass, spacing, and niche characteristics is reviewed, and the roles of moisture and altitude are evaluated. The contrast is made between forests and deserts as herpetological habitats, and some of the differences between the reptilian and amphibian components of assemblages are examined. The role of social organization in community structure, especially territoriality, is briefly mentioned.

A biotic community is an assemblage of organisms living together and interacting, and includes all such organisms, at all trophic levels. Consequently, a community is not limited to specific taxa, and a "herpetological community" by definition is not an ecologically meaningful entity. However, it is important to examine the structuring and interactions among community members of the same taxon, or of a few taxa. In the present paper I follow Heyer (1967) in referring to those segments of communities made up of reptiles, amphibians, or both as "herpetofaunal assemblages."

A biotic community (or a component assemblage) is without rank in the sense that one can treat, for example, the rain forest community, the forest floor community of the rain forest, or the community in decaying logs on the forest floor of the rain forest. In the present context the scale is determined by the few studies previously carried out.

I examined the structuring of herpetofaunal assemblages from several viewpoints: (1) numbers of species and of individuals in relation to environmental features, (2) biomass, (3) spacing within the community, and (4) patterns of interactions among species. Where there were recent reviews of a topic, I cited the review and relied heavily on it rather than citing and discussing individually the various papers contained in the review.

Nature of Herpetofaunal Assemblages

It has long been accepted that in general the numbers of species of reptiles and amphibians in the equable tropics is large and decreases toward the higher latitudes. This is exemplified by a comparison of species in two temperate and two tropical forests (Table 1) in which the tropical forests had greater species numbers than the temperate forests despite the fact that the fauna of the upper strata of the tropical forests was probably incompletely known. Porter (1972) has generalized that reptiles are restricted latitudinally and altitudinally primarily by cold, and that amphibians as a group are less cold-sensitive but tend to be restricted by dry conditions. Individual taxa do not necessarily follow these generalizations and may even show reverse trends.

The nature of the organization of species of "herps" (a reptile, amphibian, or both) in an assemblage, and the factors influencing such structure is an important aspect of community ecology. Heyer (1967) showed that four definite assemblages could be identified along a 24-km transect across the continental divide in Costa Rica which included both the Pacific and Caribbean slopes, an altitudinal range of 780 m, temperature ranges of 12°–33° C, annual rainfall of 1,700–3,800 mm, and six distinct vegetational

Table 1. Comparison of the species numbers of amphibians and lizards in drained forests (A) and swamp forests (B) in a temperate (Michigan) and a tropical (Panama) area. Data from Heatwole and Getz (1960) and Sexton et al. (1964).

Forest type	Amphibians	Lizards	Total
Michigan			
Oak-hickory (A)	2 ^a	0	2
Hardwood swamp (B)	9	0	9
Panama			
Lowland rain forest (A)	5	6	11
Swamp forest (B)	10	6	16

^aExcluding pond species.

formations. The distributions of the herpetofaunal assemblages were closely correlated with those of the vegetation zones, although some herpetofaunal assemblages spanned two vegetation zones. Individual species of herps spanned several or all of the assemblages, others were restricted to only one; however, there were areas of sharp faunal change between assemblages, and assemblages were well defined. The Pacific and Caribbean slopes were climatically different and had correspondingly different altitudinal demarcations of vegetation zones. Herpetofaunal zonation was not strictly altitudinal as samples from the same altitude on opposite sides of the divide represented different herpetofaunal assemblages. However, samples from the same vegetational zone represented the same assemblage. Heyer concluded that although the distributions of some species were limited by climatic factors, others correlated with specific microhabitats associated with particular vegetation zones. Thus, the hypothesis that zonation of herpetofaunal assemblages is primarily a direct climatic effect may be too simplistic and vegetation structure and type of habitats must also be considered.

Species Numbers

Comparisons of numbers of species among regional faunas or along latitudinal or moisture gradients could reflect differences in number of habitats in different regions, leaving the numbers of species per habitat relatively unchanged. Even

comparisons among habitats may not be entirely valid. For example, deserts and forests are not structurally equivalent. Forests often have several structural layers (such as leaf litter, low vegetation, and canopy) whereas deserts have primarily a single shrub layer. Numbers of bird species correlate well with structural complexity of the habitat (MacArthur 1972) and the same may be true of herps as well. Structural considerations may also be important on a finer scale. Tropical forests usually have more strata (several canopy layers, for example) than do temperate ones; also, Heyer (1967) noted differences in the number of stories and their heights within his subtropical-tropical transect. There may be separate assemblages in each stratum of tropical forest and if so, the greater number of species there could be an expression of the greater number of strata rather than of climate or other factors per se. Consequently, to validly express latitudinal (or other regional) differences in numbers of herp species, it is important to use an equivalent community scale and numbers of layers of the habitat or to compare structurally similar habitats. There have been only a few studies treating herpetofaunal assemblages in a way amenable for such direct comparisons; most of these have dealt with deserts or with tropical forests or its component habitats.

Tropical Forests

Quantitative studies have been carried out on the herpetofauna of the lower forest stratum in tropical Guatemala (Stuart 1951, 1958), Panama (Sexton et al. 1964; Heatwole and Sexton 1966), the Philippines (Brown and Alcala 1961; Brown 1964), Borneo (Inger 1966), Africa (Scott, this volume), and Costa Rica (Scott 1976), and on the buttress faunas in Thailand and Ecuador (Heyer and Berven 1973) and Sumatra (Voris 1977), with sufficiently similar techniques that at least broad comparisons can be made among areas. The number of herp species in a community depended on a variety of factors among which are altitude, climate, and specific geographic locality.

The greatest species numbers were found in the wet tropical lowlands, and regional differences were slight. However, there was a decrease in total number of lowland species with

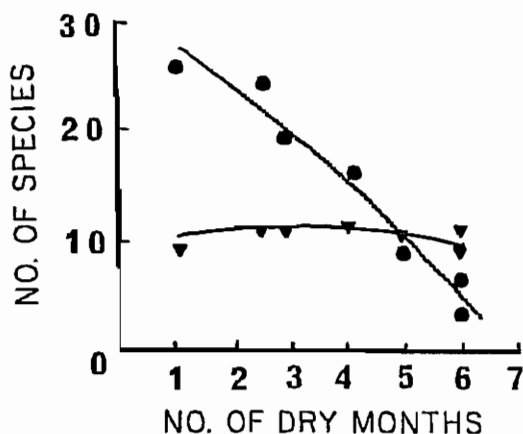


Fig. 1. Numbers of species of litter amphibians (dots) and lizards (triangles) in middle-American lowland forests with differing lengths of the dry season. Redrawn and modified from Scott (1976) with addition of data from Stuart (1958). Lines are eye-fitted.

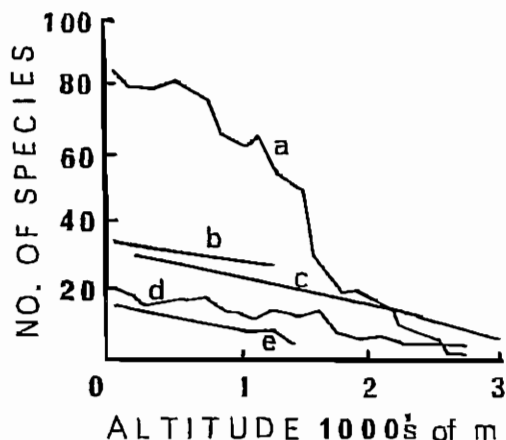


Fig. 2. Relation of tropical species-numbers to altitude. a = Costa Rican snakes; b = Costa Rican litter herps; c = Guatemalan forest herps; d = Costa Rican hylids; e = Philippine litter herps. Redrawn, modified, and horizontal axis corrected from Scott (1976) with data added from Stuart (1951, 1958).

increasing length of the dry season; this effect was especially pronounced in amphibians but slight, if at all, in lizards (Fig. 1).

Comparison of the assemblages on the buttresses in dry evergreen forest in Thailand and moist tropical forest in Ecuador is consistent with the moisture hypothesis. The dry evergreen forest had only a little more than a third of the number of species (12) as the moist tropical forest (34).

In a given geographic region and for all subgroups of the litter herpetofauna as well as for the herpetofauna as a whole, there was a tendency for decrease in species number with increasing altitude (Fig. 2). Since only a particular stratum of one habitat type (forest) was involved in these comparisons, the decreases in species number with altitude and dryness are not reflections of gross changes in habitat complexity but indicate decreases in the number of species in equivalent herpetofaunal assemblages.

A study of the total herp assemblages in Guatemala supports the conclusions based on analysis of the low-stratum assemblage alone; there was a decrease in species numbers with altitude (Fig. 2). However, in the Costa Rican transect of Heyer (1967), species numbers increased with altitude on both sides of the continental divide, perhaps reflecting community structural complexity rather than numbers per stratum or habitat. Thus the trends observed for

particular habitats or strata do not necessarily apply on a gross community scale.

In the moisture continuum, species of the forest floor stratum probably decreased because fewer species (especially of amphibians) have adapted to the more extreme physical conditions. The altitudinal correlation is less easily explained and probably encompasses historical as well as climatic considerations. Scott (1976) suggested that differential ability of lowland species to invade uplands is partly responsible.

Differences between mainland and insular assemblages were also evident. The Philippines assemblages had fewer species than equivalent moisture conditions and altitudes in Costa Rica (Fig. 2). Scott (1976) suggested that the insular depauperateness, which is especially marked at higher altitudes, results from the fact that island montane faunas will equilibrate at a lower percentage of the available lowland species than will continental montane faunas because replacements by preadapted species will be slower on islands.

Inasmuch as various taxa of herps respond differently to environmental features, habitats in different areas may have different proportional representation of amphibians, lizards, and snakes. Amphibians seem to be especially moisture-sensitive. This was previously indicated by the great difference in numbers of leaf litter

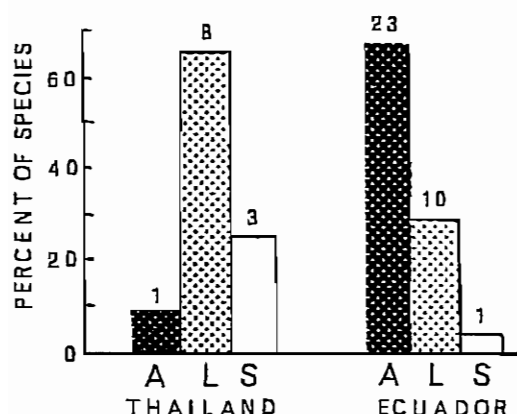


Fig. 3. Proportion of the buttress herpetofauna consisting of amphibians (A), lizards (L), and snakes (S) in Thailand and Ecuador. Numbers above histograms indicate actual number of species. Data from Heyer and Berven (1973).

frog species between forests with long dry seasons and those with short ones, compared to the relatively small differences in numbers of lizard species in the same forest floors (Fig. 1).

The composition of the buttress herpetofauna differs greatly between the Ecuadorian and Thailand forests; the proportion of amphibians is very low in the drier Thailand forest, but high in the wetter Ecuadorian one (Fig. 3). Heyer and Berven (1973) suggested that these differences arise in part because in the New World the genus *Eleutherodactylus* (which is heavily represented in the Ecuadorian buttress fauna) has direct development and is thus freed from standing water for reproduction and can consequently invade habitats closed to most amphibia; in Thailand this niche has been occupied by several lizards in the absence of frogs with direct development. The similar changes of proportional representation by amphibians along moisture gradients in the New World would suggest, however, that a sensitivity to moisture other than in terms of mode of development may also be involved.

In contrast to the sensitivity to moisture conditions, amphibians are less markedly influenced by altitude and latitude than are reptiles (cf. Costa Rican snakes and hylids in Fig. 2).

In the Guatemalan forests, increasing altitude resulted in a proportionately greater reduction in reptiles than in amphibians and the percentage

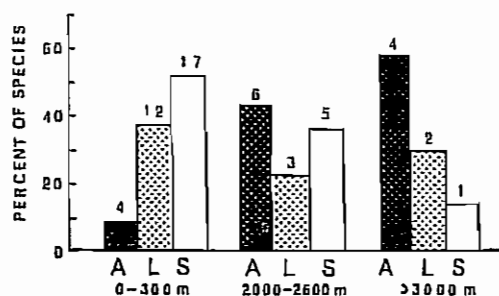


Fig. 4. Proportion of the total herpetofauna consisting of amphibians (A), lizards (L), and snakes (S) in Guatemalan forests: Tropical Dry Forest (0-300 m), Oak-Pine Forest (2,000-2,600 m), and Pine-Cypress Forest (> 3,000 m). Data from Stuart (1951, 1958). Numbers above histograms indicate actual number of species.

of the assemblages represented by amphibian species increased with altitude (Fig. 4). In contrast, an increase of 1,200 m altitude in Costa Rica, although it reduced both the numbers of litter lizards and amphibians, did not greatly alter the proportion of the two (Fig. 5). Heyer's (1967) transect revealed slight variations in

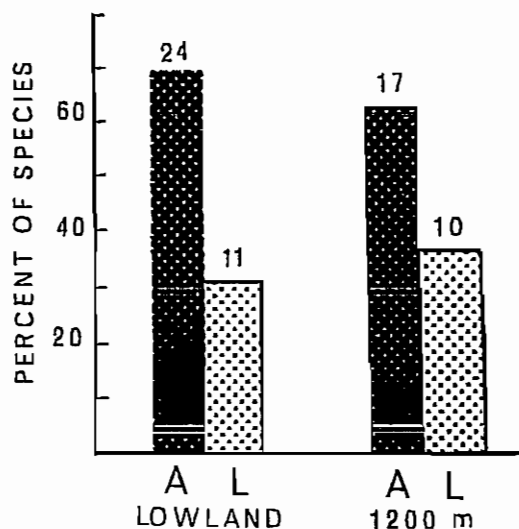


Fig. 5. Proportion of the combined numbers of lizard and amphibian species consisting of amphibians (A) and lizards (L) from wet forests in Costa Rica at different altitudes. Numbers above histograms indicate actual number of species. Data from Scott (1976).

species composition from one assemblage to another (amphibians, 37-54%; lizards, 20-27%; and snakes, 25-39%) with no consistent relation to climate or altitude. Again, one would have to analyze the separate habitats of the structurally different vegetation types for full assessment to be made of the Guatemalan data and of Heyer's transect.

In summary, the total number of species in herpetofaunal assemblages decreases with increasing latitude and altitude, with decreasing availability of moisture, and with greater insularity. The altitudinal and latitudinal effects are often influenced more strongly by decreases in reptiles than by those of amphibians, whereas the effects of moisture are the reverse. These trends can be demonstrated independent of gross changes in habitat complexity (layering), but are not always exhibited on the gross level, probably because of the added influence of community complexity.

Deserts

Numbers of species of amphibians in deserts are low and most work has concentrated on reptiles only. Pianka (1967), in a study of North American desert lizard assemblages, found that ecological time, spatial heterogeneity, length of growing season, and amount of warm-season productivity were related to the number of species occurring in an area. The most important factor was spatial (mainly vegetative) heterogeneity of the environment. He suggested that the effect was indirect and that climatic variability allows the coexistence of many plant life-forms, the variety of which in turn controls lizard species-number. Thus, the prime control factor was postulated to be climatic-vegetative. However, Pianka actually treated localities rather than habitats and part of the heterogeneity within a given locality might reflect proximity of several types of desert habitats. In a later study (Pianka 1971) of the Kalahari Desert, he found that the most important variables influencing lizard species-number seemed to be plant species diversity and mean annual precipitation. The Kalahari and American deserts were poor in number of species per locality compared to the Australian deserts (Table 2). Pianka (1969) attributed the exceptional species-numbers of Australian deserts to (1) lizards usurping ecological roles played by some worms, insects,

Table 2. Mean species density of lizards with different habitats and time niches in various localities in deserts of three continents (after Pianka 1971).

Habitat and habits	North America	Kalahari	Australia
Diurnal, terrestrial	5.4	6.3	14.4
Diurnal, arboreal	0.9	1.9	2.6
Nocturnal, terrestrial	1.1	3.5	7.6
Nocturnal, arboreal	0.0	1.6	2.6
Fossorial	0.0	1.4	1.1
Total	7.4	14.7	28.3

snakes, and mammals in North America (he considered the desert mammal and snake faunas impoverished in Australia), (2) greater temporal partitioning because of the milder and more constant Australian desert climate, (3) more narrow specialization by Australian desert lizards, and (4) greater spatial heterogeneity in Australian deserts because of an interdigitation of different habitat types, including one type, "spinifex" (*Triodia*), which is unique to Australia. Cogger (1961) previously pointed out the importance of *Triodia* in this regard. This grass has a unique life-form, occurring in dense clumps with sharp spike-like leaves interlacing and facing outward. In addition to providing a formidable defense against large predators for animals small enough to pass through the interstices, it provides an unusually equable microclimate. Diurnal humidity is higher and temperature lower than elsewhere, and shade is dense. A large number of "desert" reptiles are closely dependent on *Triodia* for conditions suitable to life and probably could not survive without this plant. Cogger (1961) argued that the fact that the life form of *Triodia* is unique to Australian deserts and has its own special reptilian fauna, may account for much of the greater species richness of Australian deserts.

As mentioned above, the real difficulty in evaluating any of the above discussion is that localities are the units of study, not habitats. As Pianka (1969) noted, a given area may have an interdigitation of habitats; part of his discussion is based on the fact that such interdigitation is greater in Australia and that each habitat has its own specialized lizard fauna as well as more ubiquitous ones. Unfortunately, he provided a breakdown by habitat only for the Australian deserts. Pianka recognized three major habitats,

Trilodia or sand-plain, mulga or shrub-acacia, and sandridges. If it can be assumed that in each American and Kalahari locality only one habitat was represented, the number of species per locality can be compared with the number per habitat type in Australia. In the Kalahari, 12 to 18 species may occur at the same locality (Pianka 1971), whereas in North America the number may be 10 or less (Pianka 1967). The mulga and sandridge habitats in Australia may contain up to 20 species each, "spinifex" up to 22, and a large number of species are not definitely assigned to any of these habitat types (Pianka 1969). Thus, it appears that even when habitat rather than localities is considered, Pianka's conclusion that the Australian deserts are richer in species than the American or Kalahari deserts is valid. If the African and American localities encompass more than one habitat, the differences would be even greater.

If one compares the species densities of lizards in deserts with that in tropical grasslands or the ground stratum of lowland forests (which are as similar structural units as can be found for comparisons between such different habitats) it is clear that deserts and tropical habitats are about equivalent; mean species densities of desert lizard species per habitat are 7.4 and 14 in the American and Kalahari deserts, respectively, about 10 for a variety of Central American forests (Fig. 1), and 6 in the grass stratum in the savannahs of the Venezuelan Llanos (Staton and Dixon 1977). This equivalence holds up although most of the deserts discussed here are at higher latitudes than are the tropical forests. In the special situation of Australia, desert habitats (20–22 species of lizard per habitat) are even richer than those of the forest floor.

One can conclude that within broad latitudinal limits and over a great range of moisture conditions, the number of lizard species in the lower strata of mainland habitats do not vary greatly, in marked contrast to that of amphibians or the herpetofauna as a whole. The greater number of species in forests would seem to reflect the additional assemblages occupying the strata found in forest but not in desert, rather than differences in the number of species in the stratum that both habitats share.

The desert environment is relatively erratic and unpredictable, and one might suspect that the large year-to-year fluctuations in the environment might be reflected in changes in the

numbers of species over time. Support for this view was obtained by Whitford and Creusere (1977) who found that during wet periods species numbers in some Chihuahuan Desert localities increased because of an expansion of suitable habitat and an influx of immigrants and transients from more mesic habitats. During dry periods these died out again.

Number of Individuals

It has been noted that number of herp species is greatest in the wet tropical lowlands of mainlands but that it decreases with increasing latitude, altitude, aridity, and insularity. Do the same or different trends apply to numbers of individuals? Few sufficiently quantitative studies have been carried out to permit evaluation; they include studies in the lower stratum of tropical forests of Panama, Costa Rica, Borneo, Africa, and the Philippines (reviewed by Scott 1976 and this volume). A surprising but consistent result was that the number of individuals increases with increasing altitude up to a certain level (Fig. 6), but thereafter decreases again, i.e., the greatest standing crops of herps occur at intermediate elevations rather than in the lowlands. There was also a difference between Asian and middle-American localities; individual numbers were lower in Asia. The numbers of individuals also decreased with increasing length of

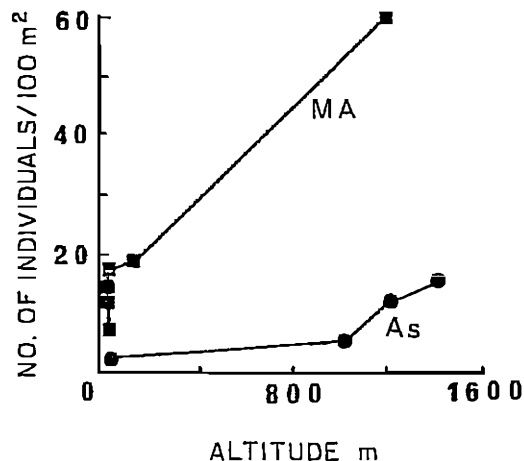


Fig. 6. Relation of numbers of individuals of leaf litter herps in tropical forests of middle America (MA, squares) and Asia (As, dots) at different altitudes.

the dry season among American tropical lowland sites (except that one locality, Silugandi, Panama, was unusually high; Scott 1976: Table 1), and at the Costa Rican localities numbers of individuals were lower in the dry than in the wet season and lower on slopes than on flat terrain. Scott (1976), although not ruling out biotic factors such as predation, suggested that all these differences were related to general productivity limits in the forest floor. He suggested that dryness (whether due to seasonal or edaphic factors) reduces productivity and that litter production may be greatest at intermediate elevations and greater in middle America than in Asia. Such productivity differences would filter through the food chain and eventually influence herps. Whitford and Creusere (1977) found that in the Chihuahuan Desert lizard densities varied directly with rainfall-induced changes in productivity and relative abundance, and activity of arthropods.

Insularity is another factor influencing densities of herps. It has been documented repeatedly that the number of species is usually smaller on islands than in equivalent mainland habitats and that the number of species on islands is a function of island size (MacArthur and Wilson 1967). However, the influence of insularity on numbers of individuals has not been studied often. Case (1975) found that on the islands in the Gulf of California, lizard numbers were inversely related to number of lizard species. The reasons for such density compensation were concluded to be differences in predation intensity, insect productivity, and possibly reduced competitive interference on small, isolated islands.

Equitability

A flurry of activity related to the concept of species diversity appears in the literature of recent years and various diversity indices have been developed. Although a few studies have applied these techniques to herpetofaunal assemblages (Lloyd et al. 1968; Heyer and Berven 1973), this aspect will not be reviewed here. I concur with Hurlbert (1971), DeBenedictus (1973), Peet (1975), and others that the concept of species diversity as expressed as an index is often biologically meaningless. It embodies two separate concepts (species richness and equitability) and a

synthesis of the two into a single index has little value. It is preferable to look at the two components of species diversity separately. One of these, species richness, has been previously examined, and the other, equitability, will be treated now. Equitability indicates how the individuals of an assemblage are distributed among species. If all species contain the same number of individuals the apportionment is equitable. If some species are abundant and others extremely rare, the distribution is highly inequitable. I will employ a graphic method of presentation in view of the frequent inappropriateness of equitability indices (Peet 1975).

The observation that some tropical forests have many species has led to the popular conception that no one species is common, i.e., that equitability in the tropics is high, and all species are rare. For example, Maiorana (1976), in a review including reptiles and amphibians, stated: "There are many species in the tropics, but generally individuals of any one of them are rare." Although this may be true for some organisms, there is abundant evidence that it is not true for amphibians or reptiles. When latitudinal comparisons are made of the population densities of herp species, it is often true that the highest population densities are encountered in tropical species (see reviews by Tinkle 1967; Turner and Gist 1970; and Heatwole 1976). There are one or a few species in each tropical herpetofaunal assemblage that are extremely abundant and account for a large proportion of the total number of individuals of the assemblage; the remaining species are relatively uncommon, i.e., equitability is low. In fact, in all but 2 of the 10 assemblages from various altitudes (lowland to 1,450 m) and localities (Panama, Costa Rica, Borneo, Philippines) reviewed by Scott (1976: Fig. 6), the most abundant species was represented by twice the number of individuals of the second-most abundant species; sometimes the differences were sixfold or more and the most abundant species contained more individuals than the rest of the species of the assemblage combined. The two exceptions were the only two assemblages represented by small samples, and even those showed considerable differences in abundance among species. Turner (1961) plotted the numerical abundance of snakes in Panama and California against their rank in abundance and got similar curves for both areas.

Although all the assemblages reviewed by Scott (1978) were inequitable, some were more inequitable than others. Equitability decreased from the lowlands to the highlands in the two areas (Costa Rica, Philippines) for which sufficient altitudinal data were available. Although there was a decrease in numbers of species with altitude, there were more individuals at the intermediate than at low altitudes. It appears that the altitudinal reduction in rare species was more than compensated by an increase in numbers of individuals of the commonest species. There was also a trend for more equitable distribution of individuals among species in the wetter as opposed to the drier American lowland assemblages, although small samples from some areas prevented a rigorous analysis. However, the data of Heyer and Berven (1973) provide a better contrast between an assemblage (butterfly fauna) from two forests differing in moisture characteristics. In dry tropical faunas (Thailand) equitability was low; the most abundant species accounted for well over half the total number of individuals, whereas in Ecuadorian wet tropical forest the distribution of individuals among species was unusually equitable. In fact, this assemblage has the highest equitability of any herpetofaunal assemblage of which I am aware. The six most common species collectively accounted for only 50% of the total individuals and the most abundant one for only 10% (Fig. 7). Although moisture conditions may have influenced these differences in equitability, it is premature to draw firm conclusions. The Thailand and Ecuadorian forests differed in ways other than moisture and continent; in Thailand the assemblage was dominated by lizards, in Ecuador by amphibians (but note that Lloyd et al. 1968 found equitability to be greater among lizards than among frogs). Furthermore, the assemblage of the Ecuadorian wet tropical forest was much more equitable than any from lowland wet forests in middle America.

The graphic portrayal of abundances of Chihuahuan Desert lizards gave equitability curves similar to those for tropical forests, i.e., the most abundant species often were twice as dense as the next most abundant species (Whitford and Creusere 1977). Considering all the above studies collectively, it is doubtful whether moisture plays a great role in influencing equitability.

On the basis of a study of Sarawak frogs, Inger

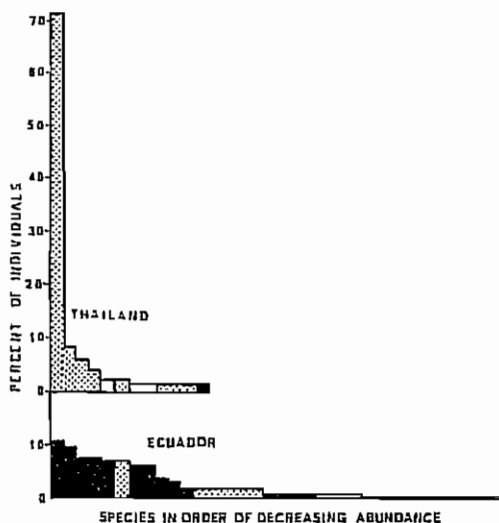


Fig. 7. Equitability in the herpetofauna of buttresses in forests in Thailand and Ecuador. Black dots on white = lizards; white dots on black = amphibians; open histograms = snakes.

(1969) implied that organization in amphibian assemblages may follow definite patterns in particular kinds of habitats, but that the role of a particular species may change from one locality to another, i.e., as one species declines in numbers, its place may be filled by an ecologically similar one that might be otherwise less numerous. He felt that the relative constancy of the frequencies of ecological types (not necessarily the same species) from stream to stream and the similarities in equitabilities meant that a given species could be added to or removed from a community without greatly affecting community structure because of the resulting changes in other species. He further hypothesized that the physical environment was ultimately responsible for community structuring in that it determined the success of particular ecological types (each of which might include a number of species). It is possible that the structuring of ecological types is determined by the physical environment, but that biotic factors influence which species of a given type predominates in the assemblage.

In summary, herpetofaunal assemblages are generally relatively inequitable; equitability decreases with altitude but with no consistent relation to moisture. It is important to obtain additional empirical data on this topic from a variety of geographic regions and across environmen-

tal gradients of different kinds. Data are at present insufficient to formulate a general theory of either the significance of equitability differences or identifications of causal factors. However, it has been suggested that particular environments determine the structuring and equitability of assemblages, and that within that structure species may be interchangeable. Clearly, much empirical data on this topic is still needed.

Biomass

A given area of habitat could theoretically support either a large number of small reptiles or a smaller number of large ones. Thus, data on numbers of individuals, as valuable as they are, do not tell the whole story. It is also essential to know the collective weight (biomass) of herps occupying a unit of habitat if community structure is to be fully understood. Although biomass values have been reported for a few individual species of herps (see review by Heatwole 1976), biomass of entire herpetofaunal assemblages have scarcely been studied (see Bury and Fitch, this volume). The work of Barbault (1970) is an exception; the mean annual biomass of the snakes (37 species) in an African savannah was 150 g/ha and the greatest values occurred during the wetter parts of the year. In the same season, there were differences between habitats (plateaus, slopes, low ground, and burned vs. unburned areas). Burned areas had a relatively low biomass compared with unburned but otherwise equivalent regions. Most of the differences among habitats were attributable to frog-eating species whose biomass changes followed those of their prey species (Fig. 8); lizard-eating species also showed biomass changes correlating with those of their prey.

Type of habitat may be important in biomass stability. Barbault (1967) found that total biomass of ground-dwelling lizards showed large seasonal fluctuation; low values occurred following fires after which they rose and reached a peak by the end of the rainy season; by contrast arboreal lizards showed little seasonal change in biomass. Lizard biomass varied by as much as twofold between comparable seasons of different years. Amphibian biomass depended largely on moisture conditions (Figs. 8, 9).

These two studies illustrate the importance of biomass studies. In the terms of the structuring of

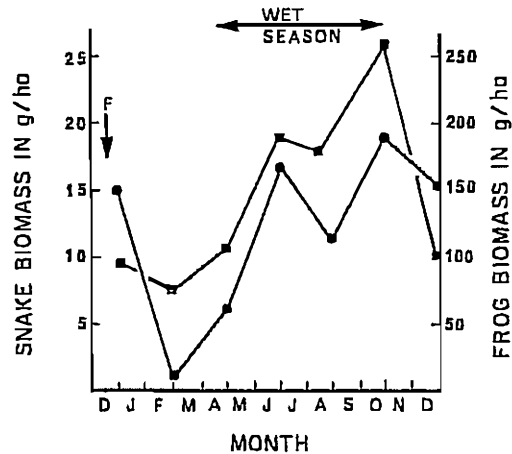


Fig. 8. Changes of mean biomass of frogs (squares) and frog-eating snakes (dots) in a savannah in Ivory Coast. F and arrow indicates fire. Redrawn from Barbault (1970).

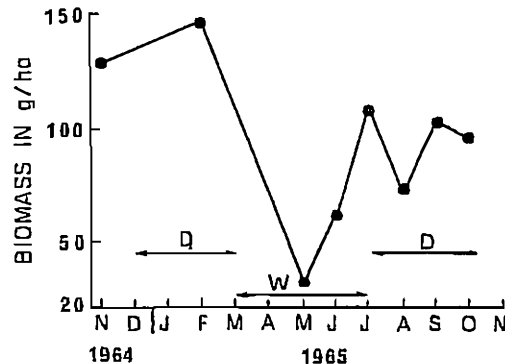


Fig. 9. Changes in amphibian biomass in a savannah in Ivory Coast in relation to the wet (W above arrow) and dry (D's above arrows) seasons of 1964-65. Data from Barbault (1967).

such assemblages, it would seem to be important to evaluate the distribution of biomass among species, i.e., look at biomass equitability. Such an approach may add a new dimension to the study of herpetofaunal assemblages and might open up fruitful avenues of research.

Spacing

The species of a herpetofaunal assemblage are not randomly distributed in space either horizon-

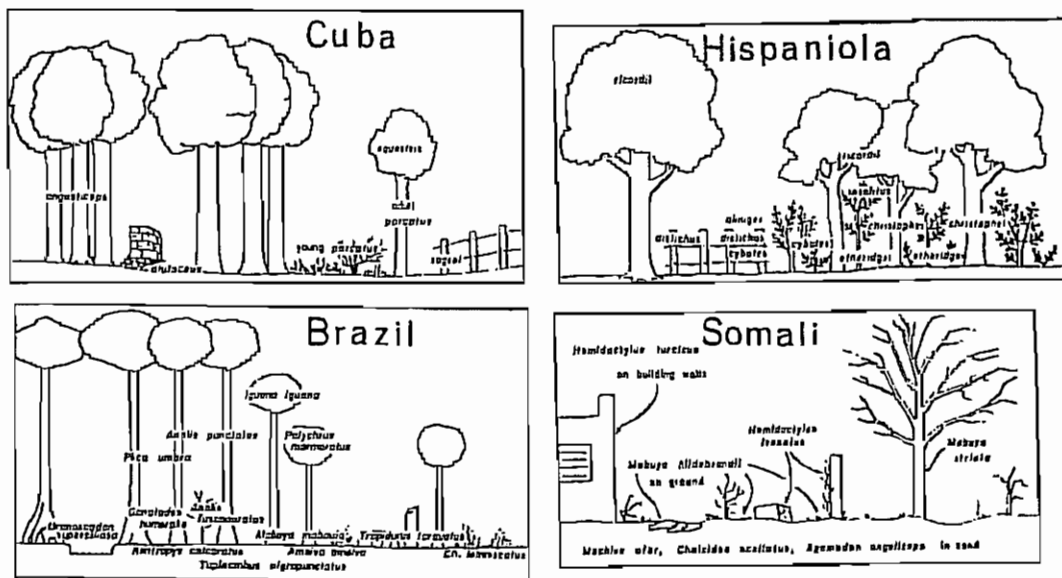


Fig. 10. Generalized schemes of spacing of lizards of the genus *Anolis* (upper two squares) and total lizard fauna (bottom two squares) in four regions. Redrawn from Collette (1961), Gans et al. (1965), Rund and Humphrey (1968), and Rund and Williams (1969).

tally or vertically; they occupy discrete microhabitats. This being true, it is presumed that the greater the spatial (structural) diversity in a habitat, the greater the number of species which can coexist there. Many investigators have qualitatively appreciated spacing patterns among herps, and diagrams indicating the nature of such spacing have appeared for a number of assemblages (e.g., Fig. 10). Where vegetation structure permits, there is often a subterranean assemblage, a leaf litter or cryptic assemblage, a low bush assemblage, a tree trunk assemblage, and one or more canopy assemblages. Where there is horizontal heterogeneity, different assemblages may occur in the more open areas than in the closed canopy areas (Fig. 11). Sea snakes show vertical and horizontal spacing (Fig. 12).

Heatwole (1977) reviewed the role of habitat selection in the spacing of reptilian assemblages and concluded (1) that spacing may in some instances arise from interspecific differences in response to the geometry of the physical environment and in others from differential responses to spatial variation in microclimatic factors, (2) that expressions of habitat selection are often modified by the presence of other species in the

same general habitat, and spacing is correspondingly affected (habitat shifts), (3) that intraspecific differences in habitat selection may tend to result in spatial separation of sexes or ontogenetic stages, but (4) that intraspecific aggression is sometimes involved in causing or maintaining such separations.

The spatial separation of the different sexes or the young from adults might maximize the number of individuals that can be maintained within a given habitat and consequently influence equitability. It would be interesting to ascertain whether common species more often have intraspecific differences in microhabitat than do rarer ones.

Biotic Interactions

Space is not the only biologically relevant dimension of a species' niche. A variety of other aspects such as food, shelter, and basking sites is also involved and the structuring of assemblages may depend on the ways species interact in partitioning such resources. Milstead (1972) suggested that for a given biome, there are a large number of finite niches, filled in different localities by

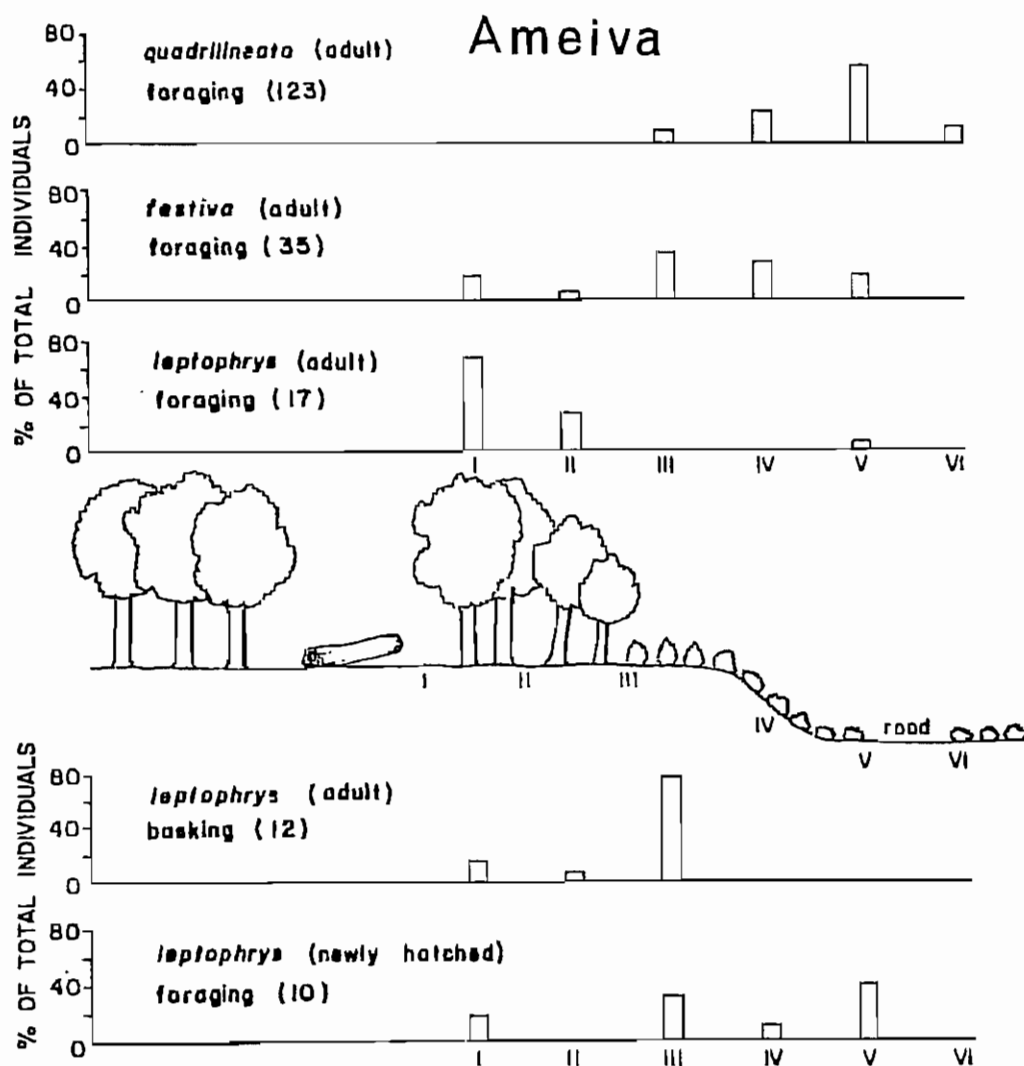


Fig. 11. Horizontal changes in habitat of lizards of the genus *Ameiva* in Costa Rica. Note the relative frequencies of individuals in the various habitats—histograms marked with Roman numerals correspond to the areas of the habitat profile of the same number. Redrawn from Hillman (1969).

convergent ecological equivalents that partition resources in similar ways.

Much of the research in resource partitioning has involved species-pairs or small groups of species rather than whole assemblages. However, the principles established by the study of small units are probably applicable to larger ones as well. Consequently, it is appropriate to briefly summarize the main points arising from these as well as from more synthetic studies (for lizards

see reviews by Milstead 1961; Pianka 1973; Schoener 1974, 1975; and the studies of Milstead and Tinkle 1969; Marcellini and Mackey 1970; Schall 1973; Hurtubia and DiCastri 1973; Scudguy and Dixon 1973; Huey and Pianka 1974; Huey et al. 1974; Fitch 1975; Simon and Miedendorf 1976; Rose 1976; Talbot 1977; for snakes see Fitch, Brown and Parker, and Reynolds and Scott, this volume; for salamanders see Jaeger 1972, 1974; Bury and Martin 1973; Fraser

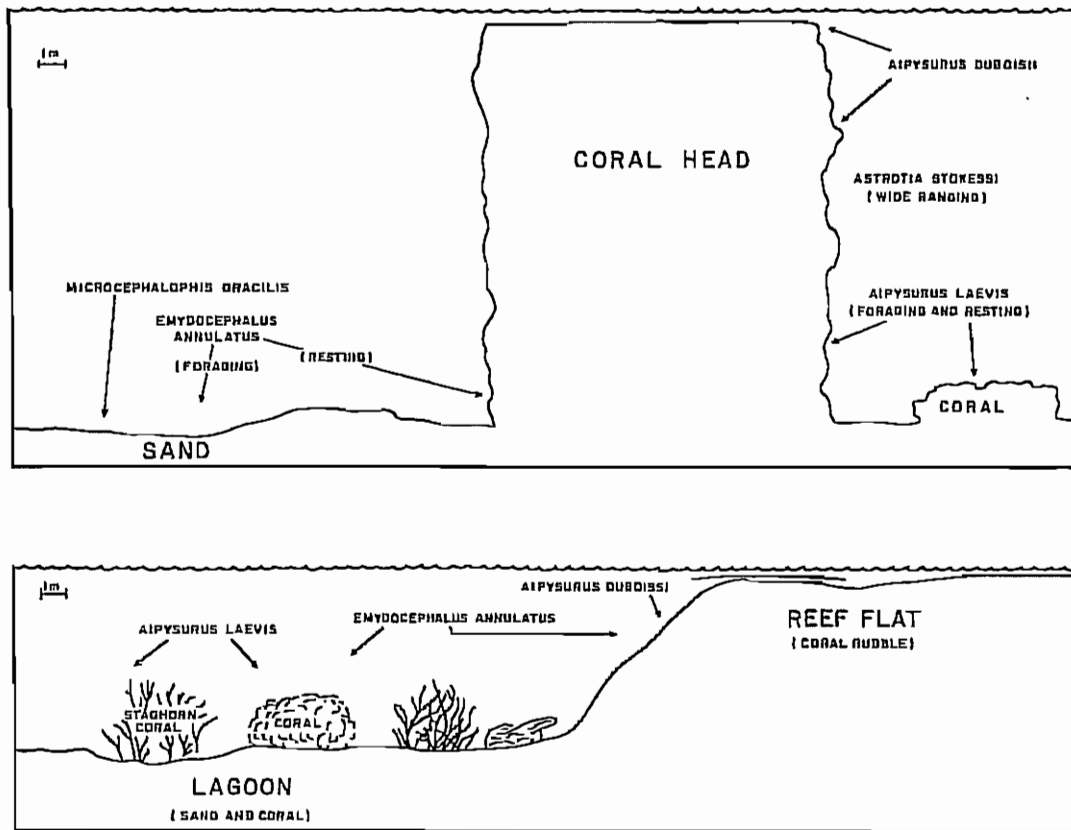


Fig. 12. Spatial separation of sea snakes on two reefs in the Coral Sea. Modified from Heatwole (1975).

1976a, 1976b; frogs are treated separately later). Resource partitioning is achieved by (1) spatial separation (also see Spacing), (2) differences in size among species, especially head size and its attendant influence on the size of prey which can be eaten, (3) differences in types, or (4) size of prey accepted or selected, and (5) the time in which activity occurs. Intraspecific differences paralleling the above-mentioned interspecific ones may also occur and result in a finer scaled partitioning. In some lizards allochronic seasonal and spatial activity may separate adults and juveniles (Whitford and Creusere 1977; Creusere and Whitford, this volume).

It is important to assess the relative importance of the various niche dimensions in separating the members of assemblages in different communities. Pianka (1973) did this for desert lizards and showed that food is a major factor separating niches of North American species, whereas in the

Kalahari, food niche separation is slight and differences in space and time are considerable. All three of these dimensions are important in separating the niches of Australian desert lizards.

Among the anoles, it would appear that separation in place and in food niches are the most important. Schoener (1975) suggested that in this group intensity of competition appears to (1) decrease with increasing differences in size between species; (2) be greater for a given size difference if the competitor is larger than if it is smaller; and (3) decrease at nonconstant rates, so that at near complete size similarity decline in intensity is more rapid for smaller than for larger competitors. It appears that the size-structure of a herpetofaunal assemblage may be an important characteristic to study, especially when coupled with information on microhabitat and on food habits (i.e., does an assemblage have an array of different-sized species in each trophic and

habitat category but few similar-sized ones in a given one?). Where anoles are released from competition from congeners (as on some islands) niche expansion occurs along the habitat, perch height, microclimate site, and prey size axes (Lister 1976).

Frogs, like lizards, tend to be generalized insectivores and many of the above considerations regarding niche separation may be expected to apply to them as well. The frog genus *Eleutherodactylus* is the ecological equivalent of the lizard genus *Anolis*; both are exceptionally large genera, have explosively radiated in tropical America, and are often represented by a number of species in the same assemblage. Like the anoles, *Eleutherodactylus* shows spatial segregation. Heatvole (1963) indicated that two species were horizontally and vertically separated in Venezuelan cloud forest; *E. terraebolivaris* occupied the tree falls, roadsides, and other open, second growth, and *E. cornutus* occupied the closed, shaded areas. Furthermore, the former leaves the litter at night and climbs up on vegetation for its activity period whereas the latter remains on the forest floor. Similarly, Cintron (1970) found that although there was considerable spatial overlap among the *Eleutherodactylus* species in Puerto Rico cloud forest, certain species tended to occupy particular strata or microhabitats (e.g., one was found primarily in bromeliads in trees, another mainly inside of the petioles of fallen palm fronds, and a third mostly under such petioles or other debris); a large species tended to feed on ants and the smaller species on small beetles. Drewry (1970) found that although the time of calling strongly overlapped, there were differences in peak of calling activity. It appears that spatial isolation is the major separating factor and a lesser difference in food and activity niches is also operative.

Inger and Marx (1961) examined the food habits of 20 species of African amphibians and found that there were interspecific differences in the food niche, and selectivity was based primarily on differences in size range of prey; there were interspecific differences in the size of prey eaten, but within a species prey size did not vary greatly with size of frog.

Heyer and Bellin (1973) examined space niche overlap (as indicated by horizontal and vertical location and vegetation type occupied) in five sympatric *Leptodactylus* in Ecuador. Three of the species had broad niches and two had narrower ones. There was considerable overlap among some of the species (Table 3). *Leptodactylus discodactylus* overlapped little with other species, in part because of distinctive calling sites used by males of that species. The species with high overlap in the spatial (habitat) niche belong to different species-groups, and Heyer and Bellin suggested that aspects other than habitat may be more important in niche differentiation among them. In any event, it is clear that although some species tend to be spatially segregated, not all are.

Dankers (1977) studied an assemblage of 18 species of frogs around a pond in eastern Australia and found that almost all were separated by differences in seasonal or daily activity period, location around the periphery of the pond, or within a given area by microhabitat. One species-pair that showed little temporal or spatial overlap differed greatly in size. (For a study of the temporal and spatial patterns of a North American frog assemblage, see Wiest, this volume.)

Inger and Greenberg (1966a) studied three species of *Rana* in Sarawak and found that spatial separation was slight and not the factor involved in their continued coexistence. Niche overlap was extensive and although coexistence is

Table 3. Niche breadth and niche overlap values for five species of *Leptodactylus* from Ecuador (from Heyer and Bellin 1973).

Species	Niche breadth	Niche overlap			
		<i>L. knudseni</i>	<i>L. mystaceus</i>	<i>L. pentadactylus</i>	<i>L. wagneri</i>
<i>L. discodactylus</i>	1.29	0.26	0.26	0.27	0.26
<i>L. knudseni</i>	2.54	—	0.99	0.63	1.00
<i>L. mystaceus</i>	2.36	—	—	0.68	0.99
<i>L. pentadactylus</i>	1.44	—	—	—	0.64
<i>L. wagneri</i>	2.53	—	—	—	—

indefinitely maintained, some competition seemed to be occurring as removal of a species resulted in increases in the density of remaining ones. They suggested that maximum population levels are fixed by intraspecific competition, a mechanism also postulated by Dankers (1977) for one of his overlapping species-pairs.

The above studies suggest that frogs are separated by much the same factors as are lizards. However, it appears that in lizards spatial components tend to be more important than in frogs but that frogs rely more heavily upon temporal separations. Ascertaining whether this impression is correct must await further comparative studies. However, it appears even at this rudimentary stage that the eleutherodactylines more closely resemble lizards in tending toward spatial segregation.

Thus far, only adult amphibians have been considered. However, given bodies of water may contain a variety of species of larvae and their potential interactions must be considered. This topic has been recently reviewed (Heyer 1976). Heyer stated that "available evidence indicates that communities of tadpoles represent nothing more than a collection of species coexisting as larvae. A tadpole community is not an integrated whole; biological interactions within the community are not important evolutionarily; there is no natural selection operating directly to integrate or partition the community." He arrived at these conclusions despite the finding of spatial and temporal separation among species, and even habitat shifts in the presence of other species, sometimes interpreted in competitive terms by the authors he cited. Heyer based his argument on the facts that (1) predation is a major organizing influence in tadpole assemblages, (2) in some instances different years result in different temporal or spatial patterns among species, (3) that he could formulate alternate hypotheses to account for presumed competition, and (4) that models had been constructed which permitted coexistence without competitive exclusion. He suggested that differences in habitat occurred as an adaptation to particular environments developed in isolation from presently coexisting species; spatial or temporal separation may arise from competition for calling or oviposition sites by adults of territorial species. He explains habitat shifts of a species when in the presence of another as a density effect independent of competition.

In critique of Heyer's views it must be mentioned (1) that although year-to-year differences in breeding times and places and with different species mixes might occur, it does not mean that such species compete at no time, nor that such competition, even if occurring occasionally, would lack selective significance in adjusting long-term trends in habitat selection or breeding phenology; (2) that ability to formulate alternate hypotheses does not necessarily disprove a pre-existing one; and (3) that models are merely highly organized, formal hypotheses and do not constitute evidence of anything. One could construct any number of models at will and arrive at any conclusions desired. Models are justified in that they stimulate empirical testing of the ideas they embody, but as an end in themselves are mere mental exercises. Heyer's main contributions, other than the empirical data on several tadpole assemblages, were the demonstration of similarity in feeding habits of various overlapping species, the providing of stimulating alternate hypotheses on organization of tadpole assemblages, and in questioning the dogma that competition is the main selective agent influencing habitat selection in larvae. In so doing, I feel he went too far in making unwarranted, blanket generalizations and in setting up the counter-dogma of no interactive affects. Further research involving detailed comparative studies of tadpole assemblages testing his ideas are clearly desirable.

Life History, Reproduction, and Community Structure

Maiorana (1976) recently reviewed the literature on the relation of life history variables to community structure, including assemblages of reptiles and amphibians. She emphasized that seasonal, temperate-zone environments select for breeding only at the most favorable time for juvenile survival. Equable tropical environments permit a greater seasonal spread of reproduction, and in general tropical lizards are characterized by early maturity, multiple but smaller clutches, and reduced life expectancy in comparison with temperate ones. However, lizards from seasonal tropical environments have reproductive strategies similar to those of lizards from the equable tropics and she suggested that tropical seasonality is not as severe as is that of temperate

regions. She concluded that (1) abiotic factors may be important in shaping the reproductive patterns of temperate lizards (length of favorable season and uncertainty in the quality of that season), (2) predation is probably important as a selective force in the life history patterns of tropical lizards but in seasonal tropical environments abiotic factors influence timing of reproduction, and (3) competition is not an important selective force in life history patterns. If these conclusions prove to be true, then it seems that in lizards, spacing and habitat selection may be influenced by competition but life history strategies more by seasonality and predation. However, Inger and Greenberg (1968b) suggested that in equable tropical forests, lack of seasonal restriction and the resulting continuous breeding of lizards may lead to increased interaction among species. Separation in space may consequently be a reflection of such interaction.

Amphibians differ considerably from lizards in some regards. Maiorana (1976) noted that many species are restricted to standing water or its vicinity for reproduction and suggested that predation pressures on larvae and competition among them in such aquatic environments are probably intense (but see Hoyer 1976). In the equable tropics, conditions favoring reproduction are extended throughout most of the year and amphibians can become temporally segregated, using breeding water sequentially in time and hence avoid larval competition. Consequently more species can coexist than in seasonal environments where favorable conditions do not persist long enough for temporal segregation of more than a few species. It is possible this is the factor which is responsible for the reduction of species numbers of frogs with increasing length of dry season noted in the section on species numbers. If coexistence or lack thereof is determined primarily by interaction at the larval stage in amphibians, rather than competition at the adult level, it would explain why adult amphibians seem to show less spatial separation but greater temporal segregation in breeding than lizards.

Hoyer (1976) concurred that the larval stage may be the bottleneck as far as population densities are concerned. He suggested that predation and weather-influenced uncertainties, such as drying or freezing of ponds, cause high mortalities and that adult population levels consequently are below the carrying capacity of the environment, except for possible scarcity of

breeding or oviposition sites in territorial species. Creusere and Whitford (1976) provided data supporting this idea.

Regardless of the factors involved, if it is true that high larval mortality results in lack of competition among adults, it explains relative lack of spatial separation among adults of different species in some amphibian groups and also explains the apparent importance of spatial separation in direct developers (see Biotic Interactions). The genus *Eleutherodactylus* has direct development and is thus freed from the high mortality imposed by aquatic environments. Predictably, the little information available suggests that like lizards, this genus shows considerable spatial segregation among adults of different species. These ideas have not been rigorously documented empirically; the data are sufficient only to be tantalizingly suggestive. Detailed empirical studies of comparative ecology and life history of various tropical amphibians, especially those with direct development, must be carried out before firm conclusions can be reached as to the role of life history variables in structuring of assemblages.

In addition to the insectivorous frogs and lizards discussed above, herpetofaunal assemblages may contain herbivorous lizards and turtles, or carnivorous members from all taxa, especially snakes, that may prey upon other herps. Most work has been done on rather generalized insectivores and the way that they segregate ecologically. Trophic structuring involving herbivorous or non-insectivorous predators in herp assemblages is a topic scarcely explained. However, Walters (1975) showed that different species of amphibian eggs and larvae have different palatabilities to their amphibian and reptilian predators. In the field there was sometimes intense predation and a negative correlation between predator presence and prey abundance.

Role of Social Organization

It is obvious that any factor which influences the numbers of individuals in an area will affect other structural aspects such as equitability, biomass, and spacing. Also, if differential mortality of various ontogenetic stages or sexes is induced by some environmental factor, the size structure and sex ratios of populations are af-

affected. Such changes in one or more component species of an assemblage affects the structure of the entire assemblage. It is beyond the scope of the present paper to review the vast literature on the influence of the physical environment on population dynamics of herps. It is also beyond the scope of this review to assess in detail the role of biotic and social factors in such processes at the level of individual populations or species. However, certain features of social organization widespread in reptiles and amphibians that have an important bearing on assemblage structure will be summarized.

A recent symposium has made it evident that reptilian social behavior is extremely varied and that it plays an important role in the ecology and evolution of the group (American Society of Zoologists 1977). Aggression is a very common element in the social repertoire of many species of reptiles and amphibians and it finds its most common expression in territoriality (Carpenter 1967). Territoriality may involve only intraspecific aggression or may operate interspecifically. In the former, aggression may be only among adult males, among conspecific adults, or take the form of adult attacks on juveniles. All of these forms of territoriality would tend to promote more uniform spacing and would limit the number of individuals that could occupy an area. This would in turn mean that successful defenders of territories in optimal habitat would have greater access to adequate food, mates, basking sites, and shelter than would less successful animals forced into marginal areas where chances of survival would be smaller. In fact, Done and Heatwole (1977a) suggested that aggression-based social systems result in a situation where, under unfavorable conditions or shortages, at least some individuals survive and breed rather than all die as a result of equally distributed but insufficient resources. Bradshaw (1971) showed that in *Amphibolurus ornatus*, adult aggression against juveniles forces the juveniles into areas where predation is higher; the surviving young migrate back into the adult areas when they reach sexual maturity. Thus, migration arising from a territorial social system may influence the structure of herpetofaunal assemblages in particular areas.

Interspecific territoriality may affect not only the number and spacing of individuals but of species as well. In some instances species occupy different horizontal or vertical zones depending

on whether the area is shared or not with congeners (Jenssen 1973; Schoener 1975). It is also possible that species numbers may be affected by the exclusion from an area of a species by another interspecifically territorial one. Thus, territoriality may affect (1) spacing within a species, (2) spacing of species relative to other species, (3) numbers of individuals, or (4) number of species in an area. These factors in turn may affect equitability and biomass.

Not all species are territorial and some can shift from territorial to hierarchical systems, at least under the artificial conditions of captivity (Carpenter 1967; Hunsaker and Burrage 1969; Done and Heatwole 1977a, 1977b). The significance of different reptilian social systems to structuring in the assemblage has scarcely been assessed except for the effect territoriality in one species has on its own numbers and spacing, and on those of the species toward which it is territorial. One can, however, ask more synthetic questions. For example, can a given assemblage contain only so many territorial species? Are the proportions of territorial to non-territorial species subject to some degree of community regulation? Are species with a particular social organization replaceable by one with a different social behavior without altering the properties of the assemblage? These and other similar questions can only be answered by empirical comparative study of different assemblages. A move in that direction has been made by Williams and Rand (1977) who showed that the relative value of the dewlap and other communicative signals in anoles varies depending on the number of anole species in the assemblage.

Conclusions

All of the topics reviewed here relate to the form or structure that herpetofaunal assemblages take under different conditions. This is just one aspect of the study of assemblages, however. The complimentary topic to that of structure is function. To fully understand an assemblage or a community, not only must its structure be known but the flow of energy and materials among species must be assessed. Both these aspects are in their infancy as far as herpetofaunal assemblages are concerned. Bioenergetic studies on herps have usually been restricted to analysis at the single species level. It is hoped that this review,

and this symposium, will stimulate herpetologists to devote increasing attention to studies involving the role of amphibians and reptiles in the structure and function of the larger community.

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Amphibian Reproductive Ecology on the Community Level

by

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Abstract

A review of amphibian reproductive ecology emphasizes the lack of integration of life history strategies and community dynamics; no data are available on the influence of interspecific interactions in shaping reproductive strategies. Certain aspects of reproductive ecology within a community matrix are suggested for future investigation. Experimental field manipulations with appropriate controls and replicates will yield the most meaningful interpretation of interspecific interactions. A list of statements and predictions concerning amphibian reproductive ecology is presented, providing a framework upon which to ask relevant questions.

The concept of a community is an abstraction because of the dynamic and boundless nature of the system. Community in the broadest sense is the entire biotic component of an ecosystem, composed of all the interacting niche-differentiated species' populations. Logistics and practicality, however, require that ecologists delimit the boundaries of such a complex system for investigation. Thus, many ecologists adopt MacArthur's (1971) definition of a community as "any set of related organisms living near each other and about which it is interesting to talk." Community ecology is more than a composite of individual population studies; a major concern is species interactions. The scope, then, is determined by the investigator and the focus is on the intermeshing influences and responses exerted and elicited by the component species.

Recently there has been increasing interest in evolution at the level of communities. Levins (1975) suggested that selection acts differently on such variables as feeding efficiency, predator avoidance, and number of offspring on the community level as compared with the species level; selection at the community level does not necessarily favor each component species. He argued that there could be strong selection for perpetuation of groups whose component species have attributes that complement each other and that favor the persistence of groups through time.

Wilson (1976) presented a model whereby selection can operate on the community level without violating the principle of Mendelian selection. It is not my intent here to enter the controversial argument on group selection, but rather to emphasize that populations do not exist in isolation from other populations.

Community organization is influenced by the simultaneous interactions of many species (MacArthur 1972; Pianka 1974; Colwell and Fuentes 1975; Whittaker 1975; Inger and Colwell 1977). Since species' responses are the result of coadaptations among sympatric populations, we must consider the organism within its entire environment to interpret adaptive strategies. Maiorana (1976a) also emphasized that a species' reproductive attributes and community ecology are interdependent and should be integrated fields of investigation. Species interactions are not simply pairwise; they are multidimensional, occurring between many if not most other populations in the community. Thus, in terms of the evolution and organization of the community, the whole is greater than the sum of its parts.

Using species interactions as the framework for community analysis, what do we know about amphibian reproductive ecology on the community versus the population level? Numerous autecological investigations have dealt with various aspects of amphibian reproductive

ecology. These range from studies such as descriptive accounts of breeding periodicity, clutch size, and survivorship to long-term analyses of fluctuations in reproductive success and population age structure. A few studies have compared reproductive ecology of conspecific populations in different environments and others have compared populations of two sympatric species. However, whenever several sympatric species have been studied, the result is an interpretation of coexisting populations. The questions have not been cast into a community framework and species interactions have not been analyzed.

In reviewing the "state of the art" of amphibian reproductive ecology, I have been continually impressed by the lack of integration of amphibian life history strategies and community dynamics. Each species exhibits a particular set of reproductive adaptations in response to its entire environment, including the structure and stability of the community to which it belongs. Interpretation of the adaptive nature of reproductive factors should include examination of the relationships of these factors with those of coexisting species within the community framework. Just as community variables are important in molding reproductive patterns, the interwoven set of reproductive tactics exhibited by the component species in turn affects community structure and stability. Since each species' response may directly affect responses of other members of the community, the interactions of the component species produce synergistic effects on the overall community.

The review of amphibian reproductive ecology presented herein and the discussion of the mutual influences of community variables and reproductive patterns are meant to provide a framework for future investigation. The purpose of this paper, then, is threefold: (1) to review current knowledge of amphibian reproductive ecology; (2) to demonstrate the relevance of analysis of reproductive ecology on the community level; and (3) to suggest fruitful areas for further investigation.

Reproduction and Species Interactions

Like all artificially delimited communities, amphibian associations are continually changing in time and space. Many species of amphibians

migrate from non-breeding areas to breeding sites (usually standing bodies of water) at appropriate times dependent on environmental conditions (see Salthe and Mecham 1974 for a review of environmental cues, breeding site location, and formation of breeding aggregations). The result at the breeding site is a different age-class distribution and sex ratio than that of the non-breeding population. In addition, species compositions at breeding sites differ from those at non-breeding sites. These compositional differences related to reproductive activity have effects on community structure, including fluctuating and overlapping resource utilization and species interactions. These effects have never been investigated. Predators of amphibians must also be affected by the transient associations with their continually changing compositions, but no data are available. Dispersal of juveniles away from the breeding site is probably the most important mechanism responsible for gene flow between populations; unfortunately, the effect of juvenile dispersal on overall community organization and stability has never been examined. The infusion of thousands of juveniles of numerous species into terrestrial habitats surely causes shifts in resource utilization among species; these shifts need to be quantified.

Although I could continue in this vein, perhaps it is more constructive to review the current status of our understanding of the mutual effects of reproductive ecology and species interactions. Two areas that have received considerable attention are reproductive isolating mechanisms and certain aspects of resource partitioning associated with breeding activity.

Reproductive Isolating Mechanisms

During the breeding season the potential for intraspecific and interspecific interactions is high because of the shift to a new community structure and a high density of individuals. Behavioral reproductive isolating mechanisms that help maintain species' identities are associated with the high potential for mismatings at temporary breeding congregations. These mechanisms include discriminatory courtship rituals such as species and sex recognition and mate selection. The most studied behavioral isolating mechanism in frogs is the mating call of males (for review see Salthe and Mecham 1974; Littlejohn 1977). The calls are species-specific with the fre-

quency of the dominant harmonic, note repetition rate, and pulse rate and length relatively uniform within a species and variable among species. Male vocalization functions in orientation of both sexes to the breeding site, formation of breeding aggregations, sex discrimination, and location of specific males by females. Analyses of acoustical variables of mating calls from a community standpoint suggest that sympatric species exhibit significant call differences with only slight overlap (e.g., Blair 1956; Creusere and Whitford 1976).

Species recognition in salamanders is based on a complex of visual, olfactory, tactile, and behavioral cues (Salthe and Mecham 1974), the significance of particular cues varying from species to species; the complex courtship patterns in salamanders are probably significant in maintaining reproductive isolation (Arnold 1977). Behavioral interactions between rival males are well documented (Arnold 1976), but nothing is known concerning community interactions. If behavioral, visual, tactile, and olfactory cues could be quantified, they could be considered as "resource states" in a similar way that W. E. Duellman (personal communication) has analyzed community variables of frogs. A species' repertoire of reproductive isolating mechanisms probably has significant consequences to species interactions as well as to members of the opposite sex.

Resource Partitioning

Communities are organized, or have structure, as a consequence of interactions among the component populations; competition and predation are two types of interactions usually considered to be primary determinants of community organization. Predation represents interactions between trophic levels, whereas competition represents interaction within a trophic level. Although competition has generally been given greater consideration as a major determinant in amphibian community organization (e.g., Inger and Colwell 1977; Krzysik 1979), Hairston (1980) emphasized the potential importance of predation in *Desmognathus* community organization; he suggested that we need to design field experiments with testable hypotheses to partition out the organizing effects of predation versus competition. As Connell (1975) pointed out, however, these two determinants may them-

selves interact. Predation may reduce species densities such that competition is reduced or prevented.

Species interactions are expected to increase at temporary breeding sites because of the high density of individuals of many species. Community studies in the past have not taken into account shifts in resource utilization resulting from changing species composition. It would be of value to compare resource utilization of members of the non-breeding community with the same species in the breeding community. Analyses of spatial or temporal partitioning of available breeding sites (Crump 1974; Collins 1975; Creusere and Whitford 1976; Wiest, this volume) and partitioning of male calling sites (Littlejohn 1959; Bogert 1960; Duellman 1967; Dixon and Heyer 1968; Channing 1978) have generally suggested that these factors organize the community; the result is reduction of species interactions and increase in space partitioning, providing order in an otherwise potentially chaotic system.

On the other hand, my observations at Santa Cecilia, Ecuador, indicate that species composition of an anuran breeding aggregation may directly affect the partitioning of calling sites. Calling site specificity seemed to be less rigid when many species called sympatrically and synchronously. No differences in calling site were noted when individual species' densities were high as contrasted to an increase in number of species. One explanation is that some species may be flexible in their tolerance of acceptable calling sites. Perhaps species are not flexible at all; when displaced from preferred calling sites during periods of intense breeding activity, those males may not be successful in attracting mates. More work needs to be done on the effects of species composition and density on calling site partitioning and how displacements affect breeding success. If population fluctuations result from competition for optimal calling sites under conditions of high species-packing, community stability and resource partitioning would be affected significantly.

Oviposition sites constitute another spatial resource that is partitioned (Crump 1974). Of all the aquatic breeding assemblages studied in Ecuador, at the most 10 species of frogs were found depositing eggs sympatrically and synchronously. These species deposit their eggs in a wide variety of sites: free-floating on the water

surface, wrapped around emergent vegetation stems in the water, on vegetation up to a meter above water, and suspended in a foam nest produced on the surface of the water. This environmental partitioning results in greater oviposition site use than if all 10 species required the same sites.

Foraging and shelter space as potentially limited resources for amphibians during the breeding period have not been investigated from a community standpoint. On the population level, many species have home ranges varying with sex, age, climatic conditions, and local geography. Sympatric species partition the environment, but whether this is indirect evidence of competition for space rather than the result of microhabitat preferences due to species differences such as in morphology, size, or physiological tolerance has not been investigated.

Food may be a major limiting resource for amphibians. One of the few studies comparing feeding habits during the breeding season with those during the non-breeding season indicated no difference in the percentage of individuals of two populations of *Pseudacris triseriata* which had food in their stomachs; about 65% of both populations had food in their stomachs (Whitaker 1971). However, significant qualitative differences were apparent. During the breeding season, vegetation and shed skin combined represented about 27% volume of stomach contents. During the non-breeding season, little vegetation was consumed (0.8%) and shed skins were not found in any stomachs. Whitaker found that *Hyla crucifer*, breeding sympatrically and synchronously with *P. triseriata*, does not feed at the breeding site. The combination of species-specific behavioral differences plus the fact that different prey items would be expected to be found in terrestrial versus aquatic sites suggest that shifting food utilization is probably extremely important to overall community organization.

When analyzing species interactions within an amphibian community, one must be aware that the system is dynamic, and species associations are constantly changing (Goin and Goin 1953; Wiest, this volume). Information for a species-pair combinations in one time frame should not be extrapolated to another life history stage. Ecologists often interpret the activities of members of a community as means of "avoiding" competition. Species differences are often labeled as "mechanisms" permitting coexistence. As pointed

out by Peters (1976) and Wiens (1977), however, the concept of competition is a tautology rather than a testable theory. Nonetheless, investigators can and should obtain quantitative measurements on available resources and determine differential utilization levels.

Mode of Reproduction, Species Richness, and Resource Partitioning

Often an obvious reproductive difference between species is the mode of reproduction, referring to a combination of egg deposition site and mode of development (including whether development is larval or direct, size and stage at hatching, and rate of development). Associated with mode of development is a wide variety of clutch sizes and egg sizes. Numerous authors have discussed evolutionary trends in amphibian reproductive modes and life history patterns (Noble 1927; Lutz 1947, 1948; Orton 1951; Jameson 1955, 1957; Goin 1960; Lynn 1961; Goin and Goin 1962; Tihen 1965; Heyer 1969). The commonly proposed trend is evolution towards greater terrestriality. In this section several questions will be addressed: (1) How much variability is there in mode of reproduction within frogs and salamanders? (2) How is clutch energy partitioning related to reproductive mode? (3) Is there a relation between diversity of reproductive modes and species richness? and (4) Does reproductive mode diversity affect partitioning of space resources?

Salthe (1969) categorized salamanders into three modes of reproduction: (1) Eggs are abandoned in open, still water; the eggs are relatively small, and hatch at comparatively early stages of development. (2) Eggs are deposited beneath objects (such as rocks) in running water; the eggs are larger than those of mode 1, the larvae hatch at a more advanced stage, and many species exhibit parental care by guarding the clutch until hatching. (3) Eggs are deposited in one mass, beneath objects on land; the eggs are larger than those of the other modes, clutch size is smaller, development is direct, and parental care is present in most species.

Anuran species with a generalized reproductive mode deposit eggs directly in water and have an aquatic larval developmental stage (modes of reproduction collectively referred to here as

Group I; from Crump 1974). Less generalized are species that deposit eggs out of water but retain an aquatic larval stage (Group II). The most specialized forms are totally independent of standing water (Group III). Some Group III species deposit terrestrial eggs that undergo direct development; in other species, development takes place within the body of the adult, within a foam nest, or in some other protective situation. Parental care is present in some species.

Quantitative variables of clutch size associated with mode of reproduction influence the genetic variability maintained by a population. The optimal balance between clutch size and egg size, or the partitioning of clutch energy, ultimately is a function of the levels of competition, predation, and environmental uncertainty to which the young are exposed (Smith and Fretwell 1974; Brockelman 1975; Wilbur 1977c). Empirical interpretations of the relation between egg size and clutch size for amphibians are provided by Salthe (1969), Salthe and Duellman (1973), Crump (1974), Kuramoto (1978), Kaplan and Salthe (1979), and Crump and Kaplan (1979). Generalized species (Group I) characteristically have large clutch sizes relative to female body size. The eggs are small and intraovular development is rapid; the resultant hatchlings are small and are at a comparatively early stage of development. These species tend to breed in the most unpredictable environments, such as temporary ponds and ditches. Species of more specialized modes of reproduction (Groups II and III) produce fewer but larger eggs relative to body size; many of these species have direct development. Groups II and III species breed in the most stable environments such as under leaf litter on the forest floor or in rotting logs; they may exhibit some form of parental care. Presumably Group I species, with larger clutch sizes, maintain higher genetic variability within local demes than do species having more specialized modes of reproduction.

One of the most notable differences in life history features of temperate versus tropical anuran communities is the increased diversity of reproductive modes in the tropics. In areas of greatest species richness there is concomitant high diversity of reproductive modes (Salthe and Duellman 1973; Crump 1974). The evolution of diverse reproductive modes in the New World tropics may have occurred in response to competition for limited breeding sites, as a

response to predation pressure on aquatic eggs, as a means of avoiding desiccation problems in ephemeral aquatic environments, as a result of larval competition for food, or any combination of these factors.

Differences in diversity of reproductive modes have been invoked to explain the considerably greater species richness in tree buttress microhabitats in Ecuador (21 species of frogs at the study site) as compared with similar microhabitat in Thailand (1 species, Heyer and Berven 1973). Four of the Ecuadorian species deposit terrestrial eggs and then transport the larvae to water; eight species deposit terrestrial eggs that have direct development and are therefore completely independent of standing water. In Thailand, the only frog in the buttress microhabitat is a microhylid that breeds in standing water. The greater species richness of lowland litter anuran communities in Costa Rica as compared with Borneo and Cameroon has also been attributed to the exploitation of the terrestrial environment in the New World tropics by direct-developing species (Scott 1976, this volume). The mode of terrestrial eggs and direct development seems to be an extremely successful strategy for avoiding stressful environmental uncertainties and fluctuations in tropical areas. It is significant that whereas all of the common leaf litter frogs in Borneo depend upon standing water for larval development, a high proportion of the fauna at various sites in Costa Rica are totally independent of aquatic sites.

Crump (1974) analyzed spatial resource partitioning of anuran breeding communities from the standpoint of modes of reproduction. In an area of 3 km², the 78 sympatric species were categorized as follows: 36 species of Group I, 25 species of Group II, and 17 species of Group III. Most of the 61 species dependent upon standing water for breeding purposes demonstrated restricted utilization of the aquatic sites. Some species preferred open, disturbed areas, whereas others were found only at ponds in mature forest; no species was distributed regularly within the habitats. Temporal differences in breeding activities were also a major segregating factor for species breeding at one site. Partitioning of the available oviposition sites was largely a function of requirements dependent on the particular mode of reproduction. Data on spatial and temporal utilization of breeding sites suggested that the reproductive diversity at Santa Cecilia is a

major factor contributing to the coexistence of the most species-rich fauna yet studied.

There have been no studies relating reproductive modes of salamanders to community ecology. However, we may predict that in communities characterized by a large diversity of modes of reproduction, increased spatial resource partitioning may be associated with fewer interspecific interactions and greater species richness, the same as it is for frog communities.

Population Variability in Life History Patterns

Considerable theory concerning contrasting life history patterns and the mechanisms leading to their evolution has been presented (see Giesel 1976; Pianka 1976; Stearns 1976, 1977; for literature reviews and syntheses of these ideas). Major factors influencing reproductive patterns are local climatic conditions and the relations between the density of a species and the availability and abundance of its resources (MacArthur and Wilson 1967; Pianka 1970). Wilbur et al. (1974) included predictability of mortality patterns as an important determinant of adaptive strategies. Habitat certainty is also important to amphibian life histories (Low 1976). Wilbur et al. (1974) and Maiorana (1976a) emphasized that since evolutionary processes result from synergistic effects, a number of factors influencing life history patterns should be considered simultaneously.

Although we have begun to interpret life history patterns on the population level, the community approach to life history patterns is at a primitive stage of development and few such studies exist. Crump (1974) and Collins (1975) discussed differences in many life history variables of anuran species within two communities. Due to the extreme difficulty in dealing with species-rich aggregations, however, the life history patterns were analyzed from a population standpoint in both studies.

A community analysis of life history patterns would provide insight as to how populations are co-adapted, or how the patterns of one species affect another's strategy. Because no such data are available, the following is a review of variability in life history patterns on the population level. These generalizations should provide a framework upon which to ask relevant questions regarding life history patterns on the community level.

Environmental Influence on Life History Patterns

A species may be thought of as a mosaic of populations, each adapted to local environmental conditions and therefore divergent in life history features (Ehrlich and Raven 1969). Rainfall, water temperature, and permanence of the aquatic breeding site exert significant influences on yearly variation in timing of reproduction and length of the larval period. Geographically separated populations of amphibians may differ in egg size, developmental rates, clutch size, age at first reproduction, and breeding periodicity, depending on environmental factors.

Geographical differences in life history features may be related to decreased activity periods of northern populations. Increasing evidence reveals biennial breeding cycles of northern populations and annual cycles for southern populations of plethodontid salamanders (Highton 1962; Sayler 1966; Hall and Stafford 1972; Nagel 1977). Some evidence suggests slower growth rates and delayed maturity in northern individuals; the higher fecundity resulting from increased body size in northern individuals perhaps compensates for the biennial breeding cycle (Highton 1962).

Altitudinal comparison of populations also reveals contrasting life history patterns. Female *Rana temporaria* are larger in mountain populations and deposit fewer but larger eggs than females in lowland populations; weight of the clutch relative to female body weight is lower in highland females, suggesting a smaller reproductive effort per breeding period (Kozłowska 1971). Berven et al. (1979) studied life history features of *Rana clamitans* along an altitudinal gradient. Transplantation experiments and laboratory studies suggest that variation in certain life history features can be environmentally induced by temperature effects alone. When grown under identical low temperatures, high-elevation larvae grew faster and completed metamorphosis earlier and at a smaller size than lowland individuals; this suggests that selection along the altitudinal gradient has minimized the effects of environmental variation and has favored the most rapid larval development possible within temperature constraints. These results agree with studies by Moore (1939) that demonstrated that cold-adapted species show faster embryonic rates of development at any given non-lethal temperature than warm-adapted species.

*Influence of Age-Specific Mortality
Predictability and Stable Environments
on Life History Patterns*

A major determinant of life history adaptations is the certainty of the environment relative to each life history stage. Amphibians demonstrate contrasting reproductive responses in unchanging environments versus fluctuating environments. Low (1976) emphasized the importance of environmental uncertainty on anuran life history strategies and pointed out that an effect of metamorphosis is an increase in independence of variation in survivorship in different life stages; in uncertain larval environments, a premium is placed on strategies that enable facultative breeding responses and reduce the chance of total reproductive failure. In unchanging environments, late maturity, multiple clutches, fewer but larger eggs, parental care, and small reproductive efforts should be favored; in fluctuating environments the reverse correlates should appear (MacArthur and Wilson 1967; Hairston et al. 1970; Pianka 1970). However, as Schaffer (1974) pointed out, life history patterns should vary depending on age-specific mortality. If the environment of the juvenile stages is uncertain, leading to high or unpredictable mortality, different strategies should be selected for as contrasted to those in environments that are uncertain for adults, leading to high or unpredictable mortality at that stage (Low 1976).

Differences in egg deposition patterns, fecundity, and parental investment of several sympatric species of *Ambystoma* are best interpreted as adaptations to adult survival and to the degree of certainty of the larval environment (Wilbur 1977c). Of the species compared, *Ambystoma laterale* breeds in the most temporary environments; this species expends the highest reproductive effort relative to body size and seemingly has sacrificed egg size for increased clutch size. Small eggs are deposited singly and hatch into larvae that develop rapidly; the ability of these larvae to metamorphose over a wide range of body sizes is considered an adaptation to unpredictable environments. *Ambystoma tigrinum*, which breeds mostly in permanent ponds, deposits its eggs in several clumps. Although larval survivorship is relatively constant from year to year, adult survivorship is low. For this reason, high reproductive output by the female is favored, as demonstrated by early maturity and high

fecundity. *Ambystoma maculatum* deposits eggs in a single mass in semipermanent ponds. Because larval survivorship is variable and adult survival is high, it is advantageous for a female to reproduce as many times as possible. By expending a low reproductive effort each year, females can reproduce more total times per lifetime to compensate for uncertain juvenile survivorship.

Darstedt (1975) studied life history characteristics of six populations of *Desmognathus fuscus* in four physiographic provinces in Maryland. Although many factors were similar in these populations, ovarian egg complement differed significantly; females from populations where adult survival was lower produced significantly more eggs. Part of the explanation is that body sizes were larger, and there is a positive size-fecundity relation. However, these females also produced more eggs per unit body size. Since egg size does not vary geographically, apparently females expend proportionately greater amounts of energy on reproduction in those populations where adult survival is lower.

Theorists predict that reduction of age at first reproduction results in a large gain in the intrinsic rate of natural increase (r ; Cole, 1954; Lewontin 1965). Early reproduction usually is indicative of fluctuating juvenile survivorship, uncertain breeding conditions, or fluctuating population densities. Several amphibian studies provide empirical support for this prediction. In Massachusetts coastal populations of *Notophthalmus viridescens* inhabiting harsh and unstable environments, selection favors a high r ; the terrestrial eft stage is omitted and individuals begin reproducing at age 2 (Healy 1974). Inland populations retain the eft stage and range from 4 to 8 years old at sexual maturity. In the more stable inland environments, individuals apparently are not under selection for a high r . Likewise, populations of *Desmognathus ochrophaeus* in contrasting environments of North Carolina differ with respect to age at maturity (Tilley 1973a, 1973b). Delayed reproductive maturity in high-elevation woodland individuals is accompanied by a larger body size and concomitant increased age-specific fecundities; unstable age structure exhibited by a low elevation woodland population suggests greater density fluctuations. Differences in life history features of populations of *Rana pretiosa* from low and high elevations support the hypothesis that earlier age at maturity should be selected for in environments of periodic reproductive failure (Licht 1975). In the lowland

area the entire reproductive effort may be lost in any given year due to drought. A markedly slower growth rate and delayed sexual maturity were evident in the high-elevation population. Clutch size was the same, but lowland females bred annually, whereas high-elevation females bred only every 2 to 3 years. Further support for the hypothesis is provided in comparative studies of *Gyrinophilus porphyriticus*. Selection has favored earlier maturity and higher size-specific fecundity in low-elevation individuals, as contrasted to high-elevation individuals (Bruce 1972). The low-elevation habitats are smaller, more isolated, and seem to be subjected to greater climatic fluctuation. These factors would increase chances of local extinction, favoring selection of life history features characteristic of colonizing species.

Individuals living in fluctuating environments should exhibit flexibility in life history features. Bruce (1975) suggested that the irregular breeding cycle of female *Pseudotriton montanus* in the Piedmont of western South Carolina is an adaptation that both favors longevity and provides for iteroparity (reproducing more than once in a lifetime) and yet allows for high fecundity. Individuals of *Batrachoseps attenuatus* in an area of California that experiences a variable, prolonged dry season, are also extremely flexible in their life history characteristics; they are able to maximize reproductive effort per lifetime even though the environment favors both longevity and high fecundity (Maiorana 1976b). Since individuals have an uncertain life expectancy (because of high predation and an unpredictable climate), selection favors a high reproductive output when energy is available.

Thus, empirical studies support the prediction for contrasting strategies in response to certainty of survivorship and habitat. The following correlate of this prediction is testable: In circumstances where larval survivorship varies unpredictably in time, smaller clutch sizes should be favored because they decrease the chances of total failure for any given breeding period. In such instances, selection favors the strategy of small numbers of young being produced at staggered times throughout the year rather than the strategy of synchronous development of a larger number of offspring (Pearson 1960; Murphy 1968; Schaffer 1974). An alternative to spreading reproductive effort throughout time is deposition

of partial clutches throughout space (Salthe 1969; Wilbur 1977c).

In virtually all amphibian populations studied, predation on young is high and juvenile mortality fluctuates more than does adult mortality. Thus, we would expect the above correlation with smaller clutch size to be true for amphibians. However, reproductive success of most amphibians is closely coupled to appropriate environmental conditions. In the temperate zone, largely because of seasonal restrictions, the breeding pattern is a rather synchronized recruitment of young into the population at widely spaced intervals; most individuals breed only once per year. An exception, however, is certain ranids that produce two clutches per year (Wells 1976; Emlen 1977). On the other hand, in climates amenable to year-round reproductive activity, the pattern seems to be continued reproduction at least by the population (Inger and Greenberg 1963; Berry 1964; Valdivieso and Tamsitt 1965; Inger and Bacon 1968; Vial 1968; Anderson and Worthington 1971; Crump 1974; Duellman 1978). Most of these studies present indirect evidence of multiple breeding per individual per year; examination of ovaries of females that have recently oviposited reveals at least one additional size class of eggs soon to be matured.

Inger and Greenberg (1966a) discussed the implications of noncyclic reproductive patterns in a nonseasonal environment. Species for which breeding activity is cyclic (characteristic of seasonal environments in both temperate and tropical areas) would be affected in a pulsating manner; the infusion of juveniles at only certain intervals might result in potential competitive interactions for limited resources. The cyclic nature would also affect the remainder of the biotic community as the young would provide only a temporary food source for predators. Noncyclic reproductive patterns are typical of many nonseasonal areas where little-fluctuating environmental conditions permit continual breeding, creating a situation of overlapping generations. Inger and Greenberg (1966a) suggested that year-round reproduction probably buffers population fluctuations and therefore may be a major factor contributing to the high species diversity of the nonseasonal tropics. Duellman (1978) supported this hypothesis in his analysis of the herpetofaunal community at Santa Cecilia, Ecuador, and pointed out that there would be

greater genetic mixing in nonseasonal habitats associated with increased matings per unit time as compared with seasonal environments.

Scattering of the eggs in space potentially increases survivorship. Many species of amphibians deposit eggs either singly or in multiple masses distributed in the habitat. On the other hand, parental care has evolved in association with deposition of a single mass of eggs, presumably as a means of increasing embryonic survivorship. A system of repeated matings by a female with different males throughout time decreases the possibility of total reproductive failure and simultaneously increases genetic variability within the population (e.g., Crump 1972; Woodruff 1976a).

Population Demographic Considerations and Community Stability

In considering population regulation, the following questions are frequently asked: (1) What is the reproductive potential of the population? (2) What is the realized reproductive performance of the population? (3) What is the environmental resistance (reproductive potential minus the realized performance of the population)? (4) How do age-specific fecundity and mortality vary in time and space? (5) What is the population turnover rate? and (6) What is the relative importance of density-dependent versus density-independent regulating factors?

Community stability is influenced not only by fluctuations of the constituent populations, but by the interactions and joint influences of coexisting species. One cannot examine community variables by dissecting out the component populations; the interactions between the species must be analyzed. No such studies have been carried out on entire amphibian communities. In fact, Turner (1962) noted that there have been few demographic analyses of anuran populations, as data on natality, mortality, and age-class distribution are extremely difficult to collect; the same is true for salamander populations. A major problem is the lack of a suitable technique for aging the animals in the field (Cagle 1956).

The size of the breeding population has considerable effect on the evolutionary processes and population dynamics (Wright 1969). The effective breeding population of most amphibians is

usually much less than the total population; generally males are many times more abundant than females in the breeding community (Blair 1943; Martof 1956; Husting 1965; Merrell 1968; Morris and Tanner 1969; Whitaker 1971; Hedeen 1972; Calef 1973b). Unfortunately, no data are available on the implications of this phenomenon to community structure.

There are few quantitative estimates of embryonic mortality in nature, but evidence suggests that mortality is low except in the event of environmental catastrophe (Woodruff 1976b). Age-specific mortality is highest in the larval stage of the amphibian life cycle (Savage 1952; Turner 1962; Moore 1963; Herreid and Kinney 1966; Licht 1968; Anderson et al. 1971; Calef 1973a; Heyer 1976) and varies widely among breeding sites in one area, geographical areas, species, and years (Pearson 1955; Martof 1956; Turner 1960; Brockelman 1969; Scott and Starrett 1974; Shoop 1974; Walters 1975); survivorship to metamorphosis often varies between 0 and 10%. For this reason, larval mortality plays a central role in regulating population size. Larval communities in temporary aquatic sites are usually characterized by highly fluctuating population sizes. The low survivorship of larvae is usually related to high predation or severe catastrophic phenomena such as evaporation of the aquatic breeding site. Walters (1975) suggested that synchronized breeding by certain palatable species of amphibians may increase survival through predator satiation. Brockelman (1969) found that high predation rates may actually benefit individual larvae by eliminating negative effects on growth by reducing crowding effects.

Experimental field and laboratory studies have shown that the proportion of a larval population that survives to metamorphosis and the mean body size at metamorphosis are inversely related to population density; in high-density experimental populations, a small number of individuals grow and metamorphose at the expense of the remainder of the cohort (Brockelman 1969; Wilbur 1972, 1976, 1977a, 1977b; Wilbur and Collins 1973; DeBenedictis 1974). The rate at which larvae feed and metamorphose is of critical importance not only in the potentially competitive and predator-rich aquatic environment (Worthington 1968; Wilbur and Collins 1973), but also from the standpoint of the ephemeral nature of

many breeding sites (Shoop 1974).

The adaptive significance of the larval stage lies in the use of abundant, but ephemeral, resources in the aquatic environment; the temporal nature of these resources is significant as it assures a time lag in the buildup of predator populations (Wassersug 1975). Amphibian larvae grow rapidly and fit a sigmoid growth model; there is considerable variability in growth rates within a population leading to a skewed distribution of body size at metamorphosis such that there are many more small individuals than large (Wilbur and Collins 1973). Species that exploit uncertain environments generally have a wider range of possible developmental times and sizes at metamorphosis than species that breed in relatively certain habitats. Some investigators conclude that food is not a limited resource in larval communities and that larval populations and communities are largely regulated by predators (Calef 1973a; Heyer 1973, 1974, 1976; Heyer et al. 1975), whereas others present data suggesting that food is limiting and serves as a density-dependent regulating factor (Savage 1952; Brockelman 1969; Wilbur and Collins 1973; DeBenedictis 1974; Wilbur 1976, 1977a, 1977b).

Anurans are particularly susceptible to snake predation during the metamorphic transition because they can neither swim as effectively as premetamorphic tadpoles nor hop as effectively as postmetamorphic frogs (Wassersug and Sperry 1977). Considering the drastic changes that take place during metamorphosis, anurans spend disproportionately little time in this stage. Wassersug and Sperry (1977) pointed out that the rapidity of transformation minimizes the amount of time spent in this vulnerable stage. In many species (e.g., *Bufo* and *Scaphiopus*), numerous individuals metamorphose in synchrony; Arnold and Wassersug (1978) suggested that metamorphic synchrony may have evolved as a mechanism for satiating predators.

Very little is known concerning juvenile survivorship between the time individuals disperse from the breeding site and their return to a breeding site when reproductively mature. Bannikov (1950) estimated mortality in *Bombina bombina* between metamorphosis and 1 year to be about 98%; mortality during the next year was about 40%, and during the third year, almost 100%. On the other hand, Green (1957) estimated postmetamorphic age-specific mortality at a constant 70% for a West Virginia popu-

lation of *Pseudacris brachyphona*. Likewise, Turner (1960) found no significant age-specific survivorship differences among age classes of a population of *Rana pretiosa*. Studies of certain species of *Rana* in the tropics indicate relatively stable postmetamorphic age structures within populations (Alcala 1955; Inger and Greenberg 1963, 1966b; Brown and Alcala 1970). Husting (1965) found that survivorship was higher for male *Ambystoma maculatum* than for females, and Organ (1961) found the same for species of *Desmognathus*; on the other hand, Bell (1977) found a lower survivorship for male *Triturus vulgaris* than for females.

Common newts (*Triturus vulgaris*) demonstrate considerable variability in life history patterns, passing through or eliminating several distinct ecological niches depending upon when in the season they metamorphose and whether they mature early or late (Bell 1977). Bell suggested that this complexity might have two effects on the population: increase in the level of genetic variability and reduction in fluctuation of population size since a disaster in one niche would not result in extinction of the entire population. In the common newt it is clear that population age structure has significant consequence to resource utilization; however, this is probably a widespread phenomenon among amphibians since there is considerable variability in age and size at metamorphosis. The effects of demography on the community level are probably of great significance to community organization and stability.

Turner (1962) suggested that if we assume that differences in metabolic rate result in different life-spans, then life expectancy should be longer in seasonal, temperate areas where growing seasons are shorter and temperatures lower than in nonseasonal tropical areas. Nonseasonal tropical communities would then be expected to consist of populations with high turnover rates. Data on a shorter life-span for *Rana erythraea* relative to temperate ranids support Turner's hypothesis (Brown and Alcala 1970). This comparison can also be viewed from a life history standpoint. Since it appears that individuals in nonseasonal regions produce smaller clutches at more frequent intervals than their counterparts in seasonal environments, a shorter life-span would be expected in nonseasonal environments based on energy budget considerations. The "live fast and die young" cliché suggests that

individuals that allocate large energy investment to reproduction rather than to somatic functions would be expected to die sooner. This prediction supports the correlate of the *r*- and *K*-selection model that associates high productivity with a short life-span (Pianka 1970), and leads to the same conclusion: nonseasonal environments should be associated with populations with higher turnover rates. How population turnover times and fluctuations affect overall community structure and stability provides a stimulating question for future ecological research. As emphasized earlier, no data are available on the extent to which sympatric amphibians influence the demography and population stability of each other nor how they affect overall community stability.

Conclusions

Although there has been a considerable number of population studies concerning the reproductive ecology of amphibians, there has been little integration of reproductive ecology and community dynamics. Because amphibians have shifting community structures and compositions, integration of these aspects is challenging. I have discussed various ways in which community structure, species interactions, community stability, and reproductive attributes of species are interdependent. Major reproductive aspects that should be related to community dynamics include (1) reproductive isolating mechanisms, (2) resource partitioning associated with breeding activity, (3) activity such as migration of adults to breeding sites and dispersal of juveniles from breeding sites, and (4) life history patterns including mode of reproduction, clutch size, iteroparity, age at first reproduction, and demographic variables.

Reproductive isolating mechanisms and resource partitioning at breeding sites are important concepts at the population level, but few studies have analyzed them from the community standpoint. Mode of reproduction has significant implications for species diversity and resource utilization: the greater the reproductive diversity the more species can coexist, perhaps because of greater resource partitioning. The spacing of recruitment of young into the population and how this relates to the overall community in terms of the patterns of coexisting species is of significance to resource utilization, species interactions, pred-

ator-prey relations, demography, and therefore ultimately to community organization and stability. Investigators are beginning to understand variability in age-specific fecundity and survivorship, age at first reproduction, age-class distribution, sex ratios, and longevity within populations. However, because natural selection favors individuals that are most successful in the overall environment (in addition to intraspecific interactions), one must integrate reproductive attributes with overall community ecology to interpret an animal's adaptations.

Using the information from the studies discussed as a base line, I submit that analysis of life history patterns on a community level is a feasible endeavor. The study of the relation between life history variability and community organization, species interactions, and community stability presents a challenging field of research. In attempting to integrate reproductive attributes and community ecology, specific questions must be asked. For practical reasons, one should begin with a relatively simple community consisting of only a few species of amphibians. Laboratory experimental studies could provide preliminary data on species interactions and influences, but eventually one would want to study a natural community. Carefully designed and executed field manipulations are essential to interpret adaptive strategies on the community level (see Connell 1975; Stearns 1976; Wiens 1977; Hairston 1980).

The following statements and predictions provide a framework upon which to ask relevant questions:

- Migration of amphibians to aquatic breeding sites and dispersal of juveniles away from sites result in different community compositions, affecting many aspects of community organization.
- Species of anurans breeding sympatrically or synchronously exhibit only slight (if any) overlap in acoustical variables of mating calls; many species have characteristic calling sites, resulting in an increase in use of spatial resources and enhancement of species recognition.
- Breeding sites within a given area are generally partitioned in time and space, resulting in greater use of the available sites and reduced species interactions.
- Species-specific requirements of oviposition sites differ such that within any mixed-species breeding aggregation there is increased utiliza-

tion of space, resulting in a greater species-packing than possible otherwise.

- Overlap in food utilization at breeding sites may be reduced by species-specific behavioral and preference differences.

- There is a positive relation between species richness and diversity in modes of reproduction; the tropics are the highest in both.

- Generalized amphibians (those that abandon eggs in open water) have larger clutch sizes relative to body size than do more specialized species (those that deposit eggs on land, often exhibiting some form of parental care). The higher fecundity of generalized species possibly results in increased variability maintained by the populations; these species usually breed in more temporary or fluctuating sites than do more specialized species, which generally deposit larger eggs with increased energy investment per offspring in more stable environments.

- Partitioning of breeding and oviposition sites related to high diversity of modes of reproduction in the tropics is a major factor contributing to the existence of species-rich communities.

- Life history patterns are in large part molded by local climatic conditions, resource availability, habitat certainty, and predictability of age-specific mortality.

- Many species exhibit latitudinal differences in various life history variables (e.g., biennial breeding cycles in northern populations versus annual cycles in southern populations). Delayed maturity, resulting in larger body sizes and therefore higher fecundity, perhaps compensates for the biennial breeding cycles of northern individuals.

- Unpredictable or otherwise harsh environments resulting in low adult survivorship favor early reproductive maturity, flexibility in life history features, and high fecundity. When adult survival is high, it is advantageous to increase iteroparity; by expending a low reproductive effort per clutch, individuals can breed more often per unit time.

- Unpredictable or otherwise harsh environments resulting in low or unpredictable larval survivorship favor either increased iteroparity with small clutches per breeding period or deposition of partial clutches scattered in space.

- Noncyclic breeding patterns (typical of nonseasonal areas) result in overlapping generations

and probably buffer population fluctuations. Genetic mixing is probably increased from the increased matings per unit time. Year-round reproduction may be a major factor contributing to high species diversity in the nonseasonal tropics.

- Larval mortality plays a central role in regulating population size. Age-specific mortality is highest during the larval stage of the amphibian life cycle and fluctuates considerably between breeding sites and from year to year.

- There is considerable variation in larval growth rates within populations leading to a skewed distribution of body sizes at metamorphosis. Species that breed in relatively certain environments exhibit a narrower range of developmental time and body size at metamorphosis than do species that exploit uncertain habitats. The proportion of a larval population that survives to metamorphosis and the mean body size at metamorphosis are inversely related to the larval population density.

- Amphibian communities in nonseasonal tropical regions are expected to be composed of individuals that have shorter life-spans than comparable species in seasonal temperate zone areas. This would result in populations with higher turnover rates, which would ultimately affect overall community organization and stability.

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AMPHIBIAN COMMUNITIES

Anuran Succession at Temporary Ponds in a Post Oak-Savanna Region of Texas

by

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Abstract

Reproductive patterns of anurans using temporary ponds in a Texas post oak (*Quercus stellata*) savanna region were studied during an abnormally wet year, September 1972 through September 1973. Anuran succession was correlated with varying environmental conditions. The overriding causes of variation in anuran reproductive patterns were fluctuations in air and water temperatures, rainfall, and possibly humidity.

Calling, breeding, and larval periods for nine species are discussed. The vocalization sequence, based on the first evening when calling was heard for each species, was as follows: *Pseudacris streckeri*, *P. triseriata*, *Scaphiopus holbrooki*, *Acris crepitans*, *Hyla versicolor*, *Bufo valliceps*, and *Gastrophryne olivacea*. Exceptions to this sequence were *Rana sphenoccephala*, which called in practically every month of the year, and *P. clarki*, which had a primary calling period in the winter-spring months and a short opportunistic calling period in late summer. *Bufo speciosus* and *B. woodhousei* were uncommon and their status in the study area is discussed. For most anurans there was a larval bloom in April and May, which were the months with the most rainfall.

The reproductive habits of the anurans of the United States are sufficiently well known to indicate that some general patterns exist in the timing of anuran reproductive activities. However, varying environmental conditions may drastically alter the time and length of the breeding season. Information is still lacking concerning the reproductive cycle of one species relative to other anuran species at any given locality. Successional studies of various durations have been reported for a few specific localities in the United States (Goin and Goin 1953; Blair 1961; Murphy 1963; Rubin 1968) and in other countries (Frazer 1956; Neal 1956; Berry 1964; Dixon and Heyer 1968; Inger 1968; Heyer 1973).

The objectives of the present study were to investigate anuran succession at temporary ponds in a post oak (*Quercus stellata*) savanna region of Brazos County, Texas, and to determine the effects of certain environmental factors on the re-

productive season of anuran species observed. The few previous anuran succession studies have been conducted in widely separated localities, and therefore more successional studies are needed before patterns of anuran reproductive activity can be properly synthesized. The particular importance of this study is that it includes observations of both adults and larvae in establishing a localized pattern of anuran succession.

Description of Study Area

Brazos County, in east-central Texas, is bordered by the Brazos River on the west and by the Navasota River on the east. This county is in the Texas Province, a broad ecotone between the forests of the Austroriparian province of eastern Texas and the grasslands in western Texas (Dice 1943; Blair 1950). The area is considered a post oak savanna region (Gould 1969), except for a small northern portion designated as blackland prairie. Typical of the post oak belt, the county

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has an elevation of 61 to 122 m; the surface slopes toward the southeast. The topography is level to gently rolling with no conspicuous relief.

Materials and Methods

Anuran succession was followed from 3 September 1972 to 28 September 1973. The study included most Brazos County anuran species that use temporary ponds for breeding. Calling dates for males were noted, as were reproductive activities such as amplexus or egg deposition. All data were collected at temporary ponds, herein defined as bodies of water which usually become dry during some portion of the year. Five temporary ponds served as the primary study areas and seven others were observed at various times throughout the study. Wiest (1974) provided a detailed description of each pond site including exact location, surrounding terrain, dimensions, depth, water clearness, periods of dryness, and vegetation in and around the ponds. Before 30 June 1973, observations of adult breeding behavior were conducted nightly, and larvae were collected every 3–4 days. Beginning 1 July 1973, night observations were made only after periods of rainfall, and larval collections were made every 2 weeks. Adult habitat, duration of day-night activity, calling sites, breeding sites, larval habitat and larval feeding, and aggregational behavior were recorded.

Larvae were collected during afternoons with a dip net. Quantitative sweeps were not taken, but rather attempts were made to sample different microhabitats and all distinctive larvae. Usually less than 10 individuals of each species were retained at each site on a given date. Air temperatures at 1 m and 2.5 cm above ground and water temperatures at depths of 2.5 and 10 cm were recorded with each afternoon larval collection. All larvae were staged according to Gosner (1960).

Environmental data were collected during evening observations to determine the effects of the environment on reproductive seasons. Air temperatures at 1 m and 2.5 cm above ground, at ground level, and the water temperature at a depth of 2.5 cm were recorded at each pond nightly. A sling psychrometer was used to determine relative humidities during evening observations. Daily maximum and minimum temperatures, daily mean wind velocity, daily wind

velocity and direction between 1900 and 2300 h, and daily rainfall were obtained, in part, from Easterwood Airport Weather Station, College Station; the Texas A&M University Weather Station, College Station; and from James R. Dixon's residence at 705 Inwood Drive, Bryan, Texas. Rainfall was recorded in millimeters and noted as to time and duration.

Climatological Considerations

The climate of Brazos County is relatively mild. From May through September, prevailing southeasterly winds from the Gulf of Mexico produce high humidities and limited temperature changes. From November through March, northerly winds become prevalent and are often accompanied by sudden temperature changes which result from the interaction of polar and tropical air masses. Cold spells are most severe and frequent from December through February. April and October are transitional months. The mean annual temperature is 18.3°C, and the maximum and minimum recorded temperatures are 43.3° and -19.4°C. The average annual precipitation is 984 mm; heaviest rainfall occurs from April through June. Droughts are common during summer months. Snow is rare and seldom accumulates. Annual relative humidity is about 70% and monthly variations are small.

Weather conditions for 8 months preceding the start of this study were normal, except rainfall was below monthly averages (Fig. 1). Weather data obtained in the field were compared with the mean monthly temperatures and rainfall data for 1933 to 1973 (taken from Climatological

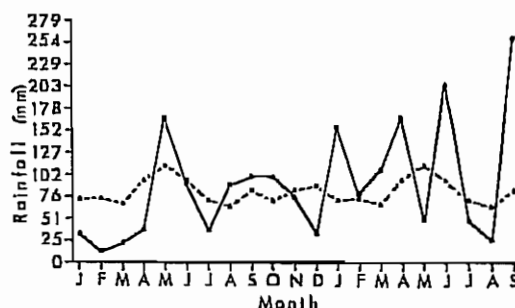


Fig. 1. Comparison of monthly means of rainfall (1933-62, dashed line) to monthly totals of rainfall (1972-73, continuous line).

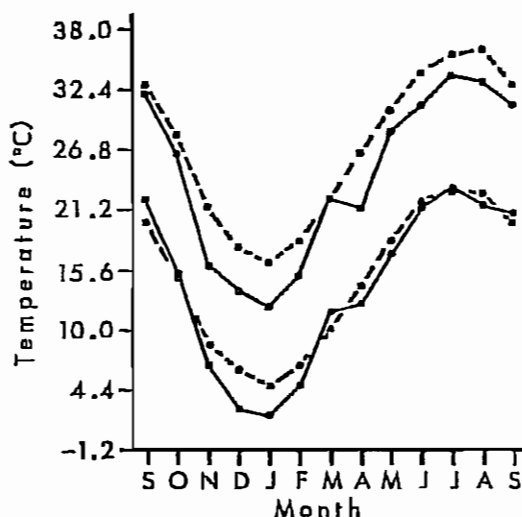


Fig. 2. Comparison of mean monthly temperatures of 1933-62 (dashed lines) to study period, September 1972-September 1973 (continuous lines). Two top lines indicate daily maximum means and two bottom lines indicate daily minimum means.

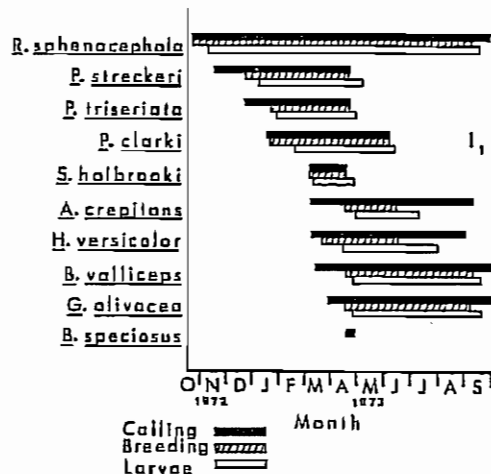


Fig. 3. Calling, breeding, and larval periods for each species during the 1972-73 study period.

Data for Texas monthly summaries, and from Climatological Summary for 1933 to 1962, both prepared by the U.S. Department of Commerce). Mean monthly temperatures were below normal during most of the study (Fig. 2). The study took place during a year which was unique in two ways to Brazos County. Two snowfalls (9 January and 8 February) occurred with appreciable accumulation, the first record of snow accumulation twice in one winter. More importantly, rainfall during the study was far above normal compared with previous years (Fig. 1). Total precipitation for Brazos County in the calendar year 1973 was 1,510 mm, which was only slightly less than the greatest recorded annual rainfall (1,577 mm).

Rainfall amounts during the study period were recorded as follows: 1,417 mm at Easterwood Airport Weather Station, 1,308 mm at Texas A&M University Weather Station, and 1,469 mm at the home of Dr. Dixon. Abundant precipitation during most of the study provided those anurans using temporary ponds with an excellent opportunity to achieve their breeding potential.

Results

A detailed account for each species' calling,

breeding, and larval periods, including the relation of air temperatures and rainfall to reproductive activities throughout the year, was given by Wiest (1974). The data clearly indicated that the calling and breeding peaks of each species were closely associated with periods of rainfall. Tables 1 and 2 summarize the environmental correlates of calling and breeding periods.

The anuran vocalization sequence, based on the first evening when calling was heard, was as follows: *Pseudacris streckeri* vocalized first, followed by *P. triseriata*, *Scaphiopus holbrooki*, *Acris crepitans*, *Hyla versicolor*, *Bufo valliceps*, and *Gastrophryne olivacea* (Fig. 3). Exceptions to this pattern were *R. sphenacephala*, which called in practically every month of the year, and *P. clarki*, which had a primary calling period in the winter-spring months and a short opportunistic calling period in late summer. *Bufo speciosus* and *B. woodhousei* are uncommon in the study area and were observed only a few times. The reproductive patterns of each species as related to air temperatures (Fig. 4) suggest the same successional pattern as presented in Fig. 3.

Larval samples collected in three of the ponds were sufficient to summarize the larval succession pattern for all ponds. The biweekly summaries of larvae collected at these three ponds is given in Figs. 5, 6, and 7.

Table 1. Calling statistics for each anuran species (air temperature and humidity at 2100 h; air temperature at 2.5 cm above ground).

Species	No. of calling nights	Calling period	Temperature (°C)	Humidity (%)
<i>Rana sphenocephala</i>	87	21 Oct 72–27 Sep 73	3.0–26.1 \bar{x} = 17.3	39–100 \bar{x} = 79
<i>Pseudacris streckeri</i>	89	15 Nov 72–18 Apr 73	1.8–21.8 \bar{x} = 12.1	39–100 \bar{x} = 76
<i>P. triseriata</i>	84	20 Dec 72–19 Apr 73	–2.5–22.0 \bar{x} = 12.8	39–100 \bar{x} = 76
<i>P. clarki</i>	60	16 Jun 73–5 Jun 73; 5–6 Sep 73	3.0–23.2 \bar{x} = 14.5	39–100 \bar{x} = 78
<i>Scaphiopus holbrooki</i>	5	6 Mar 73–15 Apr 73	13.0–18.0 \bar{x} = 16.1	63–100 \bar{x} = 75
<i>Acris crepitans</i>	85	6 Mar 73–6 Sep 73	8.7–28.3 \bar{x} = 20.1	49–100 \bar{x} = 77
<i>Hyla versicolor</i>	51	7 Mar 73–27 Aug 73	13.0–28.1 \bar{x} = 21.8	51–100 \bar{x} = 81
<i>Bufo valliceps</i>	44	12 Mar 73–27 Sep 73	18.5–28.3 \bar{x} = 23.0	62–100 \bar{x} = 81
<i>Gastrophryne olivacea</i>	34	26 Mar 73–27 Sep 73	11.3–27.2 \bar{x} = 21.7	65–100 \bar{x} = 85
<i>Bufo speciosus</i>	6	7–22 Apr 73	18.5–23.1 \bar{x} = 20.8	88–100 \bar{x} = 93

Table 2. Breeding statistics for each anuran species (air temperature and humidity taken at 2100 h; air temperature at 2.5 cm above ground).

Species	No. of breeding nights	Breeding period	Temperature (°C)	Humidity (%)	Larval period
<i>Rana sphenocephala</i>	17	22 Oct 72–5 Sep 73	11.8–25.7 \bar{x} = 17.8	68–100 \bar{x} = 84	8 Nov 72–16 Sep 73
<i>Pseudacris streckeri</i>	25	20 Dec 72–17 Apr 73	4.2–19.8 \bar{x} = 13.5	63–100 \bar{x} = 83	31 Dec 72–12 May 73
<i>P. triseriata</i>	21	19 Jan 73–17 Apr 73	6.7–19.0 \bar{x} = 14.8	62–100 \bar{x} = 79	27 Jun 73–28 Apr 73
<i>P. clarki</i>	11	20 Jan 73–5 Sep 73	11.8–21.3 \bar{x} = 17.8	68–100 \bar{x} = 84	17 Feb 73–9 May 73; 16 Sep 73
<i>Scaphiopus holbrooki</i>	5	6 Mar 73–15 Apr 73	13.0–18.0 \bar{x} = 16.1	63–100 \bar{x} = 75	10 Mar 73–24 Apr 73
<i>Acris crepitans</i>	5	17 Apr 73–12 Jun 73	18.5–23.2 \bar{x} = 21.1	65–100 \bar{x} = 88	28 Apr 73–14 Jul 73
<i>Hyla versicolor</i>	6	18 Mar 73–14 Jun 73	18.5–25.4 \bar{x} = 21.6	75–100 \bar{x} = 86	14 Apr 73–28 Jul 73
<i>Bufo valliceps</i>	16	17 Apr 73–6 Sep 73	18.5–27.2 \bar{x} = 22.1	70–100 \bar{x} = 84	24 Apr 73–16 Sep 73
<i>Gastrophryne olivacea</i>	10	15 Apr 73–5 Sep 73	18.0–26.7 \bar{x} = 22.0	70–100 \bar{x} = 87	24 Apr 73–16 Sep 73

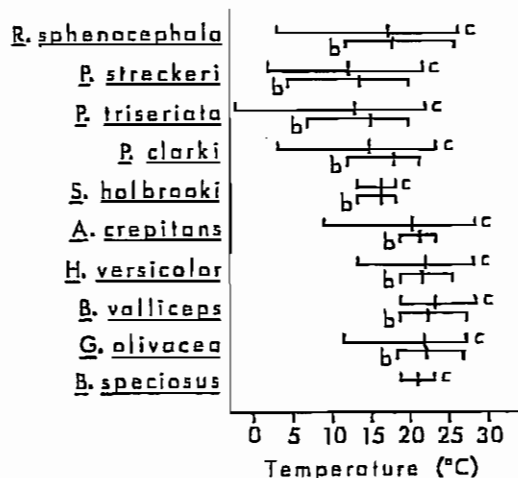


Fig. 4. Ranges and means of air temperatures (2100 h) on nights of calling (= c) and breeding (= b) for each species.

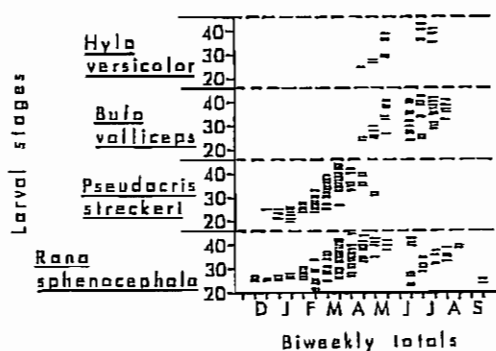


Fig. 6. Biweekly summaries of larval developmental stages from all larvae collected in pond G. Individual dashes represent larval stages (Gosner 1960), and the dashed horizontal lines indicate metamorphosis (stage 46).

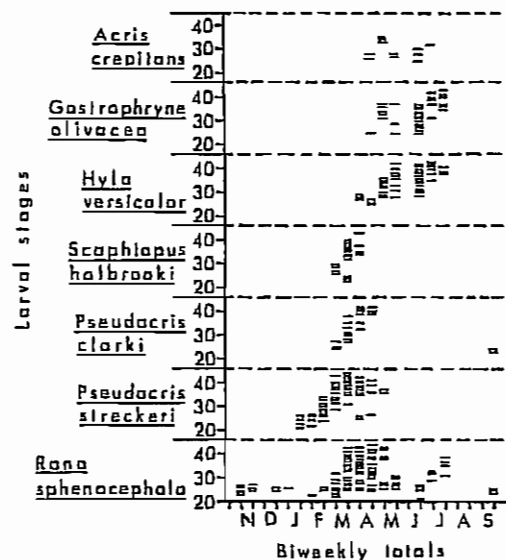


Fig. 5. Biweekly summaries of larval developmental stages from all larvae collected in pond D. Individual dashes represent larval stages (Gosner 1960), and the dashed horizontal lines indicate metamorphosis (stage 46).

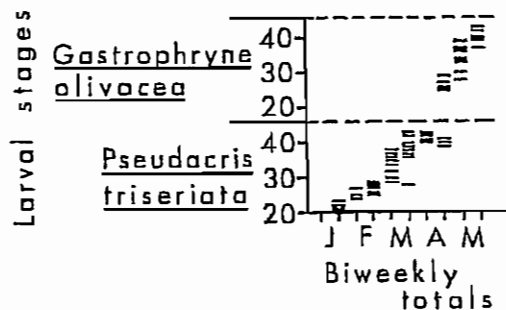


Fig. 7. Biweekly summaries of larval developmental stages from all larvae collected in pond J. Individual dashes represent larval stages (Gosner 1960), and the dashed horizontal lines indicate metamorphosis (stage 46).

Species Excluded from Study

Not all anuran species occurring in Brazos County were incorporated into this study because some used only permanent bodies of water for breeding, and a few were too rare to study in detail. *Hyla cinerea* was observed calling only at permanent ponds between 23 April and 1 August 1973. *Rana areolata*, *R. catesbeiana*, *R. clamitans*, and *R. palustris* use permanent bodies of water. Of these four species, only *R. catesbeiana* was heard calling (23 April to 10 August 1973). *Gastrophryne carolinensis* breeds in temporary ponds, but was not observed in the study area. However, during summer observations this species was common along the bottomlands of the Navasota River, Brazos County. Since *G. carolinensis* exhibits a mesic-adapted breeding pattern (Blair 1955), it possibly remains in moist forested regions which would explain its absence from the less forested upland study areas.

Post-Study Observations of Ponds

Following the wet study period, a post-study inspection of each pond was made on 2 March 1974 during an especially dry period. At this time one of the ponds had been filled in by construction work and four others were completely dry. Of the seven ponds that had water, only three approximated the dimensions and depths seen during the study period. These observations emphasize the instability characteristic of temporary ponds.

Discussion

Calling in *Rana sphenoccephala* was generally initiated by rainfall when maximum daily temperatures were above 15.0°C. This species has a winter-spring breeding season (8 February to 13 May) and a fall breeding season (22 July to 14 October) in the Austin, Texas, area (Blair 1961). The same winter-spring and fall seasons apply to the observed breeding dates in the present study (winter-spring from 17 January to 12 June; fall from 5 September to 27 November). Data from these two studies suggest that breeding can occur in any month of the year. Blair (1961) also stated that the winter-spring and fall breeding periods appeared to be of about equal importance in terms of maintenance and replace-

ment of the population. My study suggests that the winter-spring period is more significant, since many more amplexic pairs and egg masses were seen during this period; this species is more of an opportunistic and sporadic breeder in the fall.

Although all three species of *Pseudacris* are winter breeders and overlap in their reproductive seasons, they initially appeared at slightly different times of the year. *Pseudacris clarki* was clearly less tolerant of low temperatures than either *P. streckeri* or *P. triseriata*. Substantial rainfall and a drop in air temperature, followed by a sudden rise in temperatures, generally led to calling peaks and egg deposition in *Pseudacris* during the temperature rise. *Pseudacris clarki* showed more of a preference for shallow grassy pools than either *P. streckeri* or *P. triseriata*. *Pseudacris streckeri* was observed calling with *P. clarki* and *P. triseriata*, but *clarki* and *triseriata* were never heard calling from the same breeding ponds. *Pseudacris clarki* had a delayed breeding period in September which could be a population response to the possibility of spring drought as suggested by Kennedy (1958), or it could simply represent a response to weather conditions similar to those during the late stages of the normal spring breeding period. Egg masses of *Pseudacris* were attached to vegetation well below the water's surface which was a definite advantage when ice covered the ponds on several occasions.

Calling and breeding in *Scaphiopus holbrooki* coincided on five nights in March and April. My data suggest that low temperatures, possibly maximum daily temperatures below 18.9°C, inhibited breeding even when there had been sufficient rainfall. The largest choruses and most extensive breeding occurred on the evening of 15 April (maximum daily temperature = 20.6°C) following a steady rain of 52 mm. Rainfall of 40 mm and a maximum daily temperature of 17.2°C on 17 April failed to initiate calling. My data also agree with those of Wasserman (1957) who found no *S. holbrooki* breeding after May during 4 years of study in Texas. Bragg (1967) suggested that not all adult females in an area produce eggs each time breeding conditions are favorable. A staggering of egg production over several months takes advantage of all favorable situations. Possibly a related phenomenon in my study was the fact that on five occasions following breeding periods, gravid

females were found near breeding ponds on evenings when calling did not occur.

Acris crepitans was active over a wide range of temperatures and was seen in every month of the study, but this species only called in the spring and summer. This anuran usually inhabits permanent bodies of water, but also frequents temporary ponds when sufficient water is available. Calling peaks extended through three periods: 12–19 March, 12 April–14 May, and 4–18 June. Contrary to Blair (1961), my study indicates that calling peaks were generally associated with periods of heavy rainfall. Five nights of breeding between 17 April and 12 June in my study paralleled the breeding season noted by Pyburn (1958) and Blair (1961) at other Texas localities.

Hyla versicolor was not particularly common, probably because of the lack of trees in most of the study area. Trees are generally used as calling stations and play a major role in the breeding behavior of this species. Maximum daily temperatures below 20°C and evening temperatures below 16–18°C generally inhibited calling. Most calling and breeding were observed during periods of rainfall or high humidity (above 80%).

Bufo valliceps is one of the most common anurans in the study area. Blair (1960) placed emphasis on rainfall as the main initiating factor for calling in this species. My data clearly indicate that evening air temperatures below 18.5°C inhibited calling, particularly at the start of the calling season. Rainfall only became important for calling and breeding when evening temperatures were consistently above 20.0°C after mid-May. Similarly, Thornton (1960) found that sufficient rains during the breeding season did not bring out choruses of *B. valliceps* if temperatures were below 16.1°C.

Although *Bufo woodhousei* is supposedly distributed in all of east-central Texas (Stebbins 1954; Raun and Gehlbach 1972; Conant 1975), I observed this species on only a few occasions and I never heard it calling. However, during the summer of 1973, large numbers of *B. woodhousei* were encountered along the Navasota River bottom. The floodplains and lowlands along the river had sandy soils and in general were unaltered by man. This observation agrees with that of Axtell (1963), who proposed that *B. woodhousei* was not widely distributed throughout the arid Southwest, but was highly restricted to localized, stream edge habitat.

Gastrophryne olivacea was probably one of the most opportunistic breeders associated with periods of rainfall. My data indicate that air and water temperatures below 18.0°C were important factors inhibiting calling. Warm rains were necessary for initiating reproductive activities in this species.

Bufo spectosus was only observed calling on six consecutive evenings from shallow temporary pools that were formed from the overflow of an old cattle tank. Blair (1964) suggested that *B. spectosus* requires extensive (flooding) rainfall which is an adaptation for existence in the xeric Southwest. This requirement for flooding was fulfilled on numerous occasions during the study and does not afford an explanation for the limited emergence of this species. Perhaps the population numbers are so low in this marginal habitat that extensive calling and breeding are not possible.

Data collected on reproductive activities clearly indicate a successional occurrence for anurans using temporary ponds in Texas (Fig. 3). There are four basic groups of anurans that make up this sequential pattern. The first is *Rana sphenoccephala*, which is active throughout the year. The second component consists of winter-spring breeders, *Pseudacris streckeri*, *P. triseriata*, and *P. clarki*. The third component is *Scaphiopus holbrooki*, with distinctively short calling, breeding, and larval periods in the spring only. The last group consists of *Acris crepitans*, *Hyla versicolor*, *Bufo valliceps*, and *Gastrophryne olivacea*, which are most active during spring-summer months. Although there was overlap of the reproductive seasons of these species, there was an obvious temporal partitioning of the ponds. Different combinations of species occurred in each pond, and spatial separations existed between those species that were active at the same time of the year.

Males of each species initiate the calling period, and the presence of adult females determines the breeding period. Breeding periods of all species were within the broader calling periods, except in *S. holbrooki*, whose calling and breeding periods coincided. Since much more calling than breeding occurred, these data suggest that some energy is wasted on the part of males of some species. It is generally accepted, however, that calling attracts conspecific females to breeding ponds. Males of some species have been observed calling long before females arrived

to breed, and this calling may have been important in attracting other males to the pond, thus increasing the number of males at a given breeding locality. If a certain "calling volume" is necessary to attract females to the breeding pond, this increased population of calling males would be advantageous. Although this is only conjecture, the importance of calling is an unsettled question and needs to be further explored.

The range of air temperatures on nights of calling and on nights of breeding coincide in *S. holbrooki*. For all other anurans the air temperature range on calling nights is greater than on breeding nights. This suggests that females wait for certain optimal breeding conditions, in this example a narrower range of air temperatures within the range of calling males. Although not significantly different in some species, the mean humidity is higher on breeding nights than on calling nights, suggesting that females require slightly higher humidities for breeding than males need for calling.

Larvae of each species were present over a slightly different time span and various combinations of larvae occurred in the ponds (Figs. 5, 6, 7). *Rana sphenoccephala* larvae probably occur in temporary ponds throughout the year when water is available. Late April was a transitional period between the end of the winter-spring larvae (*P. streckeri*, *P. triseriata*, *P. clarki*, *S. holbrooki*) and the beginning of the spring-summer larvae (*A. crepitans*, *H. versicolor*, *B. valliceps*, *G. olivacea*). At this time there were two classes of larvae, generally larger larvae of the winter-spring species and smaller larvae of the spring-summer species. *Pseudacris clarki* broke this pattern slightly by a short larval period in late summer. In terms of both individuals and species, the greatest number of larvae were present in April and May, and this larval bloom corresponds to the time of greatest rainfall. Because temporary ponds are generally susceptible to drying, there is a definite adaptive advantage for most larvae to be in the ponds during spring months.

Certainly year-to-year fluctuations in seasonal weather conditions will alter the pattern of anuran succession as discussed herein. Numerous climatic factors are contributing to the variation in each anuran's reproductive season, but data must be accumulated for many years before appropriate analyses can determine the influence of many of these factors. My interpretation of the environmental effects on each species' reproduc-

tive season was based on data from 1 year. This study indicates the importance of fluctuations in air and water temperatures, rainfall, and possibly humidity, as the overriding causes of variation in anuran reproductive patterns in Brazos County, Texas.

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Prey Patterns and Trophic Niche Overlap in Four Species of Caribbean Frogs

by

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Abstract

Frogs in the genus *Eleutherodactylus* make up the majority of species of anurans and a high percentage of all terrestrial vertebrates in the Caribbean Islands. To examine the factors regulating the species diversity of this group on various islands, I made observations on the diet, rates of feeding, and movement for four species from the Virgin Islands and Puerto Rico. Patterns in the diet generally agree with published accounts for communities of insects from the same area, suggesting that this assemblage of species consumes prey species in the proportion in which they occur. Estimates of the competitive coefficient show trophic niche separation for most species pairs by length or prey type, suggesting trophic niche partitioning.

Since frogs in the genus *Eleutherodactylus* make up a majority of Caribbean amphibians and a high proportion of all terrestrial insectivores, it is of interest to examine their patterns of use of the insect prey base.

Schoener and Janzen (1968) reported patterns in tropical foliage insect communities in several tropical areas of Costa Rica. The present study examines prey use of four species of frogs in the genus *Eleutherodactylus* and compares patterns from stomach analyses with the sweep net studies of Schoener and Janzen. Four species of *Eleutherodactylus* occur on the Virgin Islands, and two of these species also occur on Puerto Rico. Four of the major Virgin Islands and Puerto Rico were selected for this study. These five islands provide various combinations of the four species and provide a natural experiment in resource partitioning.

Methods

From September 1973 to June 1974 four species of frogs in the genus *Eleutherodactylus*

were observed and collected on the Virgin Islands of St. Thomas, St. John, St. Croix, Tortola, and on Puerto Rico. Two of the species, *E. lentus* and *E. schwartzi* occur only on the Virgin Islands. The remaining two species, *E. cochranae* and *E. antillensis*, also occur on Puerto Rico. A collection of about 100 specimens was made for each species on each island. All specimens were preserved in the field within 2 h of capture.

Adults of each of the four species were observed while feeding and moving by means of a GTE Sylvania night-viewing device. This device allows observation under natural light conditions at night. Subjects were observed for periods of 15 min each. All feeding attacks and movements not associated with a feeding attack were tabulated. Each species was observed for 20 observational periods. The observations were made throughout the study at different times of the night and on various islands.

A small collection of insects which seemed likely to be included in the diet of *Eleutherodactylus* was made. Prey items removed from the frogs' stomachs were measured with an ocular micrometer disk inserted into a dissection microscope, compared with the initial insect col-

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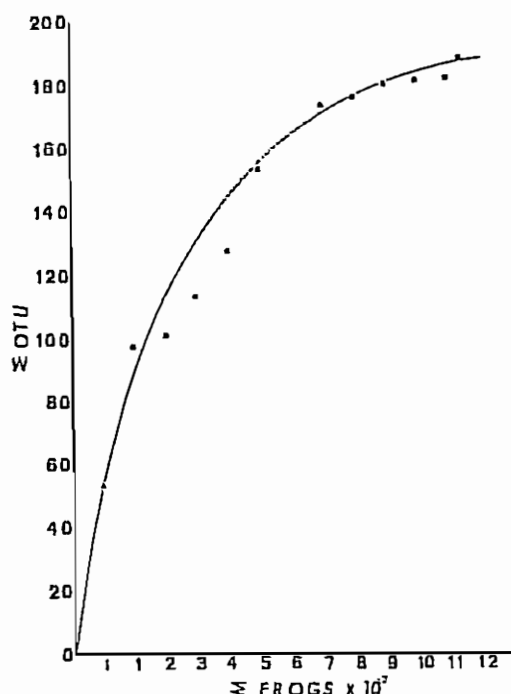


Fig. 1. Cumulative number of OTU's vs. number of frogs examined. The triangle indicates an initial reference collection. Curve was fitted by eye.

lection, and identified by the collection number. Any prey item not represented in the reference collection was assigned a number and added to the collection. No attempt was made to associate larval stages with the corresponding adult stage. All prey items assigned the same reference collection number will be referred to as belonging to the same Operational Taxonomic Unit (OTU). Any OTU may contain several morphologically similar species, and different developmental stages of the same species may have been assigned to different OTU's. A total of 190 OTU's were assigned during the study. The number of prey species represented by the 190 OTU's is unknown, but the number of OTU's in any sample is probably directly proportional to the number of prey species.

Figure 1 is a line plot of the cumulative number of OTU's against the number of frogs examined. The figure suggests that additional collecting would have added few new categories. For each OTU from each frog's stomach, the

total number, average length, and width were recorded. I calculated volume using the formula for a cylinder.

Results and Discussion

Natural History

Eleutherodactylus antillensis (mean snout-vent lengths in mm: males 23, females 27), *E. cochranae* (males 18, females 19), and *E. schwartzi* (males 24, females 29) are very similar in appearance and in general behavior. All three species call and forage mostly on foliage. Individuals use the same foraging and resting sites over long periods of time. *Eleutherodactylus lentus* (males 22, females 30) is similar to the other three species, except that the toe disks are reduced and the males are mute. This species was found exclusively on the ground. Individuals move frequently and are apparently not faithful to any given locality. The basic foraging strategy of *E. lentus* differs from that of the other three species. For convenience, *E. lentus* will be termed a searcher and the other species as sit-and-wait predators.

General Prey Patterns

Schoener and Janzen (1968) found that, in general, sizes of insects from sweep samples fit a lognormal distribution. If the four *Eleutherodactylus* species used in the present study consume prey items in the proportion in which those items occur, one would expect that the prey items removed from all of the specimens would also approximate a lognormal distribution. A histogram of all of the prey items appears to fit a lognormal distribution (Fig. 2).

Schoener and Janzen (1968) demonstrated that logarithmic transformation produced a distribution closer to normality than did the original measurements. They showed that the g_1 , g_2 , and a χ^2 statistic measuring the departure from normality are smaller in the transformed data. In the present study (Table 1) the logarithmic transformation produced g_1 and g_2 values which are closer to zero, but the curve remains leptokurtic and skewed to the right. The χ^2 statistic is smaller than in the nontransformed data indicating less departure from normality.

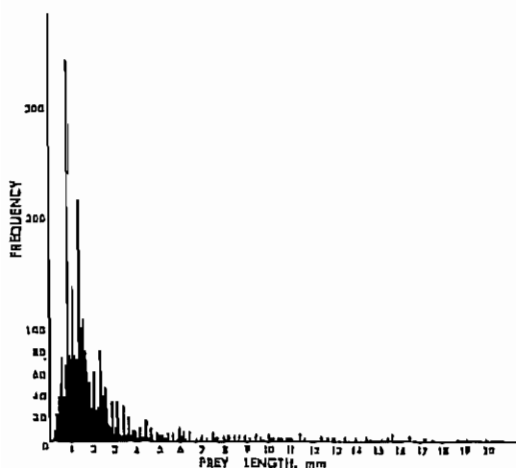


Fig. 2. Histogram of all prey items removed from stomach contents.

These results indicate that the length and volume of prey species fit a lognormal distribution better than a simple normal distribution. The g_1 and g_2 values indicate that there are more large prey items than expected. These results are in agreement with the results of the sweep sample study of Schoener and Janzen (1968).

Prey Taxa

The four species of *Eleutherodactylus* studied

Table 1. Statistical features of prey items removed from stomach contents of *Eleutherodactylus* from Puerto Rico and the Virgin Islands.

Data	Mean	SD	g_1	g_2	χ^2
Length					
Raw (mm)	2.7	2.6	5.0	50.5	14,511.3
Transformed	0.80	0.48	0.87	1.71	1,077.8
Volume					
Raw (mm ³)	10.8	7.5	1.9	4.5	136.8
Transformed	2.19	0.58	-0.27	2.63	19.7

are general arthropod predators, but they occasionally take other animals. From site to site species vary in the proportions of their diets drawn from different taxa (Table 2). On St. John, 70.1% of the prey items of *E. antillensis* are ants, but on Puerto Rico only 11.7% of the items are ants. On St. John, 44.1% of the prey items of *E. cochranae* are spiders, but on Puerto Rico only 3.5% are spiders.

Diet Overlap

Mutual use of food resources implies the potential for competition. It is not, of course, evidence for competition at any specific time. The data for mutual use of food items by OTU (Table 3) show

Table 2. Percentage of total individuals (I) and total volume (V) of various prey taxa.

Order	Puerto Rico				St. John			
	<i>E. antillensis</i>		<i>E. cochranae</i>		<i>E. antillensis</i>		<i>E. cochranae</i>	
	I	V	I	V	I	V	I	V
Hymenoptera								
Formicidae	11.7	14.3	13.4	11.5	70.1	22.1	12.0	5.4
Other	0.0	0.0	0.4	0.1	2.6	0.2	0.0	0.0
Diptera	15.8	3.5	13.0	23.0	3.9	3.4	0.4	2.2
Coleoptera	14.8	23.8	1.0	0.3	6.0	3.5	5.7	6.3
Isoptera	0.0	0.0	0.0	0.0	0.0	0.0	2.1	0.2
Homoptera	32.8	3.4	62.7	43.4	3.9	1.2	3.9	2.4
Hemiptera	4.6	4.0	1.4	12.0	0.9	8.2	2.7	7.8
Lepidoptera	3.3	13.6	0.0	0.0	2.1	23.5	3.0	2.5
Orthoptera	1.0	22.8	0.0	0.0	3.0	12.6	11.1	52.4
Acarina	0.0	0.0	3.5	0.4	0.0	0.0	0.0	0.0
Isopoda	0.5	0.2	1.1	0.9	0.9	0.1	10.2	17.1
Mollusca	0.3	7.5	0.0	0.0	0.0	0.0	0.0	0.0
Araneae	4.3	6.0	3.5	5.2	5.6	0.3	44.1	1.3
Unidentified	10.9	0.9	0.4	3.4	1.3	22.2	0.1	0.2

Table 3. Diet by OTU of *Eleutherodactylus* from Puerto Rico and the Virgin Islands.

Island, and species of <i>Eleutherodactylus</i>	Number of OTU's		Number of prey items	
	Total	Shared	Total	In shared OTU's
Puerto Rico				
<i>antillensis</i>	56	21	387	300
<i>cochranae</i>	31	21	284	263
St. Thomas				
<i>antillensis</i>	54	42	221	206
<i>cochranae</i>	53	41	952	921
<i>lentus</i>	81	51	1,627	1,508
St. John				
<i>antillensis</i>	43	19	333	209
<i>cochranae</i>	37	19	234	194
St. Croix				
<i>antillensis</i>	43	22	136	59
<i>lentus</i>	62	22	918	202
Tortola				
<i>antillensis</i>	44	26	220	184
<i>schwartzii</i>	51	31	415	344
<i>cochranae</i> ^a	15	14	39	38

^aSample based on 30 individuals only.

that all four species share some of the same OTU's with one or both congeners, and the shared categories clearly contain the majority of individual prey items for all of the species.

On Puerto Rico the diet of *E. antillensis* consisted of 56 OTU's. Thirty-five of these were not found in the diet of *E. cochranae*. The diet of *E. cochranae* consisted of 31 OTU's, only 10 of which were not found in the diet of *E. antillensis*. In the Virgin Islands, the diet of each of the two species included 50% of the OTU's that were being used solely by the other species on Puerto Rico. Only two of the 21 OTU's that were shared on Puerto Rico occurred uniquely in the diet of one of the species on the Virgin Islands. Both instances involve a small number of individuals, and this could be the result of chance. The most significant aspect of these results is the increase in the number of OTU's shared on the Virgin Islands.

An overlap in the diet of two species may be of little importance if the prey involved constitute a minor fraction of the energy budget of one or both of the species. Assuming that the energetic return is directly proportional to the prey volume, the most common items contain little volume, and presumably little caloric value. In general for the sit-and-wait frogs a few large

items contain the major portion of the volume. Based on this, one might expect that some aspect of the morphology of these frogs, such as head width, would be related to these few large categories.

Figure 3 shows a regression line, fitted by Bartlett's three-group method, for head width and modal prey volume. Each sex of each species from each island is plotted separately. The correlation for these two variables is 0.623 ($P < 0.01$).

Figure 4 is a modified copy of Fig. 3, omitting *E. lentus* and with the sit-and-wait species on each island joined by a line. The shape of the lines suggests that the relation between mean head width and modal prey volume is not rectilinear. The distance between lines suggests that there is some amount of inter-island variation in the availability of prey sizes.

Assuming that the prey base for *E. lentus* and the sit-and-wait frogs is the same, as suggested by overlap of OTU's, the differences seen in Fig. 3 could be attributed to a difference in foraging strategy.

Feeding Rates

Feeding rates were obtained in two different

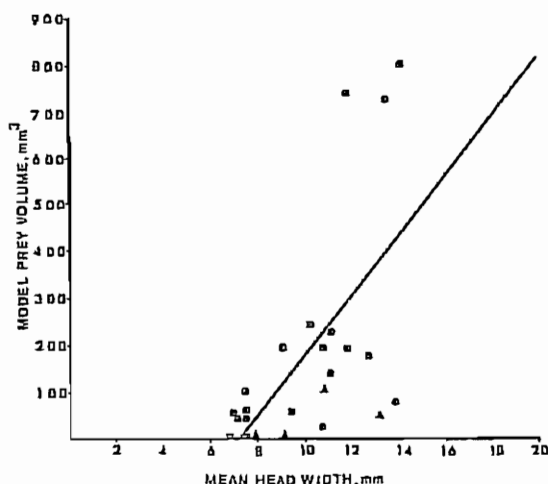


Fig. 3. Regression line for mean head width of both sexes of each species to modal prey volume in the diet. Triangles indicate *E. lentus*, circles indicate remaining three species.

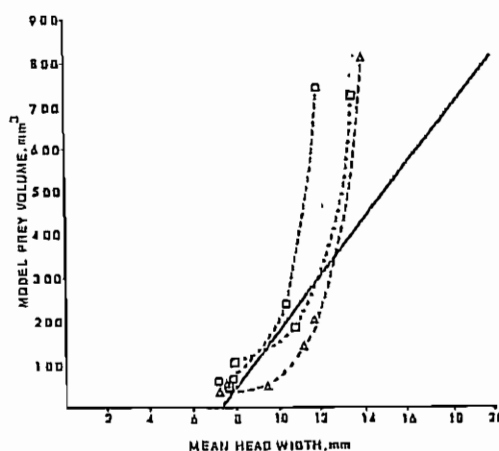


Fig. 4. Head width vs. modal prey volume for sit-and-wait frogs on three islands, Tortola (triangles), St. Thomas (circles), and St. John (squares).

ways: (1) feeding was observed directly by means of the night-viewing device, or (2) the number of prey items recovered from each collected specimen was divided by the elapsed time from dusk to capture. The second method is likely to be an underestimate of the total feeding rate, especially for specimens captured shortly before dawn. The rate at which items are transported out of the stomach is unknown, but frogs captured during the first few minutes after dark and those captured a few hours after dawn uniformly lack prey in the stomach. This suggests that feeding does not occur before dark, and that all items were moved from the stomach within a few hours after dawn.

The average feeding rate obtained by stomach analysis for *E. antillensis* was 0.8 prey/h, for *E. schwartzi*, 1.2 prey/h, and for *E. cochranae*, 1.5/h. This suggests an inverse relation between feeding rate and size within the sit-and-wait frogs. The average feeding rate for *E. lentus* was 2.8 prey/h, which is two to three times the rate of a sit-and-wait frog of the same size.

The average observed feeding rate for *E. antillensis* was 1.0 prey/h and the average non-feeding movement rate was 1.0 move/h. The average observed feeding rate for *E. schwartzi* was 0.95 prey/h and the average movement rate was 1.2 move/h. The average observed feeding rate for *E. cochranae* was 2.2 prey/h and the average observed movement rate was 1.4 move/h. The average observed feeding rate for

E. lentus was 2.6 prey/h and the average movement rate was 2.4 move/h.

The two methods of estimating feeding rates yield similar results for all four species, suggesting that neither method is strongly biased. The movement rates are also inversely related to size of animal within the sit-and-wait frogs. The *E. lentus* average movement rate is two to three times the rate of a sit-and-wait frog of the same size.

Niche Overlap

The extent to which resource use of one species overlaps that of another is a measure of possible competition between the species. Although several measures of overlap are available, it is perhaps most meaningful to measure niche overlap in terms of estimates of the competitive coefficient alpha (α).

Levins (1968) and MacArthur (1972) provided formulae for estimation of alpha based on a single resource (see Estimates of Alpha, the Competition Coefficient). Levins' formula lends itself to discrete data, whereas MacArthur's formula is more appropriate for continuous data. MacArthur's formula has the disadvantage of assuming that each species would exert the same degree of effect on the other ($\alpha_{12} = \alpha_{21}$). This is true only if the variance of resource utilization is equal.

Table 4. Alpha estimates for prey use by Antillean Eleutherodactylus. Resource axes are prey length and prey OTU.^a Alpha is read as the effect of the horizontal species on the vertical species. Intraspecific alpha is the effect of female on male.

Locality, and species of <i>Eleutherodactylus</i>	Species of <i>Eleutherodactylus</i>							
	<i>antillensis</i>		<i>cochranae</i>		<i>lentus</i>		<i>schwartzii</i>	
	Length	OTU	Length	OTU	Length	OTU	Length	OTU
St. Thomas								
<i>antillensis</i>	0.95		0.87	0.35	0.97	0.26		
<i>cochranae</i>	0.87	0.30	0.95		0.90	0.77		
<i>lentus</i>	0.97	0.42	0.90	1.29	0.84			
Tortola								
<i>antillensis</i>	0.95		0.76	0.32			0.95	0.15
<i>cochranae</i>	0.76	0.15	0.89				0.91	0.19
<i>schwartzii</i>	0.95	0.20	0.91	0.57			0.88	
St. John								
<i>antillensis</i>	0.90		0.85	0.90				
<i>cochranae</i>	0.85	0.62	1.00					
Puerto Rico								
<i>antillensis</i>	0.97		0.97	0.07				
<i>cochranae</i>	0.97	0.07	0.98					
St. Croix								
<i>antillensis</i>	1.00				0.86	0.44		
<i>lentus</i>	0.96	0.83			0.62			

^aOTU = operational taxonomic unit.

The two most likely dietary variables are length of prey and prey OTU's. Length is a continuous variable, whereas prey OTU's are discrete. The alpha estimate was computed by MacArthur's and Levins' formulae, respectively, but there are some problems in computation and interpretation of each estimate. The prey length alpha is based on frequency, whereas the prey OTU alpha is based on volume. The prey length alpha ignores the potential separation by specific type prey, and the prey OTU alpha may be underestimated because of the small sample size of the larger prey items. Finally, each frog species is treated as a homogeneous group, when in fact each sex might be acting to some unknown degree as an "ecospecies." As an indication of this effect, an intraspecific alpha estimate was computed for each dietary variable, treating the sexes as separate groups (Table 4). The prey OTU alpha estimate is omitted from the intraspecific comparisons because of small sample sizes. Within each set of interspecific alpha estimates, there are often one or more low values which indicate niche separation.

Estimates of Alpha, the Competition Coefficient

1. From Levins (1968):

$\alpha_{ij} = \sum_h P_{ih} P_{jh} / \sum_h P_{ih}^2$, where P_{ih} is probability of species i occurring in resource cell h and P_{jh} is the probability of species j occurring in cell h . In this paper, the resource cells, h , are the prey OTU's. Levins' α can be as low as 0 (no overlap) and ordinarily does not exceed 1.5.

2. From MacArthur (1972):

$\alpha = e \exp [-d^2/2(\sigma_1^2 + \sigma_2^2)]$, where σ_1 and σ_2 are the standard deviations of the resource distributions for species 1 and 2, and d is the distance between the means of these distributions. In this estimate, it is assumed that α_{12} (the effect of species 2 on species 1) equals α_{21} (the effect of species 1 on species 2). In this paper, the resource distributions are the frequency distributions of the prey lengths. MacArthur's α varies between 0 (no overlap) and 1 (complete overlap).

Conclusions

The general agreement between the sweep net sample data of Schoener and Janzen (1968) and the stomach content data in the present study indicates that all four species of *Eleutherodactylus* consume foliage insects in the proportion in which the insects occur. The lengths of insects tend to fit a lognormal distribution which is leptokurtic and skewed to the right. This indicates that a larger number of large insects exists in the combined diets than would be predicted by a lognormal distribution.

Within the four species of frogs, *E. lentus* uses a basically different foraging strategy. *E. lentus* is an active ground-dwelling species which moves and feeds two to three times faster than the other

three species. The remaining three species are mostly foliage dwellers. Within this group there is an inverse relationship between size and the rates of feeding and movement.

In the comparison of intraspecific sets, one or more low values indicate trophic niche separation.

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SNAKE COMMUNITIES

Niche Dimensions and Resource Partitioning in a Great Basin Desert Snake Community

by

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Abstract

Aspects of the population biology and community ecology of three sympatric species of snakes (*Coluber constrictor*, *Masticophis lateralis*, and *Pituophis melanoleucus*) using communal dens in a Great Basin cold desert shrub habitat were studied in northern Utah between 1969 and 1973. Food habits analysis and telemetry tracking of snakes in the field allowed quantification of the food and place dimensions of the ecological niche of each species. We also report on thermal preferences, temporal overlap at hibernacula, annual body weight changes, and survivorship of these species. Species abundance distributions and species diversity in 10 North American snake communities are surveyed.

The species were separated strongly by food habits. Major prey taken were insects (*Coluber*), lizards (*Masticophis*), and mammals (*Pituophis*). *Coluber* had the narrowest food niche, *Pituophis* was intermediate, and *Masticophis* had the broadest niche. In summer, *Masticophis* had the broadest place niche and differed from *Coluber* and *Pituophis*, which were underground most often. All three paired species comparisons showed the average overall niche overlap values were 0.79 (place) and 0.19 (food). The trophic dimension is more important in resource partitioning than is the spatial dimension for snakes in this community. Complementarity between these two niche dimensions exists.

Snakes, as a group, had lower mean activity temperatures than lizards at our study locality. Thermal preferences underground (26–27°C) were very similar among the snakes. *Pituophis* had a lower mean activity temperature (28°C) than *Coluber* and *Masticophis* (31–32°C) on the surface. At dens during spring emergence and autumn ingress, when competitive interactions may have been possible, most *Masticophis* and *Pituophis* arrived at and emerged from dens 2–3 weeks earlier than *Coluber*, but this "separation" may be more closely associated with species differences in reproductive behavior and dispersal than with competition.

Annual survival rates were similar in the three species; first-year survivorship ranged from 15 to 20% and adult survivorship ranged from 63% (*Pituophis*) to 78% (*Coluber*) and 80% (*Masticophis*). Maximum life expectancies are 16 years for *Pituophis* and 20 years for *Coluber* and *Masticophis*, according to these schedules.

Proportions of snakes that increased in body weight during 3 years varied between species. About 90% of *Masticophis* increased each year. In the other two species, 1 year each was unfavorable for *Pituophis* (1971, a wet year) and *Coluber* (1972, a dry year) when only 64–68% gained weight compared with favorable years when 83–98% of these snakes gained weight. Causal factors responsible for these different environmental responses are probably related to the proportion of rain falling during the summer months.

Rainfall may directly affect the snakes' water balance or the productivity of their prey populations. These effects probably act in different ways for each species and with different time lags through poorly understood and complex mechanisms.

Human predation has greatly altered the species composition at our desert study site over a 30-year time span, causing an almost complete shift in the dominant species (*Crotalus* and *Masticophis* in 1940, *Coluber* and *Pituophis* in 1970). At each time the diversity indices were similar ($H = 0.99$ in 1940's, $H = 1.05$ in 1970's) indicating that the replacements may be correlated with resource partitioning within the community.

In 1974 an extensive range fire destroyed the habitat around the communal dens. Subsequently, drifting sand buried the dens, completing an apparent extirpation of the snake community.

A number of studies have provided herpetological ecologists with sound biological data on single species of snakes, or have been autecological in focus (Fitch 1960, 1963, 1965, 1975; Hall 1969; Clark 1970, 1974; Brown 1973; Branson and Baker 1974; Clark and Fleet 1976) and several have dealt with two species (Platt 1969; Saint Girons 1975; Parker and Brown 1980). Only a few early studies attempted to compare three or more sympatric species (Fitch 1949; Carpenter 1952; Fouquette 1954; Fleharty 1967) and had a community outlook. Because they preceded the recent rapid growth of investigations into resource partitioning over the past 10 years or so (cf. Schoener 1974), none is couched in terms of a modern quantitative approach to community analysis, i.e., niche dimensionality and resource partitioning.

In addition to field studies cited above, some workers have explored broader patterns governing the structure of assemblages of snakes. Barbault (1970, 1971) examined population densities, biomass, and seasonal abundance of a snake fauna of a single geographic region and later analyzed these snake populations in a community context, particularly trophic relations (Barbault 1974). Other recent approaches to herpetological community studies of snakes largely have concerned food resources (Henderson 1974; Mushinsky and Hebrard 1977; Fitch, this volume) and at least three studies have treated both diet and habitat (Shine 1977; Hart 1979; Reynolds and Scott, this volume). Renewed interest in geographical patterns of species abundance and diversity was kindled largely by MacArthur (1965, 1972). Turner (1961) summarized data on relative abundance of snakes and Arnold (1972) analyzed snake community patterns to determine whether prey species density affects predator (snake) species density. Investigators seem now to be on the

verge of considering the role of snakes in community structure as begun by Barbault (1974), Henderson (1974), Shine (1977), and Hart (1979). Although Schoener (1974) warned that merely documenting differences between species with respect to resource partitioning appeals only minimally to our scientific interests, perhaps we must settle for this level of description at present because our knowledge of snakes has lagged substantially behind that of other groups of vertebrates such as birds and lizards.

For 4 years (autumn 1969 through spring 1973) we studied the natural history and ecology of snakes using communal dens in a Great Basin cold desert shrub habitat in northern Utah. Results from these studies and a description of the study area are provided by Parker and Brown (1973) and Brown and Parker (1976a). We attempt to integrate some of our findings on racers, *Coluber constrictor* (Brown 1973; Brown and Parker 1982), whipsnakes, *Masticophis taeniatus*, and gopher snakes, *Pituophis melanoleucus* (Parker and Brown 1980) with emphasis on the ecological niche of these species. Although five additional less common species have been recorded at our snake dens, we gathered data primarily on these three most abundant species. Our studies provide a data base for treating these three species as a sympatric group making up the bulk (98% by numbers, 96% by biomass) of this snake community.

We examine aspects of the biology of the three species that bear on the following questions: (1) What dimensions of the ecological niche appear to be critical and how strongly are resources partitioned? (2) Do quantitative measures of overlap among paired species comparisons imply possible interspecific competition? (3) In what ways do these snake species vary in their response to annually changing environmental conditions? (4)

How might any such differential response, along with the observed turnover in species composition and abundance in the community, reflect the ecological niche of each, and what might this tell us about community structure and population stability in snakes?

We definitely need empirical, quantitative field studies of snakes that might make this relatively specialized and morphologically homogeneous group more useful in broadening the theory of the ecological niche and of community structure in general. Whether this group of cryptic and difficult-to-study vertebrates can be used to accomplish this end remains to be seen. For many workers, snakes have proved to be attractive as research organisms. We hope to show here that they may also contribute substantially to a rapidly growing body of ecological knowledge at the community level.

Methods

Snakes were captured in spring and autumn by erecting screen wire fences around the snakes' hibernacula. Our general techniques, location of the study area, description of vegetation in the habitat (Great Basin cold desert shrub), and photographs of two of the dens and surrounding sagebrush flats, are provided by Brown and Parker (1976a). We recorded more than 1,400 individuals of seven species. Each snake was permanently marked at its first capture by clipping ventral scutes (Brown and Parker 1976b). Yearly individual body weight changes were based on successive spring or successive autumn captures that included one intervening period of winter dormancy. Inter-year variation in annual weight loss during hibernation was not significant in *Coluber* (Brown and Parker 1982) and *Pituophis* (Parker and Brown 1980) so both intervals used for determining body weight changes in these species (spring-to-spring or autumn-to-autumn) were equivalent. *Masticophis* weights were obtained at successive early spring captures, providing the most reliable data for annual changes in this species (Parker and Brown 1980).

We tracked free-ranging snakes using radiotelemetry. General procedures and equipment used are described by Brown and Parker (1976a). Besides providing data on movements and dispersal, transmitters were temperature-sensitive and enabled us to measure deep-core

body temperatures of snakes in the field. Each transmitter was calibrated in a water bath against a precision mercury thermometer before and after field use. A 1-min pulse count at each location of a snake in the field was later converted to temperature. We obtained a large number of temperature and microhabitat (location) records of all three species in the field using only those records separated by at least 15 min. Data were discarded when a snake's location or activity could not be ascertained by direct observation or inferred by thermal data. Mean number of records per day for each species were as follows: *Coluber* 2.1, *Masticophis* 3.0, and *Pituophis* 1.7.

Four primary categories of microhabitat or activity were recognized: (1) underground (U), in burrow, including burrows under rocks; (2) under rocks (UR), either surface boulders or rock piles, including hibernacula (snake usually visible); (3) moving (M), actual movement from one place to another; and (4) regulating (R), used here in the sense of thermoregulating.

These categories are recognized for analysis of the spatial dimension of the niche (place niche). The first two (U and UR) are subsurface locations and the last two (M and R) are surface activities. Snakes in concealed positions could be precisely located by disconnecting the antenna and passing the receiver close to the ground surface until a distinctly stronger signal was received. In this manner, a distinction between snakes located under rocks (UR) and underground (U) was possible. Distinction between M and R was, in most instances, based on a visual sighting of the snake. If the snake was not seen but the received signal fluctuated in intensity or faded out, the animal was actively moving. Snakes thermoregulating on the surface (R) sometimes were purposely not observed to avoid disturbing the animal. In such instances the category R was assigned by inference from (1) a high body temperature with respect to shaded ambient air and substrate temperatures and (2) lack of movement. Our R and M categories correspond to the normal activity range and basking categories of Cowles and Bogert (1944), and we use thermal data in these two categories as representing the normal activity temperatures of the snakes.

We designate seasons as follows: spring, April–May; summer, June–August; autumn, September–October. All body temperatures reported in the normal activity range of each

species pertain to clear weather conditions (< 60% cloud cover, sun visible).

Our records of food habits were obtained by palpation of live snakes captured between autumn 1969 and autumn 1972 and by examining stomach contents of preserved specimens obtained from the same habitat in areas surrounding the dens. Food items were identified from 146 individuals of the three species (102 *Coluber*, 28 *Masticophis*, 16 *Pituophis*) taken in all months between May and October. Most of the records were from individuals collected in September as they returned to hibernacula. Food items were identified to family or subfamily for insect groups, and to genus or species for vertebrates. Data reported are frequency of occurrence of each food group—proportion of stomachs containing a prey taxon to the total number of stomachs of each species of snake containing food. Although prey biomass would be superior to numbers, digestive fragmentation and small sample sizes (for *Masticophis* and *Pituophis*) would have made the estimation of prey weights from volumes difficult and would have done more to obscure than to reveal interspecific food comparisons. For analysis of the trophic niche dimension, four categories of prey are discerned: insects, lizards, snakes, and mammals.

Using proportions along food and place dimensions actually used by each species, we calculated the niche breadth (B) along any single dimension and species diversity (D) using Simpson's index of diversity (cf. MacArthur 1972)

$$D = B = \frac{1}{\sum_{i=1}^n p_i^2} \quad (1)$$

where p_i represents the proportion of the i^{th} food type or microhabitat used (calculation of B) or the proportion of the total sample belonging to the i^{th} species (calculation of D). B may vary from one to n , the number of p_i values (in our case, 3 for food and 4 for place niches).

To estimate niche overlap, we used a symmetric matrix equation introduced by Pianka (1973) and discussed by May (1975a). Our usage of this equation follows that of Pianka (1975) in the sense that it represents niche overlap (O) and is calculated as

$$O_{ij} = \frac{\sum_{k=1}^n p_{ij} p_{ik}}{\sqrt{\left(\sum_{j=1}^n p_{ij}^2\right) \left(\sum_{k=1}^n p_{ik}^2\right)}} \quad (2)$$

where p_{ij} and p_{ik} are the proportions of the i^{th} resource category used by the j^{th} and the k^{th} species respectively. This measure (range 0–1) is calculated from the relative utilization quantities, p_{ij} and p_{ik} , along the food and place dimensions.

Using the Shannon–Wiener equation, we calculated values of species diversity (H) as follows:

$$H = - \sum_{i=1}^{S_T} p_i \ln p_i \quad (3)$$

where S_T = total number of species in the community and p_i = proportion of the total sample belonging to the i^{th} species. We also calculated maximum species diversity as

$$H_{\max} = \ln S_T \quad (4)$$

and an equitability measure (E) (range 0–1) as the ratio

$$E = \frac{H}{H_{\max}} \quad (5)$$

where H is the observed species diversity according to equation (3). We use equations (3) through (5) to quantify values for several north temperate communities of snakes. We selected certain field studies where both species and numbers of individuals collected by a standard procedure were continued over a fairly long time (usually several months to several years), and where the workers specified their collecting techniques. We have deliberately avoided numerous studies reporting on snakes taken from various winter hibernating locations (cf. Parker and Brown 1973), nor have we treated tropical communities (Inger and Colwell 1977; cf. Henderson et al. 1979). The few censuses and primitive state of our knowledge of the structure of snake communities at present do not allow a comparison of temperate and tropical communities. We believe it is more important to deal with the more fundamental question: What are the relative abundances of sympatric species of snakes?

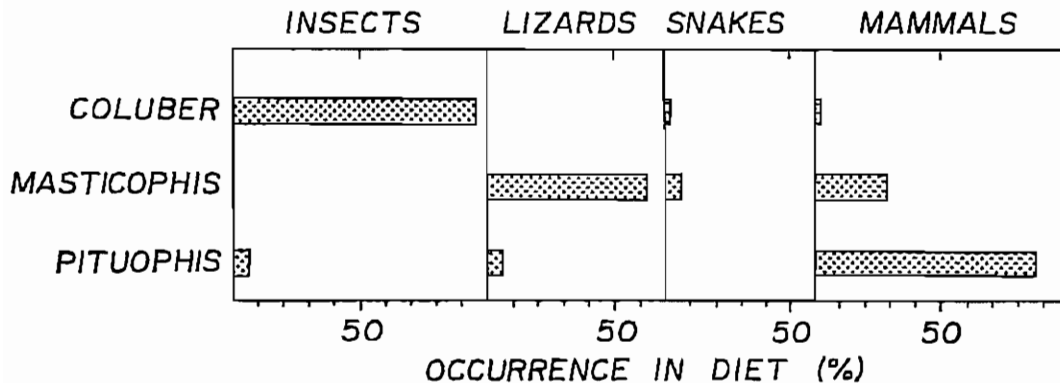


Fig. 1. Frequencies of occurrence (percentage of stomachs) of four major groups of prey taken by three species of colubrid snakes in a Great Basin cold desert shrub habitat in northern Utah.

Results

Food Niche

Food habits of the three species of snakes (Fig. 1) at our desert study area revealed that each species had eaten three of the four prey groups, and each had a dominant (preferred) prey group taken as follows: (1) *Coluber* ($n = 102$) were chiefly insectivorous. Most (96%) of the diet consisted of insects (mostly orthopterans: grasshoppers and ground crickets), whereas the remainder consisted of mammals (*Peromyscus*, 3%) and snakes (*Masticophis taeniatus*, 1%). (2) *Masticophis* ($n = 28$) ate primarily lizards (mainly *Uta stansburiana*, 84%), mammals (mostly *Peromyscus* and *Perognathus*, 28%), and snakes (*Coluber constrictor* and *Masticophis taeniatus*, 7%). (3) *Pituophis* ($n = 16$) prey consisted largely of mammals (chiefly *Microtus* and *Perognathus*, 87%). Lizards (*Uta stansburiana*, 6%) and insects (Orthoptera, 6%) made up less important items in the diet.

Using the measures B (equation 1) and O (equation 2), we show the trophic niches for each of the three species in Fig. 2. Field data are corroborated by the calculated values showing that *Coluber* has the narrowest food niche ($B = 1.08$), *Pituophis* is intermediate ($B = 1.29$), and *Masticophis* has the broadest niche ($B = 2.00$). Overlap along the food dimension is low between *Coluber* \times *Masticophis* ($O = 0.013$), intermediate between *Coluber* \times *Pituophis* ($O =$

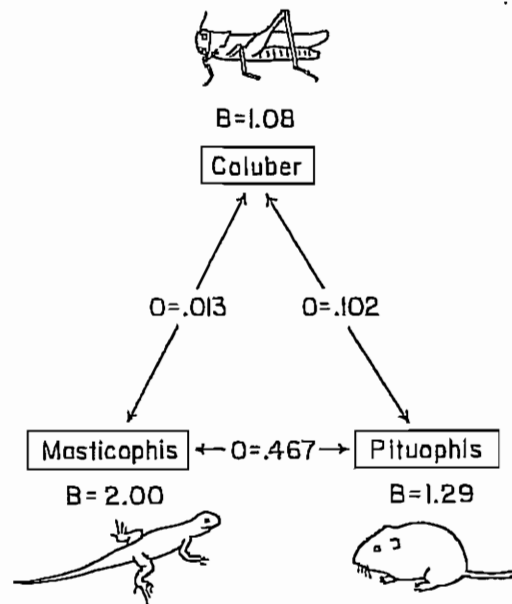


Fig. 2. Quantitative analysis of the food niche of three sympatric colubrid snake species in a Great Basin cold desert shrub habitat. Relations of the three species indicated by niche breadth values (B) at each boxed name and niche overlap values (O) midway along arrows showing comparison of each species pair. Major prey group is depicted for each.

0.102), and high between *Masticophis* \times *Pituophis* ($O = 0.467$) due to the relatively high occurrence of mammals in the diet of each of these species.

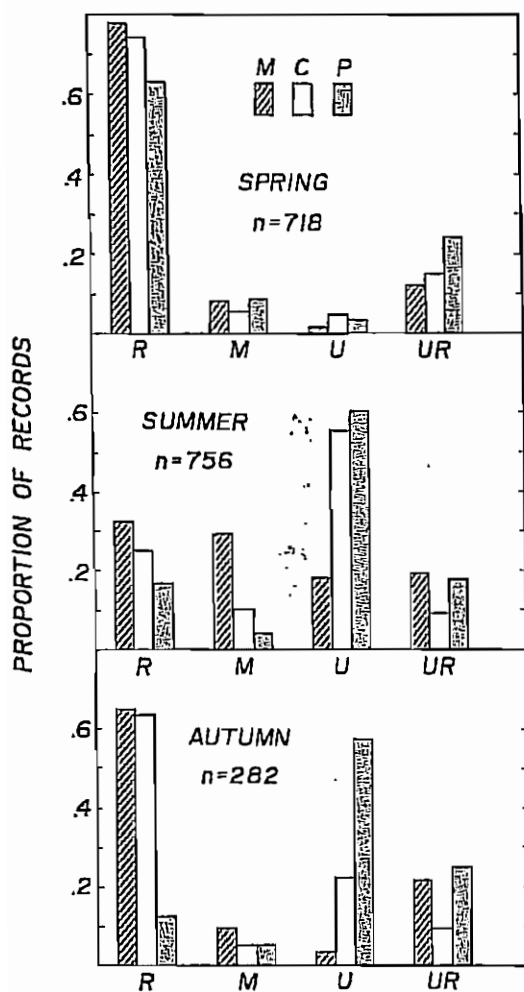


Fig. 3. Seasonal distribution of the place niche of three sympatric colubrid snake species (M = *Masticophis taeniatus*, C = *Coluber constrictor*, P = *Pituophis melanoleucus*) in a Great Basin cold desert shrub habitat. Data are microhabitat-activity categories (R = thermoregulating on surface, M = moving on surface, U = underground, UR = under rocks) recorded for free-ranging snakes in their natural habitat by radiotelemetry in 1971 and 1972. Place niche based on a total of 1,756 field records (*Coluber* 587, *Masticophis* 750, *Pituophis* 419).

Place Niche

Microhabitat-activity distributions (Fig. 3) for the three species in three seasons show several patterns of interspecific spatial-temporal responses: (1) in spring, surface thermoregulation (R) occupied the bulk of the activity of all

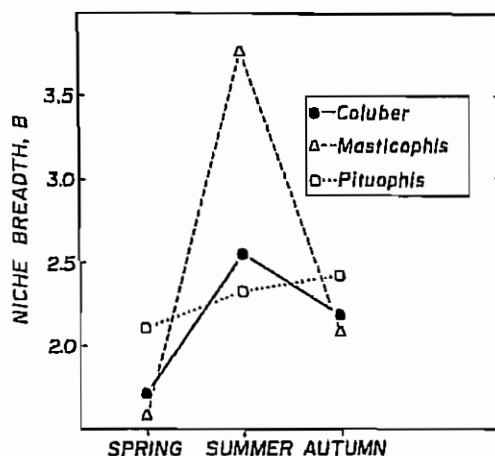


Fig. 4. Seasonal and interspecific comparisons of place niche breadth (B) occupied by three sympatric colubrid snake species in a Great Basin cold desert shrub habitat in northern Utah. Place niche quantified by proportion of location records in four categories of activity-microhabitat used by snakes. See text for calculation of niche breadth and for microhabitat-activity categories recognized.

three species; (2) in summer, most *Coluber* and *Pituophis* retreated underground; and (3) the autumn pattern was like the spring pattern for *Coluber* and *Masticophis*, but not for *Pituophis* (Fig. 3). When activity locations are grouped as to those snakes found R and M or U and UR, two notable spatial niche differences are apparent (Table 1). *Masticophis* in summer tended toward a more uniform (even) dispersion of "places," whereas *Pituophis* failed to reappear on the surface in autumn as did *Coluber*.

Niche breadths (B) for the spatial dimension were calculated for each species in the three seasons (Fig. 4). This analysis shows that (1) both *Coluber* and *Masticophis* have narrower place niches than *Pituophis* in both spring and autumn, (2) the place niches of *Coluber* and *Masticophis* are more similar to each other in spring and autumn than either is to *Pituophis*, (3) *Masticophis* has the broadest place niche in summer and differs considerably from both *Coluber* and *Pituophis*, and (4) *Coluber* and *Pituophis* are similar to each other in summer in that they are found underground most often.

Results obtained with place niche overlap computations between the species pairs (Table 2) are as follows: (1) All three paired species

Table 1. Prominent place niche (activity-microhabitat) locations as surface or subsurface records for three species of colubrid snakes in a cold desert shrub habitat in northern Utah in three seasons, 1971-72.

Species	Spring		Summer		Autumn	
	Location ^a	P ^b (n)	Location	P (n)	Location	P (n)
<i>Coluber</i> (n = 12)	R, M	0.81 (193)	U, UR	0.65 (295)	R, M	0.69 (99)
<i>Masticophis</i> (n = 14)	R, M	0.86 (343)	R, M	0.62 (264)	R, M	0.75 (143)
<i>Pituophis</i> (n = 10)	R, M	0.73 (182)	U, UR	0.79 (197)	U, UR	0.83 (40)

^aActivity-microhabitat categories: R = thermoregulating on surface, M = moving on surface, U = underground, UR = under rocks.

^bP = proportions.

comparisons show broad overlap in spring; (2) only *Coluber* × *Pituophis* overlap broadly in summer; and (3) only *Coluber* × *Masticophis* overlap broadly in autumn. Seasonal comparisons of spatial locations show autumn to have lowest overlap values; summer, intermediate place overlap; and spring, highest. Place niche overlap values averaged over all seasons show smallest overall spatial separation of *Coluber* × *Masticophis* and *Coluber* × *Pituophis* and greatest overall spatial separation of *Masticophis* × *Pituophis*.

Thermal Relations

A large number of body temperatures (T_{bs}) was obtained by telemetry from snakes monitored in the field (Brown 1973; Parker and Brown 1980). In summer, snakes located U (and therefore largely buffered from solar radiation, wind, and other environmental factors) registered the following T_{bs} listed in ascending ther-

mal levels (mean \pm 1 SE): *Masticophis* $25.6^\circ \pm 0.5^\circ$ C (17.0 – 30.6, n = 49), *Pituophis* $26.9^\circ \pm 0.3^\circ$ C (15.5 – 31.4, n = 116), and *Coluber* $27.5^\circ \pm 0.4^\circ$ C (17.5 – 35.2, n = 127). Only about 2° C separates body temperatures of the three species underground.

On the surface, we lumped R and M categories to obtain each species' overall activity body temperature. We also include, for comparative purposes, two other snakes and the six sympatric lizard species at our desert study site (Table 3). The lizards as a group had higher mean activity temperatures ($34.0^\circ - 37.6^\circ$ C) than did the snakes ($24.3^\circ - 31.8^\circ$ C). Means of the two groups did not overlap. Among the snakes, *Coluber* and *Masticophis* were the most lizard-like in their normal preferences (31.2° and 31.8° C), whereas *Pituophis* and *Crotalus* T_{bs} (27.9° and 28.3° C) were considerably lower. *Masticophis* and *Coluber*, both feeding on highly active and thermally tolerant prey (lizards, grasshoppers), may require high body

Table 2. Place niche overlap^a among three sympatric colubrid snakes in a Great Basin cold desert shrub habitat in northern Utah in each of three seasons, 1971-72.

Season	Species pair		
	<i>Coluber</i> × <i>Masticophis</i>	<i>Coluber</i> × <i>Pituophis</i>	<i>Masticophis</i> × <i>Pituophis</i>
Spring	0.997	0.985	0.978
Summer	0.724	0.976	0.639
Autumn	0.945	0.531	0.363
Mean (all seasons)	0.889	0.831	0.660

^aSee text for equation (2) used to calculate niche overlap values.

Table 3. Temperatures of active reptiles sympatric at the study location
(Great Basin cold desert shrub) in northern Utah.

Species	No.	Temperature (°C) ^a		Reference
		Mean ± 1 SE	Range	
Snakes				
<i>Coluber constrictor</i>	266	31.84 ± 0.20	18.6–37.7	Brown (1973)
<i>Masticophis taeniatus</i>	564	31.21 ± 0.13	14.9–38.4	Parker and Brown (1980)
<i>Pituophis melanoleucus</i>	206	27.87 ± 0.32	12.2–35.0	Parker and Brown (1980)
<i>Crotalus viridis</i>	81	28.32 ^b	15.5–35.0	Hirth and King (1989)
<i>Diadophis punctatus</i>	5	24.28	19.8–26.6	Parker and Brown (1974a)
Lizards				
<i>Crotaphytus wislizeni</i>	46	36.68 ± 0.32	30.6–41.5	Parker and Pianka (1976)
<i>Phrynosoma douglassi</i>	18	34.88 ± 0.64	26.3–38.8	Pianka and Parker (1975)
<i>Phrynosoma platyrhinos</i>	86	35.46 ± 0.25	28.1–40.5	Pianka and Parker (1975)
<i>Sceloporus graciosus</i>	9	34.01 ± 0.66	30.6–37.7	Parker (1974)
<i>Uta stansburiana</i>	16	35.46 ± 0.54	29.7–37.9	Parker and Pianka (1975)
<i>Cnemidophorus tigris</i>	11	37.64 ± 1.04	29.2–40.8	Parker (1974)

^aTemperatures for *Coluber*, *Masticophis*, and *Pituophis* are deep-core body temperatures (telemetrically recorded), and for other species, cloacal temperatures (recorded with a Schultheis thermometer).

^bEstimate from graph.

temperatures to maintain a scope of metabolic activity and behavior sufficient to capture their prey. Jacobson and Whitford (1971) suggested this explanation for the high activity temperature (near 33° C) of the diurnal lizard-eating snake, *Salvadora hexalepis*. In contrast, *Crotalus* and *Pituophis* eat primarily nocturnal or subterranean small mammals, and these snakes are not likely to be active at times when it would be necessary for them to maintain high T_b s to capture prey. Greenwald (1974) recorded the highest metabolic efficiency (maximal striking speed and successful prey capture) for *Pituophis* at 27° C, virtually identical to the field results obtained telemetrically by Parker and Brown (1980). Although *Coluber* and *Masticophis* share an almost identical range of activity temperatures, they are strongly separated by food habits (see *Food Niche*). *Crotalus* had a mean activity temperature very similar to *Pituophis* and, presumably, rattlesnakes once occupied a mammal-eating trophic niche similar to gopher snakes. *Crotalus* has recently been exterminated (see *Species Composition at Utah Dens*), and now *Pituophis* is the sole occupant of its overall niche as a relatively cool-bodied subterranean mammal predator.

Temporal Overlap at Hibernacula

As all three species move to and from their

summer home ranges and their winter denning retreats each year, there is opportunity for interaction or perhaps direct physical contact during the periods of fall ingress and spring emergence. We recorded the temporal sequence of arrival and departure at dens in all seasons, 1969–73 (Brown 1973; Parker 1974). In autumn 1971, for example, three main arrival peaks were clearly evident (Fig. 5): *Masticophis*, mid-September; *Pituophis*, late September; and *Coluber*, early October. *Masticophis* were active on the surface at dens for an average of about 17 days after arrival and many entered hibernation after ecdysis nearby (Parker and Brown 1980). *Coluber* and *Pituophis* were not active at dens after returning, and both species seemingly descended into hibernation immediately upon arrival at a den.

In spring 1971, *Pituophis* and *Masticophis* emerged earliest and together in mid-April, followed by *Coluber* in early May, a difference of some 3 weeks between emergence peaks (Fig. 6). The distinct emergence peaks, in general, correspond to favorable air and soil temperatures for emergence. *Masticophis* males constituted the bulk of the earliest emergers (Parker and Brown 1980), a phenomenon also noted in *Thamnophis sirtalis* and a number of other north-temperate snake species (cf. Gregory 1974). Apparently, differential interspecific emergence is related to enhancement of mating behavior in males of

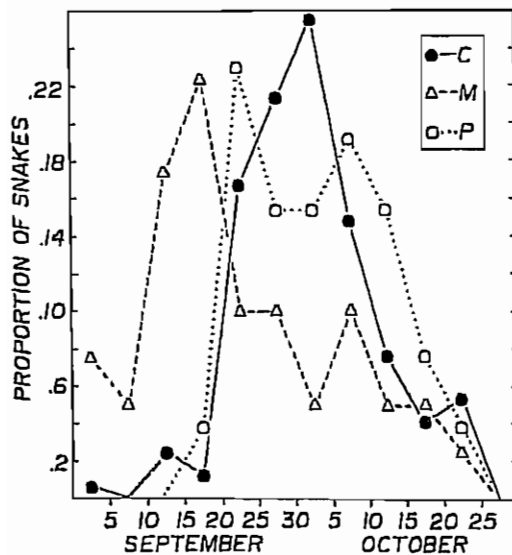


Fig. 5. Arrival of three species of colubrid snakes at den M in autumn 1971. Proportions of each species captured during each 5-day interval are shown. C = *Coluber constrictor*, M = *Masticophis taeniatus*, P = *Pituophis melanoleucus*.

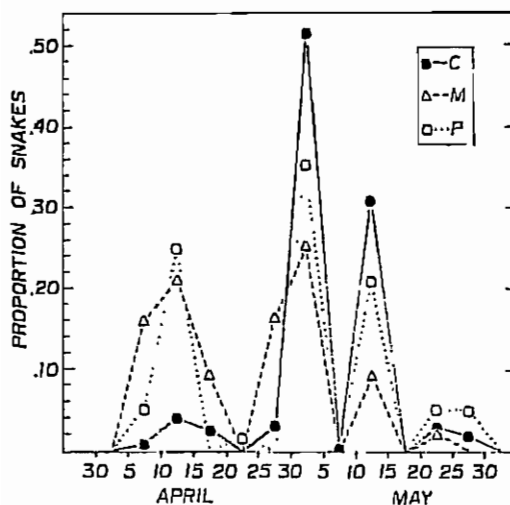


Fig. 6. Emergence of three species of colubrid snakes from den M in spring 1971. Proportions of each species captured during each 5-day interval are shown. C = *Coluber constrictor*, M = *Masticophis taeniatus*, P = *Pituophis melanoleucus*.

some species (e.g., *Masticophis*, Goldberg and Parker 1975; Bennion and Parker 1976) rather than as a mechanism to avoid possible competition, cannibalism, or interspecific predation at the hibernaculum.

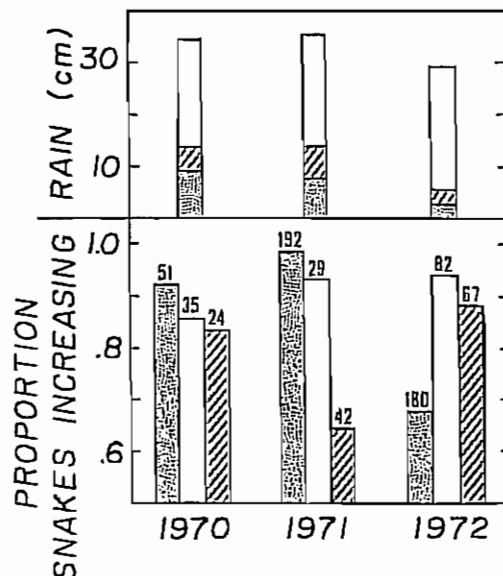


Fig. 7. Annual proportions of three species of colubrid snakes that increased in body weight in 3 successive years (1970-72) in a Great Basin cold desert shrub habitat. Weight change records (lower histogram) are for 423 *Coluber constrictor* of known age through 6 (stippled bars), 146 *Masticophis taeniatus* of all ages (open bars), and 133 *Pituophis melanoleucus* of all ages (hatched bars). Number of records above each bar. Upper histogram shows total annual rainfall (unshaded), total 5-month rainfall (May-September, hatched), and total 3-month rainfall (June-August, stippled) recorded at Grantsville, Tooele County, Utah.

Annual Body Weight Changes

We measured weight changes of snakes in each of 3 years (1970, 1971, 1972); a total of 702 individual weight difference records were accumulated for the three species. Proportions of these that showed an increase during the yearly interval appear in Fig. 7. In all 3 years, most (86-94%) *Masticophis* increased, but the responses of *Coluber* and *Pituophis* were not consistent between years except in 1970 when a majority (83-92%) of all three species showed weight gains. In 1971 only 64% of *Pituophis* gained weight (compared with 83% in 1970 and 88% in 1972), and in 1972 only 68% of *Coluber* increased (compared with 92% in 1970 and 98% in 1971). As indicated by these records, (1) all 3 years had uniformly favorable conditions for *Masticophis*, (2) the wet 1971 was unfavor-

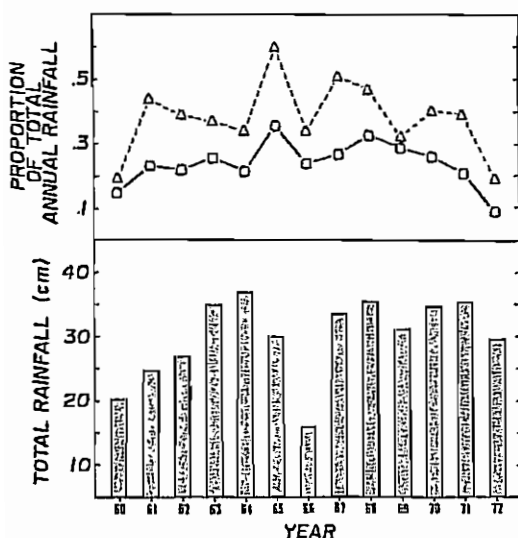


Fig. 8. Rainfall over a 13-year period (1960-72) recorded at Grantsville, Tooele County, Utah (U. S. Dep. Commerce, NOAA, Utah Climatological Data). Lower histogram shows total annual precipitation; upper graph shows proportion of total rainfall that fell in the 3-month period June-August (circles) and in the 5-month period May-September (triangles).

able for *Pituophis* and favorable for *Coluber*, and (3) the dry 1972 was a time of growth for *Pituophis* and reduced growth for *Coluber*. The validity of our designations of favorable conditions is reflected in a snake's ability to put on weight and was confirmed by the fact that *Coluber* suffered considerably higher age-specific mortality rates in 1972 than in 1971 (Brown and Parker, 1982).

The striking differential responses of the species were compared with rainfall records at Grantsville, Utah, about 4 km east of the study area. These data show a similar precipitation pattern for 1970 and 1971 (relatively wet years) compared with 1972, a relatively dry year. The 1972 drought showed up markedly during the 3- and 5-month periods of June-August and May-September when snakes are active (Fig. 7). We also plotted total annual precipitation and the proportions of rain that fell during the two periods (Fig. 8). We chose these two periods because they should be critical to a snake's ability to survive (i.e., eat and reproduce) successfully during its short (5 months) activity season. The 13-year total average rainfall was 30.0 ± 1.8

(16.0 - 36.9) cm, of which an average of 38% fell between May and September and 24% fell between June and August. Although 1972 did not receive much less total rainfall than 1970 or 1971, the critical summer periods were very dry, receiving only 19% (May-September) and 9% (June-August) of the year's total.

Species Diversity

From several studies where authors stated the number of species and individuals taken over a fairly long period of time from a specific locality, we computed various species diversity indices from which we attempted to determine what trends or patterns of species abundance, if any, are shown by communities of snakes. The communities we surveyed contained a reported range of species of 3 to 13; Shannon-Wiener functions (H) ranged from 0.592 to 2.151, Simpson's diversity indices (D) from 1.55 to 6.13, and equitability ratios (E) from 0.510 to 0.839 (Table 4). A plot of the Shannon-Wiener values against the logarithm of the number of species in each community (Fig. 9) shows that, with two exceptions, the communities fall roughly along a smooth dome-shaped curve which levels out to an upper asymptotic species number of 12-13.

At our study locality in Utah, a unique opportunity existed for calculation of community variables within a single snake community over a span of about 30 years. Woodbury (1951) earlier worked at den M (one of five major dens in a group of hibernacula called M complex) through 10 years (1940-49). Our sampling was done in the same area over a period of 4 years (1969-73). We previously documented changes in composition of the four common species (three colubrids plus *Crotalus*) during the 30-year interval at this and other dens (Parker and Brown 1973). The changes in relative abundance of these species based on proportions of the total snake fauna at each time (Fig. 10) indicate a major trend for an almost complete replacement of *Crotalus* (54% of total abundance) and *Masticophis* (37%), the two dominant species in the 1940's, by *Coluber* (65%) and *Pituophis* (14%) in the 1970's. Moderate proportions of *Masticophis* (15%) were present along with *Coluber* and *Pituophis* in our sampling period. *Pituophis* increased and *Masticophis* declined since Woodbury's (1951) study.

Table 4. Species abundance statistics for 10 North American snake communities (cf. Fig. 9). Communities are ranked in order of increasing number of species present. See text for meaning of equations for values calculated and Appendix for species, numbers of individuals, and methods of collection used by each investigator.

Locality and author	No. species (S_T)	Shannon- Wiener (H)	Simpson's Index (D)	Equitability (E)
Illinois (Selbert und Hagen 1947)	3	0.592	1.55	0.539
Iowa (Klimstra 1958)	5	1.132	2.50	0.704
Maryland (Dargan and Stickel 1949)	5	1.084	2.47	0.674
Utah (Woodbury 1951)	7	0.992	2.34	0.510
Utah (present study)	7	1.051	2.15	0.540
California (Flteh 1949)	9 ^a	1.180	2.38	0.568
Louisiana (Tinkle 1957)	10	1.472	3.00	0.639
Arizona (Pough 1966)	12	1.874	4.50	0.754
Arizona (Pough 1966)	12	1.658	3.36	0.667
Arizona (W.S. Parker, unpublished data)	13	2.151	6.13	0.839

^aNumber of individuals not given for one; calculated values pertain to eight species.

A total of eight snake species were tabulated at den M over this time, of which seven were recorded in each study. Among the four rare species, *Diadophis punctatus* and *Rhinocheilus lecontei* were recorded by both Woodbury

(1951) and by us. Woodbury caught two *Hypsiglena torquata* and we caught one *Lampropeltis triangulum* as species unique to each study.

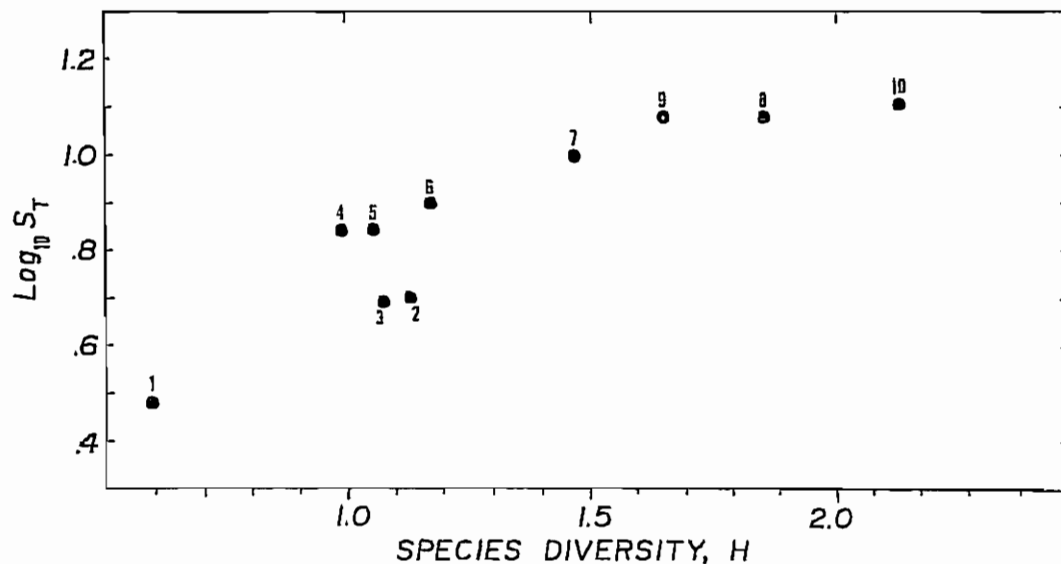


Fig. 9. Species abundance distributions in 10 North American snake communities. Shannon-Wiener diversity index (H) plotted as a function of the logarithm of the total number of species (S_T) in each community. Two communities (4 and 5) are from the same locality in Utah separated by a time span of about 30 years. Values for community 8 based on eight species (cf. Table 4 for values calculated for each community and Appendix for list of species).

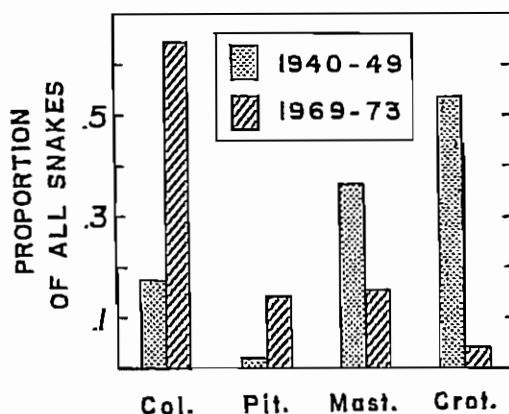


Fig. 10. Thirty-year changes in relative species abundance of a snake community at a single locality in a Great Basin cold desert shrub habitat in northern Utah. Stippled bars represent data from 1940-49 (community 4; Woodbury 1951), hatched bars data from 1969-73 (community 5; present study). Proportions of each of the four most common snakes (left to right: *Coluber constrictor*, *Pituophis melanoleucus*, *Masticophis taeniatus*, *Crotalus viridis*) are based on total individuals of all species captured at den M in each study. See Appendix for species and numbers of individuals recorded.

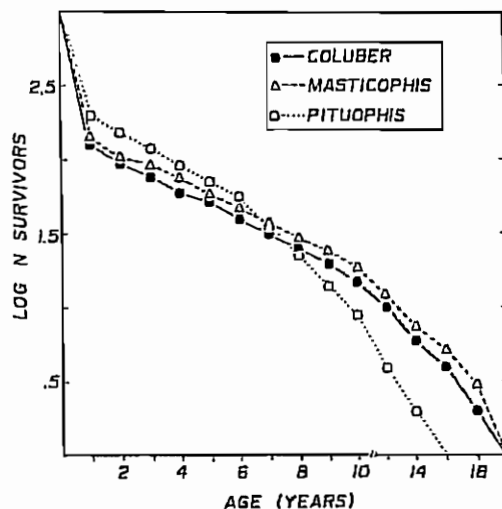


Fig. 11. Survivorship curves for females of three species of colubrid snakes in a Great Basin cold desert shrub habitat in northern Utah. Age-specific annual survival rates obtained empirically by mark-recapture studies in the field. Survivorship data pertain to 1970-72 (Parker and Brown 1980; Brown and Parker 1982).

Survivorship

We measured age-specific survival rates in 1970 and 1971 as an indicator of responses of the populations of *Coluber*, *Masticophis*, and *Pituophis* to environmental conditions. Details of the demographic aspects of our work, including age-specific growth rates, aging techniques, and fecundity rates are reported elsewhere (Parker and Brown 1980, Brown and Parker, 1982). Here we compare age-specific survivorship curves (Fig. 11). These essentially are similar in the three species, with only minor differences present in first-year (0-1) survival rates (*Coluber* 0.170, *Masticophis* 0.145, *Pituophis* 0.200) indicating generally high mortality among juveniles. Throughout adult life, *Pituophis* had somewhat lower annual survivorship (0.625) than did *Masticophis* (0.800) and *Coluber* (0.787). Some *Masticophis* and *Coluber* survive to a maximum of 20 years, and *Pituophis* to 16 years according to these schedules. Mortality is high in the first-year group, but once individuals attain an age of 1 year, annual mortality is relatively low in all three species.

Discussion

Food Niche

Various studies suggest that the role of food is a dimension of importance in resource partitioning in different communities of sympatric snakes. Carpenter (1952) indicated that differences in food habits of three species of eastern *Thamnophis* were an important factor in their coexistence. He stated that differences in the selection of size and types of prey decreased the competition for food among the three species. Similarly, Fleharty (1967) noted virtually non-overlapping food preferences among three other species of western *Thamnophis*. Schoener (1974) ranked food type first (over habitat and time of year) as the dimension in which Carpenter's *Thamnophis* were most clearly separated.

Food of snakes is one of the most readily studied aspects of their natural history (e.g., Lagler and Salyer 1945; Fox 1952; Hamilton and Pollack 1956; Brown 1958; Klimstra 1959; White and Kolb 1974) and considerable data

have accumulated on their predatory habits. Occupying high positions in the food chains of many communities has also allowed snakes to be sampled for concentrations of environmental pollutants (Fleet et al. 1972; Brisbin et al. 1974; Bauerle et al. 1975). Despite these facts, studies that have attempted to measure the use of trophic resources of more than two sympatric species of snakes are few. Recent approaches to this aspect of assemblages of sympatric snakes (Voris 1972; Mushinsky and Hebrard 1977; Shine 1977; Fitch, this volume; Reynolds and Scott, this volume) indicate that the trophic niche is indeed important to coexisting snakes.

Food clearly seems to represent an important dimension separating two of the three species pairs (*Coluber* × *Masticophis* and *Coluber* × *Pituophis*) in the Utah snake community we studied. Food also is important in resource partitioning among seven common species of snakes in Kansas (Henderson 1974; Fitch, this volume) and, apparently, in a community of seven species in Africa (Barbault 1974) and six species in Australia (Shine 1977).

Feeding responses and innate food preferences are unique aspects of behavioral ecology exhibited by snakes (Burghardt 1970a). Possibly, dietary shifts may occur in snakes from communities consisting of a number of potential interspecific competitors. This hypothesis was explored by Carr and Gregory (1978) who tested three species of neonate *Thamnophis* and compared their laboratory response profiles against the natural diets of each, but their results were limited. Still this effort might be pursued in conjunction with analyses of intraspecific geographic variation in the feeding habits of snakes both in the field and in the laboratory. The experimental approach, i.e., demonstration of innate geographic differences in populations within the same species but from different communities (Burghardt 1970b; Cove and Burghardt 1975), may yield insights into the complexities of predator-prey interactions in snake communities. Snakes may provide an excellent model vertebrate for testing hypotheses on the contrasting role of inheritance (e.g., Burghardt 1975) versus environment in shaping trophic-dynamic processes in natural communities. Food is very likely an important niche dimension separating snakes in nature. Still, its role is in need of further work.

Place Niche

The early work of Carpenter (1952) on habitat segregation of three sympatric species of *Thamnophis* in Michigan clearly demonstrates the role of this niche dimension in the ecological distribution of snakes. Schoener (1974) considered the place dimension secondary to that of food in separating Carpenter's *Thamnophis* and this interpretation appears to be correct because the major microhabitat categories ("grassy areas," "marsh grass and sedge," "water and water vegetation") were more difficult to define and quantify in the field than were food types. Also, there was considerable overlap in places occupied by these species (cf. Carpenter 1952). Fleharty (1967) used the categories "rocks," "vegetation," and "logs" to classify location preferences among three *Thamnophis* species, and he showed some species differences. The categories of their field recognition appear to us, however, to be inadequate to allow the place dimension to be compared with food.

One recent worker (Hart 1979) has categorized sympatric and allopatric microhabitats as location types of apparent importance to snakes. In allopatry, *Thamnophis sirtalis* in Manitoba, Canada, occurred near marshes and *T. radix* near ponds (Hart 1979). In sympatry, the importance of the habitat to niche discrimination between these species was reduced primarily as a result of a more limited thermal range for activity available to each species. Hart (1979) interpreted this as a behavioral reaction to the thermal limitation rather than as a reaction to the presence of another species.

Other workers have presented analyses of habitat partitioning in a community of closely related snakes (e.g., Pough 1966; Hebrard and Mushinsky 1976; Reynolds and Scott, this volume). Some studies have taken a much larger assemblage of snakes and have subdivided these into broad groups of adaptive zones (aquatic, terrestrial, arboreal, etc.), such as Henderson and Hoevers (1977) in Central America and Leston and Hughes (1968) and Barbault (1971) in Africa. The first two also classified the snake faunas in each tropical region according to activity times (nocturnal, diurnal) and major prey groups taken. Thus, at least two studies have approached snake communities from all three (spatial, temporal, and trophic) fundamental as-

pects of the niche. These analyses for snakes still provide only preliminary information, however, and data on snakes as a group continue to lag far behind similar approaches to quantify other reptilian communities, especially those of lizards (e.g., Pianka 1973, 1975).

Several related behavioral subdivisions of the place niche of snakes have been partly treated by a number of authors. These aspects seem not to have been emphasized in a parallel way by lizard ecologists, chiefly because they are biological attributes generally of more inconspicuous, secretive, or fossorial animals. They may be summarized briefly as follows: (1) thermal and moisture requirements in habitat selection, especially by small subterranean species (Warburg 1964; Clark 1967; Elick and Sealander 1972); (2) communal reproductive (mating and egg-laying) aggregations (Tinkle and Limer 1955; Brodie et al. 1969; Parker and Brown 1972; Aleksuk and Gregory 1974; Gregory 1975; Palmer and Braswell 1976; Henderson et al. 1980); (3) communal overwintering (hibernation) aggregations (Carpenter 1953; Parker and Brown 1973; Brown et al. 1974); (4) vernal dispersal from and autumnal return to some central place, usually a hibernation den (Hirth et al. 1969; Gregory and Stewart 1975; Brown and Parker 1976a); and (5) habitat conditioning and the role of olfaction in orientation (Noble and Clausen 1936; Noble 1937; Dundee and Miller 1968; Burghardt 1970a; Gehlbach et al. 1971; Porter and Czaplicki 1974; Ford 1975; Kubie and Halpern 1975).

The above attributes bear on the question, "Where does a snake find itself in space and how is that location affected by other members of its own population?" By tracking snakes carrying radio transmitters and recognizing categories of location or activity, we achieved a method for quantifying the spatial niche of snakes in the field. The telemetric tracking technique also has been used successfully to follow dispersal and home range movements (Brown and Parker 1976a; Fitch and Shirer 1971; Parker and Brown 1980). It has high potential for studying other species of snakes in other localities. Its possible adoption by many workers may be limited because it is time-consuming and physically demanding to track more than a few snakes in the field, especially if they are large or are in a migratory phase of activity.

Our computation of niche breadths using the

four categories of microhabitat-activity show definite seasonal shifts in all three species. *Coluber*, for example, is a widespread North American snake usually thought of as a diurnal ground-dwelling species. In northern Utah, however, *Coluber* was seldom found above ground during summer. Thus one cannot quantify the place niche of desert snakes in a biologically meaningful way unless the season is specified. A number of authors have examined long-term temporal aspects of snake ecology (Oliver 1947; Seibert and Hagen 1947; Klimstra 1958; Bider 1968; Barbault 1970, 1971; Nelson and Gibbons 1972; Henderson and Hoevers 1977). Patterns of seasonal abundance vary with the locality (especially due to temperate vs. tropical seasonal turnovers in temperature and rainfall) and the component species making up the community. In addition to identifying patterns of partitioning the temporal dimension over long (circannual) time, the question arises as to whether this dimension has any merit at all over short (circadian) time in partitioning this resource in snake communities. Daily time of activity (times of peak abundance since sunrise or sunset) are effective measures for quantifying the time dimension of some lizard niches (Pianka 1973; Creusere and Whitford, this volume), but little is known about snakes. Bider (1968) reported that activity of the diurnal *Thamnophis sirtalis* was bimodal on clear days but unimodal on cloudy days. Hart (1979) noted a shift in the daily activity patterns of *Thamnophis sirtalis* and *T. radix* in sympatry from the patterns present in allopatry. The nocturnal *Trimeresurus flavoviridis* underwent peak unimodal activity between 0100 and 0400 h (Tanaka et al. 1967). Parker and Brown (1980) showed that activity of *Pituophis melanoleucus* was bimodal (morning and afternoon peaks) in summer and unimodal (late afternoon peak) in spring and autumn.

Place Niche Studied by Different Methods

In 1966, A. C. King studied dispersal of snakes from the same den (den M) studied by us and the results of this work (King 1968) were later published (Hirth et al. 1969). The technique used by these workers was to tag snakes with a subdermal radioactive wire and to relocate them during the summer using a scintillo-

Table 5. Place niche data recorded in 1966 and 1971-72 for two species of colubrid snakes in a Great Basin cold desert shrub habitat. Data are proportions of radioactivity-tagged snakes located in summer 1966 (Hirth et al. 1969) and telemetry-monitored snakes located in summers 1971-72 (Brown 1973; Parker and Brown 1980).

Species	On surface		Underground		In shrubs	
	1966	1971-72	1966	1971-72	1966	1971-72
<i>Coluber constrictor</i>	0.44	0.35	0.41	0.65	0.15	0
<i>Masticophis lateralis</i>	0.49	0.62	0.10	0.38	0.41	0

meter. Results of Hirth et al. (1969) on home range biology of *Coluber* were at variance with our results (Brown and Parker 1976a). Hirth et al. (1969) presented data on proportions of *Coluber*, *Masticophis*, and *Crotalus* captured in three strata: underground, on the surface, and in shrubs (Table 5). Differences in proportional utilization for snakes found in surface locations were 0.09 for *Coluber* (higher in 1966) and 0.13 for *Masticophis* (lower in 1966). The most striking contrasts appear in proportions located underground: differences were 0.24 for *Coluber* (lower in 1966) and 0.28 for *Masticophis* (lower in 1966). Hirth et al. (1969) recorded proportions of 0.15 and 0.41 for *Coluber* and *Masticophis* in shrubs, respectively. In contrast, we found no snakes in shrubs.

Did a shift occur in the place niches of these two species during the 5 years intervening between the two studies, or could some other factor(s) be responsible for the different results? We believe that the variance was due to differences in techniques. The study of Hirth et al. (1969) apparently had three major biases. First, the investigators' peak times of searching activity (early morning) coincided with the period during which the snakes' surface activities (basking, moving) were also maximal. Second, these workers could achieve only a 3-m range for detecting a snake located 30 cm underground. Thus, they probably underestimated the frequency of snakes in this location. Third, two workers searched for 64 *Coluber* and 81 *Masticophis* in a 1,000-ha area, and a tagged snake had to be approached to within 9 m for location on the surface; detection thus depended on constant observation of the instrument rather than watching for snakes, so a *Coluber* or *Masticophis* might easily have been flushed into a shrub and then located there. A serious overestimate of snakes located off the ground likely occurred.

Among the large sample of locations (1,756) we recorded, none was an "in shrub" record. We did not observe snakes climbing in shrubs except on a few occasions when they were enclosed inside a fenced den before capture. Snakes we studied were carrying heavier and bulkier objects (constituting 5-10% of a snake's body weight) and this may have behaviorally precluded them from climbing. The snakes we tracked by telemetry, however, appeared to behave as did untagged individuals: their overall activity seemed normal and included migratory movements and home range establishment, thermoregulation and basking, and mating and egg-laying activities (Parker and Brown 1972; Brown 1973; Brown and Parker 1976a). Biases in the technique of Hirth et al. (1969), and perhaps to some extent in our own technique, make the comparative findings on temporal shifts in place niche partitioning difficult to reconcile.

Food and Place Niche Complementarity

As mentioned above, Carpenter (1952) and Schoener (1974) indicated that the food dimension assumes a more important role in separating *Thamnophis* spp. than the place dimension. Other work on snakes seems also to support this notion, particularly as shown by the preponderance of analyses of food habits in the literature as contrasted with a paucity of information on microhabitat segregation within a common space shared by three or more sympatric species. Stomach contents are considerably easier to obtain than spatial use data. In a later analysis, Schoener (1977) ranked macrohabitat (vegetation type) first in separating North American crotalids based on two studies in Arizona. Shine (1977) found only one instance of sympatry between two of six species of elapids in eastern Australia and attributed the low spatial overlap

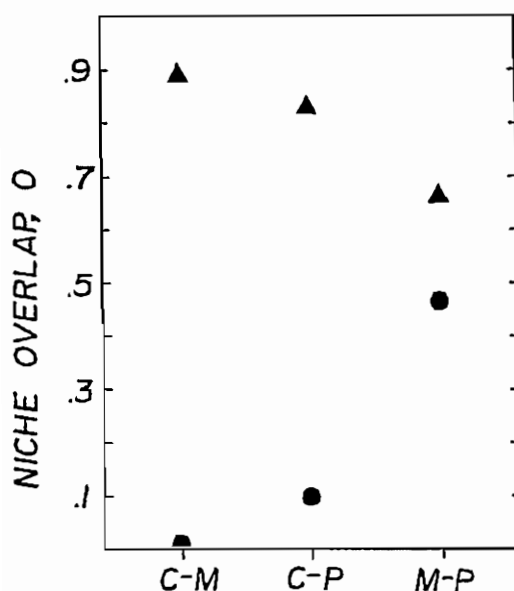


Fig. 12. Niche overlap values along two niche dimensions for each of three species pairs of colubrid snakes (C = *Coluber constrictor*, M = *Masticophis lateralis*, P = *Pituophis melanoleucus*) in a Great Basin cold desert shrub habitat. Circles show food niche; triangles place niche overlap. Overlap values for place niche are averages of separate values for each of three seasons (cf. Table 2).

to a low diversity of major prey groups with resultant segregation accounted for primarily by dietary differences.

Our results on both niche dimensions (as overlap values for all species pairs) are shown in Fig. 12. First, all three species pairs are more strongly separated along the food dimension (low overlap values) than along the place dimension (high overlap values). Second, high overlap in one dimension corresponds with low overlap in the other. This phenomenon, called "complementarity" by Schoener (1974), was described as follows: "... similarity of species along one dimension should imply dissimilarity along another, if resources are to be sufficiently distinct. Such complementarities illustrate especially well the trouble individuals and their genes seem to take to avoid other species' niches..." Schoener also documented that the most common instance of complementarity occurs in the food-habitat combination where there is a frequent tendency for species that eat different foods to overlap strongly in habitat.

Our data corroborate the occurrence of this in a snake community. The trend is strongest in *Coluber* × *Masticophis* and *Coluber* × *Pituophis* comparisons, and is present but less marked for *Masticophis* × *Pituophis*. For all three paired species comparisons, average overall overlap for place is 0.793 and for food 0.194. This is quantitative evidence for the importance of the food resource over the spatial resource and documents the complementary roles of the trophic and spatial niches in the coexistence of snakes in this particular community.

Annual Body Weight Changes

Several questions arise about the possible factors responsible for the differential interspecific responses of the snakes in years of varying amounts and proportions of summer rainfall. First, why did *Coluber* and *Pituophis* respond in opposite ways in the 2 years of markedly different rainfall patterns (1971 and 1972)? Second, why did *Pituophis* show such different responses in 2 years of virtually identical rainfall patterns (1970 and 1971)? Finally, what factors may have been involved in the very distinct species × year interactions of *Coluber* and *Masticophis*? All queries allude to a possible link between rainfall patterns and the trophic niche of each species and, perhaps, to a direct role of wetness in the habitat and physiological condition of the snakes by affecting their ability to obtain sufficient food or water, or both.

Considering first the possible role of direct effects of water deprivation and integumentary dehydration, *Masticophis* may be a more resistant species (may have lower rates of water loss through the skin) than the other two species. Although no data are available to confirm this hypothesis, Gans et al. (1968) found that desert-adapted species were much more tolerant of desiccation than were mesic-adapted forms (they reported a water loss rate much lower in the terrestrial *Pituophis melanoleucus* than in the aquatic *Nerodia sipedon*). *Masticophis* at our study locality generally occupy an epigeal (surface) niche in summer about as often as they do a subterranean one, probably in conjunction with their extensive foraging for lizard prey. This species may be less prone to water loss than either *Coluber* or *Pituophis*. *Pituophis* occupy a subterranean niche in summer and may require

higher ambient relative humidities associated with their underground retreats. If this is true, in order to have a deleterious effect on the snakes, extremely dry summers (like that of 1972) would have to result in desiccation of the soil in burrow systems to depths occupied by these snakes (usually less than 50 cm).

Rainfall effects on *Coluber* seem to be more clear-cut than for either of the other species. *Coluber* declined in weight only in the dry year of 1972. This species seems to be more directly dependent on rainfall, which we believe may affect insect populations, the chief prey of *Coluber*. We previously proposed (Parker and Brown 1973) that increasing populations of *Coluber* through the late 1960's and early 1970's may have been influenced by consistent annual rainfall at our study area since 1966 (cf. Fig. 8) and adequate orthopteran insect populations. Grasshopper populations were not censused during this study but they appeared to be less abundant in 1972 than in the 2 earlier years. In 1969 and 1970 these insects were very numerous around the dens. Greater proportions of *Coluber* stomachs contained insect prey (chiefly grasshoppers) in 1969 and 1970 than in 1971 and 1972 (Table 6).

The weight-gain responses of *Pituophis* are an enigma. Seemingly, some small mammals that this species takes were not adversely affected during the dry year (1972) and, if so, *Pituophis* food supplies may have remained ample. Certain seed-eating rodents (*Perognathus*) may be more resistant to unpredictable desert dry spells than the green plant-eating *Microtus* (both species constitute the main prey of *Pituophis*). If so, perhaps *Pituophis* is able to "switch" to the more abundant prey if the prey species are out of synchrony. Whitford (1976) reported asynchronous fluctuations in rodent populations in New Mexico between wet and dry years. Resident heteromyid rodents (*Dipodomys*, *Perognathus*) were reduced in density during a drought and recovered following a period of rainfall after a 10-12 month lag. More mesic-adapted cricetids (*Peromyscus*) responded by immigrating into previously unoccupied habitats and increasing more rapidly than resident species following a wet year (Whitford 1976). More perplexing, however, is the decline in the proportion of *Pituophis* that gained weight in 1971 from 1970 even though both years were nearly identical in total and summer rainfall patterns. Winter and

Table 6. Numbers and proportions of 340 *Coluber constrictor* that contained palpable food items in four successive autumn (September–October) sampling periods at den M in Utah.

Year	No. examined	No. containing food	Proportion containing food
1969	46	23	0.500
1970	23	15	0.652
1971	143	26	0.182
1972	128	11	0.086

spring rainfall patterns (October–April) also were similar (18.4 cm in 1969–70 compared with 22.6 cm in 1970–71). Lacking census data for small mammals, we can only offer the conjecture that 1970 may have been a favorable year for them (a peak in their population cycles), whereas 1971 may have been a poor year (low populations).

In general, the productivity of desert ecosystems is closely dependent on rainfall. Variation in rainfall should differentially influence several taxonomic components of the animal community. This apparently happened with strikingly different effects on the snakes during our study (cf. Parker and Brown 1980; Brown and Parker 1982). Sampling these animals resulted in variable annual population changes, shifting species abundance relationships, and unstable age structures through time.

Species Diversity and Competition

A number of workers have described species diversity and abundance patterns of snakes (Dunn 1949; Dunn and Allendoerfer 1949; Turner 1961; Lloyd et al. 1988; Chanter and Owen 1971; Kiester 1971; Janzen 1976; Rogers 1976). We examined the species abundances of several selected communities of snakes (cf. Fig. 9). These tentatively appear to fit an expected curve for MacArthur's broken-stick distribution as shown by May (1975b; his Fig. 5) but the broken-stick and lognormal distributions are indistinguishable for small S_T values. The assemblages of snakes we have chosen from the literature seem to be "... communities comprising a limited number of taxonomically similar species, in competitive contact with each other in a relatively homogeneous habitat . . ."

(May 1975b:94). Also, because several workers have been able to classify various assemblages of snakes into feeding guilds (Arnold 1972; Henderson and Hoevers 1977), it would appear plausible that food is the preeminent resource of consequence for snakes. Whether competitive interactions govern their utilization of food resources, however, has not been conclusively demonstrated. Wiens (1977) cautioned against attributing ecological differences between species to competitive exclusion based solely on descriptions of interspecific differences and when experimental demonstrations of competition are lacking. Wiens' critiques are further strengthened in those communities subjected to irregular climatic fluctuations (e.g., extremes in annual rainfall), where continuous competitive interactions seem not to occur. In such variable environments, competition may not be influential in affecting control over species composition (Wiens 1977). Hart (1979) reported a dietary difference between two species of garter snakes (*Thamnophis*) in sympatry but he believed that this reflected a different prey availability in the region of sympatry rather than niche displacement as a result of species interaction. Shine's (1977) demonstration of differences in body size of two species of snakes and in the mean size of their prey in an area of sympatry is consistent, however, with the interpretation that competition between the two snakes produced the observed body size and prey size divergence. In areas of allopatry such divergence did not occur (Shine 1977).

Species Composition at Utah Dens

At our desert study site, we examined the changing species composition and the factors that have influenced this community. The major observations and trends follow.

- *Crotalus* and *Masticophis* declined (nearly to extinction for the former), not because of any large-scale environmental changes, but because of killing by humans (unfortunately, rattlesnakes and whipsnakes have the behavior of remaining visible on the surface in proximity to dens for a time after spring emergence, making them vulnerable to human predators).

- *Coluber* and *Pituophis*, although also remaining largely on the surface in spring, are much more cryptic and retiring, tending not to

be conspicuous at all, even to experienced human snake collectors.

- The decline of *Crotalus*, a mammal-eater, may have sufficiently relaxed competition with *Pituophis* for this food resource so that by the late 1960's-early 1970's the *Pituophis* population responded and increased most notably sometime before and during our study.

- The dramatic rise in population sizes of *Coluber* and *Pituophis* between 1950 and 1972 may closely reflect recent changes in the entire community through sustained adequate precipitation levels in most of the years immediately preceding and during our study. There may have been a corresponding stimulation of plant productivity and increasing populations of orthopteran insects and small mammals, the principal prey of these species.

We commented on the last two points previously (Parker and Brown 1973). The observed rapid increase in the *Coluber* population was not sustained through 1972. In that year, which we considered an unfavorable one for *Coluber*, the racer population declined (Brown and Parker 1982).

The snake community in northern Utah has retained a remarkably stable species abundance pattern from Woodbury's time to ours. Despite years of man-caused perturbations to the snake fauna, there is a strong similarity in species diversity and equitability measurements between the two studies ($S_T = 7$; $D = 2.3, 2.2$; $E = 0.51, 0.54$; cf. Table 4). Human predation almost eliminated rattlesnakes and steadily reduced whipsnakes over the years, but was probably minimal in its effects on racers and gopher snakes, which have increased in recent years. The factors we have been able to identify as having produced these shifts in species composition have not created a great long-term change in the several species diversity indices for the community as a whole. They have, rather, resulted in what seem to be fairly orderly replacements of species according to abundances that might be expected if the makeup of this snake community is governed chiefly along a gradient of food resources and secondarily by microhabitat selection. An extirpated species (*Crotalus*) was seemingly replaced by its potential food competitor (*Pituophis*). A reduced species (*Masticophis*) and an increasing species (*Coluber*) may have had little direct influence on each

other or on *Crotalus* and *Pituophis*. All three colubrids were differentially affected by climatic conditions. *Coluber*, and perhaps *Pituophis*, apparently were most strongly influenced by rainfall.

The Fate of the Dens

We have stated that rattlesnakes (*Crotalus*) and whipsnakes (*Masticophis*) are easy targets for certain unprincipled humans to kill. More than all other factors, man has been the main cause for the disappearance of these two species from the den M population. An additional factor is fire. On 17 June 1974 an extensive range fire completely razed a large area which included all of the dens. This fire, by destroying the habitat of an area that more than encompasses the dispersal range of the snakes (a several kilometer radius around the dens), virtually assures the extinction of *Crotalus* (cf. Parker and Brown 1974b). Even if many snakes (mostly *Coluber* and *Pituophis*) had managed to survive the blaze by being underground as it swept through, their chances of survival for the remaining 2.5 months of summer 1974 would have been greatly reduced. Beyond this, by autumn 1974 windblown sand had begun to fill crevices between the rocks of the dens (A. C. King, personal communication). W. S. Brown revisited the dens briefly on 6 August 1976. Except for small parts of the largest rocks of dens M and 2 which were still protruding, all other dens of M complex were almost totally buried by sand and were hardly recognizable from the surrounding terrain. The communal hibernacula appeared to be permanently altered and probably now are destroyed for any future occupancy by snakes.

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Appendix

Species and numbers of individuals of snakes from community samples analyzed in text (cf. Table 4, Fig. 9).

1. Illinois (Seibert and Hagen 1947—hand captures): *Thamnophis radix* 298, *Opheodrys vernalis* 78, *Thamnophis sirtalis* 7.
2. Iowa (Klimstra 1958—observations, hand captures): *Coluber constrictor* 475, *Elaphe obsoleta* 233, *Heterodon platyrhinos* 78, *Natrix sipedon* 50, *Thamnophis sirtalis* 14.
3. Maryland (Dargan and Stickel 1949—wire traps): *Heterodon platyrhinos* 36, *Coluber constrictor* 22, *Elaphe obsoleta* 6, *Thamnophis sirtalis* 2, *Lampropeltis getulus* 1.
4. Utah (Woodbury 1951—hand captures, den fence): *Crotalus viridis* 930, *Masticophis taeniatus* 632, *Coluber constrictor* 127, *Pituophis melanoleucus* 36, *Hypsiglena torquata* 2, *Diadophis punctatus* 2, *Rhinocheilus lecontei* 1.
5. Utah (Brown and Parker 1969-1973—den M fence; all dens in parentheses): *Coluber constrictor* 332 (1,045), *Masticophis taeniatus* 79 (223), *Pituophis melanoleucus* 74 (144), *Crotalus viridis* 21 (22), *Diadophis punctatus* 5 (7), *Lampropeltis triangulum* 1 (3), *Rhinocheilus lecontei* 1 (1).
6. California (Fitch 1949—hand captures): *Crotalus viridis* 679, *Pituophis melanoleucus* 256, *Thamnophis elegans* 97, *Lampropeltis getulus* 43, *Masticophis lateralis* 26, *Thamnophis sirtalis* 24, *Rhinocheilus lecontei* 4, *Diadophis punctatus* 2, *Hypsiglena torquata* (number of individuals not reported).
7. Louisiana (Tinkle 1957—hand captures): *Thamnophis proximus* 221, *Agkistrodon piscivorus* 73, *Natrix sipedon* 60, *Natrix cyclopion* 18, *Lampropeltis getulus* 18, *Coluber constrictor* 16, *Farancia abacura* 5, *Elaphe obsoleta* 4, *Opheodrys aestivus* 3, *Natrix rigida* 2.
8. Arizona, San Simon and San Bernardino Valleys (Pough 1966—nocturnal road captures): *Crotalus scutulatus* 67, *Pituophis melanoleucus* 28, *Crotalus atrox* 23, Ari-

- zona elegans* 16, *Lampropeltis getulus* 8, *Rhinocheilus lecontei* 8, *Salvadora hexalepis* 6, *Thamnophis marcianus* 3, *Trimorphodon lambda* 3, *Hypsiglena torquata* 3, *Heterodon nasicus* 2, *Ficimia cana* 1.
9. Arizona, Portal Road (Pough 1966—nocturnal road captures): *Crotalus scutulatus* 58, *Crotalus atrox* 19, *Pituophis melanoleucus* 11, *Arizona elegans* 9, *Crotalus molossus* 7, *Rhinocheilus lecontei* 4, *Salvadora hexalepis* 2, *Trimorphodon lambda* 2, *Hysiglena torquata* 1, *Elaphe triapls* 1, *Thamnophis cyrtopsis* 1, *Heterodon nasicus* 1.
10. Arizona, Phoenix South Mountain Park (Parker, unpublished data, 1964-66—sub-surface can traps, D.O.R.): *Leptotyphlops humilis* 20, *Masticophis flagellum* 7, *Salvadora hexalepis* 6, *Hypsiglena torquata* 5, *Pituophis melanoleucus* 5, *Chilomeniscus cinctus* 5, *Crotalus mitchelli* 4, *Crotalus atrox* 2, *Crotalus cerastes* 2, *Crotalus scutulatus* 1, *Masticophis bilineatus* 1, *Phyllorhynchus decurtatus* 1, *Chionactis occipitalis* 1.

Resources of a Snake Community in Prairie-Woodland Habitat of Northeastern Kansas

by

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Abstract

In a 30-year study of a snake community at the University of Kansas Natural History Reservation, 22,093 snakes of 12 species were captured 26,346 times, and 2,360 food items were identified. The smallest species, *Diadophis punctatus*, was by far the most abundant, and its biomass was more than twice those of all other species combined. Like the two other small and abundant species, it was almost exclusively an earthworm-eater, and earthworms constituted 70% of the food biomass of all species combined. Every species overlapped several others in the composition of its food, but no two were just alike. Besides earthworms, the most abundant local species of small vertebrates made up most of the food, especially *Microtus ochrogaster*, *Sylvilagus floridanus*, *Peromyscus leucopus*, and *Rana blairi*. Each of these was important in the food of several species of snakes. Intraspecific partitioning of prey species was much more prominent in some snakes than in others. In *Agkistrodon contortrix* the first-year young and adults used different kinds of prey with little or no overlapping, and less complete partitioning between young and adults was evident in all but the earthworm-eaters. Also, some partitioning of prey species was evident between male and female, at least in *Agkistrodon contortrix*, *Coluber constrictor*, and *Thamnophis sirtalis*, in each of which one sex grows to be markedly larger than the other.

A recent trend in the study of ecology has been the detailed analysis of one taxonomic group within a biotic community, such as mammals (Rosenzweig and Sterner 1970; Brown and Lieberman 1973; Heithaus et al. 1975); birds (Cody 1974); lizards (Pianka 1973); frogs (Crump 1974); salamanders (Fraser 1976); or fish (Keast 1965) to determine how their component species coexist. Snakes are relatively difficult subjects for such investigations because of their secretive habits; consequently, little progress has been made in studying them. Unusual opportunity to gain insight into the functioning of a snake community has been afforded me as resident naturalist over 30 consecutive seasons on the University of Kansas Natural History Reservation, where 16 species of snakes are known to occur. During the 30-year interval, the entire biotic community, including its snake compo-

nent, was progressively altered by ecological succession. Also, the amount of field effort changed, as did field procedures and techniques. Nevertheless, the 30 years of records provide some basis for comparing populations of all the species, in local distribution, composition, density, stability, and impact on the community as a whole. The present account is concerned primarily with food habits and the partitioning of food resources among the 12 most common species. Henderson (1974) has already presented a brief preliminary account of resource partitioning among the snake species of the Reservation, as indicated by autecological accounts of several of them (Fitch 1960, 1963a, 1963b, 1965, 1975; Clark 1970; Fitch and Fleet 1970). Other types of snake communities are discussed by Brown and Parker, Lillywhite, and Reynolds and Scott in the present volume.

Methods and Materials

Snakes were captured by hand, in wire funnel traps, or beneath sheltering objects—strips of sheet metal, boards and flat rocks—strategically placed to attract them. Routine processing included sexing, measuring, weighing, and palpating up undigested food items from the stomach. Fecal material voided by those in traps, or those handled, was saved for study beneath a dissecting microscope for identification of prey items.

Field work began on the newly created 239-ha University of Kansas Natural History Reservation in the northeastern corner of Douglas County in July 1948, and continued through October 1977. Although much of this field effort was concentrated on a series of autecological studies of the commonest species, every available snake, regardless of species, was captured, examined, and processed (Table 1). Individual marking of *Diadophis punctatus* and *Carphophis vermis* was discontinued in 1969 but marking of the remaining species continued to the present (1977). Data published in a series of papers (Fitch 1960, 1963a, 1963b, 1965, 1975; Clark 1970; Fitch and Fleet 1970) were freely used in combination with records more recently accumulated as a basis for the present report.

Results

Habitat

The University of Kansas Natural History Reservation comprising the study area was a changing mosaic of diverse habitats during the years spanned by the study. Plant communities were mixtures of eastern deciduous forest species including climax oaks and hickories, tallgrass prairie species, and weedy species characteristic of disturbed, seral communities. At the outset about half the area was second-growth woodland dominated by large American elms (*Ulmus americana*), and the remainder was open land that had been used for grazing or for growing corn and other cultivated crops. During the 30-year interval, shrub and tree species invaded the open areas, with ever-expanding thickets, first originating along edges and gullies, and later from secondary foci in the fields.

The woodland areas were far more stable than the areas that were originally open fields. However, changes occurred in the density and composition of the forest: (1) most large elms died from phloem necrosis, breaking the continuity of the foliage canopy and causing a thickening of the undergrowth; (2) parts of the wood-

Table 1. Twelve species of snakes of the University of Kansas Natural History Reservation arranged according to total number of captures over a 30-year period, with total numbers of individuals captured and body weights.

Species	Total number of captures	Total individuals	Adult weights		Mean and range of weights of hatchlings or neonates	
			Mean (g)	Maximum (g)	(g)	
<i>Diadophis punctatus</i>	16,509	14,759	4.0	15.2	0.8	(0.6–1.6 in 43)
<i>Agkistrodon contortrix</i>	3,451	2,681	108.0	400.0	11.4	(7.6–17.0 in 63)
<i>Coluber constrictor</i>	2,376	1,414	126.0	538.0	4.2	(2.4–5.8 in 76)
<i>Thamnophis sirtalis</i>	1,938	1,569	68.0	410.0	1.9	(0.7–2.3 in 149)
<i>Elaphe obsoleta</i>	695	502	253.0	1,029.0	11.7	(7.5–1.7 in 54)
<i>Carphophis vermis</i>	276	255	6.4	14.5	1.2	
<i>Nerodia sipedon</i>	271	206	207.0	480.0	5.0	(3.6–6.8 in 57)
<i>Lampropeltis calligaster</i>	207	166	164.0	405.0	7.5	(6.0–8.0 in 6)
<i>Pituophis melanoleucus</i>	194	181	613.0	1,475.0	25.0	(12.0–34.1 in 29)
<i>Storeria dekayi</i>	186	183	4.5	12.1	0.3	(0.2–0.5 in 73)
<i>Lampropeltis triangulum</i>	134	106	50.0	105.0	2.8	(2.5–3.0 in 5)
<i>Crotalus horridus</i>	109	91	520.0	2,366.0	19.0	(23.0–46.0 in 19)
Total	26,346	22,093				

land that had been grazed before 1948 were relatively open at first, but dense undergrowth developed within a few years after livestock were removed; and (3) the general trend toward a forest climax proceeded, with trees growing larger, natural thinning taking place, and underbrush becoming sparser as the maturing trees developed a denser and more continuous leaf canopy.

Because of the interdigitating and overlapping of habitats, any of the 12 snake species studied might be found anywhere on the area. Seasonal shifts and dispersal of individuals resulted in synoptic occurrences of different species that ordinarily are separated. Each species is somewhat different from all others in its preference and range of habitats.

Agkistrodon contortrix.—Open, rocky woodland, woodland edge, and meadows with clumps of brush adjacent to woodland. Adult males wander farthest from the forest; adult females, especially nonbreeders, also move into meadows; but first-year young remain in the forest. The whole population returns to wooded hilltop rock outcrops of southern exposure to find hibernacula.

Carphophis vermis.—Chiefly in edge of woodland, especially where undergrowth is sparse and soil is loose and damp; flat rocks are used for shelter.

Coluber constrictor.—High grass and mixtures of grass and weedy vegetation or brush. In autumn most of the snakes move into woodland in search of hibernacula in rocky outcrops.

Crotalus horridus.—Deciduous forest, especially of open type, with dry, rocky areas and rugged terrain.

Diadophis punctatus.—Both forest and prairie, but especially along woodland-grassland border in situations providing abundant surface cover and sunshine. Highest densities are observed in open type of woodland on rock-strewn south-facing slope.

Elaphe obsoleta.—Woodland, especially that of open type with dry rocky areas and rugged terrain, but also in adjacent meadow and brushland; they have some affinity for edificarian situations.

Lampropeltis calligaster.—Grassland, including tallgrass prairie, grazed pasture, and meadow with brush clumps.

Lampropeltis triangulum.—Woodland glades and woodland edge where sunshine and shade

are available and ground cover, such as flat rocks, is abundant.

Nerodia sipedon.—Ponds and streams, occasionally wandering into adjacent woodland or meadow. In autumn they abandon aquatic habitats to traverse woodland areas seeking hilltop rock-fissure hibernacula.

Pituophis melanoleucus.—Tallgrass prairie and brushy meadow but more numerous on cultivated land or grazed pasture. Those caught on the Reservation were mostly stragglers or transients passing between summer ranges and hilltop rock-fissure hibernacula.

Storeria dekayi.—Woodland edge and brushy meadow, often in damp situations.

Thamnophis sirtalis.—Brushy meadow and woodland edge, with strong affinity for water in ponds, streams, marshes, or temporary puddles.

Population Density

All species included in this study are on fixed annual schedules that entail breeding after spring emergence, embryonic development extending through much of the growing season, and an annual cohort of hatchlings or neonates appearing in late summer or early autumn. Hence there is an annual cycle in numbers, from a maximum in autumn to a minimum just before the next cohort of young is added.

Other population changes are controlled by ecological succession. At the beginning of my field study, the Natural History Reservation had only recently been placed under protection as a natural area. It had been subjected to various uses, including cultivation, grazing of large blocks, and tree-cutting on wooded slopes. After cessation of these activities, secondary succession was extremely rapid at first, becoming much slower in the later years of field work.

Techniques for accurately censusing snake populations have not been established. Because of the generally secretive habits of snakes, direct counts cannot be made except under unusual circumstances. Attempts to census by capture-recapture ratios have usually been unsatisfactory, because the theoretical assumptions necessary cannot be met. Table 2 presents selected figures for population densities of five common species, based on capture-recapture data for the years when sampling by livetrapping was most intensive. In each instance, the samples used ex-

Table 2. Population densities of six species of common snakes as revealed by capture-recapture ratios of marked individuals on the University of Kansas Natural History Reservation.

Species	Mean number and range per ha	Number of censuses	Size of sampled area (ha)	Years of sampling	Source
<i>Agkistrodon contortrix</i>	7.4 (6.3-8.5)	2	46	1958-59	Fitch 1960
<i>Coluber constrictor</i>	4.7 (0.9-14.6)	37	16 and 55.5	1955-61	Fitch 1963a
<i>Diadophis punctatus</i>	1,266 (719-1,808)	7	3.8 and 5.8	1966-67; 1969-70	Fitch 1975
<i>Elaphe obsoleta</i>	0.9	1	101	1958	Fitch 1963b
<i>Thamnophis sirtalis</i>	3.7 (2.0-7.3)	6	71, 137, 151	1958-63	Fitch 1965

cluded first-year young, and the data were limited to areas of favorable habitat where sampling by trapping was considered to be most effective. The traps were not set in any geometrical pattern, but were positioned to take advantage of natural features, such as field edges, gullies, and rock outcrops, and to use available shade. Trapping for the larger species was most intensive from 1957 through 1963, and figures obtained represent population levels within that period.

The extremely high population figure indicated for *Diadophis punctatus* is more than 170 times as abundant as the next commonest species (Table 2). The suggestion that 1,266 *Diadophis* per hectare be accepted as a representative density may elicit skepticism, but supporting evidence has been assembled in an earlier report (Fitch 1975). The samples seemed adequately large, the study area was enclosed by less favorable habitats or partial barriers preventing large-scale interchange with nonresident populations, and extensive trailing of individuals equipped with radioactive tantalum tags showed that they remained on the study area for long periods (R. L. Lattis, personal communication). Large daily samples (as many as 279 snakes) always contained some that were marked, but these never made up more than a small percentage of the catch. It was evident that the many hundreds marked each season constituted only a small part of the pool of resident snakes.

Changes in population levels are normal responses to climatic trends and ecological succession. However, intensive resampling in 1977 showed that essentially the same group of species was present as in 1948, and relative abundances had not drastically changed in most instances. One exception was that of *Tantilla gracilis*. It was confined to two small areas of rocky, xeric

habitat in 1950, and not found after 1955; seemingly it was eliminated by successional habitat changes. Records of *Crotalus horridus* dwindled from 53 in the first decade of field work to 39 in the second decade and only 1 in the third. Succession in the forest, which closed the canopy and enveloped clearings by trees and brush, deteriorated the rattlesnake's habitat. Also, a rapidly growing human population in the general neighborhood and escalated traffic on a county road through the area and along its boundary, contributed to the great reduction in number of rattlesnakes, which, according to the testimony of long-time residents, were abundant in the early 1900's. *Lampropeltis getulus*, *Elaphe guttata*, and *Virginia valeriae* have been recorded only a few times and, with *T. gracilis*, are omitted from this discussion.

For seven species (*Carphophis vermis*, *Crotalus horridus*, *Lampropeltis calligaster*, *L. triangulum*, *Nerodia sipedon*, *Pituophis melanoleucus*, and *Storeria dekayi*) records were so meager and sporadic that they were inadequate for capture-recapture censuses by Petersen indices. A population estimate for each was obtained by comparing the numbers captured over a period of months or years with those of a commoner species of somewhat similar habits and local distribution (Table 3). It may be assumed that the species compared are, in every instance, somewhat different in their ecology and "catchability"; hence the population estimates indicate orders of magnitude, but cannot be considered highly accurate.

Carphophis vermis, having an estimated density of 23/ha, is much more abundant than any of the other six species (Table 3). The figure is based on the ratio of 26 *Carphophis* to 1,437 *Diadophis* trapped over the 3-year period (1965-67), on the

same area where *Diadophis* was censused by Petersen Index at 1,266/ha. In 1966 and 1967 on a 0.47-ha study area of rocky wooded pastureland on a farm near the northwest corner of the Reservation, Clark (1970) censused *C. vermis* on the basis of capture:recapture ratios. His estimate was 480 snakes per ha in 1966, and 292/ha in 1967 (a "bad" year when the earthworm prey was relatively scarce and unavailable because of drought). In similar habitat of rocky, open woodland on a south slope of the Reservation in 1957, a ratio of 40 *Carphophis* to 188 *Diadophis* was obtained; that ratio would indicate a density of 269 *Carphophis* per ha if the *Diadophis* density was the same there as on the part of the Reservation where it was censused by Petersen Index. This assumption seemed plausible. Although the figures from Clark's area and the 1957 sample on the Reservation indicate that in optimum habitat *C. vermis* may attain densities exceeding 200/ha, these figures are much too high to represent extensive areas. Support for the figure of about 23/ha is found in the *Carphophis* to *Diadophis* ratio of 255 to 14,759 in the 30-year totals, indicating a density of 22 *Carphophis* per ha.

Kinds of Prey and Frequencies of Occurrence

The composite of food items (Table 4) was assembled from data collected over many years by direct observation, palpated stomach items, and scat residues identified microscopically. As such, they are subject to various biases. The prey identified from stomachs and that from scats showed somewhat different trends, partly because some kinds of prey are digested much more rapidly and more completely than others. Also, as brought out in a later section, there are different trends between young and adults, and even between the sexes. Season and stage of succession may cause other differences.

Most prey items were determined to species, but some were determined only to genus or family, or even broader categories such as "bird" or "reptile." In Table 5 the list of prey has been shortened by lumping some categories; for instance the occasional occurrence of *Microtus* sp. and *Peromyscus* sp. has been combined with the commonest local species, *Microtus ochrogaster* and *Peromyscus leucopus*, respectively.

Table 3. Estimated densities of uncommon or secretive species based on comparison with associated species censused by capture-recapture ratios.

Species samples	Years of sampling	Commoner species compared	Ratio to commoner species	Density of commoner species (no. per ha)	Estimated density (no. per ha)
<i>Carphophis vermis</i>	1955-67	<i>Diadophis punctatus</i>	26 to 1,437 (1.81 %)	1,266.00	92.9
<i>Crotalus horridus</i>	1956-57; 1959-61	<i>Coluber constrictor</i>	40 to 615 (6.50 %)	4.72	0.306
<i>Lampropeltis callisgaster</i>	1957-61	<i>C. constrictor</i>	42 to 615 (6.82 %)	4.72	0.322
<i>L. triangulum</i>	1957-61	<i>Thamnophis sirtalis</i>	17 to 457 (3.72 %)	3.74	0.139
<i>Nerodia sipedon</i>	1957-61	<i>T. sirtalis</i>	29 to 457 (6.35 %)	3.74	0.237
<i>Pituophis melanoleucus</i>	1957-61	<i>Coluber constrictor</i>	17 to 615 (2.77 %)	4.72	0.131
<i>Storeria dekayi</i>	1966-67	<i>Diadophis punctatus</i>	183 to 14,759 (1.24 %)	1,266.00	15.7

Table 4. Food items taken by 11 snake species, Natural History Reservation, Lawrence, Kansas (n = total number of food items).

Species	No. of food items	Species	No. of food items
<i>Agkistrodon contortrix</i> , n = 602			
<i>Microtus ochrogaster</i>	116	<i>Carphophis vermis</i>	6
<i>Tibicen pruinosus</i>	93	<i>Mus musculus</i>	5
<i>Peromyscus</i> sp.	81	<i>Scincella lateralis</i>	3
<i>Diadophis punctatus</i>	45	<i>Thamnophis sirtalis</i>	3
<i>Blarina brevicauda</i>	42	<i>Coluber constrictor</i>	3
<i>Cryptotis parva</i>	35	Birds	2
Caterpillars	34	<i>Neotoma floridana</i>	2
<i>Eumeces fasciatus</i>	30	<i>Sylvilagus floridanus</i>	2
<i>Pitymys pinetorum</i>	26	<i>Synaptomys cooperi</i>	2
<i>Reithrodontomys megalotis</i>	19	<i>Terrapene ornata</i>	1
<i>Gastrophryne olivacea</i>	13	<i>Eumeces obsoletus</i>	1
<i>Rana blairi</i>	12	<i>Cnemidophorus sexlineatus</i>	1
<i>Ophisaurus attenuatus</i>	8	<i>Elaphe obsoleta</i>	1
<i>Zapus hudsonius</i>	7	Snakes	1
<i>Sigmodon hispidus</i>	7	<i>Pseudacris triseriata</i>	1
<i>Carphophis vermis</i> , n = 50			
Earthworms (<i>Allolobophora trapezoides</i> and other species, Clark 1970)			50
<i>Coluber constrictor</i> , n = 986			
Insects			
<i>Acheta assimilis</i>	144	<i>Sphargemon equalis</i>	7
<i>Ceuthophilus maculatus</i>	97	<i>Syrphula admirabilis</i>	6
<i>Arphia simplex</i>	73	<i>Conocephalus</i> sp.	6
<i>Melanoplus bivittatus</i>	71	<i>Tibicen</i> sp.	5
<i>M. femurrubrum</i>	68	<i>Macis</i> sp.	5
Insects	45	Katydid	4
<i>Acheta</i> sp.	44	<i>Orchelimum</i> sp.	4
<i>Melanoplus differentialis</i>	43	<i>Amblycorypha inasteca</i>	2
<i>Neconocephalus robustus</i>	38	<i>Melanoplus scudderi</i>	2
Unspecified beetles	17	<i>Schistocerca obscura</i>	2
<i>Melanoplus</i> sp.	17	<i>S. americana</i>	1
<i>Dissosteira carolina</i>	16	<i>Neconocephalus</i> sp.	1
<i>Orchelimum vulgare</i>	15	<i>Dahlia brevipes</i>	1
<i>O. nigripes</i>	9	<i>Tibicen pruinosus</i>	1
<i>Chortophaga ulridifasciata</i>	9	<i>T. lyrica</i>	1
Vertebrates			
<i>Microtus ochrogaster</i>	80	<i>Blarina brevicauda</i>	3
<i>Peromyscus leucopus</i>	20	<i>Eumeces obsoletus</i>	3
<i>Thamnophis sirtalis</i>	17	Reptiles	3
<i>Coluber constrictor</i>	16	Bird eggs	3
<i>Diadophis punctatus</i>	15	<i>Peromyscus maniculatus</i>	2
<i>Peromyscus</i> sp.	14	<i>Scalopus aquaticus</i>	2
<i>Microtus</i> sp.	9	<i>Sylvilagus floridanus</i>	2
<i>Reithrodontomys</i> sp.	8	<i>Cnemidophorus sexlineatus</i>	2
<i>Cryptotis parva</i>	7	<i>Pitymys pinetorum</i>	1
<i>Eumeces fasciatus</i>	5	Shrews	1
Birds	5	<i>Nerodia sipedon</i>	1
<i>Rana blairi</i>	4	<i>Ophisaurus attenuatus</i>	1
<i>Sigmodon hispidus</i>	4	<i>Gastrophryne olivacea</i>	1
<i>Elaphe obsoleta</i>	4	<i>Hyla chrysoscelis</i>	1

Table 4. Continued

Species	No. of food items	Species	No. of food items
<i>Lampropeltis calligaster</i>, n = 56			
<i>Microtus</i> sp.	15	<i>Coluber constrictor</i>	1
<i>M. ochrogaster</i>	8	<i>Ophisaurus attenuatus</i>	1
<i>Pitymys pinetorum</i>	2	<i>Synaptomys cooperi</i>	1
<i>Scalopus aquaticus</i>	5	<i>Mus musculus</i>	1
<i>Peromyscus</i> sp.	3	<i>Sigmodon hispidus</i>	1
<i>Cryptotis parva</i>	2	<i>Blarina brevicauda</i>	1
<i>Colinus virginianus</i> (eggs)	2	<i>Sylvilagus floridanus</i>	1
<i>Colinus virginianus</i>	9	<i>Diadophis punctatus</i>	1
<i>Eumeces fasciatus</i>	2		
<i>Lampropeltis triangulum</i>, n = 21			
<i>Eumeces fasciatus</i>	12	<i>Peromyscus maniculatus</i>	1
<i>Cryptotis parva</i>	4	<i>Carphophis vermis</i>	1
<i>Diadophis punctatus</i>	2	<i>Eumeces obsoletus</i>	1
<i>Nerodia sipedon</i>, n = 9			
<i>Rana catesbeiana</i>	5	<i>Acris crepitans</i>	1
<i>R. blairi</i>	2	<i>Bufo americanus</i>	1
<i>Pituophis melanoleucus</i>, n = 18			
<i>Peromyscus</i> (<i>leucopus</i> and perhaps <i>maniculatus</i>)	2	Birds	4
<i>Neotoma floridana</i>	2	<i>Pitymys pinetorum</i>	1
Bird eggs	2	<i>Sigmodon hispidus</i>	1
<i>Microtus ochrogaster</i>	4	<i>Sylvilagus floridanus</i>	1
		<i>Mus musculus</i>	1
<i>Crotalus horridus</i>, n = 28			
<i>Sylvilagus floridanus</i>	7	<i>S. niger</i>	1
<i>Microtus ochrogaster</i>	4	<i>Sigmodon hispidus</i>	1
<i>Pitymys pinetorum</i>	4	<i>Zapus hudsonius</i>	1
<i>Peromyscus leucopus</i>	3	<i>Mus musculus</i>	1
<i>Neotoma floridana</i>	3	<i>Cryptotis parva</i>	1
<i>Sciurus carolinensis</i>	1	<i>Coluber constrictor</i>	1
<i>Diadophis punctatus</i>, n = 229			
Earthworms	221	Tipulid larvae	7
		<i>Ophisaurus attenuatus</i>	1
<i>Elaphe obsoleta</i>, n = 100			
<i>Microtus ochrogaster</i>	25	Bird nestlings	3
<i>Peromyscus leucopus</i>	19	<i>Reithrodontomys megalotis</i>	2
Bird eggs	11	<i>Blarina brevicauda</i>	2
Ranid frogs	8	<i>Neotoma floridana</i>	2
<i>Sylvilagus floridanus</i>	8	<i>Eumeces fasciatus</i>	2
<i>Cyanocitta cristata</i>	6	<i>Zapus hudsonius</i>	1
Mammals	5	<i>Mus musculus</i>	1
<i>Cardinalis cardinalis</i> nestlings	4	<i>Sayornis phoebe</i>	1
<i>Thamnophis sirtalis</i>, n = 72			
<i>Rana blairi</i>	25	<i>Rana catesbeiana</i>	4
<i>Bufo americanus</i>	10	<i>Peromyscus leucopus</i>	3
Lumbricid earthworms	8	Frogs	3
<i>Hyla chrysoscelis</i>	7	<i>Microtus ochrogaster</i>	2
<i>Bufo woodhousi</i>	4	<i>Reithrodontomys megalotis</i>	1
<i>Acris crepitans</i>	4	<i>Pseudacris triseriatus</i>	1

Table 5. Estimated biomass (grams per hectare) of main prey species taken annually by 12 species of snakes, Natural History Reservation, Lawrence, Kansas.

Prey species	<i>Agkistrodon contortrix</i>	<i>Carpophis vermis</i>	<i>Coluber constrictor</i>	<i>Crotalus horridus</i>	<i>Diadophis punctatus</i>	<i>Elaphe obsoleta</i>	<i>Lampropeltis calligaster</i>	<i>Lampropeltis triangulum</i>	<i>Nerodia spilon</i>	<i>Pituophis melanoleucus</i>	<i>Sistrerea dekayi</i>	<i>Thamnophis sirtalis</i>
Earthworms												
<i>Allolobophora caliginosa</i>	—	435	—	—	14,876	—	—	—	—	—	210	12
Insects												
<i>Acheta assimilis</i>	—	—	81	—	—	—	—	—	—	—	—	—
<i>Ceuthophilus maculatus</i>	—	—	42	—	—	—	—	—	—	—	—	—
<i>Melanophis</i> spp.	—	—	135	—	—	—	—	—	—	—	—	—
Tettigoniidae	—	—	36	—	—	—	—	—	—	—	—	—
<i>Tibicen pruinosa</i>	34	—	—	—	—	—	—	—	—	—	—	—
Tipulidae	—	—	—	—	197	—	—	—	—	—	—	—
Leptidoptera	12	—	—	—	—	—	—	—	—	—	—	—
Amphibians												
<i>Acris crepitans</i>	—	—	—	—	—	—	—	—	4	—	—	—
<i>Bufo americanus</i>	—	—	—	—	—	—	—	—	10	—	—	104
<i>B. woodhousei</i>	—	—	—	—	—	—	—	—	—	—	—	42
<i>Gastrophryne olivacea</i>	9	—	—	—	—	—	—	—	—	—	—	—
<i>Hyla chrysoscelis</i>	—	—	—	—	—	—	—	—	—	—	—	73
<i>Rana blairi</i>	22	—	17	—	—	18	—	—	22	—	—	310
<i>R. catesbeiana</i>	—	—	—	—	—	—	—	—	100	—	—	83
Reptiles												
<i>Carpophis vermis</i>	7	—	—	—	—	—	—	1	—	—	—	—
<i>Coluber constrictor</i>	11	—	135	3	—	—	1	—	—	—	—	—
<i>Diadophis punctatus</i>	50	—	23	—	—	—	—	1	—	—	—	—
<i>Elaphe obsoleta</i>	4	—	35	—	—	—	—	—	—	—	—	—
<i>Eumeces fasciatus</i>	38	—	13	—	—	2	1	9	—	—	—	—
<i>E. obsoletus</i>	2	—	32	—	—	—	2	3	—	—	—	—
<i>Ophisaurus attenuatus</i>	46	—	13	—	106	—	3	—	—	—	—	—
<i>Thamnophis sirtalis</i>	5	—	145	—	—	—	3	—	—	—	—	—
Birds												
<i>Cardinalis cardinalis</i>	—	—	—	—	—	12	—	—	—	—	—	—
<i>Cyanocitta cristata</i>	—	—	—	—	—	11	—	—	—	—	—	—
Mammals												
<i>Blarina brevicauda</i>	92	—	10	—	—	3	1	—	—	—	—	—
<i>Cryptotis parva</i>	38	—	12	—	—	—	1	2	—	—	—	—
<i>Microtus ochrogaster</i>	640	—	1,010	38	—	111	57	—	—	45	—	62
<i>Mus musculus</i>	14	—	—	7	—	2	1	—	—	5	—	—
<i>Neotoma floridana</i>	15	—	—	35	—	30	—	—	—	120	—	—
<i>Peromyscus leucopus</i>	268	—	260	5	—	50	—	—	—	—	—	56
<i>P. maniculatus</i>	—	—	17	—	—	—	4	1	—	24	—	—
<i>Pitymys pinetorum</i>	143	—	—	10	—	35	5	—	—	9	—	—
<i>Reithrodontomys megalotis</i>	35	—	34	—	—	—	—	—	—	—	—	4
<i>Scalopus aquaticus</i>	—	—	75	—	—	—	37	—	—	—	—	—
<i>Sciurus carolinensis</i>	—	—	—	78	—	—	—	—	—	—	—	—
<i>S. niger</i>	—	—	—	104	—	—	—	—	—	—	—	—
<i>Sigmodon hispidus</i>	52	—	86	6	—	—	4	—	—	15	—	—
<i>Sylvilagus floridanus</i>	15	—	43	165	—	174	12	—	—	15	—	—
<i>Synaptomys conperi</i>	11	—	—	—	—	—	2	—	—	—	—	—
<i>Zapus hudsonius</i>	19	—	—	1	—	1	—	—	—	—	—	—

Relatively large prey samples were obtained from *Diadophis punctatus*, *Coluber constrictor*, *Agkistrodon contortrix*, *Elaphe obsoleta*, and *Thamnophis sirtalis*. No records were obtained for *Storeria dekayi*, but it is assumed to be an earthworm and mollusc eater (Wright and Wright 1957). Records for *Pituophis melanoleucus*, *Crotalus horridus*, *Lampropeltis triangulum*, and *Nerodia sipedon* were too few to show the full range of prey for those species.

As in other predators, snake food habits are controlled largely by prey availability (see Reynolds and Scott, this volume). Each of the 12 kinds of snakes studied depended to a large extent on one kind of prey, and in each instance it was one of the most abundant species in the local community. Four species of snakes (*Agkistrodon contortrix*, *Coluber constrictor*, *Elaphe obsoleta*, and *Lampropeltis calligaster*) had *Micratus ochrogaster* as their chief prey, and in three species (*Diadophis punctatus*, *Carphophis vermis*, and presumably *Storeria dekayi*) earthworms (mostly *Allolobophora caliginosa*) were the favorite. Other commonly taken prey were *Sylvilagus floridanus* for *Crotalus horridus*, *Neotoma floridana* for *Pituophis melanoleucus*, *Rana catesbeiana* for *Nerodia sipedon*, *Rana blairi* for *Thamnophis sirtalis*, and *Eumeces fasciatus* for *Lampropeltis triangulum*. Although insects seemed to offer the most available food sources within the size range of prey eaten by most of the snake species, they were scarcely used. Only three species ate them at all, and these took only certain types which made up a relatively small proportion of their total food volume.

Food habits of all 12 species discussed are well documented in the literature, and for each the trend shown by published records is somewhat different from that found on the Reservation. In some instances availability may be involved, but in others there may be innate preferences that differ in local populations. An outstanding example is *Diadophis punctatus*, a transectinental species differing strikingly in size, appearance, habits, and habitats in different parts of its range. In the Great Lakes region, small terrestrial salamanders make up most of its food, whereas in the southeastern States it has been recorded as feeding on a wide variety of insects and other invertebrates. In the Southwest, where it is remarkably large, it is mainly a snake eater, but on the Reservation it takes earth-

worms almost exclusively (Fitch 1975).

Biomass of Food

Any attempt to quantify the feeding of snakes must take into account the different sizes of prey species. Each kind of snake tends to take prey within a certain size range; the largest individuals take the largest prey (see Reynolds and Scott, this volume). A wide range of size exists between and within species in the local populations (Table 1). The two largest species average more than 100 times the weights of the two smallest, and in some of the species the largest individuals weigh more than 100 times as much as the smallest ones.

The intact prey retrieved from the stomachs of live snakes was weighed when feasible, and these weights were used in calculating amounts of food consumed (Tables 5 and 6). However, in many instances prey identified from scats, or from partly digested stomach items were not suitable for weighing. In lieu of individual weight, the weight considered most typical of the particular prey species was arbitrarily assigned for each such occurrence. A few of the larger prey species, notably the cottontail, were usually taken as immatures by local snakes, and this was taken into account in calculating their biomass. The insects eaten were nearly all of the largest local kinds (lepidopteran larvae, cicadas, crickets, katydids, and grasshoppers), and *Acheta assimilis*, *Ceuthophilus maculatus*, *Tibicen pruinosus*, *Melanoplus bivittatus*, *M. femurrubrum*, *M. differentialis*, *Arphia simplex*, and *Neoconocephalus robustus* made up most of the insect material. For each insect occurrence a biomass of 1 g was arbitrarily assumed. A series of earthworms from *Diadophis* stomachs averaged about 0.5 g, and this figure was used as the biomass represented by each earthworm occurrence.

For vertebrate prey, the following weights (in grams) were arbitrarily assigned to calculate biomass: *Acris crepitans* 3, "bird" 20, bird egg 10, *Blarina brevicauda* 10, *Bufo americanus* 10, *Bufo woodhousei* 10, *Cardinalis cardinalis* 20, *Carphophis vermis* 6, *Cnemidophorus sexlineatus* 10, *Coluber constrictor* (juvenile) 20, *Cryptotis parva* 5, *Cyanocitta cristata* 50, *Diadophis punctatus* 4, *Elaphe obsoleta* (juvenile) 20, *Eumeces fasciatus* 6, *Eumeces ob-*

soletus 25, "frog" (ranid) 15, *Gastrophryne olivacea* 4, *Hyla chrysoscelis* 10, *Microtus ochrogaster* 30, *Mus musculus* 15, *Peromyscus maniculatus* 18, *Peromyscus leucopus* 18, *Ophisaurus attenuatus* 30, *Pitymys pinetorum* 30, *Pseudacris triseriata* 3, *Rana blairi* 10, *Rana catesbeiana* 20, *Reithrodontomys megalotis* 10, *Sayornis phoebe* 15, *Scalopus aquaticus* 90, *Scincella lateralis* 2, *Sigmodon hispidus* 50, "shrew" 8, "snake" 50, *Sylvilagus floridanus* (juvenile) 150, *Thamnophis sirtalis* (juvenile) 20, and *Zapus hudsonius* 15.

The amount of food consumed by an individual snake varies according to the snake's size, sex, appetite, availability of prey, weather, season, and many other factors. In *Diadophis punctatus* it was determined that a single meal averaged about 12% of the snake's weight. Intervals between feedings averaged about 8 days, of which the first 4 days are required for digestion, and the snake has an empty digestive tract for the last 4 days. At this rate of feeding the snake would take about 27 meals ingesting about three times its body weight in a normal growing season estimated at 213 days. In *Diadophis*, the relatively small size of the snake itself, and the unprotected naked body and high surface-to-volume ratio in the elongate earthworm prey all promote rapid digestion and relatively large intake of food by the snake.

In contrast, *Agkistrodon contortrix* took prey averaging 18.5% of body weight. The snake has about eight meals per growing season totalling no more than 200% of body weight. Low metabolism associated with sluggish behavior reduces the food requirement, and the relatively massive prey, usually with protective hairy or scaly skin, delays digestion.

Comparable quantitative data concerning food requirements are not available for the other species studied. However, it might be expected that the two other small earthworm eaters, *Carpophis vermis* and *Storeria dekayi*, would resemble *Diadophis punctatus* in their food consumption, estimated at three times body weight annually, and the same figure is accepted for the natricines, *Thamnophis sirtalis* and *Nerodia sipedon*.

Coluber constrictor tends to maintain through behavioral thermoregulation (Fitch 1956, 1963a) a body temperature markedly higher than any of the other species. It is active and feeds on relatively small prey animals, mak-

Table 6. Samples of 19 species of snakes from the Natural History Reservation, Lawrence, Kansas, showing composition of their populations (exclusive of first-year young) with estimates of the biomass of each species, and the biomass of its annual food consumption.

Species	Time of sample	Number of snakes in sample	Ratio of adults to immatures	Ratio of males to females	Estimated biomass (kg/ha)	Estimated annual food consumption (multiples of body weight)	Estimated annual food biomass (kg/ha)
<i>Agkistrodon contortrix</i>	1977	100	4.29	1.22	0.80	2.0	1.60
<i>Carpophis vermis</i>	1949-1961	100	2.85	1.27	0.15	3.0	0.45
<i>Coluber constrictor</i>	1960-1961	100	1.33	0.98	0.60	4.0	2.40
<i>Crotalus horridus</i>	1949-1963	45	1.50	1.69	0.16	2.5	0.40
<i>Diadophis punctatus</i>	1971-1973	1,588	1.31	1.76	5.06	3.0	15.18
<i>Elaphe obsoleta</i>	1949-1977	100	5.25	1.05	0.23	2.5	0.58
<i>Lampropeltis callisgaster</i>	1949-1977	100	4.26	1.70	0.05	2.5	0.13
<i>L. triangulum</i>	1949-1976	88	2.67	1.39	0.01	2.5	0.02
<i>Nerodia sipedon</i>	1949-1976	80	3.50	0.60	0.05	3.0	0.15
<i>Pituophis melanoleucus</i>	1949-1977	100	2.57	1.20	0.08	2.5	0.20
<i>Storeria dekayi</i>	1950-1977	85	0.98	0.85	0.07	3.0	0.21
<i>Thamnophis sirtalis</i>	1964-1974	150	—	0.76	0.25	3.0	0.75

ing new captures before earlier prey is digested, so that several items may accumulate in the stomach. Because of these habits *Coluber constrictor* is believed to take a relatively greater biomass of prey than any of the other local species, and an annual food consumption four times body weight is estimated (Table 6).

The remaining five species (*Elaphe obsoleta*, *Lampropeltis calligaster*, *Lampropeltis triangulum*, *Pituophis melanoleucus*, and *Crotalus horridus*) all take relatively large prey animals which usually have protective hairy, scaly, or feather-covered surfaces and are relatively resistant to digestion. The food requirements of these species are believed to be relatively less than in *Diadophis* but more than *Agkistrodon*, and are estimated at 2.5 times body weight per growing season in Table 6. In this table, the biomass of each snake species is estimated on the basis of population density and average adult weight; and from these figures average annual food consumption for each is estimated: 2 times body weight for *Agkistrodon*, 3 times body weight for the small worm-eating species and natricines, 4 times body weight for *Coluber*, and 2.5 times body weight for the remaining species.

Diadophis punctatus, because of its great abundance, takes more food than all the other

species combined; most of the remaining biomass is taken by *Agkistrodon contortrix* and *Coluber constrictor* (Table 5). Also, the biomass of the earthworm prey exceeds that of all other prey animals combined; only a few other species (*Microtus ochrogaster*, *Sylvilagus floridanus*, *Peromyscus leucopus*, *Rana blairi*) made up significant percentages of the total biomass, and all were among the commonest local small vertebrates.

Estimates of overlap in kinds and amounts of food taken by 12 snake species are shown in Table 7. This table is based mainly on the figures for prey species shown in Table 4, but it also utilized many additional records of prey animals less specifically determined. For example, *Thamnophis sirtalis* and *Nerodia sipedon* overlapped in their feeding, both having eaten 10 g of *Bufo americanus*, 22 g of *Rana blairi*, and 83 g of *Rana catesbeiana*—altogether 115 g constituting 15% of the total prey for *Thamnophis* and 78% of the total food intake for *Nerodia*.

Most of the species' diets overlap many of the others. *Lampropeltis calligaster* and *Pituophis* each overlap strongly ($\geq 50\%$) with four other species; no other snake's diet overlaps strongly with more than two others. The food biomass of *Diadophis*, being so large, is not impacted great-

Table 7. Estimated percentage overlaps in kinds and amounts of food taken by 12 snake species, Natural History Reservation, Lawrence, Kansas. Tabled numbers are percentages of the diets of snakes in the left-hand column that are shared with the snakes listed across the top; for example, an amount equivalent to 65% of the diet of *Agkistrodon* was also taken by *Coluber*, and 6% was shared with *Crotalus*. See text for methods of calculation. T = trace, <1% shared.

Species	A. contortrix	C. vermis	C. constrictor	C. horridus	D. punctatus	E. obsoleta	L. calligaster	L. triangulum	N. sipedon	P. melanoleucus	S. dekayi	T. sirtalis
<i>Agkistrodon contortrix</i>	—	0	65	6	0	18	6	1	1	7	0	9
<i>Carphophis vermis</i>	0	—	0	0	100	0	0	0	0	0	48	3
<i>Coluber constrictor</i>	44	0	—	4	1	9	5	1	1	4	0	5
<i>Crotalus horridus</i>	25	0	22	—	0	63	15	0	0	27	0	11
<i>Diadophis punctatus</i>	0	3	T	0	—	0	T	0	0	0	1	T
<i>Elaphe obsoleta</i>	44	0	39	44	0	—	13	T	3	18	0	23
<i>Lampropeltis calligaster</i>	69	0	94	46	2	57	—	4	0	53	0	43
<i>L. triangulum</i>	86	0	91	0	0	11	29	—	0	6	0	0
<i>Nerodia sipedon</i>	15	0	12	0	0	12	0	0	—	0	0	78
<i>Pituophis melanoleucus</i>	52	0	50	54	0	51	36	1	0	—	0	23
<i>Storeria dekayi</i>	0	100	0	0	100	0	0	0	0	0	—	6
<i>Thamnophis sirtalis</i>	10	2	18	6	2	17	8	0	15	6	2	—

ly by any other species; however, the *Diadophis* diet completely overlaps the diets of the other two small earthworm-eaters. In the two partly aquatic species, *Nerodia* and *Thamnophis*, diets overlap only weakly with those of most other species.

Intraspecific Partitioning of Food Resources

The wide size range between the largest adults and the smallest hatchlings (Table 1) make possible a wide choice in size and type of prey. At one extreme hatchlings of *Carphophis vermis* and *Diadophis punctatus* and neonates of *Agkistrodon contortrix* are relatively large compared with average adults (weight ratios of young to adult 18.0, 21.0, and 10.6%, respectively) whereas at the opposite extreme neonates of *Nerodia sipedon* and *Thamnophis sirtalis* are relatively much smaller (weight ratios of young to adults 2.4 and 2.7%, respectively) and consequently have greater potential for partitioning of food resources. In the more stenophagous species, notably the earthworm-eaters (*Carphophis vermis* and *Diadophis punctatus*), young and adults differed only in the size of prey taken, but in some other species, adults and young subsist on different sets of prey.

In *Agkistrodon contortrix*, there was almost no overlap in prey species taken by adults (mainly *Microtus ochrogaster*, *Peromyscus leucopus*, *Pitymys pinetorum*, and *Blarina brevicauda*) and by first-year young (*Cryptotis parva*, *Diadophis punctatus*, *Eumeces fasciatus*, and *Gastrophryne olivacea*). Intermediate-sized second-year young overlapped both first-year young and adults in their feeding, but took some types of prey (cicadas, small mice, sphingid, and other caterpillars) more often than either.

In *Thamnophis sirtalis*, partitioning was also clear cut. Seven instances of predation on earthworms were all by first-year young (snout-vent [S-V] 226 ± 15 mm), whereas seven instances of predation on mammals were all by adults (S-V 666 ± 16 mm). Ranid frogs (*R. blairi* and *R. catesbeiana*) made up more than half the estimated total of food biomass, but even the smallest were too large for small garter snakes; the snakes that ate ranid frogs ($N = 24$) averaged S-V 541 ± 23 mm. Those that ate toads ($N = 14$) averaged S-V 428 ± 32 mm, partly

because the newly metamorphosed young of both *Bufo americanus* and *B. woodhousei* are small enough to be eaten by neonate garter snakes.

In *Coluber constrictor* the 49 prey species were almost evenly divided between vertebrates and invertebrates. Many of the former including *Sylvilagus*, *Sigmodon*, *Scalopus*, and *Microtus* were too large for any but large adult snakes. First-year snakes were poorly represented in the sample; their food (grasshoppers, crickets, cave crickets, young voles) were of the same species represented in much larger numbers in the food of adults.

The food samples of *Crotalus horridus*, *Elaphe obsoleta*, and *Pituophis melanoleucus* were too small to demonstrate whether the young of these species took kinds of prey not used by adults, but most of the adults' food biomass was obtained from species too bulky to be swallowed by young—*Sylvilagus floridanus*, *Sciurus carolinensis*, *S. niger*, *Sigmodon hispidus*, and *Neotoma floridana*.

In several of the 12 snake species, there is a pronounced size difference between the sexes; females were much larger than males in *Nerodia sipedon*, *Thamnophis sirtalis*, *Diadophis punctatus*, *Carphophis vermis*, and *Coluber constrictor*, but males were larger than females in *Agkistrodon contortrix* and *Crotalus horridus*. In a series of 38 adult *Agkistrodon* (S-V > 500 mm) containing food in 1977, 59% of the males but only 36% of the females had eaten *Microtus ochrogaster*. The remaining 64% of females had eaten smaller prey: mice of three species, lizards, ringneck snakes, shrews, and cicadas. In *Coluber constrictor*, the larger adult females took a higher proportion of vertebrate prey and the smaller adult males took more insects. In 72 instances of predation on vertebrates (mostly voles and white-footed mice) by *Coluber* (S-V > 600 mm), 30.5% were by males, but in 175 instances of predation on insects, 45% were by males. Day-to-day trailing of racers equipped with radio transmitters showed that the males spent far more time than females above ground climbing in low trees, in situations where foliage-living insects would be available (Fitch and Shirer 1971). *Thamnophis sirtalis* subsisted chiefly on amphibians, but in six instances large adult females had eaten voles (three *Microtus ochrogaster*) or large mice (three *Peromyscus leucopus*); the only instance of pre-

dation on mammals by an adult male was on the much smaller *Reithrodontomys megalotis*. In general it seems that small mammals constitute a food resource used by adult females, reducing their competition with both adult males and immatures.

Discussion and Summary

The foregoing account indicates that many species of snakes coexist in high population densities, sharing certain available resources to varying degrees. Each must affect all its ecological associates, but direct interactions are difficult to observe. Food is the most obvious limiting resource. Contests between individuals over possession of a specific food object have never been observed in nature, and must be extremely rare, although they can be elicited in snakes confined together under crowded conditions. Competition is almost always exploitative; with regard to food it consists of the eating of prey by one individual, thereby rendering it unavailable to another.

However, all the common prey animals, such as earthworms, voles, white-footed mice, frogs, and rabbits are usually present in quantities beyond the needs of the snake population and are used by various non-ophidian predators also. The prey populations are subject to much greater fluctuations than those occurring in the snakes, and at times at least, their populations seem to be controlled by density-independent climatic factors.

The generation time of the snake predator is relatively lengthy compared with that of its prey. If it attains a normal life-span, a snake lives through major changes in the level of its prey populations. The relatively long life-span and a remarkable capacity for fasting enables the snake to survive drastic changes in the status of its prey. Unlike some other types of predators the snake is neither starved out nor forced to migrate by a scarcity of the favorite prey; instead it responds by reduced reproduction and partial shift to alternate prey species. In fact, the snake population is one of the most stable components of the overall biotic community, and probably exerts a stabilizing influence on the community as a whole.

Resources other than food supply are even less liable to be objects of direct competition. Water

and shelter (for temporary resting places and hibernation) are the most obvious requirements. Dew and rain usually provide drinking water; when present at all, it is available to the entire population, and drinking by one snake does not deprive others. During periods of inactivity, shelters are readily shared, even by snake species that may, at other times, interact as predator and prey. Occupancy of a shelter by one individual does not usually prevent simultaneous use by others of the same or different species; it is common to find two or more snakes of different species together. In some instances coincidental use of a well-situated shelter may be involved, but also there may be mutual attraction as an adaptation to achieve physiological homeostasis, especially in hibernacula.

Indirect competition may function in a subtle fashion involving relations with predators and pathogens. A snake-eating predator, supported locally by a high population of one species, might have more effect on a second less common species because that species is more easily caught, or has a lower reproductive potential. Similarly, two or more coexisting species might be hosts of the same pathogen, but have different susceptibilities. If the commoner species were the less susceptible, it could act as a reservoir to maintain and transmit a pathogen severely limiting the less common species.

Earthworms, small mammals, and frogs, in that order, were the chief food resources for snakes on the study area; some 64 prey species, 40 in significant numbers, were being taken by the 12 species of snakes. Earthworms, estimated to make up just over 70% of the food biomass for the total snake population, were eaten by 99% of the individual snakes present. The three smallest species are almost entirely earthworm-eaters and occur in population densities of from 2 to 10,000 times greater than those of the nine largest species. The three small earthworm-eating species are similar in size but differ somewhat in habitat preferences (overlapping widely) and differ greatly in degree of fossorial adaptation.

Insects made up less than 10% of the prey biomass. They included mainly large orthopterans (*Acheta*, *Centrophilus*, *Melanoplus*, and *Neoconocephalus*) eaten only by *Coluber constrictor*, tipulid larvae eaten only by *Diadophis punctatus*, and cicada nymphs and sphingid larvae eaten mostly by *Agkistrodon contortrix*. All

species of small mammals occurring on the area were found in the diets of the snakes, in roughly their order of abundance: *Microtus ochrogaster* (eaten by six species), *Peromyscus leucopus* (eaten by seven species), *Sylvilagus floridanus* (eaten by three species), *Neotoma floridana* (eaten by four species), *Pitymys pinetorum* (eaten by five species), *Sigmodon hispidus* (eaten by four species), *Scalopus aquaticus* (eaten by two species), and *Blarina brevicauda* (eaten by three species). *Sylvilagus floridanus*, *Sciurus carolinensis*, and *S. niger* are too large to be eaten as adults, except by unusually large individuals of the three largest snake species—*Crataulus horridus*, *Elaphe obsoleta*, and *Pituophis melanoleucus*. *Neotoma floridana*, *Sigmodon hispidus*, *Synaptomys cooperi*, *Microtus ochrogaster*, and *Pitymys pinetorum*, are also sufficiently large that, as adults, they are generally unavailable as food to the smaller species of mammal-eating snakes (*Coluber constrictor*, *Lampropeltis triangulum*, *Thamnophis sirtalis*) and to juveniles of the larger mammal-eating species.

Of the 12 species of snakes studied in broad ecological categories based on differences and similarities in habitat, microhabitat, size, food, and numbers (Table 8), no two are the same in all categories. In 16 of 86 paired species comparisons, the compared species differed in all seven categories. The greatest similarities (five of seven categories the same) were between *Diadophis punctatus* and *Storeria dekayi*, and between *Lampropeltis calligaster* and *Pituophis melanoleucus*.

Every one of the 12 snake species in this community possesses one or more unique traits in life style, habitat, or feeding specialization that greatly reduces the potential for competition with all associated species. These unique features may be summarized as follows. *Agkistrodon contortrix*, taking relatively very large prey items, concentrates its predation on the two most abundant species of small rodents, but also takes alternatively many types of mammals, birds, reptiles, amphibians, and two types of large insects, hunting by ambush and use of venom. *Carphophis vermis* is the only species specialized for fossorial existence, and is the most stenophagous of all, taking, insofar as known, only earthworms. *Coluber constrictor*, a grassland species, is unique in its active, visual search and pursuit of prey, and in the remark-

Table 8. Major ecological groupings of snake species on the Natural History Reservation, Lawrence, Kansas.

Species	Major habitat	Microhabitat	Time of activity ^a	Method of securing prey	Adult weight range (g)	Population density per hectare	Chief food sources
<i>Agkistrodon contortrix</i>	Forest	Terrestrial	CN	Ambush, venom	75-300	1-9	Vole, mouse
<i>Carphophis vermis</i>	Forest	Fossorial	CN	Search, swallow	3-10	10-90	Earthworm
<i>Coluber constrictor</i>	Grassland	Terrestrial	D	Search, swallow	75-300	1-9	Vole, mouse
<i>Crataulus horridus</i>	Forest	Terrestrial	CN	Ambush, venom	300-1,000	<1	Rat, squirrel, rabbit
<i>Diadophis punctatus</i>	Edge	Surface litter	D	Search, swallow	3-10	>1,000	Earthworm
<i>Elaphe obsoleta</i>	Forest	Arboreal	DN	Search, constrict	300-1,000	<1	Rat, squirrel, rabbit
<i>Lampropeltis calligaster</i>	Grassland	Terrestrial	DN	Search, constrict	75-300	<1	Vole, mouse
<i>L. triangulum</i>	Edge	Surface litter	DN	Search, constrict	10-75	<1	Reptile
<i>Nerodia sipedon</i>	Riparian	Aquatic	DN	Search, swallow	75-300	<1	Anuran
<i>Pituophis melanoleucus</i>	Grassland	Terrestrial	DN	Search, constrict	300-1,000	<1	Rat, squirrel, rabbit
<i>Storeria dekayi</i>	Edge	Surface litter	DN	Search, swallow	3-10	10-90	Earthworm
<i>Thamnophis sirtalis</i>	Riparian	Aquatic	D	Search, swallow	75-300	1-9	Anuran

^aD = diurnal; C = crepuscular; N = nocturnal.

ably wide range of prey animals, including insects. *Crotalus horridus* is the largest of the species, and takes relatively large mammalian prey, too large to be taken by most of the others. It is an ambush hunter in forest habitat, using potent venom to immobilize the prey. *Diadophis punctatus* is the smallest species and is concentrated in edge habitats but is so successful and abundant that it occurs extensively in forest and grassland. It subsists almost entirely on earthworms, the most available of all prey species. *Elaphe obsoleta* is one of only two species with arboreal tendencies, and the only one with an important bird component in the diet. *Lampropeltis calligaster* is the species most limited to prairie habitat, and secures its prey by search and constriction, feeding mainly on small mammals, birds, and eggs. *Lampropeltis triangulum* is in a size range by itself, between the small and the medium-sized species; it is the only local snake that subsists chiefly on reptile prey, mostly lizards. *Nerodia sipedon* is the only strongly aquatic species. *Pituophis melanoleucus* is by far the largest of the grassland species and is specialized for predation on the pocket gopher (although no records were obtained in the small sample from the Reservation, where gophers are rare). *Storeria dekayi* is the only species known to take snails and slugs, although again, no records were obtained from the Reservation. *Thamnophis sirtalis* is most characteristic of a wetland habitat and amphibian diet.

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Use of a Mammalian Resource by a Chihuahuan Snake Community

by

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Abstract

Food habits and habitat selection were investigated in a snake community in north-eastern Chihuahua, Mexico, from 1975 to 1977. A total of 418 snakes (20 species) was collected along Highway 16 from Villa Aldama to El Pastor. Examination of snake capture sites for the plant species present, and a study of structural characteristics of the vegetation and topographic features, showed that snakes exhibited distinct habitat preferences. Rodent species present and their relative densities were assessed by 5,400 trap nights at 18 trap stations. Digestive tracts of 351 snakes of 16 species yielded 153 food items. Rodents made up 71.1% of the diets by frequency of occurrence; lagomorphs, birds, reptiles, amphibians, and arthropods accounted for the remainder. The most important snake predators on rodents were *Crotalus atrox*, *C. molossus*, *C. scutulatus*, *Elaphe subocularis*, and *Pituophis melanoleucus*. The coexistence of mammal-eating snakes in this community is chiefly due to spatial habitat differences of predators which coincide with habitat variations of prey species; different-sized snakes chose optimal-sized prey in terms of catchability, handling, and potential danger.

Factors enabling competing species to remain in sympatry are not often clear. Much attention has been focused on isolating mechanisms (Gause 1934; Hardin 1960; Mayr 1963; Dobzhansky 1970; Levin 1970; Whittaker and Woodwell 1972; Lewontin 1974; Pielou 1974; Vance 1978). These authors agree that ecological isolation is probably the most important factor to continued coexistence.

The organization of animal communities may be a function of the range and variation of resources that ultimately determine the number of predatory species and the niche space of each. Associations of sympatric species may effectively reduce competition by their differential use of the trophic, temporal, and spatial components of an area (Pianka 1974a).

It is essential to quantify resource use among community members to understand the way

resources are partitioned in a community. The ability to quantify available resources in a community is exceedingly difficult and oftentimes impossible. Community investigators to date have analyzed resource use by selecting and comparing those resource axes believed to be most important for coexistence of community members. Pianka (1974b) studied lizard communities by quantifying the use of food resources, time of activity, and habitat selection. Resource allocation in sympatric subalpine rodents was studied by Vaughn (1974) through dietary overlap, microhabitat selection, and activity. Brown and Lieberman (1973) studied the food and habitat axes of sand dune rodents. Habitat and food overlap were analyzed by Orians and Horn (1969) in a four-species black-bird community. None of these studies quantified the food resources available. Without this information, dietary overlap explains little of the dynamics of community structure (Conley 1976; Wiens 1977).

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Black (1974) studied a 17-species bat community in New Mexico and provided a detailed analysis of the insect resource available to it. He found that although the prey resources were highly diverse, only moths and beetles were very important to interactions within the bat community.

Arnold (1972) reviewed the food habits literature of sympatric snake species and provided strong empirical evidence that different species tend to eat different prey species. Shine (1977) listed other detailed studies of feeding habits in sympatric snakes that strengthen this conclusion. Arnold (1972) analyzed factors concerning species diversity gradients of predators and prey and provided four mechanisms which possibly cause sympatric snake species to eat different prey species: (1) habitat differences coinciding with habitat differences of prey species, (2) temporal differences in foraging activity coinciding with temporal differences in activity or availability of prey species, (3) differences of prey species eaten coinciding with different-sized prey species, and (4) innate differences in the tendency to strike different prey species. Arnold concluded that resource partitioning by snakes is accomplished by a variety of complex mechanisms. He believes that no single mechanism is solely responsible for relieving competition, but that all four act together to allow resource partitioning by snakes. Certainly, the importance of each mechanism will vary with any given community.

Specialized predators such as snakes are of similar basic morphology, but are different in size, foraging strategy, food capturing mechanisms, and prey eaten. Sympatry of closely related species of different sizes has been documented for a large number of animals (e.g., invertebrates—Wilson 1975; amphibians—Fraser 1976; reptiles—Schoener 1968; Pianka 1969; birds—Lack 1944; Ashmole 1968; mammals—Rosenzweig and Sterner 1970; Brown and Lieberman 1973). Size differences between the predator species and the manner in which the prey is hunted in addition to habitat segregation provide mechanisms whereby each predatory species can concentrate on a different set of prey species.

Although a number of studies have dealt with autecology of snakes (e.g., Fitch 1960, 1963, 1965; Hall 1969; Platt 1969; Clark 1970, 1974; Brown 1973; Branson and Baker 1974; Parker

1974; Clark and Fleet 1976), studies of the ecological relations of three or more snake species in the same community are few. Pough (1966) provided the first analysis of microhabitat partitioning among terrestrial snakes. The investigations by Fitch (1949) in California and those by Carpenter (1952) and Fleharty (1967) on *Thamnophis* represent the earliest such studies dealing with food resource partitioning of snakes. More recently, studies of food resource partitioning among three or more snake species include Barbault (1974), Mushinsky and Hebrard (1977), and Shine (1977). Although the above studies are important analyses of sympatric snake communities, they lack a quantitative assessment of the available prey resources.

The present study determines the use of a mammalian resource by a snake community in northeastern Chihuahua, Mexico. This is the first attempt to assess the prey resources available to a community of mammal-eating snakes. The purpose of this study was to determine to what extent coexistence of snakes in a community is related to partitioning of the food and habitat resources. Specific inquiries are posed as to the nature of food partitioning, the structure of the predator and prey communities, and the ways in which spatial and temporal niche dimensions of the individual prey and predators coincide.

Methods

Study Site

Field work was performed along an 80.5-km stretch of Mexico Highway 16, 22 km northeast of Chihuahua City from Villa Aldama to El Pastor. The area is at 29°10' N and 105°30' W at an elevation of 1,370 m. This region has hot summers and cold winters; maximum precipitation is in the summer and the average annual precipitation is 315 mm (Schmidt 1975).

The desert shrub formation of Chihuahua is uniform in physiognomy and simple in composition (Shreve 1930; Lesueur 1945). Topography consists of limestone mountains, gently falling bajadas, and broad intermont plains broken by numerous deep arroyos. The geology and soils are described by Morafka (1977). The vegetation is strongly dominated by creosote-bush (*Larrea tridentata*) in association with tarbush

(*Flourensia cernua*) where the soil is thin, or with mesquite (*Prosopis glandulosa*) where the soil is deep. The otherwise monotonous uniformity is broken by ravines, dominated by catclaw mimosa (*Mimosa blunclifera*), Wright acacia (*Acacia wrightii*), and spiny hackberry (*Celtis pallida*). In the lowest part of each basin or valley, mesquite is dominant as a shrub 1 to 2 m tall. In surface depressions where water is likely to stand during some time of the year, there are no shrubs and the prevailing vegetation is an open sod of tobosa grass (*Hilaria mutica*). Important plants of the bajadas, in addition to creosote-bush and tarbush, include mariola (*Parthenium incanum*), ocotillo (*Fouquieria splendens*), and spiny allthorn (*Koeberlinia spinosa*). On the higher parts of the bajadas, on the pediments surrounding the mountains, and on the hills and mountain slopes, the vegetation is much more diverse. The most conspicuous plants are sotol (*Dasylirion scariosa*), ocotillo, rubber-plant (*Jatropha dioica*), lechuguilla agave (*Agave lecheguilla*), mariola, and soap-tree yucca (*Yucca elata*).

Field Methods

Snakes were collected during automobile travel beginning at dusk (about 1930 h) over a period of 24 weeks between April and September 1975-77. In the course of three summers, 139 trips along Highway 16, totaling 16,713 km, provided records of 418 snakes. Additional snakes were hand-captured during the day and night while walking along the study route. Live snakes were retained in cloth bags which were examined for feces when the snake was removed. The following data were recorded for all snakes: exact location, time of capture, sex, size (snout-vent length [S-V], tail length, and head length [HL, the distance from the tip of snout to posterior end of mandible]). Measurements were recorded to the nearest millimeter on live and fresh-killed snakes with a meter stick and Peacock dial calipers. During 1975, all snakes captured alive (63) were permanently marked by clipping ventral caudal scales (Blanchard and Finster 1933) and released at the capture site. All dead snakes throughout the study, and snakes captured alive in 1976 and 1977, were preserved in 10% formalin and later transferred to a 55% isopropanol solution. They

are deposited in the Museum of Southwestern Biology, University of New Mexico, Albuquerque.

Food Habits

In 1975 records of prey items were gathered through dissection of dead snakes (111) and by palpating stomachs of living animals (41). All snakes (199) found during 1976 and 1977 were kept for dissection. The stomach and intestines of each snake were removed and examined for the presence of prey material. Condition of food items ranged from entire animals to body fragments or wads of hair retained in the lower tract. Animal fragments and hair were permanently mounted on microscope slides by techniques similar to those of Williamson (1951), Mayer (1952), and Brunner and Coman (1974). Additional slides (32) were prepared from fecal samples obtained from live snakes. Hair collected from the rodent and lagomorph species in the study area was used for reference slides for identification. Slides were examined under a dissecting microscope.

The features of hair useful for identification (medulla, cortex, cuticle) are not damaged during the digestive process (Brunner and Coman 1974). It was possible to identify hair slides to species in most instances. The only exception involved the two similar species, *Perognathus intermedius* and *P. penicillatus*, whose hair was indistinguishable. The habitat preferences of these rodents, however, are different (Anderson 1972; Findley et al. 1975). The rock pocket mouse, *P. intermedius*, was completely saxicolous, whereas *P. penicillatus* occurred in the lowest portions of the intermontane basins, often in association with mesquite. We determined which *Perognathus* species was represented on a particular hair slide on the basis of habitat (each record was considered to be a single prey item unless there were obviously more). Twelve snakes contained more than one prey item.

Rodent Size

The greatest width of a rodent skull (posterior zygomatic or bullae breadth) was used as a measure of prey size. Average measurements were obtained from Anderson (1972). This

measure is used to determine the minimum size of a snake's gape necessary to ingest a particular rodent species.

Rodent Densities

Rodent species present and their relative densities were assessed by 5,400 trap nights at 18 trapping sites along the study route. Sites were selected to sample the five major habitat types common to the area. Three habitat types were sampled four times and two were sampled three times. At each site a square grid of 100 trap stations in 10 rows and columns was maintained for three nights for a total of 300 trap nights. Folding Sherman live traps placed at intervals of 10 paces were used. Voucher specimens were preserved in 10% formalin and later transferred to a 70% ethanol solution. They are deposited in the Museum of Southwestern Biology, University of New Mexico, Albuquerque. Several factors affect trapping results in various ways (Wiener and Smith 1972). The trapping results of this study are undoubtedly biased and are not appropriate for rigorous statistical analysis, but are valuable for showing trends.

Vegetation Classifications

Five vegetation types were determined within the study area on the basis of dominant species associations. These divisions agree with the major habitat types described by Shreve (1939). They are, in order of increasing plant diversity, slope, and rocky cover, (1) tobosa, (2) mesquite-grassland, (3) creosote-tarbrush, (4), bajada, and (5) mountain pediment. The total number of road kilometers passing through each vegetation type was recorded and used to calculate the number of snakes per kilometer found in each.

Habitat Structure

Habitat structure was assessed at each snake capture site by establishing a 50- × 50-m square plot adjacent to the road in vegetation undisturbed by road construction. Conspicuous topographic features were noted (hills, rocks, alluvial fans). Plants more than 1 m tall were counted by walking in parallel lines through the plot, and those of questionable height were

measured with a meter stick. Perennial species were recorded. This analysis was simple and provided a quick quantitative measure for recording vegetational physiognomy at each snake capture site.

Arena Studies

Feeding experiments were conducted in Chihuahua during the study to determine prey acceptance of snakes. These tests provided information on the variables of snake size, snake species, rodent size, and rodent species in relation to prey acceptance by snakes. A total of 84 snakes (12 species) and 11 rodent species was used in this testing. Individual snakes were placed singly into gravel-bottomed plywood and glass behavior boxes (100 × 100 × 50 cm) in a darkened room at 24–26°C, 24 h before the introduction of a single rodent. Rodents used were live-trapped in the study area. The rodent remained in the behavior box until it was killed and eaten or until 1 h elapsed, at which time both snake and rodent were removed. Generally an individual snake was used in only one test, but on a few occasions a snake was presented with a second rodent regardless of its reaction to the first. Individual rodents were not reused because by the end of one test they tended to become wary of snakes. Testing began at dusk (about 1930 h); a low-powered light source (shaded Coleman lantern) was used for observation.

Results

Mammal Community

Abundance and Habitat Preferences

In 5,400 trap nights, 243 individual mammals (13 species and three families of rodents) were captured at the 18 sites (Table 1). The most abundant species in the traps were *Dipodomys merriami*, *Peromyscus maniculatus*, *P. eremicus*, *Perognathus intermedius*, and *P. penicillatus* and accounted for 88.5% of all rodents captured. In addition to rodents, Audubon's cottontail (*Sylvilagus auduboni*) and the black-tailed jackrabbit (*Lepus californicus*) commonly were observed in the area, but their densities were difficult to judge. The distribu-

Table 1. Total captures of rodents in study area, proportion of total catch, and proportion in snakes containing food, Chihuahua, Mexico, 1975-77. Trap data represent 5,400 trap nights at 18 stations.

Species	Total captures	Percent of total	Percent in snakes with food
<i>Dipodomys merriami</i>	126	51.9	24.2
<i>Peromyscus maniculatus</i>	45	18.5	16.4
<i>Perognathus intermedius</i>	17	6.9	7.0
<i>P. penicillatus</i>	15	6.2	7.8
<i>Peromyscus eremicus</i>	12	4.9	5.5
<i>Onychomys torridus</i>	7	2.9	—
<i>Perognathus flavus</i>	6	2.5	13.3
<i>Spermophilus spilosoma</i>	4	1.6	6.3
<i>Sigmodon hispidus</i>	4	1.6	3.1
<i>Reithrodontomys megalotis</i>	3	1.2	—
<i>Neotoma albigula</i>	2	0.8	3.1
<i>Spermophilus variegatus</i>	1	0.4	0.07
<i>Dipodomys spectabilis</i>	1	0.4	7.8

tion of mammal species in the five habitat types (Table 2) shows that *Dipodomys merriami* and *Peromyscus maniculatus* were the most abundant species and, along with *Perognathus flavus*, they occurred in four of the five habitat types. Tobosa was the only habitat supporting large numbers of *Dipodomys spectabilis* and *Spermophilus spilosoma*. These species were underrepresented in the trapping accounts, but the high density of their mounds in tobosa indicates they were common. The greatest number of species was found in mesquite-grassland, but *Dipodomys merriami*, *Perognathus penicillatus*, and *Peromyscus maniculatus* were the only common species. *Onychomys torridus* and *Sigmodon hispidus* were found only in this habitat. In the bajada and mountain pediment, *Perognathus intermedius*, *Peromyscus eremicus*, and *Spermophilus variegatus* were common.

Rodents were most noticeable during the wet months, July to September. Although extensive trapping was not conducted before the wet season, rodents were seen more frequently on the road at night with the onset of summer rains.

Predatory Community

A total of 418 individuals representing 20 species of snakes in two families was found during the three activity seasons (Table 3). Of the 11 species containing mammal remains, 5 snake

predators (*Crotalus scutulatus*, *C. atrox*, *C. molossus*, *Pituophis melanoleucus*, and *Elaphe subocularis*) accounted for 92.2% of the total predation by snakes on mammals. More than half the records of snake encounters (61.3%) were accounted for by the above five species; *C. atrox* and *C. scutulatus* alone represented 43.8%.

Of the five important mammal-eating snakes, males always averaged larger than females (Table 4). This has been previously reported for species of *Crotalus* by Klauber (1972). A comparison of the mean snout-vent length of the three *Crotalus* species reveals that *C. molossus* was the largest and *C. scutulatus* the smallest. Although it is common for *C. molossus* to be larger than *C. scutulatus*, it is unusual for it to be larger than *C. atrox*. Klauber (1972) showed that a "large adult male" of *C. atrox* was 500 mm larger than *C. molossus* and 600 mm larger than *C. scutulatus*. The largest adult males we recorded for *C. molossus* and *C. scutulatus* correspond closely to Klauber's data, but the largest *C. atrox* was 600 mm smaller than his record. The *C. atrox* from our study area were considerably smaller than those of many other areas. The two colubrids, *P. melanoleucus* and *E. subocularis*, are similar in length, but for any given size *P. melanoleucus* are heavier.

Distinct habitat preferences were found for these species in the Chihuahuan Desert shrub (Table 5). *Crotalus atrox* preferred the densest

Table 2. Ranking of rodent species trapped in five habitat types along Highway 16 from Villa Aldama to El Pastor, Chihuahua, Mexico, 1975-77. Species are ranked in descending order from most abundant. Mesquite-grassland and creosote-tarbrush were sampled three times; all others were sampled four times. See text for description of habitats and sampling method used.

Habitat and Species	Number trapped
Tobosa	
<i>Dipodomys merriami</i>	18
<i>Peromyscus maniculatus</i>	15
<i>Spermophilus spilosoma</i>	4
<i>Onychomys torridus</i>	4
<i>Perognathus flavus</i>	2
<i>D. spectabilis</i>	1
Mesquite-Grassland	
<i>D. merriami</i>	37
<i>Perognathus penicillatus</i>	10
<i>Peromyscus maniculatus</i>	10
<i>Sigmodon hispidus</i>	4
<i>Onychomys torridus</i>	3
<i>Reithrodontomys megalotis</i>	2
<i>Perognathus flavus</i>	1
<i>Neotoma albigula</i>	1
Creosote-Tarbrush	
<i>D. merriami</i>	41
<i>Peromyscus maniculatus</i>	16
<i>Perognathus penicillatus</i>	5
<i>P. flavus</i>	3
<i>Reithrodontomys megalotis</i>	1
<i>Neotoma albigula</i>	1
Bajada	
<i>D. merriami</i>	30
<i>Perognathus intermedius</i>	7
<i>Peromyscus eremicus</i>	4
<i>P. maniculatus</i>	4
<i>Perognathus flavus</i>	1
Mountain pediment	
<i>Peromyscus intermedius</i>	10
<i>P. eremicus</i>	8
<i>Spermophilus variegatus</i>	1

cover, whereas *C. scutulatus* preferred sparse shrub cover. Comparisons of shrub cover densities made between species showed a significant difference (Mann-Whitney "U," $P < 0.01$) between *C. atrox* and the other species but all other comparisons were nonsignificant. By comparing relative rodent abundances, preferences for

certain habitats were evident (Table 6, Fig. 1). *Crotalus molossus* and *E. subocularis* were found almost exclusively in rocky areas; they were most common in the mountain pediment and bajada. The remaining three species were more broadly distributed. *Crotalus scutulatus* was the most common species in tobosa and was also common with *C. atrox* in the creosote-tarbrush and bajada assemblages. *Crotalus atrox* rarely was found in tobosa. The most common species in mesquite-grassland was *P. melanoleucus*. A relation between vegetative density and lizard species densities has previously been documented in the Chihuahuan Desert of Big Bend, Texas (Degenhardt 1966, 1977).

None of the 63 snakes marked in 1975 were recaptured. Pough (1966) also obtained no recaptures of the 16 snakes he marked in southern Arizona.

Food Habits

Of 351 snakes examined, 153 (43.6%) contained food material. In addition, 32 fecal samples provided 22 identifiable items. Rodents made up 71.1% of the diets (by frequency of occurrence) and birds, reptiles, amphibians, and arthropods accounted for the remainder. There is a significant positive correlation ($r_s = 0.64$, $P < 0.05$) between rodent species abundance in traps and their frequency of occurrence in the diets of all snakes (Fig. 2).

There were important differences in the types of prey taken by different snake species that corresponded well with the habitat preferences of both predator and prey. The percentage frequency of occurrence of prey items in diets of the five mammal-eating snakes (Table 7) shows a greater number of prey species in the diets of the *Crotalus* than in the colubrids. The two most common rodents in the present study, *Dipodomys merriami* and *Peromyscus maniculatus*, were also the most common prey items. These two species, along with *Perognathus flavus*, accounted for 54.7% of the rodents found in snake stomachs.

The diet of *C. scutulatus* contained those rodents which were most abundant in tobosa. *Dipodomys merriami* was the commonest rodent in tobosa and was the most common mammal in the diet of *C. scutulatus* (Fig. 3). Likewise, tobosa supported the largest number of *Dipodomys spectabilis* and *Spermophilus*

Table 3. Number and percentage of all snakes found on Highway 16 from Villa Aldama to El Pastor, Chihuahua, Mexico, 1975-77. Snake species containing mammal remains are noted by an asterisk.

Species	1975		1976		1977		Total	
	No.	%	No.	%	No.	%	No.	%
<i>Crotalus atrox</i> *	41	20.5	24	17.3	14	17.7	79	18.9
<i>C. scutulatus</i> *	50	25.0	35	25.2	19	24.0	104	24.9
<i>C. molossus</i> *	9	4.5	6	4.3	5	6.3	20	4.8
<i>C. lepidus</i> *	1	0.5	1	0.7	1	1.3	3	0.7
<i>Elaphe subocularis</i> *	8	4.0	11	7.9	2	2.5	21	5.0
<i>E. guttata</i> *	5	2.5	2	1.4	0	—	7	1.7
<i>Pituophis melanoleucus</i> *	9	4.5	13	9.4	10	12.7	32	7.7
<i>Rhinocellus lecontei</i> *	14	7.0	9	6.5	6	7.5	29	6.8
<i>Arizona elegans</i> *	14	7.0	5	3.6	7	8.9	26	6.2
<i>Lampropeltis getulus</i> *	9	4.5	6	4.3	2	2.5	17	4.1
<i>Heterodon nasicus</i>	4	2.0	0	—	0	—	4	1.0
<i>Thamnophis marcianus</i>	16	8.0	12	8.6	2	2.5	30	7.2
<i>T. cyrtopsis</i>	3	1.5	0	—	1	1.3	4	1.0
<i>Hypsiglena torquata</i>	8	4.0	2	1.4	1	1.3	11	2.6
<i>Masticophis flagellum</i>	5	2.5	5	3.6	5	6.3	15	3.6
<i>M. lateralis</i> *	0	—	5	3.6	0	—	5	1.2
<i>Trimorphodon biscutatus</i>	2	1.0	0	—	1	1.3	3	0.7
<i>Tantilla nigriceps</i>	1	0.5	1	0.7	1	1.3	3	0.7
<i>Salpadora deserticola</i>	0	—	2	1.4	1	1.3	3	0.7
<i>Sonora semiannulata</i>	1	0.5	0	—	1	1.3	2	0.5
Total	200		139		79		418	

spilosoma, both of which had their highest frequency of occurrence in the diet of *C. scutulatus*. There is no significant positive correlation ($r_s = 0.64$, $P > 0.05$) between total rodent abundance and the frequency of occurrence of each species in the diet of *C. scutulatus*.

The most important rodents in the diets of *C. molossus* and *E. subocularis* were *Peromyscus*

gnathus intermedius and *Peromyscus eremicus* (Figs. 4 and 5). Although *C. molossus* was found most often in the mountain piedmont, where *D. merriami* is absent, this rodent constituted as large a part of the diet of *C. molossus* as *P. eremicus*, a species found only in the rocky foothills and at higher elevations. *Crotalus molossus* seems to forage in those habitats containing

Table 4. Comparison of sizes of five species of snakes from Chihuahua, Mexico, along Highway 16 from Villa Aldama to El Pastor, 1975-77.

Species	Sex	Sample size	Mean snout-vent length \pm standard error (mm)	Mean jaw length \pm standard error (mm)
<i>Crotalus atrox</i>	Male	30	757.41 \pm 2.4	38.82 \pm 0.10
	Female	7	653.1 \pm 5.1	34.64 \pm 1.0
<i>C. scutulatus</i>	Male	33	671.11 \pm 2.3	32.43 \pm 0.45
	Female	14	601.9 \pm 3.7	28.64 \pm 0.43
<i>C. molossus</i>	Male	20	780.0 \pm 9.9	40.65 \pm 0.65
<i>Pituophis melanoleucus</i>	Male	7	917.43 \pm 6.7	31.46 \pm 1.0
	Female	10	865.24 \pm 4.7	31.45 \pm 0.85
<i>Elaphe subocularis</i>	Male	5	904.8 \pm 5.4	32.0 \pm 0.67
	Female	8	894.5 \pm 5.2	31.68 \pm 0.67

Table 5. Comparison of density of plants over 1 m tall in 50- \times 50-m plots for five species of snakes in Chihuahua, Mexico, 1975-77.

Species	Number of plots	Mean number of plants \pm standard error
<i>Crotalus atrox</i>	57	41.1 \pm 0.7
<i>Pituophis melanoleucus</i>	29	33.8 \pm 1.0
<i>Elaphe subocularis</i>	17	29.4 \pm 0.9
<i>C. molossus</i>	20	27.3 \pm 0.7
<i>C. scutulatus</i>	74	26.8 \pm 0.5

D. merriami more often than the data in Table 6 indicate. No significant correlation exists between rodent species abundance and their frequency of occurrence in the diets of either *C. molossus* ($r_s = 0.68$, $P > 0.05$) or *E. subocularis* ($r_s = 0.55$, $P > 0.05$).

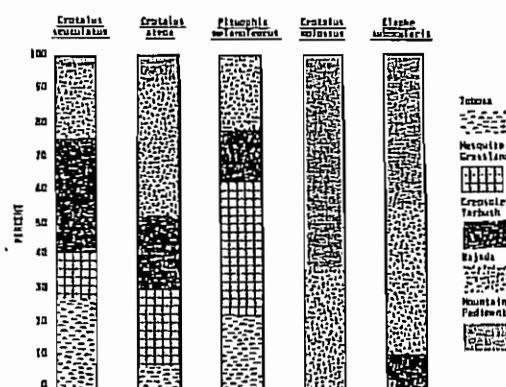


Fig. 1. Relative abundance of five mammal-eating snakes in various habitats during April-September 1975-77 from Villa Aldama to El Pastor, Chihuahua, Mexico.

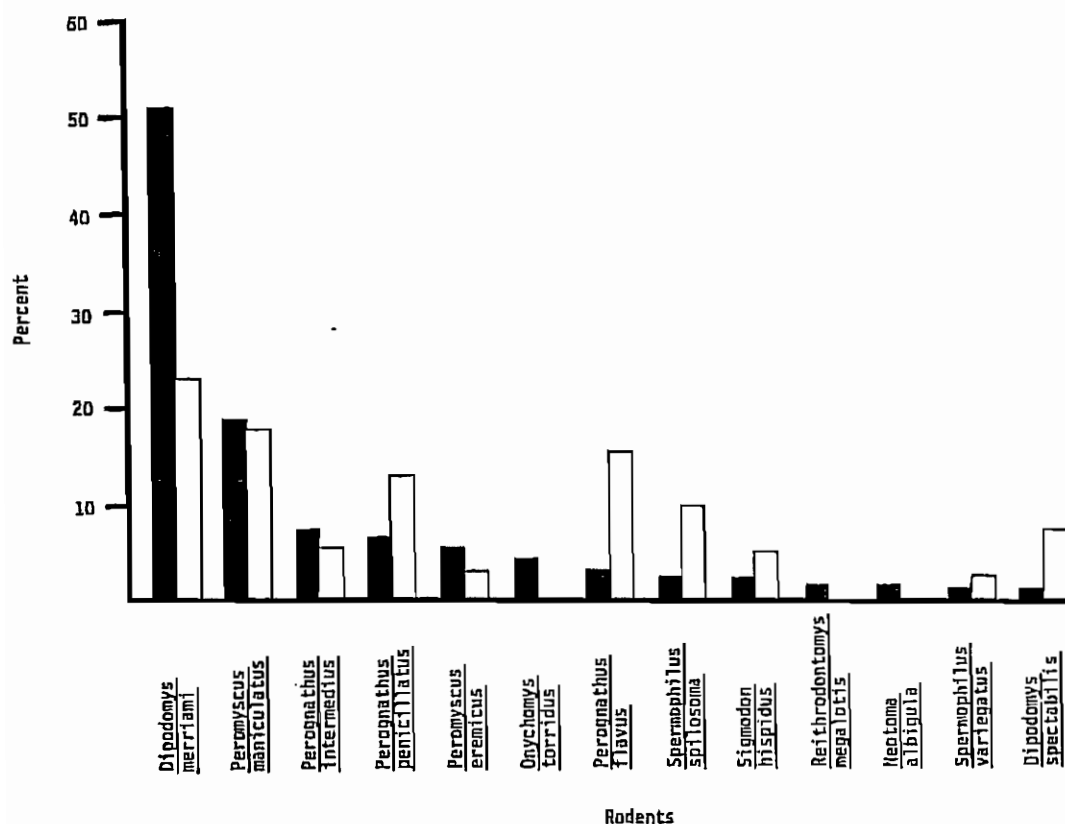


Fig. 2. Proportion of rodents trapped in study area (closed bars) and their frequency of occurrence in snakes containing mammals (open bars).

Table 6. Relative abundance (no./km) and total number (in parentheses) of snakes collected in five habitats along Highway 16, Chihuahua, Mexico, 1975-77.

Species	Habitat				
	Tobosa	Mesquite-grassland	Creosote-tarbush	Bajada	Mountain pediment
<i>Crotalus scutulatus</i> n = 104	1.98 (30)	0.99 (11)	1.46 (36)	1.36 (25)	0.21 (2)
<i>C. atrox</i> n = 79	0.33 (5)	1.62 (18)	0.89 (22)	1.58 (29)	0.52 (5)
<i>Pituophis melanoleucus</i> n = 32	0.45 (7)	1.17 (13)	0.20 (5)	0.38 (7)	—
<i>C. molossus</i> n = 20	—	—	—	0.38 (7)	1.34 (13)
<i>Elaphe subocularis</i> n = 21	—	—	0.08 (2)	0.53 (10)	0.92 (9)
Total km of each habitat	15.6	11.3	25.1	18.7	9.8
Percent of total habitat	19.37	14.03	31.18	23.22	12.17

Crotalus atrox and *P. melanoleucus* were most abundant in mesquite-grassland. The two most common rodents in the diets of each were *Dipodomys merriami* and *Peromyscus maniculatus* (Figs. 6 and 7). Both *Sigmodon hispidus*

and *Perognathus penicillatus* were associated with mesquite-grassland and had the highest frequency of occurrence in the diet of *C. atrox*, but were absent in *P. melanoleucus*. A significant positive correlation ($r_s = 0.66$,

Table 7. Percentage distribution by frequency of occurrence of prey species found in five species of snakes in the Chihuahua, Mexico, study area, 1975-77.

Prey Species	Snake species				
	<i>Crotalus atrox</i> (n = 43)	<i>Crotalus scutulatus</i> (n = 48)	<i>Crotalus molossus</i> (n = 12)	<i>Pituophis melanoleucus</i> (n = 15)	<i>Elaphe subocularis</i> (n = 12)
<i>Sylvilagus auduboni</i>	4.1	2.1	—	13.3	—
<i>Lepus californicus</i>	—	4.2	—	13.3	—
<i>Spermophilus spilosoma</i>	8.2	10.4	—	6.7	—
<i>S. variegatus</i>	2.0	—	—	—	—
<i>Perognathus flavus</i>	12.2	12.5	8.3	—	8.3
<i>P. intermedius</i>	4.1	2.1	25.0	—	16.7
<i>P. penicillatus</i>	10.2	6.2	—	6.7	—
<i>Dipodomys merriami</i>	18.4	27.1	16.7	20.0	16.7
<i>D. spectabilis</i>	6.1	12.5	—	—	—
<i>Peromyscus eremicus</i>	2.0	4.2	16.7	—	25.0
<i>P. maniculatus</i>	14.3	10.4	8.3	26.7	—
<i>Sigmodon hispidus</i>	4.1	—	—	—	—
<i>Neotoma albigula</i>	—	—	8.3	—	16.7
Birds	2.0	—	16.7	13.3	16.7
Reptiles	12.2	—	—	—	—
Arthropods	—	8.3	—	—	—

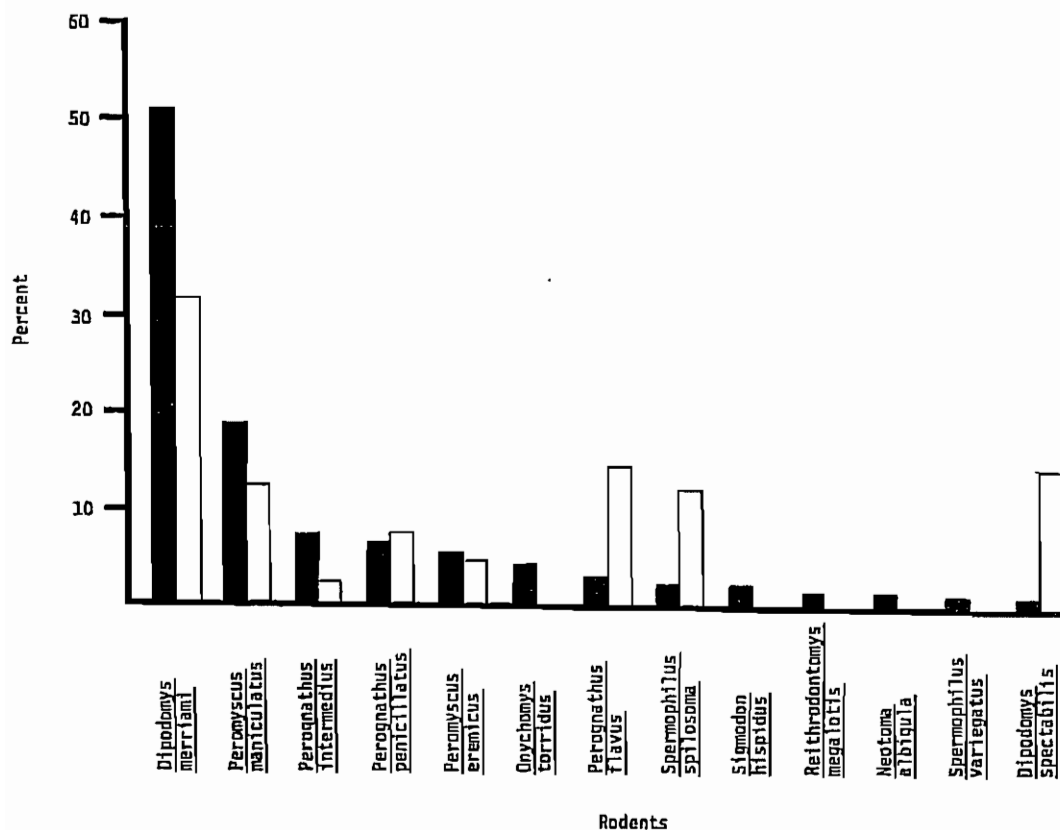


Fig. 3. Proportion of rodents trapped in the study area (closed bars) and the frequency of occurrence of each in the diet of *Crotalus scutulatus* (open bars).

$P < 0.05$) exists between the total abundance of rodents and their frequency of occurrence in the diet of *C. atrox*, but not for *P. melanoleucus* ($r_s = 0.55$, $P > 0.05$).

Present in the diets of *C. scutulatus*, *C. atrox*, and *P. melanoleucus* was *Sylvilagus auduboni*. The last two snakes also contained *Lepus californicus*. All rabbits and hares found in stomachs were immature; *Lepus californicus* was represented by nestlings.

The distributions of rodent size in individuals of *C. atrox* and *C. scutulatus* (Figs. 8 and 9) show significant ($P < 0.01$) positive correlations between snake head length and rodent skull size for each snake species, indicating that larger snakes ingested larger prey. When a snake attained a head length of 30 mm, it was able to ingest the two most common species, *Dipodomys merriami* and *Peromyscus maniculatus*. Below this head length *Perognathus flavus* was the

most common rodent in the diets. Since food is swallowed whole, it is reasonable that large food items are handled more easily by larger snakes. This relation agrees with the findings of Fitch and Twining (1946) for *Crotalus viridis* and of Beavers (1976) for *C. atrox*.

Arena Studies

Cottam et al. (1959) stated that snakes often kill prey items that are much too large to ingest suggesting that there is no discretion of prey size made by a particular snake. On an energy expenditure basis, however, this does not seem reasonable.

In testing prey items, we found that snakes selected prey on the basis of size. As shown in Figs. 10 and 11, the smallest snakes rejected prey items too large for them to eat. Also, large

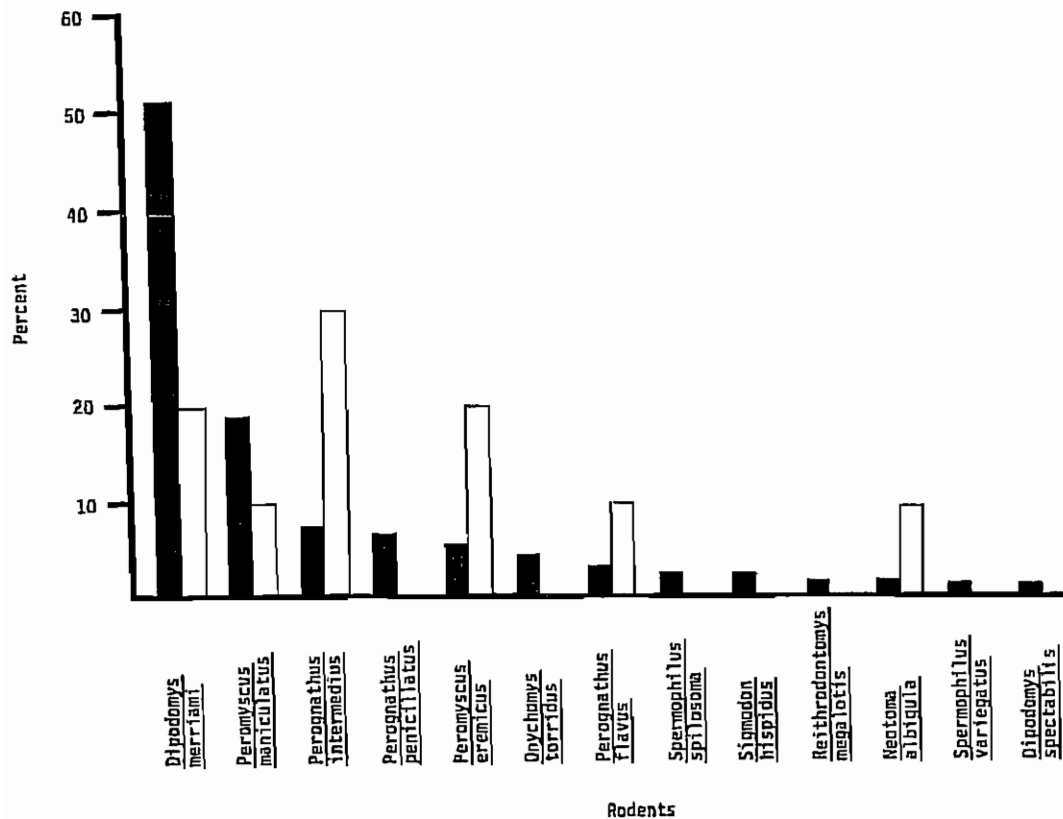


Fig. 4. Proportion of rodents trapped in the study area (closed bars) and the frequency of occurrence of each species in the diet of *Crotalus molossus* (open bars).

snakes tended to ignore the smallest prey items and concentrated on medium-sized rodents. Retreat from large rodents was exhibited by two *Crotalus scutulatus*. One snake (S-V 867 mm) moved continuously in order to maintain a maximum distance from a *Spermophilus variegatus* (the squirrel walked on the snake a number of times). The snake finally struck and disabled the squirrel, but afterwards continued to maintain a maximum distance from it. A second snake (S-V 787 mm) behaved similarly when a *Neotoma albigula* was offered. On this occasion, however, the rodent devoured a considerable amount of the snake's tail before the end of the test. During this time the snake continued to move about the arena and never attempted to strike the rodent.

The arena data show that snakes selected for catchability, handling, and potential danger of the optimal-sized prey item; they rejected indi-

viduals that were too small or too large and those that were potentially dangerous.

Discussion

Of the 20 snake species that occur in this community, 5 have sufficiently high populations to be important predators of rodents. The remaining species are limited in numbers and distribution on the study area, or do not eat mammals.

Interspecific competition may be lessened by partial ecological isolation. Habitat differences for these five snakes have been noted. Klauber's (1972) descriptions of the habitats favored by *Crotalus atrox* and *C. scutulatus* suggest that *C. scutulatus* generally is found in more barren areas than *C. atrox*. This was also true in the present study but a large degree of habitat

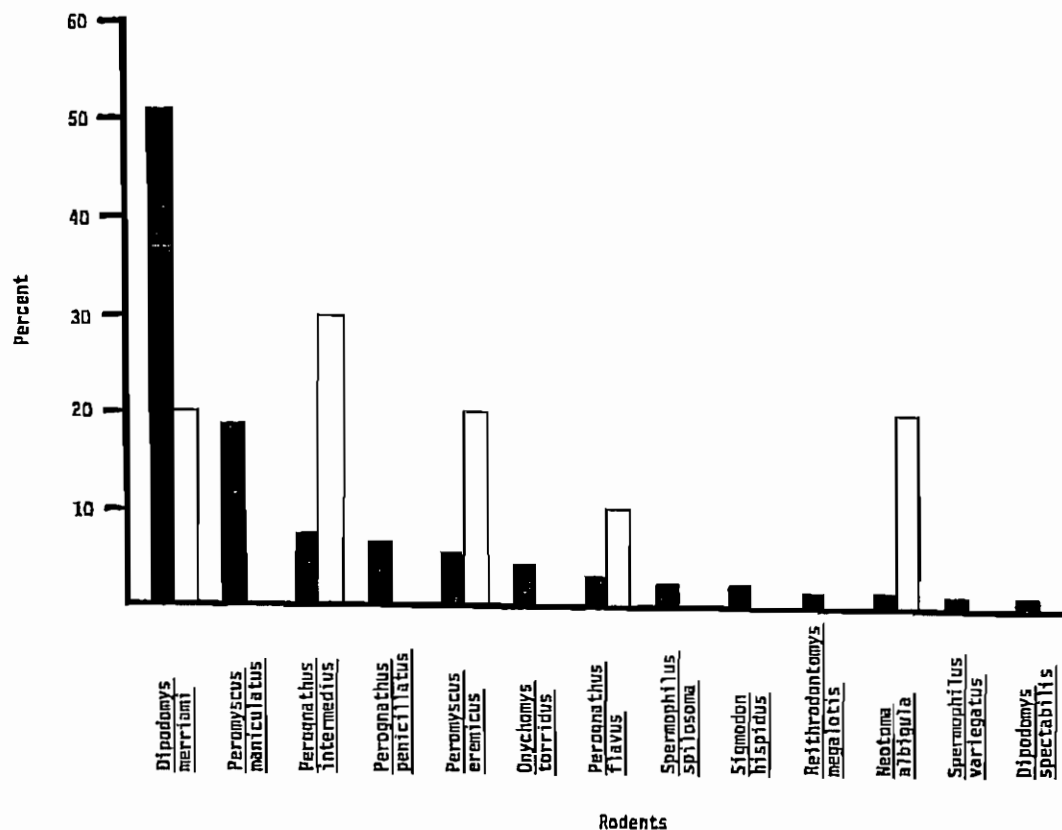


Fig. 5. Proportion of rodents trapped in the study area (closed bars) and the frequency of occurrence of each species in the diet of *Elaphe subocularis* (open bars).

overlap exists for these species and *Pituophis melanoleucus*. Pough (1966) also found considerable habitat overlap for these species in southeastern Arizona.

Although Klauber (1972) considered that sympatric populations of two or more species of rattlesnakes could be competitive, it is generally believed that this is only a temporary situation (Pough 1966 citing Mayr 1963). In this light, the broad overlap of *C. atrox* and *C. scutulatus* indicates that the species either are not competing or that the situation is unstable. Jacob (1977) described a situation in which *C. atrox* and *C. scutulatus* occur syntopically in an unstable desert grassland ecotone described by Morafka (1977) and postulated that these species may be able to coexist because their density is probably lower than in stable areas and the food supply may be exploited submaximally.

Although niche differences can be extremely subtle, apparently there is considerable similarity between the niches of *C. atrox* and *C. scutulatus*. It seems reasonable to assume, as did Klauber (1972), Damman (1961), and Pough (1966), that where they occur together these species are potential competitors. In view of their studies and the present study it appears that considerable habitat overlap is normal for these species, suggesting that their respective niches differ. Each species is most abundant in habitats and plant densities that are different from those of the other species.

In the study area *C. molossus* and *Elaphe subocularis* are almost entirely separated from *C. atrox*, *C. scutulatus*, and *P. melanoleucus*, and may experience reduced competition through differences in basic biology (size, morphology, venom vs. constriction) and foraging

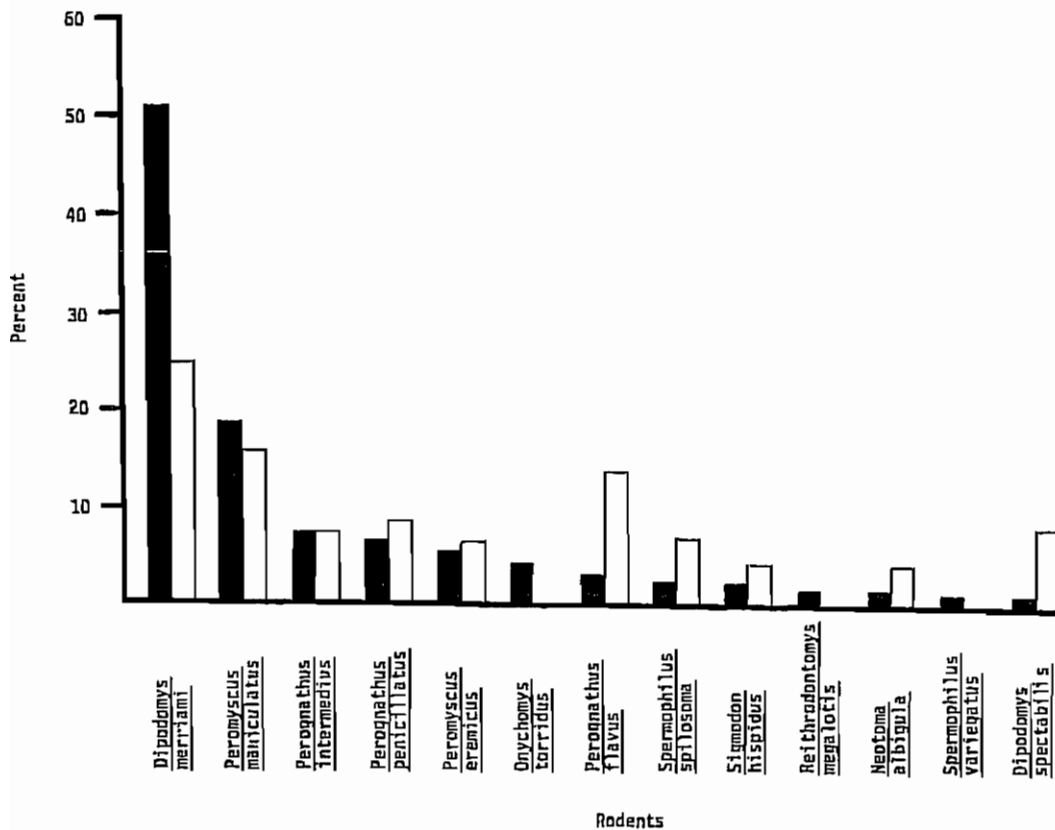


Fig. 6. Proportion of rodents trapped in the study area (closed bars) and the frequency of occurrence of each species in the diet of *Crotalus atrox* (open bars).

behavior (sit and wait vs. active foraging). Differences in biology would allow for reduced competition among *Pituophis melanoleucus*, *C. atrox*, and *C. scutulatus* where the three occur syntopically.

The prey community on which the snakes are actual or potential predators is diversified in terms of species, size, life forms, and behavior. Although a variety of rodents are used as prey, the data suggest that some are eaten more than others (e.g., *Dipodomys merriami*, *Peromyscus maniculatus*, *Perognathus flavus*). Considering that most adaptation is a compromise between biotic and abiotic selective factors, we cannot assume a priori that prey is exploited at maximum efficiency in a given predator-prey system. MacArthur and Levins (1964) provided a theoretical model in which an organism that limits the variety of resources it uses enhances its

fitness. The use of certain prey would depress a predator's fitness if it has to expend more energy obtaining the food than it receives from it. Also, the potential hazard of certain prey items would reduce a predator's fitness. The predator would do better to invest the time and energy needed to obtain this prey item searching for a more rewarding one. It is probable that certain rodents, by virtue of their size, population density, ability to escape, activity patterns, fierceness, or habitat preferences, essentially might never be exposed to certain snake predators.

Perez et al. (1978a, 1978b) found that *Neotoma micropus*, *Spermophilus mexicanus*, and *Sigmodon hispidus* have naturally occurring antihemorrhagic factors in their blood which provide them with a high resistance to *Crotalus atrox* venom. It is probable that *N. albigula* and *S. variegatus* share such resistance. Cottam et al.

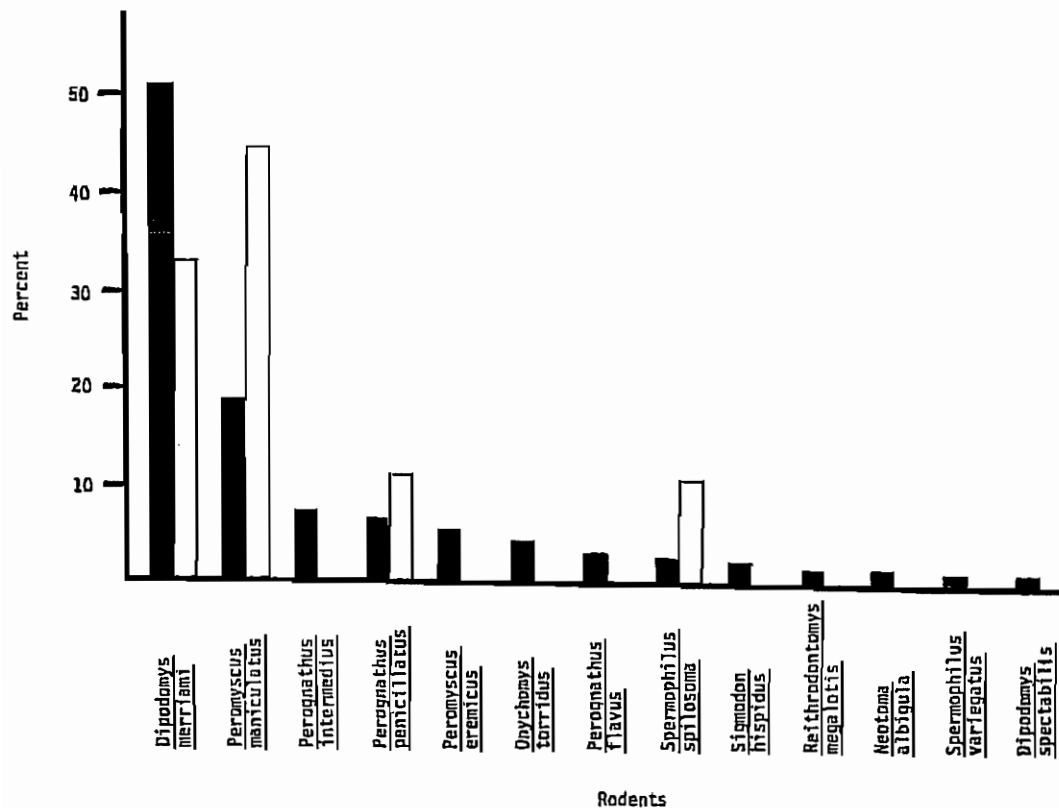


Fig. 7. Proportion of rodents trapped in the study area (closed bars) and the frequency of occurrence of each species in the diet of *Pituophis melanoleucus* (open bars).

(1959), on the Wedler Wildlife Refuge in Texas, found that the two most important food items in the stomachs of *C. atrox* were *N. micropus* and *S. hispidus*. In the present study, *C. atrox* contained *S. hispidus* and *C. molossus* had *N. albigula* in their stomachs.

Natural resistance in these rodents is not surprising because they live in the same habitat as rattlesnakes and often in the same midden as woodrats. The carnivorous diet of rattlesnakes and their cohabitation with these rodents are two possible reasons for the evolved resistance of these animals to rattlesnake venom. It is apparent, however, that this defense against rattlesnake venom is not always effective. In terms of the evolution of the predator-prey system, the relation of snake venom toxicity and the degree of rodent resistance is a dynamic situation; the rodents are constantly evolving resistance, and

snake venom is evolving to overcome this resistance. The cost of the system to the animals is unknown as is the mechanism of neutralization (Perez et al. 1978b).

Predator body size is an indicator of food size for some species of mammals (Rosenzweig 1966; McNab 1971; Brown and Lieberman 1973; Mares and Williams 1977), birds (see Schoener 1971 for references), lizards (Schoener 1968; Pianka 1969), and amphibians (Fraser 1976). Many snakes, as compared with other terrestrial endothermic vertebrates, do not sharply discontinue growth at sexual maturity. This results in more variation in adult size. The kind of prey taken depends on snake size; the smallest individuals are probably most restricted in terms of the kinds of prey used (Wilson 1975). Stomach content data (Table 7) show that lizards are included in the diet of young *Crotalus atrox* and

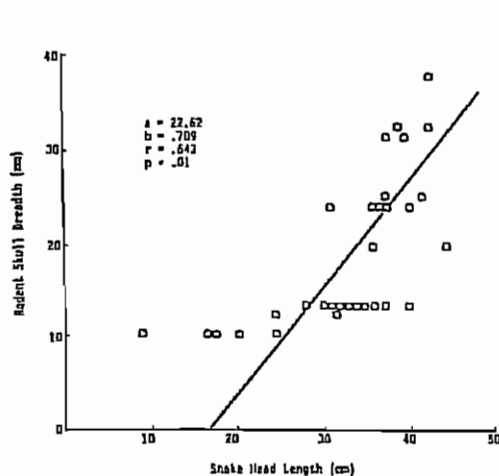


Fig. 8. Regression of head length of *Crotalus atrox* and average rodent prey skull breadth.

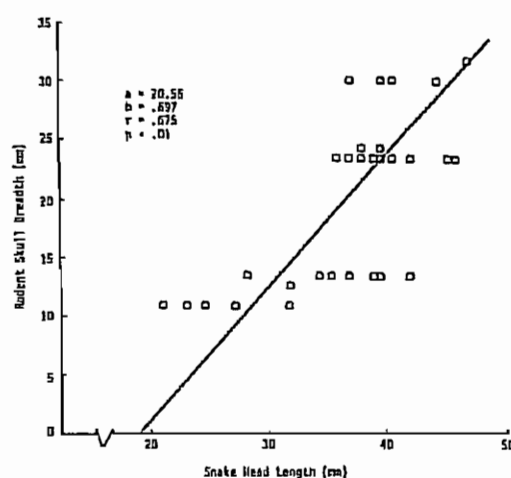


Fig. 9. Regression of head length of *Crotalus scutulatus* and average rodent prey skull breadth.

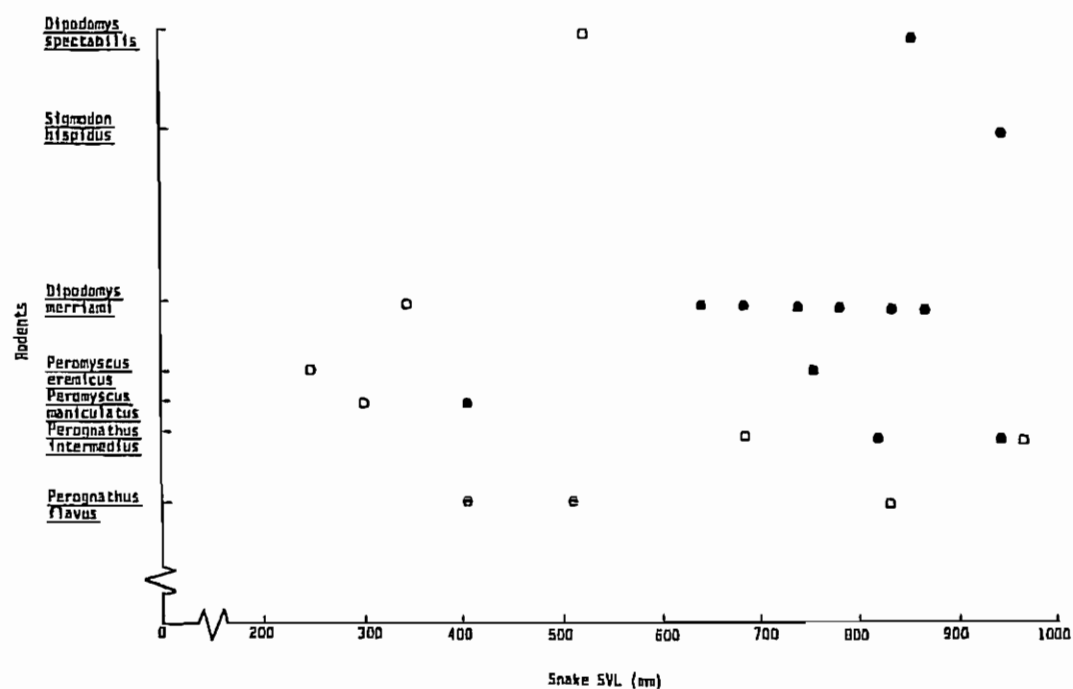


Fig. 10. Results of arena studies with *Crotalus atrox* showing acceptance (•) and rejection (◊) of rodents introduced to various-sized snakes. Rodent position on ordinate proportional to average skull breadth, smallest at bottom.

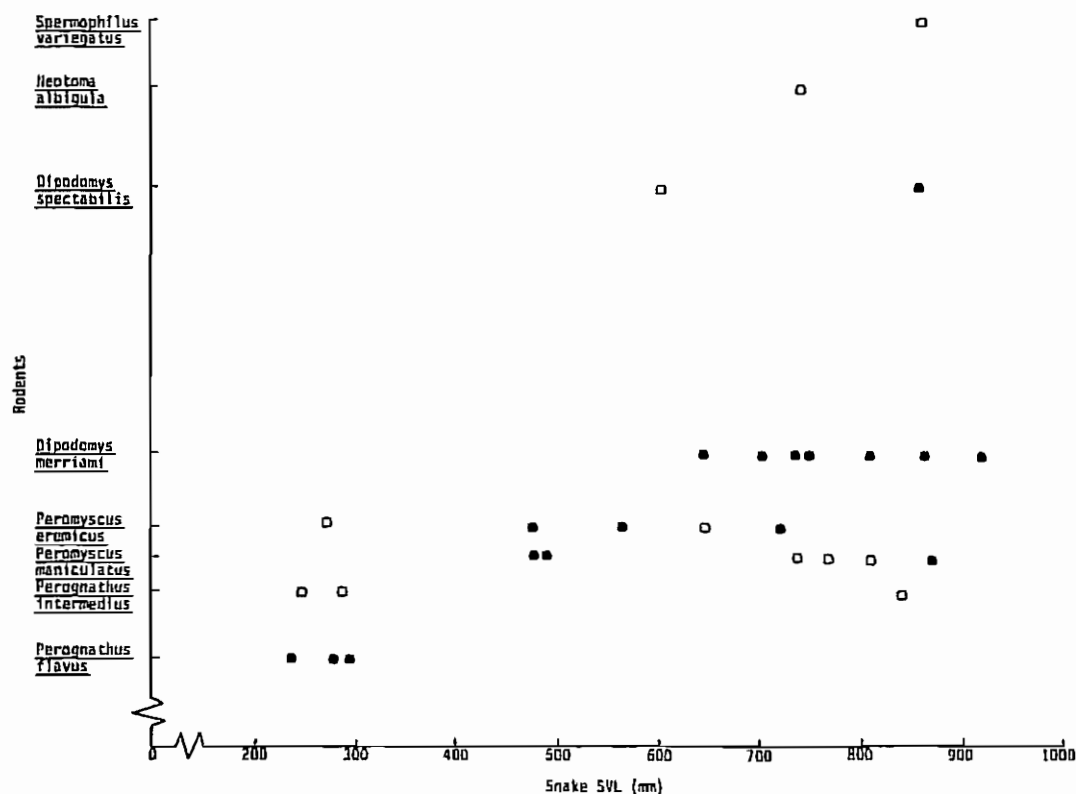


Fig. 11. Results of arena studies with *Crotalus scutulatus* showing acceptance (•) and rejection (○) of rodents introduced to various-sized snakes. Rodent position on ordinate proportional to average skull breadth, smallest at bottom.

arthropods (insects and millipedes) were taken by young *C. scutulatus*. Damman (1961) suggested that *C. scutulatus* eat more lizards than do *C. atrox* but presented no data to support this statement.

Food supply is the ultimate factor limiting snake populations (Fitch 1949). The presence of a diverse rodent community assures a reliable resource through ecological time. Also, it assures food for snakes of all sizes since certain prey species are taken largely by the young, and others predominately by larger snakes. Considering the fluctuating nature of rodent populations in desert regions (French et al. 1974; Whitford 1976), the optimum strategy of a mammal-eating snake would be that of a species generalist. Within this prey spectrum, the snake can then choose the optimal-sized prey.

In the present study, rodents such as *D. merriami*, *Peromyscus maniculatus*, and *Perog-*

nathus flavus are so abundant and widespread that they are probably not limiting to snakes and therefore there is no competition for them. They may, however, become limiting during periods of extreme population decline. *Crotalus scutulatus*, *C. atrox*, and *P. melanoleucus* are most widespread throughout the various habitats and have the greatest number of rodent prey species available to them. In comparison, *C. molossus* and *E. subocularis* are more restricted to rock habitats and have fewer common rodents available as prey. Birds represent a large proportion (16.7%) of the diets of both these species and they were the only snakes containing *Neotoma albigula*. The inclusion of birds and woodrats in the diet would provide an alternative food resource and reduce competition between these species for the remaining rodent species. Also, Degenhardt and Degenhardt (1965) noted that *E. subocularis* feeds on bats in captivity. Both *E.*

guttata and *E. obsoleta* reportedly prey on bats in nature (Herreid 1981), and it seems likely that *E. subocularis* would also. Inclusion of bats in the diet of *E. subocularis* could reduce competition between this snake and the less scansorial *C. molossus*.

Other vertebrate predators observed in our study area included canids (three species), a felid, procyonids (two species), mustelids (two species), hawks (three species), and the great-horned owl (*Bubo virginianus*). In contrast with the associated predatory mammal and bird species, snake populations occur in much higher concentrations. Fitch (1949), in an area where all predators were abundant, estimated that there were 120 rattlesnakes to each horned owl, 190 to a red-tailed hawk (*Buteo jamaicensis*), and hundreds to a coyote (*Canis latrans*). Factors favoring such concentrations are the relatively small size and the low metabolic rate of snakes allowing subsistence on small food items with long fasts intervening. Also, snakes are relatively long-lived compared with their prey species and may outlive many generations of rodents, and thus survive drastic, periodic changes in prey numbers. Birds and mammals are considerably more vagile than snakes and may respond to reductions of prey populations by moving to new areas, whereas snakes are physiologically better able to weather times of prey scarcity. Snakes, therefore, may have a more continuous influence on prey populations, especially during times of prey scarcity, than those predators whose numbers track the population cycle of prey species.

Snake predation on rodent populations on the San Joaquin Experimental Range had a minor effect on rodent population control (Fitch 1949), but combined with other vertebrate predators, predation accounts for a large part of the annual surplus of rodents. Small mammal populations probably are not predator limited. This has been shown for *Sciurus vulgaris* (Formozov 1933), *Sciurus niger* (Allen 1943), *Rattus norvegicus* (Davis 1951), *Ondatra zibethicus* (Errington 1963), and *Microtus californicus* (Pearson 1966, 1971). Presnall (1950) has similarly concluded that, although rodents are preyed upon intensively, the fluctuations in their numbers are not determined by predation. This applies to such species as the meadow mouse (*Microtus pennsylvanicus*), kangaroo rat (*Dipodomys* sp.), cottontail rabbit (*Sylvilagus floridanus*), and

jackrabbit (*Lepus californicus*) (Presnall 1950).

Foraging

Pyke et al. (1977) stated that dietary similarity is central to determination of competitive coexistence of species and that predation, as determined by the foraging behavior of all animals in a community, is the core of its structure. There is a range of possible foraging behaviors determining what prey is eaten, choice of patch type in which to hunt, allocation of time to a patch type, and the patterns and speed of movements. Differences in foraging of the predators and prey in the present study are important to limiting competitive interactions.

Crotalus atrox, *C. scutulatus*, *C. molossus*, and *E. subocularis* are primarily nocturnal, whereas *P. melanoleucus* is diurnal until the onset of summer rains when it becomes crepuscular. Among a group of mammal-eating vertebrates with similar morphologies, noncoincident feeding times could be a mechanism for reducing competition if the prey were also noncoincident in their activity. The heteromylid and cricetid rodents (except *Signodon hispidus*) and lagomorphs are primarily nocturnal or crepuscular, whereas the squirrels, *S. hispidus*, birds, and lizards are diurnal or crepuscular in activity. The opportunity to relieve competition through temporal activity differences of predators and prey is present in this community. The food items of *P. melanoleucus* contain crepuscular and diurnal prey including *S. auduboni*, *L. californicus*, *S. spilosoma*, and birds; however, this snake actively searches for prey, often raiding rodent nests (Fitch 1949). As rodent nests are generally underground, it is probable that adult rodents are taken in their burrows as the snake searches for the nest.

In the present study, *S. hispidus* was found only in the mesquite-grassland where *P. melanoleucus* had its highest frequency of occurrence. However, no *S. hispidus* were included in the diet of this snake species. It appears that *P. melanoleucus* is better adapted to foraging for rodents in underground burrows than to hunting *S. hispidus* in grass runways.

The arena tests showed that both *P. melanoleucus* and *E. subocularis* actively pursued their prey about the test arena, whereas *C. atrox*, *C. scutulatus*, and *C. molossus* employed a sit-

and-wait strategy. The three *Crotalus* species remained motionless in the behavior box until a rodent walked to within striking distance, at which time the snake would strike. A greater number of prey species were found in the diet of the *Crotalus* as compared with the colubrids (Table 7). Random draws, however, from the *Crotalus* samples to adjust for sample size differences between *Crotalus* and the colubrids show no significant differences in the number of items included in diets. The mobility of the colubrids allows the optimal use of suitable habitat patches by hunting only in those patches where the time per item caught is short. The model presented by MacArthur and Pianka (1966) predicts that "pursuers" (i.e., sit-and-wait predators) should show more restricted patch use than searchers where food is dense. The sit-and-wait *Crotalus*, as opposed to the searchers, employ a passive mode of hunting which dictates opportunism and relies on the mobility of the prey, using suitable prey in the proportion that they occur in the environment. There appears to be no differences in successfully procuring prey between the foraging methods employed by the *Crotalus* or colubrids.

Habitat Segregation

The patterns of diversity and interspecific separation of the prey and predatory communities herein described are largely based on habitat segregation. If snakes are competing for food, spatial differences in habitats of sympatric snakes will most effectively reduce competition when these differences coincide with spatial habitat differences of prey species. Schoener (1974) noted that the habitat dimension is usually more important than food type in resource partitioning among reptiles, and concluded that isolation by habitat is more important to terrestrial animals than it is to aquatic animals. In those studies dealing with aquatic or semi-aquatic snakes (Carpenter 1952; Fleharty 1967; Mushinsky and Hebrard 1977) the food dimension was found to be more important than habitat. Shine (1977), however, found that for six elapid snake species in Australia, habitat separation played a more prominent role than food type in resource partitioning. These snakes were opportunistic feeders, relatively unselective with respect to prey type or prey size, due to the limited food resources available. He found a

preponderance of lizards and frogs in the diets of all species and suggested this is due to the scarcity of small mammals and fish in Australia.

Recently, Maorana (1978) concluded that spatial dispersion of two plethodontid salamanders widely sympatric in California allowed for their coexistence and regulated population densities. The evidence suggested that burrows were the regulating resource and differences in diet simply an epiphenomenon of the spatial distribution.

The use of food and habitat dimensions are clearly complementary in the snakes studied. There are more food and habitat types available to a snake than it uses. This indicates that a snake exhibits a choice as to the habitat it occupies or prey it eats. Within a habitat type, evolution would favor those snake phenotypes that are better at extracting energy from the more available prey types.

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