CHAPTER 8

DISCUSSION

A COMPARISON OF THE HERPETOFAUNA IN DIFFERENT HABITAT TYPES IN TEMPERATE AND TROPICAL AREAS

The various adaptations and mode of life of the reptiles and amphibians have been discussed. However, to examine individual species narrowly would be to neglect them as integral parts of a community. They should, therefore, also be considered in a broader context and compared with similar groups of reptiles and amphibians in other ecological zones.

A biotic community is an assemblage of organisms living together and interacting at all trophic levels. Consequently a community is not limited to specific taxa and, therefore, to speak of a 'herpetological community' by definition is not an ecologically meaningful entity,(Heatwole 1977), but rather to call these segments of the community 'herpetofaunal assemblages'. Barbault (1976b) terms these units 'herpetocenoses'. Inger & Colwell (1977) refer in their paper to the ecological organization of the herpetofauna which they examined in Thailand. Whatever connotation one applies to these terms, it is essentially a number of similar organisms and their interactions both with their environment as well as among themselves, and within which the Nylsvley Ecosystem Study was partitioned. In this discussion the term herpetofaunal assemblage will be adhered to as outlined previously.

The nature of the organization of species of reptiles and amphibians in an assemblage and the factors affecting such structure is an important aspect. It has long been accepted that numbers of species of reptiles and amphibians increase from higher to lower latitudes. This is exemplified by a comparison of species in temperate and tropical localities (Table 51).

Table 51. Comparison of species numbers of amphibians, lizards and snakes in different habitat types in temperate and tropical areas, Barbault (1975, 1976a) and Inger *et al* (1977).

Habitat	Amphibians	Lizards	Snakes	Total
Nylsvley N.R. Tvl.	24°39'S	28°42E	630 mm	1110 m alt.
Burkea africana savanna	11	17	21	49
Combretum apiculatum savanna	7	16	17	40
Acacia tortillis savanna	12	12	19	43

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Nyl river floodplain	15	4	6	25
Total species in all habitats	17	23	29	69
*Lamto, Ivory Coast	$6^{o}13'N$	$5^{o}02'W$	1280 mm	± 140 m alt.
Herbaceous savanna	13	5	21	39
Wooded savanna	16	8	26	50
Total species in savanna	24	8	29	64
Total species in all habitats	38	17	40	95
*Sakaerat NE Thailand	$14^{o}30'N$	$101^{o}55'E$	1500 mm	± 140 m alt.
Evergreen forest	19	28	29	76
Deciduous forest	20	18	27	65
Total species in all habitats	25	31	47	103

However, as is apparent from Table 51, it is not sufficient to look at basic latitudinal differences between the faunas but also to take into consideration the structure of the habitat whether forest, savanna or desert. A forest offers a greater diversity of microhabitats, for example, than possibly a desert. Altitude, climate and substrate are also important factors. Rainfall is one of the most important limiting factors including too much or too little. Seasonal differences in this commodity are extremely important. The high rainfall areas of north-eastern Thailand exhibit the greatest number of lizards and snakes while the amphibians are most abundant at Lamto. This may be due to the greater seasonality of the former as opposed to the latter, where virtually only one month of the year is on average relatively dry. This is also reflected by the amphibians which are more diverse at Lamto than at Sakaerat. The relative paucity of lizards in the savanna at Lamto is very marked when compared to Sakaerat and Nylsvley. The diversity and structuring of the habitats are no doubt responsible for the differences while rainfall also plays a role. The high rainfall appears to limit species diversity of lizards at Lamto although Thailand in contrast exhibits a greater diversity because it experiences a longer dry season. Evergreen forest in particular exhibits a lizard species diversity unequalled by any of the other habitats under discussion (Table 51). The geckos, agamas and skinks have obviously adaptively radiated under these conditions. The first and last groups show a wide tropical distribution but both also exhibit two primary centres of radiation, one in African and one in the Indoaustralian regions while the agamids have extensively radiated into different habitats, Goin, Goin & Zug (1978). Diversity was apparently favoured at Sakaerat, particularly with arboreal species (Table 52).

Table 52. A comparison of the habitats of lizards in the three areas under discussion.

	Lamto				Sakaerat				Nylsvley			
	T	A	F	R	T	A	F	R	T	A	F	R
Geckonids	0	5	0	0	3	8	0	0	2	1	0	1
Agamids	0	0	0	1	1	7	0	0	1	1	0	0
Chameleonids	0	1	0	0	0	0	0	0	0	1	0	0
Scincids	5	2	1	0	8	2	1	0	3	1	2	1
Lacertids	0	1	0	0	1	0	0	0	5	0	0	0
Gerrhosaurids	0	0	0	0	0	0	0	0	1	0	0	1
Varanids	1	0	0	0	0	0	0	0	2	0	0	0
	6	9	1	1	13	17	1	0	14	4	2	3

T = terrestrial, A = arboreal, F = fossorial, R = rupicolous

Lamto and Sakaerat exhibit similar trends whereas Nylsvley showed the greatest terrestrial diversity while arboreal niches are lacking. Both Lamto and Sakaerat offer a greater diversity of arboreal niches. However, neither of the latter two areas exhibit rupicolous niches. At Lamto an agamid is principally found around human habitation and therefore appears to have occupied a niche not exploited by other forms. Similarly on the Nylsvley Nature Reserve, <u>Mabuya</u> <u>s</u>. <u>punctatissimus</u> occurs principally around human habitation and is rarely seen in the field and is then only arboreal. Nylsvley Nature Reserve, however, exhibits a greater number of terrestrial forms which indicate that the diversity of this habitat is greater than that offered by the other two areas. There are generally few taxonomical similarities between the African and Asian areas under discussion. Only three amphibian, three lizard and four snake genera have counterparts in Asia, while species and generic similarities between the Nylsvley Nature Reserve and Lamto are of a high order. Three species and five genera (45%) of amphibians, one species and seven genera (77%) of lizards and seven species and sixteen genera (53%) of snakes are shared by these two areas. Unfortunately a complete list of amphibians has not been seen so that relative values are approximate. One species of amphibian Kassina senegalensis and one species of snake Psammophis sibilans are common and abundant in both areas.

Figure 93 illustrates the equitability of the areas under comparison. It is apparent that both the Deciduous Forest in NE Thailand, as well as the deciduous Burkea africana savanna on the Nylsvley Nature Reserve are more equitable than either of the other habitat types. Both the Evergreen forest in NE Thailand as well as the Wooded Savanna at Lamto exhibit between the first two and the last two sites. However, in all instances illustrated, from 1 to 7 species dominate the assemblages, the remaining species being relatively uncommon. This is typical of tropical species and herpetofaunal assemblages.

Although the Nylsvley Nature Reserve lies at a considerably higher altitude than the other areas, it does nevertheless exhibit a greater degree of equitability which is in contrast to what Heatwole (loc.cit.) mentions. There does appear to be some correlation with other factors including rainfall and no doubt number of dry months in the year. The high rainfall areas depicted in Figure 93, all exhibit a similar trend with the exception of the Deciduous Forest where a greater degree of equitability was also apparent as mentioned previously. This is in contrast to what has been documented for Thailand and probably has been overlooked.

Differences between the Thailand and African herpetofaunal assemblages are also apparent. For instance, the Evergreen Forest in NE Thailand is dominated by lizards and amphibians while the Deciduous Forest is almost exclusively dominated by lizards. Although the former is largely true in the African context, snakes are more important than they are in the Asiatic context and feature more prominently. With regard to species diversity the Thailand examples show an incredible array including large numbers of rare or uncommon species which is not equalled in the African context. The Nylsvley Nature Reserve in this regard tends to exhibit an abrupt decline between the common and the not so common species and therefore not as gradual as that of the other species. Pianka (1975, from Inger & Colwell 1977)

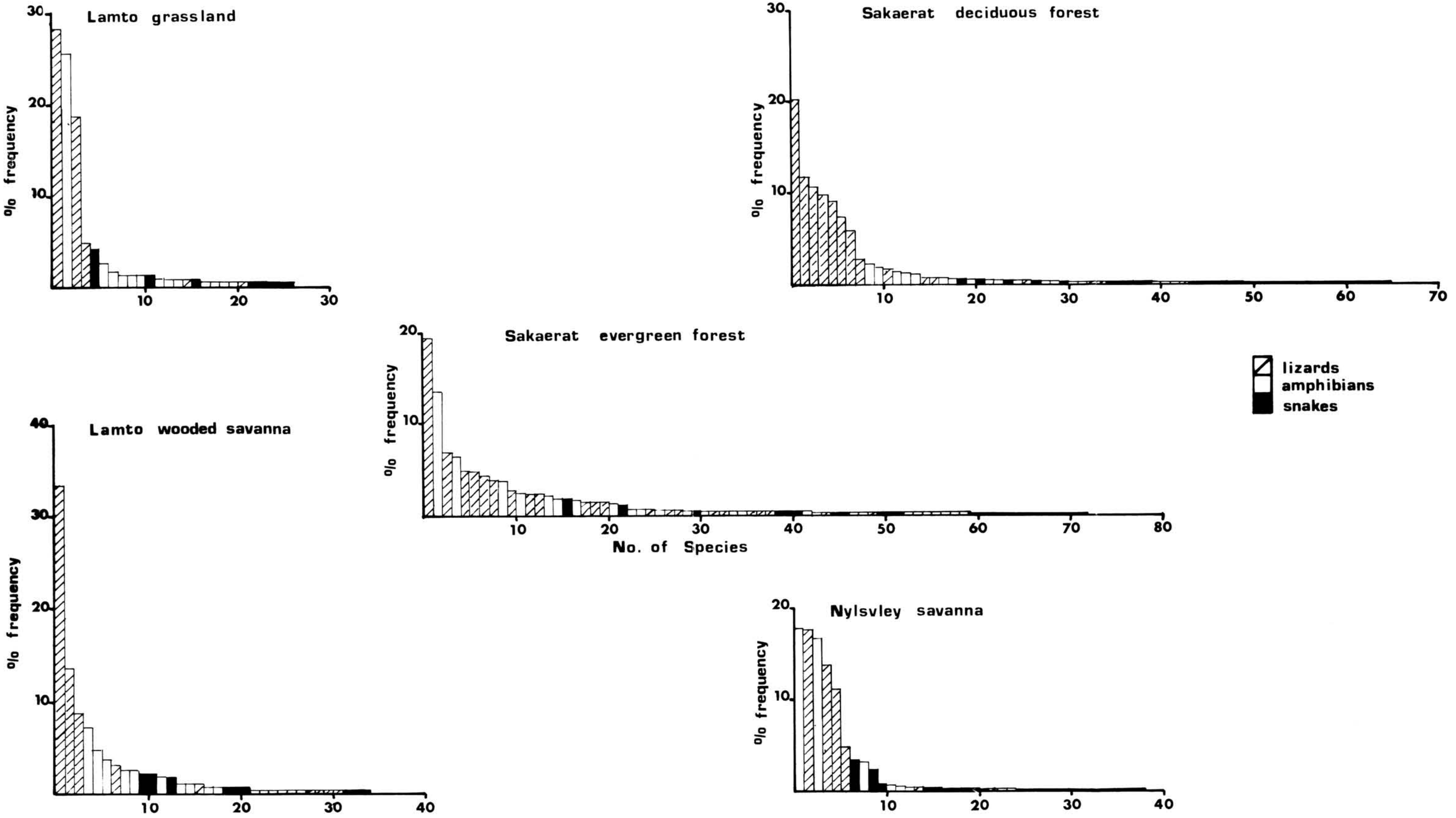

Figure 93. Equitability of different areas under comparison.

finds a positive relationship between species richness and environmental predictability which would predict greater diversity in the Tropics declining away from the Tropics although other factors may also be important.

Inger & Colwell (loc.cit.) maintain that interactions among species are important in the patterning of communities. While the physical-chemical environment demands certain minimum physiological adaptations for entrance into a community, every species must also pass the much more demanding criteria imposed by the biotic environment, particularly necessities such as finding food, coping with predation and reproducing successfully, which will be discussed presently.

Pianka (1977) states that provided that all else being equal, Assemblages with fewer different resources will support fewer species thereby indicating the basic difference between the Burkea africana Savanna and the Acacia Savanna on the Nylsvley N.R. However, although exhibiting fewer niches, there are more of each niche so that continuity is greater which therefore enables a greater density and biomass of each species which is a feature of the Acacia Savanna. This may also be the case at Lamto where there are three basic vegetation types of which the study utilized two, namely herbaceous savanna or grassland and wooded savanna including palms and other trees. Secondly, the number of species which can co-exist within an Assemblage decreases as the diversity of utilization of resources by an average species increases. Thirdly, the amount of niche overlap will affect the number of species able to exist within an environment. Fourthly, in spite of having the similarities discussed previously, the species diversity in Assemblages can still differ in the extent to which they actually support as many different species as possible or until 'saturated'. Resources seldom go unused for very long and it is perhaps the reason why such low density species, such as Mabuya capensis and Psammophis angolensis suddenly appear within the Assemblage.

Species diversity is enhanced by within-habitat partitioning of space. Considerable variations exist in the manner in which reptiles use space. In this study one snake and three lizard species are discussed, each with different requirements but generally only occupying home ranges without being territorial. Diversity of microhabitats and their use are responsible for this diversity. It is probably for this reason that the Burkea africana herpetofaunal assemblage is as diverse as that of Lamto. Differences between these areas are largely due to latitude, rainfall and habitat diversity. Latitude, as we have seen, tends to promote stability of climate the closer one gets to the Equator. Rainfall tends to enhance specific group differences such as a greater diversity of amphibians and also snakes at both Lamto and Thailand. Lizards in contrast are more diverse at Nylsvley than at Lamto, because of the greater number of niches rather than a saturation of niches. Lizards appear to diversify in a more arid environment as Pianka (1969) for example observed 39-40 species living sympatrically in parts of Australian desert areas. On the other hand, lizard species diversity in Thailand are very high as a result of the 5-6 month dry period.

Habitat, microhabitat and niche occupation may lead to physiological and anatomical adaptations such as the expanded digits of the arboreal lizards and frogs while burrowing forms develop elongated cylindrical bodies and degeneration of limbs. Snakes too have achieved a tremendous degree of variation in this respect. The snakes on the Nylsvley Nature Reserve have adapted well to their environment. Considering the ratio of tail length to : snout/vent length, a function of their anatomical adaptations correlate it with the ways in which these reptiles use space, (Figure 94).

Arboreal snakes approach a 1:1 ratio of tail to snout/vent length closest as the tail is extremely useful when moving through the tree canopy and as anchorage. The sandsnakes exhibit a close ratio which is explained by their active foraging habit which ensures adequate purchase against objects to acquire a greater speed when chasing after swift moving prey. The puff adder, however, approximates the burrowing species which again is correlated with its feeding strategies, of lying in wait along rodent tunnels in thick grass cover and acting like a mouse trap. The burrowing species and especially Typhlops are well adapted to a subterranean life. The blunt head with the large scale to force through the soils assisted by a cylindrical body, while the short blunt tail enables the animals to reverse inside the burrows, all go to make the blind snakes ultra specialised. Numerous other adaptations exist which determine the success of survival.

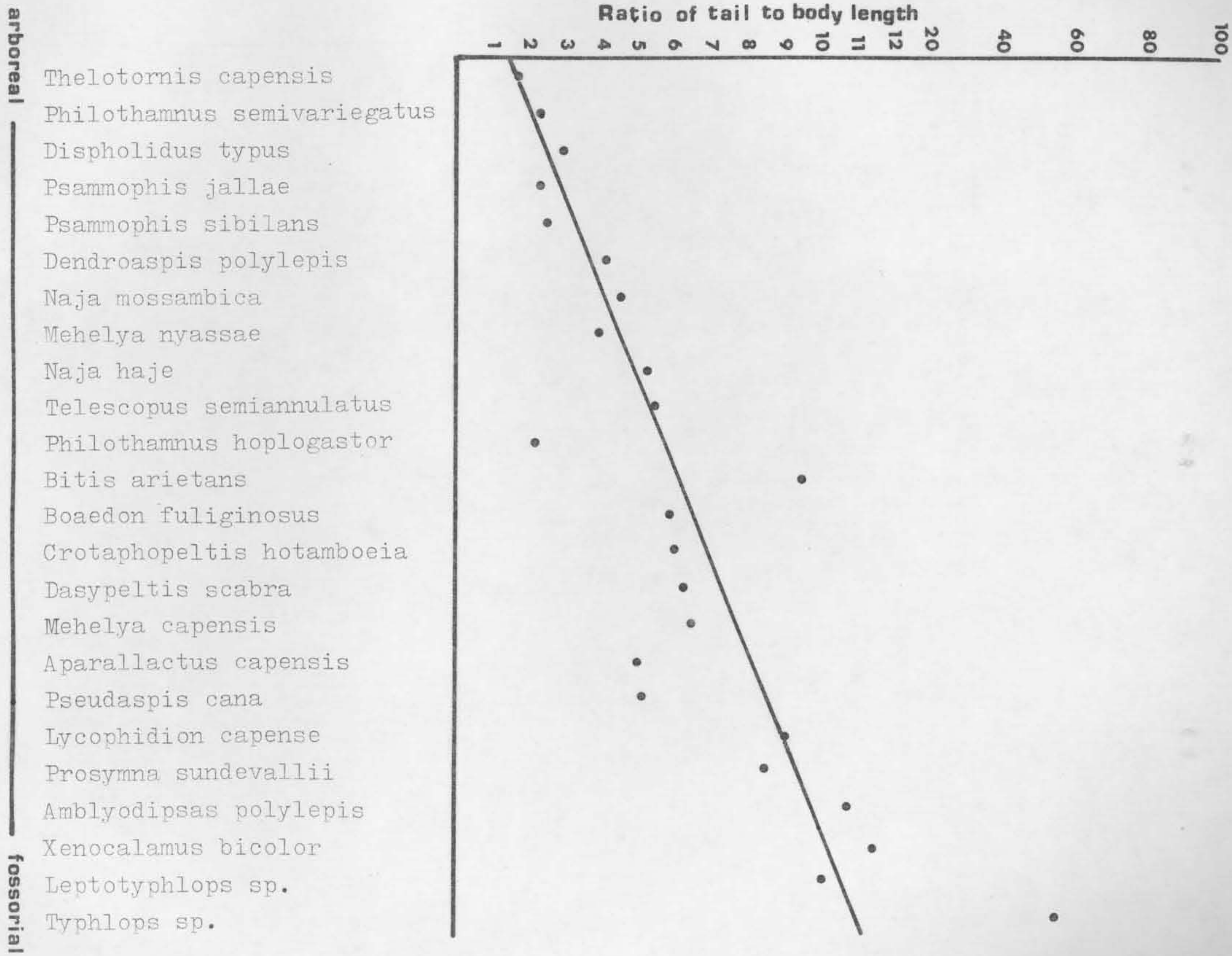

Figure 94. Ratio of tail length to snout/vent length as a function of the snakes adaptations to their respective microhabitats and niches.

Species diversity and numbers are important in a comparison of areas but in themselves are not enough. It is also essential to determine their biomass per unit of habitat if community structure is to be fully understood. Although biomass values have been reported for a few individual species of herpetofauna, the biomass of entire herpetofaunal assemblages have scarcely been studies, Heatwole (loc.cit.).He quotes the work of Barbault as an exception. Previous discussions in other Chapters have centred around the work of Barbault at Lamto on the Ivory Coast. Here mean annual biomass of snakes was 150 g/ha, lizards 89,59 g/ha and amphibians 179,42 g/ha with highest values occurring during the wetter parts of the year. A similar situation exists in the Burkea africana Savanna, where the longer dry season precluded amphibian activity, while cooler weather affected lizard and snake activity and, therefore, biomass. Seasonal influences on biomass included mortality and reproduction as some species exhibited annual life cycles. Similar situations were also apparent at Lamto where the maximum mean life expectancy after maturity (6 months of age) is about nine months for female Mabuya maculilabris, Barbault (1976a). Mean annual biomass of snakes in the Burkea africana savanna was 93,36 g/ha, for lizards 64,36 g/ha and amphibians 593,4 g/ha.

Barbault (loc.cit) suggests that the high predation pressure undergone by small tropical lizards produces selection for increasing fecundity rather than for increased adult survivorship. Although the data are fragmented, a similar situation exists in the Burkea Savanna except that the situation is compounded by the long, cold and dry winter months which suppresses growth rate of immature animals.

Type of habitat may be important in biomass stability. Barbault (1967, in Heatwole 1977) found that total biomass of terrestrial lizards showed large seasonal fluctuations; low values occurred following fires after which they rose and reached a peak by the end of the rainy season; by contrast arboreal lizards did not reflect a similar trend. This situation too is apparent on the Nylsvley Nature Reserve with the exception that fires were very rare so that seasonal turnover was rather more a function of climate, reproduction and predation. However, the arboreal and long lived Cape dwarf gecko did not fluctuate as much as did the terrestrial species which is in agreement with Barbault's conclusions.

In contrast the amphibians in the Burkea Savanna are mostly dependent on moisture. Maiorana (1976, in Heatwole 1977) states that many species are dependent on standing water or its proximity for reproduction and suggested that predation pressure on larvae and competition among them for such aquatic environments are probably intense. Therefore in the equable tropics conditions favouring reproduction are extended throughout most of the year and amphibians become temporally segregated using breeding water sequentially in time, thereby avoiding competition. Therefore, more species can co-exist than in seasonal environments, where favourable conditions do not persist long enough for temporal segregation of more than a few species. This view is supported by Barbault (1976b, c) and is illustrated by the number of amphibians at Lamto and at Sakaerat in NE Thailand in comparison to the Burkea africana Savanna. In the former, a greater and more widespread rainfall with a very short, if any, dry season, enables the amphibians to breed at different times and in a greater number and variety of habitats in comparison to either Sakaerat where the dry season persists for five to six months and the Nylsvley Nature Reserve where the dry season may last six months, while at least one month within the rainy season will also be relatively dry. Here the amphibians breed when the rains come and breeding therefore varies from year to year. If the rainfall is erratic then a poor survival rate is achieved, as opposed to a successful season when adequate water bodies are formed. Larval mortality is great in the seasonal rainfall areas and, therefore, important in regulating population densities. This is borne out by the differences in numbers of amphibians captured in the Study Area over the 1975/76 season when compared with those of the 1976/77 season (Chapter 4.) Fluctuations in numbers being largely a function of immigrating juveniles, particularly during the months of January, February and March, which are a feature not experienced to such a degree at Lamto.

Habitat selection is not confined only to breeding sites but also includes aspects such as food and shelter, particularly from predators. It was mentioned in Chapter 7 that juvenile and subadult Lygodactylus capensis were most commonly found on shrubs and trees which offer marginal shelter from predation and therefore results in spatial separation of the immature or ontogenetic stages. This enables a population to inhabit all available habitat such as the Cape Dwarf gecko (Figure 25) does. Similarly, the fact that nocturnal snakes are most prevalent in the Burkea savanna and yet feed mostly on diurnal lizards, indicates that shelter is a possible limiting factor. Skinks have been observed sheltering under leaf litter surrounding Ochna and Grewia shrubs and their reaction if molested of bursting out of their cover and running off a short distance before stopping to look at the origin of the disturbance is indication of the predation pressure involved. Most snake species at Nylsvley feed on lizards and fewer on amphibians (Chapter 5), while at Lamto most species feed on amphibians as their availability extends throughout the year. This can be attributed purely to rainfall which on the one hand appears to depress lizard diversity, such as in West Africa, but in contrast enhances diversity in Thailand to the extent that it supercedes amphibian diversity. It is apparent that both diversity of habitats and evolution play an important role in determining species diversity.

Resource partitioning among the lizards and amphibians appears to be similar. Food does not appear to be a limiting factor. The differing sizes, different feeding times and even the different emphasis on different invertebrate orders preclude competition. Some show a degree of dietary restriction, such as the agamids, which feed on ants (Hymenoptera:Formicidae), similarly Ichnotropis capensis feeds mostly on termites in the Study Area, as has been found by Broadley (1979) in Zimbabwe. Panaspis wahlbergi also feeds on termites but avoids competition by being able to forage deeper in the leaf letter than does Ichnotropis. Some predation pressure is exerted on the snake-eyed skink by the variable skink. Most lizard species are, however, opportunistic feeders as can be seen from Tables 15-18 (Chapter 5). The amphibians, although competing for food with the lizards, are nocturnal and, therefore, temporally and spatially avoid competition with lizards. Considerable overlap is experienced in their feeding behaviour but because the amphibians differ greatly in size and are mostly dependent on moisture before they become active, are able to gorge themselves should the climate and food availability become favourable. This is an adaptation not found among the lizards, which are in any event independent of moisture, except for breeding, to a limited degree.

Competition between amphibian species is avoided by differences in food and a few species are ant and termite specialists. This situation is reflected at Lamto where even more species including sympatric ones have adopted a similar approach, Barbault (1976 c).

Home ranges were determined for three lizard and one snake species. Home range size is to a degree determined by various other factors, such as food availability, shelter, breeding sites and so forth. Turner, Jennrich & Weintraub (1969, in Stamps 1977) observed a positive relationship between body mass and home range size in lizards and noted that males had larger home ranges than females. This appears to be somewhat contradictory as female mass is usually greater than that of males so that the situation should be the reverse. However, size of animal may also have a bearing on the amount of food ingested, leading back to a resource/home range size relationship.

The lizards observed on the Nylsvley Nature Reserve did not exhibit territoriality and only the dwarf gecko was observed to defend an area in his immediate vicinity, which indicates a movable site depending on whether it is used for basking, foraging or possibly shelter, although no interactions concerning the latter were observed. Both the lacertid, the Cape rough-scaled lizard as well as the variable skink displayed overlapping home ranges as did the vine snake. Unfortunately the work of Barbault at Lamto did not provide comparable results. Broadley (loc.cit.) also demarcated home ranges for the Cape rough-scaled lizard on the basis of recaptures but owing to the relative paucity of recaptures the results are highly variable but home ranges appear to be considerably smaller.

In conclusion a great deal more remains to be learned about herpetofaunal assemblages and ecosystems so that patterns and origins of species diversity, number and biomass as well as their biotic and abiotic interactions can be understood more fully. In the present study of an Assemblage the results suggest that snake species diversity is governed by habitat structure and water either directly or more probably indirectly through changes in prey community diversity. On the other hand, lizard species diversity is dependent on the diversity of habitat structure, and in biomass on the seasonality of the climate and predation. The amphibians are solely dependent on moisture and therefore breeding sites which are vital to these animals in the dry Burkea Savanna.