

BIOGEOGRAPHY OF NOCTURNAL INSECTIVORES: Historical Events and Ecological Filters

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INTRODUCTION

One of the areas of overlap between systematics and ecology that has so far proven intractable to our understanding is community organization: To what extent does history constrain the structure of ecological communities? Or, how important is ecology in filtering historical elements? To clarify the distinction between the historical and the contemporary ecological perspective, consider the two extremes: (a) ecology is unimportant but history important, versus (b) ecology is important and history unimportant. (Obviously, any given situation in the real world lies somewhere between these hypothetical end points). However, a particular example can always be viewed from either perspective. For example, consider the Australian marsupial fauna. Historical: the facts that marsupials were present, but placentals failed to reach Australia are "accidental" events that profoundly shaped the entire biota. Ecological: these marsupials radiated into numerous ecological niches (arboreal, terrestrial, herbivores, megaherbivores, insectivores, and carnivores), closely paralleling adaptive radiations of placentals elsewhere. Indeed, such convergent responses demonstrate that ecological factors direct evolutionary responses.

Major differences in the composition of faunas in different biogeographic regions constitute a perplexing dilemma for students of community organization. We consider here certain global patterns in the diversity and geographic distribution of various nocturnal insectivores, particularly lizards and frogs. We pose three questions: (a) Can the disparity between species richness of nocturnal lizards in the old and new world tropics be explained on the basis of historical events? (b) Could the paucity of nocturnal lizard species in the New World be a result of competition with frogs (or other nocturnal insectivores)? (c) Could an earlier adaptive radiation of frogs have precluded gecko diversification in the neotropics? In this context we are concerned with patterns of diversity of nocturnal lizards and frogs and their occurrence in communities in the tropical parts of the Australopapuan, Ethiopian, Neotropical, and Oriental regions.

NOCTURNAL LIZARD AND FROG DIVERSITY

Taxonomic Diversity

By far, most nocturnal lizards in the world are members of the Infraorder Gekkonomorpha which contains about 860 species (25). Of the diverse groups of gekkoideans, the family Eublepharidae (5 genera, 19 species) is primarily Holarctic. One genus enters tropical Asia and one enters the neotropics as far south as Costa Rica; two genera are endemic to Africa. The family Pygopodidae is restricted to the Australopapuan region and, according to Kluge (25), contains both the nocturnal Diplodactylinae (13 genera, 84 species), some of which are arboreal and others terrestrial, and the snakelike Pygopodinae (7 genera, 31 species), most of which are crepuscular or nocturnal. The large family Gekkonidae is pantropical in distribution. The subfamily Teratoscincinae (1 genus, 4 species) occurs in the Palearctic. The subfamily Gekkoninae is pantropical. The range of the subfamily is encompassed by members of the tribe Gekkonini (62 genera, 603 species), nocturnal lizards, some of which are arboreal and others, terrestrial. Members of the tribe Sphaerodactylini are endemic to tropical America, where they have undergone a substantial adaptive radiation (5 genera and 120 species). Most species are diurnal, but some are crepuscular (46). The majority of sphaerodactylines are terrestrial, although a few species are arboreal.

Within the American tropics, there are few nocturnal lizards, all but one of which is a gekkoidean. The exception is the xantusiid *Lepidophyma flavimaculatum*, a forest floor inhabitant in Central America. Among nocturnal gekkoideans in the New World, most species are terrestrial in xeric regions (e.g. the deserts of western South America and Argentina) or semi-arid regions characterized by scrub forest or woodland-savanna (e.g. the cerrados and caatinga of Brazil), but two species are arboreal in the caatinga (47, 49). Within the tropical rainforest in South America, the only arboreal, nocturnal

lizards are gekkonids. The species of *Hemidactylus* living there apparently arrived in South America via trans-Atlantic dispersal (24). Usually most species of *Hemidactylus* are found only on buildings in towns, and they are not considered to be components of natural communities. *Thecadactylus rapicauda*, a very large gecko, is the only nocturnal, arboreal lizard in neotropical rainforest communities (5, 6, 9). Five species of large, nocturnal, arboreal gekkonines occur in the West Indies, but usually only a single species is found at any given site.

A similar biogeographic situation exists among scincid lizards, virtually all of which are diurnal. Scincids are highly diverse in the Old World, but there is a distinct paucity of scincids in the Neotropics (18). Only lygosomine skinks occur in South America, where they are represented by 15 species of *Mabuya*, a genus with many species in Africa and Asia. This biogeographic parallel between scincids and gekkoideans deserves further study.

Principal families of nocturnal anurans in the American tropics are the Bufonidae, Centrolenidae, Hylidae (Hylinae and Phyllomedusinae), Leptodactylidae, and Microhylidae. The frog fauna of Australia is composed primarily of two endemic family groups, the Myobatrachidae and the Hylidae (Pelodryadinae). In Africa, major components are the Bufonidae, Hyperoliidae, Microhylidae, Ranidae, and Rhacophoridae (represented by only three species of *Chirromantis*). Tropical Asia differs from Africa by lacking hyperoliids and by having the Pelobatidae (Megophryinae) plus a diversity of rhacophorids.

History

Gekkoideans represent an ancient lizard lineage thought to have arisen in Asia, probably during the Late Jurassic or Early Cretaceous; a Paleocene fossil is known from Brazil (14). The present pattern of distribution of gekkoideans in all biogeographic regions reflects Late Mesozoic and Cenozoic plate movements (25), as well as dispersal. Dispersal capabilities of some geckos are considerable, as is evidenced by their presence on many oceanic islands and frequent movements via humans.

Although the earliest separation of frogs onto different continents occurred with the original break up of Pangaea in the Jurassic, the primary tectonic factors affecting major patterns of anuran distribution were the plate movements in the Cretaceous and Cenozoic (12). Frogs of the family Pipidae are known from the Cretaceous of Africa and South America. By the early Cenozoic, the families Bufonidae, Hylidae, and Leptodactylidae also are represented in South America.

Using principles of phylogenetic systematics (19), testable hypotheses of phylogenetic relationships within monophyletic groups can be proposed. Superposition of phylogenetic cladograms on geographic areas indicates past geographic histories of areas; this approach has become known as vicariance

biogeography (38, 39). Groups of organisms of approximately the same age that inhabit the same regions should show similar distributional patterns if the groups were affected by the same historical events (8). Of course, extinction of a taxon in a particular region and absence of fossils there will not support the vicariance model. Savage (40) proposed an alternative method for testing the validity of biogeographic hypotheses. He used events in earth history to predict general recurrent patterns of phylogenetic relationships; these patterns can be tested against patterns derived from phylogenetic analyses.

Unfortunately, few taxa involved have been subjected to such critical analyses. Kluge's (25) work on gekkoideans does not address relationships of Neotropical gekkonines, but Kluge (personal communication) believes that *Tarentola* in the West Indies is related to the African *Pachydactylus* and that the sister taxa of *Aristelliger* and *Thecadactylus* are probably African. With the exception of the widespread gekkonine genera *Cyrtodactylus*, *Gehyra*, *Hemidactylus*, and *Phyllodactylus* (which may not be monophyletic)—all of which are excellent dispersalists, as evidenced by their occurrence on many oceanic islands—gekkonoid evolution has paralleled earth history (Figure 1). Most notable is the endemic Pygopodidae in Australia.

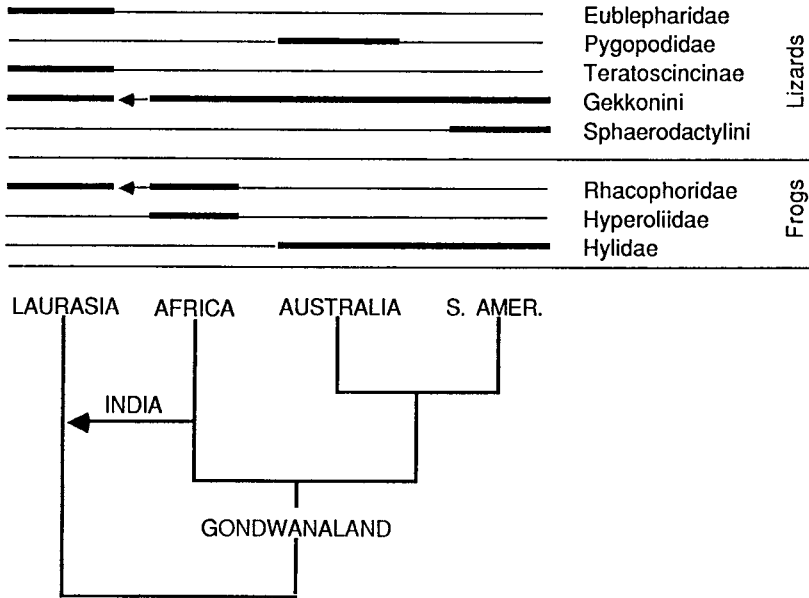


Figure 1 Area cladogram of continents and associated groups of gekkonoid lizards and major groups of arboreal frogs. Horizontal bars indicate distributions of taxa; arrows indicate transport from Gondwanaland to Laurasia via the Indian Plate.

Table 1 Species densities of nocturnal lizards (principally gekkonoids) and nocturnal frogs at various localities.

Site	Lizards		Frogs		Reference
	Terrestrial	Arboreal	Terrestrial	Arboreal	
Neotropical rainforest:					
Chinajá, Guatemala	1*	1	3	7	Duellman (10)
Barro Colorado Is., Panama	1*	1	6	17	"
Belém, Brazil	0	1	8	22	"
Santa Cecilia, Ecuador	0	1	17	52	"
Cuzco Amazónico, Peru	0	1	15	37	"
Panguana, Peru	0	1	17	34	"
Neotropical dry forest:					
Exu, Brazil	1	2	8	6	Vitt (personal communication)
Asian rainforest:					
Labang, Borneo	2	13	24	9	Inger (21)
Pesu, Borneo	0	6	34	17	"
Nanga Tekalit, Borneo	1	10	37	9	"
Ulu Gombak, Malaya	4	6	8	3	"
Bukit Lanjan, Malaya	3	5	19	11	"
Sakaeret, Thailand	3	7	10	5	Inger & Colwell (23)
African deserts:					
Bloukrans, South Africa	3	3	1	0	Pianka (32)
Ludrille, KGNP, Botswana	3	3	1	0	"
Tsabong, Botswana	3	2	1	0	"
Australian deserts:					
Laverton	10**	2	1	9	"
Red Sands	10**	4	1	0	"
E-Area	6**	5	1	0	"

* *Lepidophyma* (Xantusiidae)** Includes two non-gekkonid taxa, *Egernia* and *Eremiascincus* (Scincidae)

Frogs also have an evolutionary history associated with tectonic events. The endemic Australopapuan pygopodids are paralleled in frogs by pelodyadine hylids, whereas phyllomedusine and hylinae hylids are Neotropical, hyperoliids Ethiopian, and rhacophorids principally Oriental (Figure 1).

Communities

As has been noted by Cogger (3), nocturnal lizard faunas are impoverished throughout the New World, (Table 1). Even in nonrainforest areas, communities usually contain only a single species (31, 32). Comparable natural habitats in the Old World usually support much more diverse nocturnal lizard

faunas; for example, a dry forest in Thailand has 10 species of nocturnal gekkonids (23). Desert habitats in Australia and southern Africa support from 3 to 10 sympatric species of nocturnal gekkoideans (33, 34). Even the cold deserts of Asia seem to support a moderate to substantial diversity of gekkoideans (1, 43, 44). The fact that this pattern applies across all habitats strongly suggests that historical biogeographic factors have played a major role in gekkonid radiations.

In contrast to gekkoideans, frogs are most diverse in the American tropics; about 45% of the 3650 species of frogs (updated from Frost 17) occur there (10). Within the neotropics, the greatest diversity of anurans is in the lowland rainforests—41 and 42 species at two sites in Costa Rica, 38–84 (\bar{x} = 56) species at 10 Amazonian sites, and 35–36 (\bar{x} = 50) species at three cis-Andean sites (10). These numbers are higher than for most sites in the Old World tropics—21–51 (\bar{x} = 35) species at five sites in rainforest in Malaya and Borneo, and 19 and 20 species at two sites in seasonally dry forest in Thailand (21); 24 species at a site in seasonally dry forest in northern Australia (45); 49 species in a region of rainforest in Cameroon (30); and 20 species at each of two sites in seasonal rainforest in Nigeria (41).

Most frogs are nocturnal; at six sites in neotropical rainforests, 86–92% (\bar{x} = 88%) of the species are nocturnal (11). In the neotropics, the majority of nocturnal arboreal frogs are members of the family Hylidae, although the small centrolenids and some *Eleutherodactylus* are arboreal. For example, at Santa Cecilia in Amazonian Ecuador, 52 of 81 (64%) species are nocturnal and arboreal (6). Generally, fewer nocturnal, arboreal frogs occur in the Old World tropics. At Foulassi, Cameroon, only 19 of 49 (38%) of frogs (all hyperoliids and rhacophorids) are in this category (30). In the Oriental region, nocturnal, arboreal frogs are rhacophorids. At sites in southeastern Asia and Borneo, all frogs are nocturnal; at five sites in rainforest, 20–50% (32%) of the species are arboreal, and at two sites in seasonally dry forest 10% and 21% of the species are arboreal (21). Numbers of species of frogs are inversely related to those of nocturnal lizards (Figure 2).

EVALUATION OF DATA

Historical Events

Evidence from phylogenetic relationships of gekkonoids and frogs and from earth history neither support nor deny the notion that the great disparity in relative numbers of frogs as compared with gekkonoids between the new and old world tropics is the result of differences in historical biogeography. The earliest known fossils of gekkonoids and hylids in the neotropics date from the Paleocene of Brazil (14, 15). No earlier fossils of either group are known. Thus, both groups apparently were present on the South American plate at the time of the break up of Gondwanaland in the Late Mesozoic.

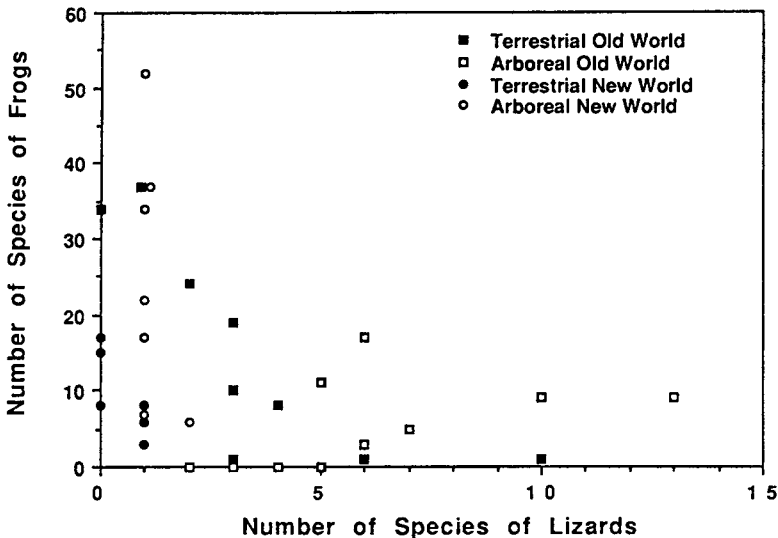


Figure 2 Frog species density plotted against nocturnal lizard species density at seven New World (circles) and 12 Old World (squares) sites. Closed symbols represent terrestrial species; open symbols are arboreal species.

Frog-Lizard Competition

If the carrying capacity of the environment limits the number of nocturnal insectivores through limited food, perches, or shelter, some sort of balance between numbers of species of nocturnal, arboreal frogs and lizards might be expected. At six sites of southeastern Asia and Borneo, Inger (21) reported 3–17 species of nocturnal, arboreal frogs and 6–13 species of arboreal gekkonoids. Ratios of species of frogs to species of lizards range from 0.40 to 2.83 ($\bar{x} = 1.25$). In contrast, at six sites in neotropical rainforests, only one species of nocturnal, arboreal gekkonoid (*Thecadactylus rapicauda*) has been found (9); at these sites the number of nocturnal, arboreal species of frogs varies from 7 to 52 ($\bar{x} = 28.2$) (10). However, as possible competitors with the large nocturnal gecko, the values for frogs in the neotropical rainforests are inflated. At these six sites the number of nocturnal, arboreal frogs having snout-vent lengths of more than 50 mm is 4–19 ($\bar{x} = 11.0$), a value that still is 8–10 times higher than those for southeastern Asia.

Abundances of frogs and lizards on the forest floor are an order of magnitude greater in the neotropics than in Indo-Malayan primary rainforest (22, 42). Presumably this disparity exists because of the comparatively lower abundance of insects (as a food supply) in the more seasonal Indo-Malayan dipterocarp forest. Nevertheless, levels of competition for food could be similar in both regions owing to the profound differential in consumer biomass.

Only one nocturnal, arboreal gecko exists on most islands in the West Indies—*Thecadactylus rapicauda* on the Lesser Antilles, *Aristelliger lar* on Hispaniola, and *Tarentola americana* on Cuba and the Bahamas. Two large, nocturnal, arboreal frogs occur on Hispaniola, but only one species is present in Cuba and the Bahamas. Thus, diversity is low, and the ratio of nocturnal, arboreal frogs to lizards in the West Indies is much closer to ratios observed in southeastern Asia than in the rainforests in Central and South America.

Daytime retreats for *Thecadactylus* include crevices under bark, cracks in tree trunks or limbs, and hollows in limbs. Although some nocturnal frogs also are found in such shelters, usually they are in more moist situations, particularly in water-filled cavities in trees or in bromeliads. Feeding sites for *Thecadactylus* are tree trunks and buttresses and large limbs, sites frequented by only a few frogs (e.g. *Osteocephalus taurinus* and *Phrynohyas venulosa*). Most nocturnal frogs in the neotropics perch on slender branches or leaves. Arthropods are principal prey of most nocturnal frogs and *Thecadactylus*. Dominant prey items identified in stomachs of *Thecadactylus* in Surinam and Ecuador were orthopterans (6, 20). Orthopterans also are common prey items of most larger treefrogs (6). However, because orthopterans are extremely abundant in neotropical forests and because feeding stations of *Thecadactylus* differ from those of most frogs, competition for food seems unlikely. Evidence for or against the existence of competition between frogs and gekkonoids for resources is hardly compelling.

Other nocturnal, insectivorous taxa that may interact with frogs and lizards include mammals, birds, and arachnids. Mouse possums (*Marmosa*) and night monkeys (*Aotus*) are abundant, nocturnal, arboreal insectivores in the American tropics; although the kinkajou (*Potos flavus*) feeds primarily on fruit at night, it also takes insects (27). Nocturnal, arboreal primates that feed on large insects also occur in the Old World (e.g. *Galago* in Africa and *Nycticebus* in southeastern Asia). Some kinds of bats glean large insects off vegetation at night. This feeding strategy is used by some phyllostomatids (e.g. *Chirotopterus*, *Phyllostomus*, and *Trachops*) in the neotropics and megadermatids (e.g. *Cardioderma* and *Megaderma*) in Africa. Also, small owls may well be important predators on insects. These endotherms could consume more large nocturnal insects than do the ectothermic gekkonoids and anurans, but quantitative data are not available. Also, nocturnal, arboreal arachnids prey on insects. Whip scorpions (Thelyphonidae, Amblypygidae, Uropygidae) and large predatory spiders, such as hirsiliids, lycosids, and theraphosids, are abundant in the tropics throughout the world and feed on relatively large prey such as orthopterans and small vertebrates. Although we have been unable to determine if there is a differential in species diversity of arachnid insectivores between the old and new world tropics, the historical biogeography of spiders parallels that of gekkonoids and anurans (35).

Adaptive Radiations

The limited fossil evidence does not support the idea that adaptive radiation on any continent of either gekkoideans or anurans preceded that of the other group. However, the diversity of living taxa certainly suggests that anuran radiation was far greater than gekkonine radiation in the neotropics. Frogs have also undergone a more extensive adaptive radiation in the neotropics than in the Old World. These differences are real unless major extinctions have occurred, but there is no basis for such speculation.

Nocturnal geckos are far more diverse and abundant in the Old World than in the New World. Lizards are generally more abundant (or at least much more conspicuous) in open habitats (e.g. deserts and savanna-woodland) than in closed-canopy forests. But this comparison of lizards as a group is unrealistic, because most lizards (gekkonoids being the principal exception) are heliophilic. The greatest diversity of nocturnal gekkonines in South America is in subarid regions, such as the cerrados and caatinga of Brazil; six species (three of which are nocturnal) occur at one site in the caatinga of northeastern Brazil (46, 47, 49, L. J. Vitt, personal communication). This number is still below that in arid regions in Africa and Australia (31, 32).

In contrast to lizards, anurans are most speciose in regions of high humidity; the richest anuran communities in the world exist in the extensive upper Amazon Basin and in the more restricted cis-Andean rainforests, where dry seasons are nonexistent or very short. Numbers of coexisting species are notably lower in monsoonal climates, such as those in tropical Africa and southeastern Asia, and decline further in deserts. Another factor contributing to the comparative paucity of arboreal anurans in the Old World tropics may be the absence there of arboreal water-holding plants (bromeliads), common diurnal retreats for neotropical anurans.

The distribution of tropical environments has changed drastically during the Late Cenozoic and Quaternary. Principally during the Pleistocene, humid tropical habitats were greatly restricted during glacial phases, whereas humid forests expanded during pluvial (or interglacial) phases. These changes have been documented in South America by Prance [(36), but see Connor (4) for a critique of interpretations]. They also are known to have occurred in Africa and Asia (16). These dramatic ecological changes have been postulated as important in determining modern distributions and patterns of speciation (7, 26, 28, 48), as well as extinctions (37).

DISCUSSION

In the absence of evidence for large-scale extinctions of gekkonines in the neotropics or of nocturnal, arboreal anurans in the Old World tropics, we suggest that both groups had similar temporal histories, but that adaptive

radiation in the two groups occurred at different rates in the Old World and in the New World. In the Old World tropics, greater climatic seasonality and the absence of bromeliads favored gecko diversification, whereas in the neotropics, less seasonal climates and the presence of bromeliads favored frog radiation.

Perhaps the difference in numbers of species of gekkonoids and frogs in the old and new world tropics reflects innate morphological and physiological design constraints of the organisms, coupled with recent climatic-ecological histories of the regions in which they live. In the extensive aseasonal rainforests in the New World, frogs have undergone a tremendous radiation; abundance of resources allows coexistence of many species. Gekkonines, most of which apparently do not tolerate environments with constantly high humidity, are much more diverse in the seasonally dry Old World tropics, where anurans are less diverse because many kinds are less capable of withstanding dry seasons. These ideas need to be tested by comparing lizard and frog communities at sites with comparable climates in Africa, Asia, and South America.

Although some evolutionary biologists (2, 13, 28, 29, 50) have included historical factors in formulating ecological hypotheses, community ecologists typically have concerned themselves with phenomena that organize communities in ecological time, such as coadjustments of patterns of resource utilization among coexisting species. Even when a coevolutionary perspective is adopted, the evolutionary time scale considered is relatively brief, such as for Pleistocene forest refugia (36). Such a "snapshot" approach provides only a brief glimpse of the factors involved in the organization of communities. Community ecology will emerge on a new level of awareness and understanding as this evolutionary time scale is broadened to include historical events and factors such as (a) biogeographic histories of taxa involved; (b) climatic histories of areas being studied; and (c) innate physiological tolerances and morphological design constraints of taxa involved.

SUMMARY

The disparity in numbers of nocturnal lizards and frogs in the old and new world tropics cannot be interpreted as owing to differences in geographic histories of lineages, nor to competition between geckos and frogs. However, clearly there has been a much greater adaptive radiation of gekkonines in the Old World as compared to the New World. In contrast, frogs have diversified to a considerably greater extent in the neotropics. These differential adaptive radiations reflect the most recent climatic-ecological histories of the regions, and the historical biogeography of important biotic components (e.g. absence of bromeliads in the Old World tropics). The example of geckos and tree frogs

underscores the necessity of considering historical events and biological constraints in the interpretation of patterns of community organization.

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