

THE AMPHIBIANS AND REPTILES OF KIBALE FOREST, UGANDA:
HERPETOFAUNAL SURVEY AND ECOLOGICAL STUDY
OF THE FOREST FLOOR LITTER COMMUNITY

By

JAMES R. VONESH

A THESIS PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

UNIVERSITY OF FLORIDA

1998

To my mother (who helped me through 3rd grade long division),
my father (who funded my science fair projects),
and Helen Burch and Mrs. Mansfield
(two teachers who made a difference early on)

ACKNOWLEDGMENTS

Not enough can be said about the role Drs. Lauren and Colin Chapman played in facilitating this project. Certainly without their support I would never have been able to conduct this research in Uganda. Both provided invaluable comments on early proposals and later manuscript drafts, facilitated getting Ugandan research clearance, and provided essential logistic support while I was in the field. But perhaps most importantly, they helped make much of the experience just plain fun.

Dr. Lillywhite, serving as the thesis committee chair, and Dr. Max Nickerson, have also provided valuable comments and suggestions throughout the process of developing this thesis, and have helped me to significantly improve the quality of the work.

Dr. Robert Drewes, Jens Vindum, and the staff of the Herpetology Department at the California Academy of Sciences, provided invaluable first hand knowledge of Ugandan frogs and superb accommodations during visits to use their collections. Visits to the collection for the purpose of identifying the Kibale specimens were financially supported by the Charles S. Stearns Grant-in-Aid of Herpetology, California Academy of Sciences, and by the California Academy of Sciences, Department of Herpetology.

I would also like to thank Christopher Amooti and Katusabe Swaibu who worked with me in the field during the leaf-litter study, and proved to be both excellent company as well as a reliable and observant field crew.

Finally, I would like to thank my fiancée, field companion, and (truth be known) initial reason for going to Uganda, Sophia Balcomb. Sophia was instrumental in providing me with the

opportunity to work in Uganda, helped me maintain my sanity throughout the field season, supported me during the difficult times, and proved a worthy cribbage adversary.

This research was supported in part by the Chicago Zoological Society.

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Abstract of Thesis Presented to the Graduate School
of the University of Florida in Partial Fulfillment of the
Requirements for the Degree of Master of Science

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By

James R. Vonesh

December, 1998

Chairman: Dr. Harvey B. Lillywhite
Major Department: Zoology

The amphibians and reptiles of Kibale National Park in western Uganda were inventoried over an 18-mo period in 1995 and 1996-97. A total of 75 species, including 28 amphibians and 47 reptiles, were collected or observed. Comparison with other equatorial African herpetofaunas confirms that the Kibale fauna is most similar to those of southwest Uganda and eastern Congo-Zaire, both hypothesized Pleistocene forest refugia. Comparison with a West Africa fauna also shows a fair degree of overlap, while almost no overlap was observed between Kibale and the forests of coastal East Africa. This confirms that the Kibale herpetofauna is an extension of the Guinea-Congolean forest faunas.

Randomly placed 5 x 5 m plots were used to sample the herpetofauna of the forest leaf-litter layer in unlogged forest, logged forest, and a neighboring exotic pine plantation. A total of 18 amphibian and reptile species were captured in the litter, a number similar to that observed in mid-elevation tropical forests in Central America and Southeast Asia. Density at Kibale was much lower than most previous studies. Analysis of the feeding ecology of the most abundant

litter species showed that most diurnal litter frogs are active foragers of hard-bodied prey such as ants; sit-and-wait predators of larger soft-bodied prey are curiously absent. Plots sampled under fruiting *Ficus natalensis* trees showed significantly higher prey densities, but litter amphibians and reptiles did not seem to respond to this increase. Of the physical and biotic factors measured in each plot, seasonal changes in soil moisture were most closely correlated with the patterns of herpetofauna abundance observed in the forest. This is consistent with the fact that Kibale receives less rain than any site where the ecology of the litter herpetofauna has been studied, and that most of the species present in Kibale are believed to have evolved in the wetter forests of eastern Congo-Zaire.

CHAPTER 1 INTRODUCTION

Rain forests currently cover about 7% of the Africa continent, and represent slightly more than one fifth of the total remaining tropical forest worldwide. While rain forests everywhere are under severe and increasing pressures, a recent survey indicates that African forests, relative to those of Asia and Latin America, are the most depleted, representing only about one-third of their historical extent (Collins, 1992). In East Africa, the moist forest diminishes as the climate becomes increasingly more arid. Forests in East Africa are found primarily in isolated patches of higher moisture; along rivers, on mountains, or among the coastal hills. These fragmented forest patches are particularly vulnerable to encroachment and exploitation, and yet these forests are home to rich plant and animal communities. Relative to the savanna ecosystem and its charismatic megafauna, the forests of East Africa have received little attention from zoologists, and what interest they have attracted has been focused primarily upon their primate, and to a lesser extent bird faunas. Our knowledge of the amphibian and reptile species of these forests, until recently, was primarily a result of the work of Arthur Loveridge, of the Harvard Museum for Comparative Zoology (*e.g.*, Loveridge, 1935, 1942*a,b,c*). The initial expeditions of Loveridge and the later work on treefrogs by Schiötz (1975) revealed two distinct forest herpetofaunas in East Africa. The first fauna is restricted to the coastal ranges of Tanzania, and is characterized by a high degree of endemism (Howell, 1993). The second fauna is the eastern-most extension of the Guinea-Congolean forests, and is characteristic of the forests of Uganda and western Kenya. Little research has followed Loveridge's work, with the notable exception of Schiötz (1975). A few of these forests have been recently surveyed for amphibians and reptiles (Drewes and Vindum, 1991; Drewes and Rotich, 1995), and Howell

(1993) has summarized his work and that of others in the forests of Tanzania. Even with these efforts, the amphibian and reptile faunas of most East Africa forests remain poorly studied, or completely unknown. Considering the extreme pressures that face many of these forests, our opportunities to learn of these faunas may be limited.

The first objective of this study was to conduct a survey of the herpetofauna of Kibale National Park in western Uganda. Kibale is a transitional lowland-montane moist forest at the eastern foot of the Ruwenzori Mountains. It is one of the better studied forests in all of tropical Africa. Research focusing primarily on primates and forest ecology has been ongoing at Kibale since the late 1960s, yet little is known about its herpetofauna; and no amphibian or reptile species list exists for the park. In Chapter 2, I present the results of a survey of the herpetofauna of Kibale National Park conducted during two trips to Uganda between 1995 and 1997. Sampling focused on the forest habitat around the Makerere University Biological Field Station at Kanyawara, but five supplementary sites, encompassing the northern and southern extremes of the park, were also sampled. The natural history of both the amphibian and reptile assemblages are summarized based on accounts from literature sources and my observations in the field.

According to previous researchers (Schiotz, 1976; Howell, 1993), the fauna of Kibale would be expected to share many species with the Guinea-Congolese forests to the west. This was examined by using Duellman's (1965) Coefficient of Biogeographic Resemblance to compare the herpetofauna of Kibale with that of eight other equatorial African sites. The similarity of these faunas is considered in the context of Pleistocene refugia theory.

The zoogeography of tropical African forests is thought to be strongly influenced by forest expansion, associated with wet interglacial periods, and forest retraction, associated with colder drier conditions during periods of glaciation. Much attention has focused on the last glacial maximum, at 18,000 years BP, when the extent of tropical forest was greatly reduced, creating hypothesized isolated forest refugia (Hamilton, 1976; Moreau, 1969). This vicariance

promoted allopatric speciation in these refugia. Warmer wetter conditions since 12,000 BP have been associated with expansion of rain forests, which reached their maximum extent at approximately 7,000 BP, and allowed mixing of previously isolated forest faunas. A number of authors have used modern patterns of distribution of forest species in order to elucidate past forest history, and have argued that patterns of richness and endemism suggest two principle core refugia, one in Cameroon and Gabon, and another in Eastern Zaire, with smaller refugia in West Africa and coastal East Africa (Hamilton, 1976, 1992; Moreau, 1969). These refugia are characterized by high species richness and a high proportion of endemic species. Kibale, located on the plateau between eastern Africa's two great rift valleys, is at an elevation approximately 800 m higher than the lowland rain forest of eastern Congo-Zaire. Due to its greater elevation, Kibale is expected to be a somewhat species poor neighbor of the hypothesized eastern Zaire forest refugia, which lies less than 100 km to the west.

Through the work of Loveridge (1935, 1942*a,b,c*) and Pitman (1974), and more recently Drewes and Vindum (1991), Howell (1993), Broadly and Howell (1991) and this study, we are beginning to get a better understanding of amphibian and reptile distributions in the forests of East Africa. However, few studies have included any detailed examination of the ecology of these herpetofaunas. One of the objectives of ecology is to determine what factors are important in determining species' distributions, both on a regional and more local scale.

The leaf-litter of most tropical forests supports a rich herpetofauna that may include frogs, salamanders, caecilians, lizards, snakes, amphisbaenids, and turtles. Comparative studies of litter herpetofaunas of southeast Asia and Central America have revealed interesting differences between the regions. The lowland forests of Central America support a similar number of species, but at much higher densities (often ten times greater) than the forest of southeast Asia. There has been a good deal of speculation as to what is responsible for this difference, and where the litter herpetofaunas of Africa fall in comparison to these regions (May,

1980). Unfortunately, comparisons with Africa at this stage are premature. For, with the exception of two preliminary studies of Coastal West Africa (Toft, 1982; Scott, 1982), the litter communities of tropical Africa have been overlooked. Neither Scott (1982), or Toft (1982) quantitatively addressed the importance of physical, biotic, or anthropogenic factors in structuring the litter herpetofaunal communities at their sites in West Africa. However, studies in Central America and Southeast Asia identified a number of physical and biotic factors that seem to influence litter herpetofaunal abundance and composition on a local scale. These studies have focused on the litter faunas' use of macrohabitat, microhabitat, food type, food size, diel time, and seasonal time (Toft, 1985). In the third chapter, I examine aspects of how the litter herpetofauna of Kibale Forest uses these resource categories and then relate the findings to existing studies from other tropical regions.

To achieve this objective, I first examine potential habitat correlates of abundance in three differently managed forest types during wet and dry seasons. This provides information on the physical and biotic factors most important in structuring the Kibale community and how it responds to anthropogenic disturbance. Next, I describe the feeding ecology of the six most common litter anurans, and use dietary overlap indices to provide an indication of the strength of interspecific interactions along this resource axis. Finally, I examine the local-scale response of litter arthropods and herpetofauna to large fruiting trees. Specifically, I test the hypothesis that litter arthropod numbers increase under fruiting fig trees, and that the litter herpetofauna increases locally in response to increased arthropod abundance. Taken collectively, the different elements of this study address the initial question of what factors are important in structuring this community. I compare these results with those from other tropical leaf-litter herpetofauna studies to see whether the Kibale fauna is similar in diversity and abundance to faunas from Central and South America and Southeast Asia, and whether the same factors appear to be important in structuring these communities.

CHAPTER 2:
THE HERPETOFAUNA OF KIBALE NATIONAL PARK, UGANDA: SPECIES
COMPOSITION AND BIOGEOGRAPHY

Introduction

Africa's tropical moist forests extend from Senegal, West Africa, to montane forests of eastern-most Somalia (Collins, 1992) and are home to an estimated 333 amphibian (Duellman, 1993), 105 snake (Hughes, 1983), 95 lizard, 16 turtle, and three crocodylian species (Bauer, 1993). While these estimates illustrate the richness of African rain forest herpetofaunas, our knowledge of these faunas is far from complete. The faunas of tropical Africa and South America have been studied since the mid-1700s, and until the beginning of this century species discovery rates were about the same for both continents (Duellman, 1993). However, after 1960 the species discovery rate in South America increased dramatically, while that of Africa remained roughly the same. In South America the increase in species descriptions coincides with an increase in the number of South American herpetologists, a phenomenon without African parallel. The relative paucity of studies from tropical Africa suggests that many species of the African rain forest are as of yet unknown to science.

The forests of Africa, like those worldwide, are disappearing at an alarming rate. Deforestation in West Africa is particularly severe, averaging 90% loss of the original forest cover from Sierra Leone to Nigeria. The forest of central Africa is also threatened from all directions, with an estimated 57% of the forest of central Congo-Zaire already being lost (World Resources Institute, 1994). Other regions of Central and East Africa are experiencing similar

loss. Deforestation has been severe in Uganda, with an estimated 86% loss of tropical moist forest (World Resources Institute, 1994). The remaining forests are primarily isolated fragments, which are vulnerable to encroachment and exploitation by a rapidly expanding, predominantly rural population.

Relative to other vertebrate groups, amphibians and reptiles in East Africa have been poorly studied, and future opportunities may be limited by the threats facing East Africa's forests. The need for baseline herpetological research in tropical Africa has been pointed out by a number of authors (*e.g.*, Mittermeier *et al.*, 1992; Lawson, 1993; Drewes and Vindum, 1997), who discussed the difficulty in conserving faunas we have so little information on.

The herpetofaunas of East African forests are generally thought to contain two non-overlapping faunas (Schiotz, 1976). The first faunal element is regarded as an eastern extension of the Congo Forest block stretching from Cameroon to Kakamega Forest in western Kenya. The second herpetofauna is that of the East African coastal forests. The herpetofaunas of the latter area have been reviewed recently by Howell (1993), however, few studies have examined the herpetofaunas of the Central African relict forests in East Africa since Loveridge (1935, 1942*a,b*, 1957). Such relicts include the Budongo, Bwamba, Kibale, Bwindi, Mbira, and Mt. Elgon forests in Uganda and reach their eastern limit in the Kakamega forest of Kenya. Of these forests, only Bwindi-Impenetrable Forest in southwestern Uganda has been inventoried specifically for herpetofauna (Drewes and Vindum, 1991).

Probably the most thoroughly studied forest in East Africa is Kibale Forest in western Uganda (Fig. 2.1). Research at Kibale, ongoing since the late 1960s, has resulted in approximately 160 scientific publications. The vast majority of these focus on Kibale's primate community (12 species); other animal taxa studied include fish, birds, small mammals, and elephants. Amphibians and reptiles have received little attention and are the only vertebrate groups at Kibale for which there are no species lists. However, there have been a few

herpetological collecting expeditions that have visited Kibale. In 1938, Harvard biologist Arthur Loveridge visited Kibale Forest and camped along the Dura River, one of the sites included in this study. He collected eight frog species during his 10-d stay (Loveridge, 1942*c*). The snakes of Uganda have been well documented primarily through the efforts of Uganda's first game warden, Captain Charles Pitman, who published "A Guide to the Snakes of Uganda" in 1938 and a revised edition in 1974. This comprehensive volume included records of 15 snake species as occurring in Kibale Forest. The tree frogs of East African have been examined in depth by Arne Schiøtz (1975) who visited Uganda in 1968 and lists six tree frogs from Kibale Forest. Based on the work of these four researchers, 14 frogs, 15 snakes and two lizards were known from Kibale prior to this study.

The first objective of this paper is to present the results of a herpetofauna survey of Kibale Forest conducted between 1995 and 1998. In combination with previous records from Kibale this study provides an overview of the amphibian and reptile richness and basic natural history of this area. Such presence-absence data are time consuming to collect, and the lack of such baseline information is likely to be one of the primary factors that has discouraged research on these taxa at Kibale. Furthermore, in light of mounting evidence of worldwide amphibian declines, it is increasingly important that baseline information on amphibian distributions be established, particularly for the poorly studied forests of tropical Africa. A second goal of this paper is to compare the herpetofaunal composition of eight equatorial African sites, one from West Africa, four from Central Africa, and three from East Africa, to reexamine the distribution of tropical forest amphibians and reptiles in the context of proposed past forest refugia, to establish which regions are most similar to Kibale, and to compare these results with those observed for other taxonomic groups.

Methods

Description of Study Sites

Kibale National Park is located in western Uganda (0°13' to 0°41'N and 30°19' to 30°32'E) near the eastern base of the Ruwenzori Mountains (Fig. 2.2). Kibale was established as a national park in 1993. Prior to that it was managed as a forest reserve with selective timber extraction and a number of exotic softwood plantations. Currently, approximately 766 km² is protected. The park is primarily characterized as a moist evergreen forest, transitional between lowland rain forest and montane rain forest (Struhsaker, 1997; Skorupa, 1988), but a variety of habitats including swamp, grassland, woodland thicket, and colonizing scrub are also represented (Struhsaker, 1997). Kibale lies on the plateau adjacent to the eastern edge of the western Great Rift Valley. The area was influenced by rifting and volcanic eruptions during the Pleistocene, and numerous crater lakes lie to the west and northwest of Kibale (Struhsaker, 1997). Soils are variable among sites, but valley bottoms often have deep, waterlogged, and dark soils characterized by low pH and fertility; hillslopes often have deep, red sandy loam; and hilltops have shallow, often rocky soils, or are covered in deep laterite (Lang-Brown and Harrop, 1962). Rainfall is typically concentrated during two distinct wet seasons, March through May and September through November. The mean annual maximum temperature measured at Kanyawara is 23.3°C, and mean annual minimum temperature is 16.2°C (Struhsaker, 1997). The management and research histories, fauna, and flora of Kibale have recently been reviewed in detail by Struhsaker (1997).

Five forest sites were sampled, Sebatoli, Kanyawara, Dura River (near Kanyanchu), Mainaro, and Ngogo. The first four sites are approximately 10-15 km apart along a N-S gradient while Ngogo is 12 km south-east of Kanyawara (Fig. 2.1). All four areas consist of a series of

moderately undulating valleys which result in a topographical relief of 150-200 m (Chapman *et al.*, 1997).

A sixth site, Lake Nyabikere, is a crater lake surrounded by areas cleared for agriculture and a few small forest patches. Lake Nyabekere lies approximately 1-2 km outside the forest along the road from Kanyawara to Kanyanchu. This site represents typical “farmbush” habitat outside the park and was sampled on January 12-13, 1997.

Kanyawara is the site of the Makerere University Biological Field Station and the area of most intensive sampling. It is situated at an elevation of 1500 m and is characterized by the steepest terrain, with an average slope of 8.7° (Chapman *et al.*, 1997). The most abundant tree species are *Uvariopsis congensis*, *Markhamia platycalyx*, and *Bosqueia phoberos*, while large emergent trees include *Parinari excelsa* and *Pseudospondias microcarpa* which reach heights of 30 m (Chapman *et al.*, 1997). Rainfall at this site averages approximately 1600 mm per year. Aquatic amphibian breeding habitat surveys focused on four Kanyawara sites: the Lower Camp Well, a permanent artificial pool ~15 x 14 m on the forest edge in a swamp forest patch; the K30 Forest Pool, a shallow natural pond ~20 m in diameter along the Nykagera stream in unlogged mature forest; the Mikana stream and seasonal flooded swamp forest; and the Karumbi Road ephemeral pools, tire ruts on an old logging road that seasonally fill with water. Forest litter sampling was also concentrated at Kanyawara with 100-140 plots in unlogged forest, selectively logged forest, and exotic pine plantation.

The Dura River site near Kanyanchu tourist center was the second most intensively sampled area. This riparian forest at 1250 m elevation along the Dura River is characterized by the lowest relief (mean slope 5.9°) and is dominated by the trees *Celtis durandii*, *Uvariopsis congensis*, and *Bequaertiodendron oblanceolatum* (Chapman *et al.*, 1997). Several habitats were sampled at Dura River including eight 5 x 5-m litter plots on the North bank of the river, dip net sampling of seasonal pools along the river, and visual searches of several stream tributaries of the

Dura and a grassy forest gap (the elephant wallow) at the Kanyanchu tourist center.

Approximately 14 d were spent sampling at this site in 1996-97, including three nocturnal samples.

Mainaro, at 1200 m, the site lowest in elevation and furthest south, is characterized by *Cynometra alexandri* forest along the Dura River (Chapman *et al.*, 1997). Here, the river seasonally inundates adjacent forest forming pools that become isolated from the river. Three day time visits were made to this site, in July-August, 1997.

Sebatoli was the northern most site visited. This site, at a slightly higher elevation of ~1590 m (Struhsaker, 1997), is characterized by riparian forest along the Mpanga River, one of two major rivers in Kibale. During heavy rains the forest is inundated. Three daytime visits were made to this site, January 13-15, 1997.

The Ngogo field station, at an elevation of 1350 m (Chapman, 1997), was visited for 3 d in early December, 1997. Nocturnal and diurnal searches were conducted along the Kanyanchu stream and surrounding forest. Ngogo receives less rain than Kanyawara, approximately 1490 mm per year. The forest is characterized by moderate topographical relief (slope 6.0°) and is dominated by *Uvariopsis congensis*, *Diospyros abyssinica*, and *Chrysophyllum albidum* (Chapman *et al.*, 1997).

Sampling

Field work was conducted in and around Kibale from May to August 1995 and November 1996, to December 1997. Collections of amphibians and reptiles were made using a variety of techniques. At Kanyawara, four amphibian breeding sites were surveyed twice weekly (nocturnal and diurnal) between November 15, 1996 and December, 1, 1997, resulting in approximately 500 total hours of active searching in these habitats. In addition, 340 5 x 5 m leaf-litter plots were sampled between March and November 1997 (See Chapter 2). Each plot was

searched for at least 1 person-hr and plots were randomly assigned locations within the forest using the Kanyawara trail grid map. Opportunistic visual searches of suitable habitats supplemented these sampling methods at Kanyawara and was the primary sampling method at the five additional sites, unless otherwise noted above.

Snakes and lizards occur at lower densities than most amphibians and are less frequently observed in the West African tropics than in comparable Neotropical forest habitats (Lawson, 1993). This is also true in Kibale, and opportunistic road cruising was the most reliable method for obtaining snake specimens. Most snakes collected in this manner were found between Kanyawara and Fort Portal or between Kanyawara and the Dura River site (Fig. 2.2). The first route runs through agricultural and farmbrush habitats while the second runs through agricultural and forest habitat.

In addition to specimens collected during my field work in 1995-1997, a number of specimens were collected by Drs. Colin and Lauren Chapman between 1990-1995. Most of these specimens were the results of by-catch in minnow traps used in their studies of the Kibale fish fauna. In total approximately 500 specimens were collected from Kibale and neighboring areas. Collection of vouchers was limited to three specimens per gender per locality within the national park boundaries. Many more individuals were observed than were collected. Specimens were preserved in the field with 10% buffered formalin and were subsequently transferred to 70% ethanol. Specimens are shared between the Makerere University Zoological Collection, Kampala, Uganda, and the California Academy of Sciences, San Francisco.

Faunal Comparisons

Herpetofaunal lists for the eight equatorial African sites compared in this study were compiled primarily from published lists: Korup National Park, Cameroon (Lawson, 1993); Parc National des Virunga, Congo-Zaire (Amphibians - Laurent, 1972; Reptiles - De Witte, 1941);

Parc National de la Garamba, Congo-Zaire (Amphibians- Inger, 1968; Reptiles - De Witte, 1966); Kibale National Park, western Uganda (this study); Bwindi-Impenetrable National Park (Amphibians - Drewes, 1991; Reptiles – Drewes and Vindum, 1997 unpub. report), Usambara Forest Reserve, northeast Tanzania (Howell, 1993); Uzungwa Forest Reserve, Tanzania (Howell, 1993); and the Arabuko-Sokoke Forest Reserve, coastal Kenya (Drewes and Rotich 1995). The nomenclature used in several of these studies is antiquated, and attempts were made to update genera and species titles. Frost (1985) was followed for most amphibians; however, I followed Duellman and Trueb (1986) and Drewes and Vindum (1991) in regarding arthroleptid frogs as a subfamily of Ranidae. I also retained the genus *Hylarana* in keeping with other African workers (e.g., Perret, 1977; Drewes and Vindum, 1991; Lawson, 1993). Lizard nomenclature follows Broadly and Howell (1991) for many species, and snake nomenclature follows Meirte (1992), Pitman (1974), and Hughes (1981, 1985).

For faunal comparisons I use Duellman's (1965) modification of Pirlot's (1956) formula

$$CBR = 2C/(N_1 + N_2)$$

where CBR is the Coefficient of Biogeographic Resemblance, C is the number of species two areas share in common, N_1 is the number of species in the first area, and N_2 is the number of species in the second area. This algorithm was used because it takes into account the size of the larger fauna and has been used in numerous comparisons of Neotropical herpetofaunas (e.g., Dixon, 1979; Hoogmoed, 1979; Duellman, 1990).

Results

Herpetofaunal inventory and natural history

Fourteen amphibian species, 13 lizard species, and 15 snake species previously unknown from Kibale were collected and/or observed during this study. The resulting herpetofauna consists of 28 frogs, 15 lizards, and 32 snakes (Table 2.1). In addition, one amphibian and six snakes are listed as expected for the park based on their presence in other nearby Ugandan forests.

All amphibians observed belonged to the order Anura (frogs). Salamanders (Caudata) are not known from sub-Saharan Africa, and caecilians (Gymnophiona) have never been collected in Uganda. Among anurans, three aquatic species (11% of fauna) of *Xenopus* were collected; *X. wittei* and *X. l. victorianus* were often found in sympatry. The terrestrial leaf litter frog assemblage consisted of nine species (32% of fauna) from three genera, *Bufo*, *Phrynobatrachus*, and *Schoutedenella*. Of the Bufonids, only *B. funereus* and *B. kisoensis* were forest-dwelling, while *B. maculatus* was abundant outside the park in farmbush habitat. Five species of *Phrynobatrachus* are known from Kibale, but two are very rare. *Phrynobatrachus dendrobates* was collected by Loveridge in 1938, but has not been collected since; and I collected the only specimen of *P. versicolor* known from Kibale. Of the remaining three species, *P. graueri* was the most commonly heard and seen frog at most sites in the park and was often found breeding at the same sites as the smaller *P. parvulus*. *Phrynobatrachus auritus* was uncommon at Kanyawara but frequently observed at the Dura Site. *Hylarana albolabris* and *Rana angolensis* were common both in and outside the forest in association with water bodies, and could best be classified as semi-aquatic species (7%). Both *Ptychadena* species were associated with forest gaps, though *P. mascarenensis* (*hyla*) appeared to be more strictly limited to the forest. Twelve arboreal or semi-arboreal frogs (43%) of the genera

Afrivalus, *Leptopelis*, *Hyperolius*, *Phlyctimantis*, and *Chiromantis* were collected or observed in the park. Of these, four *Hyperolius* species, *Leptopelis christyi*, and *Phlyctimantis verrucosus* were reported as occurring in Kibale by Schiötz (1975). The new additions to the Kibale tree frog list were *Afrivalus laevis*, known from a single specimen collected at Sebatoli; *Hyperolius platyceps langi*; *Leptopelis kivuensis*; and the rhacophorid, foam-nesting tree frog *Chiromantis rufescens* (M. Cherry, pers com.). This is the second Ugandan record for *C. rufescens*, a West and Central African species which reaches its eastern limit in Budongo Forest Reserve and Kibale in western Uganda.

Little is known about the feeding ecology of most of these frog species. Frogs typically prey upon invertebrates, but other taxa are sometimes taken. *Xenopus wittei* preys primarily upon insects while the larger *X. l. victorianus* has been observed to feed on insects, other frog larvae, and small fish (pers. obs.). The feeding ecology of the litter assemblages is examined in greater detail in Chapter 2. The two forest bufonids and the *Schoutedenella* are active foragers which feed primarily on ants, *P. graueri* feeds on Collembola, and the tree frogs *L. kivuensis* and *H. lateralis* appear to be sit-and-wait predators on soft-bodied insects.

Five reproductive strategies are exhibited by Kibale's frogs. Most species (61%) deposit their eggs in water, and eggs hatch into aquatic larvae. Seven species (25%) from three genera (one *Phrynobatrachus*, two *Afrivalus*, four *Hyperolius*) deposit their eggs on vegetation above water, which subsequently hatch and drop into the water as aquatic larvae. The two *Leptopelis* (7%) species both bury their eggs in the moist soil of depressions that later fill with water, upon which aquatic larvae hatch, and *Chiromantis rufescens* (4%) deposits eggs in arboreal foam nests from which aquatic larvae hatch. Only the arthroleptid *S. schubotzi* exhibits direct development (4%).

Lizards were uncommon within the forest. The most abundant species were those associated with the forest edge or disturbed farmbrush habitats (e.g., *H. mabouia*, *S. atricollis*, *M.*

straita, *C. ellioti*, Table 2.2). Within the forest, the two lacertids *A. africanus* and *A. vauereselli* were the most conspicuous, actively foraging in the leaf litter and basking in sun-flecks. Of these two species, *A. africanus* appeared to be more arboreal. The highly arboreal lacertid *H. guentheri* was observed only once, but its habits make it extremely difficult to collect. Of the forest chameleons, *Rhampoleon boulengeri* was the most common species, and was usually observed in low shrubs. The other two forest chameleons, *C. adolfifrigerici* and *C. ituriensis*, appear to be more arboreal in their habits.

Of the 37 species of snakes that occur or potentially occur in Kibale, 11% are fossorial or burrowing, 38% are primarily terrestrial, 51% are primarily arboreal, and less than 3% are primarily aquatic (Table 2.2). Most species are probably nocturnal or active during both day and night. The feeding ecology of Kibale's snakes can be surmised based on diets reported in Pitman (1974), the stomach contents of specimens from this study, and field observations. Of the 37 species, 8% feed primarily on invertebrate prey, 8% feed on fish, 24% prey on lizards or other snakes, 51% prey on frogs, 37% feed on small mammals such as rodents, 14% feed on birds, and 5% (*Bitis gabonica*, *Python sebae*) are capable of taking larger mammals as prey (categories add to >100% because many species prey on several taxa). Among the most specialized feeders are *Dasypeltis atra*, which feeds exclusively on bird eggs, *Duberria lutrix*, which preys on slugs, *Causus lichtensteinii*, which feeds exclusively on forest toads, and *Thelotornis kirtlandii* and *Lycophidion ornatum* which feeds on lizards.

Herpetofaunal Comparison

The herpetofauna (excluding crocodylians) from eight equatorial African sites were compared using Duellman's (1965) Coefficient of Biogeographic Resemblance (CBR). These sites ranged from Coastal West Africa (Korup - 8°4'E) to Coastal Kenya (Arabuko - 39°30'E), and from 5°N (Korup) to 7°50'S (Uzungwa) latitude (Fig. 2.2). Several broad habitat categories

are found among these sites. Korup and Virunga are composed primarily of Guinea-Congolese rain forest. Korup is mostly lowland rain forest (97% < 850 m) while the elevational range in Virunga extends from 710 m to over 5000 m in the Ruwenzori Mountains (Table 2.3). Garamba is characterized primarily by moist mixed woodlands and savanna, with gallery forests along larger streams and in deeply entrenched ravines (Inger, 1968). Both Kibale and Bwindi in western Uganda are situated upon the central African plateau between the western and eastern Rift Valleys. For that reason the lowest elevations at both sites are approximately 1100 m. However, only Bwindi, with a maximum elevation of 2607 m has true montane rain forest. Both the Tanzanian sites, the Usambaras and the Uzungwa Mountains, are characterized by moderate elevation to montane rain forest, representing a similar range of elevations as Kibale and Bwindi in Uganda. The final site, Arabuko-Sokoke, is comprised of relatively dry coastal forest. The combined species lists of these sites include 191 amphibians (APPENDIX A.), 10 turtles, 98 lizards, and 134 snake species (APPENDIX B.). This represents roughly 55% of the total estimated frog fauna of African rain forests, and a higher proportion of African forest reptiles.

All of these sites were sampled over a period of at least 3 mo, and most were sampled for considerably longer. Total species richness ranged from 167 species in Korup to 33 species in Uzungwa (forest dependent species only). The areas of these parks vary considerably; therefore, it is also valuable to consider richness controlling for area. Arabuko-Sokoke has the highest richness per area (2.4 spp/1000ha), followed by Bwindi (2.0), and Korup and Kibale (both 1.3, Table 2.3).

Kibale N. P., Bwindi N. P., Virunga N. P. exhibit the greatest similarity among the eight sites (Table 2.4). Kibale and Bwindi are separated by about 200 km along a N-S gradient in western Uganda, and share 20 species of amphibians and reptiles (Table 2.4). Both sites show strong similarity to the Virunga site (23 and 24 shared species respectively), from which they are separated by less than 100 km (Table 2.4). The lower CBR values for Kibale versus Virunga and

Bwindi versus Virunga compared to Kibale versus Bwindi are due to the larger size of the Virunga fauna. These three neighboring Central African forests exhibit the greatest similarity among the eight sites.

The herpetofauna of Korup in Cameroon is most similar to that of Virunga, 2300 km to the East, and least similar to the montane forests of Tanzania and the coastal forests of Kenya, over 3300 km distant. The Usambaras and Uzungwas are most similar to each other, and show very little similarity to any other sites. Likewise, Arabuko-Sokoke shows little similarity to other forests, however, it is interesting that it is more similar to Garamba and Virunga, over 1400 km distant, than the nearby forests of the Usambara Mts. (220 km), Uzungwa Mts. (740 km), or the intervening Ugandan forests. Reptile faunas were more similar (mean CBR 0.19) than amphibian faunas (mean CBR 0.14) among the eight areas (Table 2.4).

A comparison of mid-elevation to montane tropical rain forests from Africa, Central America, and southeast Asia show that “forest dependent” herpetofaunas of higher elevation sites range between 20 and 67 species (Table 2.5). The Virunga N. P. and Monteverde, Costa Rica supported the richest higher elevation forest herpetofaunas, N. P. and Bwindi N. P. support an intermediate number of species, while Cuernos de Negros, Philippines, and the Tanzanian Uzungwa Mts. had the lowest species richness. Reptiles outnumbered amphibians at all sights except the Uzungwas and Korup (at Korup this is likely due to low sampling effort in higher elevations). Amphibian richness was greatest in Korup, and reptile richness was highest in Virunga N. P.

Discussion

The Kibale herpetofauna consists of two main assemblages, those species which seem to be forest-dependent and those that do well in a variety of habitats, both inside and outside the

forest. Because of the lack of ecological, physiological, and behavioral studies for African forest amphibians and reptiles, it is often difficult and somewhat subjective to decide which species are truly “dependent” upon forest habitat. This difficulty has been discussed for the forest amphibians of Tanzania (Howell, 1993), East African amphibians and reptiles (Loveridge, 1935, 1957), tree frogs (Schiotz, 1967, 1975), snakes (Hughes, 1981), and birds (Moreau, 1966).

In Kibale, the non-forest dependent, or farmbush, component of the herpetofauna is characterized by the frogs *X. l. victorianus*, *B. maculatus*, *S. schubotzi*, *H. albolabris*, *P. parvulus*, *P. chrysogaster*, *P. mascarenensis*, *R. angolensis*, *A. quadrivittatus*, *H. cinnamomeoventris*, *H. kivuensis*, *H. nasutus*, and *H. viridiflavus*, roughly 46% of the frog fauna. Five lizards, *H. mabouia*, *C. ellioti*, *M. striata*, *M. maculilabris*, and *M. megalura* are found primarily outside the forest, and two, *S. atricollis* and *L. fernandi*, are edge species that were never observed in the forest interior. Of the remaining eight species, two were collected only from exotic pine plantations adjacent to the forest, and locality records for these, *C. quattuorseriatus* from Bwindi (Drewes and Vindum, 1997) and *L. aloysiisabaudiae* from Garamba (De Witte, 1966), suggest that these species also are not forest-dependent. Approximately 60% of the lizard fauna should be considered part of the farmbush assemblage. Hughes (1981) reviewed the forest, farmbush, and savanna snake faunas of tropical Africa, and I follow his classification. Accordingly, of the 37 known and expected snakes in Kibale, 32% (12) are common in both forest and savanna habitats, *A. irregularis*, *B. gabonica*, *C. hotamboeia*, *D. lutrix*, *L. ornatum*, *L. lineatus*, *N. melanoleuca*, *P. angolensis*, *P. phillipsii*, *P. sebae*, *T. angolensis*, and *T. punctatus*. *Philothamnus semivariiegatus*, known from a single specimen collected outside the park, is considered strictly a savanna form by Hughes (1981, 1985).

The transitional nature of Kibale between lowland and montane forest is evident in the herpetofauna. Among the forest-dependent species in Kibale there are elements of both a higher elevation montane fauna, consisting primarily of species endemic to Central Africa, and a

lowland forest fauna which often ranges to West Africa. Wide ranging species, characteristic of the lowland rain forest of the Guinea-Congolese forest include 14% of the frogs (*B. funereus*, *P. auritus*, *A. laevis* and *C. rufescens*), 20% of the lizards (*L. fernandi*, *A. africanus*, and *H. g. guentheri*) and 46% of the snakes (17 species). The montane forest-dependent species characteristic of Central Africa make up 28% of the Kibale frog fauna (*X. wittei*, *X. vestitus*, *B. kisoensis*, *P. dendrobates*, *P. graueri*, *P. versicolor*, *P. verrucosus* and *L. kivuensis*), 13% of the lizard fauna (*A. vauereselli*, *C. adolfifriderici*) and 9% of the snake fauna (*Philothamnus heterodermus ruandae*, *A. nitschei*, and *Dasypeltis atra*, Laurent, 1974). The remaining species represent mid-low elevation forest forms that have distributions limited to Central Africa. This category includes four frogs (*H. lateralis*, *H. platyceps*, *H. kivuensis*, and *L. christyi*) the Ituri forest chameleon, *C. ituriensis*, and four snakes (*P. christyi*, *G. depressiceps*, *T. jacksonii*, *D. jamesoni*).

Clearly the farmbrush assemblage represents a significant proportion of the Kibale herpetofauna. Bwindi-Impenetrable N. P., the site most similar to Kibale, is characterized by a higher proportion of forest-dependent species. At Bwindi, 70% of the frogs (versus 60% at Kibale) are forest-dependent. This is largely due to the existence of five montane forest tree frog species and the montane endemic *R. ruwenzorica* which do not occur in Kibale. The lizards show the same pattern: 50% are forest dependent at Bwindi (vs 40% at Kibale), and again this is largely due to the presence of two endemic montane chameleons and two endemic montane skinks. The greater representation of farmbrush species in the Kibale herpetofauna is further illustrated by the similarity of the Kibale fauna to that of Garamba, a non-forest, moist savanna woodlands site. The herpetofauna of Garamba, which is characterized by moist savanna woodlands, shares 30 species in common with Kibale, but only 16 in common with Bwindi. Hamilton (1976, 1981) and Struhsaker (1981) hypothesized that Bwindi functioned as a forest refugia during the arid conditions of the last glacial maximum. Thus, the larger number of

Albertine Rift endemic frogs and reptiles at Bwindi relative to Kibale is probably a function of its greater elevational range and age.

The zoogeography of tropical African forests is thought to be strongly influenced by forest expansion, associated with wet interglacial periods, and forest retraction, associated with colder drier conditions during periods of glaciation. Much attention has focused on the last glacial maximum, at 18,000 years BP, when the extent of tropical forest was greatly reduced, creating hypothesized isolated forest refugia (Hamilton, 1976; Moreau, 1969). This vicariance promoted allopatric speciation in these refugia. Warmer wetter conditions since 12,000 BP have been associated with expansion of rain forests, which reached their maximum extent at approximately 7,000 BP, and allowed mixing of previously isolated forest faunas. A number of authors have used modern patterns of distribution of forest species to elucidate past forest history, and have argued that patterns of richness and endemism suggest two principle core refugia, one in Cameroon and Gabon, and another in Eastern Zaire, with smaller refugia in West Africa and coastal East Africa (Hamilton, 1976, 1992; Moreau, 1969).

Those critical of refugia theory have argued that modern distribution patterns reflect recent environmental conditions and tell us little about the past. The argument most commonly used to support this criticism is based on the positive correlation between areas of high rainfall and high species richness in tropical Africa (Hamilton, 1992). Three primary responses rebut this criticism. First, Hamilton (1992) suggests that areas of current rainfall are likely to have been areas of past heavy rainfall because the broad atmospheric circulation patterns over Africa at 18,000 BP were similar to those of today. Second, the refugia are not only species and endemic rich, but they represent isolated populations of disjunct species distributions, such as the gorilla (Hamilton, 1992). Finally, few species appear to be endemic to forest regions outside the proposed refugia (Diamond and Hamilton, 1980).

Faunal comparisons among the eight sites examined here are generally consistent with forest refugia theory. The high richness of Korup N. P. and Virunga N. P. is consistent with hypothesized core refugia (Hamilton, 1988), though lack of distribution data from intervening areas precludes finer scale examination of potential gradients of declining diversity between these areas (Hamilton, 1988). Kibale, Bwindi, and Virunga are more similar to each other than to the fauna of West Africa, represented by Korup. This is consistent with the hypothesis that these areas have been connected more frequently or over a longer time period. Schiotz (1976) suggested that the forests of Uganda and western Kenya are depauperate outliers of Virunga, the eastern Zaire core area. The lower total richness observed at these two national parks is probably a function of both smaller area and their increased elevation and corresponding loss of many lowland rain forest forms present on the Zaire side of the Albertine Rift. However, when the number of species per area is considered, both Kibale and Bwindi exhibit higher values than Virunga N. P. In fact, the smaller parks consistently exhibited higher species per area values. This may be correlated with habitat degradation (L. Chapman, pers. com.), and illustrates the importance of conserving these remaining forests. These forests are now small islands, but they may have maintained many of the species that were present when they were part of larger, continuous forest.

The montane forests of Tanzania are believed to represent a minor refugia that has been isolated from the Congo forest block for millions of years, a conclusion supported by the high endemism of many taxa in these forests. In the Usambara Mountains, 87% of the amphibians and 55% of the reptiles are endemic to Tanzanian montane rain forest (Howell, 1993). Faunal comparisons with Kibale also suggest a long isolation period. The Kibale herpetofauna is five times more similar to Korup, 2420 km distant, than to the Usambaras, 1050 km away; and there is no overlap between the Uzungwa fauna and any site except Usambara.

These results also demonstrate the unique fauna of the coastal dry forest represented by the Arabuko-Sokoke site. Coastal forest is one of the most imperiled African habitats and is home to a distinctive herpetofauna unlike that of the wetter tropical forest. Interestingly, Arabuko has the greatest species overlap with moist savanna woodlands of Garamba.

Conclusions

Kibale forest supports a rich herpetofauna of more than 70 species. This relatively high species richness is derived from overlap of two primary faunal elements, farmbush species and the forest-dependent species. The relatively high number of species observed is probably related to the heterogeneous habitat of forest, swamp, grassland, and agricultural areas characteristic of Kibale. Despite the large number of farmbush species, the number of forest-dependent species in Kibale is comparable to that of other mid-elevation forests in Africa, Central America, and the Philippines. None of these species are endemic to Kibale, and only a few are restricted to the Albertine Rift. Most of the endemic amphibian and reptile species of the Albertine Rift are characteristic of higher elevation, montane forest not present at Kibale. Previous researchers have noted that the forest herpetofaunas of East Africa consist of two, non-overlapping groups. One group represents the extension of the Guinea-Congolese rain forest fauna, the second is largely endemic to the coastal mountains of Tanzania. The Kibale herpetofauna is clearly an example of the first group, as suggested by the high species overlap with the Parc National des Virunga, in eastern Congo-Zaire, and secondarily to Korup National Park in Cameroon. The high similarity among Virunga, Bwindi, and Kibale relative to the similarity of these forests to the forests of West and East Africa is consistent with the hypothesized core forest refugia of eastern Zaire.

TABLE 2.1. Ecological characteristics of the 29 species of amphibians known to occur in and around Kibale forest, Uganda. (× = Albertine Rift endemic)

Taxon	Abun ^a	Sites ^b	Habitat ^c	Diel ^d	Micro ^e	Food ^f	Repro. ^g	General Distribution ^h
Pipidae								
<i>Xenopus laevis victorianus</i>	C	1,2	FI, FE, A	ND	Aq	I, F?	Aq	E. Zaire - W. Kenya
<i>Xenopus wittei</i>	U	1,2	FI, FE	ND	Aq	I	Aq	E. Zaire, Uganda, Rwanda
<i>Xenopus vestitus</i>	R	2	FI?	?	Aq	I?	Aq	E. Zaire, Uganda, Rwanda
Bufonidae								
<i>Bufo funereus</i>	U	1-4,5	FI	D	L, U	A, I	Aq	forests; Angola to Uganda
<i>Bufo kisoensis</i>	I	1	FI	D	L, S	A, I	Aq	forests; E. Zaire and E. Africa
<i>Bufo maculatus</i>	C-U	6	A, FE	D	L	A, I?	Aq	tropical Africa
Ranidae, Arthroleptinae								
<i>Schoutedenella schubotzi</i> ×	C-U	1,2	FE, FI, A	D	L, U	A	TrDd	E. Zaire - Uganda, Rwanda?
Ranidae, Petropedetinae								
<i>Phrynobatrachus auritus</i>	I	1-3,5	FI	D	L, R	?	Aq	forests; W. Africa - Uganda
<i>Phrynobatrachus dendrobates</i> ×	R	2	FI	N	L, R	?	ArAq	forests; E. Zaire - W. Uganda,
<i>Phrynobatrachus graueri</i>	C	1-4	FI, FE	D	L, S	I, A	Aq	forests; Zaire - Uganda

TABLE 2.1

Taxon	Abun	Sites	Habitat	Diel	Micro	Food	Repro	General distribution
<i>Phrynobatrachus parvulus</i>	C-U	1	FI, FE	D	L, S	?	Aq	Angola - W. Tanzania
<i>Phrynobatrachus versicolor</i> ×	R	1	FI	ND	L, R	?	Aq	montane forest; E. Zaire, Uganda
Ranidae, Raninae								
<i>Hylarana albolabris</i>	C	1-6	FE, FI, A	N	SA	?	Aq	Liberia - Uganda
<i>Ptychadena chrysogaster</i>	U	1,2	FE	ND	T	?	Aq	mid-elevations; Uganda, Rwanda
<i>Ptychadena mascarenensis</i>	U	1,2	FI	N	T	?	Aq	forests; W. Africa - Uganda
<i>Rana angolensis</i>	U	1-6	FI, FE	N	SA	?	Aq	sub-Saharan Africa
Hyperoliidae								
<i>Afrixalus laevis</i>	R	3	FI	N	AL	?	ArAq	Cameroon - Uganda
<i>Afrixalus osorioi</i>	E	-	FI, FE	N	AL	?	ArAq	E. Zaire - Uganda
<i>Afrixalus quadrivittatus</i>	U-I	1,2	FI, FE	N	AL	?	ArAq	Cameroon - Kenya
<i>Hyperolius cinnamomeoventris</i>	C	1,2	FI, FE	N	AL	?	ArAq	Cameroon - Kenya
<i>Hyperolius kivuensis</i>	C	1,2	FI, FE	N	AL	?	ArAq	Zaire - W. Kenya
<i>Hyperolius lateralis</i>	C	1,2	FI	N	AL	I	ArAq	forests; Zaire-Kenya
<i>Hyperolius nasutus</i>	R	6?	A, FE	N	AL	?	Aq	grasslands; tropical Africa

TABLE 2.1.

Taxon	Abun	Sites	Habitat	Diel	Micro	Food	Repro	General distribution
<i>Hyperolius platyceps langi</i>	I	1,2	FI	N	AH	?	ArA	forests; E. Zaire - Uganda
<i>Hyperolius viridiflavus bayoni</i>	U	1,6	A, FI	N	AL	?	Aq	E. Zaire - Uganda
<i>Leptopelis christyi</i>	U	1-5	FI	N	AH	?	TrAq	forests; E. Zaire - Uganda
<i>Leptopelis kivuensis</i> ×	U	1-3	FI	N	AH	I	TrAq	forests; E. Zaire - Uganda
<i>Phlyctimantis verrucosus</i>	U	1,3	FI	N	AL	?	Aq	forests; E. Zaire - Uganda
Rhacophoridae								
<i>Chiromantis rufescens</i>	R	1	FE	N	A	?	FoAq	Nigeria - Uganda

Notes: *a* Abund, relative abundance: C = common—one can find many specimens; U = usual—one can find when looking in the proper habitat during the appropriate season; I = infrequent—not predictable; R = rarely seen; E = expected—not yet reported from Kibale but presence seems very likely

b Sites, collected or observed: 1 = Kanyawara; 2 = Dura River near Kanyanchu; 3 = Mpanga River at Sebatoli; 4 = Ngogo field station; Mainaro; 6 = Lake Nyabikere

c Habitat: FI = forest interior; FE = forest edge, or opening; A = agricultural areas outside the forest, farmbush

d Diel, time of activity: D = diurnal; N = nocturnal; DN = variably active either night or day

e micro, microhabitat and vertical position: Aq = aquatic; L = forest leaf litter; T = terrestrial at forest edge or opening; A = arboreal; U = upland; S = swamp forest or valley bottoms; R = riparian or streamside; AL = semi-arboreal, in low vegetation; AH = highly arboreal, in tree canopy

f Food: I = insects; A = ants, F = fish. Most preferred indicated first, if known.

g Rep. mode, reproductive strategy: Aq = eggs and larvae aquatic; ArAq = eggs arboreal, larvae aquatic; TrDd = eggs terrestrial, larvae direct developing; Tr Aq = eggs terrestrial, larvae aquatic after flooding; FoAq = eggs in arboreal foam nest, larvae aquatic

h General distribution: references include Inger (1968); Schmit and Inger (1968); Laurent (1972); De Witte (1941); Schiotz (1975)

TABLE 2.2. Ecological characteristics of the 50 reptile species found in and around Kibale forest, Uganda. (× = Albertine Rift endemic)

Taxon	Abun ^a	Sites ^b	Habitat ^c	Diel ^d	Micro ^e	Food ^f	General distribution
Sauria, Gekkonidae							
<i>Hemidactylus mabouia</i>	C	1,2,6	FE, A	N	A	I	tropical Africa
<i>Cnemaspis quattuorseriata</i>	U-I	1	A, FE	D	A	I?	forests?, E. Zaire, Uganda, Kenya, Ethiopia
Agamidae							
<i>Stellio (Agama) atricollis</i>	C	1,5,6	FE, A	D	A	?	Angola-Ethiopia & Natal
Chamaeleonidae							
<i>Chamaeleo adolfifrigerici</i> ×	R	1	FI	D	A	I	forests, E. Zaire, W. Uganda
<i>Chamaeleo ellioti</i>	C	1,6,7	A, FE	D	AL	I	S. Sudan, E. Zaire, W. Kenya, Uganda
<i>Chamaeleo ituriensis</i>	I	1,3	FI	D	A	I	forests, E. Zaire, W. Uganda
<i>Rhampoleon boulengeri</i> ×	U	1	FI, FE	D	L, AL	?	forests, E. Zaire, W. Uganda
Scincidae							
<i>Mabuya striata</i>	C	1,6,7	A, FE	D	L	I	E. Zaire-Ethiopia & Zimbabwe
<i>Mabuya maculilabris</i>	I	5?	A, FE	D	L	?	West & Central Africa
<i>Mabuya megalura</i>	I	5?	A, FE	D	L	?	

TABLE 2.2.

Taxon	Abun	Sites	Habitat	Diel	Micro	Food	General Distribution
<i>Leptosiaphos aloysiisabaudiae</i>	R	1	FE, A	D	L	?	E. Zaire-W. Uganda
<i>Lygosoma fernandi</i>	U	1,7	FE, A	D	L	?	Bioko & Cameroon, through to Uganda
Lacertidae							
<i>Adolfus africanus</i>	U	1	FI, FE	D	A, L	I	forests, Cameroon, Zaire, Uganda
<i>Adolfus vauereselli</i>	U	1	FI, FE	D	L, A	I	forests, E. Zaire, W. Uganda, W. Tanzania,
<i>Holoaspis guentheri guentheri</i>	R?	1	FI	D	AH	I	forests, Sierra Leone to Uganda
Serpentes, Typhlopidae							
<i>Typhlops angolensis</i>	I	7	A, FE	N	B	W, I	montane grasslands, Cameroon to Kenya
<i>Typhlops punctatus congestus</i>	E	-	FI	N	B	W, I	forests, Liberia to Kenya. Uganda localities: Bwamba, Budongo, Kigezi forests
Boidae							
<i>Python sebae sebae</i>	I-R	1,7	FI, FE, A	N	T, Aq	B, M	Liberia to Kenya
Colubridae							
<i>Bothrophthalmus l. lineatus</i>	U	1,8	FI	N	T, Aq?	Ro	forests, Angola & Guinea to Uganda
<i>Crotaphopeltis hotamboeia</i>	R	5?	FE, A	N	T, Aq	Am	Central and East Africa

TABLE 2.2.

Taxon	Abun	Sites	Habitat	Diel	Micro	Food	General Distribution
<i>Lamprophis lineatus</i>	C	1,7	A, FE	N	T	Ro, Re	grasslands, Seirra Leone to Uganda
<i>Lamprophis olivacea</i>	R	8	FI	N	T	Ro	forests, Liberia to Uganda
<i>Lycophidion ornatum</i>	I	1	FI, FE	N?	T	Re	forests, Zaire, Uganda
<i>Mehelya poensis</i>	E	-	FI	N	T	Re	forests, Liberia to Uganda. Uganda: Budongo, and Kigezi forests
<i>Mehelya stenophthalmus</i>	R	8	FE	N	T	Re	W. Africa to Uganda
<i>Duberria lutrix atriventris</i>	U	1,7	A, FE	N	T	Ga	grasslands, Uganda, Kenya, Rwanda
<i>Geodipsas d. depressiceps</i>	C	1	FI	DN	T	Am	forests, Nigeria, Cameroon to Uganda
<i>Psammophis phillipsii</i>	I	5	A, FE	D	T	Ro, Am	Liberia to Uganda
<i>Natriciteres olivacea</i>	U	1,5	FE, A	DN	T, Aq	Am, F	grasslands, Ghana to Kenya
<i>Philothamnus angolensis</i>	U	1,2,6?,7	A, FE	DN	A	Am	Cameroon to Uganda
<i>Philothamnus carinatus</i>	U-I	1	FI, FE	DN?	A	Am	forests, Liberia to Kenya
<i>Philothamnus heterodermus</i>	U	1	FI, FE	DN	A	Am	forest, Zaire, Uganda, Rwanda, Burundi
<i>Philothamnus semivariiegatus</i>	U	7	FE, A	DN?	A	Am	East Africa
<i>Philothamnus nitidus</i>	I	1	FE	DN?	A	Am	Liberia to Uganda

TABLE 2.2.

Taxon	Abun	Sites	Habitat	Diel	Micro	Food	General Distribution
<i>Hapsidophrys lineatus</i>	U	2,8	FE, FI	DN?	A	Am	forests, Liberia to Kenya
<i>Gastropyxis smaragdina</i>	E	-	FI	DN?	A	Am, Re	forests, Angola & Guinea to Uganda. Uganda: Bwamba, Chambura, Mbira forests
<i>Boiga blandingii</i>	I	1,8	FE, FI	DN	A	B, M	forests, Liberia to Kenya
<i>Boiga pulverulenta</i>	R	8	FI, FE	N	A	M	forests, Liberia to Kenya
<i>Dipsadoboa u. unicolor</i>	I	7,8	FE, FI	N	A	Am	forests, Liberia to Kenya
<i>Thrasops j. jacksonii</i>	C	1,2,7,8	FE, FI, A	DN	A	B, M, Re	forests, Zaire to Kenya
<i>Rhamnophis aethiopissa</i>	U	2,8	FI, FE	DN?	A	Am	forests, Liberia to Kenya
<i>Thelotornis kirtlandii</i>	I	1,2,7,8	FE, FI, A	DN	A	Re	forests, Liberia to Kenya
<i>Polemon christyi</i>	I-R	7	FE, FI, A	N?	B	Re	forests, Zaire to Kenya
<i>Dasypeltis atra</i>	U	1,8	FI	N	T, A	B eggs	montane forests, Zaire to Kenya
Viperidae							
<i>Causus lichtenstienii</i>	C	1,5	FI, FE	DN	T	Am	forests, Liberia to W. Kenya
<i>Atheris s. squamiger</i>	U-I	1,2,8	FI, FE	N	A	Ro, Am	forests, Ghana to Kenya
<i>Atheris n. nitschei</i> ×	R	1	FI, FE?	N	A	Ro, Am	montane forests, Zaire and Uganda

TABLE 2.2.

Taxon	Abun	Sites	Habitat	Diel	Micro	Food	General Distribution
<i>Bitis nasicornis</i>	U	1,3,7,8	FI, FE, A	N	T, AL	Ro, Am, F	forests, Equatorial Guinea to Kenya
<i>Bitis gabonica</i>	E	-	FE	N	T	M, B, Am	Cameroon to Kenya; Uganda: Budongo, Bwamba forests, Queen Elizabeth N. P.
Atractaspididae							
<i>Atractaspis irregularis</i>	E	-	FE, FI	N	B	Ro	E. Zaire to Kenya; Uganda: Budongo, Bwamba, Mbira, Kigezi forests
Elapidae							
<i>Naja melanoleuca</i>	I	1,5,8	FE, FI	DN	T	F, Re, Am	wide-spread through rain forest region
<i>Pseudohaje goldii</i>	E	-	FI	N	A	Am	forests, Ghana to W. Kenya below 1,500 m Uganda: Bwamba & Mbira forests
<i>Dendroaspis jamesoni</i>	U	1,7,8	FE, FI, A	N	A, T	Ro, B	forests, Zaire, W. Kenya, Uganda

Notes: a Abun, subjective relative abundance based on frequency of encounters and number of specimens: C = common, one of the most frequently seen snakes; U = usual, sighted several times over the year, more than one specimen; I = infrequent, seen only once or twice, may only have a single voucher; R = rare, reliable report, or a single specimen; E = expected, based on habitat preference and Ugandan distribution

Table 2.2

Notes:

b Sites, collected and observed: 1 = Kanyawara station; 2 = Dura River near Kanyanchu; 3= Sebatoli; 4 = Ngogo; 5 = Mainaro, or southern art of park; 6 = Lake Nyabikere; 7= agricultural area between Ft. Portal and Kanyawara; 8 = reported from Kibale by Pitman (1974).

c Habitat: FI = forest interior; FE = forest edge or opening; A = agricultural areas outside forest, farmbush

d Diel: D = Diurnal; N = Nocturnal; DN = variably active, day and night

e Micro, microhabitat and vertical position: Aq = aquatic; B = burrowing; L = forest litter; T = terrestrial; A = arboreal; AL = arboreal in low vegetation; AH = Arboreal in tree canopy

f Food: I = insect; W = annelids; Ga = Gastropods; F = fish; Am = amphibians; Re = reptiles; B = birds; M = general mammals; Ro = rodents; most information on snake diet based on Pitman (1974) and personal observations

g General distribution: primarily providing East-West range; most snake range data from Pitman (1974), lizards references include Loveridge (1942*a*) and Arnold (1989),

TABLE 2.4. Coefficients of faunal similarity for eight equatorial African herpetofaunas; Korup (KOR), Virungas (VIR), Garamba (GAR), Kibale (KIB), Bwindi (BWI), Usambaras (USA), Uzungwa (UZU), and Arabuko-Sokoke (ARA). Values > 0.50 in bold.

Amphibians								
	KOR	VIR	GAR	KIB	BWI	USA	UZU	ARA
KOR	—	18	6	6	5	1	0	1
VIR	0.26	—	13	24	23	0	0	2
GAR	0.10	0.26	—	9	5	0	0	5
KIB	0.11	0.56	0.26	—	20	0	0	1
BWI	0.09	0.54	0.15	0.73	—	1	0	1
USA	0.01	0	0	0	0.04	—	10	1
UZU	0	0	0	0	0	0.5	—	0
ARA	0.02	0.05	0.15	0.04	0.04	0.04	0	—
Reptiles								
	KOR	VIR	GAR	KIB	BWI	USA	UZU	ARA
KOR	—	33	27	23	10	4	0	6
VIR	0.36	—	43	43	33	4	0	16
GAR	0.37	0.47	—	21	11	2	0	5
KIB	0.37	0.55	0.34	—	27	3	0	5
BWI	0.18	0.46	0.20	0.67	—	4	0	4
USA	0.08	0.06	0.04	0.08	0.13	—	6	4
UZU	0	0	0	0	0	0.27	—	0
ARA	0.09	0.19	0.25	0.09	0.08	0.09	0	—

TABLE 2.4.

Amphibians and Reptiles

	KOR	VIR	GAR	KIB	BWI	USA	UZU	ARA
KOR	—	51	33	29	15	5	0	7
VIR	0.32	—	56	67	56	4	0	18
GAR	0.24	0.40	—	30	16	0	0	22
KIB	0.25	0.56	0.32	—	47	3	0	6
BWI	0.14	0.49	0.18	0.69	—	5	0	5
USA	0.05	0.04	0.02	0.05	0.09	—	16	5
UZU	0	0	0	0	0	0.38	—	0
ARA	0.06	0.14	0.22	0.07	0.07	0.07	0	—

TABLE 2.5. A comparison of the “forest-dependent” herpetofauna species richness in tropical mid-elevation-montane forests of Africa, Central America, and the Philippines.

Site	Elevation	Amphibians	Reptiles	Totals
Usambara F. R., Tanzania	1000-2286 m	23	29	52
Uzungwa F. R., Tanzania	300-2800 m	19	16	35
Kibale N. P., Uganda ^a	1400-1550 m	15	29	44
Bwindi N. P., Uganda ^b	1200-2600 m	20	21	41
Virungas N. P., Congo ^c	1300-3000 m	27	~40	67
Korup N. P., Cameroon ^d	1080-1768	33	11	44
Monteverde, Costa Rica ^e	1300-1470 m	25	36	61
Cuernos de Negros,	1050-1350 m	7	13	20
Philippines ^f				

Notes: *a* only Kibale species restricted to the forest interior are included
b species listed as extralimital by Drewes and Vindum (1991) are excluded
c only forest species found above 1300 m are included
d only species found at Mt. Yuhan (to 1079 m); Rumpi Hills (1,000-1,768), and Nta Ali (to 1,200) are included. Lawson (1993) comments that these elevations were under sampled.
e only species restricted to Timmerman’s (1981) pre-montane and lower montane zones (2-5) are included.
f only specimens in submontane and montane forest zones are included from Brown and Alcalá (1961).

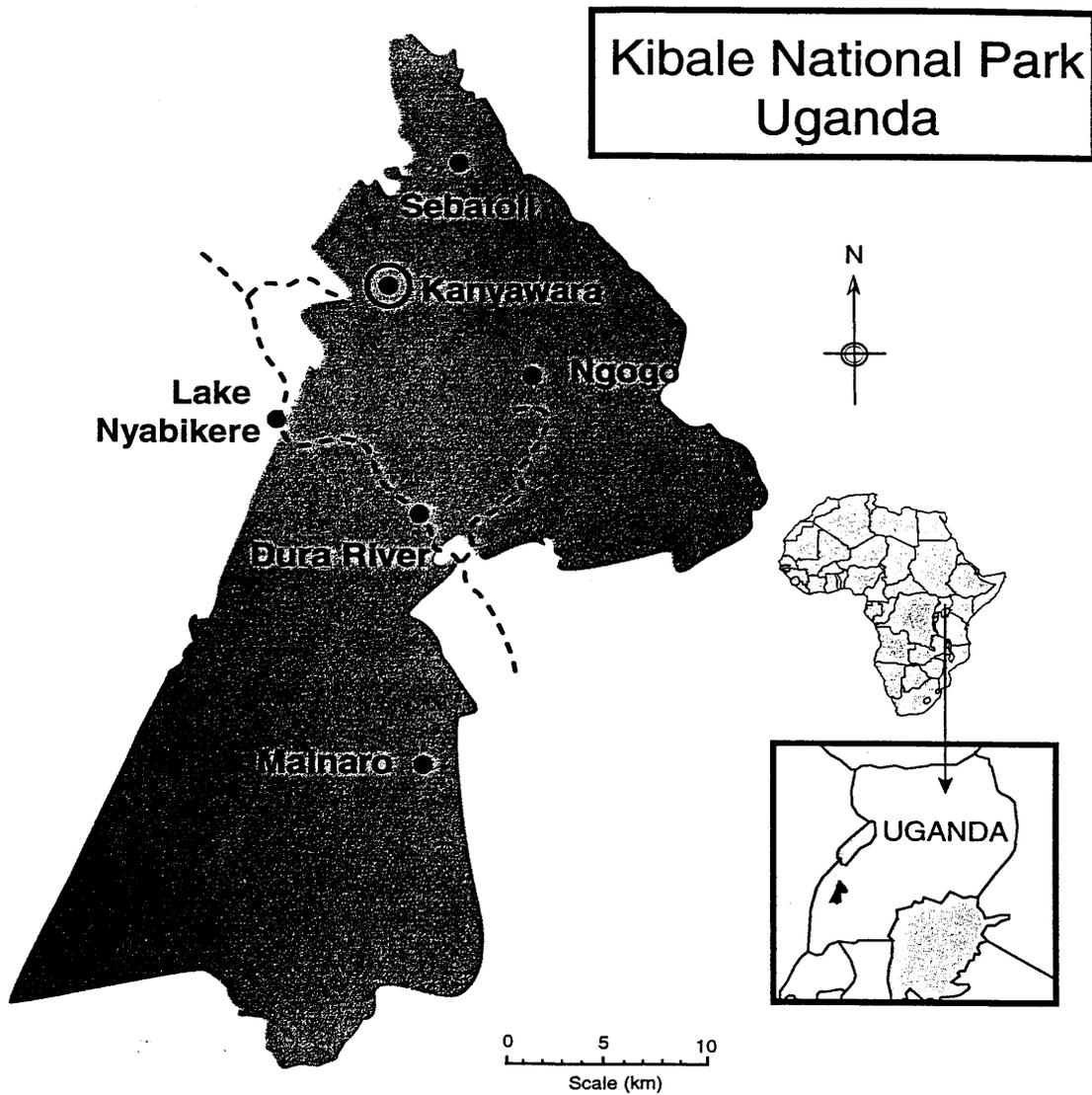


FIGURE 2.1. A map of Kibale National Park, Western Uganda, East Africa, showing Kanyawara, the primary sampling site, and five supplementary amphibian and reptile collection sites: Sebatoli, Ngogo, Lake Nyabikere, Dura River, and Mainaro.

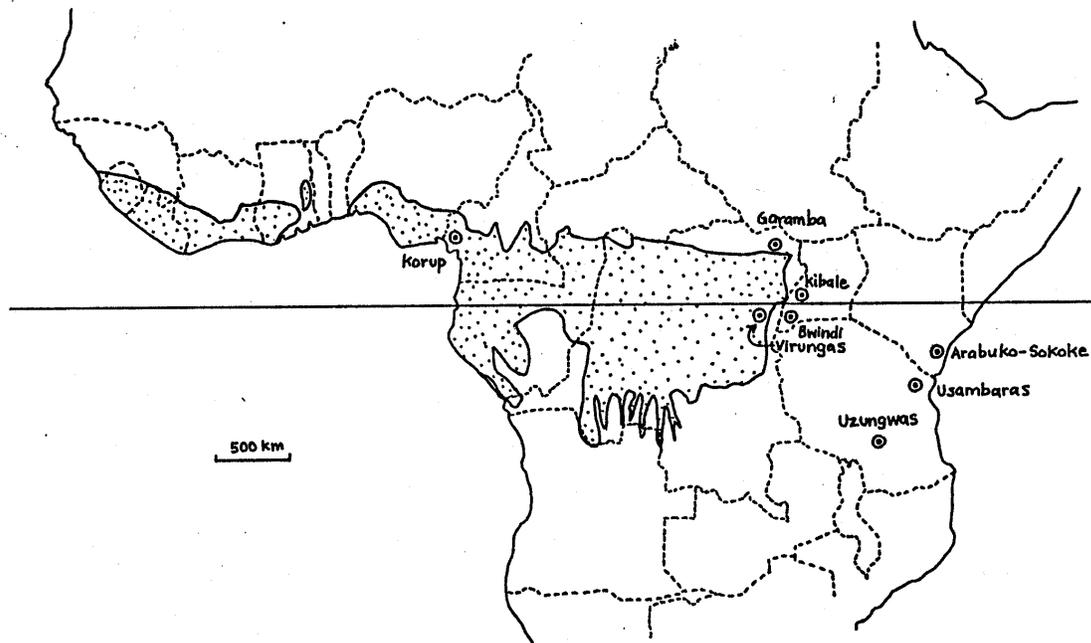


FIGURE 2.2. A map of equatorial Africa showing the eight sites that were used in comparing tropical amphibian and reptile faunas. Dots indicate estimated extent of tropical African rain forest based on Hughes (1983) and dashed lines indicate national boundaries

CHAPTER 3
ECOLOGICAL CORRELATES OF LITTER HERPETOFAUNA: RICHNESS AND
ABUNDANCE

Introduction

The leaf-litter layer of most tropical rain forests support diverse herpetofaunas which may include frogs, salamander, caecilians, amphisbaenids, lizards, snakes, and turtles. These often sizable faunas are composed of species which may be ecologically similar and phylogenetically closely related. Given these similarities, it is natural to ask, how do these species coexist? A growing number of researchers have attempted to address this question by trying to determine which physical and biotic factors are important structuring these communities, and how these communities vary among tropical regions (Lloyd *et al.*, 1968; Scott, 1976; Toft, 1980a; Allmon, 1991; Heinen, 1992; Gascon, 1996).

Comparative study of litter herpetofaunas of Southeast Asia and Central America has revealed interesting differences between the regions. The lowland forests of Central America support a similar number of species, but at much higher densities (often 10 times as great) as the forests of Southeast Asia. Unfortunately, comparisons with Africa at this stage are premature. For, with the exception of two preliminary studies of coastal West Africa (Toft, 1982; Scott, 1982), the litter communities of tropical Africa have been overlooked.

Neither Scott (1982) nor Toft (1982) quantitatively addressed the importance of physical, biotic, or anthropogenic factors in structuring the litter communities at their sites in West Africa. However, studies in Central America and Southeast Asia have identified a number of physical

and biotic factors that seem to influence litter herpetofaunal abundance and composition on a local scale. Scott (1976), Fauth *et al.* (1989), and Heinen (1992) found that litter depth was correlated with herpetofaunal abundance and diversity and Allmon (1991) found a similar relationship with dry litter mass. Physical characteristics such as elevation, slope, and moisture (Scott, 1976), and biotic characteristics such as prey abundance (Toft, 1980a; Lieberman, 1986; Guyer, 1988) and juvenile recruitment (Allmon, 1991) also correlate with litter herpetofauna abundance in some systems. Both physical and biotic factors may vary seasonally, causing corresponding changes in the litter community either directly (increased desiccation risk during the dry season) or indirectly (greater prey abundance during the dry season). Heatwole (1982) reviewed the structuring of herpetofaunal assemblages and found that species richness decreases with increasing latitude and altitude and with decreasing availability of moisture, while the animal density is highest at intermediate elevations.

Anthropogenic factors, such as implementation of different forest management strategies, may also affect in the distribution of litter amphibian and reptile species. In Costa Rica, Lieberman (1986) found increased abundance but lower diversity and evenness of litter species in anthropogenically disturbed sites relative to primary forest. Similar patterns have been reported from South America (Miyata, 1980) and Malaysia (Inger, 1980b).

Habitat, food, and time are three traditional categories of resources, which may be further divided into macrohabitat, microhabitat, food type, food size, diel time, and seasonal time (Toft, 1985). In this study I will examine aspects of how the litter herpetofauna of Kibale National Park, Uganda, uses each of these different resources and then relate these findings to existing studies from other tropical regions.

To achieve this objective, I first examine potential habitat correlates of litter herpetofaunal abundance in three differently managed forest types during both wet and dry seasons. I will use these data to identify the physical and biotic factors most important in

structuring the Kibale community and how it responds to anthropogenic disturbance. Next, I describe the feeding ecology of the six most common litter anurans, and use dietary overlap indices to provide an indication of the strength of interspecific interactions along this resource axis. Finally, I examine the local-scale response of litter arthropods and herpetofauna to large fruiting trees. Specifically, I test the hypothesis that litter arthropod numbers increase under fruiting fig trees, and that the litter herpetofauna increases locally in response to increased arthropod abundance. Taken collectively, the different elements of this study will address the initial question: “What factors are important in structuring this community?”. The next step is to compare these results with those from other tropical leaf-litter herpetofauna studies to get a better idea of whether the Kibale fauna is similar in diversity and abundance to faunas from Central and South America and Southeast Asia, and whether factors that appear to be important in structuring those communities are similar to those important in Kibale.

Methods

Study site

This study was conducted at the Makerere University Biological Field Station, Kibale National Park, in western Uganda ($0^{\circ} 13' - 0^{\circ} 41'N$ and $30^{\circ} 19' - 30^{\circ} 32'E$). The field station is located near the eastern base of the Ruwenzori mountains at an elevation of 1530 m. The forest is transitional between lowland and montane rain forest with a typical canopy height of between 20 - 30 m (Struhsaker, 1997). The general topography of the study area consists of moderately undulating hills and valleys. Mean annual rainfall at this site between 1977 and 1991 was 1622 mm, most of which fell during the two rainy seasons, March - May and September - November (Struhsaker, 1997).

Kibale received national park status in 1993. Prior to that it was managed as a forest reserve, and various compartments of the forest were commercially exploited to different degrees. As a result, the forest surrounding the field station is comprised of a mosaic of disturbed and undisturbed sections. For this study, I selected an unlogged study site, the K - 30 forest compartment, which is comprised of approximately 300 ha of undisturbed, mature, *Parinari* forest (Struhsaker, 1997). The K - 15 timber compartment served as the heavily logged study site. K - 15 was selectively logged in 1968 - 69 at an intensity of 7.4 commercial stems per hectare (Skorupa, 1988). The areas adjacent to K - 15 include lightly logged and heavily logged forest, and conifer plantations. My third study area, Nyakatojo, is a monotypic stand of mature, exotic pine (*Pinus caribaea*) on a low ridge draining into the Dura and Nyakagera Rivers, directly abutting the unlogged K - 30 compartment. This area was planted with pines between 1963 and 1965, and at that time it was dominated by elephant grass *Pennisetum purpureum* (Kingston, 1967; Chapman and Chapman, 1996). Such grassland areas in Kibale are believed to be the result of past human clearing of forest which were then maintained by frequent anthropogenic burning (Kasenene, 1987). At the time of this study, Nakatojo was characterized by a mature pine canopy, while the understory vegetation included many indigenous forest tree species (Chapman and Chapman 1996; Zanne, 1998). The greatest distance between any two of these three areas is less than 5 km.

Site and Season Comparisons

I follow Heinen (1992) in defining the litter herpetofauna as all reptiles and amphibians that live directly in the leaf litter, or were found within 0.5 m of the forest floor, and feed on other litter organisms (*e.g.*, arthropods, frogs, lizards). Using a map of the trail system in each of the three areas, I randomly generated plot sampling locations at the beginning of the study. Since statistical variances for mean densities approach an asymptote when based on 50 or more

quadrats, even in areas where densities are low (Lloyd *et al.*, 1968; Heyer *et al.*, 1994), I sampled 50 plots each season in each of the three forest types. No plot was sampled more than once. Wet season plots were sampled between March 11 - May 15, and dry season plots were sampled between June 12 - July 26, with four to eight plots being sampled in each area per week. Each plot was 5 m x 5 m (Fauth *et al.*, 1989; Allmon, 1991; Heinen, 1992) and enclosed with a clear plastic fence 50 cm high immediately prior to sampling. The bottom of the fence was secured using large nails. Once the fence was in place, 2 - 4 (usually 3) people would search the entire plot on hands and knees, overturning all litter and logs, and sifting through the first few centimeters of top-soil. A mean of 58.5 (33 - 108) person-minutes was spent searching each plot. On occasions when the *a priori* plot location fell in flooded swamp-forest, extremely dense vegetation, or in a forest gap, an alternative location was randomly generated.

All amphibians and reptiles captured were identified to species, measured (snout - vent length), and classified as adult or subadult. After voucher specimens of each species were preserved, subsequent captures were identified, measured, and released. Voucher specimens are deposited in the zoological collection of Makerere University, Kampala, Uganda, and in the herpetological collection of the California Academy of Sciences, San Francisco, U.S.A.

For each plot, I recorded: (1) air and wet bulb temperatures, (2) slope in degrees (clinometer); (3) percent soil humidity (soil humidity meter); (4) soil pH (soil pH meter); (5) wet litter mass of a randomly selected 0.5 m² subplot; (6) mean litter depth, measured to the nearest 0.5 cm, 1 m in from each corner of the plot; (7) estimated percent of low ground vegetation cover under 1 m high; (8) estimated percent shrub (1 - 3 m) cover; (9) percent canopy cover, measured using a spherical densitometer; (10) number of logs > 10 cm diameter; and (11) number of trees > 10 cm dbh (diameter at breast height).

Among forestry compartments, I compared the observed total number of species in an area (s), the Jackknife estimate of species richness (S, Heltshe and Forrester, 1983), diversity

(H'), and evenness (J'), as suggested by Hayek (1994) and Krebs (1989). To facilitate comparison with previous studies, the logarithmic base 10 was used to calculate both Shannon's H' and Pielou's J'. The Jackknife richness estimate (S), rather than the number of species observed (s) was used to estimate the maximum value of H' when calculating J'. Morisita's index of similarity (C, Morisita, 1959) was used to measure the similarity of the herpetofaunas in each forest type. Krebs (1989) recommends this index for quantitative data because, unlike many other commonly used indices, it is not affected by sample size. Data on the abundance of forest-floor arthropods in the unlogged, logged, and pine plantation areas for the wet season sampling period months of March - May and the dry season months of June - August were available from Nummelin (1989).

Among-site and within-site and season comparisons of physical and biotic variables were made using Kruskal - Wallis nonparametric analysis of variance with a Bonferroni adjusted alpha level for 12 tests (SPSS, 1997). For significantly different tests among sites multiple comparisons were conducted using the Mann - Whitney test. Nonparametric tests were used in the analysis because many of the data to be compared had unequal variances. The relationship between these physical and biotic variables and the presence or absence of amphibians and reptiles was examined within and among sites and seasons using forward stepwise logistic regression (Trexler and Travis, 1993; SPSS, 1997), which included the following variables: slope, pH, wet litter mass, litter depth, number of logs, ground vegetation cover, shrub cover, canopy cover, number of trees, and hill category. The hill category ranged from (5) = valley bottom to (1) = hill-top.

Feeding Ecology

I examined the diets of the six most abundant litter anuran species by analyzing the stomach contents of the voucher specimens from this study as well as the stomachs of other

museum specimens previously collected in Kibale forest between 1990-1997 by various other researchers. For three species, specimens from Bwindi-Impenetrable National Park, in southwestern Uganda were included in the analysis in order to increase the sample size. For these three species, the prey of Bwindi and Kibale specimens were compared to determine if large differences in the feeding ecology of these species exist. Because of the paucity of material available, and the desire to minimize the number of animals sacrificed, specimens collected in all the forest compartments adjacent to the field station during both wet and dry seasons were combined. In addition, for all six species, both genders and all age categories were also combined. All specimens were fixed in 10% formalin then stored in ethanol. The six species examined were *Phrynobatrachus graueri* (n = 46), *Bufo funereus* (n = 17), *Bufo kisoensis* (n = 11 Kibale N. P., n = 6 Bwindi N. P.), *Schoutedenella schubotzi* (n = 16 Kibale N. P., n = 3 Bwindi N. P.), *Leptopelis kivuensis* (n = 16 Kibale N. P., n = 33 Bwindi N. P.), and *Hyperolius lateralis* (n = 14). Stomachs were excised and contents were identified to at least Order. For each prey taxon, the frequency of occurrence (%F = number of stomachs containing that taxon divided by number of stomachs with contents), relative abundance (%N = number of individual prey items of that taxon divided by the total number of prey items), and percent of prey volume (%V = total estimated volume of that taxon divided by total prey volume for all specimens) were calculated for each species. Prey volume for each prey type was estimated based on the volume of a cylinder, and was calculated using an average of the length and width (nearest 0.1 mm) of several intact specimens of each prey type. The Relative Importance Index (RI) of each prey taxon was calculated using the following George and Hadley (1979), where:

$$AI = \%N + \%V + \%F,$$

$$RI = 100 \frac{AI}{\sum_{1}^{n} AI}$$

(AI) is the ‘absolute importance index’ for each prey taxa and n is the number of different prey categories. This index provides a single estimate of dietary importance by combining relative abundance (%N), frequency of occurrence (%F), and percent volume (%V). Percentage RI values were calculated by summing the RI values for each prey taxa among all species and then dividing by the number of species. Values for this index range from 0 to 1.0. The diet of each species was then compared using Horn’s modification of the Morisita’s index of similarity for percentage RI values for prey taxa:

$$C_H = (2\sum P_{ij}P_{ik})/(\sum P_{ij}^2 + P_{ik}^2)$$

In this equation C_H is the simplified Morisita’s index of similarity (Krebs, 1989) between species j and species k . P_{ij} and P_{ik} is the proportion of the prey taxa consumed by the two species.

Fruiting Fig Trees and Litter Herpetofauna Distribution

In order to determine the effect of large fruiting events on the distribution and abundance of leaf-litter arthropods and herpetofauna, I sampled five *Ficus natalensis* during their fruiting peak and again 1 mo later (between 5 September and 1 November 1997). Six randomly placed plots were sampled at each tree, three under the canopy (within the fruit-rain) and three approximately 3 m out from the canopy edge. The location of each plot was marked with flagging, and the same area was sampled 30 d post-fruiting. By 30 d post-fruiting, no fallen fruit remained in the litter, and no evidence of our first sampling was visible. All plots were sampled during the rainy season. In addition, arthropod abundance was estimated in each plot using three 50 cm² sticky traps set on the litter surface for 18 hr, two in opposite corners and one in the center of each plot. A general linear model repeated measures ANOVA (SPSS, 1997) was used to test for a significant fruiting effect, canopy effect, and fruiting-canopy interaction effect on arthropod abundance, herpetofauna abundance, and litter depth.

Results

Site and Season Comparisons

During the study, a total of 211 animals were sampled in plots, consisting of 10 frog species, five lizard species, and three species of snakes. Based on 15 mo of regular collecting and literature records (Pitman, 1974), the complete litter herpetofauna at the field station probably contains between 29 and 32 species of amphibians and reptiles (Table 3.1). This is consistent with the jackknife species richness estimate, based on all 300 plots, of 25 ± 5 species. However, plot sampling did not appear to sample all herpetofaunal taxa equally. Frogs and lizards appear to have been sampled fairly well, with the exception of the riparian *Phrynobatrachus* species. *Phrynobatrachus auritus*, *P. dendrobates*, and *P. versicolor* appear to be limited to the stream-side habitats. The latter two species are abundant in similar habitats at higher elevations in Bwindi National Park in southwestern Uganda (Drewes and Vindum, 1991). Only three of 13 possible species of terrestrial snakes were observed during the study.

Five frog species (*Bufo funereus*, *B. kisoensis*, *Phrynobatrachus graueri*, *P. parvulus*, and *Leptopelis kivuensis*) were found in all three forest types (Table 3.2). Three species were observed in two forest types. *Schoutedenella schubotzi* was absent from the logged forest samples; *Leptopelis christyi* was absent from the unlogged plots; and *Hyperolius lateralis* was found only in the logged and unlogged forests. A single *Phlyctimantis verrucosus* individual was observed in the pine plantations during the study, and a single *Rana angolensis* was found in the logged forest.

The distribution of lizard species was much less even, relative to the amphibians. Three of the five lizard species were found only in the pine plantations, (*Cnemaspis quattuorseriata*, *Rhampoleon boulengeri*, and *Leptosiaphos aloysiisabaudiae*, Table 3.2). The lacertid *Adolfus*

africanus was found in the pines as well as unlogged forest, and single *A. vauereselli* was collected from the logged forest. Observations of snakes in the plots were rare (four individuals), and only one species, *Geodipsas depressiceps depressiceps* was captured more than once. The other two species, *Bothrophthalmus lineatus* and *Dasypeltis atra* were both found in the logged forests. It is important to note that the absence of a species from the plots in a particular forest type is more a reflection of its lower abundance in that site relative to the others, not its absence. Based on opportunistic sightings in these areas, only *Cnemaspis quattuorseriata* seems to be limited to one forest type, the pines. The fossorial skink, *L. aloysiisabaudiae*, is also known only from the pines, but that is likely due to its secretive nature and rarity.

Over the entire study, more animals were captured in the logged forest than in the other two areas combined (Table 3.3). The highest density of animals (5.84 animals/100 m²) was observed in the logged forest in the wet season. Density decreased in all sites during the dry season, ranging from a 29% decrease in animals captured in the unlogged forest to a 55% decrease in the logged forest. A total of 12 species were captured in both the pines and the logged forest, while only nine were captured in the unlogged section. Richness was similar in both seasons, except in the pine plantation where it dropped from 10 species in the wet season to seven in the dry season. The decrease in abundance, while richness remained static or declined, resulted in a higher evenness (*J'*) in the unlogged and logged sites during the dry season sample. The pine plantation and unlogged forest had similar evenness measures, and both were higher than that of the logged forest (Table 3.3). The pine plantation had the highest overall diversity (*H'*), followed by the unlogged, then logged forests. Seasonally, diversity increased in the dry season, except in the pines where it remained essentially the same. Morisita's similarity indices (*C*) show a high degree of similarity between the unlogged and logged forests, and little similarity between the pine plantation and the other two habitats.

Kruskal -Wallis ANOVA and post hoc Mann - Whitney multiple comparison tests were used to compare the physical and biotic variables among the three sites during the wet and dry seasons. During the wet season, the unlogged site was significantly steeper than the other two areas, and had significantly less litter (Table 3.4). The logged forest had significantly less low ground vegetation relative to the other sites (Table 3.4). The pine plantation had significantly heavier and deeper litter, more low vegetation, less shrub cover and canopy cover than the other sites. The pines also had significantly more reptiles per plot (Table 3.4). Within the dry season samples, the unlogged remained the steepest area, and had the lowest litter mass. The logged area again had the lowest ground cover, but in the dry season had significantly higher shrub cover and the fewest trees per plot. The pines had the lowest dry season canopy cover, and significantly higher litter mass, litter depth, and number of trees per plot relative to the other areas. Seasonal changes in these three areas followed a similar pattern (Table 3.4): soil humidity, litter mass, and litter depth all decreased and soil pH increased in the dry season.

There were no significant differences in the number of frogs or reptiles among these areas during the dry season. The decrease in the number of frogs for all three sites combined in the dry season was significant (Kruskal-Wallis, $\chi^2 = 12.9$, $P < 0.001$). However, within sites the decrease was not statistically significant except in the logged forest (K-W, $\chi^2 = 10.1$, $P < 0.01$).

Stepwise logistic regression was used to identify significant environmental predictors of the presence of amphibians and reptiles for all three areas combined in the wet season and the dry season. For all three areas combined in the wet season the only significant predictor of herpetofaunal presence was soil humidity (Table 3.5). The goodness of fit of this model is indicated by the overall percent of plots correctly classified in the classification table. In this model the presence or absence of herpetofauna in plots was correctly predicted in 59.1% of 150 cases. The R statistic indicates the importance of the individual contribution of each independent variable, values for the R statistic range between -1 and +1. A positive value indicates that as the

variable increases, so does the likelihood that the plot will contain herpetofauna. A small R value for a variable indicates that the variable has a small partial contribution to the model (SPSS, 1997). Soil humidity was positively related to herpetofauna presence in plots during both seasons ($R = 0.106$, Table 3.5). Significant predictors of herpetofaunal abundance in the dry season included soil humidity, wet litter mass, number of logs and hill category (Table 3.5). Wet litter mass, soil humidity, number of logs, and shrub cover increase in a plot, so does the likelihood that the plots will contain herpetofauna (Table 3.5). It also indicates that hill category is a significant predictor of herpetofaunal presence. Of these, litter mass, hill category, and soil humidity are the best predictors, and the overall model successfully classified 80% of the plots sampled.

When forest types were analyzed separately for wet season data, there were no significant predictors of herpetofaunal presence (Table 3.5). During the dry season tree number and soil pH were both negatively related to herpetofaunal presence in unlogged forest, and overall the model successfully classified the presence or absence of herpetofauna in plots in 76% of the 50 plots. In logged forest, significant predictors included both low ground and shrub vegetation (Table 3.5). Amphibians were more likely to be found in plots with greater amounts of these vegetation types, with low vegetation being the more important of the two, and overall the model successfully classified 80% of the plots. In the pine plantation in the dry season, both canopy cover and number of logs were significant positive predictors of herpetofaunal presence in plots and overall the model successfully classified the presence or absence of animals in 79% of the 50 plots sampled.

In all three forest types, the abundance of adults and juveniles of the common species declined during the dry season, with the exception of *B. kisoensis* juveniles, which were captured only during the dry season (Table 3.6). Across all sites and excluding *B. kisoensis*, the adult abundance of the five most common species decreased by an average of 30% during the

dry season, while juveniles decreased by an average of 70%. A similar pattern was observed within areas; the proportional decline in juveniles during the dry season in each site was always higher than the decline of adults of the common species. The logged forest had the greatest decline in the overall abundance of animals during the dry season. *Phrynobatrachus graueri* juveniles were very abundant at this site during the wet season, but decreased by 82% during the dry season. The abundance of the most common species decreased by 42% in the pines, largely due to the fewer *S. schubotzi* juveniles captured, and the unlogged forest appeared least affected, with a 26% decline in common species.

Feeding Ecology

Of the 46 *P. graueri* stomachs examined (15 males, mean SVL 20 mm; 17 females, mean SVL 25 mm; 12 subadults, mean SVL 15 mm) 25 (54%) were empty (Table 3.7). The stomach contents of this species consisted of 22 invertebrate prey categories (Fig 3.1). Among frogs that contained prey, the average stomach contents consisted of 7.3 invertebrates (range = 1 to 44), and the average prey item volume was 14 mm³. Springtails (Order Collembola) were the prey group with the highest Relative Importance Index (RI = 34). They were found in 13 of the stomachs which contained prey (%F = 62%) and accounted for 64% of the prey items and comprised 34% of the total prey volume. Beetles (RI = 15; %F = 30; %N = 5, %V = 36) and ants (RI = 14; %F = 52; %N = 12; %V = 3) were the second and third most important prey taxa.

Of the 17 *B. funereus* stomachs examined (8 males, mean SVL 51 mm; 8 females, mean SVL 62 mm; 1 subadult, SVL 30 mm) 15 (88%) contained prey. The average number of prey in those 15 stomachs was 8.9 (range = 2 to 27), and the average individual prey volume was 221 mm³ (Table 3.7). Of the 12 invertebrate prey taxa, ants were clearly the most important (RI = 36; Fig. 3.1), being present in 93% of the stomachs and accounting for 69% of the prey items and 25% of the prey volume. The index for the Order Coleoptera (RI = 32) was similar to that of

ants. Beetles accounted for 17% of the prey items and 36% of the prey volume. All other prey taxa had RI indices less than seven.

Of the 17 *B. kisoensis* stomachs examined (8 male, mean SVL 57 mm; 7 female, mean SVL 71 mm; 2 subadult, mean SVL 40 mm) 13 (76%) contained prey. Five of those 13 were from Bwindi specimens, and at the level of the prey categories examined here, there were no differences in the common prey taxa observed between sites. There was an average of 18 prey per full stomach (range = 1 to 51), and the average individual prey size was 131 mm³ (Table 3.7). Again, ants (RI = 36) and beetles (combined RI = 34) were the most important of the nine invertebrate prey taxa. Ants were found in 100% of the stomachs that contained prey and they accounted for 69% of the prey items and 31% of the prey volume. Coleopterans were found in 70% of the stomachs and accounted for 20% of the prey items, and comprised 47% of the prey volume.

Of the 19 *S. schubotzi* stomachs examined (5 male, mean SVL 21 mm; 7 female, mean SVL 20mm; 7 subadult, mean SVL 16 mm) 14 (74%) contained prey representing nine prey taxa. Three of these 14 were from Bwindi specimens, and both Kibale and Bwindi specimens appear to prey predominantly upon the same taxa. Stomachs contained an average of 15 prey items (max. 47) with the average prey volume being 2 mm³. Small ants (< 3 mm length) were found in all stomachs with prey items and accounted for 80% of the prey items and 58% of the prey volume resulting in an importance index of 49 (Fig. 3.1). This was the highest index value observed for any prey taxa for any frog species. Beetles were of second greatest importance (combined RI = 19) in *S. schubotzi* diet, accounting for 65% of prey items and 16% of prey volume.

Only 16 of the 49 *L. kivuensis* stomachs (36 male, mean SVL 33 mm; 9 female, mean SVL 45 mm; 4 subadult, mean SVL 26) examined contained prey items (33%). Six of the 16 full stomachs were from Bwindi specimens. At both sites the three most common prey taxa were

taken in very similar proportions. *Leptopelis kivuensis* had the lowest number of prey items per stomach with contents (1.4 prey/frog; range = 1 to 3) and the largest average prey item volume (489 mm³). The most common prey items were orthopterans (RI = 40; %F = 38; %N = 27; %V = 62), lepidopteran larvae (RI = 21; %F = 25; %N = 18, %V = 24), and spiders (RI = 18; %F = 31; %N = 23; %V = 3). Many of the prey species found in the diet of *L. kivuensis* were associated with understory vegetation (*e.g.*, kaytidids, lepidopteran larvae) while many of the terrestrial species were absent from the diet.

Eight male (mean SVL 23 mm) and six female (mean SVL 26 mm) *H. lateralis* were examined, of which ten had prey remains in their stomachs. Those ten stomachs contained an average of four prey individuals (range = 1 to 7) with an average individual prey volume of 34 mm³ (Table 3.7). Prey from 12 taxa were represented in the diet (Fig. 3.1), with dipterans (RI = 24; %F = 80; %N = 20; %V = 19), hemipterans (RI = 17; %F = 40; %N = 10; %V = 37%), and ants (RI = 13; %F = 40; %N = 20; %V = 5) appearing most prominently (Fig. 1.2). The presence of invertebrates that are associated exclusively with the forest floor (*e.g.*, Collembola) indicates that this species does forage in the litter.

Bufo kisoensis, *B. funereus*, and *S. schubotzi* all show a high degree of similarity in their diets, as all three prey predominately upon ants (Table 3.8). However, when ants are divided into two size categories (> and < 5 mm length), this similarity is much less pronounced, particularly between *S. schubotzi*, which eats small ants, and the two toads, which feed on larger ants. The diet of *B. kisoensis* was remarkably similar to that of *B. funereus*; and many of the ant and beetle species that these two toads preyed upon appeared to be the same. However, while *B. funereus* preyed exclusively upon larger ants, the diet of *B. kisoensis* included ants of all sizes (Table 3.8). The lack of similarity between *L. kivuensis* and all the other species, even the other hyperoliid *H. lateralis*, again suggests that this species may not be feeding in the litter layer.

Fruiting Fig Trees and Litter Herpetofauna Distribution

The results of sampling under *Ficus natalensis* indicate that arthropod density increased during fruiting periods (Table 3.9), however, this increase was not entirely limited to the area directly underneath the tree canopy. With regard to herpetofauna, six anuran species (*B. kisoensis*, *B. funereus*, *P. graueri*, *H. lateralis*, *L. kivuensis*, *S. schubotzi*) totaling 16 individuals were captured during plot sampling at *Ficus natalensis*. Herpetofaunal density was significantly higher in plots under the canopy, but there was no significant effect of fruiting (Table 3.10). Frogs were found more frequently under *F. natalensis* trees than 3 m out from the canopy during, as well as after, a fruiting event. Litter depth was greater under the canopy and greater during the fruiting period, however the interaction of these two terms was not significant (Table 3.10).

Discussion

Habitat Correlates of Herpetofaunal Abundance

Several studies in the American tropics have found that seasonality is important in structuring leaf-litter herpetofaunas through seasonal changes in prey abundance (Toft, 1980a; Lieberman and Dock, 1982), litter depth (Scott, 1976), and juvenile recruitment (Allmon, 1991). The results of this study suggest that seasonal rainfall and topography interact to create moisture gradients that may be important in determining the patterns of abundance and distribution at Kibale.

For all study areas combined, there was a significant decrease in soil humidity and the number of amphibians and reptiles sampled during the dry season. During both wet and dry seasons, soil humidity was a significant predictor of herpetofaunal presence in plots. Various aspects of cover (litter mass, number of logs, ground vegetation, shrub vegetation) become more

important during the dry season, presumably due to greater desiccation risk. Upper slopes and hill tops were always drier than lower slopes and valleys, but this difference was greater during the dry season. During the wet season it was not uncommon to observe amphibians in hill-top plots. However, none were sampled from the upland habitats during the dry season. Therefore it appears that lack of moisture may limit the use of these habitats during the dry months. This may reflect a seasonal shift in habitat use similar to that observed by Toft (1980*a*), who found relatively fewer amphibians used ridge tops compared to stream bottoms during the dry season at a relatively dry site in Panama.

In contrast to this study, several others have observed higher litter herpetofaunal densities in the dry season (Toft, 1980*a*; Lieberman, 1986; Allmon, 1991). Both Toft (1980*a*) and Lieberman and Dock, (1982) found that prey densities (litter arthropods) were highest in the dry season when herpetofaunal abundance was greatest. Nummelin (1989) concluded that in Kibale forest-floor arthropod numbers peak in the late wet season, which would initially suggest that arthropod and litter herpetofaunal densities may be positively correlated. However, a closer look at Nummelin's data for unlogged, logged, and pine plantation sites during the short rains and subsequent dry season reveals a more complicated scenario. The site with the highest arthropod abundance (pines) is not the site with the highest herpetofaunal densities (logged). Nor does arthropod abundance show a similar pattern of increase or decrease among all sites during the shift from short wet to dry seasons, as herpetofaunal densities do (all decrease). However, one similarity between arthropod and herpetofaunal numbers bears mentioning. The unlogged site showed the least seasonal variation in both arthropod abundance and herpetofaunal abundance, while the logged site showed the greatest variation. While this is suggestive that prey abundance may contribute to the pattern of abundance observed in litter herpetofaunas, this is only speculation based on arthropod densities recorded more than ten years earlier. Arthropod densities at Kibale exhibit considerable year to year variation (Nummelin, 1989), and

simultaneous sampling of arthropod and herpetofaunal abundance across a range of habitats and across seasons will be necessary to test for an effect of prey abundance on herpetofaunal numbers.

Allmon (1991) concluded that juvenile recruitment was the most important factor responsible for seasonal variation in species abundance; however his study did not sample arthropods. The short duration of my study prohibits careful evaluation of the importance of recruitment. All of the amphibian species sampled except one have aquatic tadpoles and breed primarily during the two wet seasons (Vonesh, unpubl. data). However, juvenile abundance for all species declined, not increased, from the wet to dry season, with the exception of *Bufo kisoensis*. *B. kisoensis* juveniles were captured only during the dry season, and therefore may represent new recruitment. It is possible that the large number of juveniles observed for most species during the wet season may represent late metamorphs from the October-December rainy season, which is longer and is likely to be a period of greater anuran reproductive activity. Although the number of adult animals decreased, the percentage decrease was much higher for juveniles of the common species. This suggests either higher mortality among juveniles over the study period, or some aspect of juvenile behavior (*e.g.*, aggregating in valley bottom pools, retreating to burrows) that biases against their capture in the dry season. A longer study would be necessary in order to understand the importance of seasonal recruitment in structuring these communities.

In summary, it appears that seasonal variation in soil moisture and the interaction of moisture and topography, are the most important ecological variables in structuring the Kibale litter herpetofauna. The lower number of dry season captures may be due to clumping of animals in valley bottoms around water bodies, dry season mortality, and/or retreating into burrows or other refuges. All three responses suggest moisture as the limiting resource. Moisture may be particularly important, since Kibale typically receives less than 1600 mm of rain per year, one of

the lowest annual rainfalls reported for any tropical litter herpetofaunal study. Unlike a number of other studies, arthropod abundance, based on Nummelin (1989), does not seem to account for the seasonal and spatial variation in herpetofauna abundance that was observed, although this conclusion must be entertained with caution. The role of juvenile recruitment in shaping the patterns of abundance and diversity can not be determined unequivocally, but over the short period of this study it played a minor role, through the dry season recruitment of *B. kisoensis* juveniles.

Comparison of Disturbed and Undisturbed Forests

Several studies have examined how logging and conversion into tree plantations influences native herpetofaunas (Miyata, 1980; Lieberman, 1986; Heinen, 1992; Aukland *et al.*, 1997). Miyata (1980) found increased herpetofaunal densities in cacao and rubber plantations in Ecuador relative to primary forest, and Lieberman (1986) and Heinen (1992) found a similar pattern between primary forest and cacao plantations in Costa Rica. Heinen's (1992) study further suggested that the high abundance observed in recently disturbed sites decreases with time. In contrast to density trends, Heinen (1992) found that undisturbed forests in Costa Rica had higher diversity (H') and greater equitability (J') than young or older cacao plantations. Aukland *et al.*, (1997) found a very different situation in her studies in western Uganda, with higher litter frog densities and lower diversity in unlogged forest than forest that had been selectively logged in the last 5 yr. The selectively logged forest studied at Kibale was logged nearly 30 years ago, and the tree plantations are of a similar age with a dense, predominately native flora regenerating underneath the pines. My results indicate that herpetofaunal communities respond differently to different forest management strategies. Compared to the unlogged forest, the plantation had higher densities as well as greater diversity and evenness, and the logged forest had greater densities but lower diversity and evenness.

The Nyakatojo pine plantation was established on derelict land dominated by elephant grass (*Pennisetum purpureum*) adjacent to unlogged forest. This grassland is believed to have been formed through human clearing and maintained by fires which inhibit the establishment of native trees (Kasenene, 1987). Several studies (Lugo, 1992; Chapman and Chapman, 1996; Zanne, 1997) suggest that exotic tree plantations can be used to facilitate forest regeneration in cases where natural succession is very slow or arrested. Grasslands not converted to plantations in the 1960's are still dominated by elephant grass today, while many native trees and shrubs are reestablishing in the pine plantation understory (Chapman and Chapman, 1996; Zanne, 1997). However, the ability of exotic tree plantations to aid in the restoration of native herpetofaunal communities is unclear. On one hand, the pine plantation site at Kibale is home to the most diverse herpetofauna of the three sites studied. In contrast to Heinen (1992) who concluded that primary forests were an important refuge for rare species, the pine plantation, not the adjacent unlogged forest, harbored the greatest number of rare (captured 1-2 times) litter lizards and frogs (5 spp. vs 2 spp.). The greater number of rare species, higher diversity, and greater equitability all suggest that the pines' fauna is successional mature. However, the pine fauna has a very low similarity to the unlogged forest, while the logged forest and unlogged forests show a high degree of overlap. A comparison of Heinen (plantations, 1992) and Aukland *et al.*, (logged forest, 1997) suggest that logged forests are generally more similar to undisturbed native forests than plantations. In fact, though abundance decreases and diversity and evenness increase with the age of Heinen's (1992) cacao plantations, the older plantation is not any more similar to the original forest than the new plantation.

This has several implications from the perspective of faunal restoration as discussed in Heinen (1992). First, it may be inappropriate to expect abandoned plantations, be they pine or cacao, to revert to a state similar to that of the original forest, despite the availability of nearby source forests. If that is the case, what measuring stick should be used to evaluate a faunas'

relative degree of "restoration", particularly if indices of community richness, diversity, and equitability in the plantations may, in some cases, exceed that of the original forest. The implications for selective logging are different. While diversity and evenness may decrease (this study) or increase (Aukland *et al.*, 1997) with selective logging, the similarity of the disturbed fauna to that of the original may be high. In the case of selective logging then, it may be more realistic to discuss restoration of the fauna to a state similar to that of undisturbed forests.

Feeding Ecology

Several studies in the past (Toft, 1980*a,b*; Lieberman, 1986) have examined the questions of how the feeding ecology of litter species relate to their ability to coexist. Their results suggest that both diet and activity period may be important in determining the number of species that can share a habitat. Litter species can be broadly categorized as either diurnal or nocturnal, and are either active foragers, which prey upon large numbers of hard bodied arthropods such as ants or beetles which are slow to escape, or are sit-and-wait predators which tend to prey upon fewer, larger, often soft-bodied prey species (Toft, 1981). At Kibale, the six most abundant anuran species, *B. funereus*, *B. kisoensis*, *S. schubotzi*, *P. graueri*, *L. kivuensis*, and *H. lateralis*, accounted for 80% of the total number of reptiles and amphibians captured. Of these the first four are primarily diurnal while the two hyperoliid species are nocturnal.

A closer look at the diurnal species suggests that *B. funereus*, *B. kisoensis*, and *S. schubotzi* are active foragers, as indicated by the high proportion of these species that had prey in their stomachs at the time of examination and the relatively high number of prey items per stomach. All three of these species prey primarily on hard-bodied arthropods, namely ants of different species and beetles. Without prey availability data, I am unable to say whether these three species are highly selective of ants as prey or that ants are simply the most frequently encountered prey species. Regardless, ants are clearly the most important prey taxa. This is not

surprising for the two *Bufo* species; *Bufo* species around the world typically eat high proportions of ants (Inger and Marx, 1961; Toft, 1980b, 1981). What is less clear is how two species coexist with such similar diets. The Morisita's similarity index for these two species is 0.69, the highest of any species pair, and much higher than the average for all six species studied, 0.33. One subtle difference in diet is that *B. kisoensis* preys upon a wider range of ants size classes than *B. funereus*. Thirty-five percent of the ants in *B. kisoensis*' diet are smaller than 5 mm in length, while only 3% of the ants in *B. funereus*' diet fall in the smaller size category. Plot results and personal observations also suggest that these two toads may use different parts of the forest. Of the nine *B. kisoensis* captured, 7 (78%) were found in valley bottom plots, and these were all juveniles, possibly dispersing from larval habitats. No *B. kisoensis* were captured on hill-tops. Only 38% of the *B. funereus* were captured in bottom plots, and 28% , including several adults, were found on hill tops. These data support personal observations that suggest *B. kisoensis* adults are most common in dense, often seasonally flooded, vegetation in valley bottoms along streams, while *B. funereus* is more generally distributed throughout the forest. There may also be some temporal separation in the seasonal abundance of these species, *B. kisoensis* were only captured in plots during the dry season, while *B. funereus* was twice as abundant in plots during the wet season. This is similar to Toft's (1980b) findings with the species *Eleutherodactylus toftae* and *Andenomera andreae*, two non-ant specialists of similar size. *E. toftae* was only observed in the dry season, when *A. andreae* was not observed.

S. schubotzi had the highest Relative Importance Index for ants of any species in this study. Interestingly, in a phylogenetic analysis based on osteological and myological characters, Ford (1989) suggested that the family Artholeptidae, which includes the genus *Schoutedenella*, is sister group of the South American Dendrobatidae, and that the vicariance that gave rise to these two groups probably coincides with the separation of South America from Africa. The dendrobatids are also ant specialists, and derive potent defensive toxins from the ants they eat.

To the best of my knowledge, the presence or absence of defensive toxins in African arthroleptids has not been examined, but toxins in these species are probably not well developed given that they are usually cryptically colored.

The diet of *S. schubotzi* was most similar to that of the similarly sized *P. graueri*, the fourth diurnal species. Ants, beetles, and collembolans are the primary prey of both these species. However, the proportion in which they prey upon them is quite different. *Schoutedenella*, as mentioned, prey primarily upon small ants with beetles being the prey with the second highest RI index, while the important prey for *P. graueri*, based on RI indices, are collembolans, beetles, and ants, in that order. The fact that *P. graueri* preys primarily upon collembolans is rather unique. Lieberman and Dock (1982) found that almost no terrestrial anurans preyed upon Collembola, despite the fact that they were the third most abundant arthropod taxa in the litter. She concluded that they were probably very unpalatable or preferred by some non-anuran litter insectivore. Also, none of the species in Toft's studies (1980a, 1980b) preyed upon collembolans. The different body morphotypes of the collembolans in *P. graueri*'s diet suggest that it is feeding on Collembola species which dwell on the litter surface, as well as those that dwell within or under the litter.

In contrast to the diurnal species, the two nocturnal hyperoliids prey primarily upon soft-bodied arthropods. *Leptopelis kivuensis* appears to fit the model of the sit-and-wait predator, as indicated by the low number of non-empty stomachs (%33) and the large mean prey size. The diet of this species bears little resemblance to those of the other species studied, preying primarily upon orthopterans and lepidopteran larvae, which may or may not have been in the litter. Several personal observations of this species feeding suggest that it is a nocturnal forager, and probably captures most of its prey in low shrubs. It is possible that this species uses the moist litter layer only as a daytime refuge, and therefore should not really be considered part of the litter assemblage in terms of feeding ecology.

Hyperolius lateralis also preys primarily upon soft-bodied insects, in this case dipterans and hemipterans. The proportion of full stomachs suggests that this species may forage more actively than *L. kivuensis*. In addition, the presence of ants and Collembola in the diet indicate that this species does forage in the litter. In fact, the diet is much more similar to that of *P. graueri* than to *L. kivuensis*.

My results differ in some respects from those of Toft (1982), the only other study to examine the feeding ecology of an African leaf-litter anuran fauna. She examined the diets of the four most abundant litter frogs in Makokou, Gabon. These four included *Arthroleptis sylvatica*, *Cardioglossa leucomystax*, both arthroleptids, *Bufo camerunensis*, and the ranid, *Phrynobatrachus batesi*. The bufonid, as in my study, preyed primarily upon ants, but the other three species all preyed primarily upon isopterans (termites), whereas none of the species at Kibale preyed upon termites. Also, because of the preponderance of isopteran in the diets of these species, Toft (1982) observed much higher dietary similarity indices than were observed in the Kibale study. Isopteran abundance tends to be highly seasonal, and it is possible that the short duration of both this and Toft's (1982) study over or de-emphasize the importance of this taxa in the diet of African litter frogs. Toft (1982) also remarked about the absence of sit-and-wait, soft-bodied arthropod specialists in the diurnal litter frog fauna at Makokou. She found that 38% of the diurnal frog fauna specialized in non-ant prey. In this regard, Kibale resembles Makokou; all four common diurnal frogs eat hard-bodied arthropods (ants and Collembola).

Frogs and Figs

While seasonal litter arthropod abundance has been shown, in several tropical forests, to be positively correlated with herpetofaunal abundance, few studies (Guyer, 1988) have examined this on a finer scale. One question of interest is how does forest fruit-fall influence small scale changes in litter arthropod abundance, and do litter amphibians and reptiles respond to such local

scale changes, if they do exist? Inger, (1980a) hypothesized that the low litter herpetofaunal densities observed in the forest of Southeast Asia were due to the mast fruiting cycle of the dominant dipterocarp trees. He suggested that during non-mast years, the litter arthropod numbers decrease and are unable to support large amphibian and insectivorous reptile populations. However, to my knowledge, no study has demonstrated that forest-floor arthropods or herpetofauna respond in any way to forest fruit-fall. Unlike the forests of tropical Asia, Kibale is not characterized by dipterocarp trees or mast fruiting events, however litter herpetofauna might be expected to respond on a local scale to increases in availability, if only to decrease foraging effort. My results suggest that arthropods do increase under fruiting fig trees, and that this increase extends beyond the canopy edge. It does not appear that litter herpetofauna respond to this change, as herpetofaunal abundance is greater under fig trees during both fruiting and post-fruiting samples. Therefore it is possible that frogs are simply attracted to some other microhabitat characteristic associated with tree bases, such as deeper litter.

Regional Comparisons

The number of mid-elevation forest litter herpetofaunal studies is limited, relative to studies of lowland faunas, but comparison with these few is of interest. Studies from Costa Rica, the Philippines, and Africa indicate that the upland forests of these three areas support a similar number of leaf litter species (Table 3.11). San Vito, Costa Rica, appears to be an exceptional case, supporting a tremendously rich fauna (Scott, 1976), but results from a study in progress at nearby Fila Cruces (1300 m) have found a more modest 18 leaf-litter species assemblage (Schlaepfer, 1998). Animal densities vary widely within and across regions. The widely cited trend observed in lowland faunas, where densities are much higher in Central American relative to Southeast Asia, is not obvious in the mid-elevation faunas.

While the species richness of the Kibale litter fauna is comparable to that from other areas, the combined wet and dry season animals density, particularly in the unlogged forest is very low, similar to that of the depauperate lowland forests of Borneo (Lloyd *et al.*, 1968) and Thailand (Inger and Colwell, 1977). The litter herpetofauna of lowland Cameroon (Scott, 1982), which shares two frog species, and four genera with Kibale, has a fauna of similar richness, but much higher densities than either Kibale or Budongo. This contradicts the trend reported by Scott (1976) that diversity decreases, and abundance increases with increasing elevation.

Limitations

As Heinen (1992) pointed out, there are several limitations to the generalities that can be drawn from the available studies of litter herpetofaunas, including this one. First, as the areas being compared may be adjacent to one another they may not be truly independent. For example, the unlogged site in this study may serve as a source for the pines litter fauna, and studies of isolated pine plantations may yield results different to those presented here. A recent study of floral regeneration in Kibale pine plantations found that the indigenous tree species regenerating underneath the pines were more similar to natural forest species in pine plantations surrounded by forest compared with isolated plantations (Zanne, 1998). Another problem with this and other studies is pseudoreplication (Hurlburt, 1984), taking multiple samples from a single representative forest type, rather than sampling in forest type replicates. There are a number of studies at Kibale that have compared the same three areas examined here, and while pseudoreplication may limit generalization, these studies none-the-less provide valuable information and suggest directions for more rigorous, manipulative studies. Furthermore, the patterns observed in comparing the unlogged and logged forests are very similar to those observed by Heinen (1992) and Lieberman (1986) in Costa Rica, Miyata (1980) in Ecuador, and

Inger (1980*b*) in Malaysia. The similarity of the results of these studies argues for their validity and general applicability.

Conclusions

A total of 18 species were captured in the leaf-litter layer of the forest floor at Kibale, a number similar to that observed in other studies of tropical litter herpetofaunas from mid-elevation forests. The density of animals at Kibale, however, was much lower than that reported from other sites.

During the wet season, the selectively logged forest was characterized by a greater abundance of herpetofauna, but lower overall diversity and species equitability compared with the unlogged forest. This pattern has been observed in a number of studies that have examined litter herpetofaunas from disturbed and undisturbed sites. Interestingly, the exotic pine plantation exhibited the highest species diversity among all three forests. The faunal composition of the pine plantation was very different from that of the native forests, being characterized by the dominance of species adapted to more drier conditions, namely reptiles and direct developing frogs.

The most common diurnal anuran species in the litter are active foragers of small hard-bodied prey such as ants. There are no sit-and-wait predators which prey on larger soft-bodied prey. This absence of this guild is an interesting contrast with Neotropical herpetofaunas, in which predators of soft-bodied arthropods make up a large proportion of the litter anuran fauna. Two nocturnal treefrogs that are often captured in the litter appear to be sit-and-wait predators, but only one of these actively feeding in the litter, the other appears to only use it as a diurnal refuge.

Prey abundance was found to increase significantly beneath fruiting fig trees. Frog abundance was also higher under fig tree canopies than away from them, but this was the case during both fruiting and post-fruiting sampling periods. Therefore it seems likely that frogs are attracted to figs trees, but not necessarily (or only) due to increased prey availability, but perhaps due to the deeper leaf litter found under the figs.

All three forest types showed a decrease in the number of animals captured during the dry season, in contrast with most Neotropical litter herpetofaunas which reach their peak densities in the dry season. This combined with the absence of animals from the drier hilltop and upper slope forest habitats suggests that moisture is one of the most important factors in determining local patterns in herpetofauna abundance. This is not all that surprising, as Kibale is relatively dry compared to most tropical forest where litter herpetofaunas have been studied and many of the species present at Kibale are believed to have originated from the wetter lowland forests of eastern Congo-Zaire.

TABLE 3.1. Reptiles and amphibians of the forest floor leaf-litter layer, Kanyawara, Kibale National Park, Uganda, based on 15 mo of collecting and Pitman (1974). Eighteen species were sampled during the study. The jackknife species richness estimate (\pm 95% confidence interval) based on all 300 plots is 25.0 ± 5.0 species. (‡ indicates species found primarily in upland habitats; # indicates species restricted to streamside habitats; ? indicates species found at least occasionally in the litter, but the total proportion of their life that is spent in the litter layer is unknown; * indicates fossorial species; † indicates species expected to be in Kibale forest, but no record as yet; X indicates those species that were successfully sampled using plots)

Order Anura	Order Sauria
X <i>Bufo funereus</i>	X <i>Cnemaspis quattuorseriatus</i> ‡ ?
X <i>Bufo kisoensis</i>	X <i>Rhampoleon boulengeri</i>
X <i>Schoutedenella schubotzi</i> ‡	X <i>Adolfus africanus</i> ?
<i>Phrynobatrachus auritus</i> #	X <i>Adolfus vauereselli</i>
<i>Phrynobatrachus dendrobates</i> #	X <i>Leptosiaphos aloysiisabaudiae</i> ‡
X <i>Phrynobatrachus graueri</i>	<i>Lygosoma fernandi</i>
X <i>Phrynobatrachus parvulus</i>	
<i>Phrynobatrachus versicolor</i> #	Order Serpentes
X <i>Rana angolensis</i> #	<i>Typhlops punctatus</i> *
X <i>Phlyctimantis verrucosus</i> ?	<i>Causus lichtenstienii</i>
X <i>Leptopelis christyi</i> ?	<i>Bitis nasicornis</i>
X <i>Leptopelis kivuensis</i> ?	X <i>Bothrophthalmus lineatus</i>
X <i>Hyperolius lateralis</i> ?	<i>Lamprophis olivacea</i>
	<i>Mehelya poensis</i> †
	<i>Mehelya stenophthalmus</i>
	X <i>Geodipsas depressiceps</i>
	<i>Polemon christyi</i> *
	X <i>Dasypeltis atra</i>
	<i>Lycophidion ornatum</i>
	<i>Bitis gabonica</i> †
	<i>Atractaspis irregularis</i> * †

TABLE 3.2. Numbers and species of amphibians and reptiles captured in the leaf-litter of pristine, logged, and pine forest during the wet and dry seasons, Kibale National Park, Uganda. Fifty plots of 25 m² were sampled in each forest type during each season.

Family and species	Forest types						total
	Pristine		Logged		Pine		
	wet	dry	wet	dry	wet	dry	
Bufo							
<i>Bufo funereus</i>	4	4	7	2	5	1	23
<i>B. kisoensis</i>	0	5	1	4	0	4	14
Rana							
<i>Schoutedenella schubotzi</i>	2	1	0	0	14	5	22
<i>Rana angolensis</i>	0	0	1	0	0	0	1
<i>Phrynobatrachus graueri</i>	16	4	51	13	2	3	89
<i>P. parvulus</i>	1	0	1	3	2	1	8
Hyperoliidae							
<i>Phlyctimantis verrucosus</i>	0	0	0	0	1	0	1
<i>Leptopelis kivuensis</i>	3	1	7	5	1	0	17
<i>L. christyi</i>	0	0	1	0	1	0	2
<i>Hyperolius lateralis</i>	1	4	3	3	0	0	11
Gekkonidae							
<i>Cnemaspis quattuorseriata</i>	0	0	0	0	10	4	14
Lacertidae							
<i>Adolfus africanus</i>	0	1	0	0	1	0	2
<i>Adolfus vauereselli</i>	0	0	0	1	0	0	1
Chamaelonidae							
<i>Rhampoleon boulengeri</i>	0	0	0	0	0	1	1
Scincidae							
<i>Leptosiphos aloysiisabaudiae</i>	0	0	0	0	1	0	1
Colubridae							
<i>Bothrophthalmus lineatus</i>	0	0	0	1	0	0	1
<i>Geodipsas depressiceps</i>	1	0	0	1	0	0	2
<i>Dasyplectis atra</i>	0	0	1	0	0	0	1

TABLE 3.3. Density, richness, evenness, diversity, and similarity of the leaf-litter herpetofauna calculated for pristine, logged, and pine plantation forest types at Kibale National Park, Uganda.

	Unlogged			Logged			Pine plantation		
	wet	dry	total	wet	dry	total	wet	dry	total
No. individuals	28	20	48	73	33	106	38	19	57
Density (animals/100 m ²)	2.24	1.60	1.92	5.84	2.64	4.24	3.04	1.52	2.28
Richness (no. spp.)	7	7	9	9	9	12	10	7	12
Diversity (H')	0.60	0.78	0.77	0.49	0.80	0.63	0.77	0.76	0.86
Evenness (J')	0.41	0.53	0.52	0.33	0.54	0.43	0.52	0.51	0.58
Similarity (C)			0.94			0.24			
					0.42				

TABLE 3.4. Differences among the three forest types in environmental variables measures within each plot during the wet and dry seasons, expressed as the mean and ± 1 SD, and the P-values associated with each as determined by the Kruskal-Wallis ANOVA. Similar superscripts for pairs of values signify that that variable was not significantly different between those two forests. (** indicates a significant difference in that variable between wet and dry season; NS indicates value does not significantly vary between seasons, # K-W p-values compared against the Bonferroni adjusted $\alpha = 0.004$, for 12 tests)

Variable	Pristine	Logged	Pine	χ^2	K-W P-value [#]
Wet season:					
Slope	14.9 \pm 5.3 ^a	8.0 \pm 5.5 ^b	8.9 \pm 5.7 ^b	34.8	<0.001*
Soil humidity	76.6 \pm 13.7 ^a	71.9 \pm 13.7 ^a	72.7 \pm 17.05 ^a	5.2	0.073
Soil pH	6.2 \pm 0.5 ^a	6.3 \pm 0.4 ^a	6.1 \pm 0.9 ^a	5.2	0.075
Wet litter mass	0.9 \pm 0.5 ^a	0.7 \pm 0.3 ^b	1.3 \pm 0.6 ^c	40.3	<0.001*
Litter depth	2.9 \pm 1.0 ^a	3.2 \pm 0.9 ^b	5.1 \pm 1.0 ^c	81.9	<0.001*
Ground vegetation	41.9 \pm 16.0 ^a	30.7 \pm 13.1 ^b	49.3 \pm 19.2 ^a	27.8	<0.001*
Shrub cover	42.3 \pm 12.7 ^a	45.7 \pm 13.4 ^a	34.2 \pm 14.3 ^b	17.2	<0.001*
Canopy cover	93.8 \pm 1.4 ^a	93.5 \pm 2.3 ^a	88.8 \pm 2.4 ^b	74.2	<0.001*
No. logs/plot	0.3 \pm 0.6	0.4 \pm 0.8	0.5 \pm 1.0	1.3	0.525
No. trees/plot	1.8 \pm 1.5	1.5 \pm 1.2	1.9 \pm 1.2	2.0	0.361
No. frogs/plot	0.6 \pm 1.0	1.5 \pm 4.2	0.5 \pm 0.7	5.9	0.052
No. reptiles/plot	0.02 \pm 0.1 ^a	0.02 \pm 0.1 ^a	0.2 \pm 0.5 ^b	12.6	0.002*
Dry season:					
Slope	13.1 \pm 5.0 ^a NS	7.8 \pm 5.4 ^b NS	9.5 \pm 4.7 ^b NS	24.6	<0.001*
Soil humidity	57.2 \pm 20.8 ^{**}	60.4 \pm 14.8 ^{**}	52.3 \pm 12.6 ^{**}	9.2	0.01
Soil pH	6.6 \pm 0.4 ^{**}	6.7 \pm 0.3 ^{**}	6.7 \pm 0.3 ^{**}	1.4	0.505
Wet litter mass	0.4 \pm 0.2 ^{a**}	0.5 \pm 0.2 ^{b**}	0.9 \pm 0.3 ^{c**}	57.1	<0.001*
Litter depth	2.3 \pm 0.9 ^{a**}	2.6 \pm 1.1 ^{a**}	4.3 \pm 0.9 ^{b**}	71.6	<0.001*
Ground vegetation	41.5 \pm 15.2 ^a NS	28.1 \pm 10.1 ^b NS	36.3 \pm 13.5 ^{a**}	23.7	<0.001*
Shrub cover	37.2 \pm 13.4 ^a NS	44.7 \pm 12.0 ^b	32.4 \pm 15.5 ^a NS	18.3	<0.001*
Canopy cover	94.0 \pm 1.7 ^a NS	94.0 \pm 1.8 ^a NS	89.5 \pm 2.7 ^b NS	73.2	<0.001*
No. logs/plot	0.3 \pm 0.6NS	0.2 \pm 0.4NS	0.4 \pm 0.7NS	4.1	0.13
No. trees/plot	1.4 \pm 1.2 ^a NS	0.9 \pm 1.0 ^{b**}	2.0 \pm 1.2 ^c NS	22.4	<0.001*
No. frogs/plot	0.4 \pm 0.8NS	0.7 \pm 1.8 ^{**}	0.3 \pm 0.5NS	0.04	0.978
No. reptiles/plot	0.02 \pm 0.14NS	0.06 \pm 0.24NS	0.1 \pm 0.3NS	2.8	0.24

TABLE 3.5. Results of stepwise logistic regression of the presence or absence of amphibians and reptiles in leaf litter plots (Kibale National Park, Uganda) predicted by habitat variables. Independent variables included: Slope, soil humidity, soil pH, wet litter mass, litter depth, logs, % low vegetation cover, % medium vegetation cover, canopy cover, number of trees, hill category. Hill categories were: 1 = valley bottom, 2 = lower slope, 3 = upper slope, 4 = hilltop.

Habitat	Season	Classification table % correct	R	-2 log likelihood χ^2 (P value)	Predictors
All 3 habitats	wet	59.1	0.106	4.71 (0.03)	soil humidity
	dry	80.0	0.162	21.41 (0.0003)	hill category
			0.180	30.55 (<0.0001)	wet litter mass
			0.128	35.34 (<0.0001)	number of logs
			0.129	41.07 (<0.0001)	soil humidity
		0.105	45.20 (<0.0001)	med. vegetation	
Unlogged forest	wet	—	—	—	none
	dry	76.0	- 0.292	8.82 (0.003)	soil pH
- 0.165			12.95 (0.002)	no. trees	
Logged forest	wet	—	—	—	none
	dry	80.0	0.311	8.26 (0.004)	low vegetation
0.237			15.55 (0.0004)	med. vegetation	
Pine plantation	wet	—	—	—	none
	dry	79.0	0.176	6.62 (0.01)	canopy
0.266			11.59 (0.003)	no. logs	

TABLE 3.6. Numbers of adults and juveniles of the five most common leaf-litter herpetofauna in the three forest types during the wet and dry seasons. Adults identified by SVL as follows: *Phrynobatrachus graueri* > 19.0 mm; *Bufo funereus* > 35.0 mm, *Bufo kisoensis* > 40.0 mm; *Schoutedenella schubotzi* > 19.0 mm; *Leptopelis kivuensis* > 35.0 mm.

Species	Unlogged		Logged		Pines		Totals		totals
	wet	dry	wet	dry	wet	dry	wet	dry	
<i>P. graueri</i> -adult	5	5	13	5	0	3	18	13	31
<i>P. graueri</i> -juv.	9	1	39	7	1	0	49	8	57
<i>B. funereus</i> -adult	4	2	4	2	1	0	9	4	13
<i>B. funereus</i> -juv.	0	2	4	0	4	2	8	4	12
<i>B. kisoensis</i> -adult	0	0	0	0	0	0	0	0	0
<i>B. kisoensis</i> -juv.	0	5	0	4	0	3	0	8	8
<i>S. schubotzi</i> -adult	0	1	0	0	8	4	8	5	12
<i>S. schubotzi</i> -juv.	2	0	0	0	6	0	8	0	8
<i>L. kivuensis</i> -adult	0	0	0	0	0	0	0	0	0
<i>L. kivuensis</i> -juv.	3	1	7	5	1	0	11	6	17
Totals	23	17	67	21	21	12	111	50	161

TABLE 3.7. Results from the stomach content analysis of the six most common leaf-litter herpetofauna in Kibale National Park. SVL: mean length of all individuals of that species for which stomach content data was collected. N: number of stomachs examined. No. Full: number of stomachs examined which held prey remains. No. Prey: total number of prey individuals recovered. No. Items: average number of prey individuals per stomach. Prey Volume: mean prey size expressed in mm³.

Species	SVL (mm)	N	No. Full	No. Prey	No. Items	Prey Volume (mm ³)
<i>P. graueri</i>	20	46	21	154	7.0	14
<i>B. funereus</i>	55	17	15	134	9.0	221
<i>B. kisoensis</i>	61	17	13	234	18.0	131
<i>S. schubotzi</i>	19	19	14	215	15.0	2.0
<i>L. kivuensis</i>	35	49	16	22	1.0	489
<i>H. lateralis</i>	24	14	10	40	4.0	34.0

TABLE 3.8. Horn's modified Morisita's similarity indices for the six most common litter anurans. Values in parentheses indicate the similarity of those to species when ants are divided into a small (< 5 mm length) and large (> 5 mm) categories.

	<i>S. schubotzi</i>	<i>B. funereus</i>	<i>B. kisoensis</i>	<i>L. kivuensis</i>	<i>H. lateralis</i>
<i>P. graueri</i>	0.58	0.48 (0.11)	0.48 (0.3)	0.13	0.52
<i>S. schubotzi</i>	—	0.89 (0.16)	0.88 (0.41)	0.05	0.42
<i>B. funereus</i>	—	—	0.91 (0.69)	0.16	0.43 (0.15)
<i>B. kisoensis</i>	—	—	—	0.21	0.41 (0.22)
<i>L. kivuensis</i>	—	—	—	—	0.20

TABLE 3.9. Results of plot sampling around *Ficus natalensis* (n = 5) under the canopy and away from the canopy during the height of the fruiting season and 1 mo later.

Treatment	Arthropod densities (animals/50cm ²)	Herpetofauna density (animals/100m ²)	Litter depth (cm)
Fruiting/Under	70.8 ± 27.7	2.1 ± 2.0	4.4 ± 1.4
Fruiting/Away	40.2 ± 14.0	0.5 ± 0.7	2.9 ± 0.7
Post-fruiting/Under	36.4 ± 8.8	1.3 ± 2.3	3.0 ± 0.3
Post-fruiting/ Away	31.4 ± 8.4	0.3 ± 0.6	2.3 ± 0.8

TABLE 3.10. Repeated measures analysis of variance for the differences in arthropod abundance, herpetofauna abundance, and litter depth at *Ficus natalensis* trees (Kibale National Park) during and after fruiting, under and away from the canopy. Mauchley's criterion $W = 1$ in cases with only two sampling intervals.

Source of variation	df	SS	F	P	R ²
Arthropods					
Between subjects effects					
canopy	1	1584.20	4.36	0.07	29.0
error	8	363.00			7.0
Within subjects effects					
time (fruiting)	1	2332.80	12.06	0.008	44.1
time * canopy	1	819.20	4.234	0.07	15.5
error (date)	8	193.50			3.6
Herpetofauna abundance					
Between subjects effects					
canopy	1	8.71	19.262	0.025	17.1
error	8	9.158			17.9
Within subjects effects					
time (fruiting)	1	1.352	0.344	0.574	2.6
time * canopy	1	0.338	0.086	0.777	0.7
error (time)	8	31.470			61.6

TABLE 3.10.

Source of variation	df	SS	F	P	R ²
Litter depth					
Between subjects effects					
canopy	1	5.618	6.015	0.04	31.1
error	8	0.934			5.2
Within subjects effects					
time (fruiting)	1	5.202	7.437	0.026	28.8
time * canopy	1	0.722	1.032	0.339	3.9
error (time)	8	5.596			30.9

TABLE 3.11. Summary of the quantitative plot studies of mid-elevation tropical litter herpetofaunas and Scott's (1982) study in lowland West Africa. Elevation is given in meters. For richness the number of species estimated to be in the litter fauna is given first, followed by the number of those species sampled successfully using the methods referenced in study are given. Densities are given in animals per 100 m². (*) frogs only, or (†) includes a few snakes

Location	Elevation	Richness	Density	Reference
Philippines				
Cuernos de Negros	1350	12 (8)	11.3	Brown and Alcala (1961)
Cuernos de Negros	1450	4 (4)	15.0	Brown and Alcala (1961)
Costa Rica				
San Vito	1200	27 (13)	58.7	Scott (1976)
Monteverde	1500	15 (5)	6.7	Fauth et al. (1989)
Cameroon				
Lombe, Lac Tissongo	30	13 (8)	9.4	Scott (1982)
Uganda				
Kibale Unlogged	1500	19 (9)	1.9†	This study
Kibale, Logged	1500	19 (9)	4.2†	This study
Budongo, Unlogged	1100	?? (6)	6.7*	Aukland (1997)
Budongo, Logged	1100	?? (6)	5.9*	Aukland (1997)

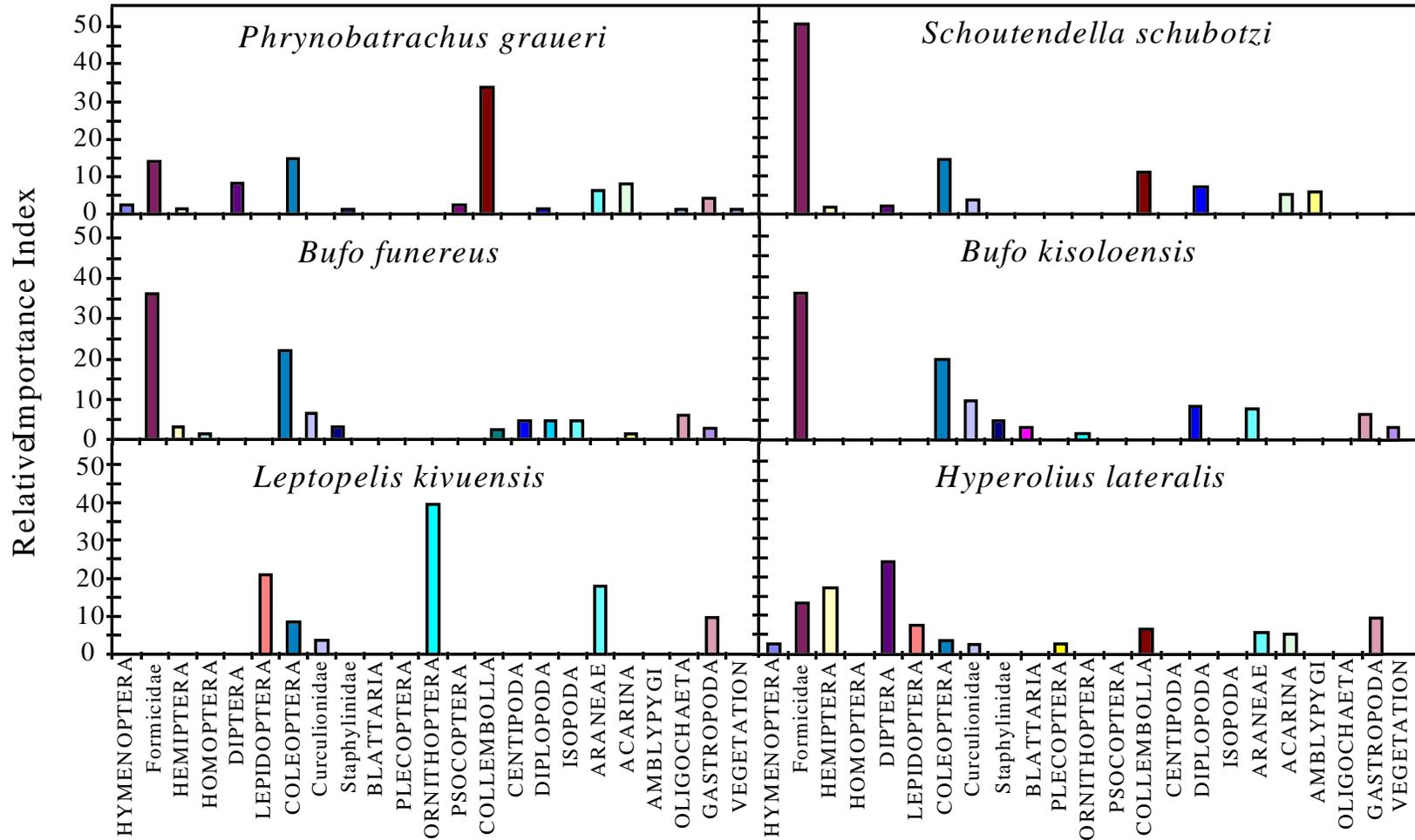


FIGURE 3.1. Feeding ecology of the six most abundant leaf-litter species in Kibale National Park, Uganda. Relative Importance indices for 23 prey categories are given for *P. graueri*, *S. schubotzi*, *B. funereus*, *B. kisoensis*, *L. kivuensis*, and *H. lateralis*

CHAPTER 4 CONCLUSIONS

Few studies have examined the herpetofaunas of East African forests. However, the need for such studies is clear given rapidly expanding human populations, the accelerating loss and disturbance of tropical forests, and the mounting recent evidence that amphibians are declining worldwide. The first objective of this study was to survey the amphibians and reptiles of the Kibale Forest and to determine its biogeographic associations by comparing the herpetofauna of Kibale to those of other tropical African sites. The second objective of this study was to examine the ecology of the leaf-litter component of the Kibale herpetofauna in order to discover which physical and biotic factors are most important in determining local patterns of herpetofauna abundance within the forest. The most important results of this study are summarized below.

1) Kibale Forest supports a rich herpetofauna that includes at least 75 species, including 28 frog species, 15 lizard species, and 32 species of snakes. This makes it one of the richest herpetofaunas in Uganda, with 13 more species than reported from Bwindi-Impenetrable Forest in southwest Uganda. This richness is derived from Kibale's transitional nature between lowland and montane forest and the mosaic of forest and grassland habitat within the park. Elements of both the endemic Central African montane and lowland Congolese herpetofaunas are present at Kibale, as are forest dependent species and farmbush/moist savanna species.

2) Comparisons with eight other equatorial African sites demonstrates the high degree of similarity among Kibale and Bwindi in Uganda, and the Virunga National Park in adjacent Congo-Zaire. These Central African forest herpetofaunas show a fair degree of overlap with the

West African fauna of Korup in Cameroon, but almost no overlap with the coastal forests of Kenya and the coastal mountains of Tanzania. These results support those that have focused on other taxa, such as primates and birds, and demonstrate that the Kibale herpetofauna is best described as an eastern extension of the Congolese fauna, as had been suggested by Schiøtz (1976), Pitman (1974), and Loveridge (1942*a,b*) for all the forests of western Uganda.

3) A total of 18 species were captured in the leaf-litter layer of the forest floor at Kibale, a number similar to that observed in other studies of tropical litter herpetofaunas from mid-elevation forests. The density of animals at Kibale, however, was much lower than that reported from other sites.

4) During the wet season, the selectively logged forest was characterized by a greater abundance of herpetofauna, but lower overall diversity and species equitability compared with the unlogged forest. This pattern has been observed in a number of studies that have examined litter herpetofaunas from disturbed and undisturbed sites. Interestingly, the exotic pine plantation exhibited the highest species diversity among all three forests. The faunal composition of the pine plantation was very different from that of the native forests, being characterized by the dominance of species adapted to more drier conditions, namely reptiles and direct developing frogs.

5) The most common diurnal anuran species in the litter are active foragers of small hard-bodied prey such as ants. There are no sit-and-wait predators which prey on larger soft-bodied prey. This absence of this guild is an interesting contrast with Neotropical herpetofaunas, in which predators of soft-bodied arthropods make up a large proportion of the litter anuran fauna. Two nocturnal treefrogs that are often captured in the litter appear to be sit-and-wait predators, but only one of these actively feeding in the litter; the other appears to only use it as a diurnal refuge.

6) Prey abundance was found to increase significantly beneath fruiting fig trees. Frog abundance was also higher under fig tree canopies than away from them, but this was the case during both fruiting and post-fruiting sampling periods. Therefore it seems likely that frogs are attracted to figs trees, but not necessarily (or only) due to increased prey availability, but perhaps due to the deeper leaf litter found under the figs.

7) All three forest types showed a decrease in the number of animals captured during the dry season, in contrast with most Neotropical litter herpetofaunas which reach their peak densities in the dry season. This combined with the absence of animals from the drier hilltop and upper slope forest habitats suggests that moisture is one of the most important factors in determining local patterns in herpetofauna abundance. This is not all that surprising, as Kibale is relatively dry compared to most tropical forest where litter herpetofaunas have been studied and many of the species present at Kibale are believed to have originated from the wetter lowland forests of eastern Congo-Zaire.

APPENDIX A
AMPHIBIAN SPECIES OF EIGHT TROPICAL AFRICAN LOCALITIES

Amphibian species of tropical Africa based on lists from Korup National Park, Cameroon (KOR; Lawson, 1993), Virungas National Park, Zaire (VIR; Laurent, 1972), Garamba National Park, northeastern Zaire (GAR; Inger, 1968), Kibale National Park, western Uganda (KIB; this study), Bwindi National Park, southeastern Uganda (BWI; Drewes, 1991; Drewes, 1998), East and West Usambara mountains, Tanzania (USA; Howell, 1993); Uzungwa National Park, Tanzania (UZU; Howell, 1993), Arabuko-Sokoke Forest Reserve (ARA; Drewes, 1995).

Taxon	KOR	VIR	GAR	KIB	BWI	USA	UZU	ARA
Gymnophiona,								
Scolecophoridae								
<i>Crotaphatrema bornmuelleri</i>	X							
<i>Scolecophorus kirkii</i>							X	
<i>Scolecophorus vittatus</i>						X		
Caeciliidae								
<i>Boulengerula boulengeri</i>						X		
<i>Geotrypetes seraphini</i>	X							
<i>Herpele multiplicata</i>	X							
<i>Herpele squalostoma</i>	X							
<i>Idiocranium russeli</i>	X							
Anura, Bufonidae								
<i>Bufo brauni</i>						X	X	
<i>Bufo camerunensis</i>	X	X						
<i>Bufo funereus</i>		X	X	X				
<i>Bufo gracilipes</i>	X							
<i>Bufo gutturalis</i>								X
<i>Bufo kisoaloensis</i>		X		X	X			
<i>Bufo latifrons</i>	X		X					
<i>Bufo maculatus</i> ¹	X	X	X	X	X			
<i>Bufo superciliaris</i>	X	X						
<i>Bufo steindachneri</i>			X					X
<i>Bufo tuberosus</i>	X							
<i>Didynamipus sjostedti</i>	X							
<i>Mertensophryne micranotis</i>								X
<i>Nectophryne afra</i>	X	X						
<i>Nectophryne batesii</i>	X	X						
<i>Nectophryne tornieri</i>						X	X	
<i>Nectophryne viviparus</i>							X	
<i>Werneria mertensiana</i>	X							
<i>Wolterstorffina parvipalmata</i>	X							
Hyperoliidae, Hyperoliinae								
<i>Alexteroon obstetricans</i>	X							

APPENDIX A.

Taxon	KOR	VIR	GAR	KIB	BWI	USA	UZU	ARA
<i>Hyperolius alticola</i> ²		X			X			
<i>Hyperolius argus</i>								X
<i>Hyperolius castaneus</i>		X			X			
<i>Hyperolius cinnamomeoventris</i>		X	X	X	X			
<i>Hyperolius concolor</i> ³	X	X	X					
<i>Hyperolius chrysogaster</i>		X						
<i>Hyperolius fusciventris</i>	X							
<i>Hyperolius frontalis</i> ⁴		X			X			
<i>Hyperolius kivuensis</i>		X		X	X			
<i>Hyperolius lateralis</i>		X		X	X			
<i>Hyperolis mitchelli</i>						X	X	
<i>Hyperolius nasutus</i>		X	X	X				
<i>Hyperolius ocellatus</i>	X	X						
<i>Hyperolius pardalis</i>	X							
<i>Hyperolius parkeri</i>								X
<i>Hyperolius phantasticus</i>	X							
<i>Hyperolius platyceps</i>		X		X	X			
<i>Hyperolius puncticulatus</i>						X	X	
<i>Hyperolius pusillus</i>								X
<i>Hyperolius mariae</i>								X
<i>Hyperolius rubripes</i>								X
<i>Hyperolius schoutedeni</i>			X					
<i>Hyperolius spinigularis</i>						X		
<i>Hyperolius sylvaticus</i>								
<i>Hyperolius tanneri</i>						X		
<i>Hyperolius tuberculatus</i>		X						
<i>Hyperolius tuberilingus</i>								X
<i>Hyperolius viridiflavus</i> ⁵		X	X	X	X			
<i>Hyperolius xenorhinus</i>		X						
Kassininae								
<i>Afrivalus dorsalis</i>	X							
<i>Afrivalus fornasinii</i>								X
<i>Afrivalus laevis</i>	X	X		X	X			
<i>Afrivalus leucostictus</i>		X						
<i>Afrivalus orophilus</i>		X			X			
<i>Afrivalus osorioi</i>		X			X			
<i>Afrivalus paradorsalis</i>	X							
<i>Afrivalus pygmaeus</i>								X
<i>Afrivalus quadrivittatus</i>		X	X	X				
<i>Afrivalus uluguruensis</i>						X	X	
<i>Afrivalus weidholzi</i>			X					
<i>Kassina senegalensis</i>		X	X					X
<i>Kassina maculosa</i>			X					
<i>Kassina maculata</i>								X
<i>Opisthothylax immaculatus</i>	X							
<i>Phlyctimantis leonardi</i>	X							

APPENDIX A.

Taxon	KOR	VIR	GAR	KIB	BWI	USA	UZU	ARA
<i>Arthroleptis stenodactylus</i>					X			X
<i>Arthroleptis tanneri</i>						X		
<i>Arthroleptis tuberosus</i>		X						
<i>Arthroleptis variabilis</i>	X	X						
<i>Astylosternus diadematus</i>	X							
<i>Astylosternus fallax</i>	X							
<i>Astylosternus laurenti</i>	X							
<i>Astylosternus schioetzi</i>	X							
<i>Cardioglossa elegans</i>	X							
<i>Cardioglossa escalerae</i>		X						
<i>Cardioglossa gracilis</i>	X							
<i>Cardioglossa leucomystax</i>	X	X						
<i>Cardioglossa nigromaculata</i>	X							
<i>Leptodactylodon bicolor</i>	X							
<i>Leptodactylodon ovatus</i>	X							
<i>Nycitbates corrugatus</i>	X							
<i>Schoutedenella schubotzi</i>		X		X	X			
<i>Schoutedenella sylvaticus</i>	X	X						
<i>Schoutedenella xenodactylus</i>						X		
<i>Scotobleps gabonicus</i>	X							
<i>Trichobatrachus robustus</i>	X							
Hemisinae								
<i>Hemisis guineensis</i>		X	X					
<i>Hemisis marmoratus</i>			X					X
<i>Hemisis olivaceus</i>		X						
Petropedetinae								
<i>Arthroleptides martiensseni</i>						X	X	
<i>Dimorphognathus africanus</i>	X							
<i>Petropedetes cameronensis</i>	X							
<i>Petropedetes johnstoni</i>	X							
<i>Petropedetes newtoni</i>	X							
<i>Petropedetes parkeri</i>	X							
<i>Petropedetes perreti</i>	X							
<i>Phrynobatrachus acridoides</i>								X
<i>Phrynobatrachus auritus</i>	X	X		X				
<i>Phrynobatrachus bequaerti</i>		X						
<i>Phrynobatrachus calcaratus</i>	X	X						
<i>Phrynobatrachus cornutus</i>	X							
<i>Phrynobatrachus cricogaster</i>	X							
<i>Phrynobatrachus cryptotis</i>			X					
<i>Phrynobatrachus dendrobates</i> ⁶		X		X	X			
<i>Phrynobatrachus graueri</i>				X	X			
<i>Phrynobatrachus krefftii</i>						X		
<i>Phrynobatrachus natalensis</i>		X	X					
<i>Phrynobatrachus parvulus</i> ⁷		X		X	X			
<i>Phrynobatrachus parkeri</i>			X					

APPENDIX A.

Taxon	KOR	VIR	GAR	KIB	BWI	USA	UZU	ARA
<i>Phrynobatrachus perpalmatus</i>			X					
<i>Phrynobatrachus scapularis</i>			X					
<i>Phrynobatrachus ukingensis</i>								X
<i>Phrynobatrachus uzungwensis</i>							X	
<i>Phrynobatrachus versicolor</i>		X		X	X			
<i>Phrynodon sandersoni</i>	X							
Raninae								
<i>Aubria subsigillata</i>	X							
<i>Conraua crassipes</i>	X							
<i>Conraua robusta</i>	X							
<i>Euphlyctis occipitalis</i>	X		X	*				
<i>Hylarana albolabris</i>	X	X	X	X	X			
<i>Hylarana amnicola</i>	X							
<i>Hylarana bravana</i>								X
<i>Hylarana galamensis</i>			X					X
<i>Hylarana lepus</i>	X							
<i>Ptychadena c.f. aequiplicata</i>	X							
<i>Ptychadena chrysogaster</i>				X	X			
<i>Ptychadena huguettae</i>			X					
<i>Ptychadena macCarthyensis</i>			X					
<i>Ptychadena mascareniensis</i>	X		X*	X*	X*			X
<i>Ptychadena oxyrhynchus</i>	X		X					
<i>Ptychadena perreti</i>			X					
<i>Ptychadena straeleni</i>			X					
<i>Ptychadena taenioscelis</i>			X					
<i>Ptychadena tournieri</i>			X					
<i>Ptychadena trinodis</i>			X					
<i>Pyxicephalus edulis</i>								X
<i>Rana angolensis</i> ⁸		X		X	X			
<i>Rana ornata</i>			X					
<i>Rana ruwenzorica</i>		X			X			
Rhacophoridae								
<i>Chiromantis rufescens</i>	X	X		X				
<i>Chiromantis xerampelina</i>								X
	79	58	42	28	27	24	16	25

Notes: ¹ includes *Bufo regularis*

² includes *Hyperolius discodactylus* after Drewes (1991)

³ includes *Hyperolius balfouri*

⁴ includes *Hyperolius diaphanus*

⁵ includes subspecies *H. v. bayoni*, *H. v. pitmani*, *H. v. ornatus*, *H. v. xanthogrammus*, *H. v. pachydermus*

⁷ includes *Phrynobatrachus minutus* (Laurent, 1972)

⁸ includes *Rana daesageri* (Laurent, 1972)

APPENDIX B
REPTILES OF EIGHT TROPICAL AFRICAN LOCALITIES.

Reptiles of eight tropical African localities. Species lists were from the following sources; Korup National Park (KOR; Lawson, 1993); Virungas National Park (VIR; DeWitte, 1941); Garamba National Park (GAR; DeWitte, 1966); Kibale National Park (KIB; this study; Pitman, 1974); Bwindi National Park (BWI; Drewes, 1998); Usambara mountains (USA; Howell, 1993); Uzungwa National Park (UZU; Howell, 1993); Arabuko-Sokoke Forest Reserve (ARA; Drewes and Rotich, 1995).

Taxon	KOR	VIR	GAR	KIB	BWI	USA	UZU	ARA
Testudines, Testudinidae								
<i>Kinixys erosa</i>	X	X						
<i>Kinixys homeana</i>	X							
<i>Kinixys belliana</i>			X					X
<i>Geochelone pardalis</i>								X
Pelomedusidae								
<i>Pelomedusa subrufa</i>		X	X					
<i>Pelusios castaneus</i>	X		X					
<i>Pelusios gabonensis</i>		X						
<i>Pelusios niger</i>	X							
<i>Pelusios nigricans</i>		X						
Trionychidae								
<i>Trionyx triunguis</i>	X							
Squamata, Agamadae								
<i>Agama agama</i>	X		X					
<i>Agama atricollis</i>		X		X	X			X
<i>Agama cyanogaster</i>								X
Chamaeleonidae								
<i>Bradypodion fisheri</i>						X		
<i>Bradypodion oxyrhinum</i>							X	
<i>Bradypodion spinosum</i>						X		
<i>Bradypodion tenue</i>						X		
<i>Chamaeleo adolfifriderici</i>		X		X	X			
<i>Chamaeleo bitaeniatus</i>		X						
<i>Chamaeleo carpenteri</i>		X						
<i>Chamaeleo cristatus</i>	X							
<i>Chamaeleo deremensis</i>						X		
<i>Chamaeleo dilepis</i>								X
<i>Chamaeleo eisentrauti</i>	X							
<i>Chamaeleo ellioti</i>		X		X	X			
<i>Chamaeleo gracilis</i>		X	X					
<i>Chamaeleo goetzei</i>							X	
<i>Chamaeleo ituriensis</i>				X				

APPENDIX B.

Taxon	KOR	VIR	GAR	KIB	BWI	USA	UZU	ARA
<i>Chamaeleo johnstoni</i>		X			X			
<i>Chamaeleo laterispinis</i>							X	
<i>Chamaeleo montium</i>	X							
<i>Chamaeleo oweni</i>	X							
<i>Chamaeleo rudis</i>		X			X			
<i>Chamaeleo senegalensis</i>		X	X					
<i>Chamaeleo tempeli</i>							X	
<i>Chamaeleo werneri</i>							X	
<i>Chamaeleo xenorhinus</i>		X						
<i>Rhampoleon boulengeri</i>		X		X	X			
<i>Rhampoleon brevicaudatus</i>						X	X	
<i>Rhampoleon kirstenii</i>								X
<i>Rhampholeon spectrum</i>	X	X						
<i>Rhampoleon temporalis</i>						X		
Cordylidae								
<i>Cordylus tropidosternum</i>								X
Gekkonidae								
<i>Cnemaspis africana</i>						X		
<i>Cnemaspis dickersoni</i>		X					X	
<i>Cnemaspis koehleri</i>	X							
<i>Cnemaspis spinicollis</i>	X							
<i>Cnemapsi quattuorseriatus</i>		X	X	X	X			
<i>Cnemaspis uzungwe</i>							X	
<i>Hemidactylus ansorgii</i>	X							
<i>Hemidactylus brookii</i>	X		X					X
<i>Hemidactylus echinus</i>	X							
<i>Hemidactylus fasciatus</i>	X		X					
<i>Hemidactylus ituriensis</i>		X						
<i>Hemidactylus mabouia</i>		X		X	X			X
<i>Hemidactylus platycephalus</i>								X
<i>Hemidactylus squamulatus</i>								X
<i>Lygodactylus conradti</i>						X		
<i>Lygodactylus cf conraui</i>	X							
<i>Lygodactylus gravis</i>						X		
<i>Lygodactylus picturatus</i>		X	X					X
<i>Lygodactylus williamsi</i>							X	
<i>Pachydactylus bibronii</i>		X						
<i>Urocotyledon wolterstorffi</i>						X		
Gerrhosauridae								
<i>Gerrhosaurus major</i>			X					X
<i>Gerrhosaurus flavigularis</i>								X
<i>Gerrhosaurus nigrolineatus</i>								X
Lacertidae								
<i>Adolfus africanus</i>		X	X	X	X			
<i>Adolfus jacksoni</i>		X			X	X		
<i>Adolfus vauereselli</i>		X		X	X			

APPENDIX B.

Taxon	KOR	VIR	GAR	KIB	BWI	USA	UZU	ARA
<i>Eremias nitida</i>			X					
<i>Gastropholis prasina</i>						X		X
<i>Heliobolis spekii</i>		X						
<i>Holoaspis guentheri</i>	X			X		X		
<i>Ichnotropis capensis</i>			X					
<i>Latastia longicaudata</i>		X						X
Scincidae								
<i>Feylinia currori</i>		X						
<i>Lygosoma afer</i>								X
<i>Lygosoma fernandi</i>	X	X	X	X	X			
<i>Lygosoma modestum</i>								
<i>Lygosoma pembanum</i>								X
<i>Lygosoma sundevallii</i>		X	X					
<i>Leptosiaphos aloysiisabaudiae</i>		X	X	X				
<i>Leptosiaphos blochmanni</i>		X						
<i>Leptosiaphos graueri</i>		X				X		
<i>Leptosiaphos hackarsi</i>		X				X		
<i>Leptosiaphos luberoensis</i>		X						
<i>Leptosiaphos meleagris</i>		X						
<i>Leptosiaphos rhomboidalis</i>							X	
<i>Mabuya affinis</i>			X					
<i>Mabuya blandingii</i>	X	X	X					
<i>Mabuya boulengeri</i>		X						
<i>Mabuya brevicollis</i>								X
<i>Mabuya maculilabris</i>	X	X	X	X				
<i>Mabuya megalura</i>		X		X	X			
<i>Mabuya perroteti</i>			X					
<i>Mabuya planifrons</i>								X
<i>Mabuya quinquetaeniata</i>			X					
<i>Mabuya striata</i>		X		X	X			
<i>Mabuya sudanesis</i>			X					
<i>Mabuya varia</i>		X						X
<i>Melanoseps ater</i>						X	X	
<i>Proscelotes eggeli</i>						X		
Varanidae								
<i>Varanus albigularis</i>								X
<i>Varanus niloticus</i>	X	X	X					X
<i>Varanus exanthematicus</i>			X					
Zonuridae								
<i>Chamaesaura tenuior</i>		X						
Serpentes								
Atractaspidae								
<i>Atractaspis aterrima</i>		X					X	
<i>Atractaspis bibronii</i>								X
<i>Atractaspis corpulenta</i>	X	X						
<i>Atractaspis irregularis</i> ¹		X						

APPENDIX B.

Taxon	KOR	VIR	GAR	KIB	BWI	USA	UZU	ARA
<i>Atractaspis reticulata</i>	X							
Boidae								
<i>Calabaria (Eryx) rienhardtii</i>	X							
<i>Eryx colubrinus</i>								X
<i>Python sebae</i>	X	X	X	X				X
<i>Python regius</i>	X		X					
Colubridae								
<i>Afronatrix anascopus</i>	X							
<i>Aparallatus guentheri</i>						X		X
<i>Aparallatus modestus</i>	X	X						
<i>Aparallatus turneri</i>								X
<i>Aparallatus weneri</i>						X		
<i>Boiga blandingii</i>	X	X	X	X				
<i>Boiga pulverulenta</i>	X	X		X				
<i>Bothrophthalmus lineatus</i>	X	X	X	X	X			
<i>Calamelaps cf unicolor</i>			X					X
<i>Crotaphopeltis hotamboeia</i>		X	X	X				
<i>Crotaphopeltis tornieri</i>						X	X	
<i>Dasypeltis atra</i>				X	X			
<i>Dasypeltis fasciata</i>	X		X					
<i>Dasypeltis macrops</i>		X						
<i>Dasypeltis medici</i>								X
<i>Dasypeltis scabra</i>	X	X	X					
<i>Dipsadoboa duchesnii</i>	X	X						
<i>Dipsadoboa elongata</i>	X							
<i>Dipsadoboa unicolor</i>	X	X	X	X	X			
<i>Dipsadoboa weneri</i>						X		
<i>Dispholidus typus</i>		X	X					X
<i>Dromophis lineatus</i>			X					
<i>Duberria lutrix</i>		X		X	X			
<i>Gastropyxis smaragdina</i>	X	X	X					
<i>Geodipsas depressiceps</i>		X		X	X			
<i>Geodipsas vauerocegae</i>						X		
<i>Gonionotophis brussauxi</i>	X							
<i>Grayia caesar</i>	X							
<i>Grayia ornata</i>		X	X					
<i>Grayia smithii</i>	X		X					
<i>Grayia tholloni</i>			X					
<i>Hapsidophrys lineatus</i>		X		X	X			
<i>Hemirhagerrhis nototaenia</i>			X					X
<i>Homonotus (Lamprophis) modestus</i>	X							
<i>Lamprophis fuliginosus</i>			X		X			X
<i>Lamprophis lineatus</i>		X		X				
<i>Lamprophis olivaceus</i>	X	X		X	X			
<i>Lamprophis virgatus</i>	X							

APPENDIX B.

Taxon	KOR	VIR	GAR	KIB	BWI	USA	UZU	ARA
<i>Lycophidion capense</i>		X	X					X
<i>Lycophidion depressirostre</i>								X
<i>Lycophidion laterale</i>	X							
<i>Lycophidion meleagis</i>						X		X
<i>Lycophidion oratum</i>		X	X	X	X			
<i>Mehelya capensis</i>		X	X					
<i>Mehelya guirali</i>	X							
<i>Mehelya nyassae</i>			X					X
<i>Mehelya poensis</i>	X	X	X					
<i>Mehelya stenophthalmus</i>	X	X	X	X				
<i>Meizodon cornatus</i>			X					
<i>Meizodon semiornatus</i>								X
<i>Natriciteres fuliginoides</i>	X							
<i>Natriciteres olivacea</i>	X	X	X	X				
<i>Natriciteres variegata</i>	X							
<i>Philothamnus angolensis</i>		X*		X	X			
<i>Philothamnus carinatus</i>		X		X	X			
<i>Philothamnus heterodermus</i> ²	X	X		X	X			
<i>Philothamnus heterolepidotus</i>	X		X					
<i>Philothamnus hoplogaster</i>		X	X					
<i>Philothamnus irregularis</i> ³	X							
<i>Philothamnus macrops</i>						X		
<i>Philothamnus nitidus</i>	X			X				
<i>Philothamnus punctatus</i>								X
<i>Philothamnus semivariiegatus</i>	X	X	X	X				
<i>Polemon barthii</i>	X							
<i>Polemon christyi</i>		X	X	X				
<i>Polemon collaris</i>	X							
<i>Polemon gabonensis</i>	X	X						
<i>Prosymna ambigua</i>			X					X
<i>Psammophis biseriatus</i>		X						X
<i>Psammophis phillipsii</i>	X			X				X
<i>Psammophis punctulatus</i>								X
<i>Psammophis sibilans</i>		X	X					
<i>Psammophis subtaeniatus</i>		X						X
<i>Pseudoaspis cana</i>		X						
<i>Rhamnophis batesii</i>	X							
<i>Rhamnophis aethiopissa</i>	X	X	X	X				
<i>Rhamphiophis acutus</i>		X	X					
<i>Rhamphiophis oxyrhynchus</i>								X
<i>Rhamphiophis rostratus</i>								X
<i>Rhamphiophis rubropunctatus</i>								X
<i>Scaphiophus albopunctatus</i>	X	X	X					X
<i>Telescopus semiannulatus</i>		X						X
<i>Telescopus obtusus</i>								X
<i>Thelotornis kirtlandii</i>	X	X	X	X	X			

APPENDIX B.

Taxon	KOR	VIR	GAR	KIB	BWI	USA	UZU	ARA
<i>Thelotornis capensis</i>								X
<i>Thrasops flavigularis</i>	X							
<i>Thrasops jacksonii</i>		X	X	X				
<i>Thrasops occidentalis</i>	X							
Elapidae								
<i>Boulengerina annulata</i>			X					
<i>Dendroaspis augusticeps</i>								X
<i>Dendroaspis jamesonii</i>	X	X	X	X				
<i>Dendroaspis polylepis</i>								X
<i>Elapsoidea guntherii</i>		X						
<i>Elapsoidea laticincta</i>			X					
<i>Elapsoidea nigra</i>						X	X	
<i>Naja haje</i>		X	X					
<i>Naja melanoleuca</i>	X	X	X	X	X	X		X
<i>Naja nigricollis</i>		X	X		X			X
<i>Pseudohaje goldii</i>	X	X						
Leptotyphlopidae								
<i>Leptotyphlops emini</i>		X						
<i>Leptotyphlops longicaudus</i>								X
<i>Leptotyphlops monticola?</i>		X						
<i>Leptotyphlops nigricans</i>		X						
Typhlopidae								
<i>Typhlops angolensis</i>				X				
<i>Typhlops avakubae?</i>		X						
<i>Typhlops lineolatus (boulengeri)</i>			X					
<i>Typhlops congestus</i>			X					
<i>Typhlops gierrai</i>						X	X	
<i>Typhlops lestradei?</i>		X						
<i>Typhlops punctatus</i>	X	X	X					
<i>Typhlops sudanensis?</i>			X					
<i>Typhlops unitaeniatus</i>								X
<i>Rhinotyphlops schlegelii</i>								X
<i>Rhinotyphlops lumbriciformis</i>								X
Viperidae								
<i>Adenorhinos barbouri</i>							X	
<i>Atheris ceratophorus</i>						X	X	
<i>Atheris nitschei</i>		X		X	X			
<i>Atheris squamiger</i>	X	X		X	X			
<i>Bitis arietans</i>		X	X					X
<i>Bitis gabonica</i>	X	X	X		X	X		
<i>Bitis nasicornis</i>	X	X		X	X	X		
<i>Causus defilippii</i>		X						X
<i>Causus lichtenstienii</i>	X	X		X				
<i>Causus maculatus</i>	X							
<i>Causus resimus</i>		X						X
<i>Causus rhombeatus</i>		X	X					

APPENDIX B.

Taxon	KOR	VIR	GAR	KIB	BWI	USA	UZU	ARA
Totals	76	109	74	46	35	28	17	63

Notes: 1 synonymous with *A. schoutedeni*, *A. conradsi*, and *A. babaulti* of DeWitte (1941).

2 includes *P. ruandae* of Hughes (1885)

3 following Hughes (1985) for range of *P. irregularis*

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BIOGRAPHICAL SKETCH

James Richard Vonesh was born on July 11, 1969, in Madang, Papua New Guinea, to Richard and Naomi Vonesh. He earned his degree of Bachelor of Science in biology from Eckerd College, St. Petersburg, Florida. Upon graduation he spent three years teaching English in Takamatsu, Japan. In 1994 he returned to the United States to pursue graduate studies in zoology at the University of Florida.