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Patterns of Richness and Abundance in a Tropical African Leaf-litter Herpetofauna[1]

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ABSTRACT

I compared species richness and habitat correlates of leaf-litter herpetofaunal abundance in undisturbed and selectively logged forests, and an abandoned pine plantation in Kibale National Park, Uganda. I sampled 50 randomly located 25 m^2 litter plots in each area during the wet and dry seasons in 1997. Ten anuran, five lizard, and three snake species were captured in plots over the study. Assemblage composition was most similar at logged and unlogged sites. The logged forest herpetofauna had higher species richness and abundance than the unlogged forest, but diversity was greater in the unlogged forest due to greater evenness. In contrast, the pine plantation site had the highest richness, abundance, and evenness of the three study sites, but species composition was distinct from the other areas. Herpetofaunal densities were significantly lower in all three areas during the dry season than in the wet season. During the dry season, soil moisture, litter mass, topography, shrub cover, and number of fallen logs were significant positive predictors of herpetofaunal presence in litter plots, but only soil moisture was significant in the wet season. The interaction of moisture and topography appears to be important in determining seasonal patterns of litter herpetofaunal distribution. Comparison of litter herpetofaunal studies across the tropics have shown that mid-elevation faunas generally support fewer species than lowland faunas. Compared with other tropical mid-elevation litter faunas, Kibale supports an intermediate number of species, but at lower densities than observed at any other mid-elevation site reported in the literature.

Key words: *Africa; amphibian; conservation; density; diversity; habitat alteration; leaf litter; logging; plantation; reptile; Uganda.*

THE LEAF-LITTER HERPETOFAUNAS OF TROPICAL AFRICAN RAIN FORESTS are poorly known relative to those of tropical America and Asia. Studies in the Neotropics and southeast Asia have demonstrated that species composition and abundance of litter amphibians and reptiles can be influenced by a variety of environmental characteristics, and may vary on both a diel and seasonal basis (Lieberman 1986, Slowinski *et al.* 1987). Habitat characteristics that correlate with litter herpetofaunal richness and abundance include climate, elevation (Scott 1976, Fauth *et al.* 1989, Giaretta *et al.* 1999), moisture, leaf-litter depth, (Scott 1976, Allmon 1991), understory vegetation density (Pearman 1997), and leaf-litter arthropod abundance (Lieberman 1986, Guyer 1988). In addition, human disturbances (*e.g.*, logging or planting nonnative tree plantations) have also been shown to influence litter amphibian and reptile communities. Disturbed sites are frequently characterized by lower species richness and evenness compared to similar undisturbed sites (Inger 1980a, Lieberman 1986, Heinen 1992). To date, only two studies have examined the leaf-litter herpetofaunas of tropical Africa (Scott 1982, Toft 1982). Both were conducted in the lowland forests of West Africa, and only Scott (1982) provided estimates of litter herpetofaunal densities. Neither study examined the relationships among habitat characteristics, seasonal changes, or human disturbances and leaf-litter herpetofaunal richness or abundance.

In addition to examining local habitat correlates of litter herpetofaunal diversity, previous studies have revealed regional differences among tropical herpetofaunas (May 1980, Inger 1980a). Allmon (1991) reviewed biogeograpical trends in species richness and abundance for litter amphibians of the tropical Old and New World lowland rain forests. While species richness was similar, densities differed among regions. Central American lowland forests supported the densest litter amphibian faunas, followed by Africa, South America, and southeast Asia. No one has compared the richness and abundance of tropical litter herpetofaunas found at higher elevations in these four regions, because no data were available from Africa.

This study describes seasonal patterns of leaf-litter amphibian and reptile richness and abundance in disturbed and relatively undisturbed mid-elevation forest sites in Kibale National Park, western Uganda, and examines the habitat characteris-

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tics correlated with their abundance among sites and seasons. This study is the first to examine the litter herpetofauna of a mid-elevation African forest. With these new data, I compare mid-elevation sites from tropical Asia, Africa, and America, and discuss if patterns observed among the lowland litter herpetofaunas of these regions are also observed among mid-elevation faunas.

MATERIALS AND METHODS

STUDY SITES.—I conducted this study at the Makerere University Biological Field Station (MUBFS), Kibale National Park, in western Uganda (0°13′–0°41′N, 30°19′–30°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 20 to 30 m (Struhsaker 1997). The general topography of the study area consists of moderately undulating hills and valleys. Mean annual rainfall at this site is 1622 mm (1977–1991), most of which falls during the two rainy seasons, March–May and September–November (Struhsaker 1997).

The forest surrounding the field station is comprised of a mosaic of undisturbed and selectively logged forest and pine plantations. The unlogged site I studied was the K30 forest compartment, which consists of 282 ha of mature evergreen forest (Struhsaker 1997). The selectively logged site was the 347 ha K15 forest compartment, which was selectively logged from 1968–1969 at an intensity of 8.6 stems/ha, resulting in a 47 percent reduction in basal area for all species (Skorupa 1988). The pine plantation site, Nyakatojo, is a 86.2 ha monotypic stand of Caribbean pine (*Pinus caribaea*) initially planted during 1967–1968. During this study, Nyakatojo was characterized by a mature pine canopy, while the understory vegetation included many saplings and seedlings of indigenous forest trees (Chapman & Chapman 1996, Zanne 1998).

SAMPLING METHODS.—I sampled 50 litter plots each season per site. Wet season plots were sampled 11 March–15 May 1997, and dry season plots were sampled 12 June–26 July 1997; 4–8 plots were sampled in each area per week. Plots were 5 × 5 m (Fauth *et al.* 1989, Allmon 1991, Heinen 1992) and enclosed with a clear plastic fence 50 cm high immediately prior to sampling. Each plot was randomly selected within the MUBFS trail grid system at the beginning of the study. Once the fence was in place, two to four people searched the entire plot, overturning litter and logs, and sifting through the topsoil until the entire area had been covered and 15 minutes had passed without a new capture. Animals found directly on or in the litter, or within 0.5 m of the forest floor, were included in the results. A mean of 58.5 (33–108) person-minutes was spent searching each plot.

For each plot, I recorded: slope (% incline, measured with a clinometer); percent soil humidity (measured with a soil humidity meter); soil pH; wet litter mass of a randomly selected 0.5 m^2 subplot (kg); mean litter depth (measured to the nearest 0.5 cm, 1 m in from each corner of the plot); estimated percent area covered by low ground vegetation cover less than 1 m high; estimated percent area of shrub (1–3 m) cover; percent area canopy cover; number of logs greater than 10 cm diameter; number of trees greater than 10 cm diameter at breast height (DBH); and topographic category. Topographic category was a subjective index ranked 1–5, where a rank of 1 indicated that the plot was located on a valley bottom, a rank of 3 denoted a plot that fell mid-slope, and a rank of 5 specified a hill- or ridgetop plot. Amphibians and reptiles captured were identified to species and measured. All captured animals were released after initial voucher specimens were preserved. Voucher specimens are housed at Makerere University, Kampala, Uganda, and at the California Academy of Sciences, San Francisco, California (specimens listed in: Vonesh in press).

ANALYSES.—Among sites and seasons, I compared species richness, diversity (H'; Pielou 1966), and evenness (J'; Pielou 1966). Morisita's (1959) index of similarity (C) was used to measure the similarity of the herpetofaunas in each forest type. A jackknife species richness estimate based on all 300 plots was calculated to estimate the total number of species (95% ci) in the litter herpetofauna (Heltshe & Forrester 1983). Among-site and season comparisons of physical and biotic variables were made using the Kruskal-Wallis test with a Bonferroni adjusted alpha level for three tests (Conover 1980). The Kruskal-Wallis test statistic *H* approximates the chi-square distribution, and I report chi-square values for Kruskal-Wallis analyses (SPSS 8.0, Chicago, Illinois). For significantly different tests among sites, multiple comparisons were conducted using Bonferroni adjusted Mann-Whitney *U*-tests. Plots in each of the five topographical categories were compared during both seasons; however, the pine plantation plots were excluded from this anal-

TABLE 1. *Species of leaf-litter amphibians and reptiles found in Kibale National Park, Uganda. Data from this study (marked with *), Pitman (1974), and Vonesh (1998).*

Order Anura	Order Sauria
**Bufo funereus*	**Cnemaspis quattuorseriata*
**B. kisoloensis*	**Rhampholeon boulengeri*
**Schoutedenella schubotzi*	**Adolfus africanus*
Phrynobatrachus auritus	**A. vauereselli*
P. dendrobates	**Leptosiaphos aloysiisabaudiae*
**P. graueri*	*Lygosoma fernandi*
**P. parvulus*	**Order Serpentes**
P. versicolor	*Typhlops punctatus*
**Rana angolensis*	*Causus lichtensteinii*
**Phlyctimantis verrucosus*	*Bitis gabonica*
**Leptopelis christyi*	*B. nasicornis*
**L. kivuensis*	**Bothropthalamus lineatus*
**Hyperolius lateralis*	*Lamprophis olivacea*
	Mehelya poensis
	M. stenophthalmus
	**Geodipsas depressiceps*
	Polemon christyi
	**Dasypeltis atra*
	Lycophidion ornatum
	Atractaspis irregularis

ysis because there were no plots in the valley bottom (rank 1) and lower slope (rank 2) categories at this site. The relationship between 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 & Travis 1993). Variables included in the logistic regression analysis were: slope, soil pH, wet litter mass, litter depth, number of logs, ground vegetation cover, shrub cover, canopy cover, number of trees, and topographic category (SPSS 8.0, Chicago, Illinois).

RESULTS

General description of the litter herpetofauna.—A total of 18 species was captured in the plots, including ten anurans, five lizards, and three snakes (Table 1). The jackknife estimate of the total litter herpetofaunal richness for the three study sites combined (300 plots) was 25 ± 5 species. This was consistent with estimates based on 15 month of regular collecting and literature records for the Kibale area (Pitman 1974), which indicated that the complete litter herpetofauna of the park should include 29–32 amphibian and reptile species (Table 1; Vonesh in press). Plot sampling was effective in capturing anurans (10 of 13 spp.) and lizards (5 of 6 spp.), but poor at capturing terrestrial and fossorial snakes (3 of 13 spp.). Anurans comprised 89, lizards 9, and snakes only 2 percent of the animals captured (Table 2). The aquatic-breeding cricket frog *Phrynobatrachus graueri* was the most abundant litter species (42% of captures), followed by the toad *Bufo funereus* (11%), the direct-developing frog *Schoutedenella schubotzi* (10%), and the toad *B. kisoloensis* (7%). The diurnal gecko *Cnemapis quattuorseriata* was the most abundant reptile (6% of captures). Among the species captured within litter plots, several were probably refugee species (*sensu* Scott 1976) that are typically found in other parts of the forest but may occasionally be found in the litter. These species included *Rana angolensis, Phylctimantis verrucosus,* both *Leptopelis* species, and *Hyperolius lateralis* (Table 2).

Habitat characteristics and herpetofaunal distribution.—The logistic regression model for predicting the presence or absence of amphibians and reptiles in plots for all areas during the wet season correctly classified only 59 percent of the plots, and included one significant variable: soil humidity. The model for all areas combined during the dry season correctly classified 80 percent of the plots and included five significant variables: wet litter mass, hill category, soil humidity, number of logs, and shrub cover (Table 3).

The seasonal interaction between topography and moisture appeared to strongly influence herpetofaunal distributions. In the dry season, there were no significant differences in the number of animals captured in the five topographic categories from the logged and unlogged sites (logged: $\chi^2_{[4]} = 3.19$, $P = 0.53$; unlogged: $\chi^2_{[4]} = 7.32$, $P = 0.12$). During the dry season, however, no animals were captured in hilltop (rank 5) or upper slope (rank 4) plots in either area (logged: $\chi^2_{[4]} = 21.79$, $P < 0.001$; unlogged: $\chi^2_{[4]} = 14.74$, $P = 0.005$). During both seasons, soil humidity was lower in hill top and upper slope plots than bottom and lower slope plots, but this difference was more pronounced during the dry season (wet season: $\chi^2_{[4]} = 9.64$, $P = 0.47$; dry season: $\chi^2_{[4]} = 20.43$, $P < 0.001$). For both unlogged and logged areas, plots that contained animals were characterized by higher soil humidity ($\chi^2_{[4]} = 14.01$, $P < 0.001$).

Comparison of habitat characteristics among study areas.—Both across and within seasons, there were no differences in soil humidity or pH among the three study areas (Table 4). During both seasons, the pine plantation had the deepest and

TABLE 2. *Numbers of amphibians and reptiles captured in the leaf litter of unlogged, selectively logged, and pine plantation sites during the wet and dry seasons (March–June 1997), Kibale National Park, Uganda. Fifty 25 m^2 plots were sampled per site each season. * indicates refugee species not considered part of the regular litter fauna (*sensu *Scott 1976).*

	Unlogged		Logged		Pine		
Species	Wet	Dry	Wet	Dry	Wet	Dry	Total
B. funereus	4	4	7	2	5	1	23
B. kisoloensis	0	5	1	4	0	4	14
S. schubotzi	2	1	0	0	14	5	22
*R. angolensis**	0	0	1	0	0	0	1
P. graueri	16	4	51	13	2	3	89
P. parvulus	1	0	1	3	2	1	8
*P. verrucosus**	0	0	0	0	1	0	1
*L. kivuensis**	3	1	7	5	1	0	17
*L. christyi**	0	0	1	0	1	0	2
*H. lateralis**	1	4	3	3	0	0	11
C. quattuorseriata	0	0	0	0	10	4	14
A. africanus	0	1	0	0	1	0	2
A. vauereselli	0	0	0	1	0	0	1
R. boulengeri	0	0	0	0	0	1	1
L. aloysiisabaudiae	0	0	0	0	1	0	1
B. lineatus	0	0	0	1	0	0	1
G. depressiceps	1	0	0	1	0	0	2
D. atra	0	0	1	0	0	0	1
TOTALS	28	20	73	33	38	19	
	48		106		57		211

heaviest leaflitter and the least canopy cover, while the unlogged forest was significantly steeper than the other two areas. During the wet season, ground vegetation cover was significantly lower in the logged area, and shrub cover was significantly lower in the pine plantation. During the dry season, however, ground cover and soil humidity were lowest in the pines, and shrub cover greatest in the logged area. Across all three sites, soil humidity, wet litter mass, and litter depth decreased during the dry season, and soil pH increased (Table 4).

COMPARISON OF HERPETOFAUNAS AMONG STUDY AREAS.—A total of 106 animals was captured in the logged site, compared to 48 animals in the unlogged site and 57 in the pine plantation (Table 5). Differences in amphibian densities among areas neared statistical significance during the wet ($\chi^2_{[2]} = 5.9$, $P = 0.052$), but not in the dry ($\chi^2_{[2]} = 2.8$, $P = 0.978$) season. Reptile densities were significantly greater in the pines during the wet season ($\chi^2_{[2]} = 12.6$, $P = 0.002$) but not in the dry season ($\chi^2_{[2]} = 2.8$, $P = 0.24$). Qualitatively, overall species richness was greater in the logged forest and pine plantation sites (12 spp.) than the unlogged forest site (9 spp.), and species equitability was highest in the pines and unlogged forest. Thus, species diversity was highest in the pine plantation,

TABLE 3. *Results of stepwise logistic regression of the presence or absence of amphibians and reptiles in leaf-litter plots predicted by habitat variables. Independent variables included slope, soil humidity, soil pH, wet litter mass, litter depth, logs, percentage low vegetation cover, percentage medium vegetation cover, canopy cover, number of trees, and topographic category (1 = valley to 5 = hilltop).*

Season	Classification table (% correct)	*R*	−2 log likelihood χ^2 (*P*-value)	Predictors
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 (<0.001)	wet litter mass
		0.128	35.34 (<0.001)	no. logs
		0.129	41.07 (<0.001)	soil humidity
		0.105	45.20 (<0.001)	shrub cover

TABLE 4. *Differences among forest types in environmental variables measured during the wet and dry seasons ($\bar{x} \pm SD$). Kruskal-Wallis χ^2, and* P*-values are provided for site comparisons. For site comparisons within a season, statistically different variables are indicated with * next to the* P*-value in the far right column with significantly different variables indicated by different letter superscripts; nonsignificant differences are indicated by NS next to the* P*-value. For comparisons of habitat variables within site between seasons, significant (*) and nonsignificant (NS) differences are indicated after the letter superscript following the dry season value.*

Variable	Unlogged	Logged	Pine	χ^2	*P*-value
WET SEASON					
Slope (°)	14.9 ± 5.3^{a}	8.0 ± 5.5^{b}	8.9 ± 5.7^{b}	34.8	<0.001*
Soil humidity (%)	76.6 ± 13.7	71.9 ± 13.7	72.7 ± 17.05	5.2	0.073NS
Soil pH (pH)	6.2 ± 0.5	6.3 ± 0.4	6.1 ± 0.9	5.2	0.075NS
Wet litter mass (kg)	0.9 ± 0.5^{a}	0.7 ± 0.3^{b}	1.3 ± 0.6^{c}	40.3	<0.001*
Litter depth (cm)	2.9 ± 1.0^{a}	3.2 ± 0.9^{b}	5.1 ± 1.0^{c}	81.9	<0.001*
Ground cover (%)	41.9 ± 16.0^{a}	30.7 ± 13.1^{b}	49.3 ± 19.2^{a}	27.8	<0.001*
Shrub cover (%)	42.3 ± 12.7^{a}	45.7 ± 13.4^{a}	34.2 ± 14.3^{b}	17.2	<0.001*
Canopy cover (%)	93.8 ± 1.4^{a}	93.5 ± 2.3^{a}	88.8 ± 2.4^{b}	74.2	<0.001*
No. logs/plot (*N*)	0.3 ± 0.6	0.4 ± 0.8	0.5 ± 1.0	1.3	0.525NS
No. trees/plot (*N*)	1.8 ± 1.5	1.5 ± 1.2	1.9 ± 1.2	2.0	0.361NS
DRY SEASON:					
Slope	13.1 ± 5.0^{a}NS	7.8 ± 5.4^{b}NS	9.5 ± 4.7^{b}NS	24.6	<0.001*
Soil humidity	57.2 ± 20.8^{a}*	60.4 ± 14.8^{a}*	52.3 ± 12.6^{b}*	9.2	0.01*
Soil pH	6.6 ± 0.4*	6.7 ± 0.3*	6.7 ± 0.3*	1.4	0.505NS
Wet litter mass	0.4 ± 0.2^{a}*	0.5 ± 0.2^{b}*	0.9 ± 0.3^{c}*	57.1	<0.001*
Litter depth	2.3 ± 0.9^{a}*	2.6 ± 1.1^{a}*	4.3 ± 0.9^{b}*	71.6	<0.001*
Ground cover	41.5 ± 15.2^{a}NS	28.1 ± 10.1^{b}NS	36.3 ± 13.5^{a}*	23.7	<0.001*
Shrub cover	37.2 ± 13.4^{a}NS	44.7 ± 12.0^{b}NS	32.4 ± 15.5^{a}NS	18.3	<0.001*
Canopy cover	94.0 ± 1.7^{a}NS	94.0 ± 1.8^{a}NS	89.5 ± 2.7^{b}NS	73.2	<0.001*
No. logs/plot	0.3 ± 0.6NS	0.2 ± 0.4NS	0.4 ± 0.7NS	4.1	0.13NS
No. trees/plot	1.4 ± 1.2^{a}NS	0.9 ± 1.0^{b}*	2.0 ± 1.2^{c}NS	22.4	<0.001*

followed by the unlogged and the logged forest sites (Table 3).

Across all three areas, herpetofaunal abundance and density decreased significantly during the dry season ($\chi^2_{[2]} = 12.9$, $P < 0.001$). Diversity tended to increase in the logged and unlogged sites during the dry season, due to similar richness and greater equitability, than during the wet season. In the pine plantation, richness was similar among seasons (Table 3).

TABLE 5. *Density, richness, evenness, diversity, and similarity of the leaf-litter herpetofauna calculated for pristine, logged, and pine plantation forest types in Kibale National Park, Uganda.*

Variable	Unlogged			Logged			Pine plantation		
	wet	dry	total	wet	dry	total	wet	dry	total
No. individuals	28	20	48	73	33	106	38	19	57
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
Density (/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
Similarity (C)				0.94			0.24		
					0.42				

TABLE 6. *A comparison of mid-elevation tropical liter herpetofaunas. Richness estimates are the total number of amphibians and lizards estimated to be in the litter herpetofauna. For Kibale, richness and density estimates are provided for all animals captured, and for regular litter species (*sensu *Scott 1976) with refugee species excluded.*

Location	Elevation (m)	Richness (No. spp)	Density (/100 m^2)	Source
SOUTHEAST ASIA				
Philippines				
Cuernos de Negros	1425	4	15.0	Brown and Alcala (1961)
Cuernos de Negros	1010	12	5.1	Brown and Alcala (1961)
AFRICA				
Uganda				
Kibale (unlogged)	1500	19 (14)	1.9 (1.6)	This study
CENTRAL AMERICA				
Costa Rica				
San Vito	1200	27	58.7	Scott (1976)
Monteverde	1500	15	6.7	Fauth *et al.* (1989)
SOUTH AMERICA				
Brazil				
Atlantic Forest	1200	14	4.6	Giaretta *et al.* (1999)

The unlogged and logged forest herpetofaunas were similar, and both demonstrated low similarities to the pine plantation (Table 5). The litter herpetofaunas of the logged and unlogged areas were dominated by the frogs *P. graueri* and *B. funereus,* while the most common species in the pines were the frog *S. schubotzi* and the gecko *C. quatteroseriata,* which were rare or absent from the other areas (Table 2).

DISCUSSION

Habitat characteristics and herpetofaunal distribution.—Results from this study suggest that the Kibale litter herpetofauna is sensitive to environmental characteristics similar to those observed by previous researchers. Topography (Scott 1976, Toft 1980a), moisture, litter mass (Scott 1976, Fauth *et al.* 1989, Allmon 1991), number of logs, and shrub cover (Pearman 1997) were important in predicting the presence of animals in plots in Kibale; however, with the exception of soil moisture, the significance of these variables was only apparent during the dry season (Table 3). Moisture and cover during the dry season may be particularly critical, since Kibale typically receives only 1600 mm of rain per year, less than that reported at other tropical sites where the litter herpetofauna has been studied (for review, see Scott 1976, Allmon 1991). The seasonal shift in the number of animals captured in upslope plots in Kibale was similar to that observed by Toft (1980a) at a relatively dry site in Panama. Toft (1980a) found the highest density of amphibians shifted from ridgetops to stream bottoms during the dry season.

Several Neotropical studies have found that herpetofaunal abundance peaks during the dry season when prey arthropod abundance is greatest (Toft 1980a,b; Lieberman 1986; Allmon 1991). In Kibale, herpetofaunal numbers were highest during the wet season. Two possible explanations for this difference are: (1) moisture may be more limiting at Kibale than in other areas previously studied; and (2) Kibale litter arthropod numbers peak in the late wet season (Nummelin 1989). Thus, the peak in Kibale herpetofaunal abundance may occur when desiccation is unlikely and prey are abundant.

Comparison of disturbed and undisturbed sites.—The large scales at which natural and anthropogenic forest disturbances occur frequently make experimental manipulation and replication difficult. Because of these challenges, many studies (including this one) that examine the effects of forestry management practices are unreplicated or pseudoreplicated (Hurlbert 1984). In the absence of replication, it is difficult to assign causation to the observed response; however, by comparing the response of herpetofaunas from different studies and different tropical regions to similar classes of disturbance (*e.g.,* selective logging, clearing, and conversion to plantations), it may be possible to detect general trends that hold under a variety of conditions.

Several common patterns emerge from studies in tropical America and southeast Asia. Miyata (1980), Lieberman (1986), Heinen (1992), and Inger (1980b) all observed increased herpetofaunal abundance or density in tree plantations relative to undisturbed forests. Similarly, Inger (1980b) found increased herpetofaunal abundance in logged forests relative to undisturbed forest. The results from this study are consistent with Inger's (1980b) observations: herpetofaunal densities were lowest in the unlogged site and highest in the logged and plantation sites. In this study, species richness was also greater in both of the disturbed sites. Two recent studies have reported a similar response in richness to selective logging (Pearman 1997, Lemckert 1999). Miyata (1980) observed a similar pattern when comparing forest to cacao plantation sites, but Heinen (1992) observed higher richness in primary forest. At Kibale, diversity was greatest in the pine plantation, followed by the logged, then unlogged forests. Diversity indices, however, failed to reveal important differences in species composition among the three areas in this study. Similarity indices revealed that although the pine plantation was not dramatically different in species richness or abundance, the fauna of this area was distinct from those of the two native forest areas. The seasonally drier pine plantation fauna was dominated by the direct-developing frog *S. schubotzi* and the *Cnemaspis* gecko, which were rare or absent from the other sites. The amphibians that were most abundant in the native forests have aquatic reproductive strategies and thus may be less common in the pine plantation, in part because the pines lie along a low ridge several hundred meters from any aquatic habitats.

Regional comparisons.—This is only the second study to provide richness and density data for a tropical African litter herpetofauna, and the first from a mid-elevation forest. With this new information, some of the patterns observed previously in comparisons of lowland and mid-elevation, and Old and New World litter herpetofaunas can be reexamined (Scott 1976, Inger 1980a, May 1980). These earlier studies reported that species richness decreased and abundance increased with elevation and that Old World and New World lowland litter herpetofaunas had similar species richness; however, densities in the New World studies were an order of magnitude greater than those in Old World forests. In addition, Old World litter herpetofaunas were predominantly comprised of lizards, while American faunas were dominated by amphibians.

Species richness of the regular leaf-litter herpetofauna (*sensu* Scott 1976) from mid-elevation sites averaged 15.2 (N = 6) species and ranged from 15 to 27 species in Central America (Scott 1976, Fauth *et al.* 1989), 14 species in Africa (this study), 14 species in South America (Giaretta *et al.* 1999), and 4 to 12 species in southeast Asia (Brown & Alcala 1961). The lowland sites reviewed by Allmon (1991) had higher average species richness ($\bar{x}$ = 19.4, N = 11) than the mid-elevation sites reviewed here, but showed similar variation (range: 13–26). Thus, preliminary evidence suggests similar heterogeneity in species richness between mid-elevation and lowland sites and supports earlier observations that mid-elevation sites tend to support fewer species (Scott 1976, Fauth *et al.* 1989).

Lowland litter herpetofaunal densities estimates (animals/100 m^2) reported in Allmon (1991) were highest in Central American sites ($\bar{x}$ = 16.4, N = 14), followed by Africa ($\bar{x}$ = 9.4, N = 1), South America ($\bar{x}$ = 7.2, N = 5) and southeast Asia ($\bar{x}$ = 1.64, N = 3). Estimates from mid-elevation tropical forests were also highest in Central America (58.7 and 15 animals/100 m^2), followed by southeast Asia (5–15), South America (4.6), and Africa (1.6). Across all sites, lowland forests had lower litter herpetofaunal densities ($\bar{x}$ = 8.7, N = 14) compared to mid-elevation sites $\bar{x}$ = 15.2, N = 6), but this trend was due in large part to the high densities observed at San Vito, Costa Rica (Scott 1976). Excluding this site, average litter herpetofaunal densities were slightly lower in mid-elevation forests ($\bar{x}$ = 6.6, N = 5). Considering only the two African sites, litter herpetofaunal densities were much higher in the lowland sites studied by Scott (1982) in Cameroon (9.4 animals/100 m^2) than in the undisturbed mid-elevation forest at Kibale (1.6 animals/100 m^2).

The relative proportion of amphibians and lizards at Kibale is not consistent with expectations for the Old World, based on observations in southeast Asian forests. In southeast Asian forests, the litter herpetofauna was predominantly comprised of lizards, while amphibians dominated in Kibale. The proportion of lizard species in the Kibale fauna (32%) was similar to that reported for Costa Rica (La Selva 26%; Osa 31%; Scott 1976) and Cameroon (32%; Scott 1982), but lower than reported for Borneo (47%; Lloyd *et al.* 1968); however, lizard densities in the native forest sites were much lower than any previously reported for any tropical rain forest site. In Kibale, only two individuals were captured in 200 plots (0.0004 individuals/100 m^2), while densities from other tropical sites using similar sampling methods ranged from 0.25 individuals/100 m^2 in Borneo (Inger 1980a) to 15.4 individuals/100 m^2 in Silugandi, Panama (Heatwole & Sexton 1966). Lizards were also notably absent from the litter fauna studied by Scott (1982) in Cameroon. Scott (1976, 1982) suggested that, because of their ability to reproduce by direct development in terrestrial habitats, frogs of the genera *Eleutherodactylus* and *Arthroleptis* were ecological replacements for small lizards in the American and African forests. This, however, does not seem to account for the absence of lizards in Kibale, since direct-developing anurans were rare in native forest.

In summary, Kibale supports herpetofaunal diversity similar to other mid-elevation tropical forests, but at very low densities. Litter herpetofaunal abundance varied seasonally, and topography and moisture appear to be two of the most important habitat characteristics in predicting the herpetofaunal presence or absence. In addition, this and previous studies suggest that human disturbances may have lasting effects on herpetofaunal assemblage composition and abundance. This is the first study to describe and provide densities for a Central or East African leaf-litter herpetofauna. Given recent concerns about global amphibian declines (Houlahan *et al.* 2000), this provides valuable baseline data from a poorly studied region of the tropics.

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