

Herpetofaunal Diversity and Abundance in Tropical Upland Forests of Cameroon and Panama¹

Ulrich Hofer²

Department of Vertebrates, Natural History Museum, Bernastrasse 15, 3005 Berne, Switzerland

and

Louis-Félix Bersier

Zoological Institute, University of Neuchâtel, rue Emile-Argand 11, 2007 Neuchâtel, Switzerland

ABSTRACT

Two tropical upland forests, Mount Kupe in Cameroon and Bosque Protector Palo Seco in Panama, were compared in terms of herpetofaunal species richness and density of individuals. Based on rarefaction, whereby samples are standardized for abundance, Palo Seco had significantly more species of frogs and lizards. Extrapolations to total local species richness, by fitting the Michaelis–Menten equation to the species accumulation curves and by using Chao's estimator, yielded divergent results: more lizard species on Mount Kupe, and an equal number of frogs at both sites. These disparities can be accounted for by differences in evenness, which was higher in Palo Seco. Frog density was significantly higher on Mount Kupe, snake density significantly higher in Palo Seco, and lizards exhibited no density difference. Overall, the results revealed a less consistent pattern and more moderate differences than what is known from southeast Asian–Central American comparisons. This outcome is discussed in the light of available knowledge, but quantitative data from African forests are too sparse to allow general conclusions.

RESUMEN

Se comparó la herpetofauna de dos bosques tropicales húmedos ubicados en las montañas, Mount Kupe en Camerún y Bosque Protector Palo Seco en Panamá, en relación a la riqueza específica y la densidad de individuos. Con base en el método de rarefacción, en el cual los muestreos se estandarizan en base a su abundancia, Palo Seco presenta significativamente más especies de anuros y lagartos. Extrapolaciones con respecto a la riqueza específica total de los sitios, mediante un ajuste de la ecuación de Michaelis–Menten a las curvas de acumulación de especies, y utilizando el índice de Chao, produjeron resultados divergentes: más especies de lagartos en Mount Kupe, y el mismo número de especies de anuros en ambos sitios. Dichas diferencias pueden resultar de una equitatividad más alta en Palo Seco. La densidad de anuros resultó significativamente más alta en Mount Kupe, mientras que la densidad de serpientes fue significativamente más alta en Palo Seco, y no se encontró una diferencia entre la densidad de lagartos en ambos sitios. En general los resultados muestran patrones menos consistentes y diferencias más moderadas de las que se conocen entre el Sureste de Asia y Centroamérica. Se discuten los resultados con base en la información disponible, sin embargo, la existencia de datos cuantitativos para bosques africanos es demasiado escasa como para permitir conclusiones generales.

Key words: Amphibia; Cameroon; density; evenness; Panama; Reptilia; species richness; tropical wet forest.

COMPARING SAMPLES OF AMPHIBIANS AND REPTILES from Neotropical and southeast Asian lowland rain forests revealed that both diversity and density are higher in the Neotropics. Samples usually encompassed the leaf litter zone or a single type of microhabitat. Heyer and Berven (1973) and Voris (1977) analyzed the tree buttress microhabitat and based their comparisons on average species diversity per individual, thus incorporating both species richness and evenness. Diversity of amphibians and

reptiles found on tree buttresses was higher in the Neotropical collection and the authors concluded that overall herpetofaunal diversity in a given rain forest largely determines the diversity associated with a particular microhabitat. Scott (1976) and Inger (1980a) compared the densities of non-riparian leaf litter herpetofaunas. Standardized to the number of individuals per 100 m², Central American lowland forest densities were about an order of magnitude higher than in Indo-Malayan ones, a result supported by further data from Central American sites (Toft 1980, Lieberman 1986, Fauth *et al.* 1989). Scott (1976) also included upland sites and found densities of Costa Rican leaf litter her-

¹ Received 19 February 1999; revision accepted 9 November 1999.

² Corresponding author: E-mail: Ueli.Hofer@cscf.unine.ch

petofaunas almost six times higher than those reported by Brown and Alcalá (1961) for the same elevations on Cuernos de Negros, Philippine islands. Scott (1976) attributed these differences to greater litterfall and faster decomposition rates in Neotropical forests. Finding no such difference in ecosystem function, Inger (1980a) suggested that population levels in the Indo-Malayan forests are kept below those achieved in Neotropical forests primarily by a reduced food supply. The latter would result from the synchronized mast fruiting of the dipterocarp trees dominating these forests, which reduces the number of seed-eating insects and associated arthropod predators on the forest floor. In a brief review of the topic, May (1980) favored Inger's explanation, but emphasized the need for a confirmation of the postulated arthropod density differences.

While the cited studies revealed consistent differences between Central America and southeast Asia in diversity and density of lowland forest amphibians and reptiles, Afrotropical herpetofaunas remained virtually excluded from such comparisons, as data sets equivalent to those from the other two continents were scarce. Scott (1982) presented the first inter-site comparison, based on a sample of 15 forest litter plots and 66 person-hours of collecting effort in a Cameroonian lowland forest on white-sand soil. The herpetofaunal species richness in the African leaf litter samples was about half that found in equivalent-sized samples from lowland forests of Borneo and Costa Rica (Scott 1982). Densities of individuals were *ca* 60 percent of those found in Central America, but six times the densities on Borneo. Using simple life history data on habitat, activity period, breeding site, and size class, Lawson (1992) assessed the similarity in ecological structure of the herpetofaunal assemblages of Korup, Cameroon, and Santa Cecilia, Ecuador. Frogs exhibited little overlap in distribution among life history types, a finding attributed to differences in types of breeding sites available; squamates showed such a dissimilarity, although they were ecologically more diverse in Korup. The two sites had similar species numbers, but this comparison was not standardized for area or effort. On a broad level, Duellman (1993) and Bauer (1993) provided comprehensive comparisons of the amphibian and reptile faunas of Africa and South America. Standardized to a 10⁶-km² scale, amphibian species density in montane rain forests of South America was 1.7 times that of Africa, while for lowland forests, density in Africa was 1.2 times that of South America (Duellman 1993). For reptiles, Bauer (1993) com-

pared continent-wide totals of taxa and country by country summaries for the major groups, but did not include standardizations for area and vegetation types.

In this paper, we compare local species richness, evenness, and density of amphibians and reptiles in an Afrotropical and a Central American upland forest. We use two original data sets obtained by the same sampling method from Mount Kupe in Cameroon, and from Bosque Protector Palo Seco in western Panama. As Voris (1977) has pointed out, comparisons of diversity between sites often are biased by unresolved differences in the length of the collecting period, the number of major habitats sampled, and the size of the area censused, thus affecting sample sizes and total numbers of species. We accounted for these concerns by adjusting both data sets in a way that total sampling effort, forest type, elevational range, and season were comparable.

METHODS

STUDY SITES.—Mount Kupe (4°45'N) in the southwest province of Cameroon, is a steep-sided, cone-shaped mountain 2064 m in height and situated *ca* 100 km northeast of Mount Cameroon. It forms part of the Cameroon Highlands, an extensive volcanic mountain range in western Cameroon, running from Mount Cameroon in the southwest tip of the country (*ca* 500 km toward the northeast to the Bamenda and Adamawa Highlands). At the time of the sampling, the upper slopes of the mountain (between 900 m and the summit) were covered by *ca* 2100 ha of undisturbed closed canopy submontane forest, characterized by a fairly uniform structure with a sparse ground layer and a thin understory. Below 900 m, the forest has been logged or severely degraded except for a few patches on the southwestern and southern slopes. In the primary forest, we found permanent streams between 900 and 1500 m and at 1900 m. The single standing body of water found within the primary forest was a puddle on a log in a treefall. Mount Kupe receives a mean annual rainfall of 4891 mm (Suchel 1972), with monthly precipitation never < 70 mm. The rainy season lasts for seven months (April–October).

The Bosque Protector Palo Seco (8°47'N) in Bocas del Toro province of Panama, is situated on the Caribbean slope of the Cordillera Central. It is a vast area of primary forest extending vertically from the lowlands up to the continental divide, with ridgetops and peaks at *ca* 1400 to 2200 m.

TABLE 1. *Sampling characteristics in two tropical upland forests: Bosque Protector Palo Seco, Panama, and Mount Kupe, Cameroon.*

	Palo Seco, Panama	Mount Kupe, Cameroon
Elevational range (m)	800–1600	900–1700
Total transect length (m)	2610	2820
Number of sampling bouts	32	56
Person-hours of sampling	9.8 h/bout	3.8 h/bout
Number of days	935	35
Start day	4 May 1998	9 May 1994

Horizontally, Palo Seco extends from the main road that crosses the divide and links the two provinces of Chiriquí and Bocas del Toro farther west to Costa Rica.

Despite the status of a protected forest, human impact is increasing, with pastures along the valley bottoms and plantations on the adjacent slopes. Estimated from regional climate maps (Instituto Geográfico Nacional Tommy Guardia 1988), Bocas del Toro province receives an annual rainfall from *ca* 3000 mm in the lowlands to 5000 mm at higher elevations. Other than on the Pacific slope, rainfall is abundant throughout the year, and without a pronounced dry season. We found permanent streams at all elevations sampled, whereas puddles along an unpaved road outside the forest were the only standing water located. As on Mount Kupe, most stream bottoms are bedrock, with moderate to steep gradients, rapids, and splash zones. Most herpetological work in western Panama has focused on the Pacific side and the vicinity of Reserva La Fortuna, but the Palo Seco area has received little attention from herpetologists.

DATA ACQUISITION.—At both sites, the sampling method adopted was “cruise collecting”; (*i.e.*, three to five people walked slowly along a transect, moving floor debris, turning logs and stones, ripping apart rotten wood, digging soil in the root system of big trees and under logs, and inspecting the herb and shrub layer up to *ca* 10 m; Inger & Colwell 1977). In riparian zones, the streambed also was examined. The data on Mount Kupe were acquired between March and November 1994, in the primary forest on the western slope of the mountain between 900 m and the summit; procedures are outlined in more detail in Hofer *et al.* (1999). Data in the Palo Seco area were acquired between April and June 1998. Fieldwork was restricted to the primary forest between 800 and 1600 m elevation at the eastern edge of the forest reserve. The transect samples were taken along 430 m of a trail maintained by workers from the Instituto de Recursos

Hidráulicos y Electrificación and by the local citizens, along 1360 m of trails opened by our field crew and along 820 m of streambanks. Basic information on sampling at both study sites is summarized in Table 1.

On Mount Kupe, animals we did not collect as vouchers were marked and released at the end of each sampling bout, and recaptured animals were excluded from all analyses. The abundance data of two chameleon species we failed to mark reliably were retained in the data set. The mean recapture rate of all species reliably marked was 2.75 percent. Due to a drastic decline in amphibian populations in Costa Rica and adjacent western Panama (see Discussion), our research permits restricted collecting efforts to the minimum number of individuals necessary for accurate species identification, and banned marking of individuals. For the latter reason, the abundance of some species may be overestimated. Assuming a similar mean recapture rate as on Mount Kupe, this sampling error would be five individuals. Voucher specimens from the two sites were deposited at the Natural History Museum of Berne, the Alexander Koenig Zoological Research Institute and Zoological Museum in Bonn, and in the collections of the Mount Kupe Forest Project, Nyasoso, Cameroon, and those of the *Círculo Herpetológico de Panamá*.

ANALYSIS.—Customarily, tropical herpetofaunas have been compared on the basis of species richness, evenness, density, and dominance. We restricted our analyses to the first three measures, and as suggested by Gotelli and Graves (1996), used indices that had a probabilistic basis and tended to be unbiased by sample size. First, we applied an interpolation procedure: species richness of the two samples was compared by rarefaction (Sanders 1968, Hurlbert 1971, Simberloff 1972), whereby samples were standardized for abundance. Second, we extrapolated to total species richness by fitting a Michaelis–Menten equation (Raaijmakers 1987) to the species accumulation curves, and by com-

puting Chao's (1984) nonparametric estimator. As an evenness measure, we computed Hurlbert's (1971) probability of an interspecific encounter. Means and standard errors of this index were estimated by a bootstrap procedure with 1000 iterations (Efron & Tibshirani 1993). Due to the small number of snakes obtained on Mount Kupe, we excluded the snakes from all estimates of species richness.

As a consequence of the field methods chosen, two properties of the data set had to be accounted for. First, because trails were searched repeatedly in the course of sampling both sites, trails could not be treated as an equivalent to leaf litter plots of previous studies (*e.g.*, Inger & Colwell 1977, Scott 1982, Lieberman 1986). We therefore used samples standardized by time effort to calculate animal densities (number of frogs, lizards, or snakes encountered per person-hour of sampling). For each sampling bout, we computed the time-based density; from these densities, means and standard errors were estimated for both sites. Second, samples based on cruise collecting encompassed a wider array of species than litter plots and usually included taxa associated chiefly with microhabitats above the forest floor. We therefore split three taxonomic groups (frogs, lizards, and snakes) into an "arbo-real" (species known to feed in vegetation) and a "terrestrial" subset, and again computed the parameters for these six categories. Because such splitting led to very small sample sizes for some subsets, we do not present the results in tabular form, but refer to them in the Discussion.

We accounted for differences between sites and sampling efforts in two ways. First, we restricted the analysis to data acquired within primary forest (including riparian habitats). Furthermore, we adjusted the elevational range and the lengths of sampling periods by reducing the larger sample (Mount Kupe). This resulted in data sets accumulated over the same number of days starting with the onset of the rainy season. Thus, our density and local species richness estimates were based on data sets obtained by the same methodology from comparable forest types, elevational ranges, and seasons. Second, differences in sampling effort (Table 1) were further taken into account by using rarefaction methods.

For the extrapolations that predicted the total regional species richness, we left the elevational ranges adjusted, but used all data available for the entire collecting period at both sites. We based the accumulation curves on a similar number of sampling bouts (some chronologically adjacent sam-

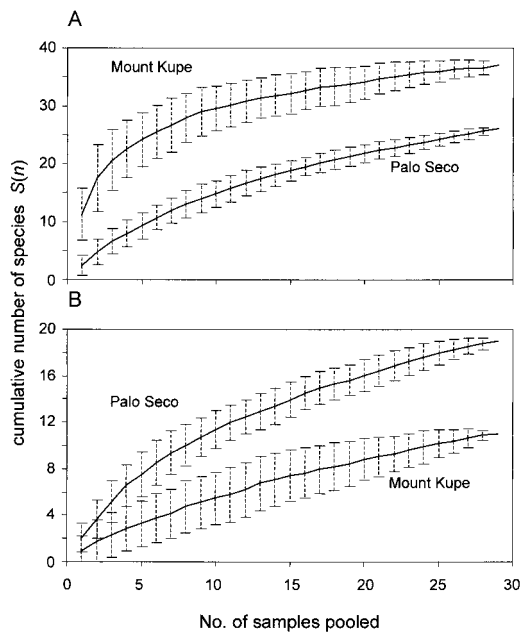


FIGURE 1. Species accumulation curves for (a) frogs and (b) lizards. Due to small sample sizes, no curves were drawn for the snakes. Error bars indicate ± 1 SD.

pling bouts were pooled). We followed Colwell and Coddington's (1994) procedure to generate species accumulation curves, performing 100 randomizations of the order of sample bouts. The Michaelis–Menten equation was fitted directly by use of a nonlinear regression module in the SPSS package (SPSS 1990). We used the sum of absolute values of the residuals as the loss function, to avoid giving too much weight to outliers. Confidence intervals of Michaelis–Menten parameters were computed by a bootstrap procedure included in SPSS (1990).

RESULTS

The species list from Palo Seco is given in the Appendix, the corresponding data from Mount Kupe are published in Hofer *et al.* (1999). Rarefaction of such data entails several assumptions (Gotelli & Graves 1996). First, the communities compared must be taxonomically similar, come from similar habitats, and be sampled with similar techniques, concerns we accounted for as explained previously. Second, sample size must be sufficient to correctly characterize the parent distribution. From inspection of the species accumulation curves (Fig. 1), the frog and lizard sample sizes appear adequate. Finally, the spatial distribution of individuals must

TABLE 2. Results of the runs tests (Zar 1974) performed to evaluate clumping of conspecifics within sampling bouts. For both sites, frogs and lizards were analyzed separately for four bouts selected at random from those that contained >7 specimens.

		Number of runs			P
		Ob-	Expected		
	Bout	served			
Frogs	Mount Kupe	1	7	5.99	0.93
		2	18	19.67	0.15
	Palo Seco	3	8	8.44	0.33
		4	10	8.66	0.85
Lizards	Mount Kupe	1	7	7.42	0.37
		2	7	6.93	0.51
		3	5	5.83	0.19
		4	9	9.17	0.42
	Palo Seco	1	9	8.35	0.69
		2	7	6.89	0.53
		3	5	5.80	0.21
		4	8	6.50	0.92
Lizards	Palo Seco	1	8	6.50	0.92
		2	12	11.30	0.68
		3	8	7.79	0.56
		4	6	5.27	0.75

be random. In the context of an elevational gradient, this assumption is likely to have been violated to some extent, since many species exhibited gaussian-like abundance curves along the gradient; however, the rarefaction model is mostly affected by clumped distributions of conspecifics (Simberloff 1986). We controlled statistically for this property by a runs test (Zar 1974), performed at each site on a random selection of four sampling bouts with > 7 individuals. The tests were run separately for frogs and lizards. The power of the tests was evaluated to ascertain that rejection of H₀ was not due to small sample size, which resulted in the elimination of one sampling bout for the frogs at Palo Seco. We found no indication of clumping of conspecifics (Table 2). The fitting of a Michaelis–Menten equation to the species accumulation curves assumes homogeneity of the habitat. The homogeneity can be assessed by comparing the empirical species accumulation curves to those obtained by a random assignment of individuals to sampling bouts (Colwell & Coddington 1994). In a homogeneous habitat, the empirical curves will fit the theoretical ones; in a heterogeneous one, they will lie below. We found no strong departure from the assumption of homogeneity, the empirical curves lying at most 1.95 SDs below the theoretical ones (Table 3).

Based on equal sample sizes, Palo Seco exhibited a significantly higher richness in frog and lizard

TABLE 3. Distances between empirical species accumulation curves and those obtained by 100 random assignments of individuals to sampling bouts. Distances are expressed in units of SD (N = 100). The higher the value, the stronger the departure from the homogeneity of the habitat.

		Distance in SD units	
		\bar{x}	Maximum
Frogs	Mount Kupe	0.45	0.63
	Palo Seco	0.16	0.33
Lizards	Mount Kupe	0.77	1.46
	Palo Seco	1.33	1.95

species than Mount Kupe (Fig. 2). The two extrapolation methods yielded divergent estimates of local species richness, especially for frogs, but variance around these estimates was large (Table 4). Despite their differences, the species accumulation curves (Fig. 1) produced similar estimates to those of the Michaelis–Menten equation, except for the number of lizard species which was higher on Mount Kupe (Table 4). With the Chao estimator, differences between the two sites were accentuated: however, based on nonoverlapping 95 percent confidence intervals, the higher number of lizard species on Mount Kupe was the only significant dif-

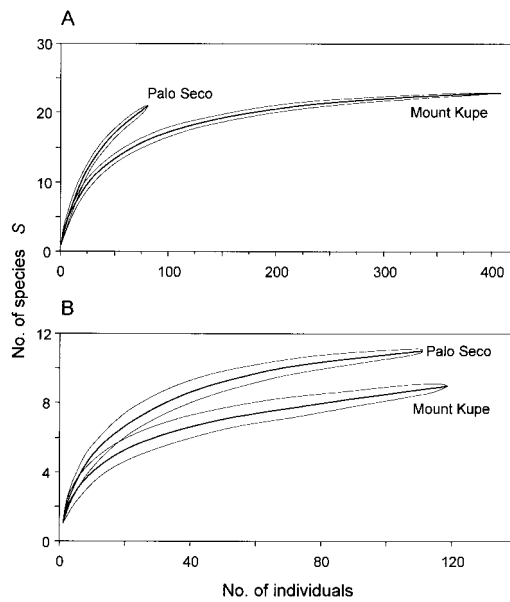


FIGURE 2. Rarefaction curves for (a) frogs and (b) lizards. Due to small sample sizes, no curves were drawn for the snakes. Envelopes indicate the 95 percent confidence limits.

TABLE 4. Diversity and density parameters in two tropical upland forests. Expected species richness for equal sample sizes was estimated by rarefaction; the sizes of the smaller samples are given in parentheses. The number of species at both sites was extrapolated by fitting the Michaelis–Menten equation, and by computing Chao's (1984) estimator. Evenness is expressed as the probability of an interspecific encounter. Densities refer to numbers of individuals per person-hour of sampling. When appropriate, the 95 percent confidence intervals (ci) are added. Asterisks (*) indicate significant differences between Panama and Cameroon ($P \leq 0.05$). Due to small sample sizes, snakes were omitted from all species richness estimates.

	Palo Seco, Panama		Mount Kupe, Cameroon	
Observed number of species				
Frogs	21		23	
Lizards	11		9	
Snakes	13		3	
	Estimate	95% ci	Estimate	95% ci
Species richness based on rarefaction				
Frogs ($N = 82$)	21	—*	16.1	15.4–16.7
Lizards ($N = 111$)	11	—*	8.8	8.5–9.1
Species richness extrapolated				
(a) Fitted Michaelis–Menten equation				
Frogs	38.1	37.6–38.6	37.7	37.0–38.4
Lizards	13.6	13.4–13.8*	16.6	16.4–16.8
(b) Chao's (1984) estimator				
Frogs	53.3	41.5–65.0	44.0	40.2–47.8
Lizards	13.0	10.8–15.2*	19.5	15.9–23.1
Probability of an interspecific encounter				
Frogs	0.85	0.80–0.91	0.79	0.75–0.81
Lizards	0.77	0.71–0.82	0.65	0.57–0.73
Density of individuals (N /sampling hour)				
Frogs	0.25	0.16–0.35	2.33	1.65–3.00
Lizards	0.35	0.23–0.47	0.57	0.36–0.77
Snakes	0.14	0.08–0.20*	0.02	0.00–0.04

ference. The probability of an interspecific encounter among frogs and lizards was higher in Palo Seco. Although the differences were not significant, the 95 percent confidence intervals overlapped only marginally, particularly for lizards (Table 4). Standardized to the number of specimens encountered per person-hour of sampling, there was no difference in lizard density (t -test, two-tailed; $P = 0.14$); however, frog density was nine times higher on Mount Kupe (t -test, two-tailed; $P < 0.0001$), and snake density seven times higher in the Palo Seco forest (t -test, two-tailed; $P < 0.0001$).

DISCUSSION

AMPHIBIAN DECLINE IN CENTRAL AMERICA.—Because no quantitative data are available for the Palo Seco area prior to an amphibian decline reported for Costa Rica and adjacent Panama (Lips 1998, 1999), the effect of this recent disturbance on the abundance and species richness of amphibians and reptiles observed today is unknown; however, the watershed of the Río Chiriquí on the Pacific side of Panama, where Lips (1999) found a sudden and massive decline in anuran abundance and diversity in late 1996, is separated only by a narrow ridge from the

nearest watercourse of the Palo Seco area, hardly sufficient to prevent spreading of the suspected fungal pathogen to the adjacent Atlantic side. Furthermore, our frog density estimates were as low as those found by Lips (1999) after the decline. We therefore consider it probable that the phenomenon also affected frog populations in Palo Seco, accounting for the remarkable difference in density observed between this site and Mount Kupe. The difference is largely attributable to higher numbers of individuals (of species) dwelling on the forest floor (leaf litter and riparian) of Mount Kupe. Effects on species richness and evenness are less comprehensible, because these properties tend to be biased if some species show a particularly strong response to the pathogen. Lips (1998, 1999) found streamside anurans with an aquatic stage to be more affected than other taxa. The density of these species in Palo Seco was 0.05 individuals/person-hour of sampling, while on Mount Kupe it was 0.7.

SPECIES RICHNESS AND EVENNESS.—Standardized for sample size, frog and lizard species numbers were significantly higher in Panama. Frog species richness in the Palo Seco forest was 1.3 times greater than on Mount Kupe, but below the value evalu-

ated by Duellman (1993) on a continent-wide 10^6 -km² scale; in that study, amphibian species density in montane rain forests of South America was 1.7 times that of Africa. Inequalities in seasonality and dry season length, factors invoked to explain differences in species richness between other sites (Inger 1980b, Scott 1982), were presumably of minor importance in our case. High annual rainfall and the lack of a pronounced dry season at both sites should minimize potential effects of climatic properties. The higher species richness in the Palo Seco forest, when standardized for sample size, may result simply from a species–area relationship and an island effect (MacArthur & Wilson 1967). As part of an extended forest range covering the entire Caribbean slope of the Cordillera Central from sea level to ca 2300 m, Palo Seco supports more species than the relatively isolated forest block on Mount Kupe, which is situated in a highland area where ca 50 percent of the anuran species and at least 40 percent of the lizards are endemic. Of the 46 species of amphibians and reptiles endemic to Panama (R. Ibáñez, pers. comm.), 5 amphibian (*Dendrobates speciosus*, *Eleutherodactylus emcelae*, *E. museosus*, *Bolitoglossa minutula*, and *Caecilia volcani*) and 2 lizard species (*Anolis casildae* and *A. exsul*) were found at Palo Seco, along with 5 undescribed taxa that may be endemic to the area.

Estimates of total species richness did not differ between the two sites for frogs, but lizard species are probably more numerous on Mount Kupe. Mount Kupe is situated in an area known for exceptional herpetofaunal diversity. The Cameroon Highlands may exhibit the highest level of herpetofaunal endemism in all of mainland Africa; more than 60 amphibian species are restricted to this region (Jenkins & Hamilton 1992) and a large number of lizard taxa are undescribed. The adjacent Korup National Park is among the most herpetologically diverse areas in the world (Lawson 1992). Due to colonization from two directions (South America and the northwest), however Panama probably has the most diverse herpetofauna in Central America. (R. Ibáñez pers. comm.). Duellman (1993) has explained that the higher amphibian species richness in South America results, in part, because of an influx from Central America of taxa inhabiting humid environments, while no equivalent dispersal has occurred into sub-Saharan Africa.

An intriguing result of our study was the discrepancy between rarefaction and extrapolation estimates for the lizards; interpolation indicated higher species richness for Palo Seco, while both extrapolation methods found the opposite. This inconsis-

tency can be explained by inter-site differences in evenness, differences in the degree of heterogeneity of the habitats, or both. On one hand, the more uneven the distribution of species abundances, the sooner species are eliminated in a rarefaction procedure. On the other hand, given the same species abundance profiles, the more heterogeneous a habitat, the higher the probability of finding new species during the entire sampling period; consequently, the species accumulation curve in a heterogeneous habitat will not attain an asymptote as rapidly as in a homogeneous one. Thus higher estimates of species richness will be produced. We found that Palo Seco exhibited a slightly higher degree of heterogeneity than Mount Kupe; thus, differences in habitat heterogeneity cannot explain the conflicting estimates. More likely, they resulted from a difference in evenness between the two sites, suggested by the higher probability of an interspecific encounter among lizards in Palo Seco (Table 4). This outcome may have reflected divergent community structures, in that the Mount Kupe lizard assemblage was dominated by a few abundant species. It further demonstrates that the use of different estimators of species richness can reveal subtle differences in community organization otherwise easily overlooked.

DENSITY.—The remarkable inequality in snake abundance resulted from a much higher density of arboreal species in Palo Seco. The species most commonly encountered in Panama were the arboreal colubrids *Sibon dimidiatus* and *Imantodes cenchoa*, while on Mount Kupe, the small leaf litter colubrid *Buboma depressiceps* was observed most frequently. The conspicuous difference in relative representation of arboreal and terrestrial taxa in the two snake faunas may have resulted from the lack of a lineage of arboreal gastropod-feeders in the African snake fauna, a niche filled by a group of xenodontine colubrids in the Neotropics (in Palo Seco, represented by the genus *Sibon*). In a qualitative comparison of the equatorial amphibians and reptiles in Africa and South America, Laurent (1973) found several examples of empty niches on both continents. An impact of phylogeny and historical events on contemporary patterns of community organization was also suggested by Cadle and Greene (1993) to explain differences in composition and species richness among Neotropical rain forest snake assemblages.

Murphy *et al.* (1994) compared snake densities from several tropical areas based on catch per day. A lack of detailed information on sampling effort and crew sizes for most sites prevented standardi-

zations to catch per person-day, and the numbers of people involved in sampling undoubtedly accounted in part for observed differences. Despite its inherent inaccuracy, the stet-per-stet measure revealed that Palo Seco and Mount Kupe fell at opposite ends of the range reported by others. The 2.1 encountered in Palo Seco is close to the 2.25 of Dunn's (1949) large snake collection obtained in Panama and greater than the rates from three South American lowland sites: 0.39 snakes/d in Santa Cecilia, Ecuador (Duellman 1978) and Kartabo, Guiana (Beebe 1946), and 0.47 snakes/d in Manaus, Brazil (Zimmerman & Rodriguez 1990). Our encounter rates at Palo Seco also exceed rates from Southeast Asia (0.97 in lowland sites on Borneo [Murphy *et al.* 1994] and Thailand [Inger & Colwell 1977]). With 0.2 snakes/d, Mount Kupe fell at the lower end of this range. Janzen (1976) has suggested that the biomass of African reptiles is depressed by increased predator pressure, a factor that may have contributed to the strikingly low snake density on Mount Kupe.

Unlike the snakes, the lizard faunas at the two sites were similar both in density and in relative representation of arboreal and terrestrial taxa. Frog density was higher on Mount Kupe, but, provided that the current frog density in the Palo Seco forest resulted from a recent disturbance depressing population levels in western Panama, the difference ultimately may become less pronounced.

Together with Scott's (1982) estimates, our results suggest that frog and lizard densities of African forests may be intermediate to Central American and Asian sites, but closer to the former; however, additional quantitative data from African forests are needed to confirm such a trend. The finding of a consistent pattern may stimulate research related to the mast fruiting hypothesis (Inger 1980a).

Our results suggest that there is no simple relationship between species richness and density of individuals. Within the samples at each site, the two parameters showed a significant positive correlation ($r = 0.60$, $P (0.001)$ and $r = 0.85$, $P (0.001)$ for all species at Mount Kupe and Palo Seco, respectively), a result also found by Lieberman (1986) for litter plots at La Selva, Costa Rica. When comparing the two sites, however, the higher

frog species richness at Palo Seco was not coupled with higher frog density, while the higher number of snake species observed at this site was. Attempts to link herpetofaunal density and species richness between sites have led to contradictory conclusions. Scott (1976) has suggested that density and species richness of leaf litter herpetofaunas are inversely correlated. From his Table 1 (p. 43), we found the trend to be strongly affected by a single site (Sarawak, Borneo). Removal of this site resulted in a correlation in the opposite direction, but neither correlation was significant. Fauth *et al.* (1989) found a significantly positive correlation among several Costa Rican sites. Part of the conflicting results may stem from major differences in site characteristics and in overall geographic range covered by the sites compared. Even so, we doubt that species richness and density are linked in a systematic way (Begon *et al.* 1996); instead, they result from different processes in which their relative importance depends strongly on the regions considered, a fact that is difficult to account for in comparisons involving both parameters.

ACKNOWLEDGMENTS

Fieldwork in Cameroon was supported by grants from the Swiss Development Corporation, the Swiss Academy of Sciences, and the Natural History Museum of Berne. The Mount Kupe Forest Project provided logistic help and housing in Nyasoso. E. J. Ebung, E. H. Njume, and N. S. Epie assisted the whole, and C. Wild and I. C. Ojiawum, parts of the fieldwork. C. Wild introduced U. Hofer to the study area. U. Hofer greatly appreciates the support of the Bakossi people stet Nyasoso; in particular, K. E. Epie and E. E. Ewang. J.-L. Amiet, J.-L. Perret, W. Böhme, A. Schmitz, and B. Hughes helped with the identification of the collected specimens. Fieldwork in Panama was supported by the Natural History Museum of Berne. L. Indermaur, M. A. Aguirre, A. Gonzáles, and O. Samudio assisted the data acquisition. R. Ibáñez D. and the Círculo Herpetológico de Panamá helped with the identification of the collected specimens. For logistic support, U. Hofer is indebted to M. A. Aguirre, R. Ibáñez D., N. Gómez, R. Borrell, the Smithsonian Tropical Research Institute, the Instituto de Recursos Naturales y Renovables, and the Instituto de Recursos Hidráulicos y Electrificación. For help and constructive criticism of the manuscript, we thank R. F. Inger, N. J. Scott Jr., R. Ibáñez D., B. Benrey, and an anonymous reviewer. L.-F. Bersier was supported by the Swiss National Science Foundation grant 31-52566.97 and the Novartis Foundation.

LITERATURE CITED

- BAUER, A. M. 1993. African-South American relationships: a perspective from the Reptilia. In P. Goldblatt (Ed.), Biological relationships between Africa and South America, pp. 244-288. 37th Annual Systematics Symposium, St. Louis, Missouri.

- BEEBE, W. 1946. Field notes on the snakes of Kartabo, British Guiana, and Caripito, Venezuela. *Zoologica* 31: 11–51.
- BEGON, M., J. L. HARPER, AND C. R. TOWNSEND. 1996. *Ecology: individuals, populations, and communities*, 3rd edition. Blackwell Scientific, Oxford, England. 1068 pp.
- BROWN, W. C., AND A. C. ALCALA. 1961. Populations of amphibians and reptiles in the submontane and montane forests of Cuernos de Negros, Philippine islands. *Ecology* 42: 628–636.
- CADLE, J. E., AND H. W. GREENE. 1993. Phylogenetic patterns, biogeography, and the ecological structure of Neotropical snake assemblages. In R. E. Ricklefs and D. Schluter (Eds.). *Species diversity in ecological communities. Historical and geographical perspectives*, pp. 281–293. University of Chicago Press, Chicago, Illinois.
- CHAO, A. 1984. Non-parametric estimation of the number of classes in a population. *Scand. J. Stat.* 11: 265–270.
- COLWELL, R. K., AND J. A. CODDINGTON. 1994. Estimating terrestrial biodiversity through extrapolation. *Philosophic Trans. R. Soc. Lond. B* 345: 101–118.
- DUELLMAN, W. E. 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. *Univ. Kansas Misc. Publ.* 65: 1–352.
- . 1993. Amphibians in Africa and South America: evolutionary history and ecological comparisons. In P. Goldblatt (Ed.). *Biological relationships between Africa and South America*, pp. 200–243. 37th Annual Systematics Symposium, St. Louis, Missouri.
- DUNN, E. R. 1949. Relative abundance of some Panamanian snakes. *Ecology* 30: 39–57.
- EFRON, B., AND R. J. TIBSHIRANI. 1993. *An introduction to the bootstrap*. Chapman and Hall, New York, New York. 436 pp.
- FAUTH, J. E., B. I. CROTHER, AND J. B. SLOWINSKI. 1989. Elevation patterns of species richness, evenness, and abundance of the Costa Rican leaf litter herpetofauna. *Biotropica* 21: 178–185.
- GOTELLI, N. J., AND G. R. GRAVES. 1996. *Null models in ecology*. Smithsonian Institution Press, Washington, DC. 368 pp.
- HEYER, W. R., AND K. A. BERVEN. 1973. Species diversities of herpetofaunal samples from similar microhabitats at two tropical sites. *Ecology* 54: 642–645.
- HOFER, U., L.-F. BERSIER, AND D. BORCARD. 1999. Spatial organization of a herpetofauna on an elevational gradient revealed by null model tests. *Ecology* 80: 976–988.
- HURLBERT, S. H. 1971. The non-concept of species diversity: a critique and alternative parameters. *Ecology* 52: 577–586.
- INGER, R. F. 1980a. Densities of floor-dwelling frogs and lizards in lowland forests of southeast Asia and Central America. *Am. Nat.* 115: 761–770.
- . 1980b. Relative abundances of frogs and lizards in forests of southeast Asia. *Biotropica* 12: 14–22.
- , AND R. K. COLWELL. 1977. Organization of contiguous communities of amphibians and reptiles in Thailand. *Ecol. Monogr.* 47: 229–253.
- INSTITUTO GEOGRAFICO NACIONAL TOMMY GUARDIA. 1988. *Atlas Nacional de la Republica de Panama*. Instituto Geografico Nacional Tommy Guardia City, Panama. 222 pp.
- JANZEN, D. H. 1976. The depression of reptile biomass by large herbivores. *Am. Nat.* 110: 371–400.
- JENKINS, M., AND A. HAMILTON. 1992. Biological diversity. In J. A. Sayer, C. S. Harcourt, and N. M. Collins (Eds.). *The conservation atlas of tropical forests: Africa*, pp. 26–32. Macmillan, London, England.
- LAURENT, R. F. 1973. A parallel survey of equatorial amphibians and reptiles in Africa and South America. In B. J. Meggers, E. S. Ayensu, and W. D. Duckworth (Eds.). *Tropical forest ecosystems in Africa and South America: a comparative review*, pp. 259–266. Smithsonian Institution Press, Washington, DC.
- LAWSON, D. P. 1992. The herpetofauna of Korup National Park, Cameroon: biogeography and comparative biodiversity of a tropical African rainforest. M.S. thesis, University of Texas, Arlington, Texas.
- LIEBERMAN, S. S. 1986. Ecology of the leaf litter herpetofauna of a Neotropical rain forest: La Selva, Costa Rica. *Acta Zool. Mex. (N.S.)* 15: 1–71.
- LIPS, K. 1998. Decline of a tropical montane amphibian fauna. *Conserv. Biol.* 12: 106–117.
- . 1999. Mass mortality and population declines of anurans at an upland site in western Panama. *Conserv. Biol.* 13: 117–125.
- MACARTHUR, R. H., AND E. O. WILSON. 1967. *The theory of island biogeography*. Monographs in population biology. 1. Princeton University Press, Princeton, New Jersey. 216 pp.
- MAY, R. M. 1980. Why are there fewer frogs and lizards in southeast Asia than in Central America? *Nature* 287: 105.
- MURPHY, J. C., H. K. VORIS, AND D. R. KARNS. 1994. A field guide and key to the snakes of the Danum Valley, a Bornean tropical forest ecosystem. *Bull. Chi. Herpetol. Soc.* 29: 133–151.
- RAAIJMAKERS, J. G. W. 1987. Statistical analysis of the Michaelis–Menten equation. *Biometrics* 43: 793–803.
- SANDERS, H. L. 1968. Marine benthic diversity: a comparative study. *Am. Nat.* 102: 243–282.
- SCOTT, N. J., JR. 1976. The abundance and diversity of the herpetofaunas of tropical forest litter. *Biotropica* 8: 41–58.
- . 1982. The herpetofauna of forest litter plots from Cameroon, Africa. In N. J. Scott Jr. (Ed.). *Herpetological communities*, pp. 145–150. A symposium of the Society for the Study of Amphibians and Reptiles and the Herpetologists' League, August 1977. Wildlife Research Report 13. U.S. Fish and Wildlife Service, City, State.
- SIMBERLOFF, D. 1972. Properties of the rarefaction diversity measurement. *Am. Nat.* 106: 414–418.
- . 1986. Are we on the verge of a mass extinction in tropical rain forests? In D. K. Elliott (Ed.). *Dynamics of extinction*, pp. 165–180. John Wiley and Sons, New York, New York.
- SPSS. 1990. *SPSS advanced statistics 7.5*. SPSS Corporation, Chicago, Illinois. 579 pp.
- SUCHEL, J. B. 1972. La répartition des pluies et les régimes pluviométriques du Cameroun. *Travaux et Documents de*

- Géographie Tropicale, Centre d'Etude de Géographie Tropicale—Centre National de la Recherche Scientifique 5: 1–287.
- TOFT, C. A. 1980. Seasonal variation in populations of Panamanian litter frogs and their prey: a comparison of wetter and drier sites. *Oecologia* 47: 34–38.
- VORIS, H. K. 1977. Comparison of herpetofaunal diversity in tree buttresses of evergreen tropical forests. *Herpetologica* 33: 375–380.
- ZAR, J. H. 1974. *Biostatistical analysis*, 3rd edition. Prentice-Hall, Upper Saddle River, New Jersey. 662 pp.
- ZIMMERMAN, B. L., AND M. T. RODRIGUES. 1990. Frogs, snakes, and lizards of the INPA-WWF Reserves near Manaus, Brazil. *In* A. H. Gentry (Ed.). *Four Neotropical rainforests*, pp. 426–454. Yale University Press, New Haven, Connecticut.
-

APPENDIX. *Amphibians and reptiles recorded in the Bosque Protector Palo Seco, Bocas del Toro Province, Panama, between 800 and 1600 m, April–June 1998. The abundance figures given are those used for further analyses and refer to the numbers of animals taken during the timed sampling bouts. Taxa with no abundances given were encountered outside sampling bouts, belong to orders not found on Mount Kupe (Plethodontidae and Caeciliidae), or were only found in disturbed habitats (*), and therefore not included in the analyses. Total number of frog, lizard, and snake species was 82, 111, and 44, respectively.*

Amphibia		Reptilia	
Bufonidae		Gekkonidae	
<i>Bufo coniferus*</i>		<i>Lepidoblepharis xanthostigma</i>	4
<i>B. marinus*</i>		Gymnophthalmidae	
Centronelidae		<i>PtychoGLOSSUS plicatus</i>	4
<i>Centrolene prosoblepon</i>	3	Polychrotidae	
<i>Hyalinobatrachium vireovittatum</i>	3	<i>Anolis aquaticus</i>	13
Dendrobatidae		<i>A. biporcatus</i>	5
<i>Colostethus nubicola</i>	1	<i>A. casildae</i>	3
<i>Dendrobates speciosus</i>	2	<i>A. exsul</i>	2
Hylidae		<i>A. humilis</i>	44
<i>Agalychnis spurrelli</i>	3	<i>A. limifrons</i>	9
<i>Hyla debilis</i>	1	<i>A. pachypus</i>	25
<i>H. lancasteri</i>	1	<i>Anolis</i> sp. A	1
<i>H. picadoi</i>	1	<i>Anolis</i> sp. B	1
<i>Smilisca phaeota*</i>			
Leptodactylidae		Colubridae	
<i>Eleutherodactylus bransfordii</i>	4	<i>Amastridium veliferum</i>	1
<i>E. caryophyllaceus</i>	27	<i>Chironius grandisquamis</i>	2
<i>Eleutherodactylus</i> cf. <i>diastema</i>		<i>Colubridae</i> sp. nov.	2
<i>E. crassidigitus</i>	2	<i>Dendrophidion paucicarinatum</i>	
<i>E. cruentus</i>	11	<i>Geophis brachycephalus</i>	1
<i>E. diastema</i>	4	<i>Imantodes cenchoa</i>	11
<i>E. emclae</i>	1	<i>Leptodeira septentrionalis</i>	2
<i>E. fitzingeri</i>	1	<i>Liophis epinephalus</i>	1
<i>E. gollmeri</i>		<i>Sibon argus</i>	3
<i>E. melanostictus</i>	1	<i>S. dimidiatus</i>	17
<i>E. museosus</i>	1	<i>S. nebulatus</i>	2
<i>E. pardalis</i>	6	<i>Urotheca decipiens</i>	1
<i>E. podiciferus</i>	3	<i>U. euryzona</i>	
<i>E. ridens</i>	1	<i>Xenodon rabdocephalus*</i>	
<i>Eleutherodactylus</i> sp. nov.	5	Elapidae	
		<i>Micrurus alleni*</i>	
Plethodontidae		Viperidae	
<i>Bolitoglossa colonnea</i>		<i>Bothriechis lateralis</i>	
<i>B. minutula</i>		<i>Bothrops asper*</i>	
<i>Bolitoglossa</i> sp. nov.		<i>Lachesis stenophrys</i>	1
Caeciliidae			
<i>Caecilia volceni</i>			
<i>Dermophis mexicana</i>			