

The herpetofauna of the cloud forests of Honduras

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Abstract.—The cloud forest amphibians and reptiles constitute the most important herpetofaunal segment in Honduras, due to the prevalence of endemic and Nuclear Middle American-restricted species. This segment, however, is subject to severe environmental threats due to the actions of humans. Of the 334 species of amphibians and reptiles currently known from Honduras, 122 are known to be distributed in cloud forest habitats. Cloud forest habitats are found throughout the mountainous interior of Honduras. They are subject to a Highland Wet climate, which features annual precipitation of >1500 mm and a mean annual temperature of <18°C. Cloud forest vegetation falls into two Holdridge formations, the Lower Montane Wet Forest and Lower Montane Moist Forest. The Lower Montane Wet Forest formation generally occurs at elevations in excess of 1500 m, although it may occur as low as 1300+ m at some localities. The Lower Montane Moist Forest formation generally occurs at 1700+ m elevation. Of the 122 cloud forest species, 18 are salamanders, 38 are anurans, 27 are lizards, and 39 are snakes. Ninety-eight of these 122 species are distributed in the Lower Montane Wet Forest formation and 45 in the Lower Montane Moist Forest formation. Twenty species are distributed in both formations. The cloud forest species are distributed among restricted, widespread, and peripheral distributional categories. The restricted species range as a group in elevation from 1340 to 2700 m, the species that are widespread in at least one of the two cloud forest formations range as a group from sea level to 2744 m, and the peripheral species range as a group from sea level to 1980 m. The 122 cloud forest species exemplify ten broad distributional patterns ranging from species whose northern and southern range termini are in the United States (or Canada) and South America, respectively, to those species that are endemic to Honduras. The largest segment of the herpetofauna falls into the endemic category, with the next largest segment being restricted in distribution to Nuclear Middle America, but not endemic to Honduras. Cloud forest species are distributed among eight ecoregions, with the largest number being found in the Northwestern Highlands, followed by the North-Central Highlands and the Southwestern Highlands. The greatest significance of the Honduran herpetofauna lies in its 125 species that are either Honduran endemics or otherwise Nuclear Middle American-restricted species, of which 83 are distributed in the country's cloud forests. This segment of the herpetofauna is seriously endangered as a consequence of exponentially increasing habitat destruction resulting from deforestation, even given the existence of several biotic reserves established in cloud forest. Other, less clearly evident environmental factors also appear to be implicated. As a consequence, slightly over half of these 83 species (50.6%) have populations that are in decline or that have disappeared from Honduran cloud forests. These species possess biological, conservational, and economic significance, all of which appear in danger of being lost.

Resumen.—Los anfibios y reptiles de los bosques nublados constituyen el segmento más importante de la herpetofauna de Honduras, debido a la prevalencia de especies endémicas y restringidas a la Mesoamérica Nuclear. Este segmento, sin embargo, está sometido a fuertes amenazas medioambientales debido a acciones humanas. De las 334 especies de anfibios y reptiles que se conocen en Honduras en el presente, 122 se conocen que están distribuidas en las habitaciones de los bosques nublados. Las habitaciones del bosques nublados se encuentran a través de las montañas del interior de Honduras. Ellos están sujetos a un clima lluvioso de tierras altas, el cual tiene una precipitación anual de más de 1500 mm y una temperatura anual promedia de menos de 18 grados centígrados. La vegetación de los bosques nublados cae entre dos formaciones de Holdridge, la de Bosque Lluvioso Montano Bajo y la de Bosque Húmedo Montano Bajo. La formación de Bosque Lluvioso Montano Bajo generalmente ocurre a elevaciones en exceso de 1500 m, aunque puede ocurrir tan bajo como 1300 m en algunas localidades. La formación Bosque Húmedo Montano Bajo generalmente ocurre a 1700 m o más de elevación. De las 122 especies de los bosques nublados, 18 son salamandras, 38 son anuros, 27 son lagartijas y 39 son culebras. Noventa y ocho de estas 122 especies están distribuidas en la formación Bosque Lluvioso Montano Bajo y 45 en la formación Bosque Húmedo Montano Bajo. Viente especies están distribuidas en ambas formaciones. Las especies de los bosques nublados están distribuidas entre categorías distribucionales restringidas, amplias, y periféricas. Las especies restringidas se encuentran como grupo en un rango de elevaciones de los 1340 a los

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2700 m, las especies que tienen una distribución amplia en al menos entre una de las dos formaciones de los bosques nublados como grupo tiene un rango desde el nivel del mar hasta 2744 m, y las especies periféricas como grupo tiene un rango desde el nivel del mar hasta 1980 m. Las 122 especies de los bosques nublados ejemplifican 10 patrones distribucionales amplios con rangos de especies para las cuales los rangos terminales norteño y sureño están en los Estados Unidos (o Canadá) y América del Sur, respectivamente, hasta esas especies que son endémicas de Honduras. El segmento más grande de la herpetofauna cae en la categoría endémica, con el próximo segmento más grande siendo restringido en distribución a la Mesoamérica Nuclear, pero no endémico de Honduras. Las especies de los bosques nublados están distribuidas entre ocho áreas ecofisiográficas, con el grupo más grande encontrándose en las tierras altas hacia el noroeste y seguido por las tierras altas norte-central y las tierras altas del suroeste. La importancia más grande de la herpetofauna hondureña cae en sus 125 especies que son endémicas de Honduras o de otra manera restringidas a la Mesoamérica Nuclear, de las cuales 83 están distribuidos en los bosques nublados del país. Este segmento de la herpetofauna está seriamente amenazado a consecuencia de la destrucción exponencial de sus habitaciones, el cual es el resultado de la destrucción de los bosques, aunque existen varias reservas bióticas establecidas en los bosques nublados. Otros factores medioambientales menos claramente evidentes parecen estar implicados. Como consecuencia, un poco más de la mitad de estas 83 especies (50.6%) tiene poblaciones que están disminuyendo o que han desaparecido de los bosques nublados hondureños. Estas especies poseen significancia biológica, de conservación, y económica, todas las cuales parecen estar en peligro de ser perdidas.

Key words. Cloud forests, Honduras, amphibians, reptiles, herpetofauna

Introduction

After decades of warnings by environmental scientists, population biologists, and demographers (see especially Osborn 1948; Carson 1962; Ehrlich 1968; Meadows et al. 1972), it is becoming increasingly apparent to an enlarging group of people that the Earth is entering a sixth spasm of mass extinction of life, at least comparable to and, perhaps, exceeding in scope the five episodes that have preceded it (Ehrlich and Ehrlich 1981, 1996; E. Wilson 1988, 1992; E. Wilson and Perlman 2000). What has come to be known as biodiversity decline is best documented in areas where the flora and fauna are most completely understood, e.g., the United States, and correspondingly less well understood in the areas of the world supporting the greatest amount of biodiversity—the tropics.

To use as an example the country that has been the focus of our research for more than three decades—Honduras—and the group upon which we have specialized—the herpetofauna, it is evident that the modern study of the Honduran herpetofauna began with the research of John R. Meyer that led to his dissertation, which appeared in 1969. Meyer's (1969) study documented a known herpetofauna of 196 species, including 53 amphibians and 143 reptiles. The current tally is 334 species, including 117 amphibians and 217 reptiles (McCrane and Wilson 2002; Wilson and McCranie 2002). With respect to the total count, there has been an increase of 138 species or 41.3% in the 33 years since 1969 to the present (although Meyer did not include five marine turtles species then known to occur in Honduran waters, nor five species of reptiles known in Honduran territory only from the Swan Islands, which are included in the total count of 334). Meyer (1969) included 35 species in the cloud forest herpetofauna of Honduras, although one species included by him (*Ungaliophis continentalis*) is not so included by us. Presently, we can document the presence of 122 species in one or more cloud forest regions of Honduras. This increase of 88 species (or 72.1% of the total now known) is largely a result of our field work in the

country. Forty-two of these 88 species (47.7%) have been described as new species since 1979. In addition, populations of two species reported from cloud forest by Meyer (1969) have been described as new species (*Ptychohyla spinipollex* and *Ninia lansbergi* cloud forest populations of Meyer equal *P. hypomykter* and *N. espinali*, respectively).

There is still significant mountainous terrain in Honduras supporting cloud forest that has been incompletely sampled herpetofaunally. Such is the case with the Yoro Highlands, the Agalta Highlands, and the Santa Barbara Highlands. Given the frequency with which new taxa have been added to the Honduran cloud forest herpetofauna (2.3 taxa per year since 1972), it can be expected that additional forms await discovery in these yet poorly known ranges.

Acting in contraposition, however, is a more recent trend toward decline of herpetofaunal populations, which has been documented in Honduras by Wilson and McCranie (1998, 2003 a and b) and McCranie and Wilson (2002). This trend has been most evident in regions of the country in excess of 900 m in elevation and has most obviously affected the species composing the most distinctive group, i.e., those that are endemic to Honduras or otherwise restricted in distribution to Nuclear Middle America. Of the 125 species belonging to this group, 52 or 41.6% are considered to have declining populations, to be extinct, or to be extirpated in Honduras. This trend is extremely alarming, given the fact that the 125 species involved do not occur outside of Nuclear Middle America.

In light of the importance of the cloud forest environments of Honduras as centers of herpetodiversity and the accumulating evidence of the decline and disappearance of a significant amount of this diversity, it is the purpose of this paper to update our current understanding of the composition and distribution (both geographic and ecological) of this herpetofauna, to discuss its biodiversity significance, to examine its current conservation status, and to speculate on the future for this segment of the Honduran herpetofauna.

Materials and methods

Fieldwork upon which this paper is based has been conducted by one or both of us since 1968. The material collected has been reported in a number of publications written by one or both of us since 1971 and summarized in Meyer and Wilson (1971, 1973), Wilson and Meyer (1985), and McCranie and Wilson (2002, *in preparation*).

The Coefficient of Biogeographic Resemblance algorithm (Duellman 1990) was used to demonstrate herpetofaunal relationships among the cloud forest ecophysiographic areas examined in this study. The formula is $CBR = 2C/(N_1 + N_2)$, where C is the number of species in common to both formations, N_1 is the number of species in the first formation, and N_2 is the number of species in the second formation.

Physiography

Honduras contains within its borders a major segment of the mountains of Nuclear Middle America (West 1964). Many of the ranges found within the country have portions high enough to support cloud forest (Fig. 1). Descriptions of the physiography of Honduras have appeared in Wilson and Meyer (1985) and McCranie and Wilson (2002), so this description will be limited to only those mountain ranges upon which cloud forest vegetation occurs.

Elevations high enough to support cloud forest are distributed throughout the *Serranía*, the mountainous interior of Honduras, which is a portion of the Nuclear Middle American highlands (Fig. 1). The *Serranía* is traditionally divided into the Northern Cordillera and the Southern Cordillera, the latter distinguishable from the former by an overlay of Pliocene volcanic ejecta deposits (Wilson and Meyer 1985). Both of these cordilleras are interrupted by an irregular graben, called the Honduran depression, traceable from north to south through the Ulúa-Chamelecón Plain, the Valley of Humuya, the Comayagua Plain, and the Valley of Goascorán (Wilson and Meyer 1985). In effect, these physiographic features divide the mountainous interior of Honduras into four sectors, three of which are recognized as ecophysiographic areas on the basis of this division. They are the Northwestern Highlands, the Southwestern Highlands, and the Southeastern Highlands. The fourth sector is significantly larger than any of the other three and is broken into four ecophysiographic areas (see below).

Climate

Savage (2002), in his opus on the amphibians and reptiles of Costa Rica, noted "the term cloud forest is often applied to forests that develop at an altitude where the temperature (6 to 10°C) causes water condensation that produces clouds, fog, and rain. This zone may be at any elevation, and its degree of development is related to the amount of water vapor in the air. Cloud forests usually occur where there are prevailing onshore winds that have their air masses uplifted along ocean-facing mountains. In Central America, cloud forests develop principally on the windward slopes affected by the northeast trade winds. In the Holdridge (1967) system, cloud forests are regarded as atmospheric association within bioclimates that, in Central America, usually develop in the lower portion of the lower montane life zone under the influence of strong pre-

vailing winds. During much of the year these forests receive precipitation in the form of light mists. In the drier seasons, much of the time they are enveloped in dense, dripping fog."

Areas supporting cloud forest in Honduras are generally subject to a Highland Wet climatic regime (Wilson and Meyer 1985). This climatic type is broadly characterized by annual rainfall of >1500 mm and a mean annual temperature of <18°C. The cloud forest regions occurring in the Southern Cordillera generally receive less rainfall than do those in the Northern Cordillera, part of the general effect of the dissipation of moisture in clouds carried by the prevailing winds arising over the Caribbean Sea as they sweep inland.

Climatic data are available for the nuclear zone and the buffer zone of Parque Nacional El Cusuco, a cloud forest reserve in the Sierra de Omoa in northwestern Honduras (Fundación Ecologista "Hector Rodrigo Pastor Fasquelle" 1994). Annual precipitation in the nuclear zone is 2995 mm and in the buffer zone 2580 mm. The雨iest months, in both cases, are October, November, and December, accounting for 45.1% of total rainfall in both zones. The least雨iest months are March, April, and May, when only 12.1% of rainfall occurs in both zones. Monthly temperatures range from 12.9°C in December to 20.2°C in April, with a mean of 16.7°C, in the nuclear zone and from 17.5°C in December to 23.1°C in April, with a mean of 20.6°C, in the buffer zone.

Vegetation

The vegetation of the Honduran cloud forests is referable to two forest formations, as slightly modified from the work of Holdridge (1967), which differ from one another on the basis of the amount of annual precipitation (Wilson and Meyer 1985). The formation characteristic of the cloud forests of the Northern Cordillera is the Lower Montane Wet Forest formation. It is characterized by annual precipitation of >2000 mm. The formation typical of the cloud forests of the Southern Cordillera is the Lower Montane Moist Forest formation. It features an annual precipitation of <2000 mm.

Wilson and McCranie (*in preparation a*) presented information on the vegetation of Parque Nacional El Cusuco (Lower Montane Wet Forest formation), as follows: "Fundación Ecologista 'Hector Rodrigo Pastor Fasquelle' (1994) indicated that this forest formation, called 'Zona de Vida Bosque Muy Húmedo Montano Bajo Sub-Tropical,' is characterized by the presence of three strata. The uppermost stratum consists of a closed canopy of trees attaining heights of 35 to 40 m of the following species: *Quercus* spp.; *Podocarpus oleifolius*; *Clusia massoniana*; and *Liquidambar styraciflua*. The middle stratum is composed of the forgoing species lying in the shade of the taller conspecifics mixed with *Persea vesticula* and *Myrica cerifera*. The lowermost stratum is comprised of seedlings of the species in the middle and uppermost strata intermixed with palms such as *Chamaedorea costaricana* and *C. oblongata*, as well as *Geonoma congesta* and a great variety of ferns. Many epiphytic orchids, bromeliads, and mosses are present, as well as lianas and vines."

Espinal et al. (2001) presented similarly limited data on floristic composition at two sites (at 1570 and 1650 m) in Parque Nacional La Muralla (both in Lower Montane Wet Forest formation), located in the Ocote Highlands of the northwestern portion of the department of Olancho. They stat-

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Table 1. Geographic and ecological distribution, relative abundance, and conservation status of the cloud forest herpetofauna (122 species) of Honduras. Abbreviations include: Formations—LMWF = Lower Montane Wet Forest formation, LMMF = Lower Montane Moist Forest formation; Forest Formation Distribution—W = widespread in that formation, R = restricted to that formation, P = peripherally distributed in that formation; Primary Microhabitat—A = arboreal, T = terrestrial, F = forest inhabitant, P = pondsides inhabitant, S = streamsides inhabitant; Relative Abundance—C = common, I = infrequent, R = rare; Conservation Status—S = stable populations at least at one cloud forest locality, D = all known cloud forest populations declining, E = extinct or extirpated from all known cloud forest localities, N = no data on population status. See text for explanation of Broad Distribution Pattern abbreviations.

Species	LMWF	LMMF	Elevational	Broad	Primary	Relative	Conservation
			Range (m)	Distribution Pattern			
Salamanders (18 species)							
<i>Bolitoglossa carri</i>	—	R	1840-2070	J	A, F, S	C	D
<i>Bolitoglossa celaque</i>	—	R	1900-2620	J	A, T, F, S	C	S
<i>Bolitoglossa conanti</i>	W	W	1370-2000	I	A, F	C	S
<i>Bolitoglossa decora</i>	R	—	1430-1550	J	A, F	C	S
<i>Bolitoglossa diaphora</i>	R	—	1470-2200	J	A, F	I	S
<i>Bolitoglossa dofleinii</i>	P	—	650-1370	I	T, F	I	D
<i>Bolitoglossa Dunnii</i>	W	—	1200-1600	I	A, F	I	S
<i>Bolitoglossa longissima</i>	R	—	1840-2240	J	A, F	C	S
<i>Bolitoglossa porrassorum</i>	W	—	980-1920	J	A, F, S	C	S
<i>Bolitoglossa rufescens</i> complex	P	—	30-1400	I	A, F	C	D
<i>Bolitoglossa synoria</i>	—	R	2150	I	A, S	R	D
<i>Cryptotriton nasalis</i>	W	—	1220-2200	J	A, F	R	S
<i>Dendrotriton sanctibarbarus</i>	W	—	1829-2744	J	A, T, F	C	S
<i>Nototriton barbouri</i>	W	—	860-1990	J	A, F	C	S
<i>Nototriton lignicola</i>	R	—	1760-1780	J	T, F	I	S
<i>Nototriton limnospectator</i>	R	—	1640-1980	J	A, T, F	C	S
<i>Oedipina cyclocauda</i>	P	—	0-1780	H	T, F	I	S
<i>Oedipina gephya</i>	R	—	1580-1810	J	T, F	C	D
Anurans (38 species)							
<i>Atelophryniscus chrysophorus</i>	W	—	750-1760	J	T, F, S	C	D
<i>Bufo coccifer</i>	—	W	0-2070	E	T, P	C	S
<i>Bufo leucomyos</i>	W	—	0-1600	J	T, F	C	S
<i>Bufo valliceps</i>	P	—	0-1610	E	T, F, P	C	S
<i>Hyalinobatrachium fleischmanni</i>	P	—	0-1550	D	A, S	C	D
<i>Duellmanohyla soralia</i>	P	—	40-1570	I	A, S	C	D
<i>Hyla bromeliacia</i>	W	—	1250-1790	I	A, F	C	S
<i>Hyla catracha</i>	—	R	1800-2160	J	A, S	C	D
<i>Hyla insolita</i>	R	—	1550	J	A, S	C	S
<i>Hyla salvaje</i>	R	—	1370	I	A, F	R	D
<i>Phrynohyas venulosa</i>	P	—	0-1610	D	A, T, P	C	S
<i>Plectrohyla chrysopleura</i>	W	—	930-1550	J	A, T, S	I	D
<i>Plectrohyla dasypus</i>	R	—	1410-1990	J	A, S	C	D
<i>Plectrohyla exquisita</i>	R	—	1490-1680	J	A, S	C	S
<i>Plectrohyla guatemalensis</i>	W	W	950-2600	I	A, S	C	D
<i>Plectrohyla hartwegi</i>	—	R	1920-2700	I	A, F, S	I	N
<i>Plectrohyla matudai</i>	P	W	770-1850	I	T, S	C	D
<i>Plectrohyla psiloderma</i>	—	R	2450-2530	I	A, T, S	C	D
<i>Ptychohyla hypomykter</i>	W	W	620-2070	I	A, S	C	D
<i>Ptychohyla salvadorensis</i>	—	W	1440-2050	I	A, T, S	C	S
<i>Ptychohyla spinipollex</i>	P	—	160-1580	J	A, S	C	S
<i>Smilisca baudinii</i>	P	—	0-1610	B	A, P	C	S
<i>Eleutherodactylus anciano</i>	—	W	1400-1840	J	T, S	I	E
<i>Eleutherodactylus aurilegulus</i>	P	—	50-1550	J	T, S	C	E
<i>Eleutherodactylus charadra</i>	P	—	30-1370	I	T, S	C	E
<i>Eleutherodactylus cruzi</i>	R	—	1520	J	T, S	R	E
<i>Eleutherodactylus emleni</i>	—	W	800-2000	J	T, S	R	E
<i>Eleutherodactylus laevissimus</i>	—	P	100-1640	H	T, S	I	E
<i>Eleutherodactylus loki</i>	R	—	1370	F	T, F	R	N

Continued on page 38.

Table 1. Continued.

Species	LMWF	LMMF	Elevational	Broad	Primary Microhabitat	Relative Abundance ¹	Conservation Status
			Range (m)	Distribution Pattern			
<i>Eleutherodactylus milesi</i>	W	—	1050-1720	J	T, S	C	E
<i>Eleutherodactylus rostralis</i>	W	—	1050-1800	I	T, F	I	D
<i>Eleutherodactylus saltuarius</i>	R	—	1550-1800	J	T, F	I	D
<i>Eleutherodactylus stadelmani</i>	W	—	1125-1900	J	T, S	C	E
<i>Leptodactylus silvаниmbus</i>	—	W	1470-2000	J	T, P	C	D
<i>Hypopachus barberi</i>	—	W	1470-2070	I	T, P	C	S
<i>Hypopachus variolosus</i>	P	—	0-1610	B	T, P	C	S
<i>Rana berlandieri</i> ²	P	W	0-2200	C	T, P	C	S
<i>Rana maculata</i>	W	W	40-1980	I	T, S	C	D
Lizards (27 species)							
<i>Abronia montecristoi</i>	R	—	1370	I	A, F	R	D
<i>Abronia salvadorensis</i>	—	R	2020-2125	J	A, T, F	R	D
<i>Celestus bivittatus</i>	—	P	1510-1980	I	T, F	C	D
<i>Celestus montanus</i>	P	—	915-1372	J	A, F	R	N
<i>Celestus scansorius</i>	R	—	1550-1590	J	A, F	R	N
<i>Mesaspis moreletii</i>	W	W	1450-2530	I	T, F	C	S
<i>Sceloporus malachiticus</i>	W	W	540-2530	H	A, F	C	S
<i>Norops amplisquamösus</i>	R	—	1530-1720	J	A, F	C	S
<i>Norops crassulus</i>	—	W	1200-2020	I	A, F	C	S
<i>Norops cusuco</i>	R	—	1550-1935	J	A, F	C	S
<i>Norops heteropholidotus</i>	—	R	1860-2200	I	A, F	C	S
<i>Norops johnmeyei</i>	R	—	1340-1825	J	A, F	C	S
<i>Norops kreutzi</i>	R	—	1670-1690	J	A, F	I	D
<i>Norops laeviventris</i>	W	W	1150-1900	E	A, F	I	S
<i>Norops loveridgei</i>	P	—	ca. 550-1600	J	A, F	I	S
<i>Norops muralla</i>	R	—	1440-1740	J	A, F	C	D
<i>Norops ocelloscapularis</i>	P	—	1150-1370	J	A, F	I	D
<i>Norops petersii</i>	R	—	1340-1370	F	A, F	R	N
<i>Norops pijolensis</i>	W	—	1180-2050	J	A, F	C	S
<i>Norops purpurgularis</i>	R	—	1550-2040	J	A, F	C	S
<i>Norops rubribarbaris</i>	R	—	1700	J	T, S	R	N
<i>Norops sminthus</i>	—	W	ca. 1450-2200	J	A, F	C	S
<i>Norops tropidonotus</i>	P	P	0-1900	F	A, T, F	C	S
<i>Norops uniformis</i>	P	—	30-1370	F	A, T, F	C	D
<i>Norops yoroensis</i>	P	—	1180-1600	J	A, F	I	S
<i>Sphenomorphus cherriei</i>	P	P	0-1860	E	T, F	C	S
<i>Sphenomorphus incertus</i>	P	—	1350-1670	I	T, F	R	S
Snakes (39 species)							
<i>Typhlops stadelmani</i>	P	—	850-1370	J	T, F	I	D
<i>Boa constrictor</i>	P	—	0-1370	D	T, F	I	N
<i>Adelphicos quadrivirgatus</i>	P	—	0-1740	F	T, F	C	S
<i>Coniophanes bipunctatus</i>	P	—	0-1370	E	T, P	I	N
<i>Dryadophis dorsalis</i>	W	W	635-1900	I	T, F	I	S
<i>Drymarchon corais</i>	P	—	0-1555	A	T, F	I	N
<i>Drymobius chloroticus</i>	W	W	780-1900	F	T, F, S	I	D
<i>Drymobius margaritiferus</i>	P	—	0-1450	A	T, F, P	C	S
<i>Geophis damiani</i>	R	—	1750	J	T, F	R	N
<i>Geophis fulvoguttatus</i>	W	W	1680-1900	I	T, F	R	D
<i>Imantodes cenchoa</i>	P	—	0-1620	D	A, F	C	S
<i>Lampropeltis triangulum</i>	P	—	0-1370	A	T, F	I	N
<i>Leptodeira septentrionalis</i>	W	W	0-1940	A	A, P, S	I	S
<i>Leptophis ahaetulla</i>	P	—	0-1680	D	A, T, P, S	C	N
<i>Leptophis modestus</i>	—	R	1890-2020	I	T, F	R	D
<i>Ninia diademata</i>	P	—	0-1370	F	T, F	I	D

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The herpetofauna of the cloud forests of Honduras

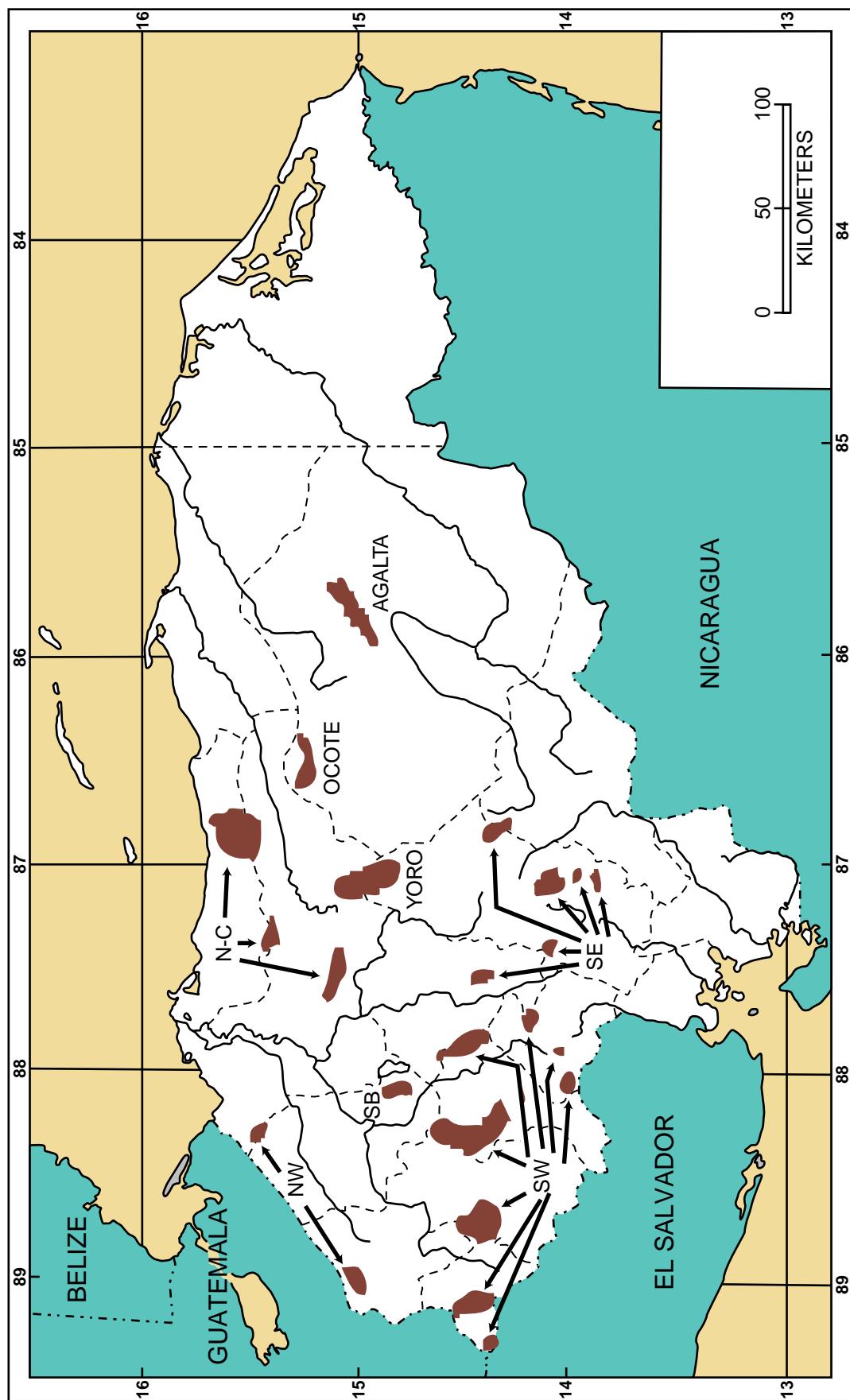


Figure 1. Generalized map of the cloud forest areas of Honduras. Abbreviations are as follows: NW = Northwestern Highlands; N-C = North-Central Highlands; SW = Southwestern Highlands; SE = Southeastern Highlands; SB = Santa Bárbara Highlands; Ocote = Ocote Highlands; Yoro = Yoro Highlands; Agalta = Agalta Highlands.
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Table 1. Continued.

Species	LMWF	LMMF	Elevational	Broad	Primary Microhabitat	Relative Abundance ¹	Conservation Status
			Range (m)	Distribution Pattern			
<i>Ninia espinali</i>	W	W	1590-2242	I	T, F	C	D
<i>Ninia sebae</i>	P	—	0-1650	E	T, F	C	S
<i>Pliocercus elapoides</i>	P	—	0-1670	F	T, F	I	S
<i>Rhadinaea godmani</i>	W	W	1450-2160	H	T, F	I	S
<i>Rhadinaea kinkelini</i>	W	W	1370-2085	I	T, F	I	D
<i>Rhadinaea lachrymans</i>	R	—	2050	I	T, F	R	N
<i>Rhadinaea montecristi</i>	W	W	1370-2620	I	T, F	I	S
<i>Rhadinaea tolpanorum</i>	R	—	1900	J	T, F	R	N
<i>Sibon dimidiatus</i>	P	—	950-1600	E	A, F	I	D
<i>Sibon nebulatus</i>	P	—	0-1690	D	A, F, S	C	S
<i>Stenorhina degenhardtii</i>	P	—	100-1630	D	T, F	I	S
<i>Storeria dekayi</i>	—	P	635-1900	C	T, F	R	N
<i>Tantilla impensa</i>	W	—	635-ca. 1600	I	T, F	R	D
<i>Tantilla lempira</i>	—	P	1450-1730	J	T, F	I	D
<i>Tantilla schistosa</i>	P	—	950-1680	E	T, F	I	S
<i>Thamnophis fulvus</i>	—	W	1680-2020	I	T, P, S	C	S
<i>Tropidodipsas fischeri</i>	—	W	1340-2150	I	T, F	I	D
<i>Micrurus browni</i>	—	R	1900	F	T, F	R	N
<i>Micrurus diastema</i>	P	—	100-1680	F	T, F	I	S
<i>Micrurus nigrocinctus</i>	P	—	0-1600	G	T, F	C	S
<i>Bothriechis marchi</i>	W	—	ca. 500-1840	J	A, S	I	D
<i>Bothriechis thalassinus</i>	W	W	1370-1750	I	A, S	R	D
<i>Cerrophidion godmani</i>	W	W	ca. 1300-2620	H	T, F	I	S
Total 122 species							

¹Historical. For example, species that were common at one time during our field experience, but may now be declining or extinct.

²LMMF specimens represent *Rana berlandieri* x *Rana forreri* hybrids (see McCranie and Wilson 2002).

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ed the following (p. 102): “At the 1570 m site, of 38 species with chest-high diameters of 5 cm or more, seven species were considered most important [based on numerical prevalence]. These species, in order of importance, are: *Persea* sp. (aguacate); *Calatola mollis* (nogál); *Quercus sapotaefolia* (encinillo); *Calophyllum brasiliense* (aceite de maría); *Elaeagia auriculata* (oreja de macho); *Quercus skinneri* (bellota); *Chamaedorea neurochlamys* (palma pacaya).

At the 1650 m site, a group of 6 species (out of 30) were judged most important, based on frequency of occurrence. These species, in order of importance, are: *Calophyllum brasiliense* (aceite de maría); *Quercus sapotaefolia* (encinillo); *Persea* sp. (aguacate); *Quercus skinneri* (bellota); *Elaeagia auriculata* (oreja de macho); *Alchornea latifolia* (amargoso). Five of these six species are of greatest importance as well at the 1570 m site.”

Wilson and McCranie (*in preparation b*) included data on the floristic makeup of the vegetation of the Lower Montane Moist formation in Parques Nacionales de Celaque and La Tigra, as follows: “The undisturbed forest is composed of three strata. The upper stratum is composed of trees 25 to 30 m in height, principally of the species *Quercus skinneri* (bellota), *Liquidambar styraciflua* (liquidámbar), *Pinus pseudostrobus* (pinabete), *P. oocarpa* (ocote), and *Persea* sp. (aguacate suerte). These trees carry a moderate amount of epi-

phytic mosses, orchids, bromeliads, and aroids. The middle stratum consists of *Quercus* sp. (curtidor), *Q. oleoides* (encino), *Clethra macrophylla* (alámico blanco), *Cedrela oaxacensis* (cedro), *Inga* sp. (guama), and various species of laurals. The lower stratum consists of shrubs belonging to the families Compositae, Myrsinaceae, Rubiaceae, Saurauiaeae, and Verbenaceae and the genera *Cleyera*, *Miconia*, *Piper*, *Psidium*, and *Vismia*.“

Composition of the cloud forest herpetofauna

The herpetofauna of the cloud forests of Honduras is known to consist of 122 species (Table 1), including 18 salamanders (14.8% of total), 38 anurans (31.1%), 27 lizards (22.1%), and 39 snakes (32.0%). The salamanders are all members of the family Plethodontidae. The anurans belong to six families, including the Bufonidae (4 species), Centrolenidae (1 species), Hylidae (17 species), Leptodactylidae (12 species), Microhylidae (2 species), and Ranidae (2 species). The lizards are members of four families, the Anguidae (6 species), Phrynosomatidae (1 species), Polychrotidae (18 species), and Scincidae (2 species). The snakes belong to five families, including the Typhlopidae (1 species), Boidae (1 species), Colubridae (31 species), Elapidae (3 species), and Viperidae (3 species).

Distribution and distributional relationships of the cloud forest herpetofauna

Distribution within forest formations

More than twice as many of the 122 cloud forest species are distributed in the Lower Montane Wet Forest formation (98 or 80.3% of total) than in the Lower Montane Moist Forest formation (45 or 36.9%). Twenty-one species (17.2%) are found in both formations (Table 1). The Coefficient of Biogeographic Resemblance (CBR) for these two forest formations is 0.29.

The species distributed in cloud forests fall into three distributional categories, viz., restricted, widespread, and peripheral (Table 1). Restricted species are those whose distribution is limited to a particular cloud forest formation. Widespread species are those that are widespread in distribution in a particular cloud forest formation or both cloud forest formations, as well as, perhaps, outside those forest formations. Finally, peripheral species are those whose distribution is largely peripheral to a particular cloud forest formation.

The Lower Montane Wet Forest formation is inhabited by 26 restricted species (26.5% of the total of 98 in this formation), including six salamanders, seven anurans, ten lizards, and three snakes. Thirty-two species (32.7%) are widespread in this formation, including six salamanders, ten anurans, four lizards, and 12 snakes. Finally, 40 species (40.8%) are peripherally distributed in this formation, including three salamanders, 11 anurans, eight lizards, and 18 snakes.

The Lower Montane Moist Forest formation is home to ten restricted species (22.2% of the total of 45 in this formation), including three salamanders, three anurans, two lizards, and two snakes. Twenty-nine species (64.4%) are widespread in this formation, including one salamander, 11 anurans, five lizards, and 12 snakes. Finally, there are six species (13.3%) peripherally distributed in this formation, including one anuran, three lizards, and two snakes. Notably, there are proportionately more peripheral and widespread species than restricted species in the Lower Montane Wet Forest formation. In the Lower Montane Moist Forest formation, most species are widespread ones, followed by relatively few restricted and peripheral species. The relative prevalence of peripheral species in the Lower Montane Wet Forest formation apparently is due to the grading of this type of cloud forest into highland rain forest (Premontane Wet Forest formation) at elevations usually around 1500 m, whereas the Lower Montane Moist Forest formation grades into upland pine forest (Premontane Moist Forest) typically.

As noted above, 21 species are distributed in both cloud forest formations (Table 1). The largest number of these species (17) are widespread in both formations. Two species are peripheral in distribution in both formations, and, finally, two species are widespread in one formation and peripheral in the other.

Distribution with respect to elevation

The Lower Montane Wet Forest formation is generally found at elevations in excess of 1500 m, although in some locales it occurs at elevations down to 1300+ m. The Lower Montane Moist Forest formation usually occurs at 1700+ m elevation. Thus, it is expected that patterns of elevational occurrence would be related to the patterns of occurrence in the two forest formations elucidated above. That is to say, the widespread and peripheral species would be expected to have broader overall elevational ranges than those whose distribution is restricted to cloud forest vegetation, with the peripheral species more broadly distributed overall than the widespread ones.

The restricted species, as a group, range from 1340 to 2700 m. The mean elevational range for this group of 36 species is 209.6 m. The species that are widespread in at least one of the two cloud forest formations, as a group, range from sea level to 2744 m. The mean elevational range for this group of 44 species is 1000.4 m. The species that occur peripherally in at least one of the two cloud forest formations, as a group, range from sea level to 2200 m. The mean elevational range for this group of 44 species is 1260.3 m (two species are peripheral in one formation and widespread in the other).

Broad distribution patterns

As did Wilson and Meyer (1985), Wilson et al. (2001), and McCranie and Wilson (2002), we placed the cloud forest species into a set of distributional categories based on the entire extent of their geographic range. Two of the categories used by Wilson et al. (2001) do not apply to this paper (marine species and insular and/or coastal species). The applicable categories are as follows:

- A. Northern terminus of the range in the United States (or Canada) and southern terminus in South America.
- B. Northern terminus of the range in the United States and southern terminus in Central America south of the Nicaraguan Depression.
- C. Northern terminus of the range in the United States and southern terminus in Nuclear Middle America.

Table 2. Summary of numbers of taxa exhibiting various Broad Patterns of Geographic Distribution (see text for explanation of categories).

Groups	Broad Patterns of Distribution									
	A	B	C	D	E	F	G	H	I	J
Salamanders (18 species)	—	—	—	—	—	—	—	1	5	12
Anurans (38)	—	2	1	2	2	1	—	1	13	16
Lizards (27)	—	—	—	—	2	3	—	1	6	15
Snakes (39)	4	—	1	5	4	6	1	2	11	5
Totals 122	4	2	2	7	8	10	1	5	35	48

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Table 3. Distribution of the Honduran cloud forest herpetofauna within eight ecophysiographic areas. Abbreviations are: W = widespread in that area; R = restricted to that area; P = peripherally distributed in that area; HL = Highlands.

Species	SE	SW	N-Central	Yoro	Ocote	Agalta	NW	Santa Bárbara	Total
	HL	HL	HL	HL	HL	HL	HL	HL	
<i>Bolitoglossa carri</i>	R								1
<i>Bolitoglossa celaque</i>		R							1
<i>Bolitoglossa conanti</i>		P					W		2
<i>Bolitoglossa decora</i>					R				1
<i>Bolitoglossa diaphora</i>							W		1
<i>Bolitoglossa dofleini</i>							P		1
<i>Bolitoglossa Dunnii</i>							W		1
<i>Bolitoglossa longissima</i>						R			1
<i>Bolitoglossa porrasorum</i>			W						1
<i>Bolitoglossa rufescens</i> complex							P		1
<i>Bolitoglossa synoria</i>	R								1
<i>Cryptotriton nasalis</i>							W		1
<i>Dendrotriton sanctibarbarus</i>								R	1
<i>Nototriton barbouri</i>		W							1
<i>Nototriton lignicola</i>					R				1
<i>Nototriton limnospectorator</i>								R	1
<i>Oedipina cyclocauda</i>					W				1
<i>Oedipina gephyra</i>			R						1
<i>Atelophryniscus chrysophorus</i>			W						1
<i>Bufo coccifer</i>	W	W							2
<i>Bufo leucomyos</i>			P	P	W				3
<i>Bufo valliceps</i>							P	P	2
<i>Hyalinobatrachium fleischmanni</i> ¹			P		P				2
<i>Duellmanohyla sororita</i>							P		1
<i>Hyla bromeliacia</i>							W		1
<i>Hyla catracha</i>	R								1
<i>Hyla insolita</i>			R						1
<i>Hyla salvaje</i>							R		1
<i>Phrynohyas venulosa</i>								P	1
<i>Plectrohyla chrysopleura</i>			P						1
<i>Plectrohyla dasypus</i>							R		1
<i>Plectrohyla exquisita</i>							R		1
<i>Plectrohyla guatemalensis</i>	W	W	W		W		P		5
<i>Plectrohyla hartwegi</i>		R							1
<i>Plectrohyla matudai</i>		W					P		2
<i>Plectrohyla psiloderma</i>		R							1
<i>Ptychohyla hypomykter</i>	W	W			W		W		4
<i>Ptychohyla salvadorensis</i>	W	W							2
<i>Ptychohyla spinipollex</i>			P						1
<i>Smilisca baudinii</i>			P	P	P		P	P	5
<i>Eleutherodactylus anciano</i>		P							1
<i>Eleutherodactylus aurilegulus</i>			P		W				2
<i>Eleutherodactylus charadra</i>							P		1
<i>Eleutherodactylus cruzi</i>			R						1
<i>Eleutherodactylus emleni</i>	W								1
<i>Eleutherodactylus laevissimus</i>	P								1
<i>Eleutherodactylus loki</i>							R		1
<i>Eleutherodactylus milesi</i>							W		1
<i>Eleutherodactylus rostralis</i>			P				W		2
<i>Eleutherodactylus saltuarius</i>			R						1
<i>Eleutherodactylus stadelmani</i>			W		W				2
<i>Leptodactylus silvaniimbus</i>	W								1
<i>Hypopachus barberi</i>	W								1
<i>Hypopachus variolosus</i>							P		1

Continued on page 43.

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Table 3. Continued.

Species	SE	SW	N-Central	Yoro	Ocote	Agalta	NW	Santa	Total
	HL	HL	HL	HL	HL	HL	HL	Bárbara	
<i>Rana berlandieri</i> ²	W	W					P	P	4
<i>Rana maculata</i>	W	W	P		P		W		5
<i>Abronia montecristoi</i>							R		1
<i>Abronia salvadorensis</i>		W							1
<i>Celestus bivittatus</i>		P							1
<i>Celestus montanus</i>							P		1
<i>Celestus scansorius</i>			R						1
<i>Mesaspis moreletii</i>	W	W			W		W		4
<i>Sceloporus malachiticus</i>	W	W	W	P	P	W	W		7
<i>Norops amplisquamosus</i>							R		1
<i>Norops crassulus</i>		W							1
<i>Norops cusuco</i>							R		1
<i>Norops heteropholidotus</i>		R							1
<i>Norops johnmeyeri</i>							W		1
<i>Norops kreutzi</i>			R						1
<i>Norops laeviventris</i>	P	P					P	W	4
<i>Norops loveridgei</i>			W						1
<i>Norops muralla</i>					X	X			2
<i>Norops ocelloscapularis</i>							P		1
<i>Norops petersii</i>							R		1
<i>Norops pijolensis</i>			W						1
<i>Norops purpurgularis</i>			R						1
<i>Norops rubribarbaris</i>								R	1
<i>Norops sminthus</i>	W								1
<i>Norops tropidonotus</i>	P		P		W				3
<i>Norops uniformis</i>							P		1
<i>Norops yoroensis</i>			P	P					2
<i>Sphenomorphus cherriei</i>	P				P		P		3
<i>Sphenomorphus incertus</i>			P						1
<i>Typhlops stadelmani</i>							P		1
<i>Boa constrictor</i>							P		1
<i>Adelphicos quadrivirgatus</i>							P		1
<i>Coniophanes bipunctatus</i>							P		1
<i>Dryadophis dorsalis</i>		W	W	P	P		P		5
<i>Drymarchon corais</i>							P		1
<i>Drymobius chloroticus</i>	P	P	W				W		4
<i>Drymobius margaritiferus</i>							P		1
<i>Geophis damiani</i>			R						1
<i>Geophis fulvoguttatus</i>		W					W		2
<i>Imantodes cenchoa</i>			P		P		P		3
<i>Lampropeltis triangulum</i>							P		1
<i>Leptodeira septentrionalis</i>		W	W				P		3
<i>Leptophis ahaetulla</i>					W		W		2
<i>Leptophis modestus</i>		R							1
<i>Ninia diademata</i>							P		1
<i>Ninia espinali</i>		W					W		2
<i>Ninia sebae</i>								P	1
<i>Pliocercus elapoides</i>			P		W		P		3
<i>Rhadinaea godmani</i>	W	W	W						3
<i>Rhadinaea kinkelini</i>		W	W				P		3
<i>Rhadinaea lachrymans</i>						R			1
<i>Rhadinaea montecristi</i>		W					W		2
<i>Rhadinaea tolpanorum</i>			R						1
<i>Sibon dimidiatus</i>							P		1
<i>Sibon nebulatus</i>			W						1

Continued on page 44.

Table 3. Continued.

Species	SE HL	SW HL	N-Central HL	Yoro HL	Ocote HL	Agalta HL	NW HL	Santa Bárbara HL	Total
<i>Stenorhina degenhardtii</i>					P		P		2
<i>Storeria dekayi</i>		P							1
<i>Tantilla impensa</i>							W		1
<i>Tantilla lempira</i>		P							1
<i>Tantilla schistosa</i>							W		1
<i>Thamnophis fulvus</i>	P	W							2
<i>Tropidodipsas fischeri</i>		W							1
<i>Micrurus browni</i>		R							1
<i>Micrurus diastema</i>							W		1
<i>Micrurus nigrocinctus</i>			P						1
<i>Bothriechis marchi</i>			P				W		2
<i>Bothriechis thalassinus</i>		P					W	P	3
<i>Cerrophidion godmani</i>	W	W	W				W		4
Totals	19	39	39	5	21	4	60	11	—

¹North-Central Highlands records based on calling males that could not be located.

²*Rana berlandieri* from the Southeastern and Southwestern Highlands equal *R. berlandieri* × *R. forreri* (see McCranie and Wilson 2002).

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- D. Northern terminus of the range in Mexico north of the Isthmus of Tehuantepec and southern terminus in South America.
- E. Northern terminus of the range in Mexico north of the Isthmus of Tehuantepec and southern terminus in Central America south of the Nicaraguan Depression.
- F. Northern terminus of the range in Mexico north of the Isthmus of Tehuantepec and southern terminus in Nuclear Middle America.
- G. Northern terminus of the range in Nuclear Middle America and southern terminus in South America.
- H. Northern terminus of the range in Nuclear Middle America and southern terminus in Central America south of the Nicaraguan Depression.
- I. Restricted to Nuclear Middle America (exclusive of Honduran endemics).
- J. Endemic to Honduras.

The data on broad distributional patterns in Table 1 are summarized in Table 2. These data indicate that the largest number of species (48 or 39.3% of the total of 122 species) fall into the J category, i.e., that containing the species endemic to Honduras. The next largest category is I, with 35 species (28.7%), containing those species not endemic to Honduras but restricted in distribution to Nuclear Middle America. Together, these two categories contain 68.0% of the cloud forest species. The other eight categories contain from one to ten species and harbor, as a group, 32.0% of the total number. These data again point to the biogeographic and conservation importance of the Honduran cloud forest herpetofauna.

Primary microhabitat distribution

We used the same microhabitat categorization as did Espinal et al. (2001). In terms of vertical positioning, we scored species as either terrestrial or arboreal. With respect to occurrence in the three major microhabitats found in cloud forest,

species were scored as being found in the forest proper, along streams, or around ponds (Table 1).

In terms of vertical positioning within the primary microhabitats, 49 species (40.2%) were usually found only in arboreal situations, 62 species (50.8%) only in terrestrial situations, and 11 (9.0%) in both. With respect to occurrence in the three major microhabitats (forest proper, streamside, pondside), 76 species (62.3%) were found exclusively in the forest proper, 26 (21.3%) only along streams, eight (6.6%) only around ponds, seven (5.7%) in the forest and along streams, three (2.5%) around ponds and along streams, and two (1.6%) in the forest and around ponds (Table 1).

If the two sets of categories, vertical positioning in primary habitat and microhabitats, are combined, it can be demonstrated that 94 species (77.0%) fall into four groups, as follows (Table 1): 40 terrestrial forest inhabitants (32.8%); 31 arboreal forest inhabitants (25.4%); 12 arboreal streamside inhabitants (9.8%); and 11 terrestrial streamside inhabitants (9.0%). The terrestrial forest inhabitants include four salamanders, four anurans, four lizards, and 28 snakes. The arboreal forest inhabitants are eight salamanders, two anurans, 19 lizards, and two snakes. The arboreal streamside inhabitants are one salamander, nine anurans, and two snakes. The terrestrial streamside inhabitants are ten anurans and one lizard.

Relative abundance

In discussing relative abundance, we used the following categorization: common (C: found on a regular basis, many individuals can be found); infrequent (I: unpredictable, few individuals seen); rare (R: rarely seen). These classifications are historical (i.e., based largely on earlier trips to cloud forest localities) and do not take into consideration the population declines taking place for many species (see *Biodiversity significance and conservation status of the cloud forest herpetofauna*). Sixty-three species (51.6%) are classified as being common (11 salaman-

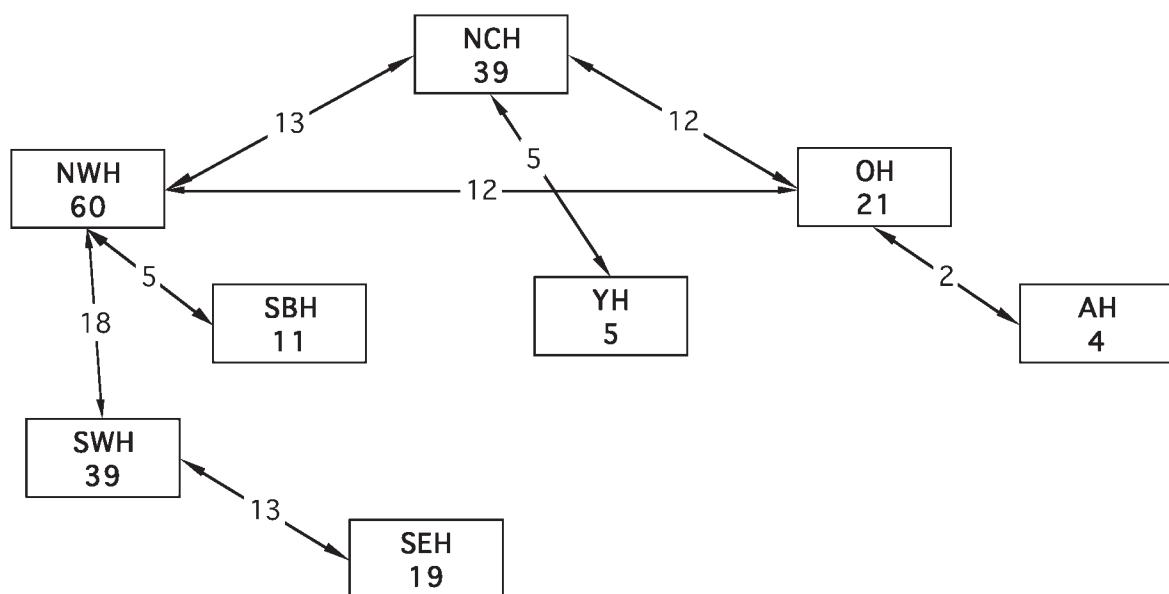


Figure 2. Greatest shared species diagram of eight cloud forest areas in Honduras. See text for explanation of abbreviations. Numbers in boxes are the number of species in each area; numbers on arrows indicate the number of species shared between areas connected and represent the greatest shared value for each area. Position of the boxes in the diagram is roughly reflective of their geographic relationships in Honduras.

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ders, 28 anurans, 15 lizards, and nine snakes), 37 (30.3%) as being infrequent (five salamanders, six anurans, five lizards, and 21 snakes), and 22 (18.0%) as being rare (two salamanders, four anurans, seven lizards, and nine snakes).

Patterns of distribution among ecophysiographic areas

Wilson et al. (2001) recognized eight ecophysiographic areas that contain cloud forest vegetation. Two of these areas, the Southeastern Highlands and Southwestern Highlands, are located in the Southern Cordillera. The remaining six areas are situated in the Northern Cordillera. The distribution of the members of the Honduran cloud forest herpetofauna among these eight cloud forest ecophysiographic areas is indicated in Table 3. Perusal of the data in this table allows for several conclusions, as follows:

1. The numbers of species in these eight areas range from four (Agalta Highlands) to 60 (Northwestern Highlands).

2. Significantly more species are known from the Northern Cordillera areas (98 or 80.3% of total) than those in the Southern Cordillera (45 or 36.9%) areas. Only 20 species (16.4%) are distributed in both cordilleras (the *Rana berlandieri* listed in Table 3 from the Southern Cordillera are considered *R. berlandieri* x *R. forreri* hybrids—see McCranie and Wilson 2002).
3. The above pattern is seen in each of the major herpetofaunal groupings. Only four salamanders are found in the Southern Cordillera cloud forests, compared to 15 in the Northern Cordillera cloud forests. Only a single species (*Bolitoglossa conanti*) is distributed in both cordilleras (although the population in the Southern Cordillera likely represents an undescribed species). Fifteen species of anurans occur in the Southern Cordillera cloud forests, as opposed to 28 in the Northern Cordillera forests. Only four species (*Plectrohyla guatemalensis*, *P. matudai*, *Ptychohyla hypomykter*, and *Rana maculata*; the

Table 4. CBR matrix of herpetofaunal relationships for the eight ecophysiographic areas supporting cloud forest. **N** = species in each region; **N** = species in common between two regions; **N** = Coefficients of Biogeographic Resemblance. See text for explanation of the abbreviations. No distinction is made between *Rana berlandieri* and *R. berlandieri* x *R. forreri* for this analysis.

	SEH	SWH	NCH	YH	OH	AH	NWH	SBH
SEH	19	13	7	1	7	1	10	2
SWH	<u>0.45</u>	39	9	2	6	1	18	2
NCH	<u>0.24</u>	<u>0.23</u>	39	5	12	1	13	1
YH	<u>0.08</u>	<u>0.09</u>	<u>0.23</u>	5	4	1	3	1
OH	<u>0.35</u>	<u>0.20</u>	<u>0.40</u>	<u>0.31</u>	21	2	12	1
AH	<u>0.09</u>	<u>0.05</u>	<u>0.05</u>	<u>0.22</u>	<u>0.16</u>	4	1	0
NWH	<u>0.25</u>	<u>0.36</u>	<u>0.26</u>	<u>0.09</u>	<u>0.30</u>	<u>0.03</u>	60	5
SBH	<u>0.13</u>	<u>0.08</u>	<u>0.04</u>	<u>0.13</u>	<u>0.06</u>	<u>0.00</u>	<u>0.14</u>	11

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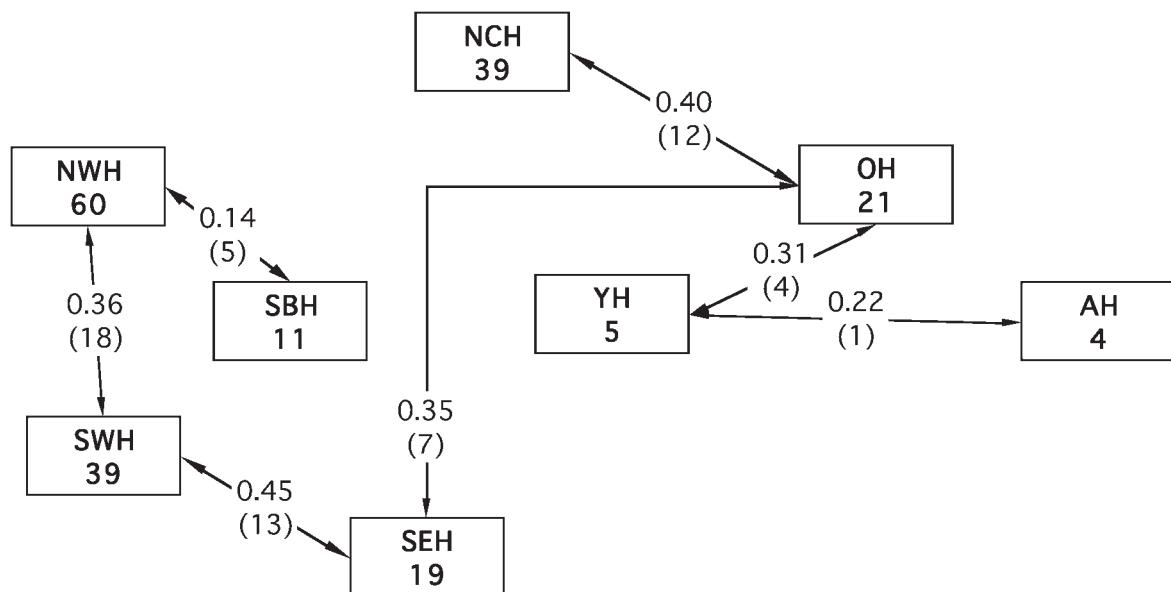


Figure 3. Coefficient of Biogeographic Resemblance diagram for the eight cloud forest areas in Honduras. See text for explanations of abbreviations. Numbers in boxes are the number of species in each area; decimal numbers on arrows indicate the CBR value shared between areas connected and represent the highest value for each area; absolute numbers in parentheses indicate the number of species shared between the areas connected. Position of the boxes in the diagram is roughly reflective of their geographic relationships in Honduras.

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Rana berlandieri listed in Table 3 from the Southern Cordillera are considered *R. berlandieri* x *R. forreri* hybrids—see McCranie and Wilson 2002) occur in both regions. Ten species of lizards are distributed in the Southern Cordillera forests, whereas 22 are in the Northern Cordillera forests. Only five species (*Mesaspis moreletii*, *Sceloporus malachiticus*, *Norops laeviventris*, *N. tropidonotus*, and *Sphenomorphus cherriei*) are found in both areas. Finally, 16 species of snakes occupy the Southern Cordillera cloud forests and 33 the Northern Cordillera forests. Ten species (*Dryadophis dorsalis*, *Drymobius chloroticus*, *Geophis fulvoguttatus*, *Leptodeira septentrionalis*, *Ninia espinali*, *Rhadinaea godmani*, *R. kinkelini*, *R. montecristi*, *Bothriechis thalassinus*, and *Cerrophidion godmani*) are distributed in both areas.

4. Most of the 122 species (102 or 83.6%) occur in only one or two cloud forest ecophysiological areas. The most broadly-distributed species occur in seven ecophysiological areas (*Sceloporus malachiticus*) or in five ecophysiological areas (*Plectrohyla guatemalensis*, *Smilisca baudinii*, *Rana maculata*, and *Dryadophis dorsalis*). The average area occurrence is 1.6.

A greatest shared species diagram of the eight cloud forest physiographic areas is presented in Figure 2. The areas are abbreviated as follows: Southeastern Highlands - SEH; Southwestern Highlands - SWH; North-Central Highlands - NCH; Yoro Highlands - YH; Ocote Highlands - OH; Agalta Highlands - AH; Northwestern Highlands - NWH; Santa Bárbara Highlands - SBH. The number of species shared between areas ranges from two to 18. In general, the greater

the total herpetofaunas of any two compared areas, the greater is the number of species shared.

Generation of Coefficient of Biogeographic Resemblance (CBR) values allows for a more robust analysis of herpetofaunal resemblances. Thus, a matrix of CBR values for the eight ecophysiological areas is summarized in Table 4, and these values are used to produce a CBR diagram (Fig. 3) indicating highest values for each ecophysiological area. These values indicate that the herpetofauna of a given ecophysiological area most closely resembles that of another area occupied by the same forest formation and/or lying in close geographic proximity. For example, the Southeastern Highlands and the Southwestern Highlands are both occupied by the Lower Montane Moist Forest formation and they share 13 species. Also, as an example, the Northwestern Highlands and the Southwestern Highlands are in close geographic proximity and share 18 species. Geographic proximity, however, appears to be the more important determinant of the degree of herpetofaunal resemblance, inasmuch as Figure 3 illustrates a western and southern grouping of areas (NWH, SBH, SWH, and SEH) and a northern and eastern grouping of areas (NCH, OH, YH, and AH). These two groups are connected by a relatively high CBR value between SEH and OH.

Averaging all CBR values provides a gauge of herpetofaunal distinctiveness, as follows: SEH (0.23); SWH (0.21); NCH (0.21); YH (0.16); OH (0.25); AH (0.09); NWH (0.20); SBH (0.08). The most distinctive herpetofauna is that of the SBH (average CBR value of 0.08), the least that of the OH (average CBR value of 0.25). The distinctiveness of the SBH herpetofauna is an artifact of being poorly known. The fewer the species known from a given area, the fewer there are to be shared with other areas.

Biodiversity significance and conservation status of the cloud forest herpetofauna

As noted in the Introduction, the herpetofauna of Honduras is being subjected to the same anthropogenic pressures as have been demonstrated to be in effect elsewhere in the tropics. The most substantial pressure is created by habitat loss as a result of deforestation (Wilson et al. 2001; Wilson and McCranie 2003 a and b). Also significant is a threat of unsubstantiated origin (but see Duellman 2001, for a discussion of events elsewhere in the tropics) that is decimating amphibian populations in the country occurring at elevations in excess of 900 m (Wilson and McCranie 1998; McCranie and Wilson 2002), thus conceivably impacting all cloud forest areas.

That these threats are impinging on herpetofaunal populations at 900 m and above is especially poignant, inasmuch as the herpetodiversity of greatest significance is distributed in these regions, especially those supporting cloud forest. This most significant herpetodiversity consists of those species endemic to Honduras and those otherwise restricted to Nuclear Middle America. Of the 334 species now known to constitute the Honduran herpetofauna (including six marine reptiles), 78 are country endemics (23.4% of total) and 47 are Nuclear Middle American-restricted species (14.1%). A greater percentage of the amphibian species fall into these two categories than do the reptilian species. There are 41 amphibian Honduran endemics (35.0% of total of 117 species) and 25 Nuclear Middle American-restricted amphibian species (21.4%), compared to 37 (17.1% of total of 217 species) and 22 (10.1%) such reptilian species, respectively. Thus, a total of 125 species of amphibians and reptiles (37.4%) are either endemic to Honduras or otherwise restricted to Nuclear Middle America.

Of these 125 species, 83 or 66.4% are distributed in cloud forests in Honduras (Table 2). Of the remaining 209 Honduran species not found in cloud forests, only 42 species or 20.1% are Honduran endemics or Nuclear Middle American-restricted. It is obvious that the large majority of the species of greatest biodiversity significance is found in cloud forests.

As indicated above, deforestation is eroding forest resources throughout the country. Wilson and McCranie (2003 a) presented estimates, based on a computer model in E. Wilson and Perlman (2000), suggesting that the current deforestation rate is -2.3%, giving rise to a halving rate of 30.1 years. At this rate, only a half a million hectares of forest will remain in Honduras by the year 2085 and none will remain by the end of the current century.

This trend has been affecting cloud forests in Honduras, just as it has everywhere else in the country, and continues to the present day. It has been abated somewhat by the establishment of biotic reserves in several of the ranges supporting cloud forest (Wilson et al. 2001). This establishment largely has been the result of an effort to secure water supplies for populated areas. As noted by Wilson et al. (2001), however, most of these reserves are incompletely developed, such that deforestation still proceeds in many, if not all of them (e.g., Espinal et al. 2001), as a result of illegal logging and subsistence farming.

It has been demonstrated in recent years that populations of many Honduran amphibians and reptiles are in decline or

have disappeared altogether, as part of a global pattern (Duellman 2001). Wilson and McCranie (2003 a) have provided the most recent assessment of this trend for the Honduran herpetofauna. However, their assessment differs somewhat from the one undertaken here. Wilson and McCranie (2003 a) considered the range as a whole for each species when classifying whether a given species had stable populations somewhere in their range. However, a few species may have stable populations at some low elevation localities, but may be extirpated from their known cloud forest localities (e.g., *Eleutherodactylus charadra*). Thus, the conservation status categories in this paper refer only to cloud forest populations. Table 1 lists the conservation status for each of the 122 species at their known cloud forest localities. These data indicate that 40 species (32.8%) have populations that are in decline, eight species (6.6%) have disappeared altogether from cloud forests, and 16 species (13.1%) are too poorly known to determine their status in Honduran cloud forests. Fifty-eight species (47.5%) appear to have stable populations in at least one cloud forest locality.

When one considers only the two most important components of the Honduran cloud forests (the Honduran endemics and the Nuclear Middle American-restricted species), then 15 of the 48 Honduran endemics (31.3%) have declining populations, six endemics (12.5%) have disappeared, five endemics (10.4%) are too poorly known to determine their status, and 22 endemics (45.8%) appear to have stable populations in at least one cloud forest locality. Of the 35 Nuclear Middle American-restricted species, 20 (57.1%) have declining populations, one (2.9%) has disappeared, two (5.7%) are too poorly known, and 12 (34.3%) appear to have stable populations in at least one cloud forest locality. Thus, about one half of the 83 Honduran endemics or Nuclear Middle American-restricted species have declining populations (35 species or 42.2%) or have disappeared from Honduran cloud forests (seven species or 8.4%). Of the six Honduran endemic species that have disappeared from cloud forests, five are feared extinct. These are shocking statistics, considering the importance of these species not only biologically, but also from conservation and ecotourist standpoints.

From simply a biological standpoint, the systematics of the majority of the 83 cloud forest notables (Honduran endemics and Nuclear Middle American-restricted species) are insufficiently understood to be subjected to cladistic analysis, a requirement for reconstructing their phylogenies, and, beyond this, their biogeographic histories. These species are particularly important in our effort to understand the general patterns of evolution of the herpetofauna and to take that understanding beyond the work done on this subject to date.

From the perspective of conservation biology, we have demonstrated here and elsewhere (Wilson and McCranie 1998, 2003 a and b; Wilson et al. 2001; McCranie and Wilson 2002, *in press*) that the herpetofauna is anything but the pedestrian compendium alluded to in Lynch and Fugler's (1965, p.15) conclusions when they wrote that, "The anuran fauna seems to be derived from largely widespread species and species with northern affinities." Quite to the contrary, the work that has been accomplished since Lynch and Fugler published their paper 38 years ago has shown that slightly more than a third (37.4%) of the Honduran herpetofauna is com-

posed of endemics or otherwise Nuclear Middle American-restricted species. Our work in cloud forests has provided the major support for that conclusion.

The economic value of the Honduran cloud forests for ecotourism is only beginning to be calculated. It is stunningly evident to us, however, based on the several decades of our field work in the country, that efforts to develop an ecotourist-generated component to the Honduran economy is likely to be doomed by the uncontrolled human population growth that continues to stymie efforts to conserve the considerable biodiversity of the country.

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References

- Carson, R. L. 1962. *Silent Spring*. Houghton Mifflin, Boston, Massachusetts. 368 p.
- Duellman, W. E. 1990. Herpetofaunas in neotropical rainforests: comparative composition, history, and resource use, p. 455-505 in Gentry, A. H. (editor). *Four Neotropical Rainforests*. Yale University Press, New Haven, Connecticut. 627 p.
- Duellman, W. E. 2001. *The Hylid Frogs of Middle America*. Society for the Study of Amphibians and Reptiles, Contributions to Herpetology **18**:1-694, 695-1159.
- Ehrlich, P. 1968. *The Population Bomb*. Ballantine Books, New York. 223 p.
- Ehrlich, P. and Ehrlich, A. 1981. *Extinction: the causes and consequences of the disappearance of species*. Random House, New York. 305 p.
- Ehrlich, P. and Ehrlich, A. 1996. *Betrayal of Science and Reason: how anti-environmental rhetoric threatens our future*. Island Press, Covelo, California. 335 p.
- Espin, M. R., McCranie, J. R., and Wilson, L. D. 2001. The herpetofauna of Parque Nacional La Muralla, Honduras, p. 100-108 in Johnson, J. D., Webb, R. G., and Flores-Villela, O. A. (editors). *Mesoamerican Herpetology: systematics, zoogeography, and conservation*. Centennial Museum, University of Texas at El Paso, Special Publication 1:1-200.
- Fundación Ecologista "Hector Rodrigo Pastor Fasquelle." 1994. *Evaluación Ecológica Rápida (EER)*. Parque Nacional "El Cusuco" y Cordillera del Merendón. The Nature Conservancy and PACA (Proyecto Ambiental para Centro América). 129 p.
- Holdridge, L. R. 1967. *Life Zone Ecology*. Revised Edition. Tropical Science Center, San José, Costa Rica. 206 p.
- Lynch, J. D. and Fugler, C. M. 1965. A survey of the frogs of Honduras. *Journal of the Ohio Herpetological Society* **5**(1):5-18.
- McCranie, J. R. and Wilson, L. D. 2002. *The Amphibians of Honduras*. Society for the Study of Amphibians and Reptiles, Contributions to Herpetology **19**:1-625.
- McCranie, J. R. and Wilson, L. D. *In press*. The Honduran amphibian fauna: perched on the brink of decline, in Wilkinson, J. W. (editor). *Declining Amphibian Populations Task Force Combined Working Group Report 2001*. IUCN, Gland, Switzerland.
- McCranie, J. R. and Wilson, L. D. *In preparation*. *The Reptiles of Honduras*.
- Meadows, D. H., Meadows, D. L., Randers, J., and Behrens, W. W. 1972. *The Limits to Growth*. Universe, New York. 207 p.
- Meyer, J. R. 1969. A biogeographic study of the amphibians and reptiles of Honduras. Unpublished Ph.D. Dissertation, University of Southern California, Los Angeles. 589 p.
- Meyer, J. R. and Wilson, L. D. 1971. A distributional checklist of the amphibians of Honduras. *Los Angeles County Museum of Natural History, Contributions in Science* **21**:1-47.
- Meyer, J. R. and Wilson, L. D. 1973. A distributional checklist of the turtles, crocodilians, and lizards of Honduras. *Los Angeles County Museum of Natural History, Contributions in Science* **24**:1-39.
- Osborn, F. 1948. *Our Plundered Planet*. Pyramid Books, New York. 176 p.
- Savage, J. M. 2002. *The Amphibians and Reptiles of Costa Rica: a herpetofauna between two continents, between two seas*. University of Chicago Press, Chicago. 934 p.
- West, R. C. 1964. Surface configuration and associated geology of Middle America, p. 33-83 in West, R. C. (editor). *Natural Environment and Early Cultures*. Volume 1, *Handbook of Middle American Indians* (R. Wauchope general editor). University of Texas Press, Austin. 570 p.
- Wilson, E. O. (editor). 1988. *Biodiversity*. National Academy Press, Washington, D.C. 521 p.
- Wilson, E. O. 1992. *The Diversity of Life*. Belknap Press of Harvard University Press, Cambridge, Massachusetts. 424 p.
- Wilson, E. O. and Perlman, D. L. 2000. *Conserving earth's biodiversity with E. O. Wilson* (CD-ROM). Island Press, Covelo, California.
- Wilson, L. D. and McCranie, J. R. 1998. Amphibian population decline in a Honduran national park. *Froglog* **25**:1-2.
- Wilson, L. D. and McCranie, J. R. 2002. Update on the list of reptiles known from Honduras. *Herpetological Review* **33**(2):90-94.
- Wilson, L. D. and McCranie, J. R. 2003 a. The conservation status of the herpetofauna of Honduras. *Amphibian and Reptile Conservation* **3**(1):6-33.
- Wilson, L. D. and McCranie, J. R. 2003 b. Herpetofaunal indicator species as measures of environmental stability in Honduras. *Caribbean Journal of Science* **39**(1):50-67.
- Wilson, L. D. and McCranie, J. R. *In preparation* a. The herpetofauna of Parque Nacional El Cusco, Honduras.
- Wilson, L. D. and McCranie, J. R. *In preparation* b. The herpetofauna of Parques Nacionales de Celaque and La Tigra, Honduras.
- Wilson, L. D., McCranie, J. R. and Espinal, M. R. 2001. The ecology of the Honduran herpetofauna and the design of biotic reserves, p. 109-158 in Johnson, J. D., Webb, R. G., and Flores-Villela, O. A. (editors). *Mesoamerican Herpetology: systematics, zoogeography, and conservation*. Centennial Museum, University of Texas at El Paso, Special Publication 1:1-200.
- Wilson, L. D. and Meyer, J. R. 1985. *The Snakes of Honduras*. Second edition. Milwaukee Public Museum. 150 p.

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