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## BATS IN TIME: HISTORICAL AND GEOGRAPHIC DISTRIBUTION IN HONDURAS

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### ABSTRACT

Bat records from Honduras reported herein are based on 11,163 individuals representing 113 species and eight families, recorded from 1860 to 2020. The Global Biodiversity Information Facility (GBIF) and published records were used to document the history of bat collecting in Honduras, and the number of species expected for the country and their relative abundance were estimated. Herein, the first checklist available for each department in Honduras is provided, as well as a discussion of the history of bat research in the country, including three peaks that occurred in 1967–69, 1983, and 2001. The geographic position of Honduras and the variety of its ecosystems combine to promote a diversity of bat species that are typical of regions to both the north and the south of Honduras. Despite the relatively large number of specimens known from the country, details of the distribution and natural history of each species remain understudied.

Key words: Central America, Chiroptera, Honduras, natural history, relative abundance

### RESUMEN

Los registros de murciélagos de Honduras que se describen en este documento se basan en 11,163 individuos que representan 113 especies y ocho familias, registrados desde 1860 hasta 2020. El Fondo de Información sobre Biodiversidad Global (GBIF) y los registros publicados se utilizaron para documentar la historia de la recolección de murciélagos en Honduras. Además se estimó el número de especies esperadas para el país y se describe la abundancia relativa de todas las especies. Aquí, se proporciona la primera lista de verificación disponible para cada departamento en Honduras, así como una discusión de la historia de la investigación de murciélagos en el país, incluyendo tres picos que ocurrieron en 1967–69, 1983 y 2001. La posición geográfica de Honduras y la variedad de sus ecosistemas se combinan para promover una diversidad de especies de murciélagos que son típicas de las regiones tanto del norte como del sur de Honduras. A pesar de la cantidad relativamente grande de especímenes que se conocen en el país, los detalles de la distribución y la historia natural de cada especie siguen siendo poco estudiados.

Palabras clave: abundancia relativa, Centroamérica, Chiroptera, Honduras, historia natural

## INTRODUCTION

Perhaps because of its proximity to Mexico, the United States, and Canada, Central America has been an early leader in the investigation of tropical bats. The establishment of the Smithsonian Tropical Research Institute in Panama in 1923 spearheaded a long period of tropical bat research there that continues today, conducted primarily by US and European bat biologists. The Organization for Tropical Studies, a US-based entity founded in 1963, chose Costa Rica for its tropical biology courses and research stations, among which La Selva is internationally famous. Beginning in the 1960s, an increasing number of bat researchers carried out their work in Costa Rica. Partially as a result of this activity, participating Costa Rican biologists began to investigate bats, resulting in a cadre of highly qualified and active native Costa Rican bat biologists. LaVal and Rodríguez-H (2002) summarized much of this work.

In Nicaragua, young biologists interested in bats participated in workshops given by Costa Rican and US biologists (with biologists from Honduras and Guatemala also participating), the most recent being in 2012. These young biologists have been very active in the last decade investigating the bats of Nicaragua, and Medina-Fitoria (2014) summarized much of this work. More recently, Martínez-Fonseca et al. (2020) produced an updated checklist of the bats of Nicaragua.

Guatemala has a similar history, but relatively little has been published on bats in the country. Although there are now a few young biologists in Guatemala interested in bats, no major investigations have yet been undertaken, to the best of our knowledge. However, Kraker-Castañeda et al. (2016) published the most recent checklist of the bats of Guatemala.

Honduras was visited during early decades by US bat biologists mainly for the purpose of collecting specimens for museum collections, which became extensive. During the last few years several young and enthusiastic bat biologists have emerged in Honduras, resulting in a modern synthesis of what is known about the taxonomy and distribution of the species occurring there. With an area of 112,492 km<sup>2</sup>, Honduras is the second largest country in Central America (Hernández Oré et al. 2016). The vast territory includes a variety of ecosystems, from mangroves to pine forests, from

rain forests to cloud forests, from dry forests to riparian forests.

Unfortunately, each forest type is being affected negatively by conservation problems, usually exacerbated by humans. For example, pine forests have been strongly affected by weevil plagues and intentional fires (Portillo Reyes and Elvir 2016). Dry forests, among the least studied of the ecosystems, are threatened by extensive cattle raising (Medina et al. 2020). Tropical rain forests are considered one of the most important ecosystems because they house the highest biodiversity in the country (McCranie et al. 2019), but unfortunately, they are subjected to illegal ranching, narcotrafficking activities, and plantations of exotic trees and other plants (Dávalos et al. 2011; Medina-Fitoria and Turcios-Casco 2019; Martínez et al. 2020).

The bat fauna of Honduras remains poorly known, despite the importance of bats in all of these ecosystems (Turcios-Casco et al. 2020g). The two primary references available regarding the bats of Honduras are Goodwin (1942) and McCarthy et al. (1993), and mainly based on their efforts, the basic distribution of bats in Honduras came to be understood between 1950 and 2000 [see Turcios-Casco et al. (2020g) for a brief resume of the history of bat studies in Honduras]. McCarthy et al. (1993) attributed the first significant collection of bats in northern Central America to O. Salvin and F. D. Godman, who increased (Alston 1879–82) the number of species in Nicaragua and Guatemala. The history of bat research in Central America has led to confusion concerning the localities of some specimens, especially from Belize, because Belize was previously known as British Honduras (McCarthy et al. 1976). However, Honduras was a term generally used to refer to the region that extends from southern Quintana Roo in Mexico, southeastward to northern Honduras in the 19th century (McCarthy 1987; McCarthy et al. 1993). According to McCarthy et al. (1993), G. F. Gaumer, on behalf of O. Salvin and F. D. Godman, collected bats from the islands off the coast of the Yucatán Peninsula and the Bay of Honduras. McCarthy et al. (1993) also attribute to G. F. Gaumer the first reported bat specimens from the Honduran island of Roatán, including specimens of *Artibeus jamaicensis*, *Glossophaga soricina*, *Molossus*

*molossus*, and *Saccopteryx bilineata* (Thomas 1888; McCarthy et al. 1993). In 1887, when Gaumer was on Roatán, Islas de la Bahía, he met C. H. Townsend, and even though Townsend had more interest in the bird fauna of the Islas del Cisne and the Mosquitia Coast (Monroe 1968), he made a substantial mammal collection including the holotype of *Ectophylla alba*, described by Allen (1892). After Goodwin (1942), the main reference for the bats of each Central American country until the late 1990s was McCarthy et al. (1993), which listed 99 bat species from Honduras.

Bats have gained more attention during the 2000s, but certain types of studies are lacking. For

example, currently there are no population studies of any bat species in Honduras. Additionally, there are no vouchers to confirm the occurrence of many bat species expected in the country based on literature records (e.g., *Glyphoncycteris daviesi*, *Tadarida brasiliensis*, *Eptesicus brasiliensis*). Most of the vocalization records that have been collected recently are due to the efforts of the PCMH (Programa para la Conservación de Murciélagos de Honduras). Most of the specimens in collections have never been published, so compiling this data is the first step in documenting their occurrence in the country. Thus, the first checklist of bats for each department in the country is provided herein.

## METHODS

The database of the Global Biodiversity Information Facility ([www.GBIF.org](http://www.GBIF.org) 2020) was used as the basis for the occurrence of bats in Honduras (Fig. 1), including more than 9,100 records. Additionally, records were obtained from [www.inaturalist.org](http://www.inaturalist.org) (2020) but were used only if they included photos that showed distinguishable features that could verify identifications. All records lacking geographic coordinates and/or known locality data were excluded. Further, a search on Google Scholar was conducted for documents referring to the bats of Honduras, with the concepts: bats + Chiroptera + Honduras + Central America. Again, the records of species that could not be verified, lacked reliable data (e.g., manuscripts with no description of how specimens were identified), or without the year of the record, were excluded. The following works were used for the analyses: Goodwin (1940), Sanborn (1941), Goodwin (1942), Rinker (1948), Davis and Carter (1964), Davis et al. (1964), Carter et al. (1966), LaVal (1969), Valdez and LaVal (1971), Pine (1972), LaVal (1973), Greenbaum and Jones (1978), Dolan and Carter (1979), Benshoof et al. (1984), Dolan (1989), Lee and Bradley (1992), McCarthy et al. (1993), Birmingham et al. (1998), Estrada-Villegas et al. (2007), Mora and López (2010), Espinal and Mora (2012), Mora (2012), Dick (2013), Divoll and Buck (2013), PCMH (2013), Mérida and Cruz (2014), Mora et al. (2014), Miller (2014), Hernández et al. (2016), Espinal et al. (2016), Mora et al. (2016), Portillo Reyes et al. (2015, 2016), Gilroy (2017), Bocanegra et al. (2017), PCMH (2018a,b), GBIF.org (2019), Medina-Fitoria and Tur-

cios-Casco (2019), PCMH (2019), Turcios-Casco and Medina-Fitoria (2019), Turcios-Casco et al. (2019a,b), Ávila-Palma et al. (2019, 2020), iNaturalist.org (2020), Medina-Fitoria et al. (2020), Ordoñez-Mazier et al. (2020), and Turcios-Casco et al. (2020a,b,c,d,e,f,g,h).

New records based on the sampling efforts of the first and last author also were added to the records obtained from the published literature and GBIF data. This information was used to create a relative abundance dataset of the 113 species that are known to occur in Honduras, comprised of data from 1860 to 2020. Species richness was estimated based on the estimators Chao 1, ACE, and Bootstrap using the software EstimateSMac 910 with 100 randomizations to eliminate the specific order of the data (Colwell and Coddington 1994; Colwell 2013). Additionally, the Shannon-Wiener and the True Diversity indexes were estimated for Honduras, with the same software [considering the latter as the exponential of the inverse of the Shannon-Wiener index (Jost 2006)]. Finally, the species were represented as relative abundance with a range-abundance graph using logarithm of base 10.

For taxonomy, Wilson and Mittermeier (2019) was followed with modifications based on the most recent revisions regarding the bats of Honduras (Turcios-Casco et al. 2020g). *Micronycteris minuta* and *M. tresamici* were treated as conspecific because Siles and Baker (2020) recommended that both species be evaluated to determine if they are sympatric or allopatric.

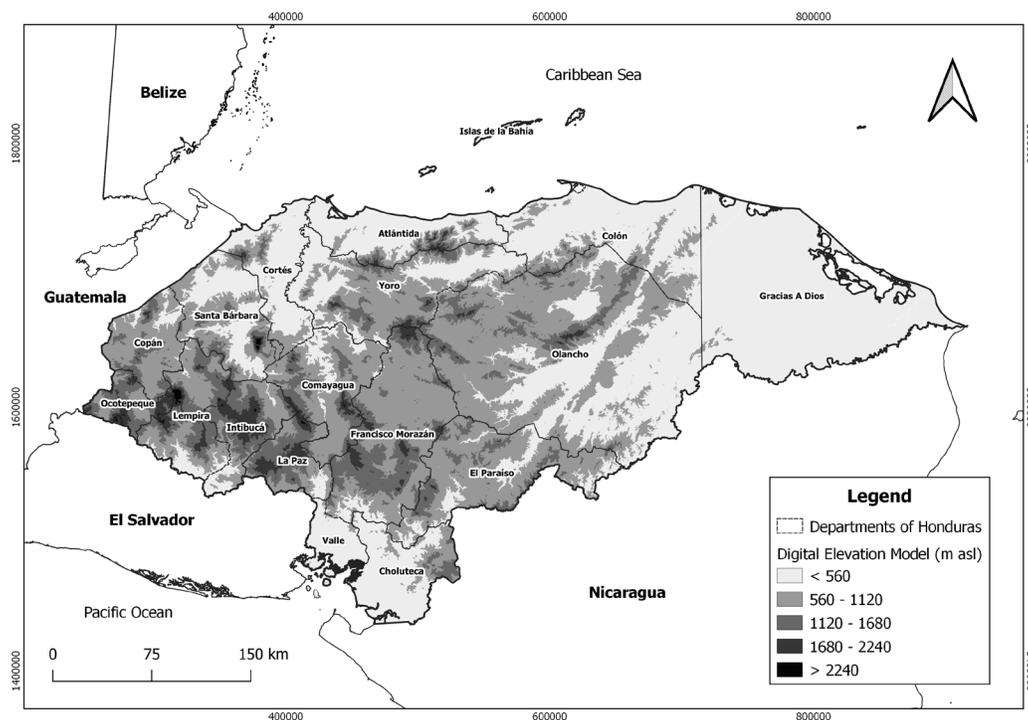


Figure 1. Map of Honduras depicting departments and elevation. Note that the highest elevations in Honduras are in the western region of the country.

## RESULTS

For the years 1860 to 2020, a total of 11,163 records were compiled of the 113 species in Honduras (Table 1). Of these, 32.7% of the species are known from five or fewer records. Of the 10.6% of species that are known only from a single record, three species (*Centronycteris centralis*, *Diaemus youngii*, and *Glyphonycteris daviesi*) were reported in the published literature but lack museum specimens. Only 20.4% of the species are known from more than 100 records in Honduras. *Artibeus jamaicensis* ( $n = 1,287$ ), *Glossophaga soricina* ( $n = 1,022$ ), and *Sturnira parvidens* ( $n = 862$ ) have been recorded most frequently with more than 28.4% of the records. Many species (44.2%) are known from ten or fewer records. By family, Phyllostomidae has the most records (79.3%), followed by Mormoopidae (5.8%), Molossididae (5.4%), Emballonuridae (4.0%), Vespertilionidae (3.3%), Natalidae (0.8%), and Thyropteridae (0.1%).

These numbers are supported by the Shannon-Wiener (evenness of diversity) and True Diversity

(diversity) indexes, respectively, with 3.53 and 20.93 (Fig. 2). Based on the estimator indices, between 63.7% (Bootstrap) and 94.7% (ACE) of the expected number of species were recorded that may occur in Honduras (Fig. 2), which indicates that with more sampling effort additional species may be found. Of the 18 departments of Honduras, Cortés ( $n = 70$ ) and Olancho ( $n = 66$ ) are the most diverse, followed by Atlántida ( $n = 58$ ), Francisco Morazán ( $n = 54$ ), and Choluteca and Gracias a Dios with 49 species each. The least diverse, without considering Islas de la Bahía (a group of islands;  $n = 12$ ), are Ocotepeque ( $n = 18$ ), Intibucá ( $n = 23$ ), Yoro ( $n = 25$ ), and La Paz ( $n = 26$ ). The three most important years for bat research, based on the number of individuals captured in each, were 1967 ( $n = 2,125$ ), 1983 ( $n = 1,128$ ), and 2001 ( $n = 1,026$ ), comprising almost half (38.3%) of all the captured individuals (Figs. 3–4).

Table 1. Bat species recorded in Honduras by department. New records reported here based on the efforts of the authors are represented by a red X.

Family/Species	Atlántida	Choluteca	Colón	Comayagua	Copán	Cortés	El Paraíso	Francisco Morazán	Gracias a Dios	Intibucá	Islas de la Bahía	La Paz	Lempira	Ocotepeque	Olancho	Santa Bárbara	Valle	Yoro	Individuals	Relative Abundance
<b>Emballonuridae</b>																				
<i>Balantiopteryx io</i>				X															6	0.0005
<i>Balantiopteryx plicata</i>		X		X				X								X	X		168	0.0150
<i>Centronycteris centralis</i>			X																1	0.0001
<i>Diclidurus albus</i>					X	X			X									X	4	0.0004
<i>Peropteryx kappleri</i>				X	X	X		X				X				X			24	0.0021
<i>Peropteryx macrotis</i>							X	X							X		X		58	0.0052
<i>Rhynchonycteris naso</i>	X		X		X	X	X	X	X						X	X	X		79	0.0071
<i>Saccopteryx bilineata</i>	X	X			X	X	X	X	X		X				X		X	X	89	0.0080
<i>Saccopteryx leptura</i>	X	X	X								X						X		23	0.0021
<b>Phyllostomidae</b>																				
<i>Desmodus rotundus</i>	X	X	X	X	X	X	X	X	X	X					X	X	X	X	375	0.0336
<i>Diaemus youngii</i>			X																1	0.0001
<i>Diphylla ecaudata</i>	X	X	X		X	X		X		X				X	X	X	X		52	0.0047
<i>Anoura geoffroyi</i>	X			X	X	X	X	X		X				X	X				40	0.0036
<i>Choeroniscus godmani</i>	X	X		X	X	X	X	X		X									25	0.0022
<i>Choeronycteris mexicana</i>						X		X											2	0.0002
<i>Glossophaga commissarisi</i>	X	X		X	X	X	X	X	X						X	X	X		164	0.0147
<i>Glossophaga leachii</i>	X	X	X	X	X	X	X	X		X				X		X	X		76	0.0068
<i>Glossophaga soricina</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	1,022	0.0916
<i>Hylonycteris underwoodi</i>	X					X		X	X						X				9	0.0008

Table 1. (cont.)

Family/Species	Atlántida	Choluteca	Colón	Comayagua	Copán	Cortés	El Paraíso	Francisco Morazán	Gracias a Dios	Intibucá	Islas de la Bahía	La Paz	Lempira	Ocatepeque	Olancho	Santa Bárbara	Valle	Yoro	Individuals	Relative Abundance
<i>Leptoncyteris yerbabuena</i>		X															X		7	0.0006
<i>Lichonycteris obscura</i>															X				2	0.0002
<i>Chrotopterus auritus</i>	X				X				X						X			X	15	0.0013
<i>Glyphonycteris daviesi</i>																			1	0.0001
<i>Glyphonycteris sylvestris</i>			X																6	0.0005
<i>Lonchorhina aurita</i>			X			X		X			X					X			11	0.0010
<i>Lophostoma brasiliense</i>	X			X		X	X		X							X			23	0.0021
<i>Lophostoma evotis</i>	X																		3	0.0003
<i>Lophostoma sylvicolum</i>	X								X						X				7	0.0006
<i>Macrophyllum macrophyllum</i>	X						X		X						X	X			6	0.0005
<i>Micronycteris hirsuta</i>	X						X		X						X				5	0.0004
<i>Micronycteris microtis</i>	X	X	X	X		X	X	X	X				X		X	X			56	0.0050
<i>Micronycteris minuta</i>	X													X					7	0.0006
<i>Micronycteris schmidtorum</i>	X										X					X			9	0.0008
<i>Mimon cozumelae</i>	X		X			X			X						X				21	0.0019
<i>Gardnerycteris keenani</i>									X	X					X				1	0.0001
<i>Phylloderma stenops</i>								X	X	X					X				7	0.0006
<i>Phyllostomus discolor</i>	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X	X		251	0.0225
<i>Phyllostomus hastatus</i>	X	X	X			X			X			X			X	X		X	68	0.0061
<i>Tonatia bakeri</i>	X								X										10	0.0009
<i>Trachops cirrhosus</i>	X		X			X			X				X						55	0.0049

Table 1. (cont.)

Family/Species	Atlántida	Choluteca	Colón	Comayagua	Copán	Cortés	El Paraíso	Francisco Morazán	Gracias a Dios	Intibucá	Islas de la Bahía	La Paz	Lempira	Ocatepeque	Olancho	Santa Bárbara	Valle	Yoro	Individuals	Relative Abundance
<i>Vampyrum spectrum</i>	X								X						X				5	0.0004
<i>Carollia castanea</i>	X		X		X	X	X	X	X						X				121	0.0108
<i>Carollia perspicillata</i>	X	X	X	X	X	X	X	X	X	X					X	X			688	0.0616
<i>Carollia sowelli</i>	X	X	X	X	X	X	X	X	X	X					X	X			613	0.0549
<i>Carollia subrufo</i>	X	X	X	X	X	X	X	X	X						X	X			163	0.0146
<i>Sturnira parvidens</i>	X	X	X	X	X	X	X	X	X	X					X	X			862	0.0772
<i>Sturnira hondurensis</i>	X			X	X	X	X	X	X	X					X				340	0.0305
<i>Artibeus inopinatus</i>		X		X			X	X		X						X			474	0.0425
<i>Artibeus jamaicensis</i>	X	X	X	X	X	X	X	X	X	X					X	X			1,287	0.1153
<i>Artibeus intermedius</i>	X		X	X	X	X		X		X									11	0.0010
<i>Artibeus lituratus</i>	X	X	X	X	X	X	X	X	X	X					X	X			648	0.0580
<i>Dermanura azteca</i>		X		X		X		X		X					X				13	0.0012
<i>Dermanura phaeotis</i>	X	X	X	X	X	X	X	X	X	X					X	X			180	0.0161
<i>Dermanura tolteca</i>	X	X	X	X	X	X	X	X	X	X					X	X			160	0.0143
<i>Dermanura watsoni</i>	X	X		X		X		X	X						X	X			94	0.0084
<i>Centurio senex</i>	X	X	X	X	X	X	X	X	X	X					X	X			58	0.0052
<i>Chiroderma salvini</i>		X		X	X	X	X	X	X						X	X			121	0.0108
<i>Chiroderma gorgasi</i>								X											2	0.0002
<i>Chiroderma villosum</i>	X	X		X		X	X	X	X	X					X	X			53	0.0047
<i>Ectophylla alba</i>								X							X				23	0.0021
<i>Enchisthenes hartii</i>		X		X		X	X	X											6	0.0005

Table 1. (cont.)

Family/Species	Atlántida	Cholulteca	Colón	Comayagua	Copán	Cortés	El Paraíso	Francisco Morazán	Gracias a Dios	Intibucá	Islas de la Bahía	La Paz	Lempira	Ocatepeque	Olancho	Santa Bárbara	Valle	Yoro	Individuals	Relative Abundance
<i>Platyrrhinus helleri</i>	X	X	X	X			X		X				X		X				63	0.0056
<i>Uroderma convexum</i>	X	X	X				X		X	X					X	X			300	0.0269
<i>Uroderma davisi</i>						X				X							X		161	0.0144
<i>Uroderma magnirostrum</i>		X															X		9	0.0008
<i>Vampyressa thyone</i>	X				X	X			X						X				28	0.0025
<i>Vampyriscus nymphaea</i>														X	X				1	0.0001
<i>Vampyrodes major</i>	X			X		X	X		X						X				35	0.0031
<b>Mormoopidae</b>																				
<i>Mormoops megalophylla</i>	X	X		X		X		X				X			X	X		X	48	0.0043
<i>Pteronotus psilotis</i>		X		X	X	X							X	X	X	X			71	0.0064
<i>Pteronotus fulvus</i>	X	X	X	X	X	X	X	X		X		X		X	X	X		X	156	0.0140
<i>Pteronotus gymnonotus</i>				X		X	X	X							X			X	10	0.0009
<i>Pteronotus mesoamericanus</i>	X	X	X	X	X	X		X	X	X		X	X	X	X	X		X	362	0.0324
<b>Noctilionidae</b>																				
<i>Noctilio leporinus</i>	X					X			X		X				X	X		X	36	0.0032
<i>Noctilio albiventris</i>	X					X	X		X						X		X		92	0.0082
<b>Thyropteridae</b>																				
<i>Thyroptera tricolor</i>						X		X	X										13	0.0012
<b>Natalidae</b>																				
<i>Natalus mexicanus</i>		X		X	X	X	X	X							X	X			85	0.0076
<i>Natalus lanatus</i>						X		X											2	0.0002

Table 1. (cont.)

Family/Species	Relative Abundance	Individuals	Yoro	Valle	Santa Bárbara	Olancho	Ocatepeque	Lempira	La Paz	Islas de la Bahía	Intibucá	Gracias a Dios	Francisco Morazán	El Paraíso	Cortés	Copán	Comayagua	Colón	Choluteca	Atlántida	
<b>Molossidae</b>																					
<i>Cynomops greenhalli</i>	0.0001	1															X				
<i>Cynomops mexicanus</i>	0.0004	4																X	X	X	
<i>Eumops auripendulus</i>	0.0011	12			X											X					
<i>Eumops nanus</i>	0.0001	1										X									
<i>Eumops ferrox</i>	0.0006	7							X		X		X				X				
<i>Eumops hansae</i>	0.0001	1																		X	
<i>Eumops underwoodi</i>	0.0004	5							X										X		
<i>Molossus aztecus</i>	0.0005	6							X												
<i>Molossus bondae</i>	0.0007	8							X			X						X			
<i>Molossus molossus</i>	0.0011	12						X		X		X	X					X	X	X	
<i>Molossus nigricans</i>	0.0262	292							X	X			X	X			X	X	X	X	
<i>Molossus alvarezi</i>	0.0222	248											X	X			X	X		X	
<i>Nyctinomops aurispinosus</i>	0.0001	1																	X		
<i>Nyctinomops laticaudatus</i>	0.0001	1																			
<i>Nyctinomops macrotis</i>	0.0002	2																	X		
<i>Promops centralis</i>	0.0004	4									X										
<i>Tadarida brasiliensis</i>	0.0003	3																			
<b>Vespertilionidae</b>																					
<i>Eptesicus brasiliensis</i>	0.0001	1													X				X	X	
<i>Eptesicus furinalis</i>	0.0082	92																	X	X	

Table 1. (cont.)

Family/Species	Atlántida	Choluteca	Colón	Comayagua	Copán	Cortés	El Paraíso	Francisco Morazán	Gracias a Dios	Intibucá	Islas de la Bahía	La Paz	Lempira	Ocatepeque	Olancho	Santa Bárbara	Valle	Yoro	Individuals	Relative Abundance
<i>Eptesicus fuscus</i>	X						X	X		X									25	0.0022
<i>Lasiurus frantzii</i>					X	X	X	X					X						5	0.0004
<i>Lasiurus cinereus</i>								X											1	0.0001
<i>Lasiurus egregius</i>														X					2	0.0002
<i>Lasiurus ega</i>		X		X		X		X		X						X	X		16	0.0014
<i>Lasiurus intermedius</i>								X	X					X			X		2	0.0002
<i>Rhogeessa bickhami</i>		X		X			X	X	X			X					X		79	0.0071
<i>Rhogeessa menchuae</i>	X				X	X									X	X		X	10	0.0009
<i>Perimysotis subflavus</i>	X	X												X	X				6	0.0005
<i>Bauerus dubiaquercus</i>						X								X	X				4	0.0004
<i>Myotis albescens</i>	X	X				X										X			12	0.0011
<i>Myotis elegans</i>	X				X										X	X			7	0.0006
<i>Myotis pilosatibialis</i>		X				X		X					X		X	X	X		70	0.0063
<i>Myotis nigricans</i>		X			X	X	X		X			X	X		X	X	X		28	0.0025
<i>Myotis riparius</i>							X		X						X				7	0.0006
<i>Myotis velifer</i>						X		X						X					5	0.0004
TOTAL	58	49	33	42	30	70	43	54	49	23	12	26	30	18	66	47	37	25	11,163	1

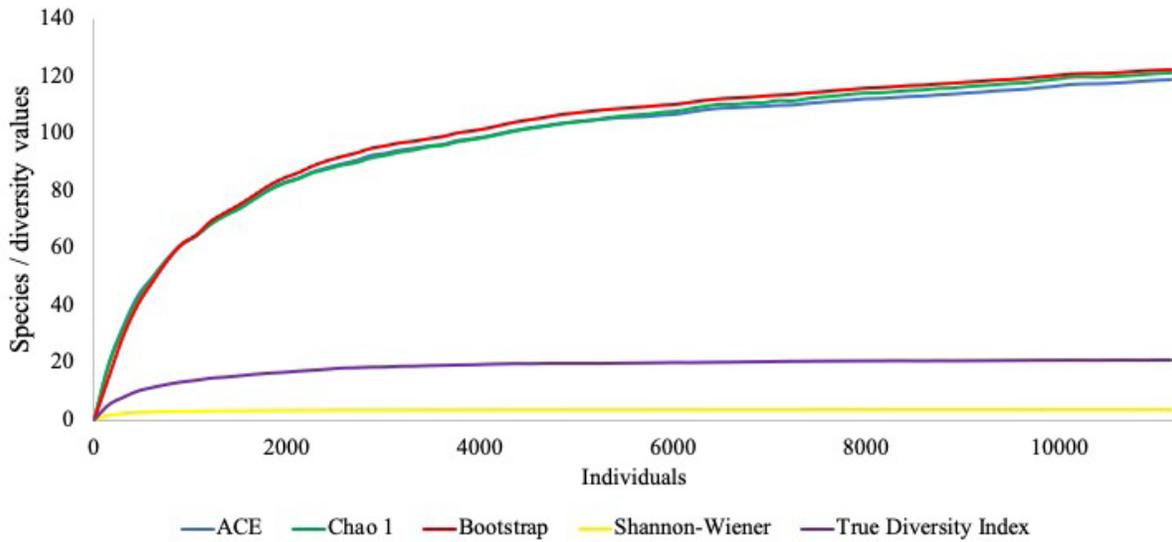


Figure 2. Accumulation curves of estimators and diversity indexes based on the 11,163 individuals that were found in the literature. Note that the estimator indexes have not reached the asymptote.

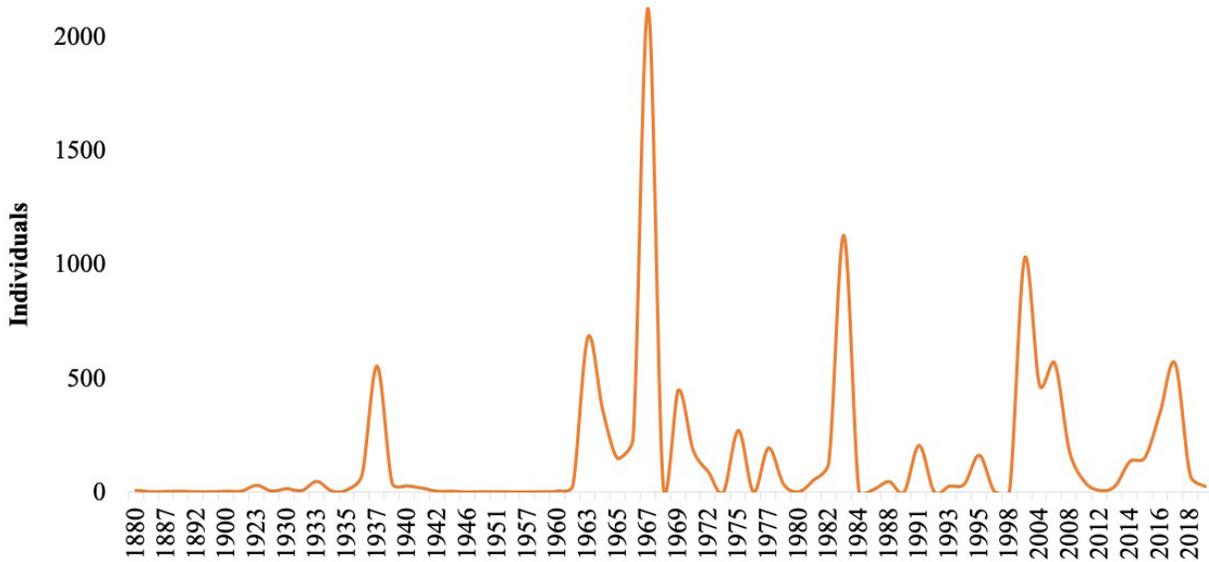


Figure 3. Fluctuations of the number of individuals recorded each year since 1860. Note the three largest peaks in Honduran bat research history in 1967–69, 1983, and 2001.

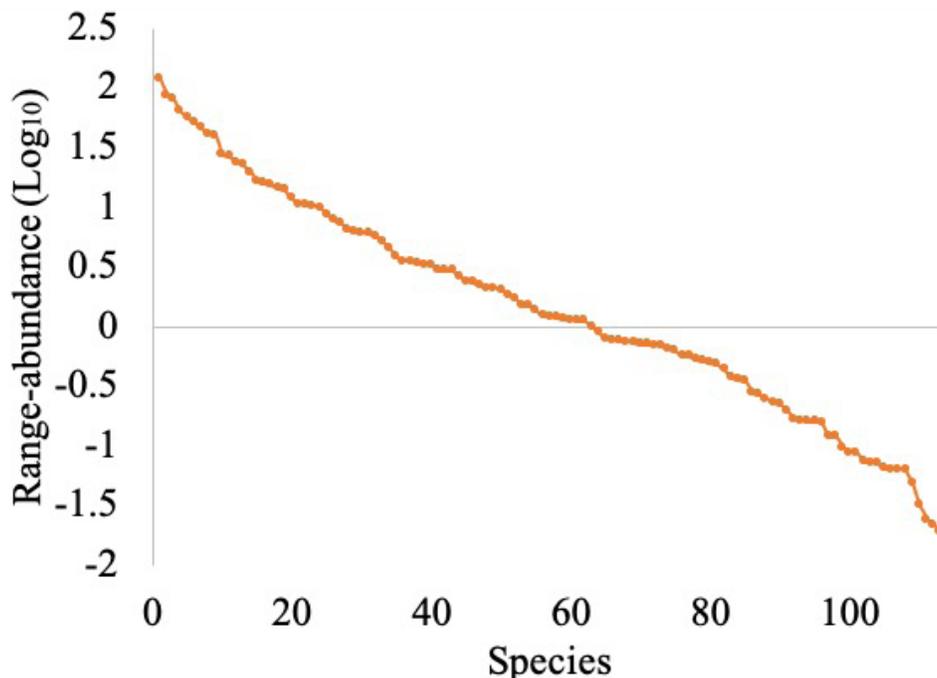


Figure 4. Range abundance of the 113 bat species of Honduras based on logarithm of base 10.

## DISCUSSION

*Diversity, geography, and history of the bats of Honduras.*—In reviewing the 160 years of bat research in Honduras, phyllostomid bats are the group with the most records. One reason may be that most of the collecting done in the country has been by mist-netting, and much less has been directed toward searching for bat roosts, making audio recordings of echolocation calls, mark and recapture, using harp traps, or searching for bat caves. Among the leaf-nose bats, frugivorous species (*A. jamaicensis* and *S. parvidens*) are responsible for the most records (19.3%), followed closely by the nectarivore/omnivore *G. soricina*. In this review, only *A. jamaicensis* and *G. soricina* were found to be distributed in all 18 departments. Ten species are known only from one department (*Centronycteris centralis*, *Diaemus youngii*, *Gardnerycteris keenani*, *Glyphonycteris daviesi*, *Eumops hansae*, *E. nanus*, *Vampyriscus nymphaea*, *Nyctinomops aurispinosus*, *N. macrotis*, and *Lasiurus cinereus*). Literature records of insectivorous species often provide only occurrence data without quantifying the number of individuals.

Two families are known by relatively few records: Natalidae with 87 and Thyropteridae with 13.

Individuals of both families are difficult to capture in mist nets, suggesting that their scarcity may be due to a lack of searching for roosting sites. On the other hand, the relative abundance of certain insectivorous groups (emballonurids, molossids, and vespertilionids) may not be represented accurately by the specimen records available, for two reasons. First, there have been no studies using canopy or subcanopy nets to capture and study insectivorous bats in Honduras. Secondly, there has been a lack of appropriate sampling effort in some cases. For example, *Tadarida brasiliensis*, one of the most widely distributed molossid bats (Cleveland et al. 2006) is represented only by three records in this study. Roost sites in Central America may differ from the common cave roosts in North America (e.g., RKL has only seen one live specimen of *T. brasiliensis* in Costa Rica in 47 years). It is almost certain that the knowledge of the distribution of the species in these three insectivorous families will be greatly augmented once comprehensive audio recording has been carried out. Common species play an important role in seed dispersal and pollination (Kunz et al. 2011), as documented by the abundance of *A. jamaicensis*, *G. soricina*, in Honduran forests.

In comparison to the number of species documented in Colombia (209 – Ramírez-Chaves et al. 2020), Brazil (181 – Garbino et al. 2020), Peru (187 – Velazco 2020), Ecuador (176 – Tirira et al. 2020), and Mexico (140 – Ramírez-Pulido et al. 2014; Rivas-Camo et al. 2020), the bat diversity of Honduras may seem less impressive. However, considering the relatively small area of Honduras and its geographic location (Medina-Fitoria et al. 2020), the number of species is significant. With 113 species that have been confirmed in the country, it is the third most bat-diverse country in Central America behind only Panama (118 species – Samudio and Pino 2014) and Costa Rica (120 species – York et al. 2019). If more species of probable occurrence as mentioned by Hernández (2015), Mora et al. (2018), and Turcios-Casco et al. (2020g) are added, there may be six to nine more species. The “three great moments” in the bat history of Honduras are 1967–69, 1983, and 2001. Considering the efforts after 2001, fewer than 24% of the records have been reported recently, and no other peak has yet been reached. Most of the collecting efforts causing those big peaks were conducted by international researchers (e.g., the biggest museum collections holding Honduran specimens are at Texas Tech University and Texas A&M University).

Richard K. LaVal and colleagues collected specimens in Honduras in 1969, but field work was interrupted by the football war between Honduras and El Salvador. Although the war only lasted from 14 to 18 July of 1969 (approximately 100 hours), most of the economic and social activities ceased for both countries (Kapusinski 1990), and at the time, most of the researchers that were in the country were forced to leave. Had the war not happened, 1969 may have been another peak in Honduran bat research history. For example, the records presented by Valdez and LaVal (1971) were collected in the summer of 1969, before the war.

Another interesting remark was made by Goodwin (1942:108) when he presented the results of the collection made by Cecil F. Underwood. He stated “Mr. Underwood was greatly indebted to the President of Honduras, General Tiburcio Carías. Both the president and his wife, Dona Elena, treated him with exceptional good will officially and personally.” This statement is important in the mammalian history of Honduras because it suggests the interest of political entities at least in the early 1900s.

*Species counts from the most diverse departments to the least diverse.*—Medina-Fitoria et al. (2020) reported 57 species for the Caribbean side of Honduras (including Gracias a Dios and Colón) and Nicaragua, of which 40 were recorded from Honduras. We list 49 species for Gracias a Dios, and it could be one of the most important for conservation. It includes Río Plátano Biosphere Reserve (RPBR) (Hernández 2015; Portillo-Reyes et al. 2015; Mora et al. 2018; Ávila-Palma et al. 2019; Martínez et al. 2020; Ordoñez-Mazier et al. 2020; Turcios-Casco et al. 2020a,b,c,h), the region with the most pristine and unstudied areas of Honduras (Martínez et al. 2020; Turcios-Casco et al. 2020h). It contains species that are considered of special interest because of rarity, such as *Gardnerycteris keenani* and *Macrophyllum macrophyllum*. Probably the conservation of bats in the RPBR would be even more effective because it comprises three departments Olancho, Colón, and Gracias a Dios.

In contrast, the western region still is one of the least studied and even with the efforts of Goodwin (1940, 1942), the bats of this region remain poorly known, especially in Ocotepeque and Intibucá. Additionally, the western regions have the highest mountains in Honduras, in Lempira (2849 m asl) and Santa Bárbara (2770 m asl) (McCranie and Castañeda 2007). However, La Paz, Intibucá, Copán, and Ocotepeque also have regions of high elevations (> 1500 m asl) (Goodwin 1942; McCarthy et al. 1993; McCranie and Castañeda 2007). Collecting at these high elevations [e.g., most of the records provided by Goodwin (1940, 1942) were collected in La Paz] where the sampling effort has been low, could augment the diversity that is known from this region, especially for phyllostomid bats (Arias-Aguilar et al. 2020). As shown elsewhere, in Cusuco National Park, there are many species at these higher elevations (Medina-Van Berkum et al. 2020), some of them found only at high elevations.

The archipelago of Islas de la Bahía is part of the mountainous complex of Nuclear America from the Sierra Madre in Chiapas, Mexico, to the Sierra de Omoa in Cortés, Honduras (Harborne et al. 2001; McCranie and Castañeda 2007). The islands closest to the mainland (Cayos Cochino and Utila) are part of the continental mass, and they became separated from the mainland between 13,000 and 18,000 years ago; Guanaja and Roatán are part of the oceanic platform (McCranie and Castañeda 2007), and the majority of

the bat records of this department are from Roatán. However, there are no studies suggesting the possibility of endemic subspecies or species in the region.

An important area of species richness is Francisco Morazán, the department of the capital, Tegucigalpa, and one of the most urbanized (Jansen et al. 2005). Records for many species are based on their earlier occurrence, for example *Phylloderma stenops* and *Thyroptera tricolor*. According to Goodwin (1942) they were recorded from near Tegucigalpa, in Las Flores Archaga and San Marcos de Guaimaca, respectively. McCarthy et al. (1999) mentioned how von Hagen (1940) observed and captured a three-toed sloth (*Bradypus variegatus*) which had been previously attacked by a harpy eagle (*Harpia harpyja*) in the Montaña de la Flor in northern Francisco Morazán. Three of these four species are dependent on primary forests, whereas *P. stenops* is also known from other habitat types such as llanos, xeric shrubs, and dry forests in Colombia (Martínez-Cerón et al. 2019). However, none of these species has been recorded recently in the department. Additionally, the other two most industrialized departments, Atlántida and Cortés, were among the most diverse. In contrast to Francisco Morazán, they still contain remnants of well conserved forest sustained in protected areas, such as Lancetilla Botanical Garden in Atlántida and Cusuco National Park in Cortés. Based on the recent work of Medina-Van Berkum et al. (2020), Cusuco National Park contains 59 bat species, containing 52.2% of the bat diversity of Honduras. Cortés department, the most diverse department regarding richness, includes the Sula Valley, which is a mixture of lowlands connected with the highlands of Comayagua and Santa Bárbara, and the limits of the largest natural lake of Honduras, Lago de Yojoa. Additionally, two of the most important rivers of Honduras, the Ulúa and Motagua, cross the department. The northern limits of Cortés border on the Atlantic Ocean. All this diverse geography creates different mountainous regions throughout the department, creating different ecosystems and housing different bat species. If the efforts of Medina-Van Berkum et al. (2020) are augmented by recording of bat vocalizations and searches for bat tents and roosts, the number of species in Cusuco National Park will almost certainly increase. Undoubtedly, this National Park is among the most important protected areas for bat conservation in Honduras. Choluteca is an important area for bat conservation as well, consid-

ering its habitats (e.g., from dry to transitional forest). Despite its high species richness and important records (e.g., *Leptonycteris yerbabuena* and *Artibeus inopinatus*), the region still needs more scientific research (Mora et al. 2018).

Of the bat species that are known from fewer than eleven records (excluding *Thyroptera tricolor* with 13 and *Ectophylla alba* with 23), special attention should be given to searching for *Bauerus dubiaquercus*, *Choeronycteris mexicana*, *Diaemus youngii*, *Gardnerycteris keenani*, *Glyphonycteris daviesi*, *Leptonycteris yerbabuena*, *Lichonycteris obscura*, *Lophostoma evotis*, *Macrophyllum macrophyllum*, *Micronycteris hirsuta*, *Perimyotis subflavus*, and *Vampyrum spectrum*. The reason for *Bauerus dubiaquercus*, *Ectophylla alba*, *Leptonycteris yerbabuena*, and *Perimyotis subflavus* being listed is that internationally, the first three are categorized as Near Threatened and the last as Vulnerable (Rodríguez and Pineda 2015; Medellín 2016; Solari 2018a,b). *Diaemus youngii* was recently reported but its occurrences have been debated since the first bat checklist for Honduras (Turcios-Casco et al. 2020g). *Choeronycteris mexicana* and *Lichonycteris obscura* are nectarivorous species that have not been recorded since 1971 (GBIF.org 2019) and 2001 (GBIF.org 2020), respectively, and they are currently affected by anthropogenic disturbance. The other species are sensitive based on their specific roosting requirements, (e.g., *Lophostoma evotis*, *Thyroptera tricolor*, and *Uroderma magnirostrum*) (Rodríguez-Herrera et al. 2007; Garbino and Tavares 2018), intolerance to disturbance (*Micronycteris hirsuta* and *Vampyrum spectrum*) (Medellín et al. 2000), and dependence on primary forests or on a specific habitat (*Macrophyllum macrophyllum*). All these species are very uncommon or rare in Honduras and throughout their range. In the case of *Artibeus inopinatus*, Honduras holds the northern-most records of the species (Turcios-Casco et al. 2020f,g). It has a very restricted distribution in Central America (Reid and Medina 2016), and there are no population studies (Turcios-Casco et al. 2020e,f).

*Main threats and recommendations.*—A surprising discovery was that *Artibeus inopinatus* was ranked seventh in number of records in Honduras. Currently, its distribution is restricted to Nicaragua, El Salvador, and Honduras (Reid 2009; Reid and Medina 2016; Turcios-Casco et al. 2020e,f) and it is categorized as Data

Deficient (DD) by the IUCN (Reid and Medina 2016). Specimen records indicate the species is common in some parts of the country [e.g., the suburban region of Sabanagrande in south-central Honduras (Ávila-Palma et al. 2020; Turcios-Casco et al. 2020e,f,g)]. Studies of population trends of *A. inopinatus* are recommended in order to determine its status in Honduras.

A recent threat to bats in Honduras is wind turbines. Mora et al. (2018) considered *Lasiurus ega*, *L. frantzii*, *L. intermedius*, and *Balantiopteryx plicata* as the species most frequently killed by these machines, and three new records were added to the Honduran fauna based on deaths at wind farms; *Lasiurus cinereus*, *Nyctinomops aurispinosus*, and *Nyctinomops macrotis*. More information is needed to understand this phenomenon, but see Mora et al. (2018) for recommendations for wind farms.

Areas of extensive ranching contain barbed-wire fences for the delimitation of properties and control of movements of livestock. It is common to see bats (e.g., specimens of *A. lituratus* and *Centurio senex*) impaled on these fences in cattle-raising areas. Of the five records of *Vampyrum spectrum* that are known from Honduras, one was reported by McCarthy et al. (1993:200) as “a dried carcass was found hanging from a barbed wire fence”.

Extensive audio recordings throughout the country are recommended to learn more about the species of insectivorous bats present, their distribution, and their relative abundance. Searches for bat tents, and for roost sites like tree hollows, caves, and buildings, will add more information on the distribution of many species.

Each Life Zone in Honduras is facing its own type of threat. However, there are some threats that are happening in several Life Zones. For example, both moist [in eastern Honduras, see Turcios-Casco et al. (2020a,g,h)] and dry forests [in western Honduras, see Turcios-Casco et al. (2019a)] have been affected by excessive ranching and changes of the landscape to agricultural fields. But, whereas the dry forests are affected by bushfires, moist forests are being affected by the raising of exotic plants and illegal access to the core zone, especially by hunters. Exotic plant crops are known to change land use in protected areas; for example, HDAP recently encountered a cardamom farm

in the core zone of National Park Cusuco. Coffee plantations are another issue of concern. Of major impact is logging of forests to plant grass for cattle grazing, or for marijuana crops; these are common in the department of Colón. Considering this, the impact of hunters (e.g., such as destroying tents and/or refuges of some bat species) may be minimal compared to the aforementioned impacts on habitat. However, all of these activities are threats to bat populations. For example, in eastern Honduras, hunters make their camp beds and shelters using leaves of Araceae and Aracaceae, plants that are often used as tents by stenodermatine bats (Rodriguez et al. 2007). In eastern Honduras, sometimes tents of *Ectophylla alba* are destroyed or altered by native people because the heliconias used for these tents are considered to be weeds in their crops. The pine forests of Honduras are periodically affected by pests. For example, from 1962 to 1965, more than two million hectares were affected by the bark beetle, *Dendroctonus frontalis* (Billings et al. 2004). Species of special interest such as *Artibeus inopinatus* have been recorded in pine forest in Honduras (Turcios-Casco et al. 2020f). In general, an estimated 122,061,763 board feet of wood are extracted each year (ICF 2017). The cloud forest of Cusuco National Park might also be affected by deforestation (Medina-Van Berkum et al. 2020), and CONADEH (2015) documented more than 80,000 ha of Honduran forests affected by fires in 2014.

Among natural events, hurricanes are one of the biggest disasters affecting Honduras. Two of the destructive hurricanes that have impacted the Central American region are Hurricane Fifi-Orlene in 1974 and Hurricane Mitch in 1998. In the first, more than 10,000 people died, in the latter between one and two million people became homeless (Glantz and Jamieson 2000). Obviously, these events also affected many species, however, there were no attempts to estimate damages to specific taxonomic groups. More recently, hurricanes Eta and Iota both struck Honduras in November 2020. Damage, although extensive, is still being assessed. While reviewing the historical occurrence of bats in Honduras, we found that the apparent abundance of bats from 1860 to 1972 (before Hurricane Fifi-Orlene) was lower than after Hurricane Fifi-Orlene (1976 to 2020). However, the apparent abundance of Mormoopidae, Noctilionidae, Natalidae, Molossidae, and Vespertilionidae was lower after hurricane Fifi-Orlene (Table 2). There also was a reduction when comparing the

Table 2. Comparison of the relative abundance before and after Hurricane Fifi-Orlene and Hurricane Mitch. Records from each event, 1974 and 1998, respectively, were not taken into consideration.

Family	Before Hurricane Fifi-Orlene (1860–1972)	After Hurricane Fifi-Orlene (1976–2020)	Before Hurricane Mitch (1880–1997)	After Hurricane Mitch (2001–2020)
Emballonuridae	223	229	339	113
Phyllostomidae	3,844	5,012	5,655	3,201
Mormoopidae	425	222	519	128
Noctilionidae	80	48	118	10
Thyropteridae	1	12	1	12
Natalidae	55	32	55	32
Molossidae	397	211	556	52
Vespertilionidae	193	179	288	84
Total	5,218	5,945	7,531	3,632

apparent abundance of bats from 1880 to 1997 (before Hurricane Mitch) with those from 2001 to 2020 (after Hurricane Mitch); additionally, there was a decrease in the apparent abundances of all bat families except Thyropteridae (Table 2). It is difficult to determine if this decrease in bat apparent abundance was due to effects of the hurricanes, because we must consider that during these years the sampling efforts and techniques were always different. This is a major problem when comparing the apparent decrease in bat abundance after hurricanes. However, we strongly suspect that the hurricanes had an influence on this decrease.

There are many negative effects of tropical storms and hurricanes on bat populations (see Rodríguez-Duran and Kunz 2001), although it has been proposed that passive dispersal by tropical storms is responsible for insular dispersal, as in the case of *Phyllops falcatus*, which was recently recorded on the island of Cozumel in Mexico and was known from the Cuban archipelago (Rivas-Camo et al. 2020). In the case of Honduras, we can conclude that we have found no positive effects on bat abundances. Another interesting fact of how hurricanes affect bat populations was demonstrated by Gannon and Willig (1994), in which population levels of three common phyllostomid bats (*Artibeus jamaicensis*, *Stenoderma rufum*, and *Monophyllus redmani*)

were negatively affected by Hurricane Hugo in Puerto Rico, including a change in age structure and a decline in reproductively active females.

Two more important threats to bats in Honduras are stigmatization of bats and vampire control. The first is one of the oldest threats towards bats because they are associated with conjuring and witchcraft. Together with the repercussions of the COVID-19 pandemic, the pressures to which bats are being subjected will likely increase (Rocha et al. 2020). The stigmatization of bats has created a demonized concept resulting in the belief among many persons that all bats are vampires. In several regions of Honduras, people set fires to caves or old mines containing bats. In addition, and related to the increase in extensive cattle raising, the use of vampiricides—substances that are used to kill vampire bats—also has increased. In Honduras, these products are now easy to buy in stores that sell products for cattle and agriculture. Technicians capture vampire bats near cattle with mist nets and apply the vampiricide to the fur on their backs. When the bats return to their roost, other bats ingest the toxic substance in the process of mutual grooming. Indirectly, they can thus poison other bats in the caves because of this social behavior (Carter et al. 2018).

*Conclusion.*—The first key for the identification of bats in Honduras was published only four years ago (Mora 2016) and, four years later, the most recent systematic checklist for the country (Turcios-Casco et al. 2020g) was produced. Now we provide the first checklist for each department based on the historical occurrence of the bats in Honduras. Compiling the complete record of bat collecting in Honduras shows that there was more effort before 2000 than after. However, to our knowledge, there are many private collections due to consultancy works by biologists in Honduras, and the access to these collections is restricted. The geographical position of Honduras in the heart of Central America permits the occurrence of

species from both the Nearctic and from farther south in the Neotropical Region, and it is likely that the number of species presented herein underestimates the number of bat species in Honduras. Efforts to understand the geographical occurrence of bats in Honduras have been affected by different circumstances: from local wars to the lack of national financial support; from a lack of interest on the part of researchers (alleviated somewhat by enthusiastic new researchers) to bureaucratic processes; and from the superstitions against bats to the increase of threats of all types. Clearly, the occurrence of bats and how they are distributed has just begun to be understood in Honduras.

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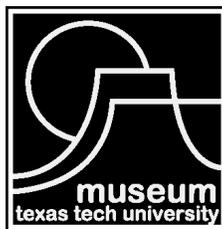


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