ECOTROPICA 18: 105–118, 2012

REVIEW OF SPECIES RICHNESS AND BIOGEOGRAPHY OF BATS (CHIROPTERA) FROM THE GUIANA SUBREGION OF SOUTH AMERICA WITH COMMENTS ON CONSERVATION

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Abstract. Our study is the first review of the species richness, biogeography, and conservation status of bats from the Guiana subregion of northern South America, which includes southern Venezuela, Guyana, Suriname, French Guiana, and northern Brazil. Current knowledge of biodiversity across this region is uneven, particularly because of poorly sampled areas in Brazil. Nonetheless, 148 species of bats have been documented, of which six are endemic to the Guiana subregion (*Lonchorhina fernandezi, Lophostoma schulzi,* an undescribed species of *Artibeus, Platyrrhinus aurarius, Lasiurus atratus,* and *Molossus barnesi*). The main influence on biogeography is the Guiana uplands, a plateau above c. 400 m in elevation that includes flat-topped mountains (tepuis) reaching 3000 m. The only species of bat endemic to these upland areas is *Platyrrhinus aurarius*, which has a relatively recent origin from the Andes during the Pleistocene. The Amazon Basin has also been an area of range expansion during biotic diversification, as seen in the speciation of emballonurid bats where the Guiana Shield was a stable core area during range contractions in the Miocene. Environmental threats associated with human encroachment are more prevalent in the more populated areas of northern Brazil and southern Venezuela. There are two species of bats (*Lonchorhina fernandezi* and *L. orinocensis*) from Venezuela in the conservation categories Endangered and Vulnerable, respectively, on the Red List of Threatened Species. Implementation of a comprehensive regional protected areas system in the Guiana subregion, such as transnational conservation corridors, and participation in international climate change treaties will maintain the essential ecosystem services such as seed dispersal, flower pollination, and insect control that are provided by a healthy bat fauna.

Keywords: Brazil, Chiroptera, French Guiana, Guyana, Suriname, Venezuela.

INTRODUCTION

Until recently the only summary of mammals from the Guiana region of northern South America was a study by Tate (1939), but only non-volant species were included. At that time, bats were only opportunistically collected by hand or shotgun at roost sites and thorough surveys of volant mammals were only possible after the introduction of Japanese mist nets as a standard sampling technique (Dalquest 1954). Since then there have been comprehensive studies of bats from countries in the Guianas, including Venezuela (Handley 1976, Linares 1987, 1998), Guyana (Lim & Engstrom 2001, Engstrom & Lim 2002), Suriname (Husson 1962, 1978), and the overseas department of French Guiana (Brosset & Charles-Dominique 1990, Simmons & Voss 1998, Charles-Dominique *et al.* 2001). Although there is a monograph on the bats of Brazil (Reis *et al.* 2007), information specific to the Guianan portion, such as distribution, is not easily parsed. There is a summary of the conservation priorities for mammals in the Guiana Shield highlighting this knowledge gap in northern Brazil (Lim & Engstrom 2003). The bats of the Guianas (not including Brazil) were reviewed in an annotated checklist of mammals (Lim *et al.* 2005) and there is a publication on the biogeography of Guianan mammals (Lim 2012). In the present paper we provide the first overview of the species richness, biogeography, and conservation status of bats from the Guiana subregion, including the portion in northern Brazil that represents approximately half of this area. In general the taxonomy follows Simmons (2005) with modifications as reported in Lim *et al.* (2005) and Lim (2012), unless noted otherwise.

Our area of study is the Guiana subregion, which occupies the northern extent of tropical South

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America and encompasses the contiguous Amazonian rainforest including other habitats contained within. It has an area of approximately 2 million km^2, consisting of French Guiana, Suriname, Guyana, Venezuela south of the Orinoco River (Delta Amacuro, Bolívar, and Amazonas states) and Brazil north of the Rio Negro and lower Amazon River (northeastern Amazonas, Roraima, northern Pará, and Amapá states; Fig. 1). This area was first recognized as a biogeographic zone during a study of platyrrhine monkeys and was originally referred to as the Guiana district "north of the Amazon and Rio Negro" (Wallace 1852). In a study of non-volant mammals, the boundaries were further defined as "the connected waters of the Orinoco, Cassiquiare and Amazon Rivers" and called the Guiana region (Tate 1939). We follow the most recent terminology of Guiana subregion, as used in a summary of diversity patterns in Neotropical mammals (Voss & Emmons 1996), but for convenience include the complete state of Amazonas in Venezuela.

The Guiana subregion represents most of the ancient geological Guiana Shield, except for parts of southeastern Colombia (Gibbs & Barron 1993). The main topographic feature is the Guiana uplands, a plateau above *c*. 400 m with flat-topped mountains (tepuis) of sandstone from the Roraima formation that begin at 1500 m and reach elevations of over 3000 m in southern Venezuela, west-central Guyana, and extreme northwestern Brazil (Huber 1995, 2006). Tafelberg in central Suriname is a tepui that is an eastern outlier of the Roraima formation, and there are also other mountains below 1000 m that are scattered throughout the lowlands of this area. Forest is the primary vegetation across the Guiana subregion, with the lowlands roughly southwest and northeast of the plateau referred to as the Negro-Amazonian forest and the east Guiana forest, respectively (Tate 1939). There are also substantial patches of savanna, including the large *Llanos* in central Venezuela, but only a portion is on the northwestern edge of the subregion. There are three other smaller

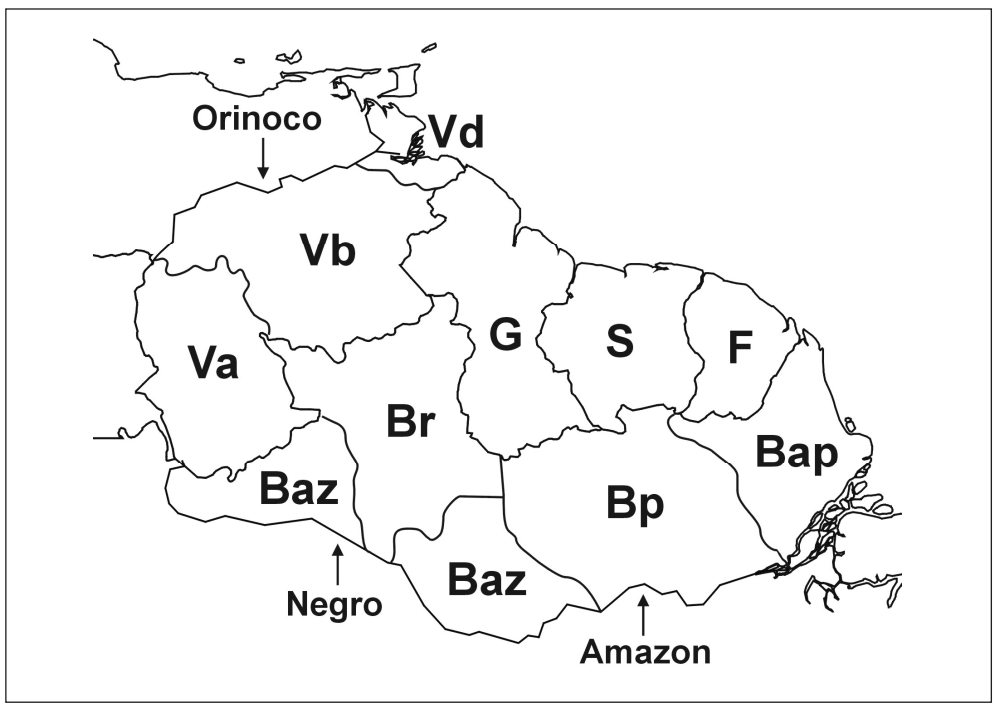

FIG. 1. Map of the Guiana subregion of northern South America bounded by the Orinoco, Negro, and Amazon Rivers. Political units include French Guiana (F), Suriname (S), Guyana (G), Venezeulan Delta Amacuro (Vd), Venezuelan Bolívar (Vb), Venezuelan Amazonas (Va), Brazilian Amazonas (Baz), Brazilian Roraima (Br), Brazilian Pará (Bp), and Brazilian Amapá (Bap).

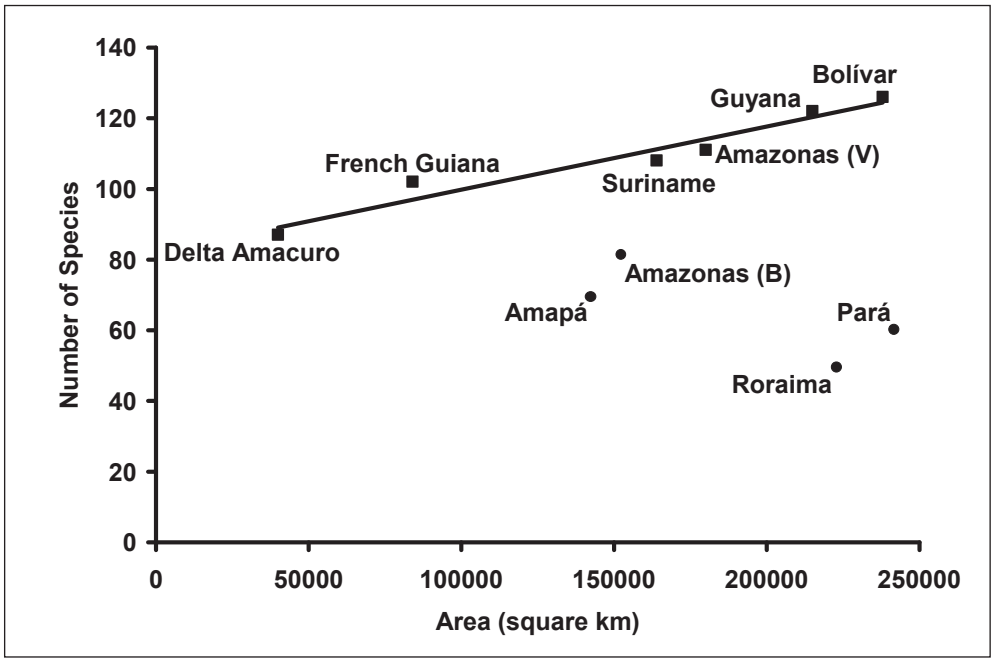

FIG. 2. Documented species diversity for areas of political units in the Guiana subregion including French Guiana, Suriname, Guyana, and states within Venezuela (V) and Brazil (B). The linear regression for non-Brazilian areas (squares) has an R^2 of 0.9447 and they are more diverse than the undersurveyed Brazilian areas (circles).

savannas that are located within the Guianan forest. The largest of these are formed by the contiguous upland Gran Sabana in Venezuela, and the lowland Rio Branco in Brazil and Rupununi in Guyana. The smallest grassland area is composed of the Sipaliwini in Suriname and the Paru in adjacent Brazil. The Amapá savanna further east in Brazil is intermediate in size. There are also patches of grasslands along the Atlantic coast and north bank of the lower Amazon that are more closely associated with and affected by human habitation.

SPECIES RICHNESS

A total of 148 species representing 9 families of bats has been reported from the Guiana subregion (Appendix 1). In Venezuela, Amazonas has 111 species, Bolívar 126 species, and Delta Amacuro has 87 species; Guyana has 122 species; Suriname has 108 species, and French Guiana has 102 species (Lim *et al.* 2005, Lim 2009). The four states in the Brazilian Guiana subregion are Amapá with 74 species (Martins *et al.* 2006, Martins *et al.* 2011), Pará with 56 species (V.C. Tavares, unpublished data), Roraima with 48 species (Robinson 1998), and Amazonas with 80 species (Sampaio *et al.* 2003, Bernard *et al.* 2011). The only new addition from Brazil to the species diversity of the Guianas is *Molossus currentium*, which was listed as *M. bondae* from Manaus (Sampaio *et al.* 2003). Previously, *M. bondae* was considered widely distributed from Central America to Argentina (Burnett *et al.* 2001), but was synonymized under *M. currentium* based on priority (López-González & Presley 2001). However, Eger (2008) recognized *M. bondae* as a valid species restricted to Central America and northwestern South America.

In general, our knowledge of species occurrence across the Guiana subregion is uneven. For example, there is a positive correlation (r = 0.97) of increasing species diversity with increasing area in the relatively well-surveyed northern portion in Venezeula, Guyana, Suriname, and French Guiana. In contrast, the states within Brazil are clearly undersampled, which hinders the broader study of biogeography in northern South America (Fig. 2). Delta Amacuro in Venezuela is the smallest political unit in the Guiana

subregion but has higher documented species diversity than any of the larger Brazilian states (Appendix 1). This is undoubtedly an artifact of a lack of comprehensive surveys in the extensive and remote areas of northern Brazil. For example, the second most speciose family of bats in the Guiana subregion (Molossidae) is poorly documented in the four Brazilian states. Molossid bats are high-flying aerial insectivores that require specialized canopy netting or sustained inventory efforts for opportunistic capture in the forest understory.

The most diverse family of bats in the Guiana subregion is Phyllostomidae, which accounts for half of the total species (74), followed by Molossidae (28), Vespertilionidae (18), and Emballonuridae (16). The other 5 families combined account for less than 10% in total (Fig. 3). Within Phyllostomidae, two subfamilies (Phyllostominae and Stenodermatinae) comprise 75% of the species diversity.

Notwithstanding the disproportional geographic sampling, there are six species of bats that are endemic to the Guiana subregion: 1) *Lonchorhina fernandezi* is known from two localities in the *Llanos* savanna of Venezuela on the northwestern edge of the subregion (Ochoa G & Sánchez 1988); 2) *Lophostoma schulzi* is relatively uncommon but widely distributed throughout the lowland rainforest in the eastern portion of the Guiana subregion and currently undocumented from Venezuela and Roraima (Williams & Genoways 2008, Martins *et al.* 2011); 3) *Artibeus* sp. is an undescribed species from the Caura watershed in Bolívar (J. Ochoa G, pers. comm.; Lim *et al.* 2005); 4) *Platyrrhinus aurarius* occurs in upland areas ranging in elevation from 340 to 2100 m in Venezuela, Brazil, Guyana, and Suriname (Gardner 1990, Velazco & Gardner 2009); 5) *Lasiurus atratus* is known from lowland areas in eastern Venezuela, Guyana, Suriname, French Guiana, and northern Brazil (Handley 1996, Lim *et al.* 1999, Sampaio *et al.* 2003). Two specimens from Brazil were originally listed as "*Lasiurus* cf. *castaneus*" (Sampaio *et al.* 2003) and considered referable to the species reported from French Guiana by Masson & Cosson (1992), which was subsequently identified as *L. atratus* in the description of this new species (Handley 1996), and 6) *Molossus barnesi*, known from only 3 specimens from coastal lowland French Guiana (Simmons & Voss 1998). However it is also considered by some authors to be a subspecies of a more widely distributed *M. coibensis* in Central and South America (Dolan 1989, Eger 2008).

There are 27 species that occur in all countries and states of the Guiana subregion (Appendix 1). In contrast, 11 species are found in only one of the 10 political units: *Enchisthenes hartii* in Amazonas (Venezuela); *Artibeus* sp., *Eptesicus diminutus*, and *Myotis keaysi* in Bolívar; *Eptesicus andinus*, *Eumops nanus*, *Molossus* sp., and *Thyroptera devivoi* in Guyana; *Rhogeessa hussoni* in Suriname; *Molossus barnesi* in French Guiana, and *Molossus currentium* in Amazonas (Brazil). Only two of these species (*Artibeus* sp. and *Molossus barnesi*) are endemic to the Guiana subregion, whereas the others are more widespread but sparsely distributed or poorly known over a larger area.

In a review of the biogeography of the mammals of the Guianas (Lim 2012), 86 species of bats were documented in the Guiana upland plateau (> 400 m elevation), of which 17 were also reported in highland regions above 1500 m elevation (*Anoura caudifer, A. geoffroyi, A. latidens, Artibeus bogotensis, Carollia brevicauda, Histiotus humboldti, Lasiurus cinereus, Lophostoma schulzi, Micronycteris megalotis, Molossus molossus, Myotis oxyotus, M. riparius, Nyctinomops macrotis, Platyrrhinus aurarius, Sturnira lilium, S. tildae,* and *Trachops cirrhosus*). Most species of bats occur in the surrounding western (134) and eastern (127) lowlands, with southward extensions into the contiguous forested Amazonian basin.

BIOGEOGRAPHY

The Guiana subregion is located in an area of South America where there are faunal associations with neighboring biogeographic regions, such as the Andes and Amazon Basin (Lim 2012). For example, a phylogenetic study of broad-nosed bats placed the Guiana upland endemic *Platyrrhinus aurarius* within an Andean clade of 7 other species in the genus (Velazco & Patterson 2008). This suggests that the Guiana plateau (> 400 m) acted as an area of range expansion from the Andes in the early Pleistocene during the diversification of *Platyrrhinus*.

For emballonurid bats, a phylogeny based on an analysis of molecular markers representing each of the 4 components of genetic transmission in mammals (mitochondrial genome and nuclear autosomal, X and Y chromosomes) recovered a monophyletic New World clade (tribe Diclidurini; Lim *et al.* 2008). Ancestral state reconstructions identified Africa as the origin of the most recent common ancestor of Diclidurini, and molecular dating indicated that most biotic differentiation occurred during the Miocene

(Lim 2007). Historical biogeography suggested two main episodes of taxon pulse diversification centered in the northern Amazon, with the Guiana Shield acting as a stable core area during changing paleoenvironments resulting from marine incursions from the Caribbean, appearance of savanna within rainforest, and uplifting of the northern Andes (Lim 2008). Correlation of ear morphology, echolocation call parameters, and foraging behavior with episodes of rapid speciation supports an adaptive radiation in heterogeneous forest and savanna habitats during the diversification of New World emballonurid bats in the Miocene of South America (Lim & Dunlop 2008).

A recent summary of the biogeography of mammals from the Guianas found several examples of non-volant mammals (rats and opossums) with phylogeographic patterns suggesting that the Guiana lowlands were an area of multiple faunal exchange with the contiguous Amazon Basin region (Lim 2012). The affinities between the Guianas and the Amazon are undoubtedly similar for bats, but there is a paucity of distributional data (Bernard *et al.* 2011) and species-level phylogenies that hinder interpretation of biogeography. However, an earlier study of 18 Neotropical lowland forest sites that have been well surveyed for bats used Jaccard's coefficients to assess patterns of faunal similarity (Lim & Engstrom 2001). A clustering algorithm grouped the northern Guiana sites within the eastern Amazon, which grouped with the western Amazon to the exclusion of Central American sites. Within the Neotropics, the Guiana subregion has a relatively low level of bat diversity at any given site, with approximately 90 species expected compared with 110 species in the western Amazon, 100 species for eastern Panama, and 80 species for southern Mexico (Voss & Emmons 1996).

CONSERVATION

The Guiana subregion represents the northern portion of the Amazon Basin, which is recognized as one of three major tropical wilderness areas in the world harboring high levels of biodiversity (Mittermeier *et al.* 1998). It has the highest percentage of intact rainforest coupled with the lowest population density in the tropics and accounts for approximately 25% of the tropical forest in the world (Huber & Foster 2003). In particular, the countries or department wholly within the subregion (Guyana, Suriname, and French Guiana) are relatively pristine, with low populations (< 800 000) that live primarily on the Atlantic coast, and remote interiors with minimal transportation infrastructure. Approximately 80% of the natural habitat is intact, with primary environmental concerns being deforestation by timber companies and water pollution from mining operations. However, plans for upgrading the Georgetown to Lethem road in Guyana and a new road connecting Paramaribo to Brazil will inevitably increase human migration and development in this area. Venezuelan Guayana, in particular Bolívar, is more populated and developed with access via a paved all-weather road. The southern portion of the Guiana subregion in Brazil, primarily Amazonas, poses higher conservation concerns because of a large city (Manaus) with over 1 million people, a more extensive highway system, and larger navigable rivers leading into the interior. The imminent threat in this area is colonization and development associated with human disturbance and clear-cutting of forest for large-scale monoculture crops, such as soybeans.

Approximately 25% of the Guiana subregion is protected as national parks, nature reserves, or heritage sites (Flores 2003). However coverage is uneven, with half of Venezuelan Guayana designated as protected areas whereas only 2% of Guyana is protected by one national park and two other conservation units. However Guyana and Suriname are active participating countries in Reducing Emissions from Deforestation and forest Degradation (REDD), which is a United Nations Framework Convention on the Climate Change initiative whereby greenhouse gases are reduced by the preservation of forest in developing countries. Guyana is also pursuing a Low Carbon Development Strategy (LCDS) that promotes economic development with the reduction of climate change.

In addition, there needs to be a concerted commitment of financial and human resources from governments to properly implement national protected areas systems beyond parks on paper maps (Huber 2001). Another concern is the legal enforcement of conservation policies in these typically remote areas, where a continuous presence of research and security is necessary as a deterrent to illegal colonization and activities detrimental to the environment, such as mining (Butler 2004).

There are two species of bats in the Guiana subregion with conservation concerns according to the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species. *Lonchorhina*

fernandezi is listed as endangered because it is known from only two localities in the Venezuelan savanna on the western edge of the Guiana subregion (Ochoa G & Sánchez 1988). The natural grassland habitat where this endemic species occurs is being altered by increased cattle grazing and human encroachment. *Lonchorhina orinocensis* is listed as vulnerable because of declining populations in savanna and forest habitats of southwestern Venezuela and southeastern Colombia that are being degraded by human disturbance (Ochoa G & Molinari 2010).

CONCLUSIONS

There are 148 species of bats currently known from the Guiana subregion, but areas in northern Brazil require more faunal surveys to attain a comparable level of species diversity and distributional occurrence to the other countries to enable more detailed studies of community ecology. Moreover, the dearth of species phylogenies for bats needs to be addressed because they are typically the most speciose group of mammals in lowland areas of the Neotropics and this would give a better understanding of biogeography in South America. The loss of natural habitat and an increase in road infrastucture are the primary conservation concerns. However full implementation and coordination of protected areas across the Guiana subregion, such as conservation corridors and participation in international treaties on climate change, will ensure a healthy bat fauna to maintain essential ecosystem services such as seed dispersal, flower pollination, and insect control.

ACKNOWLEDGMENTS

This paper formed the basis of an invited symposium presentation at the 15th International Bat Research Conference in Prague, Czech Republic, on 25 August 2010. We are grateful for the ongoing interest and support of the permitting agencies in the countries and overseas department of the Guiana subregion (Brazil, Venezuela, Guyana, Suriname, and French Guiana) that have enabled us to compile this review. The second author thanks the MRN company for supporting field work in Trombetas and allowing the publication of data. Primary funding for fieldwork and research has been generously provided to the first author by the Royal Ontario Museum Governors and Department of Natural History at the ROM.

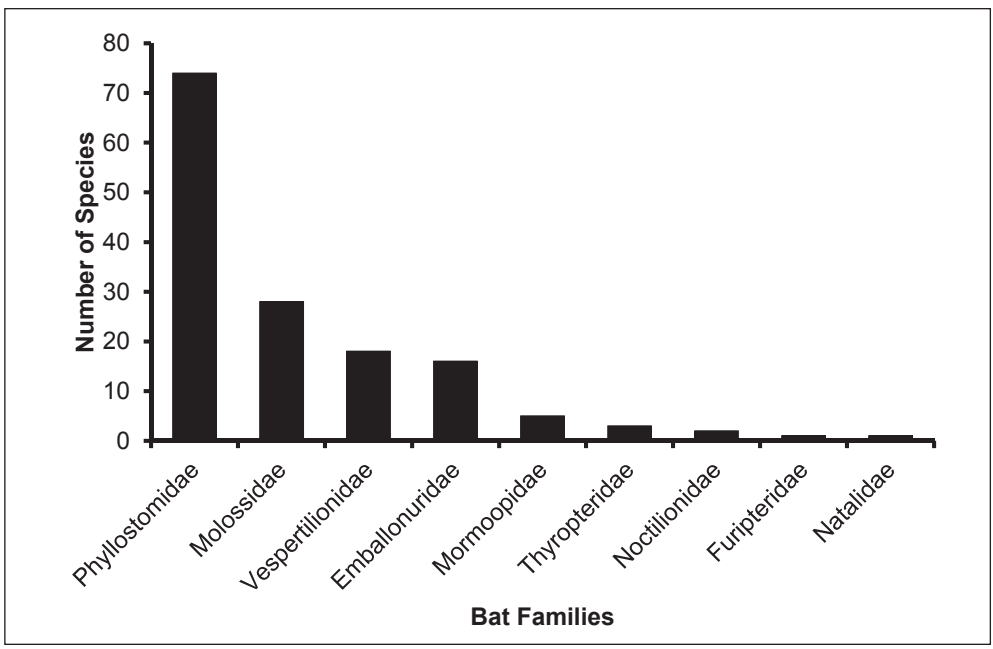

FIG. 3. There are 9 families and 148 species of bats documented from the Guiana subregion. The most diverse family is Phyllostomidae with half of the total species (74), followed by Molossidae (28), Vespertilionidae (18), and Emballonuridae (16). The other 5 families combined account for less than 10% of the total species diversity.

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APPENDIX 1

The 148 species of bats documented from the Guianan subregion of northern South America. Geographic distribution is updated based on current taxonomy (Simmons 2005). There are 6 species endemic to the Guianan subregion (*). The species list is modified and revised from Lim et al. (2005), and includes occurrence in Amazonas (Va), Bolívar (Vb), and Delta Amacuro (Vd) in Venezuela, Guyana (G), Suriname (S), and French Guiana (F), and the addition of Amapá (Bap; Martins et al. 2006, Martins et al. 2011), Pará (Bp), Roraima (Br; Robinson 1998), and Amazonas (Baz; Bernard et al. 2011, Sampaio et al. 2003) in Brazil. Records from Pará are unpublished data of V. C. Tavares. Some records from Roraima are unconfirmed species identifications (Br?).

	Va	**Vb**	**Vd**	**G**	**S**	**F**	**Bap**	**Bp**	**Br**	**Baz**
Emballonuridae (16)	**13**	**13**	**11**	**15**	**13**	**15**	**9**	**5**	**5**	**11**
Centronycteris maximiliani	Va	Vb		G	S	F	Bap	Bp		Baz
Cormura brevirostris	Va	Vb	Vd	G	S	F		Bp	Br	Baz
Cyttarops alecto				G	S	F				
Diclidurus albus	Va	Vb	Vd	G	S	F	Bap			Baz
Diclidurus isabellus	Va	Vb	Vd	G						
Diclidurus ingens	Va	Vb	Vd	G		F				
Diclidurus scutatus	Va	Vb		G	S	F	Bap			Baz
Peropteryx kappleri		Vb	Vd	G	S	F	Bap			Baz
Peropteryx leucoptera	Va			G	S	F		Bp		Baz
Peropteryx macrotis	Va	Vb	Vd	G	S	F	Bap			Baz
Peropteryx trinitatis	Va	Vb	Vd			F				
Rhynchonycteris naso	Va	Vb	Vd	G	S	F	Bap		Br	Baz
Saccopteryx bilineata	Va	Vb	Vd	G	S	F	Bap	Bp	Br	Baz
Saccopteryx canescens	Va	Vb	Vd	G	S	F	Bap		Br	Baz
Saccopteryx gymnura				G	S	F				
Saccopteryx leptura	Va	Vb	Vd	G	S	F	Bap	Bp	Br	Baz
Noctilionidae (2)	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**1**	**1**	**2**
Noctilio albiventris	Va	Vb	Vd	G	S	F	Bap	Bp		Baz
Noctilio leporinus	Va	Vb	Vd	G	S	F	Bap		Br	Baz
Mormoopidae (5)	**4**	**5**	**5**	**3**	**3**	**3**	**2**	**1**	**3**	**2**
Mormoops megalophylla		Vb	Vd							
Pteronotus davyi	Va	Vb	Vd							
Pteronotus gymnonotus	Va	Vb	Vd	G	S	F			Br	Baz
Pteronotus parnellii	Va	Vb	Vd	G	S	F	Bap	Bp	Br	Baz
Pteronotus personatus	Va	Vb	Vd	G	S	F	Bap		Br	
Phyllostomidae (74)	**66**	**67**	**46**	**65**	**59**	**57**	**49**	**43**	**34**	**54**
Phyllostominae (29)	**26**	**26**	**17**	**27**	**25**	**27**	**20**	**14**	**15**	**24**
Chrotopterus auritus	Va	Vb	Vd	G	S	F	Bap	Bp		Baz

	Va	**Vb**	**Vd**	**G**	**S**	**F**	**Bap**	**Bp**	**Br**	**Baz**
Glyphonycteris daviesi	Va	Vb		G	S	F				Baz
Glyphonycteris sylvestris	Va	Vb		G	S	F	Bap	Bp	Br	Baz
Lampronycteris brachyotis	Va	Vb	Vd	G	S	F				Baz
*Lonchorhina fernandezi**	Va	Vb								
Lonchorhina inusitata	Va	Vb		G	S	F			Br	
Lonchorhina orinocensis	Va	Vb								
Lophostoma brasiliense	Va	Vb	Vd	G	S	F	Bap		Br	Baz
Lophostoma carrikeri	Va	Vb		G	S	F		Bp		Baz
*Lophostoma schulzi**				G	S	F	Bap			Baz
Lophostoma silvicolum	Va	Vb	Vd	G	S	F	Bap	Bp	Br	Baz
Macrophyllum macrophyllum	Va	Vb	Vd	G	S	F	Bap			Baz
Micronycteris brosseti				G		F				
Micronycteris hirsuta	Va	Vb	Vd	G	S	F			Br	Baz
Micronycteris megalotis	Va	Vb	Vd	G	S	F	Bap		Br	Baz
Micronycteris microtis	Va	Vb	Vd	G	S	F	Bap	Bp		Baz
Micronycteris minuta	Va	Vb	Vd	G	S	F	Bap	Bp	Br	Baz
Micronycteris schmidtorum	Va	Vb		G		F	Bap			Baz
Mimon bennettii	Va			G	S	F	Bap			
Mimon crenulatum	Va	Vb	Vd	G	S	F	Bap	Bp	Br	Baz
Phylloderma stenops	Va	Vb		G	S	F	Bap		Br	Baz
Phyllostomus discolor	Va	Vb	Vd	G	S	F	Bap	Bp	Br	Baz
Phyllostomus elongatus	Va	Vb	Vd	G	S	F	Bap	Bp	Br	Baz
Phyllostomus hastatus	Va	Vb	Vd	G	S	F	Bap	Bp	Br	Baz
Phyllostomus latifolius		Vb		G	S	F				Baz
Tonatia saurophila	Va	Vb	Vd	G	S	F	Bap	Bp	Br	Baz
Trachops cirrhosus	Va	Vb	Vd	G	S	F	Bap	Bp	Br	Baz
Trinycteris nicefori	Va	Vb	Vd	G	S	F	Bap	Bp	Br	Baz
Vampyrum spectrum	Va	Vb	Vd	G	S	F	Bap	Bp		Baz
Glossophaginae (11)	**9**	**11**	**5**	**10**	**8**	**7**	**6**	**3**	**3**	**6**
Anoura caudifer	Va	Vb		G	S	F	Bap	Bp		Baz
Anoura geoffroyi	Va	Vb		G	S	F	Bap			
Anoura latidens	Va	Vb	Vd	G						
Choeroniscus godmani		Vb	Vd	G	S					
Choeroniscus minor	Va	Vb	Vd	G	S	F	Bap		Br?	Baz
Glossophaga longirostris	Va	Vb	Vd	G						
Glossophaga soricina	Va	Vb	Vd	G	S	F	Bap	Bp	Br	Baz

	Va	**Vb**	**Vd**	**G**	**S**	**F**	**Bap**	**Bp**	**Br**	**Baz**
Lichonycteris obscura		Vb		G	S	F				Baz
Lionycteris spurrelli	Va	Vb		G	S	F	Bap			Baz
Lonchophylla thomasi	Va	Vb		G	S	F	Bap	Bp	Br?	Baz
Scleronycteris ega	Va	Vb								
Carolliinae (5)	**5**	**3**	**3**	**3**	**3**	**3**	**3**	**5**	**2**	**3**
Carollia brevicauda	Va	Vb	Vd	G	S	F	Bap	Bp		Baz
Carollia castanea	Va							Bp		
Carollia perspicillata	Va	Vb	Vd	G	S	F	Bap	Bp	Br	Baz
Rhinophylla fischerae	Va							Bp		
Rhinophylla pumilio	Va	Vb	Vd	G	S	F	Bap	Bp	Br?	Baz
Stenodermatinae (27)	**24**	**25**	**19**	**23**	**21**	**18**	**18**	**20**	**13**	**19**
Ametrida centurio	Va	Vb	Vd	G	S	F	Bap	Bp		Baz
Artibeus amplus	Va	Vb		G	S			Bp		
Artibeus bogotensis	Va	Vb	Vd	G	S			Bp		
Artibeus cinereus	Va	Vb	Vd	G	S	F	Bap	Bp		Baz
Artibeus concolor	Va	Vb	Vd	G	S	F	Bap	Bp	Br	Baz
Artibeus gnomus	Va	Vb	Vd	G	S	F	Bap	Bp	Br?	Baz
Artibeus jamaicensis	Va	Vb	Vd							
Artibeus lituratus	Va	Vb	Vd	G	S	F	Bap	Bp	Br	Baz
Artibeus obscurus	Va	Vb	Vd	G	S	F	Bap	Bp	Br	Baz
Artibeus planirostris	Va	Vb		G	S	F	Bap	Bp	Br	Baz
Artibeus sp.*		Vb								
Chiroderma trinitatum	Va	Vb	Vd	G	S	F	Bap	Bp		Baz
Chiroderma villosum	Va	Vb	Vd	G	S	F	Bap	Bp	Br	Baz
Enchisthenes hartii	Va									
Mesophylla macconnelli	Va	Vb	Vd	G	S	F	Bap	Bp	Br	Baz
*Platyrrhinus aurarius**	Va	Vb		G	S					Baz
Platyrrhinus brachycephalus		Vb	Vd	G	S	F				
Platyrrhinus helleri	Va	Vb	Vd	G	S	F	Bap	Bp	Br?	Baz
Sphaeronycteris toxophyllum	Va	Vb								Baz
Sturnira lilium	Va	Vb	Vd	G	S	F	Bap	Bp	Br	Baz
Sturnira tildae	Va	Vb	Vd	G	S	F	Bap	Bp	Br	Baz
Uroderma bilobatum	Va	Vb	Vd	G	S	F	Bap	Bp	Br	Baz
Uroderma magnirostrum	Va	Vb	Vd	G			Bap	Bp	Br	Baz
Vampyressa bidens	Va	Vb	Vd	G	S	F	Bap	Bp	Br?	Baz
Vampyressa brocki				G	S	F		Bp		Baz

	Va	**Vb**	**Vd**	**G**	**S**	**F**	**Bap**	**Bp**	**Br**	**Baz**
Vampyressa thyone	Va	Vb		G			Bap	Bp		
Vampyrodes caraccioli	Va	Vb	Vd	G	S	F	Bap			
Desmodontinae (2)	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**1**	**1**	**2**
Desmodus rotundus	Va	Vb	Vd	G	S	F	Bap	Bp	Br	Baz
Diaemus youngii	Va	Vb	Vd	G	S	F	Bap			Baz
Natalidae (1)	**0**	**1**	**0**	**1**	**1**	**1**	**0**	**0**	**0**	**0**
Natalus tumidirostris		Vb		G	S	F				
Furipteridae (1)	**1**	**0**	**0**	**1**	**1**	**1**	**0**	**0**	**0**	**0**
Furipterus horrens	Va			G	S	F				
Thyropteridae (3)	**1**	**1**	**1**	**2**	**2**	**2**	**1**	**1**	**0**	**2**
Thyroptera discifera					S	F				Baz
Thyroptera devivoi				G						
Thyroptera tricolor	Va	Vb	Vd	G	S	F	Bap	Bp		Baz
Vespertilionidae (18)	**11**	**13**	**10**	**11**	**11**	**8**	**6**	**4**	**3**	**5**
Eptesicus andinus				G						
Eptesicus brasiliensis	Va	Vb	Vd	G	S		Bap	Bp	Br?	
Eptesicus chiriquinus		Vb	Vd	G	S	F		Bp		Baz
Eptesicus diminutus		Vb								
Eptesicus furinalis	Va	Vb	Vd	G	S	F	Bap			
Histiotus humboldti	Va	Vb								
*Lasiurus atratus**		Vb		G	S	F				Baz
Lasiurus blossevillii	Va		Vd	G	S	F	Bap	Bp		
Lasiurus cinereus	Va		Vd							
Lasiurus ega	Va	Vb	Vd	G	S					
Lasiurus egregius					S	F				
Myotis albescens	Va	Vb	Vd	G	S	F	Bap		Br	Baz
Myotis keaysi		Vb								
Myotis nigricans	Va	Vb	Vd	G	S	F	Bap		Br	Baz
Myotis oxyotus	Va	Vb								
Myotis riparius	Va	Vb	Vd	G	S	F	Bap	Bp		Baz
Rhogeessa hussoni					S					
Rhogeessa io	Va	Vb	Vd	G						
Molossidae (28)	**13**	**24**	**12**	**22**	**16**	**13**	**5**	**1**	**2**	**4**
Cynomops abrasus		Vb		G	S	F		Bp		Baz
Cynomops greenhalli		Vb	Vd		S	F				Baz
Cynomops paranus		Vb		G	S	F				

	Va	**Vb**	**Vd**	**G**	**S**	**F**	**Bap**	**Bp**	**Br**	**Baz**
Cynomops planirostris	Va	Vb	Vd	G	S	F				
Eumops auripendulus	Va	Vb	Vd	G	S	F				
Eumops nanus				G						
Eumops dabbenei		Vb	Vd							
Eumops glaucinus	Va	Vb		G	S					
Eumops hansae	Va	Vb	Vd	G		F				
Eumops maurus		Vb		G	S	F				
Eumops trumbulli		Vb		G	S		Bap			
Molossops neglectus		Vb		G	S					
Molossops temminckii		Vb		G						
Molossus aztecus		Vb	Vd							
*Molossus barnesi**						F				
Molossus coibensis	Va	Vb	Vd	G						
Molossus currentium										Baz
Molossus molossus	Va	Vb	Vd	G	S	F	Bap		Br	Baz
Molossus pretiosus		Vb	Vd	G						
Molossus rufus	Va	Vb	Vd	G	S	F	Bap			
Molossus sinaloae		Vb	Vd	G	S	F				
Molossus sp.				G						
Neoplatymops mattogrossensis	Va	Vb		G						
Nyctinomops gracilis	Va	Vb	Vd							
Nyctinomops laticaudatus	Va	Vb		G	S	F	Bap		Br	
Nyctinomops macrotis	Va	Vb		G	S					
Promops centralis	Va	Vb		G	S	F				
Promops nasutus	Va	Vb		G	S		Bap			
Total	**111**	**126**	**87**	**122**	**108**	**102**	**74**	**56**	**48**	**80**