Rev. Inst. Med. Trop. Sao Paulo
57(1):63-72, January-February, 2015
http://dx.doi.org/10.1590/S0036-46652015000100009

BAT-BORNE RABIES IN LATIN AMERICA

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SUMMARY

The situation of rabies in America is complex: rabies in dogs has decreased dramatically, but bats are increasingly recognized as natural reservoirs of other rabies variants. Here, bat species known to be rabies-positive with different antigenic variants, are summarized in relation to bat conservation status across Latin America. Rabies virus is widespread in Latin American bat species, 22.5%[75] of bat species have been confirmed as rabies-positive. Most bat species found rabies positive are classified by the International Union for Conservation of Nature as "Least Concern". According to diet type, insectivorous bats had the most species known as rabies reservoirs, while in proportion hematophagous bats were the most important. Research at coarse spatial scales must strive to understand rabies ecology; basic information on distribution and population dynamics of many Latin American and Caribbean bat species is needed; and detailed information on effects of landscape change in driving bat-borne rabies outbreaks remains unassessed. Finally, integrated approaches including public health, ecology, and conservation biology are needed to understand and prevent emergent diseases in bats.

KEYWORDS: Rabies virus; Bats; Geographic distribution; Biodiversity.

INTRODUCTION

Bats offer diverse cultural and economic contributions to human situations, such as ecotourism, vector control, guano, medicinal products, and religious significance, among others[42]. Bat diets include insects, fruits, leaves, flowers, nectar, pollen, fish, other vertebrates, and blood[41]. Insectivorous bats consume large quantities of insects and other arthropods under natural conditions or related to anthropogenic activities, controlling important agricultural pests and potential disease vectors[39,40,42]. Nectarivorous bats help to maintain diversity in forests through dispersal of seeds and pollen, essential to many plant species with high economic, biological, and cultural value[42]. With around 1230 species, bats are the second most diverse mammal order (after rodents), with an impressively broad ecological and geographic distribution[41,42].

Rabies virus is the most important virus in the genus *Lyssavirus* because, from a global perspective, its distribution, human cases (> 55,000 deaths per year), wide range of potential reservoirs, and veterinary and economic cost implications make it the most important viral zoonosis[73]. Rabies transmission cycles in wild and domestic carnivores have existed almost worldwide, whereas bat-mediated transmission of rabies virus occurs only in North, Central, and South America; in Europe, Africa, Asia, and Australia, bats are reservoirs of different *Lyssavirus* species[44,55,72,87]. In America, bats now constitute the principal rabies reservoir[73,74], rabies is thought to have occurred in tropical America since pre-Hispanic times, being transmitted predominantly by hematophagous vampire bats[3], although recent phylogenetic reconstructions suggest that rabies virus in the Americas is unlikely to have originated from vampire bats[46]. The first scientific report of rabies in America was by CARINI (1911), in São Paulo, Brazil[7]. Advances in diagnostic techniques have now contributed to an understanding of bat-rabies dynamics[83].

In Latin America, human rabies cases have decreased in recent decades[57-61], with mortality rates estimated at 0.01-0.60 per 100,000 individuals[29,37]. Between 1993 and 2002, annual incidence of human rabies in Latin America was 105 cases, ranging 0.00-0.09 per 100,000 individuals in South America, 0.00-0.10 in Central America, and 0.00-0.06 in the Caribbean[9]. Brazil, Peru, Mexico, and Colombia are the countries with most human cases of rabies in the region[80], although on a *per capita* basis Peru and Colombia dominate.

In fact, by 2013, human and canine rabies rates in Latin America had decreased by 95% compared to previous years (Fig. 1). Epidemiological surveillance is considered to have been essential for control of rabies in Latin America[79]. However, while reports of rabid dogs in Latin America have declined, the number of bat rabies cases appears stable (Fig. 1). Although further data compilation is needed for a clearer picture of this phenomenon, in Latin America, data on rabies are woefully limited and biased by uneven surveillance effort.

Antigenic variants of rabies (AgV) can be identified by monoclonal antibody techniques[29]. Dog rabies (variants 1 and 2) has decreased

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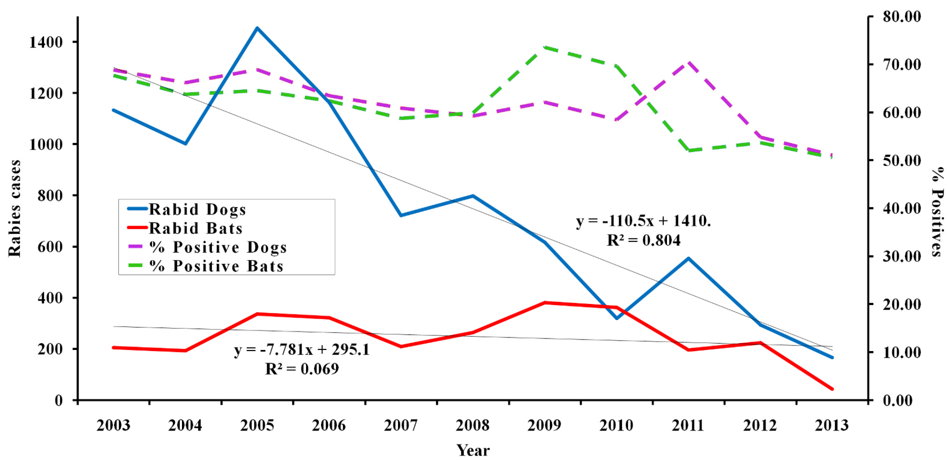

Fig. 1 - Dog (blue line) and bat (red line) rabies cases during 2003-2013, based on samples from Latin American and Caribbean countries considered in this study. Belize, Costa Rica, Ecuador, Guatemala, Guyana, French Guyana, and Haiti did not have reports for this period. Notice the linear trend (black line) for each host group. Proportion of positive bat (green dash line) and dog samples (purple dash line) is shown. Source: SIEPI-PANAFTOSA/PAHO-WHO, data available on http://siepi.panaftosa.org.br/

dramatically (Fig. 1), and now occurs only in circumscribed areas of Latin America. Hence, according to current epidemiological reports, bats now constitute the principal reservoir in Latin America[73,74]. Cross-species spillover is well appreciated in bat-borne rabies[19]. Since 1975, at least 500 bat-associated cases of human rabies have been reported from across Latin America[2]. In 2004, the Regional Program for the Elimination of Rabies of the Pan American Health Organization (PAHO) reported for the first time more human cases of rabies derived from wild animals (bats, other small mammals) than from dogs[78]: for example, in 2005, 13 cases of human rabies derived from dogs were reported, compared with 60 human cases derived from bats[80]. Indeed, even in Latin American countries considered "dog rabies free," human cases caused by bats have been reported[4,21].

Both vampire and non-vampire bats have been involved in these events[4,21]. Hence, after vampire bats, insectivorous bats have assumed a greater role as sources of the virus in Latin America[10,26,38,75,78,90]. In spite of the significant economic, ecological, and cultural stigmas and fears associated with this disease[9], rabies surveillance in bats is limited in developing countries[44]. Consequently, the aim of this article is to review rabies occurrence in bats, evaluate geographic patterns in species richness of potential bat rabies reservoirs, and summarize knowledge of antigenic variants, ecology, food habits, and conservation status in key bat species. This article aims to characterize potential bat rabies reservoirs and guide new steps in research.

METHODS

For information on bat species (geographic distribution, diet, conservation status), data from the current, online IUCN database (www.iucn.org; accessed 13 Jan 2013) were used. To identify potential bat rabies reservoirs, summaries were made of bat species reported rabies-positive by country (i.e., Argentina, Belize, Bolivia, Brazil, Chile, Colombia, Costa Rica, Cuba, Dominican Republic, Ecuador, El Salvador, Guatemala, French Guyana, Guyana, Haiti, Honduras, Mexico, Nicaragua, Panama, Paraguay, Peru, Suriname, Trinidad and Tobago, Uruguay, and Venezuela). First, the Web of Science was searched for articles related to "bat rabies" in Latin American countries between 1953 and 2012 in English and Spanish, a number of articles from this search were used as search effort in posterior analysis. Because several articles from Latin American journals were not available via Web of Science, Google Scholar was searched for articles, theses, and official sources available online using the same criteria. Publications including rabies diagnosis based on histopathology, direct fluorescent antibody tests, or molecular techniques were included. When multiple manuscripts source the same bat species or antigenic variants from the same country, only the older such reference was cited (Table 1). To date, the most valuable compilation of rabies-positive bat species in Latin America was published by CONSTANTINE (2009), so part of this article's analysis is based on his data. For preliminary bat distributional information, vector-format based maps (shapefiles) from IUCN[36] were used; maps were handled using ArcGIS 9.3 (ESRI). Chi-square tests were used to evaluate associations ($\alpha = 0.05$) between the response variable (i.e., number of rabies-positive species) and factors such as bat family, diet, and conservation status. Linear regressions were conducted to evaluate association between bat species (richness) with rabies-positive species and the number of manuscripts from the Web of Science (i.e., research effort) by country and rabies antigenic variants with bat species rabies positive by country. Statistical analyses were carried out in R[71].

RESULTS

Bat species richness patterns: In all, 333 bat species were documented from 24 Latin American and Caribbean countries[36]. The countries with the highest species richness were Colombia (172 species), Brazil (155 species), and Venezuela (152 species; Fig. 2). Fifty-two species were endemic to single countries: Mexico had 17, and Brazil and Peru had nine each. None of these single-country endemic species were reported as rabies-positive. The number of species by family was Phyllostomidae (168 species), Vespertilionidae (82 species), Molossidae (38 species), Emballonuridae (21 species), Mormoopidae (nine species), Natalidae (seven species), Thyropteridae (four species), and Noctilionidae and Furipteridae (two species each).

Table 1.
Bat species known to be rabies-positive in Latin America and the Caribbean

Insectivorous	Frugivorous	Nectarivorous	Omnivorous	Carnivorous	Hema-tophagous	AgV
Argentina						
Eumops auripendulus†[12] Eumops patagonicus†[10] Histiotus montanus*[10] Myotis sp*[10] Myotis nigricans*[10] Tadarida brasiliensis†[10,33] Eptesicus furinalis*[69] Molossus molossus†[69] Lasiurus blossevillii*[69] Lasiurus cinereus*[33,69] Lasiurus ega*[69]	Artibeus lituratus•[15]				Desmodus rotundus•[69]	V3[69] V4[33,69] V6[33,69] E[69] H[69] M[69]
Belize						
Myotis fortidens*[12] Myotis nigricans*[12] Molossus molossus†[12] Molossus sinaloae†[12]	Artibeus jamaicensis•[12] Artibeus lituratus•[12]		Phyllostomus discolor•[12]		Desmodus rotundus•[12]	-
Bolivia						
	Artibeus jamaicensis•[12] Artibeus lituratus•[12]				Desmodus rotundus•[12]	V3[22] V5[22]
Brazil						
Cynomops abrasus†[82] Cynomops planirostris†[82] Eptesicus diminutus*[82] Eptesicus furinalis*[82] Eptesicus brasiliensis*[82] Eumops glaucinus†[82] Eumops perotis†[82] Eumops auripendulus†[82] Histiotus velatus*[82] Lasiurus blossevillii*[82] Lasiurus cinereus*[82] Lasiurus ega*[82] Lasiurus egregius*[82] Lonchorhina aurita•[82] Lophostoma brasiliense•[82] Micronycteris megalotis•[82] Molossus molossus†[82] Molossops neglectus†[82] Molossus rufus†[82] Molossus sinaloae†[12] Myotis albescens*[82] Myotis levis*[82] Myotis nigricans*[82] Myotis riparius*[82] Nyctinomops laticaudatus†[82] Nyctinomops macrotis†[82] Promops nasutus†[12] Tadarida brasiliensis†[82]	Artibeus jamaicensis•[12] Artibeus lituratus•[82] Artibeus planirostris•[82] Carollia perspicillata•[82] Platyrrhinus lineatus•[82] Sturnira lilium•[12] Uroderma bilobatum•[82] Vampyrodes caraccioli•[12]	Anoura caudifer•[82] Anoura geoffroyi•[82] Glossophaga soricina•[82]	Phyllostomus hastatus•[82]	Chrotopterus auritus•[82] Trachops cirrhosus•[82]	Desmodus rotundus•[82] Diaemus youngi•[82] Diphylla ecaudata•[82]	V3[26,35] V4[26,35] V5[26] V6[26,35] E[26] H[26] Eu[26] N[26] Lb[26]
Colombia						
Eptesicus brasiliensis*[65] Molossus molossus†[65]	Carollia perspicillata•[53]				Desmodus rotundus•[68]	V3[68] V4[68]

Table 1.
Bat species known to be rabies-positive in Latin America and the Caribbean (cont.)

Insectivorous	Frugivorous	Nectarivorous	Omnivorous	Carnivorous	Hema-tophagous	AgV
Costa Rica						
					Desmodus rotundus•[4]	*V3*[4]
Cuba						
*Eptesicus fuscus**[12] *Eumops glaucinus*†[54]						-
Chile						
*Histiotus macrotus**[23,24] *Histiotus montanus**[23,24] *Lasiurus borealis**[23,24] *Lasiurus cinereus**[23,24] *Myotis chiloensis**[23,24] *Tadarida brasiliensis*†[23,24]						*M*[20,23,24,92] *V4*[20,23,24,92] *V6*[20,23,24,92] *H*[20,23,24,92]
Ecuador						
					Desmodus rotundus•[27]	*V3*[27]
El Salvador						
					Desmodus rotundus•[12]	-
Guatemala						
Molossus sinaloae†[12] *Myotis fortidens**[12]	*Artibeus lituratus*•[12]		*Phyllostomus discolor*•[12]		*Desmodus rotundus*•[12]	-
French Guyana						
					Desmodus rotundus•[52]	*V3*[52]
Honduras						
Molossus sinaloae†[1]					*Desmodus rotundus*•[13]	-
Mexico						
*Antrozous pallidus**[12] *Eptesicus fuscus**[12] *Lasiurus blossevillii**[12] *Lasiurus cinereus**[12] *Lasiurus ega**[12] *Lasiurus intermedius**[12] *Lasiurus seminolus**[12] *Macrotus waterhousii*•[12] *Molossus rufus*†[12] *Mormoops megalophylla*£[1] *Myotis velifer**[12] *Nyctinomops laticaudatus*†[12] *Nyctinomops macrotis*†[12] *Pteronotus personatus*£[12] *Pipistrellus subflavus**[12] *Pteronotus parnellii*£[12] *Pteronotus davyi*£[12] *Rhogeessa parvula**[1] *Rhogeessa tumida**[12] *Tadarida brasiliensis*†[90]	*Artibeus jamaicensis*•[90] *Artibeus lituratus*•[1] *Carollia subrufa*•[12]	*Glossophaga soricina*•[1] *Leptonycteris nivalis*•[1] *Leptonycteris yerbabuenae*•[12]	*Phyllostomus discolor*•[12]	*Noctilio leporinus*‡[1]	*Desmodus rotundus*•[90] *Diaemus youngi*•[12] *Diphylla ecaudata*•[1]	*V3*[17,43,50,89] *V4*[17,43,50,89] *V5*[17,43,50,89] *V6*[17,43,50,89] *V8*[17,43,50,89] *V9*[17,43,50,89] *V11*[17,43,50,89]
Nicaragua						
					Desmodus rotundus•[12]	-

Table 1.
Bat species known to be rabies-positive in Latin America and the Caribbean (cont.)

Insectivorous	Frugivorous	Nectarivorous	Omnivorous	Carnivorous	Hema-tophagous	AgV
Panama						
Cynomops planirostris[†1] *Micronycteris megalotis*[•12] *Molossus coibensis*[†1] *Molossus currentium*[†12] *Molossus molossus*[†12] *Myotis nigricans*[*1]	*Artibeus jamaicensis*[•1] *Uroderma bilobatum*[•1]			*Noctilio sp.*[‡12]		-
Paraguay						
Lasiurus ega[*81] *Tadarida brasiliensis*[†8]	*Artibeus jamaicensis*[•8]				*Desmodus rotundus*[•12]	*V6*[81] *V3*[64]
Peru						
Myotis nigricans[*12] *Micronycteris megalotis*[•12] *Molossus molossus*[†12]	*Artibeus* sp.[•75] *Artibeus concolor*[•12] *Artibeus lituratus*[•12] *Carollia* spp.[•75] *Carollia perspicillata*[•12] *Platyrhinus* sp.[•12] *Platyrrhinus lineatus*[•12] *Uroderma* sp.[•75]	*Glossophaga soricina*[•12]	*Phyllostomus hastatus*[•12] *Phyllostomus elongatus*[•12]		*Desmodus rotundus*[•75]	*V3*[91]
Dominican Republic						
Tadarida brasiliensis[†62]						-
Trinidad and Tobago						
Diclidurus albus[ʃ31] *Molossus molossus*[†31] *Pteronotus davyi*[£31] *Pteronotus parnellii*[£12]	*Artibeus jamaicensis*[•31] *Artibeus lituratus*[•31] *Carollia perspicillata*[•31]				*Desmodus rotundus*[•31] *Diaemus youngi*[•31]	-
Uruguay						
Lasiurus cinereus[*69] *Lasiurus ega*[*69] *Molossus molossus*[†32] *Myotis* spp.[*69] *Tadarida brasiliensis*[†69]					*Desmodus rotundus*[•69]	*V4*[69] *V3*[32]
Venezuela						
Molossus rufus[†16]					*Diphylla ecaudata*[•1] *Desmodus rotundus*[•16]	*M*[16] *V3*[16] *V5*[16]

Family: *Vespertilionidae; •Phyllostomidae; †Molossidae; £Mormoopidae; ‡Noctilionidae; ʃEmballonuridae. **AgV:** Antigenic variants by country. **E:** Antigenic variant for *Eptesicus* spp.; **Eu:** Eumops; **H:** Antigenic variant for *Histiotus* spp.; **Lb:** *Lasiurus borealis*; **M:** Antigenic variant for *Myotis* spp.; **N:** *Nyctinomops*; **V3, V5, V8, V11:** Antigenic variant for *D. rotundus*; **V4, V9:** *T. brasiliensis*; **V6:** *Lasiurus* spp.

The largest host geographic distributions were for *Lasiurus cinereus* (39.2 x 10^6 km^2), *L. blossevillii* (22.6 x 10^6 km^2), and *Tadarida brasiliensis* (17.7 x 10^6 km^2), all insectivorous. Considering other diets, the species with the largest distributions were *Sturnira lilium* 16.4 x 10^6 km^2 (frugivorous), *Glossophaga soricina* 15.7 x 10^6 km^2 (nectarivorous), *Noctilio leporinus* 15.5 x 10^6 km^2 (carnivorous), and *Desmodus rotundus* 19.3 x 10^6 km^2 (hematophagous).

In all, 75 (22.5%) Latin American bat species have been confirmed as rabies-positive, at least as incidental records (see Table 1). The countries with more bat species rabies-positive reports were Brazil (43), Mexico (31), and Argentina (13; Fig. 3). Only Guyana, Suriname, and Haiti are countries lacking bat-rabies records. It was found that the number of rabies-positive species is not related to number of bat species (richness) reported per country (r^2 = 0.1238, df = 24, p = 0.078). From the first search of articles (i.e., Web of Science), no association was found (r = 0.2768, df = 7, P = 0.4708) between the number of bat species and publications by country; for example, Chile, with the fewest bat species, has nine publications about bat-borne rabies while Colombia with the highest number of bat species has only four publications. An association was found between number of

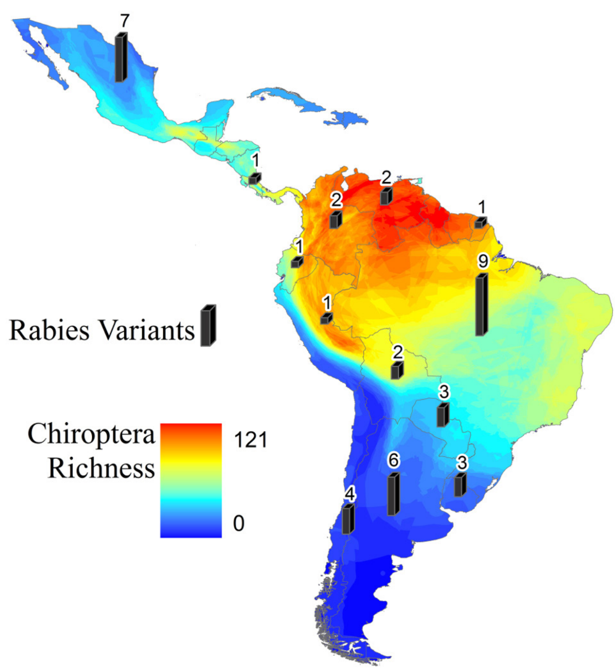

Fig. 2 - Bat richness showing the number of bat species (rabies positive or not) present in Latin America (colored shading) and number of antigenic variants of bat rabies reported (gray bars).

publications and rabies AgV by country ($r = 0.775$, df = 7, $p = 0.0142$), as well as an association between the number of publications and the number of bat species rabies-positive by country ($r = 0.883$, df = 7, $p = 0.001$).

In terms of numbers of species known to be rabies-positive by family, significant effects of family were found ($X^2 = 24.29$, $p = 0.001$); the most consistently rabies-positive family was Vespertilionidae 64% (25 species), followed by Noctilionidae 50% (one), Mormoopidae 44% (four), Molossidae 42% (16), Phyllostomidae with 17% (29), and Emballonuridae 5% (one species; see Table 1). Considering diet type, significant effects of diet on rabies positivity were found ($X^2 = 23.29$, $p = 0.0002$): the highest proportions of species rabies-positive were hematophagous 100% (three), carnivorous 60% (three), insectivorous 27% (50), followed by nectarivorous 19% (five), frugivorous 13% (10 species), and omnivorous 11% (four).

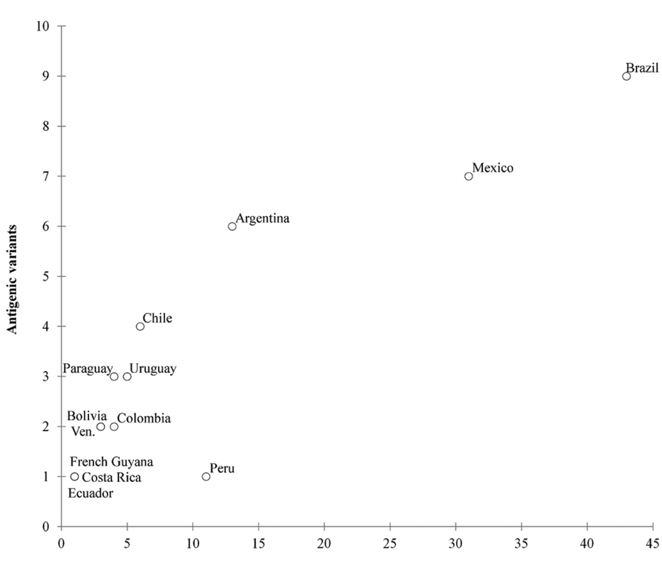

Fig. 3 - Numbers of rabies-positive species and antigenic variants of rabies reported by country (Table 1). Ven. = Venezuela.

Antigenic variants: Only 13 (60%) countries with rabies-positive bats reported information on antigenic variants (Fig. 2; Table 1). Significant relationships were found between the number of rabies-positive species and the number of antigenic variants reported by countries ($r^2 = 0.83$, $P < 0.001$; Fig. 3). Brazil had the highest number of rabies-positive bat species (43 species), with nine antigenic variants; in contrast, Mexico had fewer rabies-positive bat species, but an impressive number (seven) of antigenic variants. Indeed, in Mexico, four variants are in vampire bats and three in non-hematophagous bats, primarily insectivores (Fig. 3). Chile is the Latin American country with the fewest bat species, but four viral variants are known (Fig. 3); this number is impressive in comparison with Argentina and Mexico, which are known to have six and seven variants, respectively, but with much greater bat diversity (Fig. 2). The most frequent variants reported by country were AgV3 (12 countries), found mainly in *D. rotundus*; AgV4 (six countries), in *T. brasiliensis*; and AgV6 (five countries), in *Lasiurus* spp.

Conservation of bats in Latin America: Only one species from the rabies-positive group had increasing populations (*Eptesicus fuscus*); most (90%) rabies-positive species are considered as Least Concern (Fig. 4). Indeed, rabies-positive species are more likely to be classed as Least Concern when compared with species where rabies virus has not been detected ($X^2 = 41.13$, $p < 0.001$). Bat species rabies-positive in Latin American and the Caribbean include one endangered species (*Leptonycteris nivalis*), and three species (*L. yerbabuenae*, *Eumops perotis*, *Mormoops megalophylla*) that have decreasing populations[36]. According to IUCN (2012), information was insufficient to classify the conservation threat status for 44 (13%) bat species reported in Latin America.

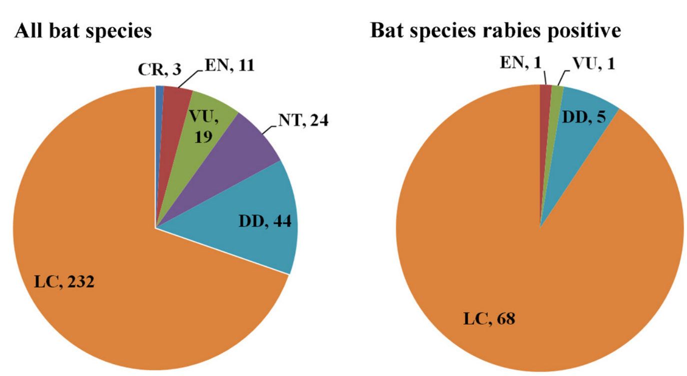

Fig. 4 - Conservation status for all bat species and rabies positive bat species in Latin America and the Caribbean. CR: Critically Endangered, EN: Endangered, VU: Vulnerable, NT: Near Threatened, LC: Least Concern, DD: Data Deficient.

DISCUSSION

Bat-borne rabies in Latin America and the Caribbean presents a complex and incompletely understood situation. Across the region, bats of all diet types have been found infected with rabies, but insectivorous bats include the highest number of rabies-positive species (184 species), but the lowest proportion of species diversity (27%); for hematophagous and carnivorous species high proportions of rabies-positive species were found (100% and 60% respectively), but numbers of species for these diets were low. Because only three hematophagous bat species are known, and only three carnivorous species were reported as rabies-positive, results from these chi-square tests must be considered with caution, as the low numbers of observations may render the results unreliable. In light of frequent commensalism with humans, insectivorous bats present risk of rabies transmission to humans[63], as in the case of the insectivorous bat *T. brasiliensis*, found abundantly in urban environments from Mexico to Argentina and Chile[10,25,76,90].

Hematophagous bats include only three species, but a significant role in numerous rabies outbreaks in humans and livestock has been attributed to *D. rotundus* populations, possibly in light of their ecological plasticity and wide geographic distribution[47]. The diet and cryptic behavior of vampire bats represent an overt source of human and animal bite contact, compared to other bat diet types[88]. Viral characterization using monoclonal antibodies gives clues about the mammal reservoir involved[4,21,69], but, considering the high diversity of viral lineages in Latin America, molecular genetic tools are often used for confirmation[25,32,67,69,90,92]. The number of bat species rabies-positive and rabies AgV by country appear to be linked to research effort, but not to bat species richness by country. More antigenic variants were reported in countries where more bat species rabies-positive are found (Fig. 3). This close association between amount of rabies-positive species and number of antigenic variants is strong evidence that more lineages could be found if countries with high bat biodiversity increase research effort. For example, a report was found of *T. brasiliensis* as rabies-positive for Dominican Republic, but no reports were found for Haiti, even though the two countries share a single island[62].

However, substantial gaps exist in the knowledge of bat-rabies ecology, such as how the virus spreads among populations[86]. Seasonal migrations of species of bats in the genus *Lasiurus* may link to the spread of rabies virus over thousands of kilometers along migration routes[43]. Nevertheless, rabies virus variants linked to this genus have not been reported in all Latin American and Caribbean countries where the species is present. Geographic origins of rabies in the Americas remain unclear, but recent evidence indicates that vampire strains may not be the source of bat-borne rabies in the Americas[46].

Antigenic variants differ among bat species and geographic locations. For instance, *T. brasiliensis* is widely distributed in Latin America, and across its distribution, diverse rabies antigenic variants have been reported[44]. In Mexico, *T. brasiliensis* is the main reservoir of AgV9, but in South America the same species carries AgV4[89]. *Lasiurus* spp., on the other hand, carry AgV6 across their broad geographic distribution[43], although with some exceptions[26] and rabies lineages from other bat species have been found in *Lasiurus* genus, suggesting cross-species transmission[70,93], contrasting with a report from North America, where *Lasiurus* are more likely to be donors than recipients of spillover[83]. These differences in the distribution of virus variants may result from geographic isolation and host behavior[55], showing the complex dynamics of rabies in bat populations[90]. Bat rabies antigenic variants have also been found in skunks (*Mephitis mephitis*) and gray foxes (*Urocyon cinereoargenteus*) of North America, demonstrating successful bat-borne rabies host shift events to novel host species with viral persistence and adaptation for transmission[45,48]. In Latin America, bat-borne antigenic variants of rabies have been found in domestic carnivores (dogs and cats) in Mexico, Costa Rica, Colombia, Brazil, Argentina, and Chile[4,65,69,76,90,92]. Bat rabies outbreaks have been associated with habitat disturbance and ecosystem alteration[44], with some historic and current evidence in Latin America[5,14,32,49,51,56,77]; a recent key article highlighted the need to understand how anthropogenic perturbation triggers outbreaks of bat-borne diseases[34], and this phenomenon demands deeper study.

The rabies literature presently focuses largely on disease diagnosis and detection of rabies; few studies have sought to understand host-virus dynamics or the ecology of these interactions[18,28,83-85]. An understanding of virus and host ecology is fundamental, however, to preventing outbreaks in humans and animals. Indeed, a series of significant research gaps, were found as follows: 1) Relatively few countries report antigenic variant identifications. As a result, virus variant distributions are poorly characterized geographically. To date, the most relevant and complete phylogenetic studies of bat-borne rabies have not included spatial analyses[11,83]; detailed geographic and environmental characterization of bat rabies could enhance future phylogeographic research. Better characterization of rabies lineages in Latin America brings the opportunity to identify bat-borne rabies in humans and understand how climate is linked to rabies lineage distributions in the Americas. STREICKER *et al.* (2012b), found effects of climate on viral evolution of bat rabies across temperate and tropical regions, although more detailed analysis is needed for tropical lineages. 2) Little is known about the ecology of rabies-bat dynamics. In Latin America, few ecological studies have been undertaken regarding rabies persistence mechanisms (but see BLACKWOOD *et al.,* 2013); further research should focus on longitudinal serologic studies to understand temporal and spatial infection dynamics of rabies in bat populations[30,34]. 3) Bat species carrying rabies are not reported in all countries: such epidemiological gaps delay human rabies diagnosis and prevention[4]. 4) Latin American bat species population status is frequently poorly known. Understanding of bat population dynamics is indispensable in comprehending the ecology of this and other infectious diseases[34]. Finally, 5) effects of habitat fragmentation on virus occurrence in bats and transmission to humans are poorly studied: although land-use change has been suggested as related to rabies outbreaks, no scientific quantification of this phenomenon exists[34].

Density of mammals in human settlements (mainly cats and dogs) may prove more important than just bat presence in determining transmission risk of non-hematophagous bat rabies to people[4,22,45,65,66,68,92], in view of low prevalence in bat colonies[24]. Considering that bats are natural rabies hosts, an integrated approach should seek equilibrium among public health, agriculture, and biodiversity conservation interests. Public health agencies should include bat ecologists in their teams, to understand bat population dynamics for rabies prevention[34]; unfortunately, such links are still missing. A strategic opportunity to reduce the gap between ecology and public health is the Red Latinoamericana para la Conservación de Murciélagos (Latin American Network for Bat Conservation; www.relcomlatinoamerica.net). On the other hand, present laboratory-based rabies surveillance in Latin America has been advancing programs to eliminate dog rabies, a valuable source of data for bat-borne rabies studies[34]. Finally, bat conservation has become a significant concern in recent years[72], but an important number of species in the region are deficient in data to ascertain their conservation status.

RESUMEN

Rabia transmitida por murciélagos en Latino América

La situación de rabia en América es compleja: la rabia en perros ha disminuido drásticamente pero los murciélagos están siendo reconocidos cada vez más como reservorios naturales de otras variantes de rabia. Aquí compilamos las especies de murciélagos reconocidas como positivas a rabia con diferentes variantes antigénicas, así como su relación con el estado de conservación de los murciélagos a lo largo de América Latina. El virus de rabia está ampliamente distribuido en las especies de murciélagos de América Latina, 22.5% (75) de las especies de murciélagos conocidas han sido confirmadas como especies positivas a rabia. La mayoría de las especies de murciélagos reportadas como positivas a rabia son clasificadas por la Unión Internacional para la Conservación de la Naturaleza como "Preocupación Menor". De acuerdo al tipo de dieta, los murciélagos insectívoros tuvieron la mayor cantidad de especies reconocidas como reservorio del virus rabia, mientras en proporción los hematófagos fueron los más importantes. Investigaciones a escala gruesa deben buscar entender aspectos de ecología de la rabia; es necesaria la información básica sobre la distribución y dinámica poblacional para muchas especies de murciélagos de América Latina y el Caribe; y el efecto del cambio del paisaje en la generación de brotes de rabia transmitida por murciélagos permanece sin ser evaluado. Por último, para entender y prevenir enfermedades emergentes a partir de los murciélagos es necesario un enfoque integral incluyendo salud pública, ecología y biología de la conservación.

ACKNOWLEDGMENTS

Special thanks to the Programa para la Conservación de los Murciélagos de Chile (PCMCH) for promoting the development of this review, and Emma Stapleton who donated the ArcGIS license. Thanks also to Ruben Barquéz, who reviewed an earlier version of this manuscript, and to Valeska Rodriguez for assistance in data compilation. Universidad Andres Bello provided the grant DI-412-13/I. LEE is student in the Conservation Medicine Program at the Universidad Andres Bello, this manuscript is part of the fulfillment of his PhD degree.

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Received: 2 August 2013
Accepted: 9 May 2014