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, 22.5-73% 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 others42. Bat diets include insects, fruits, leaves, flowers, nectar, pollen, fish, other vertebrates, and blood41. 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 vectors97,40,42. 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 value4. With around 1230 species, bats are the second most diverse mammal order (after rodents), with an impressively broad ecological and geographic distribution41,42.

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 zoonosis23. 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 species73,44,15,72,87. In America, bats now constitute the principal rabies reservoir15,23; rabies is thought to have occurred in tropical America since pre-Hispanic times, being transmitted predominantly by hematophagous vampire bats4, although recent phylogenetic reconstructions suggest that rabies virus in the Americas is unlikely to have originated from vampire bats46. The first scientific report of rabies in America was by CARINI (1911), in São Paulo, Brazil7. Advances in diagnostic techniques have now contributed to an understanding of bat-rabies dynamics43.

In Latin America, human rabies cases have decreased in recent decades77,74, with mortality rates estimated at 0.01-0.60 per 100,000 individuals9,37. 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 Caribbean4. Brazil, Peru, Mexico, and Colombia are the countries with most human cases of rabies in the region36, 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 America79. 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 techniques29. Dog rabies (variants 1 and 2) has decreased...
In Latin America, rabies surveillance in bats is limited in 1975. Since 1975, at least 500 bat-associated cases of human rabies have been reported from across Latin America. 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: for example, in 2005, 13 cases of human rabies derived from dogs were reported, compared with 60 human cases derived from bats. Indeed, even in Latin American countries considered “dog rabies free,” human cases caused by bats have been reported.

Both vampire and non-vampire bats have been involved in these events. Hence, after vampire bats, insectivorous bats have assumed a greater role as sources of the virus in Latin America. Cross-species spillover is well appreciated in bat-borne rabies. Since 1975, at least 500 bat-associated cases of human rabies have been reported from across Latin America. 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; for example, in 2005, 13 cases of human rabies derived from dogs were reported, compared with 60 human cases derived from bats. Indeed, even in Latin American countries considered “dog rabies free,” human cases caused by bats have been reported.

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. For preliminary bat distributional information, vector-format based maps (shapefiles) from IUCN were used; maps were handled using ArcGIS 9.3 (ESRI). Chi-square tests were used to evaluate associations between bat species (richness) with 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.

**RESULTS**

**Bat species richness patterns:** In all, 333 bat species were documented from 24 Latin American and Caribbean countries. 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 I.
Bat species known to be rabies-positive in Latin America and the Caribbean

| Insectivorous | Frugivorous | Nectarivorous | Omnivorous | Carnivorous | Hematophagous | AgV |
|---------------|-------------|---------------|------------|-------------|---------------|-----|
| **Argentina** |             |               |            |             |               |     |
| Eumops auripendulus* |             |               |            |             |               | V2⁸⁰ |
| Eumops patagonicus⁴⁰       |             |               |            |             |               | V⁴³⁻⁶⁰ |
| Histiotus montanus⁴⁰       |             |               |            |             |               | H⁸⁰  |
| Myotis sp⁴⁰             |             |               |            |             |               | V⁴³⁻⁶⁰ |
| Myotis nigricans⁴⁰       |             |               |            |             |               | V⁴³⁻⁶⁰ |
| Eptesicus furinalis⁸⁹      |             |               |            |             |               | V⁴³⁻⁶⁰ |
| Molossus molossus⁶⁹       |             |               |            |             |               | V⁴³⁻⁶⁰ |
| Lasiusus blossveillii⁴⁰   |             |               |            |             |               | V⁴³⁻⁶⁰ |
| Lasiusus cinereus⁸³⁶⁹      |             |               |            |             |               | V⁴³⁻⁶⁰ |
| Lasiusus ega⁹⁹           | Artibes lituratus¹⁵ |         |            |             |               | V⁴³⁻⁶⁰ |
| **Belize**              |             |               |            |             |               |     |
| Myotis fortidens⁴¹²      |             |               |            |             |               |     |
| Myotis nigricans⑩²        |             |               |            |             |               |     |
| Molossus molossus⑩²      |             |               |            |             |               |     |
| Molossus sinaloae⑩²      |             |               |            |             |               |     |
| **Bolivia**             |             |               |            |             |               |     |
| Artibes jamaicensis⑩²   | Artibes lituratus⑩² |           |            |             |               |     |
| **Brazil**              |             |               |            |             |               |     |
| Cynomops abrustrus⁸²       |             |               |            |             |               |     |
| Cynomops planirostris⁸²   |             |               |            |             |               |     |
| Eptesicus diminutus⁸²      |             |               |            |             |               |     |
| Eptesicus furinalis⁸²      |             |               |            |             |               |     |
| Eptesicus brasiliensis⁸²   |             |               |            |             |               |     |
| Eumops glaucinus⑩²        |             |               |            |             |               |     |
| Eumops perotis⑩²         |             |               |            |             |               |     |
| Eumops auripendulus⑩²    |             |               |            |             |               |     |
| Histiotus velatus⑩²      |             |               |            |             |               |     |
| Lasiusus blossveillii⑩²  |             |               |            |             |               |     |
| Lasiusus cinereus⑩²      |             |               |            |             |               |     |
| Lasiusus ega⑩²           |             |               |            |             |               |     |
| Lasiusus egretius⑩²      |             |               |            |             |               |     |
| Lonchorhina aurita⑩²     |             |               |            |             |               |     |
| Lophostoma brasiliense⑩² |             |               |            |             |               |     |
| Micronycteris megalotis⑩²|             |               |            |             |               |     |
| Molossus molossus⑩²      |             |               |            |             |               |     |
| Molossops neglectus⑩²    |             |               |            |             |               |     |
| Molossus rufus⑩²         |             |               |            |             |               |     |
| Molossus sinaloae⑩²      |             |               |            |             |               |     |
| Myotis albescens⑩²      |             |               |            |             |               |     |
| Myotis levis⑩²          |             |               |            |             |               |     |
| Myotis nigricans⑩²      |             |               |            |             |               |     |
| Myotis riparius⑩²       |             |               |            |             |               |     |
| Nyctinomops laticaudatus⑩²|             |               |            |             |               |     |
| Nyctinomops macrotis⑩²   |             |               |            |             |               |     |
| Promops nasutus⑩²        |             |               |            |             |               |     |
| Tadarida brasiliensis⑩² |             |               |            |             |               |     |
| **Colombia**            |             |               |            |             |               |     |
| Eptesicus brasiliensis⁴⁶⁵ | Carollia perspicillata⑤³ |         |            |             |               |     |
| Molossus molossus⁴⁶⁵      |             |               |            |             |               |     |

**Notes:**
- * indicates species that are known to be rabies-positive.
- † indicates species that are known to be bat-borne rabies carriers.
- AgV refers to the specific antigenic variants detected in each species.
### Table 1.
Bat species known to be rabies-positive in Latin America and the Caribbean (cont.)

| Insectivorous | Frugivorous | Nectarivorous | Omnivorous | Carnivorous | Hematophagous | Ag V |
|---------------|-------------|---------------|------------|-------------|---------------|------|
| **Costa Rica** |             |               |            |             |               |      |
|                |             |               |            |             | Desmodus rotundus⁴ | V³⁴ |
| **Cuba**      |             |               |            |             |               |      |
| Epitesicusfuscus⁴¹² |             |               |            |             |               |      |
| Eumops glauinus⁵⁴ |             |               |            |             |               |      |
| **Chile**     |             |               |            |             |               |      |
| Histiotusmacrotus⁶²³,²⁴ |             |               |            |             |               |      |
| Histiotusmontanus⁶²³,²⁴ |             |               |            |             |               |      |
| Lasiurus borealis⁶²³,²⁴ |             |               |            |             |               |      |
| Lasiuruscinereus⁶²³,²⁴ |             |               |            |             |               |      |
| Myotis chiloensis⁸³,²⁴ |             |               |            |             |               |      |
| Tadarida brasiliensis⁷⁵³,²⁴ |             |               |            |             |               |      |
| **Ecuador**   |             |               |            |             | Desmodus rotundus⁷³⁷ | V³⁷⁷ |
|                |             |               |            |             |               |      |
| **El Salvador** |             |               |            |             | Desmodus rotundus¹² |      |
|                |             |               |            |             |               |      |
| **Guatemala** |             |               |            |             | Desmodus rotundus¹² |      |
| Molossus sinaloae¹² |             | Artibeus lituratus¹² | | Phyllostomus discolor¹² | Desmodus rotundus¹² |      |
| Myotis fortidens⁵¹² | |                |            |             |               |      |
| **French Guyana** |             |               |            |             | Desmodus rotundus⁵² | V³⁵² |
|                |             |               |            |             |               |      |
| **Honduras** |             |               |            |             | Desmodus rotundus¹³ |      |
| Molossus sinaloae¹¹ |             |               |            |             |               |      |
| **Mexico**    |             |               |            |             | Desmodus rotundus⁹⁰ | V³⁷⁵,³⁴,³⁵,⁸⁹ |
| Antrozous pallidus¹⁰² |             |               |            |             |               |      |
| Eptesicusfuscus⁹¹² |             |               |            |             |               |      |
| Lasiurusblossevillii⁹¹² |             |               |            |             |               |      |
| Lasiuruscinereus⁹¹² |             |               |            |             |               |      |
| Lasiurus ega⁹¹² |             |               |            |             |               |      |
| Lasiurus intermediate⁹¹² |             |               |            |             |               |      |
| Lasiurus seminolus⁹¹² |             |               |            |             |               |      |
| Macrota waterhouesti¹² |             |               |            |             |               |      |
| Molossus rufus¹² |             |               |            |             |               |      |
| Mormoops megalophylla⁴¹ |             |               |            |             |               |      |
| Myotis velifer⁸¹² |             |               |            |             |               |      |
| Nyctinomops latcaudatus¹¹² |             |               |            |             |               |      |
| Nyctinomops macrotis¹¹² |             |               |            |             |               |      |
| Pteronotus personatus¹³² |             |               |            |             |               |      |
| Pipistrellus subflavus¹² |             |               |            |             |               |      |
| Pteronotus parnellii¹² |             |               |            |             |               |      |
| Pteronotus davyi¹² |             |               |            |             |               |      |
| Rhogeessa parvula⁷¹ |             |               |            |             |               |      |
| Rhogeessa tumida⁸¹² |             |               |            |             |               |      |
| Tadarida brasiliensis⁹⁰ |             |               |            |             |               |      |
| **Nicaragua** |             |               |            |             | Desmodus rotundus¹² |      |
Table 1.
Bat species known to be rabies-positive in Latin America and the Caribbean (cont.)

| Insectivorous | Frugivorous | Nectarivorous | Omnivorous | Carnivorous | Hematophagous | AgV |
|---------------|-------------|---------------|------------|-------------|---------------|-----|
| **Panama**    |             |               |            |             |               |     |
| Cynomops planirostris* |             |               |            |             |               |     |
| Micronycteris megalotis†12 |             |               |            |             |               |     |
| Molossus coibensis†1 |             |               |            |             |               |     |
| Molossus currentium12† |             |               |            |             |               |     |
| Molossus molossus12† |             |               |            |             |               |     |
| Myotis nigricans* |             |               |            |             |               |     |
| **Paraguay**  |             |               |            |             |               |     |
| Lasiusus ega*81 | Artibeus jamaicensis* | Desmodus rotundus12 | V6*1 |           |               |     |
| Tadarida brasiliensis18 |             |               |            |             |               |     |
| **Peru**      |             |               |            |             |               |     |
| Myotis nigricans*12 |             |               |            |             |               |     |
| Micronycteris megalotis†12 |             |               |            |             |               |     |
| Molossus molossus12† |             |               |            |             |               |     |
| **Dominican Republic** |             |               |            |             |               |     |
| Tadarida brasiliensis*62 |             |               |            |             |               |     |
| **Trinidad and Tobago** |             |               |            |             |               |     |
| Diclidurus albus*31 |             |               |            |             |               |     |
| Molossus molossus*11 | Artibeus jamaicensis* | Desmodus rotundus12 | V4*31 |           |               |     |
| Pteronotus davii*31 | Artibeus lituratus* | Diaemus youngi*31 | -         |            |               |     |
| Pteronotus parnelli*112 |             |               |            |             |               |     |
| **Uruguay**   |             |               |            |             |               |     |
| Lasiusus cinereus*49 |             |               |            |             |               |     |
| Lasiusus ega*49 |             |               |            |             |               |     |
| Molossus molossus*12 |             |               |            |             |               |     |
| Myotis spp.*60 |             |               |            |             |               |     |
| Tadarida brasiliensis*60 |             |               |            |             |               |     |
| **Venezuela** |             |               |            |             |               |     |
| Molossus rufus*16 |             |               |            |             |               |     |
| Family: *Vespertilionidae; †Phyllostomidae; ‡Molossidae; §Mormoopidae; †Noctilionidae; ‡Emballonuridae. AgV: Antigenic variants by country. E: Antigenic variant for Eptesicus spp.; Eu: Eumops; H: Antigenic variant for Histiotus spp.; Lb: Lasiusus borealis; M: Antigenic variant for Myotis spp.; N: Nyctinomops; V3, V5, V8, V11: Antigenic variant for D. rotundus; V4, V9: T. brasiliensis; V6: Lasiusus spp. |

The largest host geographic distributions were for *Lasiusus 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
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).

**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 (*Leptonycteris yerbabuenae*, *Eumops perotis*, *Mormoops megalophylla*) that have decreasing populations. According to IUCN (2012), information was insufficient to classify the conservation threat status for 44 (13%) bat species reported in Latin America.

**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 humans43, as in the case of the insectivorous bat T. brasiliensis, found abundantly in urban environments from Mexico to Argentina and Chile30,56,90.

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. The diet and cryptic behavior of vampire bats represent an overt source of human and animal bite contact, compared to other bat diet types. Viral characterization using monoclonal antibodies gives clues about the mammal reservoir involved21,69, but, considering the high diversity of viral lineages in Latin America, molecular genetic tools are often used for confirmation. 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. 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.

However, substantial gaps exist in the knowledge of bat-rabies ecology, such as how the virus spreads among populations. Seasonal migrations of species of bats in the genus Lasius are may link to the spread of rabies virus over thousands of kilometers along migration routes. 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-rabies outbreaks in the Americas.

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 reported44. In Mexico, T. brasiliensis is the main reservoir of AgV9, but in South America the same species carries AgV49. Lasius spp., on the other hand, carry AgV6 across their broad geographic distribution4, although with some exceptions and rabies lineages from other bat species have been found in Lasius genus, suggesting cross-species transmission63,91, contrasting with a report from North America, where Lasius are more likely to be donors than recipients of spillover49. These differences in the distribution of virus variants may result from geographic isolation and host behavior49, showing the complex dynamics of rabies in bat populations. 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 transmission44,45. 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 Chile64,65,66,70,92. Bat rabies outbreaks have been associated with habitat disturbance and ecosystem alteration46, with some historic and current evidence in Latin America5,14,32,49,51,56,72, a recent key article highlighted the need to understand how anthropogenic perturbation triggers outbreaks of bat-borne diseases47, 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 interactions48,83-85. 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 antigen 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 analyses1,87; 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 populations30,34. 3) Bat species carrying rabies are not reported in all countries: such epidemiological gaps delay human rabies diagnosis and prevention. 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 diseases44. 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 exists44.

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 people42,43,45,65,66,68,92, in view of low prevalence in bat colonies44. 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 prevention49; 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 studies48. Finally, bat conservation has become a significant concern in recent years72, but an important number of species in the region are deficient in data to ascertain their conservation status.
RESUMEN

Rabia transmitida por murciélagos en Latinoamérica

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 antigenéticas, 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.

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