
Enzootic and Epizootic Rabies Associated with Vampire Bats, Peru

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During the past decade, incidence of human infection with rabies virus (RABV) spread by the common vampire bat (*Desmodus rotundus*) increased considerably in South America, especially in remote areas of the Amazon rainforest, where these bats commonly feed on humans. To better understand the epizootiology of rabies associated with vampire bats, we used complete sequences of the nucleoprotein gene to infer phylogenetic relationships among 157 RABV isolates collected from humans, domestic animals, and wildlife, including bats, in Peru during 2002–2007. This analysis revealed distinct geographic structuring that indicates that RABVs spread gradually and involve different vampire bat subpopulations with different transmission cycles. Three putative new RABV lineages were found in 3 non-vampire bat species that may represent new virus reservoirs. Detection of novel RABV variants and accurate identification of reservoir hosts are critically important for the prevention and control of potential virus transmission, especially to humans.

Rabies virus (RABV; family *Rhabdoviridae*, genus *Lysavirus*) is a bullet-shaped, single-stranded, negative-sense RNA virus with a 12-kb genome that encodes 5 structural proteins: nucleoprotein (N), phosphoprotein, matrix protein, glycoprotein, and polymerase (P). Over the course of its evolutionary history, RABV has established independent transmission cycles in diverse species of mesocarnivores and bats. Rabies disease remains a serious public health concern in several countries of Asia, Africa, and the Americas, where it is estimated that >50,000 fatal infections occur annually (2).

In Latin America, rabies diseases are classified into 2 major epidemiologic forms, urban rabies and sylvatic rabies. For the former, dogs are the main viral reservoir

host; for the latter, several species of wild carnivores and bats maintain independent rabies enzootics. Because of the widespread control of urban rabies through vaccination of domestic dogs, the common vampire bat (*Desmodus rotundus*) has emerged as the principal RABV reservoir host along the species' natural range from Mexico to South America (3,4). The transmission and maintenance of RABV in natural populations of *D. rotundus* bats remains poorly understood, particularly within ongoing epizootics and enzootics occurring in different regions of the Americas (5,6). Active programs for the control of vampire bat-associated rabies in Latin America rely primarily on reduction of vampire bat populations by culling (7,8). Nonetheless, cross-species transmission to humans and domestic animals persists, even in areas where culling occurs regularly.

In Peru and other countries within the Amazon rainforest region, RABV transmitted by vampire bats has acquired greater epidemiologic importance because of the more frequent detection of human rabies outbreaks. This increase may reflect enhanced laboratory-based surveillance; increased awareness among public health stakeholders; or ecologic changes that promote greater contact between bats and humans, such as depletion of vampire bats' natural prey community through hunting or habitat fragmentation. During 2002–2007, a total of 293 (77%) of the rabies cases diagnosed by the Instituto Nacional de Salud in Peru were associated with vampire bat RABV variants; the remaining 87 (23%) were attributed to RABV variants associated with dogs. In communities where vampire bats commonly feed on humans, the frequency of outbreaks depends on the transmission dynamics within the local vampire bat populations (9,10). Unfortunately, recent outbreaks in native communities of the Amazon region have been poorly characterized because of cultural constraints and local beliefs that have precluded investigators from obtaining diagnostic specimens (11).

Molecular epidemiology has been extensively used to determine RABV reservoir hosts in a given region or country, define the geographic distribution of the disease associated with those hosts, infer the temporal and spatial spread of the disease, identify spillover infections to nonreservoir

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species, describe novel RABV variants, and detect putative host shifts (12). The spatiotemporal epidemiology and genetic diversity of vampire bat-associated rabies in Peru have not been explored; a laboratory-based investigation conducted in 1999 addressed the comprehensive characterization of RABV in only 2 humans (11). Given the increasing importance of vampire bat-associated rabies in the Peruvian Amazon, comprehensive surveys of virus diversity and elucidation of geographic boundaries are needed to clarify the frequency and duration of rabies outbreaks. The goals of our study were to 1) determine the genetic diversity and geographic distribution of RABV infection associated with vampire bats; 2) clarify disease dissemination trends among affected areas; 3) detect the origins of spillover infections to other mammals; and 4) identify novel RABV lineages.

Materials and Methods

Virus Samples

During 2002–2007, decentralized units of the Ministry of Health of Peru collected 157 brain samples from multiple species and geographic regions of Peru (online Technical Appendix Table 1, wwwnc.cdc.gov/EID/article/19/9/13-0083-Techapp1.pdf). Samples were selected on the basis of identification of vampire bat or any other bat-associated rabies virus variant by using a panel of 8 monoclonal antibodies, as described (12). The specimens included samples from 98 cows, 26 bats, 12 humans, 9 horses, 5 goats, 2 dogs, 2 donkeys, 1 kinkajou, 1 pig, and 1 sheep. Most samples ($n = 118$) originated from the departments of Apurimac, Ayacucho, Cusco, Madre de Dios, and Puno, located in the southern region of the country, which is made up of inter-Andean valleys and Amazon rainforest. Twenty-six samples were from the departments of San Martin, Amazonas, Cajamarca, and Lambayeque, located in the northern region, which comprises the Andean mountains and Amazonian forests. The remaining 13 samples were from the departments of Pasco, Huanuco, and Ucayali in the central Amazon. All samples were submitted to the reference laboratory of the Instituto Nacional de Salud for RABV confirmation by fluorescent antibody testing (13).

PCR and Sequencing

Total RNA was extracted from each sample after a single passage in mouse brains by using TRIzol (Invitrogen, Carlsbad, CA, USA), according to the manufacturer's specifications. Amplification of the complete N gene was achieved by reverse transcription PCR through 2 overlapping reactions by use of 3 published primers (Lys 001, 550F, and 304) and a modified version of primer 1066degB (14–16). The primer sets were used in

the following combinations: Lys001, 5'-ACGCTTAAC-GAMAAA-3'; 1066degB, 5'-TCYCTGAAGAATCTTC-TYTC-3'; 550F, 5'-ATGTGYGCTAAYTGGAGYAC-3'; and 304, 5'-TTGACGAAGATCTTGCTCAT-3' (14–16). PCR products were visualized on 1.5% agarose gels, and expected size amplicons were purified by using ExoSAP-IT (USB Products Affymetrix, Inc., Cleveland, OH, USA). Cycle sequencing reactions were conducted by using Big Dye Terminator v1.1 Cycle Sequencing Kit (Applied Biosystems, Foster City, CA, USA), according to the manufacturer's instructions. Products were analyzed on an ABI 3730 DNA analyzer (Applied Biosystems, Grand Island, NY, USA). Chromatograms were edited by using BioEdit (17), and sequences were assembled by using the fixed RABV SADB19 (GenBank accession no. M31046) as a template (18). Multiple alignments were attained by using ClustalW (19).

Phylogenetic Analysis

For phylogenetic reconstructions, we retrieved complete and partial RABV sequences from GenBank that represented historical and ongoing rabies epizootics in the Americas (online Technical Appendix Table 2). Other *Lyssavirus* species, such as European bat lyssavirus (EBLV) 1 (U22845) and EBLV-2 (U22846), were included as outgroups (20). Phylogenetic reconstructions using complete N gene sequences of the 157 isolates from Peru and 83 from GenBank were generated by using the neighbor-joining (NJ) method in MEGA 4.0 (21), assuming the maximum composite likelihood nucleotide substitution model. The statistical significance of branch partitions was assessed with 1,000 bootstrap replicates. We also estimated a time-scaled phylogenetic tree for the dataset comprising RABVs associated with *D. rotundus* (154 isolates from Peru and 58 from GenBank) by using BEAST version 1.7 (22), which uses a Bayesian coalescent framework to estimate evolutionary parameters from many possible genealogies through Markov chain Monte Carlo sampling. Our analysis used the Bayesian skyline model of population growth as a flexible demographic prior and the relaxed lognormal molecular clock to allow for rate variation among branches of the tree. Substitution models for coding positions 1+2 (CP12) and CP3 were unlinked, and substitution models in each coding position were selected by Akaike Information Criterion in jModeltest (23). The general time reversible model, including invariant sites and Γ distributed site heterogeneity, was applied to CP12, and time reversible model + Γ was applied to CP3. Four replicate Markov chain Monte Carlo analyses were run for 60 million generations each and combined for final estimates and construction of the maximum-clade credibility tree. Convergence across runs, appropriate burn-in periods, and effective sample sizes >200 were assessed by using Tracer (<http://beast.bio.ed.ac.uk/Tracer>).

Results

Phylogeny of RABV Isolates

Complete N gene sequences (1,350 nt, excluding the stop codon) were obtained from 157 specimens from humans, domesticated animals, and wildlife from 12 of the 24 departments of Peru (online Technical Appendix Table 1). Pairwise similarity ranged from 85.9% to 100%, with an average pairwise identity of 97.3%. The NJ phylogenetic analysis demonstrated 2 major RABV clusters, 1 associated with *D. rotundus* bats and 1 associated with insectivorous bats. The *D. rotundus* cluster was subsequently subdivided into 4 lineages, I–IV, each with a distinctive geographic distribution within Peru; the RABVs associated with insectivorous bats segregated into 3 independent RABV lineages not previously reported in Peru (Figure 1).

Sequences within lineage I showed a widespread spatiotemporal distribution. Isolates were obtained from the departments of Amazonas, San Martin, Cajamarca, Huanuco, Ucayali, Pasco, Ayacucho, Cusco, and Madre de Dios. Inclusion of the reference sequences from GenBank revealed that lineage I had an extended spatiotemporal distribution over northern regions of South America, encompassing Ecuador and Colombia, during 1997–2007

(Figure 1) (24). Conversely, isolates in lineage II were detected predominately during a human rabies outbreak in the Madre de Dios and Puno departments in 2007. This lineage also grouped with an isolate from a sample found in the Cusco department in 2003 (GenBank accession no. JX648444) and with several RABV sequences reported in Brazil and Uruguay during 2004–2008 (24). These findings indicate that lineage II has been circulating within a larger geographic scale, perhaps reflecting virus dispersion across the Amazon region and southern South America (Figures 1). Two isolates (GenBank accession nos. JX648544 and JX648543) grouped into lineage III as an independent cluster unrelated to any previously described RABV (Figure 1). These samples were collected in 2006 from the Pozuzo district, which is located in the eastern side of the Pasco department in the central Peruvian Amazon.

Lineage IV was the most frequently identified lineage among the isolates collected in Peru, encompassing 98 of the 157 isolates captured during 2002–2007. These results indicate this lineage’s high prevalence in cattle in the Andes. Its geographic distribution comprised the valleys of Ayacucho and Apurimac, located at 1,200–3,500 m above sea level and extended into Cusco and north into San Martin, Lambayeque, and northern Colombia. Although this

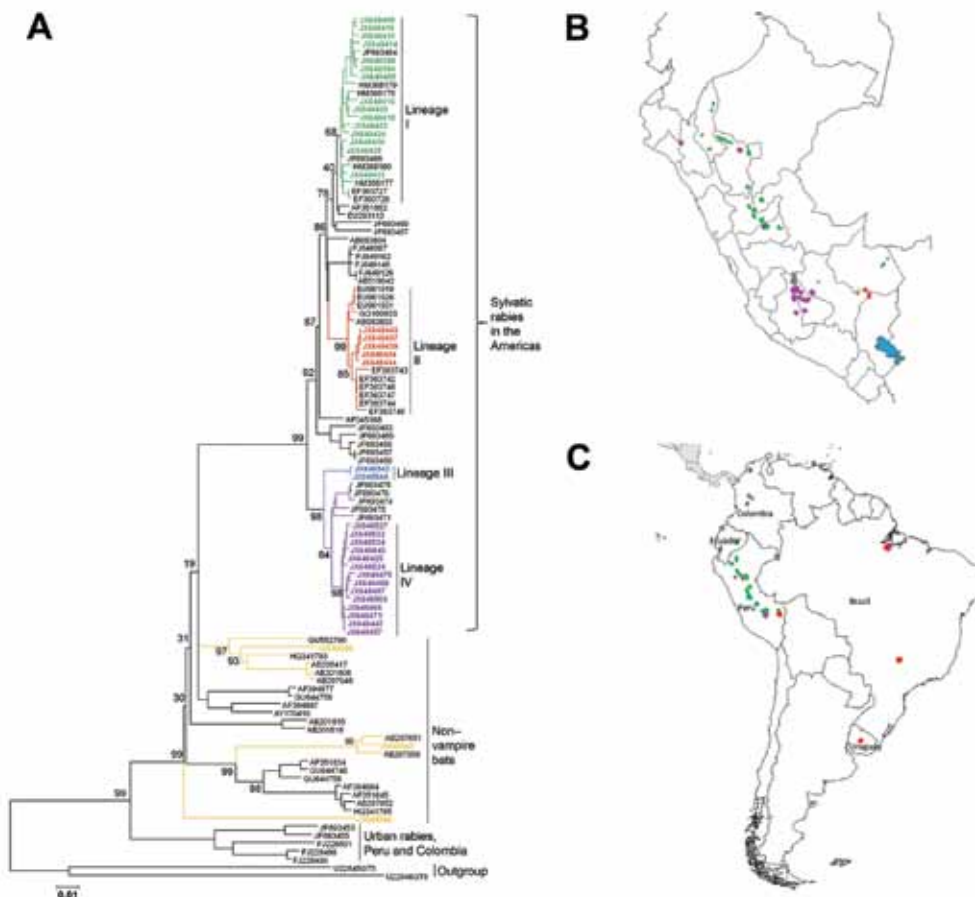


Figure 1. Phylogenetic and geographic comparisons of rabies virus isolates collected in Peru during 2002–2007 with representative rabies viruses circulating in South America. A) Phylogenetic tree showing relationships among virus isolates; B) locations from which viruses were isolated in Peru and South America. Colors indicate isolates from this study: green, lineage I; red, lineage II; blue, lineage III; purple, lineage IV. Gold indicates the 3 isolates collected in Peru from non-vampire bats. Additional lineage I isolates were found in Ecuador and Colombia; lineage II, Brazil and Uruguay; and lineage IV, Colombia. GenBank accession numbers are indicated. Scale bar indicates nucleotide substitutions per site.

lineage was predominately collected from livestock, it was also obtained from vampire bats ($n = 24$).

Evolution of Vampire Bat–Associated RABV in Peru

By applying a Bayesian coalescent analysis to 212 serially sampled partial N sequences (1,275-bp), we inferred the time scale of RABV evolution in lineages associated with vampire bats. Consistent with previous estimates, the median rate of nucleotide substitution of vampire bat–associated RABV was 9.76×10^{-4} substitutions per site per year (95% highest posterior density [HPD] 6.81×10^{-4} to 1.3×10^{-3}). These results would place the most recent common ancestor (MRCA) of contemporary vampire bat–associated RABVs as occurring in Peru in 1933 (95% HPD 1889–1962) (25). The maximum clade credibility tree (Figure 2) demonstrated similar topology to the NJ tree (Figure 1) when broader datasets were used, with vampire bat–associated RABVs differentiated into 4 phylogenetic lineages (Figure 2). As in the NJ trees, a deep division at the MRCA of vampire bat–associated RABVs separated lineages I and II from lineages III and IV (posterior probability [PP] 1.0). Major lineages appear to have been circulating for similar periods in Peru, each originating 33–44 years ago (when including the stem branch leading to current viral diversity), with extensive overlap of the 95% HPDs of the time since the MRCA for each lineage. Each RABV lineage in Peru except lineage III shared common ancestors with viruses circulating in other Latin American countries, indicating multiple viral dispersion events into or out of Peru; how-

ever, overlap of the 95% HPDs on the age of samples from Peru compared with those from other countries limited direct inference on the directionality of movement between countries. Within lineage I, samples from Ecuador and Colombia were interspersed with contemporary samples from Peru, which suggests a relatively recent spatial spread among countries. In addition, historical introductions of a similar RABV were indicated by strong posterior support (PP 0.99) for an MRCA between lineage I and samples from Colombia, Trinidad, and French Guyana in about 1973. Isolates related to lineage II were detected in Brazil and Uruguay; however, strong spatiotemporal clustering apparently separated distinct epizootics in Brazil in 2004 and Uruguay and Brazil in 2007–2008 from the human outbreak in southern Peru in 2007. A sample from a cow collected in 2003 in Peru was ancestral to samples from the 2007 human outbreak in Peru (PP 1), rather than grouping with the more contemporaneous viruses circulating in Brazil in 2004, indicating that this virus may have circulated in Peru for ≥ 4 years before the 2007 outbreak.

As in the NJ tree, lineage III was most closely related to lineage IV (PP 0.99) but was highly divergent, sharing an MRCA in 1963 (95% HPD 1940–1979). The large genetic distance from other lineages indicates that these sporadic cases were not recently introduced from other RABV lineages circulating elsewhere in Peru but rather were part of a previously unknown vampire bat–associated rabies enzootic. No samples from other countries clustered with the lineage IV samples from Peru, suggesting that this

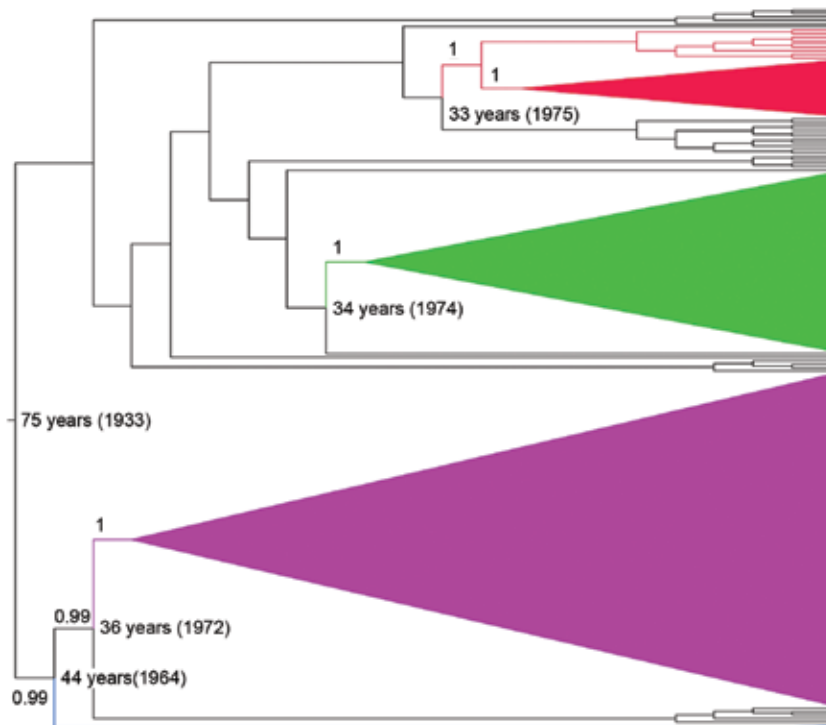


Figure 2. Phylogenetic tree generated by using Bayesian analysis for a 1,274-nt portion of the gene-coding sequences of rabies virus isolates collected in Peru during 2002–2007. Red, lineage II (found in Peru, Brazil, and Uruguay); green, lineage I (found in Peru, Ecuador, and Colombia); purple, lineage IV (found in Peru and Colombia); blue, lineage III (found in Peru). Posterior probabilities and lineage ages are shown for all major nodes.

virus has been maintained independently as a widespread rabies focus that covers the inter-Andean valleys (Aya-cucho, Apurimac) and the rainforest of northern Peru (San Martin). The closest relatives of lineage IV were viruses collected in Colombia during 1994–2008, which diverged from the samples from Peru around 1972 (95% HPD 1957–1984), consistent with the enzootic maintenance of rabies over long periods within Peru.

Novel RABV Associated with Other Wildlife in Peru

We identified 3 novel RABV variants in wildlife other than vampire bats in the southeastern region of Peru. The first variant (GenBank accession no. JX648546) was isolated from a kinkajou (*Potus flavus*) in Madre de Dios in the Amazon rainforest in southern Peru. This variant was not closely related to any previously described RABV but grouped within the larger diversity of bat-associated RABVs in the Americas (Figure 1). A second RABV variant (GenBank accession no. JX648545) was isolated from a small big-eared brown bat (*Histiotus montanus*) in Puno in southern Peru. This variant was related to RABVs found in bats of the genera *Histiotus*, *Nyctinomops*, and *Tadarida* from Chile and Brazil but appears to be an independent lineage; its branch length and pairwise average divergence of 5% separate it from its closest relatives. A third variant (GenBank accession no. JX648547) was found during 2008 in Paucartambo, Cusco, which is located in an inter-Andean valley at 2,900 m altitude. This sample clustered with sequences from unidentified bats from Brazil (GenBank accession nos. AB297651 and AB297656). Unfortunately, the bat from which this sample was obtained was not available for taxonomic identification.

Discussion

Rabies epidemiology has experienced dramatic changes in Latin America during the past 4 decades because of the implementation of highly effective strategies for prevention and control of infection in dogs and the procurement of adequate postexposure prophylaxis for humans. In 2003, human rabies cases transmitted by bats outnumbered cases transmitted by dogs in Latin America (4), and that trend has continued. The increasing detection of RABV infection in humans in the Peruvian Amazon and the persistence of vampire bat-transmitted RABV infection in livestock highlight the need to clarify the diversity of RABV lineages circulating in Peru and the spatiotemporal dynamics of RABVs associated with vampire bats. We completed phylogenetic analysis of bat-associated RABVs collected in Peru, using samples collected from rabies-endemic areas in the Andes, during sporadic human outbreaks in the Amazon, and from previously unsurveyed wildlife host species. Our study revealed that at least 4 phylogenetic lineages of RABV are circulating in vampire bat populations in Peru; these lineages appeared to display

distinctive spatiotemporal dynamics across their geographic ranges. Three of the lineages had wide geographic distributions in Peru and recent and historical relationships linked to rabies outbreaks occurring in other parts of South America (24,26–32). Dissemination of vampire bat-associated RABV appears to be gradual rather than involving long-distance dispersal events, as might be expected by the absence of long-distance migration and small home range of the reservoir species (33,34). Spatiotemporal analysis of lineage I, II, and IV RABVs showed that the ample distribution ranges were covered over periods no shorter than 3–4 decades. The specific movement of vampire bat-associated RABVs is difficult to assess, but the phylogenetic and evolutionary analyses we conducted indicate that lineages I and IV spread from north to south, whereas lineage II spread from south to north. Lineage III had restricted distribution in central Peru, which suggests it was part of a long-term vampire rabies enzootic that disappeared from Peru around 2006. Hence, in contrast to lineages I and IV, the local dynamics for lineage 3 were epizootic rather than enzootic. Understanding factors linked to the limited geographic distribution and apparent extinction of lineage III are important for preparing improved prevention and control practices.

Vampire bats are not a migratory species and usually inhabit places below 1,800-m altitude. Nonetheless, they may occasionally move relatively long distances and inhabit higher altitudes in response to limited food or roost availability. Movement encouraged by food supplementation may be illustrated by the distribution dynamics observed for lineage IV, which currently is mainly found along the inter-Andean valleys, an important cattle raising area in Per, which has an average altitude >2,000 m (35). Our data suggest that the incursion of lineage IV into the inter-Andean valleys is relatively recent (30–40 years ago) and probably occurred from northern lower lands, consistent with the likely ancestors of this lineage coming from Colombia and Ecuador (Figure 2). Because of the detrimental economic effects of vampire bat-associated rabies in the livestock industry in this region, in 2010, the government of Peru initiated intense control and prevention measures that included culling vampire bats. However, the frequency of rabies cases in livestock has been unaffected (6).

Our study showed that different RABV lineages may overlap temporally and geographically, which indicates that, within a rabies enzootic region, convergence or co-circulation of ≥ 1 RABV lineage may occur, perhaps in association with the maintenance of independent rabies foci by distinct vampire bat metapopulations. This observation could affect effective planning of prevention and control strategies because 1 focal point might be vulnerable to rabies reintroduction from adjacent foci, a process that could explain the persistence of the disease. Studies of population structure, gene flow, and dispersal of vampire bats

within Peru and throughout the South America are necessary for corroborating observations on the dissemination dynamics of rabies associated with this species.

Although it was not the intent of this study to identify the role of rabies transmission and maintenance among species other than vampire bats, we circumstantially discovered 3 potentially novel RABV lineages in non-vampire bat hosts. This finding stresses the potential emergence of novel RABV reservoirs in the country and the need for enhanced surveillance for lyssaviruses in potential wild animal reservoirs. In Peru, the surveillance system for the detection and monitoring of human rabies cases associated with bats and other wild animals is passive; that is, cases are recorded only as they are reported. Operationally, the system is less than ideal because, even though most clinical cases of rabies in humans may be recorded, few are laboratory confirmed; consequently, the RABV variants associated with them are not typed. Rabies associated with insectivorous bats is commonly encountered in countries such as the United States, where 1 or 2 cases of rabies occur in humans each year (36). A bat rabies surveillance system such as the one in place in the United States, which tests >20,000 bats and confirms ≈1,400 infections each year, relies heavily on submissions of sick or dead bats to rabies diagnostic facilities from the general public (36). This public participation in the process has been augmented by active educational programs that emphasize the potential risk for rabies transmission from bats to humans, pets, and livestock. Human rabies associated with insectivorous bats has been reported in other countries in Latin America, such as Chile and Mexico (37,38), but the role of these bats in rabies transmission to humans is largely unknown in Peru. Therefore, better understanding of these transmission cycles and better programs for the taxonomic identification of bats with rabies should be implemented.

We also identified RABV in a kinkajou; this strain that was not closely related to any known RABV. We could not determine whether this animal represented a single spillover infection from a previously unknown bat reservoir or an emerging host shift with ongoing transmission within kinkajous. Kinkajous are in the same taxonomic family (*Procyonidae*) as raccoons (*Procyon lotor*) (39), which are a well-established rabies reservoir in North America. This relationship suggests that kinkajou could serve as an emerging RABV reservoir if the traits that enable the establishment of RABV reservoirs are conserved along the phylogeny of procyonids. Serologic surveys and enhanced surveillance would be useful for further exploring this possibility.

In conclusion, our study demonstrates the presence of diverse RABV lineages associated with vampire bats and several other species in Peru. Although our research was limited by the restrictions of passive surveillance data, RABV lineages in vampire bats appear to show distinct

spatiotemporal patterns, with 2 lineages that were abundant and widely distributed throughout the study period and 2 others that occurred more sporadically, consistent with enzootic and epizootic dynamics. Further discrimination of transmission cycles and their drivers will be crucial for prediction of the frequency of outbreaks in humans and domestic animals and, ultimately, for the design of informed strategies for rabies control in this region.

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Mr Condori is a guest researcher at the Centers for Disease Control and Prevention and has 10 years of experience in rabies diagnosis and molecular typing. He has a special interest in molecular epidemiology and ecology of rabies.

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Enzootic and Epizootic Rabies Associated with Vampire Bats, Peru

Technical Appendix

Technical Appendix Table 1. Isolates of rabies virus from Peru included in this study*

No.	Identification no. and genetic cluster	Animal source	Department	Province	District	Year	GenBank no.	Lineage
1	PERAPUBV1539_02	Bovine	Apurimac	Andahuaylas	Pacucha	2002	JX648538	IV
2	PERAYABV2138_02	Bovine	Ayacucho	La Mar		2002	JX648457	IV
3	PERAPUBV3040_02	Bovine	Apurimac	Andahuaylas	Pacucha	2002	JX648540	IV
4	PERAPUHR3981_02	Horse	Apurimac	Andahuaylas	Andarapa	2002	JX648525	IV
5	PERAPUBV3982_02	Bovine	Apurimac	Andahuaylas	Pacucha	2002	JX648541	IV
6	PERAPUBV5119_02	Bovine	Apurimac	Andahuaylas	Pacucha	2002	JX648539	IV
7	PERAYABV10574_02	Bovine	Ayacucho	La Mar		2002	JX648460	IV
8	PERAYAGT10576_02	Goat	Ayacucho	La Mar	Chilcas	2002	JX648471	IV
9	PERAYAGT10578_02	Goat	Ayacucho	Huamanga		2002	JX648497	IV
10	PERAPUBT12725_02	Bat	Apurimac	Chincheros	Ongoy	2002	JX648518	IV
11	PERHUABV14643_02	Bovine	Huanuco	Puerto Inca	Codo de Pozuzo	2002	JX648402	I
12	PERSMADG15667_02	Dog	San Martin	Rioja	Awajun	2002	JX648426	I
13	PERAYABV17556_02	Bovine	Ayacucho	La Mar	Chilcas	2002	JX648465	IV
14	PERSMABV18452_02	Bovine	San Martin	Rioja	Elias Soplin	2002	JX648427	I
15	PERAYABV19596_02	Bovine	Ayacucho	La Mar	San Miguel	2002	JX648458	IV
16	PERAYABV24974_02	Bovine	Ayacucho	La Mar	San Miguel	2002	JX648456	IV
17	PERAPUBV25686_02	Bovine	Apurimac	Chincheros	Ongoy	2002	JX648522	IV
18	PERAPUBV25773_02	Bovine	Apurimac	Abancay	Huanipaca	2002	JX648528	IV
19	PERAPUBV25775_02	Bovine	Apurimac	Abancay	Huanipaca	2002	JX648529	IV
20	PERSMHR27577_02	Horse	San Martin	Lamas	Lamas	2002	JX648532	IV
21	PERAPUBV27641_02	Bovine	Apurimac	Chincheros	Huaccana	2002	JX648498	IV
22	PERAYHR27817_02	Horse	Ayacucho	Huamanga	Ocros	2002	JX648505	IV
23	PERAYABV27821_02	Bovine	Ayacucho	La Mar	San Miguel	2002	JX648472	IV
24	PERAYABV29517_02	Bovine	Ayacucho	La Mar	Anco	2002	JX648468	IV
25	PERAYABV32068_02	Bovine	Ayacucho	La Mar	san Miguel	2002	JX648475	IV
26	PERAPUBT32653_02	Bat	Apurimac	Abancay	Huanipaca	2002	JX648533	IV
27	PERAPUBT32717_02	Bat	Apurimac	Abancay	Huanipaca	2002	JX648537	IV
28	PERSMABV33299_02	Bovine	San Martin	San Martin	Tarapoto	2002	JX648412	I
29	PERSMABV33842_02	Bovine	San Martin	San Martin	Tarapoto	2002	JX648413	I
30	PERSMHR35351_02	Horse	San Martin	Lamas	Lamas	2002	JX648424	I
31	PERAMABV36425_02	Bovine	Amazonas	Utcubamba	Cajaruro	2002	JX648400	I
32	PERAYABV39012_02	Bovine	Ayacucho	La Mar	San Miguel	2002	JX648463	IV
33	PERAPUBV41363_02	Bovine	Apurimac	Chincheros	Huaccana	2002	JX648501	IV
34	PERAPUBV197_03	Bovine	Apurimac	Chincheros	Huaccana	2003	JX648507	IV
35	PERAPUBV249_03	Bovine	Apurimac	Chincheros	Huaccana	2003	JX648508	IV
36	PERAPUBV250_03	Bovine	Apurimac	Chincheros	Huaccana	2003	JX648500	IV
37	PERAYABV1234_03	Bovine	Ayacucho	La Mar	San Miguel	2003	JX648467	IV
38	PERSMHR6074_03	Horse	San Martin	San Martin	Chazuta	2003	JX648419	I
39	PERAYABV12387_03	Bovine	Ayacucho	La Mar	Anco	2003	JX648474	IV
40	PERAYHR17815_03	Horse	Ayacucho	La Mar	San Miguel	2003	JX648466	IV
41	PERUCAHM23580_03	Human	Ucayali	Padre Abad	Irazola	2003	JX648418	I
42	PERAYAGT24135_03	Goat	Ayacucho	La Mar	San Miguel	2003	JX648531	IV
43	PERAYABV24139_03	Bovine	Ayacucho	Huamanga	Ocros	2003	JX648536	IV
44	PERUCAHM24278_03	Human	Ucayali	Padre Abad	Padre Abad	2003	JX648416	I
45	PERAYABT26736_03	Bat	Ayacucho	La Mar	San Miguel	2003	JX648530	IV
46	PERAYASH26745_03	Sheep	Ayacucho	Huamanga	Ocros	2003	JX648504	IV
47	PERAYABV29265_03	Bovine	Ayacucho	La Mar	Chungui	2003	JX648535	IV
48	PERCUSBV38910_03	Bovine	Cusco	Paucartambo	Kosñipata	2003	JX648444	II
49	PERHUABV39200_03	Bovine	Huanuco	Leoncio Prado	José Crespo y	2003	JX648414	I

No.	Identification no. and genetic cluster	Animal source	Department	Province	District	Year	GenBank no.	Lineage
					Castillo			
50	PERHUABV41340_03	Bovine	Huanuco	Leoncio Prado	José Crespo y Castillo	2003	JX648415	I
51	PERPASBV43903_03	Bovine	Pasco	Oxapampa	Pozuzo	2003	JX648417	I
52	PERAYABV10421_04	Bovine	Ayacucho	Huamanga	Ocros	2004	JX648502	IV
53	PERAYABV11462_04	Bovine	Ayacucho	Huamanga	Ocros	2004	JX648503	IV
54	PERAYABT13771_04	Bat	Ayacucho	La Mar	Tambo	2004	JX648459	IV
55	PERSMABV14677_04	Bovine	San Martin	Tocache	Tocache	2004	JX648401	I
56	PERLAMDG16670_04	Dog	Lambayeque	Ferreñafe	Incahuasi	2004	JX648489	IV
57	PERAYABV17034_04	Bovine	Ayacucho	Vilcashuaman	Concepcion	2004	JX648495	IV
58	PERSMABV17048_04	Horse	San Martin	Rioja	Nueva Cajamarca	2004	JX648429	I
59	PERSMABV17053_04	Horse	San Martin	Rioja	Nueva Cajamarca	2004	JX648428	I
60	PERAYABV24247_04	Bovine	Ayacucho	La Mar	Chilcas	2004	JX648506	IV
61	PERAYABT24249_04	Bat	Ayacucho	Huamanga	Ocros	2004	JX648499	IV
62	PERCUSHR24845_04	Horse	Cusco	La Convencion	Vilcabamba	2004	JX648534	IV
63	PERCUSBV26090-04	Bovine	Cusco	La Convencion	Echarate	2004	JX648393	I
64	PERMDIBV30578_04	Bovine	Madre de Dios	Tambopata	Laberinto	2004	JX648404	I
65	PERAPUBV43925_04	Bovine	Apurimac	Chincheros	Ongoy	2004	JX648447	IV
66	PERSMABV54395_04	Bovine	San Martin	Picota	Picota	2004	JX648431	I
67	PERAMAPG2034-05	Pig	Amazonas	Condorcanqui	Rio Santiago	2005	JX648408	I
68	PERAMABV2039_05	Bovine	Amazonas	Condorcanqui	Rio Santiago	2005	JX648409	I
69	PERAMABV2040_05	Bovine	Amazonas	Condorcanqui	Rio Santiago	2005	JX648406	I
70	PERAPUBV5736_05	Bovine	Apurimac	Andahuaylas	Pacobamba	2005	JX648527	IV
71	PERAPUBV5737_05	Bovine	Apurimac	Andahuaylas	Pacobamba	2005	JX648526	IV
72	PERAYABV14916_05	Bovine	Ayacucho	Huamanga	Ocros	2005	JX648448	IV
73	PERPASBV25193_05	Bovine	Pasco	Oxapampa	Puerto Bermudez	2005	JX648394	I
74	PERPASBV27761_05	Bovine	Pasco	Oxapampa	Puerto Bermudez	2005	JX648395	I
75	PERMDIBV29509_05	Bovine	Madre de Dios	Tambopata	Las Piedras	2005	JX648405	I
76	PERAYABV35266-05	Bovine	Ayacucho	Huamanga	Acoria	2005	JX648450	IV
77	PERAMABV37027_05	Bovine	Amazonas	Condorcanqui	Nieva	2005	JX648403	I
78	PERAMABV41508_05	Bovine	Amazonas	Condorcanqui	Nieva	2005	JX648420	I
79	PERAYADK47065_05	Donkey	Ayacucho	La Mar	Anco	2005	JX648542	IV
80	PERAYADK50031_05	Donkey	Ayacucho	Huanta	Sivia	2005	JX648422	I
81	PERSMABV1897_06	Bovine	San Martin	El Dorado		2006	JX648399	I
82	PERSMABV1898_06	Bovine	San Martin	El Dorado		2006	JX648398	I
83	PERAPUBT4220_06	Bat	Apurimac	Chincheros	Huaccana	2006	JX648482	IV
84	PERAPUBT4221_06	Bat	Apurimac	Chincheros	Huaccana	2006	JX648492	IV
85	PERAMABV4953_06	Bovine	Amazonas	Condorcanqui	Rio Santiago	2006	JX648407	I
86	PERPASBV5714_06	Bovine	Pasco	Oxapampa	Pozuzo	2006	JX648544	III
87	PERAPUBT7039_06	Bat	Apurimac	Chincheros	Huaccana	2006	JX648483	IV
88	PERAPUBT7043_06	Bat	Apurimac	Chincheros	Huaccana	2006	JX648493	IV
89	PERAPUBT9773_06	Bat	Apurimac	Andahuaylas	Talavera	2006	JX648520	IV
90	PERAPUBT9776_06	Bat	Apurimac	Andahuaylas	Talavera	2006	JX648523	IV
91	PERAPUBT10342_06	Bat	Apurimac	Chincheros	Ongoy	2006	JX648524	IV
92	PERAPUBV12463_06	Bovine	Apurimac	Chincheros	Chincheros	2006	JX648484	IV
93	PERPASBV14803_06	Bovine	Pasco	Oxapampa	Pozuzo	2006	JX648543	III
94	PERAPUBV16406_06	Bovine	Apurimac	Chincheros	Chincheros	2006	JX648494	IV
95	PERAPUBT18510_06	Bat	Apurimac	Chincheros	Chincheros	2006	JX648480	IV
96	PERAPUBV20237_06	Bovine	Apurimac	Chincheros	Chincheros	2006	JX648491	IV
97	PERAPUBV24266_06	Bovine	Apurimac	Andahuaylas	Andarapa	2006	JX648521	IV
98	PERAPUBV28489_06	Bovine	Apurimac	Chincheros	Cocharcas	2006	JX648490	IV
99	PERAYABV28771_06	Bovine	Ayacucho	La Mar	Anco	2006	JX648453	IV
100	PERAYABV30524_06	Bovine	Ayacucho	Huamanga	Ocros	2006	JX648461	IV
101	PERAYABV31905_06	Bovine	Ayacucho	La Mar	Anco	2006	JX648452	IV
102	PERAYABV32674_06	Bovine	Ayacucho	La Mar	San Miguel	2006	JX648462	IV
103	PERAPUBV35975_06	Bovine	Apurimac	Chincheros	Anco Huallo	2006	JX648496	IV
104	PERAPUBT36009_06	Bat	Apurimac	Chincheros	Anco Huallo	2006	JX648481	IV
105	PERAYABT37810_06	Bat	Ayacucho	La Mar	San Miguel	2006	JX648470	IV
106	PERAYABV37818_06	Bovine	Ayacucho	La Mar	San Miguel	2006	JX648473	IV
107	PERAPUBV40999_06	Bovine	Apurimac	Andahuaylas	Andarapa	2006	JX648519	IV
108	PERAPUBT42668_06	Bat	Apurimac	Andahuaylas	Andahuaylas	2006	JX648510	IV
109	PERAPUBT42684_06	Bat	Apurimac	Andahuaylas	Andahuaylas	2006	JX648515	IV
110	PERAYAGT42935_06	Goat	Ayacucho	La Mar	San Miguel	2006	JX648469	IV
111	PERAPUBT44948_06	Bat	Apurimac	Andahuaylas	Andahuaylas	2006	JX648512	IV

No.	Identification no. and genetic cluster	Animal source	Department	Province	District	Year	GenBank no.	Lineage
112	PERAPUBV45653_06	Bovine	Apurimac	Andahuaylas	Kishuara	2006	JX648514	IV
113	PERAPUBT46404_06	Bat	Apurimac	Chincheros	Huaccana	2006	JX648488	IV
114	PERAMABV51713_06	Bovine	Amazonas	Luya	Ocalli	2006	JX648430	I
115	PERMDIHM1710_07	Human	Madre de Dios	Tambopata	Inambari	2007	JX648434	II
116	PERMDIKN1766_07	<i>Potus flavus</i>	Madre de Dios	Tambopata	Las Piedras	2007	JX648546	NA
117	PERMDIHM2987_07	Human	Madre de Dios	Tambopata	Inambari	2007	JX648435	II
118	PERAYABV5591_07	Bovine	Ayacucho	Vilcashuaman	Vilcashuaman	2007	JX648487	IV
119	PERAYAGT5592_07	Goat	Ayacucho	Vilcashuaman	Vilcashuaman	2007	JX648486	IV
120	PERMDIHM5710_07	Human	Madre de Dios	Tambopata	Inambari	2007	JX648437	II
121	PERMDIHM5711_07	Human	Madre de Dios	Tambopata	Inambari	2007	JX648436	II
122	PERPUNHM7172_07	Human	Puno	Carabaya	Ayapata	2007	JX648441	II
123	PERAPUBV7745_07	Human	Cusco	Quispicanchi	Marcapata	2007	JX648442	II
124	PERCUSHM8217_07	Human	Cusco	Quispicanchi	Marcapata	2007	JX648440	II
125	PERSMABV8429_07	Bovine	San Martin	Tocache	Shunte	2007	JX648423	I
126	PERCUSHM8714-07	Human	Cusco	Quispicanchi	Marcapata	2007	JX648443	II
127	PERPUNHM9090_07	Human	Puno	Carabaya	San Gaban	2007	JX648439	II
128	PERCUSHM9449_07	Human	Cusco	Cusco	San Sebastian	2007	JX648438	II
129	PERAYABV9870_07	Bovine	Ayacucho	Huamanga	Ocros	2007	JX648449	IV
130	PERAPUBV10320_07	Bovine	Apurimac	Chincheros	Cocharcas	2007	JX648479	IV
131	PERAPUBT10370_07	Bat	Apurimac	Andahuaylas	Pacucha	2007	JX648516	IV
132	PERSMABV10590-07	Bovine	San Martin	Moyobamba	Moyobamba	2007	JX648432	I
133	PERAPUBV10742_07	Bovine	Apurimac	Chincheros	Cocharcas	2007	JX648485	IV
134	PERCUSBV10999_07	Bovine	Cusco	La Convencion	Kimbiri	2007	JX648396	I
135	PERCUSBV11000_07	Bovine	Cusco	La Convencion	Kimbiri	2007	JX648392	I
136	PERAPUBT11043_07	Bat	Apurimac	Chincheros	Cocharcas	2007	JX648478	IV
137	PERAPUBT11045_07	Bat	Apurimac	Chincheros	Chincheros	2007	JX648477	IV
138	PERAYABV11313_07	Bovine	Ayacucho	La Mar	San Miguel	2007	JX648411	I
139	PERAYABV11314_07	Bovine	Ayacucho	Huamanga	Ocros	2007	JX648464	IV
140	PERAYABV11316_07	Bovine	Ayacucho	La Mar	San Miguel	2007	JX648455	IV
141	PERAPUBT12448_07	Bat	Apurimac	Andahuaylas	Andarapa	2007	JX648517	IV
142	PERAPUBV12450_07	Bovine	Apurimac	Andahuaylas	Andarapa	2007	JX648511	IV
143	PERAYABV12690_07	Bovine	Ayacucho	La Mar	Luis Carranza	2007	JX648445	IV
144	PERHUABV13139_07	Bovine	Huanuco	Leoncio Prado	Hermilio Valdizan	2007	JX648410	I
145	PERAPUBV13361_07	Bovine	Apurimac	Chincheros	Huaccana	2007	JX648476	IV
146	PERAYABV13485_07	Bovine	Ayacucho	La Mar	San Miguel	2007	JX648446	IV
147	PERPUNBT13526_07	<i>Histiotus montanus</i>	Puno	Carabaya	Ayapata	2007	JX648545	NA
148	PERCAJBV13590_07	Bovine	Cajamarca	San Ignacio	San Ignacio	2007	JX648433	I
149	PERAPUBV13695_07	Bovine	Apurimac	Andahuaylas	Kishuara	2007	JX648509	IV
150	PERHUABV13735-07	Bovine	Huanuco	Leoncio Prado	Rupa Rupa	2007	JX648425	I
151	PERPASBV13969-07	Bovine	Pasco	Oxapampa	Puerto Bermudez	2007	JX648421	I
152	PERAYABV14465_07	Bovine	Ayacucho	La Mar	Chungui	2007	JX648454	IV
153	PERAPUBV15558_07	Bovine	Apurimac	Andahuaylas	Kishuara	2007	JX648513	IV
154	PERCUSBV15589-07	Bovine	Cusco	La Convencion	Kimbiri	2007	JX648391	I
155	PERAYABV1200456_07	Bovine	Ayacucho	La Mar	Luis Carranza	2007	JX648451	IV
156	PERSMABV1209567_07	Bovine	San Martin	Moyobamba	Moyobamba	2007	JX648397	I
157	PERCUSBT0812565_08	Non-vampire bat	Cusco	Paucartambo	Paucartambo	2008	JX648547	NA

*NA, not applicable.

Technical Appendix Table 2. Representative strains from the Americas included in this study

No.	Identification no. and genetic cluster	Animal source	Country	Year	GenBank no.	Reference
1	H02/08	Human	Colombia	2008	JF693457	Velasco-Villa et al. (unpub. data)
2	H01/08	Human	Colombia	2008	JF693456	Velasco-Villa et al. (unpub. data)
3	CT1/06	Cat	Colombia	2006	JF693458	Velasco-Villa et al. (unpub. data)
4	H04/08	Human	Colombia	2008	JF693460	Velasco-Villa et al. (unpub. data)
5	BV6/97	Cattle	Colombia	1997	JF693463	Velasco-Villa et al. (unpub. data)
6	BRhr31	Horse	Brazil	1998	AB083804	Ito et al. (1)
7	BRbv30	Cattle	Brazil	1999	AB083803	Ito et al. (1)
8	8MarellaSP1700B	Cattle	Brazil	2008	GQ160938	Macedo et al. (2)
9	IP6770U/08	Cattle	Uruguay	2008	EU981919	Guarino et al. (unpub. data)
10	IP6775U/08	Equine	Uruguay	2008	EU981923	Guarino et al. (unpub. data)
11	IP6781U/08	Cattle	Uruguay	2008	EU981929	Guarino et al. (unpub. data)
12	IP6778U/08	Cattle	Uruguay	2008	EU981926	Guarino et al. (unpub. data)
13	IP6785U/07	<i>D. rotundus</i>	Uruguay	2007	EU981931	Guarino et al. (unpub. data)
14	08IacriSP3577B	Cattle	Brazil	2008	GQ160933	Macedo et al. (2)
15	08IacriSP4001B	Cattle	Brazil	2008	GQ160934	Macedo et al. (2)
16	IP3066P/04H	Human	Brazil	2004	EF363742	Castilho et al. (3)
17	IP3072P/0H4	Human	Brazil	2004	EF363747	Castilho et al. (3)
18	IP3068P/0H4	Human	Brazil	2004	EF363744	Castilho et al. (3)
19	IP3522P/04H	Human	Brazil	2004	EF363748	Castilho et al. (3)
20	IP3067P/Portel Para	Human	Brazil	2004	EF363743	Castilho et al. (3)
21	IP3070P/04H	Human	Brazil	2004	EF363746	Castilho et al. (3)
22	IP2617	Cattle	Brazil	2000	FJ649126	Carnieli et al. (4)
23	BR-DR1	<i>D. rotundus</i>	Brazil	2000	AB519642	Mochizuki et al. (5)
24	IP7518	Cattle	Brazil	2001	FJ649170	Carnieli et al. (4)
25	IP3602	Cattle	Brazil	1999	FJ649087	Carnieli et al. (4)
26	IP1959	Cattle	Brazil	2000	FJ649125	Carnieli et al. (4)
27	IP5347	Cattle	Brazil	2000	FJ649146	Carnieli et al. (4)
28	IP5458	Cattle	Brazil	2001	FJ649168	Carnieli et al. (4)
29	IP6261	Cattle	Brazil	2000	FJ649152	Carnieli et al. (4)
30	brdrusp100/07	<i>D. rotundus</i>	Brazil	2007	GU592648	Campos et al. (6)
31	IP1501	Cattle	Brazil	2001	FJ649167	Carnieli et al. (4)
32	IP1064	Cattle	Brazil	2001	FJ649162	Carnieli et al. (4)
33	HR1/02	Horse	Colombia	2002	JF693469	Velasco-Villa et al. (unpub. data)
34	H02/07	Human	Colombia	2007	JF693470	Velasco-Villa et al. (unpub. data)
35	BV1/03	Cattle	Colombia	2003	JF693468	Velasco-Villa et al. (unpub. data)
36	BV7/97	Cattle	Colombia	1997	JF693467	Velasco-Villa et al. (unpub. data)
37	DR.Td2; V325	Cattle	Trinidad Tobago	1995	AF351852	Nadin-Davis et al. (7)
38	IP4405EQ/07BOV	Cattle	Ecuador	2007	HM368176	Castilho et al. (3)
39	IP4404EQ/07BOV	Cattle	Ecuador	2007	HM368180	Castilho et al. (3)
40	IP4406EQ/07BOV	Cattle	Ecuador	2007	HM368177	Castilho et al. (3)
41	IP4407EQ/07BOV	Cattle	Ecuador	2007	HM368178	Castilho et al. (3)
42	IP2293EQ/05H	Human	Ecuador	2005	EF363727	Castilho et al. (3)
43	IP2294EQ/05H	Human	Ecuador	2005	EF363728	Castilho et al. (3)
44	BV1/06	Cattle	Colombia	2006	JF693466	Velasco-Villa et al. (unpub. data)
45	IP4403EQ/07BOV	Cattle	Ecuador	2007	HM368179	Castilho et al. (3)
46	BV8/97	Cattle	Colombia	1997	JF693465	Velasco-Villa et al. (unpub. data)
47	CT1/97	Cat	Colombia	1997	JF693464	Velasco-Villa et al. (unpub. data)

No.	Identification no. and genetic cluster	Animal source	Country	Year	GenBank no.	Reference
48	9001FRA	Dog	French Guyana	1990	EU293113	Delmas et al. (8)
49	pehm3230	Human	Peru	1996	AF045166	Warner et al. (9)
50	484	Cattle	Argentina	1996	KC758860	Included in this study
51	109	Cattle	Argentina	2001	KC758861	Included in this study
52	795	Cattle	Argentina	2007	KC758862	Included in this study
53	02	Cattle	Argentina	1999	KC758863	Included in this study
54	CT2/06	Cat	Colombia	2006	JF693474	Velasco-Villa et al. (unpub. data)
55	H02/94	Human	Colombia	1994	JF693476	Velasco-Villa et al. (unpub. data)
56	H04/95	Human	Colombia	1995	JF693475	Velasco-Villa et al. (unpub. data)
57	H03/08	Human	Colombia	2008	JF693478	Velasco-Villa et al. (unpub. data)
58	CT1/94	Cat	Colombia	1994	JF693471	Velasco-Villa et al. (unpub. data)
59	IP1992/05	<i>Histiotus velatus</i>	Brazil	2005	GU552790	Oliveira et al. (10)
60	Hm860	<i>H. macrotus</i>	Chile	2007	HQ341793	Yung et al. (unpub. data)
61	BR-Pbt4	<i>Molossus molossus</i>	Brazil	2003	AB206417	Shoji et al. (11)
62	BR-NL3	<i>Nyctinomops laticaudatus</i>	Brazil	2001	AB201808	Kobayashi et al. (12)
63	BR-TL1	<i>Tadarida laticaudata</i>	Brazil	1990	AB297648	Kobayashi et al. (13)
64	905	<i>Plecotus townsendii</i>	USA	1989	AF394877	Rohde et al. (14)
65	CA178	<i>Corynorhinus townsendii</i>	USA	2003	GU644759	Streicker et al. (15)
66	804	<i>Eptesicus fuscus</i>	USA	1987	AF394887	Rohde et al. (14)
67	5441	Skunk	USA	2001	AY170410	Leslie et al. (16)
68	BR-MM1	<i>M. molossus</i>	Brazil	1999	AB201815	Kobayashi et al. (12)
69	BR-MM2	<i>M. molossus</i>	Brazil	2002	AB201816	Kobayashi et al. (12)
70	BR-BAT13	Non-vampire bat	Brazil	2003	AB297651	Kobayashi et al. (13)
71	BR-BAT27	Non-vampire bat	Brazil	2006	AB297656	Kobayashi et al. (13)
72	SHCAN	<i>Lasionycteris noctivagans</i>	Canada	1992	AF351834	Nadin-Davis et al. (7)
73	MI1100	<i>Myotis lucifugus</i>	USA	2005	GU644748	Streicker et al. (15)
74	TX5168	<i>Perimyotis subflavus</i>	USA	2004	GU644758	Streicker et al. (15)
75	446	<i>Lasiurus cinereus</i>	USA	1982	AF394884	Rohde et al. (14)
76	LC1- 92RABL2108	<i>L. cinereus</i>	Canada	1992	AF351845	Nadin-Davis et al. (7)
77	BR-BAT15	Non-Vampire	Brazil	2003	AB297652	Kobayashi et al. (13)
78	Lc1564	<i>L. cinereus</i>	Chile	2009	HQ341795	Yung et al. (unpub. data)
79	C14/95	Dog	Colombia	1995	JF693453	Velasco-Villa et al. (unpub. data)
80	H01/00	Human	Colombia	2000	JF693455	Velasco-Villa et al. (unpub. data)
81	4355Perudg2004	Dog	Peru	2004	FJ228498	Velasco-Villa et al. (unpub. data)
82	26200PeruFx2004	Fox	Peru	2004	FJ228501	Velasco-Villa et al. (unpub. data)
83	4352Perudg2004	Dog	Peru	2004	FJ228499	Velasco-Villa et al. (unpub. data)

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