

# Potential Geographic Distribution of Hantavirus Reservoirs in Brazil

Stefan Vilges de Oliveira<sup>1,2</sup>, Luis E. Escobar<sup>3</sup>, A. Townsend Peterson<sup>4</sup>, Rodrigo Gurgel-Gonçalves<sup>5\*</sup>

**1** Postgraduate Program in Tropical Medicine, Universidade de Brasília, Brasília, Brazil, **2** Unidade Técnica de Vigilância de Zoonoses, Ministério da Saúde, Brasília, Brazil, **3** Conservation Medicine Program, Facultad de Ecología y Recursos Naturales, Universidad Andres Bello, República 440, Santiago, Chile, **4** Biodiversity Institute, University of Kansas, Lawrence, Kansas, United States of America, **5** Laboratório de Parasitologia Médica e Biologia de Vetores, Universidade de Brasília, Brasília, Brazil

## Abstract

Hantavirus cardiopulmonary syndrome is an emerging zoonosis in Brazil. Human infections occur via inhalation of aerosolized viral particles from excreta of infected wild rodents. *Necromys lasiurus* and *Oligoryzomys nigripes* appear to be the main reservoirs of hantavirus in the Atlantic Forest and Cerrado biomes. We estimated and compared ecological niches of the two rodent species, and analyzed environmental factors influencing their occurrence, to understand the geography of hantavirus transmission. *N. lasiurus* showed a wide potential distribution in Brazil, in the Cerrado, Caatinga, and Atlantic Forest biomes. Highest climate suitability for *O. nigripes* was observed along the Brazilian Atlantic coast. Maximum temperature in the warmest months and annual precipitation were the variables that most influence the distributions of *N. lasiurus* and *O. nigripes*, respectively. Models based on occurrences of infected rodents estimated a broader area of risk for hantavirus transmission in southeastern and southern Brazil, coinciding with the distribution of human cases of hantavirus cardiopulmonary syndrome. We found no demonstrable environmental differences among occurrence sites for the rodents and for human cases of hantavirus. However, areas of northern and northeastern Brazil are also apparently suitable for the two species, without broad coincidence with human cases. Modeling of niches and distributions of rodent reservoirs indicates potential for transmission of hantavirus across virtually all of Brazil outside the Amazon Basin.

**Citation:** Oliveira SVd, Escobar LE, Peterson AT, Gurgel-Gonçalves R (2013) Potential Geographic Distribution of Hantavirus Reservoirs in Brazil. PLoS ONE 8(12): e85137. doi:10.1371/journal.pone.0085137

**Editor:** Fausto Baldanti, Fondazione IRCCS Policlinico San Matteo, Italy

**Received:** August 16, 2013; **Accepted:** November 24, 2013; **Published:** December 31, 2013

**Copyright:** © 2013 Oliveira et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

**Funding:** Stefan Vilges de Oliveira received financial support (scholarship) from CAPES, Brazil (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, www.capes.gov.br). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

**Competing interests:** The authors have declared that no competing interests exist.

\* Email: gurgelrg@hotmail.com

## Introduction

Hantaviruses (family *Bunyaviridae*, genus *Hantavirus*) are zoonoses that have been appreciated increasingly in the last two decades, particularly across the Americas. Human infections occur by inhalation of aerosolized viral particles from excreta of infected wild rodents. The disease manifests in different clinical forms: hemorrhagic fever with renal syndrome (HFRS) and hantavirus cardiopulmonary syndrome (HCPS); HCPS is an emerging disease, particularly in the Americas [1]. The first documented cases of HCPS emerged apparently as a result of weather phenomena that favored exposure of human populations to wild rodents [2,3].

In Brazil, the first recorded occurrence of HCPS was in 1993, in the city of Jucituba, state of São Paulo [4]. Since then, knowledge of the disease has expanded and its range is now known to extend to all regions of the country [5]. Among rodent species found infected with hantavirus in Brazil, *Necromys*

*lasiurus* and *Oligoryzomys nigripes* are widely distributed in the Cerrado and Atlantic Forest biomes, respectively [6,7]. Some studies indicate that regional distributions of hosts and pathogen are related to climatic and environmental factors [8-11]; these studies also show associations between occurrence of human cases of hantavirus and areas of high probability of occurrence of rodent reservoirs, suggesting that analysis of ecological niche models of hosts could offer valuable information. Therefore, assessment of potential distributions of rodent reservoirs in different biomes and analysis of the influence of environmental factors on hantavirus transmission can be useful in understanding spatial patterns of transmission risk of the disease.

This study explores a series of approaches. We estimated ecological niches and geographic distributions for *N. lasiurus* and *O. nigripes* in the Cerrado and Atlantic Forest regions, and analyzed environmental factors associated with their occurrence. We estimated the ecological niche for hantavirus

transmission in Brazil based on the distribution of infected rodents detected during 2000-2010. Finally, we compared distributions with respect to climatic conditions for the two rodent species and for HCPS cases in humans, to ascertain whether they occur under distinct environmental circumstances.

## Materials and Methods

### Occurrence data

All data were obtained from public databases; full names and information for accessing data (websites) are provided below. All data were anonymized. Distributional data for *N. lasiurus* and *O. nigripes* were obtained from speciesLink (<http://splink.cria.org.br>), Global Biodiversity Information Facility (<http://data.gbif.org>) and VertNet (<http://www.vertnet.org>); our searches included the old name of *N. lasiurus* (*Bolomys lasiurus*). We also consulted various published studies on these rodent species [12-33]. When only textual georeferences were provided we georeferenced them based on two internet resources (<http://www.fallingrain.com/world/> and <http://www.ibge.gov.br/>). Records were georeferenced with an uncertainty of  $\leq 5$  km to the nearest  $0.01^\circ$  (records presenting greater uncertainty were removed). We eliminated duplicate records and records presenting obvious errors of georeferencing or identification (e.g., records in the ocean). We also excluded records in oversampled locations based on subsampling among very close pairs of points to reduce sampling bias [34]. Based on occurrence data, we created buffers of 400 km around known occurrences, which were used as a hypothesis of the accessible area **M** [35] which is the area most appropriately used for model calibration.

For information on rodents infected with hantavirus, we used technical reports of research activities undertaken by the Brazilian Ministry of Health. We also extracted occurrence data from published records of infections in these two rodent species during 2000-2010 [7,30,36-48].

Finally, we included records of HCPS cases reported from municipalities falling within the bounds of the Atlantic Forest and Cerrado biomes, reported by the Brazilian Ministry of Health during 2000-2010. We considered in particular suspected infection location, where human infection by the pathogen apparently occurred. Locations for infected rodents and humans were georeferenced as described above.

### Environmental data

To characterize environmental variation across Brazil, we used seven climatic variables: annual mean temperature, diurnal temperature range, maximum temperature in the warmest month, minimum temperature in the coldest month, annual precipitation and precipitation in the wettest and driest months. We obtained these variables from the WorldClim project ([worldclim.org](http://worldclim.org)), which were developed via interpolation of mean monthly climatic data from meteorological stations over 30-50 (1950-2000) years, depending on data availability at stations [49]. To summarize aspects of vegetation and land cover, we used multitemporal (monthly) normalized difference vegetation index values (NDVI, a "greenness" index) drawn

from the Advanced Very High Resolution Radiometer (AVHRR) satellite (<http://daac.gsfc.nasa.gov/avhrr/>) (1982-1992). All environmental databases used in our analyzes covered areas of accessibility for each of the rodent species (see above), resampled to a spatial resolution of  $2.5'$  ( $\sim 5$  km).

### Ecological niche models

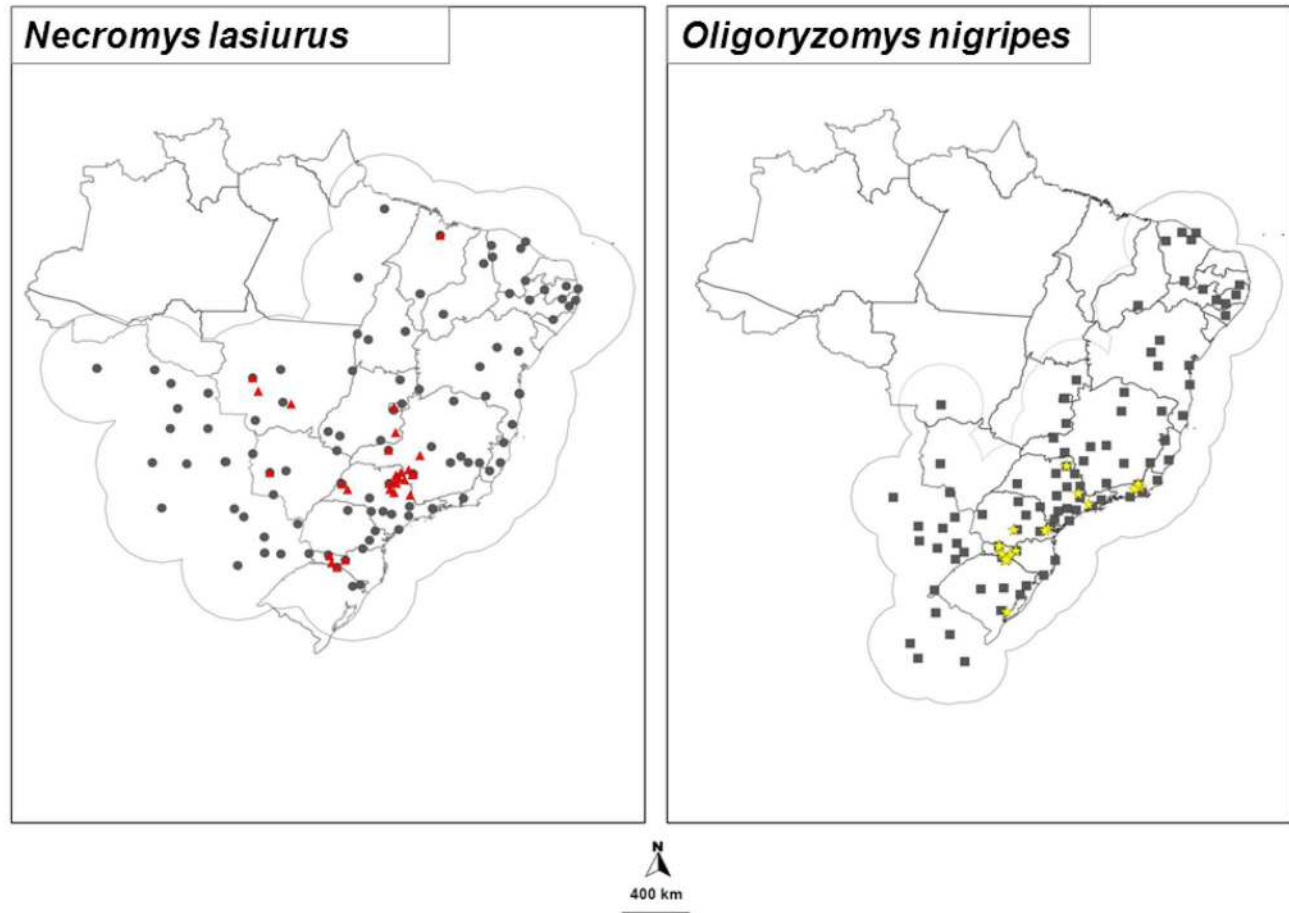
Ecological niche models were produced using Maxent version 3.2.1 [50]. We used a random seed to generate 10 replicate analyses based on bootstrap subsampling. We used median output grids as a hypothesis of suitability, and imported the results into ArcView 3.3 for assessment and analysis.

Distributional data for *N. lasiurus* and *O. nigripes* were separated into two sets: one for model calibration (75% of points) and one for model evaluation (25% of points). For infected rodents, in light of smaller sample sizes, we considered all points in the analysis. Raw Maxent outputs were converted into binary maps of suitability or unsuitability for each species based on a threshold that includes 95% of the records of each species used in model calibration [51]. This threshold takes into consideration an estimate of the likely amount of error among the occurrence data ( $E = 5\%$ ) [52].

### Model evaluation

We assessed model accuracy by examining omission rates associated with test points [53]. To test model significance, we compared predictive success of models against null expectations using a cumulative binomial test [34]. In particular, we assessed whether each test point fell in areas identified by the model as suitable, and compared this success rate with overall proportions of pixels identified as suitable or unsuitable for that species. Statistical significance was assessed via a cumulative binomial probability calculation in Excel. We also used Maxent's jackknife test to identify variables that most influenced model predictions [50].

Finally, we used randomization tests to assess the degree to which the environmental footprint of distributions of the two putative rodent reservoirs and human cases differed. That is, if one or the other of the rodents were not involved in transmission of the virus to humans, its ecological niche might differ from that of human cases. We used the background similarity tests of Warren et al. [54], on the basis that these tests allow specification of an accessible area (**M**) particular to each of the species involved, which is key in erecting appropriate tests [55]. Specifically, we compared ecological niche model outputs thresholded at minimum training presence in terms of the similarity indices *D* and *I* [54], and compared these observed similarities to a distribution of 'background' similarities, in which one species' occurrences were replaced by a similar number of random points drawn from across its **M**. All resampling and similarity calculations were performed in ENMTools version 1.3 [56]. Smaller numbers of variables were generated for this analysis through a principal component analysis (PCA) of the environmental variables used for niche modeling using NicheA version 1.2 [57]. For a visualization of rodent and human cases environmental use, niches were determined by a minimum-volume ellipsoid calculated around



**Figure 1. Distribution of rodent species.** *Necromys lasiurus* (circles) and *Oligoryzomys nigripes* (squares). The access area "M" is approximated by buffers of 400 km. Distribution of hantavirus-infected rodents (*N. lasiurus*, red triangles and *O. nigripes*, yellow stars) is also shown.

doi: 10.1371/journal.pone.0085137.g001

occurrences with a strict threshold ( $E = 10\%$ ; H. Qiao, pers. comm.).

## Results

We obtained 114 records for *N. lasiurus* and 30 records of hantavirus-infected *N. lasiurus* (Figure 1). For *O. nigripes*, we found 105 unique records and 19 records of hantavirus-infected *O. nigripes* (Figure 1).

Niche models generated for rodents were statistically robust. For *N. lasiurus*, only one test point fell outside the predicted area of presence (3% omission error), such that binomial tests indicated statistical significance ( $p = 0.02$ ). In *O. nigripes* comparisons, all test points were included in the predicted suitable area (0% omission), and models were thus highly statistically significant ( $p < 0.01$ ).

When niche models were displayed in geographic space *N. lasiurus* showed a wide potential distribution in Brazil. Highest climate suitability for *O. nigripes* was observed along the Brazilian Atlantic coast (Figure 2).

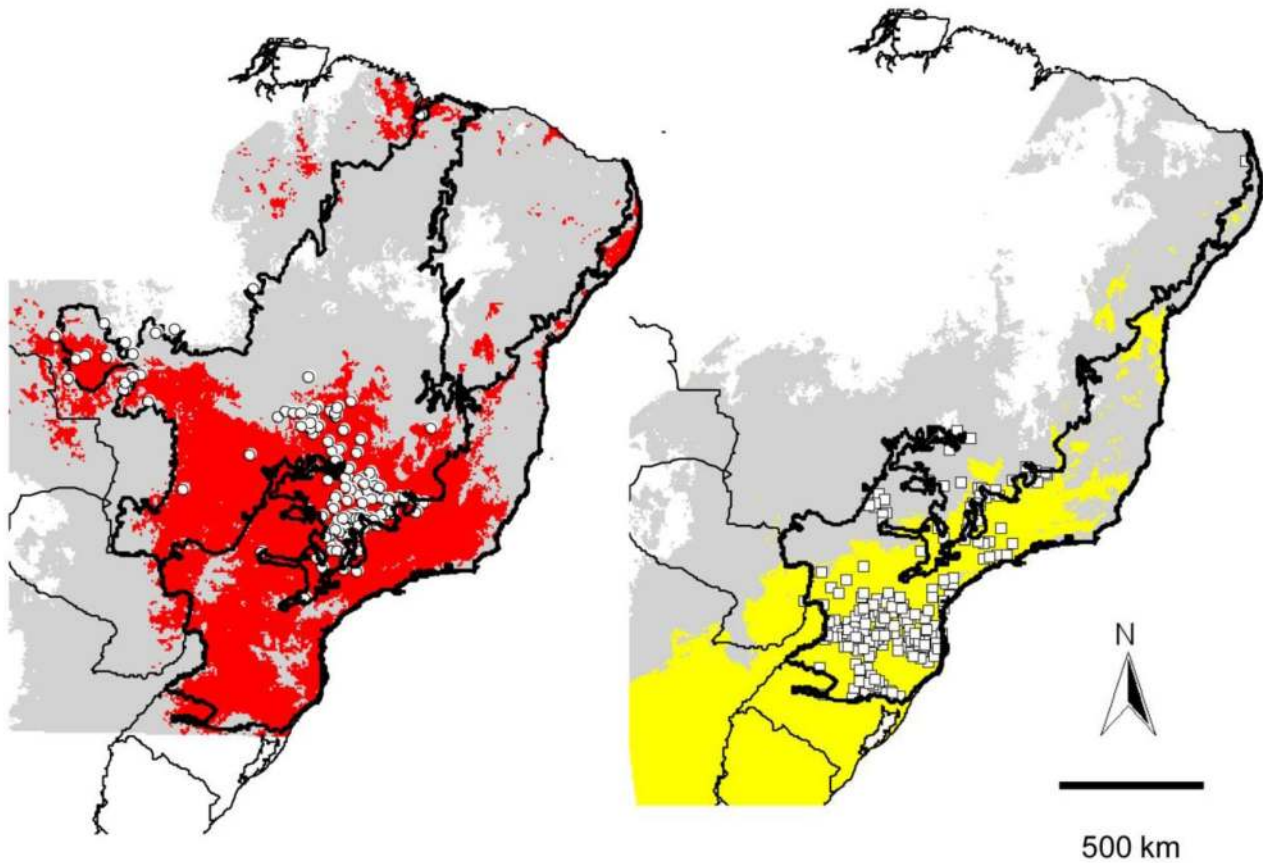
When contribution of environmental variables was explored, maximum temperature in the warmest months was the variable that most influenced models of *N. lasiurus*; NDVI had low contribution. For *O. nigripes* annual precipitation was the variable that most influenced models, and NDVI data showed low contribution.

Models based on occurrences of infected rodents estimated a broad area of hantavirus transmission in southeastern and southern Brazil, coinciding with the distribution of 280 and 188 human cases of HCPS in the Cerrado and Atlantic Forest respectively (Figure 2). Parts of northern and northeastern areas of Brazil were also suitable for occurrence of *N. lasiurus* and *O. nigripes* (Figure 2), yet show few human HCPS reports.

Background similarity tests, in all comparisons, failed to reject the hypothesis of niche similarity (Table 1). That is, observed similarity values fell within the null distribution of background similarity values. In this sense, no evidence was available that suggested that these two rodent species could not be involved in hantavirus transmission. The first three axes from PCA analyses explained 90% of the variance;

*Necromys lasiurus*

*Oligoryzomys nigripes*



**Figure 2. Ecological niche models projected as potential distributions for rodent reservoirs of hantavirus in Brazil (gray shading).** *Necromys lasiurus* (left) and *Oligoryzomys nigripes* (right). Areas identified as suitable based on all occurrence records are shown in pale gray, whereas areas identified as suitable based only on infected rodents database are shown for *N. lasiurus* (red) and *O. nigripes* (yellow). Bold lines indicate the range of the Cerrado and Atlantic Forest. Cases of human infections with hantavirus in Cerrado (circles) and Atlantic Forest (squares) were superimposed on the models.

doi: 10.1371/journal.pone.0085137.g002

**Table 1. Background similarity test results for two similarity metrics (*I* and *D*) for comparisons of *Necromys lasiurus* and *Oligoryzomys nigripes* (putative reservoirs) and human cases.**

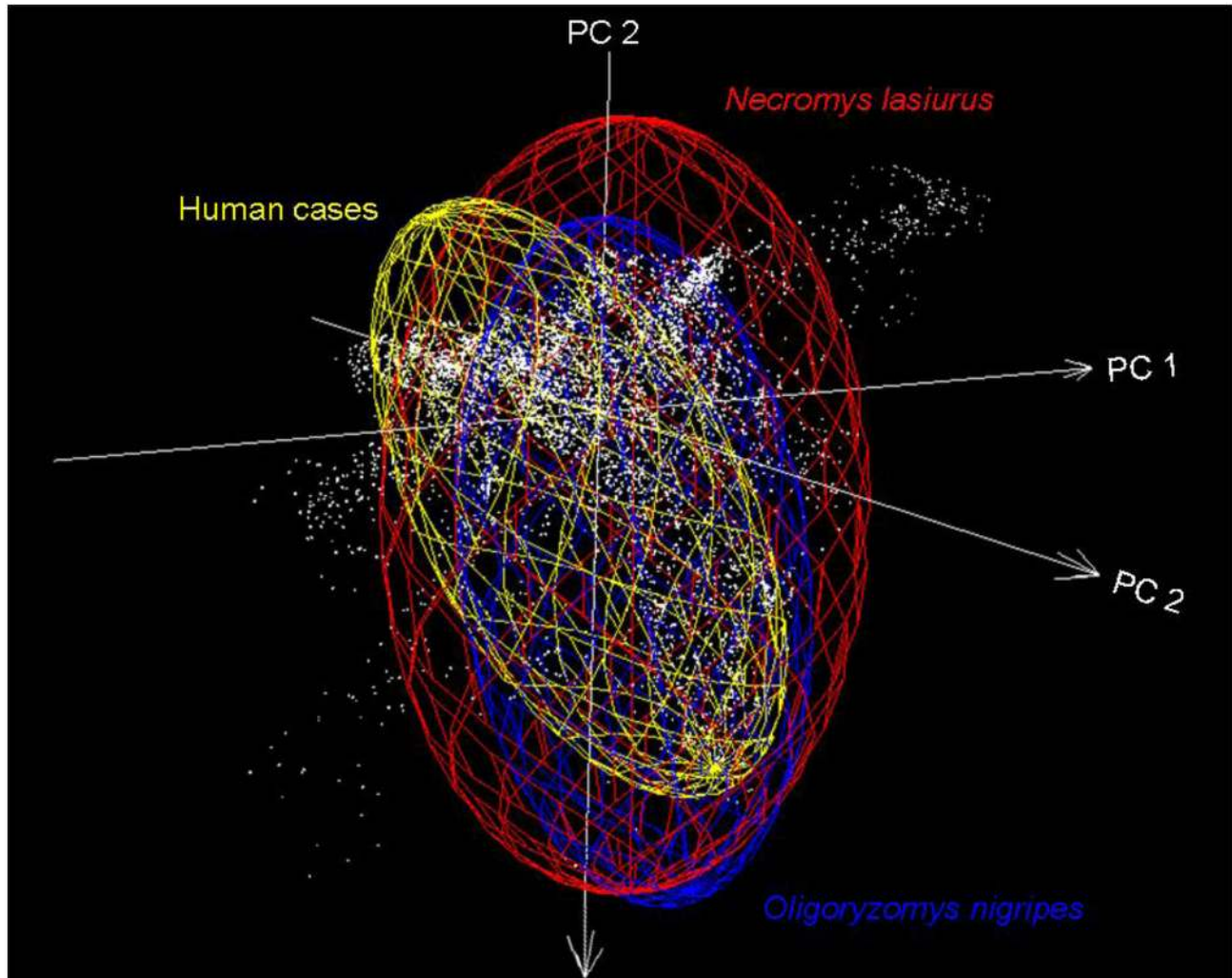
Target versus background	Observed overlap		<i>I</i>		<i>D</i>	
	<i>I</i>	<i>D</i>	5%	95%	5%	95%
Human cases versus <i>Necromys lasiurus</i> background	0.895	0.849	0.861	0.947	0.809	0.929
Human cases versus <i>Oligoryzomys nigripes</i> background	0.925	0.909	0.869	0.944	0.811	0.929
<i>Necromys lasiurus</i> versus <i>Oligoryzomys nigripes</i> background	0.918	0.856	0.846	0.919	0.834	0.867
<i>Oligoryzomys nigripes</i> versus <i>Necromys lasiurus</i> background	0.918	0.856	0.882	0.961	0.840	0.940

Observed overlap values can be compared against the 5% (dissimilar) and 95% (similar) values for the null distributions. As can be appreciated, all observed values fell within null expectations; i.e., the hypothesis of niche similarity could not be rejected.

doi: 10.1371/journal.pone.0085137.t001

visualization of niches in the environmental space allows appreciation of overlap between rodent species and human

cases (Figure 3), this overlap corroborated our similarity test results.



**Figure 3. Visualization of niches of hantavirus in rodents and humans.** White points indicate environments in the study area (background). Ellipsoids are the representation of niches for hantavirus in *N. lasiurus* (red), *O. nigripes* (blue), and human cases (yellow). Environmental space based on components 1 to 3 from a principal component analysis (PCA) of climatic and NDVI variables. Note that, while the ellipsoids for the different species do show some difference, so also do the environments represented within each species' **M**; here, the results of the background similarity test become key.

doi: 10.1371/journal.pone.0085137.g003

## Discussion

This study updates the picture of the geographic distribution of *N. lasiurus*. Bonvicino et al. [6] showed only limited occurrence of *N. lasiurus* in the Atlantic Forest biome. We found records of *N. lasiurus* in many municipalities of Atlantic Forest, albeit largely on the interior slopes of the coastal mountain ranges. These occurrences could be favored by presence of *Brachiaria* spp. as has been suggested [7,58], in open areas or near remnants of Atlantic Forest. *N. lasiurus* can be found in many habitats, but prefer open and dry areas, being absent or infrequent in moist forest environments [59,60]. Occurrence of *N. lasiurus* has also been observed in areas of agricultural and urban expansion [58], suggesting that

deforestation over recent years favors occurrence of the species in the Atlantic Forest biome. The reproduction of *N. lasiurus* occurs throughout the year with seasonal peaks. Litter sizes of these species are similar, varying from 1 to 13 new individuals [61]. Annual population fluctuations appear to be regulated by food availability, influenced by rainfall [62].

Our results also extend the limits of the distribution of *O. nigripes* in Brazil, including areas in the extreme south (Rio Grande do Sul), northeast (Ceará) and Midwest (Mato Grosso and Mato Grosso do Sul) of the country. Predictive models indicated favorable conditions for occurrence of the species outside the limits of the Atlantic Forest within the Cerrado and Pantanal biomes. In these areas, *O. nigripes* is associated with gallery forest, secondary forest, and forest edges [63].

Our model results agree with analyses carried out in Argentina by Carbajo & Pardiñas (2007) [8], indicating that aspects of both temperature and precipitation were essential to explain the distribution of *O. longicaudatus*. Those authors also found an association between occurrences of human hantavirus cases in areas with a higher suitability for *O. longicaudatus*.

Recently, Donalísio & Peterson [10], seeking to identify environmental factors influencing occurrence of hantavirus cases in southern Brazil, found that winter precipitation and high photosynthetic mass were most closely related to distributions of cases of HCPS; the authors explored distributions of four species of *Oligoryzomys* in relation to areas of hantavirus transmission in southern Brazil. NDVI showed low contribution to our models, in contrast with results of Donalísio & Peterson [10].

We found a broad potential distributional area for infected rodents in Mato Grosso do Sul, in the southwestern Cerrado region, where only one HCPS case was registered. Low reporting owing to diagnostics by local health services may be involved in the low incidence of HCPS in the predicted area. Future studies should evaluate rates of infection in rodents, using records collected via careful planned sampling in areas with lack of information but with suitable environments predicted by our models in order to fill epidemiological gaps.

Most HCPS cases in Brazil (85%) occurred within the Cerrado and Atlantic Forest biomes. These biomes cover 37% of the area of Brazil, where ~140 million people live, representing 73% of the population of the country (<http://www.ibge.gov.br>). Our exclusion of the Amazon Basin from analyses was owing to unavailability of information on reservoirs and their occurrences. Recent studies in Mato Grosso showed that *Oligoryzomys utaritensis* [64] is involved in hantavirus transmission to humans [65]; indeed, studies

showing involvement of *Calomys callidus* [66] and *O. fornesi* in transmission [66] indicate that these species are also involved in the virus cycle in Brazil.

Considering the high rodent species richness in the Cerrado (78 species) and Atlantic Forest (98 species) [67] biomes, with little knowledge of enzootic cycles of hantavirus in these biomes, it is clear that we are still far from fully understanding the natural history of hantaviruses in Brazil. Our ecological niche models for *N. lasiurus* and *O. nigripes* indicate that climatic variables are fundamental to explaining distributions of these species, at least over the broad extent of this study. At the spatial scale explored, niches of *N. lasiurus* and *O. nigripes*, and human hantavirus reports were not significantly different, highlighting a role for *N. lasiurus* and *O. nigripes*, at least in part, in the host-parasite cycle of hantavirus and eventual transmission to humans. We stress the importance of knowledge of true participation of these rodents in epidemiological cycles of the disease, because the predictive model of infected rodents included sites of HCPS cases in Cerrado and Atlantic Forest.

## Acknowledgements

We are thankful to the staff of the Unidade Técnica de Vigilância de Zoonoses do Ministério da Saúde, Brazil. M.R. Donalísio, P. Tauil, and M.T. Obara provided helpful comments on earlier drafts of this manuscript.

## Author Contributions

Conceived and designed the experiments: ATP RGG. Performed the experiments: SVO LEE. Analyzed the data: SVO RGG. Contributed reagents/materials/analysis tools: RGG LEE. Wrote the manuscript: RGG SVO ATP.

## References

- Nichol ST, Spiropoulou CF, Morzunov S, Rollin PE, Ksiazek TG et al. (1993) Genetic identification of a novel hantavirus associated with an outbreak of acute respiratory illness in the southwestern United States. *Science* 262: 914-917. doi:10.1126/science.8235615. PubMed: 8235615.
- Glass GE, Cheek JE, Patz JA, Shields TM, Doyle TJ, Thoroughman DA et al. (2000) Using remotely sensed data to identify areas at risk for hantavirus pulmonary syndrome. *Emerg Infect Dis* 6: 238-247. doi: 10.3201/eid0603.000303. PubMed: 10827113.
- Glass GE, Yates TL, Fine JB, Shields TM, Kendall JB et al. (2002) Satellite imagery characterizes local animal reservoir populations of Sin Nombre virus in the southwestern United States. *Proc Natl Acad Sci U S A* 99: 16817-16822. doi:10.1073/pnas.252617999. PubMed: 12473747.
- Silva MV, Vasconcelos MJ, Hidalgo NTR, Veiga APR, Canzian M et al. (1997) Hantavirus pulmonary syndrome: Report of the first three cases in São Paulo, Brazil. *Rev Inst Med Trop S Paulo* 39: 231-234. PubMed: 9640788.
- Brasil (2009) Guia de Vigilância Epidemiológica. Brasília: Ministério da Saúde. Secretaria de Vigilância em Saúde. Departamento de Vigilância Epidemiológica. 816 pp.
- Bonvicino CR, Oliveira JA, D'Andrea PS (2008) Guia dos roedores do Brasil com chaves para gêneros baseadas em caracteres externos. Rio de Janeiro: Centro Pan-Americano de Febre Aftosa. 120 pp.
- Suzuki A, Bisordi I, Levis S, Garcia J, Pereira LE et al. (2004) Identifying rodent hantavirus reservoirs, Brazil. *Emerg Infect Dis* 10: 2127-2134. doi:10.3201/eid1012.040295. PubMed: 15663849.
- Carbajo AE, Pardiñas UF (2007) Spatial distribution model of the hantavirus reservoir, the long-tailed colilargo (*Oligoryzomys longicaudatus*), in Argentina. *J Mammal* 88: 1555-1568. doi: 10.1644/06-MAMM-A-183R1.1.
- Zhang WY, Fang LQ, Jiang JF, Hui FM, Glass GE et al. (2009) Predicting the risk of hantavirus infection in Beijing, People's Republic of China. *Am J Trop Med Hyg* 80: 678-683. PubMed: 19346399.
- Donalísio MR, Peterson AT (2011) Environmental factors affecting transmission risk for hantaviruses in forested portions of southern Brazil. *Acta Trop* 119: 125-130. doi:10.1016/j.actatropica.2011.04.019. PubMed: 21605537.
- Loehman RA, Elias J, Douglass RJ, Kuenzi AJ, Mills JN et al. (2012) Wagoner prediction of *Peromyscus maniculatus* (deer mouse) population dynamics in Montana, USA, using satellite driven vegetation productivity and weather data. *J Wild Dis* 48: 348-360. doi: 10.7589/0090-3558-48.2.348.
- Mello DA (1982) Roedores, marsupiais e triatomíneos silvestres capturados no município de Mambai-Goiás: Infecção natural pelo *Trypanosoma cruzi*. *Rev Saúde Publica* 16: 282-291.
- Moura RT (2003) Distribuição e ocorrência de mamíferos na Mata Atlântica do sul da Bahia In: PI PradoEC LandauRT MouraLPS PintoGAB Fonseca. Corredor de biodiversidade da Mata Atlântica do Sul da Bahia. Ilhéus: Conservation International do Brasil. pp.1-22.
- Oliveira JA, Gonçalves PR, Bonvicino CR (2003) Mamíferos da Caatinga. Recife: Editora Universitária, Universidade Federal de Pernambuco. pp.275-333.
- Cherem JJ (2004) Lista dos mamíferos do estado de Santa Catarina, sul do Brasil. *Mastozool Neotrop* 11: 151-184.
- Gazeta GS, Carvalho RW, Avelar RF, Amorim M, Aboud-Dutra AE (2004) Ocorrência de *Babesia* sp. em pequenos roedores no Brasil.

- Arq Brasileiro Med Vet Zootec 56: 741-744. doi:10.1590/S0102-09352004000600007.
17. Oliveira FF, Langguth A (2004) Pequenos mamíferos (Didelphimorphia e Rodentia) de Paraíba e Pernambuco, Brasil. Rev Nord Biol 18: 19-86.
  18. Paresque R, Souza WP, Mendes SL, Fagundes V (2004) Composição cariotípica de roedores e marsupiais de duas áreas de Mata. Atlântica do Espírito Santo, Brasil. Bol Mus Biol Mello Leitão 17: 5-33.
  19. Sousa MAN, Langguth A, Gimenez EA (2004) Mamíferos dos brejos de altitude Paraíba e Pernambuco. In: KC PortoJJP CabralM Tabareli. Brejos de altitude em Pernambuco e Paraíba história natural, ecologia e conservação. Brasília: Ministério do Meio Ambiente. pp. 229-254.
  20. Bonvicino CR, Lemos B, Weksler M (2005) Small mammals of Chapada dos Veadeiros National Park (Cerrado of central Brazil): ecologic, karyologic, and taxonomic considerations. Braz J Biol 65: 395-406. doi:10.1590/S1519-69842005000300004. PubMed: 16341417.
  21. Ghizoni IR-Jr., Layme VMG, Lima AP, Magnusson WE (2005) Spatially explicit population dynamics in a declining population of the tropical rodent, *Bolomys lasiurus*. J Mammal 86: 677-682. Available online at: doi:10.1644/1545-1542(2005)086[0677:SEPDIA]2.0.CO;2
  22. Weksler M, Bonvicino CR (2005) Taxonomy of pygmy rice rats genus *Oligoryzomys* Bangs, 1900 (Rodentia, Sigmodontinae) of the Brazilian Cerrado, with the description of two new species. Arq Museu Nac Rio De Janeiro 63: 113-130.
  23. Astúa D, Moura RT, Grelle CEV, Fonseca MT (2006) Influence of baits, trap type and position for small mammal capture in a Brazilian lowland Atlantic Forest. Bol Mus Biol Mello Leitão 19: 31-44.
  24. Becker RG, Paise G, Baumgarten LC, Vieira EM (2007) Estrutura de comunidades de pequenos mamíferos e densidade de *Necromys lasiurus* (Rodentia, Sigmodontinae) em áreas abertas de Cerrado no Brasil central. Mastozool Neotrop 14: 157-168.
  25. Lustosa GS, Leite FH, Marques-Oliveira FN, Santos MP (2007) Análise da composição e riqueza de pequenos mamíferos em três fitofisionomias na Fazenda Bonito, município de Castelo do Piauí. Anais do VIII Congresso de Ecologia do Brasil, 23 a 28 de Setembro de 2007, Caxambu, Minas Gerais, Brasil
  26. Paresque R, Silva MJJ, Yonenaga-Yassuda Y, Fagundes V (2007) Karyological geographic variation of *Oligoryzomys nigripes* Olfers, 1818 (Rodentia, Cricetidae) from Brazil. Genet Mol Biol 30: 43-53. doi: 10.1590/S1415-47572007000100010.
  27. Cademartori CV, Saraiva M, Miranda JA (2008) Nota sobre a fauna de pequenos roedores em mosaico antropogênico com remanescente florestal do domínio mata atlântica, sul do Brasil. Biod Pamp 6: 34-38.
  28. D'elia G, Pardini UF, Jayat J, Salazar-Bravo J (2008) Systematics of *Necromys* (Rodentia, Cricetidae, Sigmodontinae): Species limits and groups, with comments on historical biogeography. J Mammal 89: 778-790. doi:10.1644/07-MAMM-A-246R1.1.
  29. Bezerra AMR, Carmignotto AP, Rodrigues FH (2009) Small non-volant mammals of an ecotone region between the Cerrado hotspot and the Amazonian rainforest, with comments on their taxonomy and distribution. Zool Stud 48: 861-874.
  30. Chioratto GTS, Costa CEV, Sobreira M, Almeida AM (2010) Soroprevalência da infecção por hantavírus em roedores do estado do Ceará, Brasil. Rev Patol Trop 39: 1-6.
  31. Alho CJR, Camargo G, Fischer E (2011) Terrestrial and aquatic mammals of the Pantanal. Braz J Biol 71: 297-310. PubMed: 21537603.
  32. Machado LF, Paresque R, Christoff AU (2011) Anatomia comparada e morfometria de *Oligoryzomys nigripes* e *O. flavescens* (Rodentia, Sigmodontinae) no Rio Grande do Sul, Brasil. Pap Avulsos Zool 51: 29-47
  33. Saavedra RC, Dias JP (2011) Infecção por *Yersinia pestis*, no estado da Bahia: Controle efetivo ou silêncio epidemiológico? Rev Soc Bras Med Trop 44: 223-227
  34. Peterson AT, Soberón J, Pearson RG, Anderson RP, Martínez-Meyer E et al. (2011) Ecological niches and geographic distributions. Princeton: Princeton University Press. 314 pp.
  35. Barve N, Barve V, Jiménez-Valverde A, Lira-Noriega A, Maher SP et al. (2011) The crucial role of the accessible area in ecological niche modeling and species distribution modeling. Ecol Modelling 222: 1810-1819. doi:10.1016/j.ecolmodel.2011.02.011.
  36. Vasconcelos MI, Lima VP, Iversson LB, Rosa MD, Travassos Da Rosa AP et al. (1997) Hantavirus pulmonary syndrome in the rural area of Juquitiba, São Paulo metropolitan area, Brazil. Rev Inst Med Trop S Paulo 39: 237-238. PubMed: 9640790.
  37. Romano-Lieber NS, Yee J, Hjelle B (2001) Serologic survey for hantavirus infections among wild animals in rural areas of São Paulo state, Brazil. Rev Inst Med Trop Sao Paulo 43: 325-327. PubMed: 11781602.
  38. Katz G, Williams RJ, Burt MS, de Souza LT, Pereira LE et al. (2001) Hantavirus pulmonary syndrome in the state of São Paulo, Brazil, 1993-1998. Vector Borne. Zoo - Drosophila Inf Service 1: 181-190.
  39. Caldas EP (2003) Epidemiologia de infecções por hantavírus no Rio Grande do Sul. Porto Alegre: Dissertação (Mestrado Em Ciências Veterinárias) Universidade Federal do Rio Grande: 63.
  40. Lemos ER, D'Andrea PS, Bonvicino CR, Famadas KM, Padula P et al. (2004) Evidence of hantavirus infection in wild rodents captured in a rural area of the state of São Paulo, Brazil. Pesq Vet Bras 24: 71-73.
  41. Rosa ES, Mills JN, Padula PJ, Elkhoury MR, Ksiazek TG et al. (2005) Newly recognized hantaviruses associated with hantavirus pulmonary syndrome in northern Brazil: Partial genetic characterization of viruses and serologic implication of likely reservoirs. Vector Borne Zoon. Drosophila Inf Service 5: 11-19.
  42. Pereira LE (2006) Estudo ecoepidemiológico de hantavírus em roedores das regiões da mata atlântica e cerrado do Brasil. São Paulo: Tese de Doutorado Coordenadoria de Controle de Doenças. Secretaria de Estado de Saúde de São Paulo: 165.
  43. Sobreira M, Souza GT, Moreli ML, Borges AA, Morais FA et al. (2008) A serosurvey for hantavirus infection in wild rodents from the states of Rio de Janeiro and Pernambuco, Brazil. Acta Trop 107: 150-152. doi: 10.1016/j.actatropica.2008.05.018. PubMed: 18619568.
  44. Travassos da Rosa ES (2008) Associação vírus-hospedeiro e epidemiologia molecular de hantavírus em distintos ecossistemas amazônicos: Maranhão e Pará - Mato Grosso. Rio de Janeiro: Tese de Doutorado. Instituto Oswaldo Cruz. 162 p
  45. Oliveira RC, Teixeira BR, Mello FC, Pereira AP, Duarte AS et al. (2009) Genetic characterization of a Juquitiba-like viral lineage in *Oligoryzomys nigripes* in Rio de Janeiro, Brazil. Acta Trop 112: 212-218. doi:10.1016/j.actatropica.2009.07.029. PubMed: 19660427.
  46. Raboni SM, de Borba L, Hoffmann FG, de Noronha L, Azevedo ML (2009) Evidence of circulation of Laguna Negra-like hantavirus in the central west of Brazil: case report. J Clin Virol 45: 153-156. doi: 10.1016/j.jcv.2009.03.015. PubMed: 19395308.
  47. Raboni SM, Hoffmann FG, Oliveira RC, Teixeira BR, Bonvicino CR et al. (2009) Phylogenetic characterization of hantaviruses from wild rodents and hantavirus pulmonary syndrome cases in the state of Paraná (southern Brazil). J Gen Virol 90: 2166-2171. doi:10.1099/vir.0.011585-0. PubMed: 19439554.
  48. Oliveira RC, Padula PJ, Gomes VR, Martínez VP, Bellomo C et al. (2011) Genetic characterization of hantaviruses associated with sigmodontine rodents in an endemic area for hantavirus pulmonary syndrome in southern Brazil. Vector Borne Zoo Dis 11: 302-3011.
  49. Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. Int J Climatol 25: 1965-1978. doi:10.1002/joc.1276.
  50. Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. Ecol Modelling 190: 231-259. doi:10.1016/j.ecolmodel.2005.03.026.
  51. Pearson RG, Raxworthy CJ, Nakamura M, Peterson AT (2007) Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. J Biogeogr 34: 102-117.
  52. Peterson AT, Pape SM, Soberón J (2008) Rethinking receiver operating characteristic analysis applications in ecological niche modeling. Ecol Modelling 213: 63-72. doi:10.1016/j.ecolmodel.2007.11.008.
  53. Anderson RP, Gómez-Laverde M, Peterson AT (2002) Geographical distributions of spiny pocket mice in South America: Insights from predictive models. Global Ecol Biogeogr 11: 131-141. doi:10.1046/j.1466-822X.2002.00275.x.
  54. Warren DL, Glor RE, Turelli M (2008) Environmental niche equivalency versus conservatism: Quantitative approaches to niche evolution. Evolution 62: 2868-2883. doi:10.1111/j.1558-5646.2008.00482.x. PubMed: 18752605.
  55. Peterson AT (2011) Ecological niche conservatism: A time-structured review of evidence. J Biogeogr 38: 817-827. doi:10.1111/j.1365-2699.2010.02456.x.
  56. Warren DL, Glor RE, Turelli M (2010) ENMTools: A toolbox for comparative studies of environmental niche models. Ecography 33: 607-611.
  57. Qiao H, Soberón J, Campbell L, Peterson AT (2013) NicheA. version 1.2 beta. Available: <http://biodiversity-informatics-training.org/software-data-sources/nichea/>. Accessed 01 August 2013
  58. Santos JP, Steinke ET, Garcia-Zapata MT (2001) Land use and occupation and hantaviruses dissemination in the São Sebastião region, Federal District: 2004- 2008. Rev Soc Bras Med Trop 44: 53-57

59. Alho CJ, Souza MJ (1982) Home range and use of space in *Zygodontomys lasiurus* (Cricetidae, Rodentia) in the Cerrado of central Brazil. *Ann Carneg Mus* 51: 127-132.
60. Vieira EM, IOB G, Briani DC, Palma AR (2005) Microhabitat selection and daily movements of two rodents (*Necomys lasiurus* and *Oryzomys scotti*) in Brazilian Cerrado, as revealed by a spool-and-line device. *Mammal Biol* 70: 359-365.
61. Oliveira JA, Bonvicino CR (2006) Ordem Rodentia. In: NR ReisAL PeracchiWA PedroIP Lima. *Mamíferos do Brasil*. Londrina: Universidade Estadual de Londrina. pp. 347-406.
62. Bergallo HG, Magnusson WE (1999) Effects of climate and food availability on four rodent species in southeastern Brazil. *J Mammal* 80: 472-486. doi:10.2307/1383294.
63. Eisenberg JF, Redford KH (1999) *Mammals of the Neotropics*. Chicago: University of Chicago Press. 609 pp.
64. Agrellos R, Bonvicino CR, Rosa ES, Marques AA, D'Andrea OS et al. (2012) The taxonomic status of the Castelo dos Sonhos hantavirus reservoir, *Oligoryzomys utiariensis* Allen 1916 (Rodentia: Cricetidae: Sigmodontinae). *Zootaxa* 3220: 1-28.
65. Rosa ES, Medeiros DB, Nunes MR, Simith DB, Pereira AS et al. (2011) Pygmy rice rat as potential host of Castelo dos Sonhos hantavirus. *Emerg Infect Dis* 17: 1527-1530. doi:10.3201/eid1708.101547. PubMed: 21801642.
66. Rosa EST, Medeiros DB, Nunes MR, Simith DB, Pereira AS, Elkhoury MR et al. (2012) Molecular epidemiology of Laguna Negra Virus, Mato Grosso State, Brazil. *Emerg Infect Dis* 18: 982-985. doi:10.3201/eid1806.110948. PubMed: 22607717.
67. Paglia AP, Fonseca GA, Rylands AB, Herrmann G, Aguiar LM, Chiarello AG et al. (2012) Annotated checklist of Brazilian mammals. Arlington: Conservation International. p. 76. Occasional Papers in conservation biology