

Original Contribution

Modeling Potential Distribution of *Oligoryzomys longicaudatus*, the Andes Virus (Genus: *Hantavirus*) Reservoir, in Argentina

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Abstract: We constructed a model to predict the potential distribution of *Oligoryzomys longicaudatus*, the reservoir of Andes virus (Genus: *Hantavirus*), in Argentina. We developed an extensive database of occurrence records from published studies and our own surveys and compared two methods to model the probability of *O. longicaudatus* presence; logistic regression and MaxEnt algorithm. The environmental variables used were tree, grass and bare soil cover from MODIS imagery and, altitude and 19 bioclimatic variables from WorldClim database. The models performances were evaluated and compared both by threshold dependent and independent measures. The best models included tree and grass cover, mean diurnal temperature range, and precipitation of the warmest and coldest seasons. The potential distribution maps for *O. longicaudatus* predicted the highest occurrence probabilities along the Andes range, from 32°S and narrowing southwards. They also predicted high probabilities for the south-central area of Argentina, reaching the Atlantic coast. The Hantavirus Pulmonary Syndrome cases coincided with mean occurrence probabilities of 95 and 77% for logistic and MaxEnt models, respectively. HPS transmission zones in Argentine Patagonia matched the areas with the highest probability of presence. Therefore, colilargos presence probability may provide an approximate risk of transmission and act as an early tool to guide control and prevention plans.

Keywords: Argentina, hantavirus reservoir, logistic regression, MaxEnt algorithm, *Oligoryzomys longicaudatus*, potential distribution

INTRODUCTION

The “colilargo” (*Oligoryzomys longicaudatus* Bennet 1832) belongs to a genus of small mice in the New World Tribe Oryzomyini (Muridae: Sigmodontinae). It is primarily distributed in humid and highly vegetated areas, such as

woods and shrublands in Chile and southwestern Argentina where it is usually found in high abundances (Murúa and Gonzalez 1982; Pearson 1983; Larrieu et al. 2003; Piudo et al. 2005). However, it has also been captured in steppe and, in disturbed habitats such as borders of cultivated fields, peridomestic settings and pastures (Monjeau et al. 1997; Pardiñas et al. 2003; Piudo et al. 2005, 2011; Polop et al. 2010). The species is of great practical importance because of its role as the natural reservoir for the Andes

South virus (ANDV), one of the lineages of hantavirus that causes Hantavirus Pulmonary Syndrome (HPS) in southern South America (Lopez et al. 1996; Levis et al. 1998; Padula et al. 2000).

Hantaviruses are zoonotic, host-specific, RNA viruses that persistently infect rodents of the families Muridae and Cricetidae. Each virus establishes a chronic, asymptomatic infection in its rodent host that involves the shedding of infectious virus into the environment in rodent urine, feces, and saliva. These characteristics are key to the transmission of the virus both to humans and among rodents. The virus is transmitted to humans by inhalation of aerosols of urine and feces, and/or mucosal secretions (Botten et al. 2002; Padula et al. 2004) and it is maintained in rodent populations mainly through bites and aggressive encounters among adults (Glass et al. 1988; Mills et al. 1997).

HPS is a severe and frequently (30–50% of cases) fatal cardiopulmonary disease (Yahnke et al. 2001). Since the first cases of HPS reported in 1993, at least 23 hantaviruses have been described throughout the Americas and about half of them are known to cause HPS. ANDV has been responsible for the HPS cases recorded in southern Argentina and Chile since 1995 (Lopez et al. 1996; Padula et al. 2000). Antibody prevalence rates in *O. longicaudatus* show spatial and temporal variations, reaching values of almost 50% in some springs (Cantoni et al. 2001; Larrieu et al. 2003; Padula et al. 2004, 2005, 2011; Polop et al. 2010). Three other species have been found to have antibodies against ANDV in Argentina: *Abrothrix longipilis*, *A. olivaceus*, and *Loxodontomys micropus* (Cantoni et al. 2001, Piudo et al. 2005, 2011) but there are no reports of these species transmitting ANDV to humans. However, ANDV epidemiology is slightly complicated by occasional person-to-person transmission (Martinez et al. 2005). The control and prevention of rodent-borne diseases (e.g., HPS) largely depend upon understanding the biology and ecology of the host in which describing and explaining its geographic distribution is key (Mills and Childs 1998). Epidemiologic analysis and planning of preventive measures also require knowing the geographic distribution and ecological conditions relevant to the occurrence of the host and the circulation of a pathogen (Kosoy et al. 1997). Since the virus is directly transmitted to humans by the rodent reservoir, basic studies about the colilargo may provide useful information to establish risk of human disease, to direct prevention programs, and improve our understanding of the relationships between environment, host populations, and occurrence of disease cases.

For many South American rodents involved in zoonoses, basic aspects such as geographic distribution remain poorly known. Developing predictive habitat distribution models, or niche modeling, as applied in many fields, such as biogeography, evolution, ecology, epidemiology, conservation, and invasive-species management may provide an important tool to address this challenge (Anderson et al. 2003; Guisan and Zimmermann 2000). Species distribution models identify the set of conditions that best predict the geographic distribution of a species using one of several modeling algorithms with environmental data from georeferenced sites of known species occurrence (Pearson and Dawson 2003; Elith et al. 2006). Each algorithm is designed to extract the relationship between environmental variation and species occurrence. This relationship is used to predict the species distribution in unsampled locations given the environmental conditions of the area of interest (Richards et al. 2007). Methods for modeling species distributions differ in how they select relevant predictor variables, weight the individual variables contribution, and predict patterns of occurrence (Guisan and Zimmermann 2000; Elith et al. 2006). Additionally, whereas some algorithms rely on presence data alone, others require both presence and absence data. Ultimately, the choice of modeling algorithm should be based on both the intended use of the resulting distribution estimates and the available data. However, newer algorithms such as maximum entropy methods (MaxEnt) and boosted regression trees, appear to empirically outperform several of the more established methods in comparisons across a number of species and geographic regions (Elith et al. 2006).

The study of the relationship between environment, host distribution and abundance, and HPS cases have recently begun in Argentina. Two previous attempts to describe *O. longicaudatus* distribution for the whole country have examined maximum likelihood classification (Porcasi et al. 2005) and logistic regression (Carbajo and Pardiñas 2007). However, the approach described here uses a larger number of presence and absence records and higher resolution environmental data. We also compare two different methods: classical logistic regression and MaxEnt, which has been characterized as one of the three most reliable techniques for predicting species distributions (Phillips et al. 2006; Elith et al. 2006).

Given the public health significance of *O. longicaudatus* and the possibility of human-to-human transmission of ANDV in southern Argentina, it is of great interest to determine the best approaches to identify environmental

variables associated with the occurrence of this rodent host. Likewise, it is important to assess the relationship between host distribution and HPS cases to recognize those areas of high risk for humans. The goal is to identify locations and times when the risk of hantaviral disease occurrence will be high, allowing public health authorities to focus surveillance and concentrate resources where the need is greatest.

METHODS

Rodent host and HPS cases data

We generated an extensive database of *O. longicaudatus* presence and absence records from published studies (Monjeau et al. 1997; Pearson 2002; Pardiñas et al. 2003, 2004; Porcasi et al. 2005; Piudo et al. 2005; Jayat and Pacheco 2006; Jayat et al. 2006; Pardiñas and Teta 2007; Carbajo and Pardiñas 2007; Rivera et al. 2007; Cueto et al. 2008; Ferro and Bárquez 2008; Nabte et al. 2009) and our own surveys in northwestern Chubut province (V. Andreo, unpublished, Table 1). Presence was defined by voucher specimens, osteological remains in owl pellets or the trapping of the animal in the field. Absence was defined, based on sites where owl pellets with the remains of at least 100

rodents were examined without detecting any sign of *O. longicaudatus* (see Carbajo and Pardiñas (2007) for further details on collections surveyed) or, sites where researchers trapped mice but did not capture colilargos. We deleted presence or absence points that were less than 3 km apart to avoid autocorrelation issues. A randomly selected subset of locations (~20% of presences and absences) was withheld for validation studies.

Data on human HPS cases was provided by Health Ministries from Neuquén, Río Negro and Chubut provinces. HPS localities were considered just once when more than one case was recorded at a site and when secondary transmission was confirmed or suspected.

Records of *O. longicaudatus* and HPS localities were incorporated into a geographic information system (GIS) using ArcMap, version 9.3 (Environmental Systems Research Institute, Redlands, CA).

Environmental data

Environmental data layers of topography, climate, and land cover were compiled for southern South America. Altitude and climatic data layers as 19 'bioclimatic variables' were drawn from the WorldClim data set (Hijmans et al. 2005,

Table 1. Number of presence and absence records used as training and test data sets obtained from published studies and our own field surveys in northwestern Chubut province, Argentina

Source	Training data set			Test data set			Total
	Absence	Presence	Subtotal	Absence	Presence	Subtotal	
Carbajo and Pardiñas (2007)	60	93	153	22	24	46	199
Cueto et al. (2008)	7	–	7	1	–	1	8
Ferro and Bárquez 2008	1	–	1	1	–	1	2
Jayat and Pacheco (2006)	60	–	60	11	–	11	71
Jayat et al. (2006)	23	–	23	4	–	4	27
Monjeau et al. (1997)	6	3	9	2	–	2	11
Nabte et al. (2009)	20	–	20	3	–	3	23
Palma et al. (2005)	–	1	1	–	1	1	2
Pardiñas and Teta (2007)	6	1	7	1	–	1	8
Pardiñas et al. (2003)	8	5	13	–	1	1	14
Pardiñas et al. (2004)	14	–	14	4	–	4	18
Pearson (2002)	–	3	3	–	–	–	3
Piudo et al. (2005)	1	6	7	–	–	–	7
Porcasi et al. (2005)	42	9	51	–	–	–	51
Rivera et al. (2007)	–	1	1	13	2	15	16
V.A. surveys (unpublished)	2	8	10	–	4	4	14
Total	250	130	380	62	32	94	474

<http://www.worldclim.org>). These products are derived from monthly weather station measurements of altitude, temperature, and rainfall. They are biologically meaningful variables that capture annual ranges, seasonality and limiting factors useful for species distribution modeling. The Worldclim data set we used is at $\sim 1 \text{ km}^2$ spatial resolution and corresponds to averages over a 50-year period (1950–2000, Hijmans et al. 2005). Land cover data was drawn from the Vegetation Continuous Fields collection (VCF-MOD44B, collection 3, Hansen et al. 2003), which contains proportional estimates for vegetative cover types: woody vegetation, herbaceous vegetation, and bare ground. The product was derived from the seven bands of the Moderate-resolution Imaging Spectroradiometer (MODIS) sensor and it was aggregated from an initial 0.5 km pixel to 1 km² to match the resolution of the climatic variables. The environmental layers were imported into ArcMap, version 9.3 (Environmental Sciences Research Institute, Redlands, CA).

Modeling

Two modeling approaches to characterize the probability of presence for *O. longicaudatus* were compared: Multiple logistic regression models (generalized linear models with binomial error) and MaxEnt algorithm (Maximum Entropy, Phillips et al. 2006; Phillips and Dudík 2008).

Exploratory analysis compared environmental variables between sites with and without *O. longicaudatus* using a Kruskal–Wallis test. We also conducted univariate logistic regressions to determine the associations between colilargos occurrence probability and altitude, climate, and land cover. Variables that were not different between sites or that were not significant in univariate logistic regressions were not included in further analysis. Multivariate logistic analysis was performed including variables with *P* values < 0.10 from the univariate analyses as covariates to increase sensitivity. The significance of variables was evaluated with a *t* test. Variance inflation factors (VIFs) and pairwise Pearson correlation coefficients were computed to evaluate collinearity among the independent variables. Variables with VIF lower than 10 (or that yielded an average VIF of 5) were retained. For pairwise Pearson correlation coefficients larger than 0.6 the variable responsible for the greater change in deviance was retained, and the other was excluded from further analyses. We ran models using either only altitude, climatic or land cover variables, and then we tried with combinations of all of them to assess the contribution of each category to

O. longicaudatus distribution. We did not consider interactions among variables to simplify models.

The explanatory power of the models was estimated with D^2 , the ratio of the residual to null deviance. To select the most parsimonious model with the best predictive power, Akaike Information Criterion (AIC) and D^2 were used to rank the models. The model with the lowest AIC and highest D^2 was selected to build distribution maps and draw inferences. We also performed a Moran test on the residuals of this model to assess whether the unexplained variation was randomly distributed (Software Passage version 2.0, Rosenberg and Anderson 2011). The potential distribution map for the logistic model was built by applying the model formula pixel to pixel in the geographic information system. R 2.12.0 (The R-Development Core Team 2010) and ArcMap version 9.3 were used for modeling and mapping, respectively.

The MaxEnt algorithm was applied using the same combination of predictor variables as in the best logistic model. MaxEnt is a machine learning technique that estimates a target probability distribution for species occurrence that maximizes the entropy, subject to the constraint that the expected value for each environmental variable under this distribution matches the empirical average generated from environmental values associated with occurrence data (Phillips et al. 2006). The target probability is calculated using the pixels with known species occurrence records and the associated environmental variables. The obtained distribution approximates the species potential geographic distribution (Phillips et al. 2006, for more details on MaxEnt statistical functioning see Elith et al. 2011). MaxEnt algorithm was run using MaxEnt software, version 3.3.1 (<http://www.cs.princeton.edu/~schapire/maxent/>) with SWD format (“samples with data”) which allows the inclusion of both presence and absence data. We used the logistic map as output with values ranging from 0 to 1. Therefore, pixels with values close to 1 showed the best environmental conditions for the occurrence of *O. longicaudatus* and indicated a higher probability of finding it, while pixels with values close to 0 indicated unsuitable conditions for the species and a very low probability of occurrence. All other parameters were maintained at default settings.

To assess the predictive accuracy of the logistic and MaxEnt models, we used both threshold dependent and independent measures for training data set. Receiver operating characteristic (ROC) curves were used to assess the overall discrimination ability of each model on the basis of

the area under the ROC curve (AUC) as threshold independent measures. Following Araújo and Guisan (2006), a rough guide for classifying the model accuracy was: 0.50–0.60 = insufficient; 0.60–0.70 = poor; 0.70–0.80 = average; 0.80–0.90 = good; 0.90–1 = excellent. However, predictive modeling and some practical applications of species distribution models may require an arbitrary threshold probability at which to accept the presence of the target organism. Therefore, to complement the former evaluation, we converted the probabilities to a binary value. Three different criteria for the optimal probability cut-off value were evaluated: the prevalence (the proportion of sites in which the species was recorded as present), the point where the sum of sensitivity and specificity was maximized, and the cut-off value where sensitivity equaled specificity. The latter two approaches have proven to work best in comparing methods for threshold selection (Liu et al. 2005). For each threshold for logistic and MaxEnt models we constructed a confusion matrix of the predicted and observed values using the training data set and we estimated accuracy and error measures (Table 2). Finally, we compared the performance of the models using only threshold independent measures for test data set. Both threshold dependent and independent measures were estimated using the package ROCR version 1.0-4 (Sing et al. 2005) for R (The R-Development Core Team 2010).

RESULTS

The database consisted of 162 presence and 312 absence records. Thirty-two presence and 62 absence records were

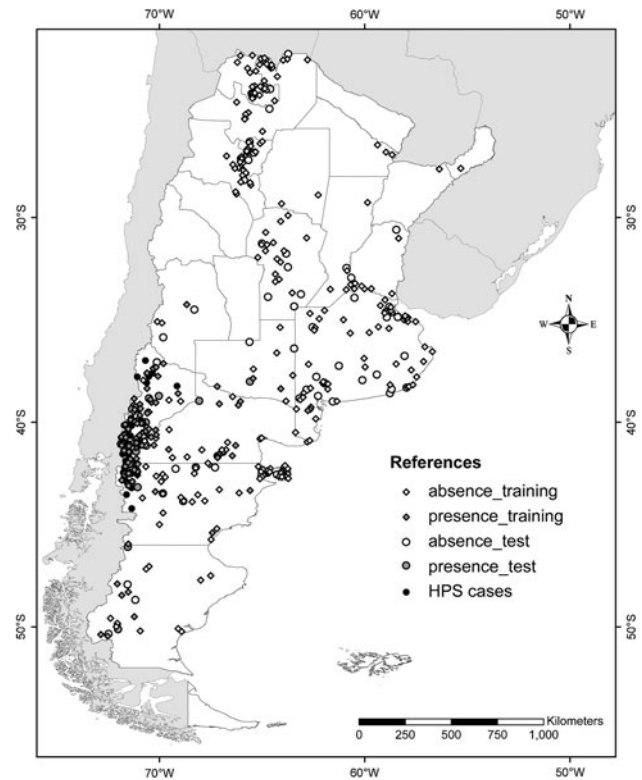


Figure 1. Training and test samples for presence and absence of *O. longicaudatus* in Argentina.

used as validation test points and 130 presence and 250 absence records were the training set used to perform exploratory analysis and develop models. The distribution of *O. longicaudatus* was represented by a thematic point map with the sites where the rodent was present or absent (Fig. 1).

Table 2. Threshold dependent measures used for assessing the predictive performance of models

Performance measure	Definition	Formula
Overall accuracy	Proportion of all cases correctly predicted	$(TP + TN)/(P + N)$
Error rate	Proportion of all cases erroneously predicted	$(FP + FN)/(P + N)$
Sensitivity (true positive rate)	Proportion of true presences correctly predicted	TP/P
Specificity (true negative rate)	Proportion of true absences correctly predicted	TN/N
False positive rate		FP/N
False negative rate		FN/P
Positive predictive value (precision)	Percentage of predicted presences that were real	$TP/(TP + FP)$
Negative predictive value	Percentage of predicted absences that were real	$TN/(TN + FN)$

TP number of presence points correctly classified as presences, *TN* number of absence points correctly classified as absences, *FP* number of actual absence points classified as presences, *FN* number of actual presence points classified as absences, *P* total number of actual presences, *N* total number of actual absences

Sites with and without *O. longicaudatus* differed significantly for most of the environmental variables that were examined (Table 3). In univariate logistic regression, mean temperature and precipitation of the wettest quarter (bio8 and bio19, respectively) explained the highest proportion of deviance, followed by mean annual temperature (bio1), mean temperature of the warmest quarter (bio10), and mean temperature of the coldest quarter (bio11). Most of these variables were negatively associated with colilargos occurrence except for precipitation of the wettest quarter which showed a positive relationship (Table 3).

The best logistic models (m1 and m2, Table 4) included tree and grass cover, mean diurnal temperature range (bio2), mean temperature of the driest season (bio9), and precipitation of the warmest and coldest seasons (bio18 and bio19, respectively). All variables but precipitation of the warmest quarter (bio18) were positively related to *O. longicaudatus* occurrence probability. We chose the second model (m2) to draw inferences and build the potential distribution map, because it was simpler (less variables), it showed very similar AIC and equal D^2 values with m1 (i.e., it explained the same proportion of deviance). In MaxEnt algorithm using the same predictors as m2, environmental variables showed a similar general pattern of association with *O. longicaudatus* occurrence, although for bio 18 and bio 19 the relationship was non-linear. These precipitation-related variables explained the highest proportion of deviance in the logistic model and had the highest contribution in the MaxEnt algorithm.

Maps of potential distribution of *O. longicaudatus* (Fig. 2) predicted high habitat suitability or high occurrence probability along the Andean range from northern Mendoza province (32°S) and narrowing southward. Both models also predicted a high suitability area in the northwest and south of La Pampa, south of Buenos Aires and north of Río Negro provinces, following the trajectory of two major rivers: Río Negro and Río Colorado. The Patagonian central plateaus (Chubut and Santa Cruz provinces) showed low probabilities in the logistic model with some patches of high suitability, and moderate to low values in MaxEnt predictive map. The MaxEnt potential distribution map showed high suitability for colilargos all along Andes range to Tierra del Fuego (55°S) and intermediate probabilities for the Atlantic coast of Chubut and Santa Cruz provinces, describing a more gradual change in habitat suitability from west to east than logistic map. In contrast, the latter did not predict the presence of colilargos southwards beyond 49°S. The probability of occurrence decreased

towards the northeast in Buenos Aires and Córdoba provinces in both predictive maps.

In terms of vegetation types, high likelihood of presence areas corresponded to most of the Subantarctic forests (perennial and deciduous forests, 800–5000 mm precipitation annually), the western part of the Patagonian steppe (shrub and grass steppes, 100–300 mm annually), southern part of the Espinal (scrublands and low trees, 340–600 mm precipitation annually) and the Monte (shrub-grass steppes, 250–800 mm precipitation annually) phytogeographic regions.

Both the logistic regression and MaxEnt models performed similarly as measured by threshold independent measures (Fig. 3). According to ROC curves, sensitivity and specificity plots and sensitivity plus specificity plots, both models had highly satisfactory performances with AUC values of 0.96 and 0.97, for logistic and MaxEnt models, respectively. In the threshold-dependent evaluation approach (Table 5), differences in predictive performance between models were more noticeable when we used prevalence as threshold than for the other two criteria. Differences were also evident in the presence–absence maps (Fig. 4). For the logistic model the best criteria for threshold selection seemed to be sensitivity = specificity and prevalence, which had higher sensitivity values and lower false negative rates. In MaxEnt, even though the prevalence criterion showed the highest sensitivity and lowest false negative rate, it had a very low specificity and high false positive rate, wrongly predicting presence all over Patagonia. Therefore, 0.5 (the cut-off value where sensitivity equals specificity) seemed to be the best threshold selection criterion for this model. When comparing models with the threshold-dependent approach, sensitivity = specificity seemed to be the criterion that better balanced these measures along with false positive and negative rates and, positive and negative predictive values (Table 5). Using this criterion we chose MaxEnt model as the best representation of *O. longicaudatus* distribution. To complement the predictive performance assessment we used the threshold-independent ROC curve and AUC on test samples. Again, models behaved nearly equally as measured by AUC, with MaxEnt showing a slightly higher value (0.94 and 0.95, for Logistic and MaxEnt models, respectively).

Finally, almost all HPS cases recorded in Patagonia were encompassed in the highest predicted probability of *O. longicaudatus* presence, which coincided with forests and shrublands areas. The mean predicted probability of coli-

Table 3. Univariate statistics for the environmental variables considered in *O. longicaudatus* distribution modeling

Variable	Description and units	O.l.	Mean	sd	Median	K-W	B	D ²
ALT	Elevation above sea level (m)	0	913.72	1125.05	416.00	15.44***	-6.6×10^{-5} ns	0.00
BARE	Percentage of surface with bare soil cover (%)	1	857.54	332.17	858.50			
		0	24.26	28.88	11.00	0.27 ns	-0.003 ns	0.00
HERB	Percentage of surface with grass cover (%)	1	22.19	21.49	20.00			
		0	65.64	26.81	68.50	9.76**	-0.01*	0.01
TREE	Percentage of surface with tree cover (%)	1	59.25	20.73	62.00			
		0	10.11	16.84	3.00	18.44***	0.019***	0.03
BIO1	Annual mean temperature (°C × 10)	1	18.56	24.96	7.00			
		0	136.83	38.49	138.00	118.25***	-0.042***	0.28
BIO2	Mean diurnal range (Mean of monthly (max tem - min tem))	1	90.00	24.81	84.50			
		0	131.97	21.52	131.00	6.32**	-0.010 [†]	0.01
		1	127.88	16.13	124.00			
BIO3	Isothermality ((bio2/bio7) × 100)	0	49.71	4.91	48.50			
		1	50.88	2.52	51.00	29.57***	0.063*	0.01
BIO4	Temperature seasonality (standard deviation × 100)	0	4623.57	577.02	4634.00			
		1	4544.15	501.81	4417.00	3.23 ns	-0.00026 ns	0.00
BIO5	Maximum temperature of the warmest month (°C × 10)	0	272.36	39.64	273.50			
		1	232.96	37.11	224.50	77.93***	-0.026***	0.16
BIO6	Minimum temperature of the coldest month (°C × 10)	0	10.40	41.21	18.00			
		1	-15.81	14.72	-14.50	57.52***	-0.023***	0.10
BIO7	Temperature annual range (bio5 - bio6) (°C × 10)	0	261.95	26.34	263.00			
		1	248.77	27.51	240.00	27.31***	-0.019***	0.04
BIO8	Mean temperature of the wettest quarter (°C × 10)	0	159.40	68.36	181.00			
		1	48.48	43.10	37.00	162.04***	-0.028***	0.41
BIO9	Mean temperature of the driest quarter (°C × 10)	0	110.38	45.40	107.00			
		1	133.53	29.08	136.50	26.86***	0.015***	0.06
BIO10	Mean temperature of the warmest quarter (°C × 10)	0	194.04	39.51	197.00			
		1	148.40	30.37	141.50	102.51***	-0.034***	0.23
BIO11	Mean temperature of the coldest quarter (°C × 10)	0	76.28	39.45	78.00			
		1	32.15	20.12	30.50	104.69***	-0.043***	0.27
BIO12	Annual precipitation (mm)	0	530.21	329.64	457.50			
		1	679.66	351.93	653.00	16.62***	0.0013***	0.03

Table 3. continued

Variable	Description and units	O.I.	Mean	sd	Median	K-W	B	D ²
BIO13	Precipitation of the wettest month (mm)	0	83.10	48.12	86.00	29.75***	0.012***	0.07
BIO14	Precipitation of the driest month (mm)	1	118.76	63.78	118.50	31.82***	0.013*	0.01
BIO15	Precipitation seasonality (coefficient of variation)	1	20.28	11.27	17.00	3.84*	0.003 ns	0.00
BIO16	Precipitation of the wettest quarter (mm)	0	54.20	31.99	40.00	32.69***	0.0045***	0.07
BIO17	Precipitation of the driest quarter (mm)	1	56.42	14.76	61.00	33.15***	0.0050**	0.01
BIO18	Precipitation of the warmest quarter (mm)	0	222.39	131.51	226.00	46.67***	-0.012***	0.19
BIO19	Precipitation of the coldest quarter (mm)	1	318.12	162.79	328.50	154.92***	0.014***	0.42

O.I. (0), *O. longicaudatus* absence; O.I. (1), *O. longicaudatus* presence; SD, standard deviation; K-W, Kruskal-Wallis Chi-squared statistic; B, univariate logistic regression parameter; D², ratio of the residual to null deviance.

*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; † $P < 0.1$; ns $P > 0.1$.

Table 4. Multivariate logistic regression models for *O. longicaudatus* presence/absence

Model	Variables	AIC	D^2
m1	TREE + HERB + BIO2 + BIO9 + BIO18 + BIO19	194.20	0.63
m2	TREE + HERB + BIO2 + BIO18 + BIO19	194.49	0.63
m3	BIO7 + BIO18 + BIO19	203.35	0.60
m4	BIO2 + BIO18 + BIO19	204.63	0.60
m5	HERB + BIO18 + BIO19	204.75	0.60
m6	TREE + HERB + BIO9 + BIO13 + BIO18	206.08	0.60
m7	TREE + HERB + BIO3 + BIO9 + BIO13 + BIO18	206.80	0.61
m8	HERB + BIO9 + BIO13 + BIO18	207.84	0.59
m9	BIO18 + BIO9 + BIO19	207.95	0.59
m10	BIO3 + BIO5 + BIO6 + BIO8 + BIO9 + BIO18 + BIO19	208.03	0.61
m11	TREE + HERB + BIO3 + BIO8 + BIO9 + BIO13 + BIO18	208.42	0.61
m12	BIO5 + BIO18 + BIO19	209.88	0.59
m13	BIO3 + BIO18 + BIO19	210.16	0.59
m14	BIO18 + BIO19	210.22	0.58

HERB percentage of surface with grass cover, *TREE* percentage of surface with tree cover, *BIO2* mean diurnal range, *BIO3* isothermality, *BIO5* maximum temperature of the warmest month, *BIO6* minimum temperature of the coldest month, *BIO7* temperature annual range, *BIO8* mean temperature of the wettest quarter, *BIO9* mean temperature of the driest quarter, *BIO13* precipitation of the wettest month, *BIO18* precipitation of the warmest quarter, *BIO19* precipitation of the coldest quarter, *AIC* Akaike information criterion value, D^2 ratio of the residual to null deviance.

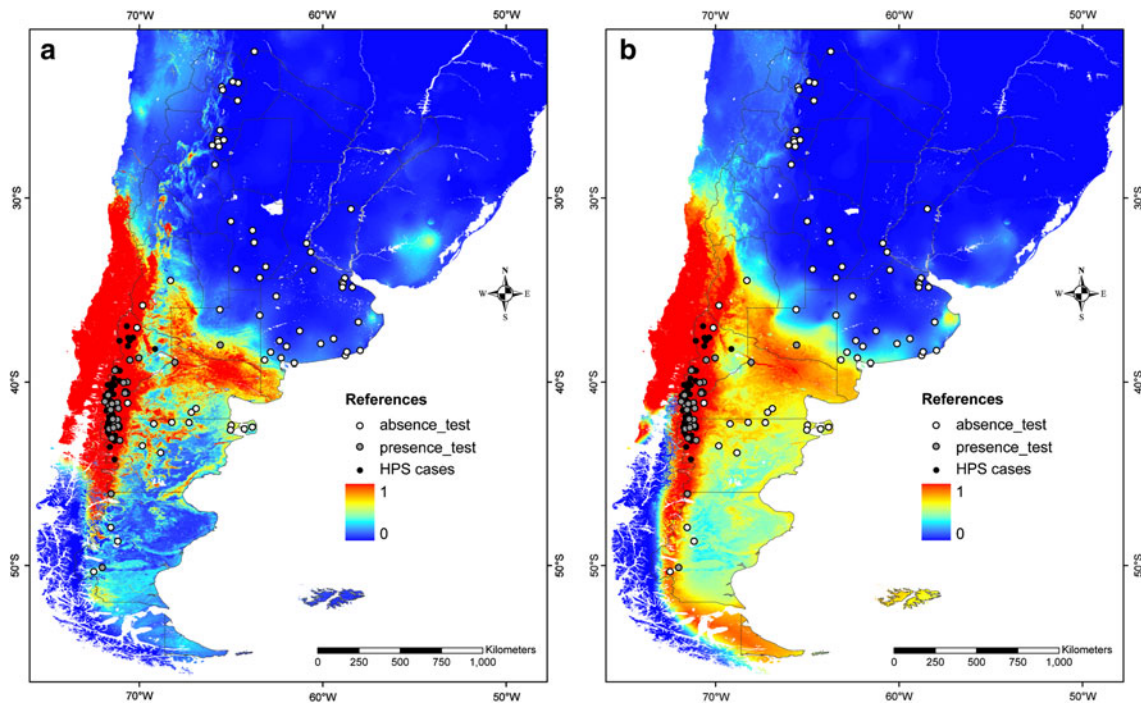


Figure 2. Predicted potential geographic distribution of *O. longicaudatus* for logistic model (a) and MaxEnt algorithm (b).

largos presence for sites with HPS cases was 0.77 (min = 0.42, max = 0.86) for MaxEnt model and 0.95 (min = 0.2, max = 1) for the logistic model. The minimum

probability value for both maps corresponded to a locality called El Morado in the northeast of Neuquén province, an area phytogeographically characterized as Monte.

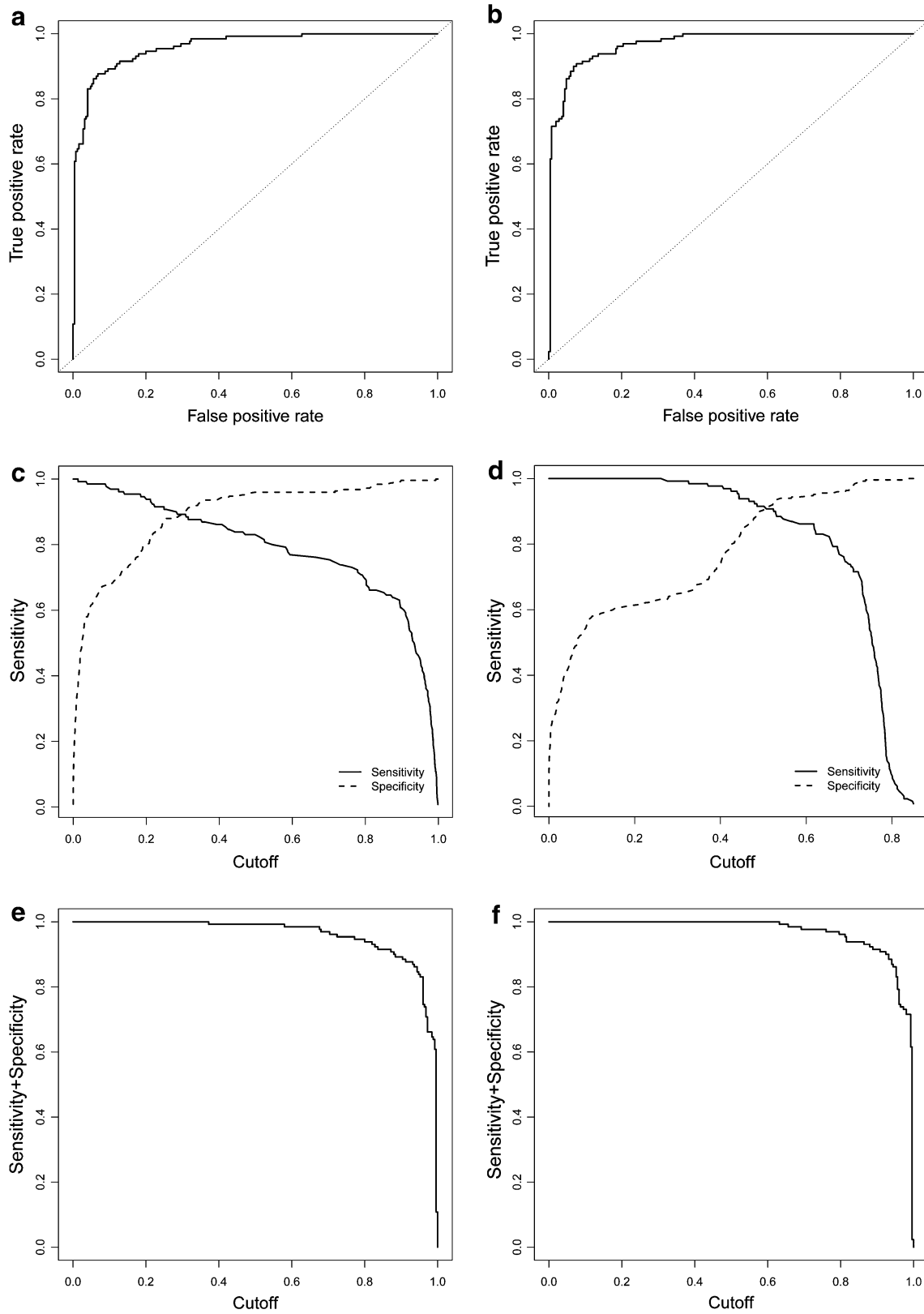


Figure 3. Receiver operating characteristic (a, b), sensitivity and specificity (c, d) and sensitivity plus specificity (e, f) curves for logistic and MaxEnt models based on training data.

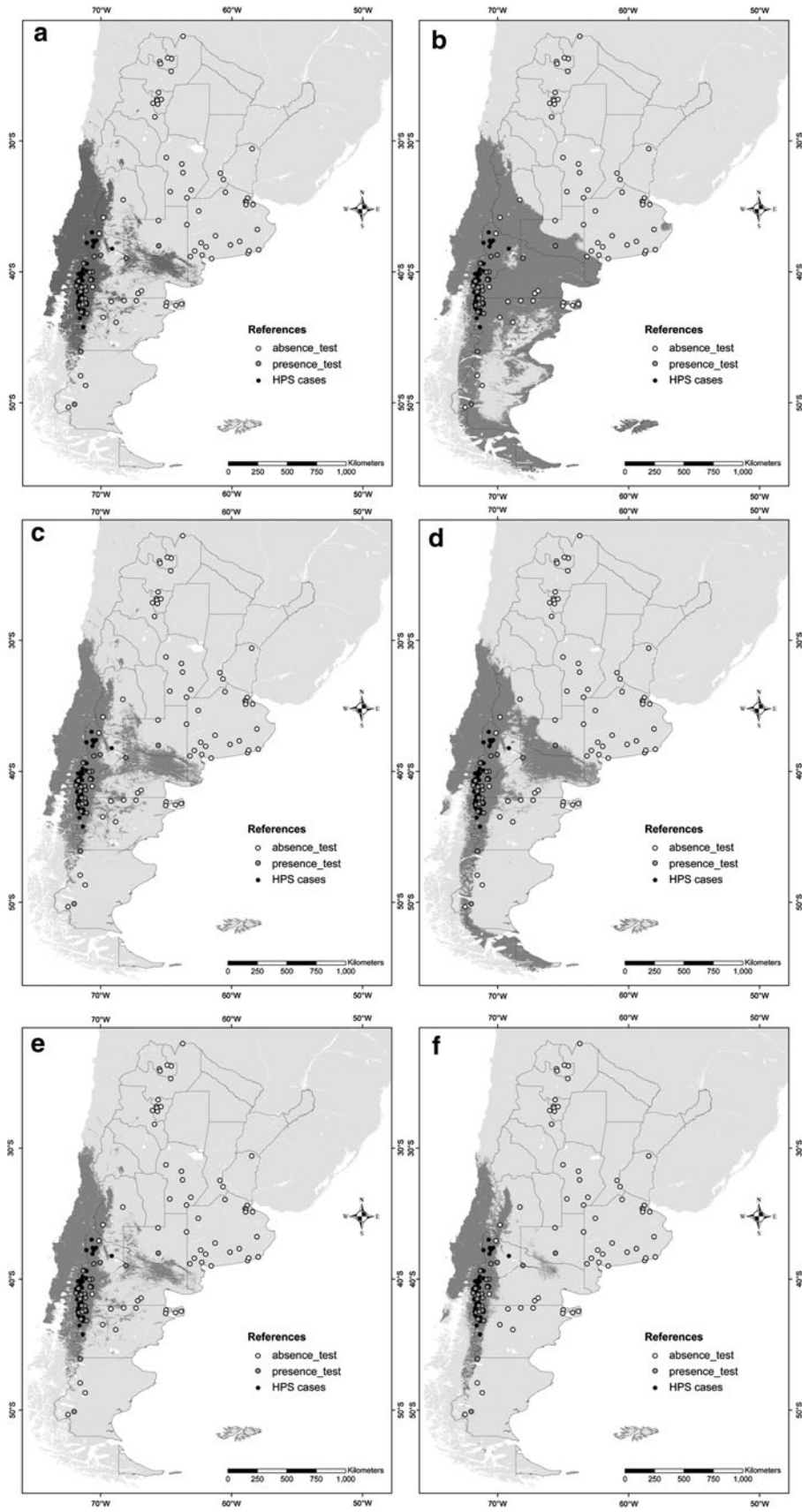
Table 5. Comparison of models performance using different criteria for threshold selection

Threshold selection criteria	Model	Threshold	Overall accuracy	Error rate	Sensitivity	Specificity	False positive rate	False negative rate	Positive predictive value	Negative predictive value
Prevalence	Logistic	0.34	0.91	0.094	0.88	0.92	0.080	0.123	0.85	0.93
	MaxEnt	0.34	0.78	0.221	0.98	0.67	0.330	0.015	0.61	0.99
Sensitivity = Specificity	Logistic	0.30	0.89	0.087	0.90	0.90	0.104	0.107	0.82	0.94
	MaxEnt	0.50	0.91	0.092	0.92	0.92	0.096	0.085	0.83	0.95
Max Sensitivity + Specificity	Logistic	0.36	0.91	0.087	0.87	0.94	0.064	0.131	0.88	0.93
	MaxEnt	0.63	0.91	0.087	0.83	0.96	0.044	0.170	0.91	0.92

DISCUSSION

The distribution of *O. longicaudatus* can be accurately modeled as a function of environmental (land cover) and climatic variables. At a univariate level, there were significant differences between presence and absence sites for most of these variables. In univariate logistic regressions several climatic variables explained between 15 and 42% of models deviance. *O. longicaudatus* should be present in sites with cooler temperatures (Table 3) and drier conditions during the warmest season (i.e., 77 mm for presence sites vs. 194 mm for absence sites). Thus, colilargos tend to occur in cooler, drier locations during the warm season in the region while they are most probably found in sites with high precipitations in the winter rainy season in southwestern Argentina (297 vs. 74 mm for presence and absence sites, respectively). When combined at a multivariate level, the number of significant variables was reduced, but it seems likely that tree and grass cover, mean diurnal temperature range (bio2), mean temperature of the driest season (bio9), and precipitation of the warmest and coldest seasons (bio18 and bio19, respectively) have some effect on the distribution of this hantavirus reservoir. Most of the variables under consideration were positively related to *O. longicaudatus* occurrence probability.

There are potential biases in relying only on published literature as papers rarely report negative information (no captures) and samples are the locations where extensive sampling efforts were done. To some extent we controlled for that by including sites where the same authors did not catch *O. longicaudatus*, but this is not as efficient as designing a sampling strategy that evaluates all the major habitats in an unbiased manner. Obviously, places that were sampled by collectors and the data were not published were not accessible and represent yet another source of bias. We are also aware that there may be some effect of the different sources and methodologies used to build our data base. However, as we are just using presence/absence data (not abundance) and considering the spatial scale of the study, we do not believe those effects could greatly influence our results. Thus, sites with only a single capture are considered to be equally indicative of species presence as sites with substantially more captures, whether this reflects biases in detection or effort. There also may be limitations in using climate data averaged over a 50-year period. However, the rodent sample records were collected from the 1970s through the 2000s—an approximately comparable period.



◀ **Figure 4.** Maps of presence and absence (*dark gray* and *light gray*, respectively) for *O. longicaudatus* built using different thresholds. **a, b** Using prevalence; **c, d** using the cut-off value where sensitivity equals specificity; and **e, f** using the cut-off value where the curve sensitivity plus specificity reaches its maximum for logistic and MaxEnt models, respectively.

These climate data represented the best available information for the entire country (regarding timing and spatial resolution). The extensive time period may hide temporal dynamical changes that might be detected by finer resolution climate information but generating a new nationwide data set would, itself, be subject to further concerns of its accuracy. These climate data were chosen, in part, because of the consistent methods in the construction (Hijmans et al. 2005) and because they have been applied successfully in earlier species distribution modeling studies in Argentina (Jayat et al. 2009; Tognelli et al. 2009; Martin 2010; Torres and Jayat 2010).

The potential distribution maps for *O. longicaudatus* predicted the highest occurrence probabilities along the Andes range, from 32°S and narrowing southwards. They also predicted high probabilities of presence for northwestern and southern La Pampa, southern Buenos Aires and central-northern Río Negro provinces, reaching the Atlantic coast. These high suitability areas corresponded to four phytogeographic regions: Subantarctic forests, Patagonian steppes, Monte and Espinal. The logistic model predicted some other patches of high probability in central Chubut (central plateaus) and a very small patch in western Santa Cruz province, while the MaxEnt model extended the distribution of this hantavirus reservoir almost continuously to Tierra de Fuego (55°S), and predicted moderate to low probabilities in central and eastern Chubut and Santa Cruz provinces.

Although both models performed quite similarly in terms of AUC and threshold-dependent measures, MaxEnt algorithm showed slightly higher values in most cases. We consider that the predictive map generated with MaxEnt algorithm was the best representation of *O. longicaudatus* distribution for a number of reasons: (a) it predicted the range expansion of this species as far as 55°S that was confirmed by Belmar-Lucero et al. (2009) through genetic studies; (b) it correctly predicted very low or null occurrence probabilities northwards 32°S, while logistic model predicted some very high probability patches in this area, (c) it predicted moderate occurrence probabilities in areas where training points density was low, but the colilargo is known to occur (such as the Atlantic coast and central

plateaus), whereas logistic model yielded low presence probability for those areas, and (d) it predicted *O. longicaudatus* presence in western Santa Cruz province whereas the southernmost predicted presence of the logistic model was southern Chubut province. The better performance of MaxEnt over the logistic model was evident in both threshold-dependent and -independent measures and in the resulting predictive map. This may be related to the higher flexibility of MaxEnt algorithm in allowing for nonlinear relationships between response and predictor variables (Phillips et al. 2006). Interestingly, this model also accurately predicted colilargos known distribution in Chile (Palma et al. 2005; Belmar-Lucero et al. 2009), even though we did not include any records for that country.

Our MaxEnt potential distribution map was similar to that presented by other workers (Porcasi et al. 2005; Carbajo and Pardiñas 2007) which may be because many presence points were obtained from their studies (Table 1). However, our predictive map was accurate in not predicting colilargos northward of 32°S where another *Oligoryzomys* species is responsible for the HPS human cases recorded (Gonzalez-Ittig et al. 2002; Rivera et al. 2007).

Both temperature and rainfall variables were good predictors of the rodent occurrence, consistently with previous studies (Porcasi et al. 2005; Carbajo and Pardiñas 2007). However, despite the usefulness of temperature and precipitation for the delimitation of suitable or unsuitable areas for *O. longicaudatus*, higher resolution bioclimatic variables used in the present study ($\sim 1 \text{ km}^2$), aside from being more specific and capturing more environmental variability, may also indicate potentially favorable or limiting conditions for the distribution of the species (both generally and for specific times of the year). In this sense, there were several bioclimatic variables with high predictive power (Table 3) some of which were retained in multivariate models (Table 4). Although climate has traditionally been regarded as a major determinant of species distribution, we found that land cover variables, such as tree and grass cover were also positively related to colilargos occurrence, which is in agreement with previous studies on this species (González et al. 2000; Monjeau et al. 2011). It seems then, that at least at this spatial scale, both biotic (land cover) and abiotic (climate) variables contribute in the explanation of *O. longicaudatus* distribution. These results are also consistent with previous temporal studies on the species suggesting a high sensitivity to climatic factors and fluctuations in resource levels (Murúa et al. 1987, 2003).

Oligoryzomys longicaudatus inhabits subantarctic forests, where woods are abundant, and extends into the steppe along shrublands adjacent to streams and roads (Murúa and Gonzalez 1982; Pearson 1983). Generally, it seems to prefer humid areas with extensive cover (Pearson and Pearson 1982; Pearson 1983) and studies in patagonian provinces (Neuquén, Río Negro, and Chubut) revealed that the highest abundances corresponded to woods and shrublands habitats, and the lowest to the steppe (Cantoni et al. 2001; Larrieu et al. 2003; Piudo et al. 2005, 2011; Polop et al. 2010). Moreover, in a wood-steppe ecotone, captures were associated with shrub cover and spiny shrubs, such as wild rose and blackberry (Lozada et al. 2000). These habitats coincide with the phytogeographic regions where our model predicted presence. In Chile, *O. longicaudatus* is also most abundant in mesic areas of the Temperate and Patagonian Forests in the south. However, this species has expanded northward as far as 28°S in the Mediterranean region where more open and almost xeric areas prevail (Mann 1978). In this latter region this species has colonized and adapted to distinct vegetation types such as scrublands, but seems to be always associated with humid areas (Mann 1978). Within its extended geographical range, the species appears to be adapted to very distinct vegetative types and climatic conditions both in Chile and Argentina, which supports the view that it has an opportunistic and vagile nature (Murúa et al. 1986).

There were few sites in the southwest of Argentina where *O. longicaudatus* was recorded present but models predicted low or moderate occurrence probabilities (in the eastern part of Chubut province against the Atlantic coast, central-western Chubut, and central-southwestern Santa Cruz provinces). This may reflect the low number of presence records for those areas limiting the representation of those environmental conditions in the environmental space evaluated for the species. On the other hand, there were areas predicted as highly suitable for colilargos (such as Mendoza province), but with very few or no presence points to perform a thorough assessment. These areas, however, may also be seen as a great opportunity to test our model predictive ability by performing field surveys there. Both situations require further research to clarify these results and to generate better knowledge of this hantavirus reservoir distribution (and of the virus).

The HPS cases recorded in Patagonia (caused by ANDV) are encompassed in the highest probability of occurrence area. The mean colilargos predicted presence probability for sites with HPS cases was 0.77 for MaxEnt

model and 0.95 for the logistic model. Thus, MaxEnt provides a more conservative tool for risk mapping. This high probability area coincided with the highest ANDV prevalence area (Cantoni et al. 2001; Larrieu et al. 2003; Piudo et al. 2005; Polop et al. 2010). Infected *O. longicaudatus* have been captured along the Andes range in Neuquén, Río Negro, and Chubut provinces in Argentina but there are no records of ANDV eastwards (Cantoni et al. 2001; Piudo et al. 2005). In the Chilean side, infected *O. longicaudatus* have been captured all over its range along the Andes (Belmar-Lucero et al. 2009). The distribution of this reservoir species indicate the maximum potential extent of HPS and in Argentine Patagonia, transmission zones matched the areas with the highest probability of colilargos presence. These findings suggest that presence probability of colilargos may indicate an approximate risk of transmission and that this kind of models could be used as an early tool to guide control and prevention plans.

CONCLUSIONS

The distribution of *O. longicaudatus*, the ANDV reservoir in southern Argentina and Chile, can be understood and modeled as a function of environmental and climatic variables, such as tree and grass cover, mean diurnal temperature range, mean temperature of the driest season, and precipitation of the warmest and coldest seasons. The potential distribution maps predicted high probabilities of occurrence along the Andes range (from 32°S and narrowing southwards) and in south-central areas of Argentina reaching the Atlantic coast. MaxEnt model predictions extended the distribution of this hantavirus reservoir almost continuously to Tierra de Fuego (55°S) and showed slightly higher values of AUC and threshold-dependent measures in most cases. This better performance of MaxEnt over logistic model may be due to the higher flexibility of this algorithm in allowing for nonlinear relationships (Phillips et al. 2006). Since almost all HPS cases recorded in Patagonia were encompassed in the highest probability of occurrence area, we presume that the probability of colilargos presence may indicate an approximate risk of transmission. These potential distribution maps might be used as early tools to guide control and prevention plans. However, a more comprehensive and accurate approach would also include pathogen and human population distribution as well as the other hantavirus host species in the country. The next step would be to more precisely define

risk by determining the relationship of host abundance with prevalence of infection in particular habitats at landscape and local scales. We have an ongoing study focused in northwestern Chubut province aiming at determining those associations. These results will likely collaborate in the comprehension of the relationships between environment, host populations and occurrence of disease cases, providing potentially useful information to establish the risk area for human disease and direct prevention programs.

ACKNOWLEDGMENTS

This research was made possible by grants from the Fondo para la Investigación Científica y Tecnológica (FONCYT) and Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET). This article was written as a result of an internship of V.A. funded by Fulbright and Bunge and Born Foundation at the Johns Hopkins Bloomberg School of Public Health, Baltimore, USA. V.A. thanks Fulbright and Bunge and Born Foundation for the financial assistance and the host institution for great working facilities. We are also grateful to two anonymous reviewers who provided valuable comments and suggestions on an early version of the manuscript.

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