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PREDICTIVE DISTRIBUTION MAPS OF RODENT RESERVOIR SPECIES OF ZONOSES IN SOUTHERN AMERICA

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ABSTRACT: We model potential distribution for three species of rodents known to be reservoirs of zoonotic diseases: *Calomys musculinus*, *Oligoryzomys flavescens* and *O. longicaudatus*. These models provide general distribution hypotheses obtained using environmental data from record localities. Satellite remote sensing is then used to extrapolate climatic and ecological features of potentially suitable habitats for these rodents. In the three species mapped, we found high overall correspondence between predicted (based on environmental data) and specimen based distributions. The maps proposed here provide several advantages over dot and shaded outline maps. First, the predictive maps incorporate geographically explicit predictions of potential distribution into the test. Second, the validity of the predictive map can be appreciated when localities of previous records of the studied species, not used as training sites or used as control sites, are overlaid on the map. In this approach, environmental factors, criteria and analytical techniques are explicit and can be easily verified. Hence, we can temporally fit data in more precise distribution maps.

Key words. Environmental factors. Geographic distribution. Rodent reservoirs.

INTRODUCTION

The distributions of many taxa are poorly known in most of the Neotropics in general and Argentina in particular (e.g., Redford and Eisenberg, 1992). For example, most regions in Argentina have only received cursory and unevenly distributed surveys. However, the geographic distributions of species have a growing number of applications in conservation biology, evolutionary studies, viral disease host and invasive-species management (Mc Arthur, 1972; Ricklefs and Schluter, 1993; Kerr and Ortovsky, 2003).

Museum records constitute the primary documentation in the process of outlining the boundaries of a species. Distribution maps constructed based on these data represent the probable geographic space inhabited by individuals of the same species. Historically, two types of maps based on museum records have been produced: dot maps and shaded outline maps. Dot maps (documented localities plotted on a map) depict a species' range of distribution in a very conservative way, leaving the reader to draw conclusions regarding the true distribution. By contrast, shaded outline maps attempt to extrapolate a species range among and be-

yond known localities. They are highly dependent on subjective knowledge of the group under consideration, on the study region (Jamas and McCulloch, 2002), and on the assumption that a species' spatial distribution is linked to specific habitat requirements. These associations constitute approximations of a species' realized ecologic niche, defined as the conjunction of ecological conditions within which it can maintain populations without immigration (Grinnell, 1917a, b; Mac Arthur, 1972; Peterson et al., 1999; Peterson et al., 2002a, b).

Recent advances in remote sensing of climatic and ecological features via satellite have begun to be used to identify particular environments that are suitable for different species. Techniques that model species' requirements using environmental characteristics of localities of known occurrence represent a great advance in the production of range maps (Walker and Cocks, 1991; Carpenter et al., 1993; Skov, 2000; Peterson, 2001). Plant species composition and vegetation structure are important determinants of habitat quality. Furthermore, the spatial arrangement of different habitat types within heterogeneous landscapes has been shown to be a strong influence on the size and persistence of animal populations. Factors such as terrain slope and elevation, temperature, humidity, soil texture, and vegetation, exert a profound influence over the distribution of many species (Wilcove et al., 1986). Geographic information systems (GIS) use these environmental data from locations of a species' known occurrence to produce a model of its requirements in those environmental dimensions, and then projects them onto geographic space in order to create a map of the species potential distribution based on the modeled environmental parameters (Hay et al., 1996; Engelthaler et al., 1999; Pikula et al., 2002). Predictive distribution maps suggest where the species is likely to be present (Ricklefs and Schluter, 1993). Models used in ecology to predict species abundance have been based on linear relationships among environmental variables (Manel et al. 1999), and assumed to be normally distributed, raising statistical and theoretical concerns (Austin and

Meyers, 1996; Lek et al., 1996). New modeling paradigms (e.g., logistic regressions) account for these shortcomings by accommodating binomial errors and have been successfully used (Osborne and Tigar, 1992; Green et al., 1994; Austin and Meyers, 1996). Anderson et al. (2003) suggest that use of the Genetic Algorithm for Rule selection (GARP), which works with stochastic elements and yields multiple solutions, can be successfully employed in cases where only presence data are available.

Modeling approaches provide a new global framework in epidemiologic studies by accessing new variables which could improve epidemiological modeling for emerging infectious diseases (Linthicum et al., 1987; Croner et al., 1996; Beck et al., 1997; Cheek et al., 1998; Dale et al., 1998; Engelthaler et al., 1999; Beck et al., 2000; Boone et al., 2000; Glass et al., 2000; Anderson et al., 2002; Chaput et al., 2002; Pikula et al., 2002). One of the most basic pieces of information for designing and directing a prevention program for any disease is a more accurate knowledge of the geographic distribution of the reservoir species that defines the potential endemic area of the disease (Mills, 1999; Singleton et al., 1999).

Two rodent-borne diseases have been considered major public health problems in Argentina (Sabattini and Maiztegui, 1970; Sabattini et al., 1977; Maiztegui et al., 1986; Mills et al., 1994; Calderón et al., 1999; Mills, 1999; Enria et al., 2000). Argentine Hemorrhagic Fever (AHF) is a human disease produced by Junín virus. The virus is maintained in nature in the sigmodontine rodent *Calomys musculinus* and is transmitted to humans predominantly through aerosolized particles of contaminated rodent excreta. The disease occurs in a small but expanding area on the central Argentine pampa, representing only a small portion of the total distributional range of the reservoir species.

Calomys musculinus has been captured in disturbed fields of crops and stable habitats (De Villafañe et al., 1977; Kravetz, 1978; Kravetz and Polop, 1983; Mills et al., 1991; Polop and Sabattini, 1993). The mice exhibit

distinct habitat associations within their range, and detailed studies of physical and environmental factors influencing their distribution have been carried out (Crespo et al., 1970; De Villafañe, 1970; Contreras and Rossi, 1980; Kravetz and de Villafañe, 1981; Kravetz and Polop, 1983; Busch et al., 1984; Zuleta et al., 1988; Bilenca, 1993; Polop and Sabattini, 1993).

The other rodent-borne disease is Hantavirus Pulmonary Syndrome (HPS). In Argentina, five genotypes are associated with human disease: Orán (ORN) and Bermejo (BMJ) viruses in northwestern Salta province, Lechiguanas (LEC) and HU 39694 viruses in central Buenos Aires and Santa Fe provinces, and Andes (AND) virus in southwestern Río Negro province (Enría and Levis, 2004). Hantaviruses are maintained in nature in their species-specific rodent hosts and transmitted to humans through aerosolized particles from contaminated excreta. The natural reservoirs are rodents of the genus *Oligoryzomys*: *O. longicaudatus* is the host for ORN and AND; *O. chacoensis* for BMJ, and *O. flavescens* for LEC and HU 39694 (Levis et al., 1997, 1998). These rodent species have been captured in disturbed (cultivated fields and edge areas), as well as grasslands and forests areas (Massoia and Fornes, 1966; Massoia, 1973; Contreras and Berry, 1983; Pearson, 1983; Mills et al., 1991; Redford and Eisenberg, 1992; Polop and Sabattini, 1993; Monjeau et al., 1998; Pardiñas et al., 2000; Pardiñas et al., 2003).

Oryzomys longicaudatus and *O. flavescens* are found predominantly in stable disturbed habitats (pastures, forests, roadsides, and railroad right-of-way) (Kravetz and Polop, 1983; Mills et al., 1991; Andrades-Miranda et al., 2001; Delfraro et al., 2003).

The regional distribution of *C. musculinus*, *O. longicaudatus* and *O. flavescens* is poorly known (Thomas, 1927; Hershkovitz, 1962; Massoia and Fornes, 1966; Olog and Lucero, 1981; Redford and Eisenberg, 1992; Massoia and Pardiñas, 1994; Monjeau et al., 1994, 1997, 1998; Saba et al., 1995; Pardiñas, 1999; Pardiñas et al., 2000; Pardiñas et al., 2003; Pardiñas et al., 2004). Because these species

are known from localities with differing ecological conditions, extrapolation is necessary to estimate the species' distributions. The objective of this study was to develop a predictive ecological distribution map of *C. musculinus*, *O. flavescens* and *O. longicaudatus* using digital databases of potential environmental determinants.

MATERIALS AND METHODS

Appendix 1 shows the localities of field trapping used to define each species' presence sites as "training sites", these localities were obtained from both authors' field data and bibliography. In order to evaluate the potential distributional range of *C. musculinus*, *O. flavescens* and *O. longicaudatus* we used geographic computer databases on spatial distribution of environmental factors including the following data:

1) **Precipitation:** A latitude-longitude rasterized grid of 30-year-monthly mean rainfall (1930-1960) with a spatial resolution of 30 min (Leemans and Cramer, 1991; Cramer and Leemans, 2001). IIASA database, Luxemburg, Austria. Available from <http://www.daac.ornl.gov>

2) **Vegetation Index:** A 1982-1992 time series of Normalized Difference Vegetation Index (NDVI) from meteorological satellite of National Oceanic and Atmosphere Administration/Advanced Very High Resolution Radiometer (NOAA/AVHRR) with a pixel of 8 x 8 km. $NDVI = (Ch2 - Ch1) / (Ch2 + Ch1)$, Ch is the channel of AVHRR sensor. This index represents greenness but does not distinguish between primary, agricultural, or disturbed habitats

3) **The Land Surface Temperature (LST)** of the former temporal series $LST = Ch4 + 3.33(Ch4 - Ch5)$ (Price, 1984).

4) **Digital Elevation Model (DEM):** 1 km x 1 km of spatial resolution data from AVHRR sensor, provided by USGS, 1998. Eros Data Center. Available from <http://edcdaac.usgs.gov/gtopo30/gtopo30.asp>

Environmental data were geo-referenced to a latitude-longitude coordinate system and were re-sampled using nearest neighbor algorithm to adjust the pixels size to 1 km x 1 km. ENVI 3.5 (System Research) was used in all geographic analyses. The resulting raw data have 737 x 1037 pixels and include South America between 13° and 56° S and 33° and 82° W. The analysis includes data derived from monthly averaged satellite images. Temporal series covered the period 1982-1992. Eastman and Fulk (1993) suggest the use of standardized princi-

pal component analysis (PCA), because it decomposes the time-series into a sequence of spatial and temporal components that may often be interpreted as corresponding to particular environmental features or events. Typically the first component indicates the characteristic value of the variable, whereas subsequent components represent change elements of decreasing magnitude. In PCA, spatial variation is registered by the first component, and the temporal variation of this vegetation index is represented by the second and third components. Due to the different units of measures for the variables under consideration herein, a standardization of each new variable (i.e. the components obtained from PCA) and DEM product was done before integrating them into an image composed of seven bands, and analyses carried out afterwards. We used a PCA of a NDVI time series of South America obtained by Gorla (2002). Here, the first two components of each environmental variable accounted for more than 99% of the total variance of each series. Thus, both first and second components of each environmental variable and DEM were used in classification analysis. We elaborated a multi-dimensional map in which each geographic area was characterized by this set of seven variables (first and second component of NDVI, precipitation and LST, and DEM) and where "training sites" or "classes" represent the environmental conditions for the presence or absence of *C. musculus*, *O. flavescens*, and *O. longicaudatus*.

Minimum size of training sites (number of pixels) required for classification analysis increase directly with the number of variables included. Thus, presence sites (**Appendix 1, 2, 3**) were composed of the pixel with the exact geographical coordinates of field sampling sites and its closest eight neighbor pixels (we assume similar values in those pixels due to the fact that they are environmental variables).

Field absent sites were not homogeneously distributed over a wide area. To characterize all geographic regions involved in the "absence" class (which is the largest area in all species at the considered scale), we decided to add to that absence localities, random points over South America (excluding the area where presence of each species was confirmed). As the field absence points represent a low proportion of total absence training sites, and random points need to be confirmed as true absence, we could name it "pseudo absence class" as is suggested by Anderson et al. (2003).

Mean and dispersion of environmental variables characterized presence and absence sites. The multivariate distribution function of presence and absence sites should be different enough to enable us to unambiguously identify between the classes (pres-

ence and absence) that are analyzed to characterize the habitat of each species. To verify this point, Divergence Transformed (Chuvieco, 1996) and Jeffries-Matusita (Matusita, 1966) tests were performed between presence-absence class pairs.

After the suitability test of each site was defined, we selected the number of variables and performed Maximum Likelihood algorithm for classification. The method considered the likelihood distribution function of each class defined and also the covariance among different variables intervening in the analysis. The probability of each pixel belonging to a certain class is calculated, and then the pixel is assigned to those with major likelihood. It was also possible to choose the threshold for the inclusion of a pixel in each class based on its probability function. Values of threshold closer to 1 indicated strict inclusion of pixels whose values were closer to the means of training sites; while when threshold values tended to 0, the inclusion of pixels took into account major dispersion of the values.

The accuracy of the thematic map obtained (presence-absence map) was evaluated with other presence control points (**Appendix 1, 2, 3**) that were taken at random among all localities available and that were not used to characterize training sites. A confusion matrix that shows discrepancies between "real data" with those derived from classification was made; throughout the matrix, commission errors (false positives), omission errors (false negatives), as well as an overall accuracy (the percentage of correctly classified over all map) could be calculated (Congalton, 1991; Chuvieco, 1996). Due to the asymmetry in the input data (because of "pseudo-absence class"), commission error includes true commission (overprediction) and apparent commission errors (correctly predicted areas not verifiable as such, primarily because of the lack of adequate sampling). The interpretation of these measures needs to be done carefully (Anderson et al., 2003).

Due to the wide distribution of the rodent species (particularly *C. musculus* and *O. flavescens*, which cover diverse biogeographic regions) classifications were performed with a strict inclusion threshold (between 0.9 and 0.99) to limit the resulting presence area to very similar "training site" values. Cabrera's phytogeographic regions (Cabrera, 1976) were used in this work.

RESULTS

The PCA analysis performed in NDVI, LST and rainfall time series are summarized in **Table 1**; 99.70% of the variance in rainfall,

99.72 % in NDVI, and 99.97 % in LST was explained by first principal component.

The Jeffries-Matusita test among all pairs of training sites is shown in **Table 2**. Values greater than 1.9 indicate good differentiation among classes. A good definition was observed between *O. longicaudatus* and *C. musculus* (1.99), and *O. longicaudatus* and *O. flavescens* (1.99), but only a small one between *C. musculus* and *O. flavescens* (1.52). *Calomys musculus* and *O. longicaudatus* presence training sites had the highest value. These classes could be used together if, for example, the possibility of competitive exclusion between these species is considered.

We generated potential distribution maps using the method of Maximum Likelihood for *C. musculus* (**Fig. 1**); *O. flavescens* (**Fig. 2**) and *O. longicaudatus* (**Fig. 3**). In Argentina, a widespread distribution of *C. musculus* was observed (**Fig. 1**). The estimated area of presence covered from northern Formosa province (25° 30' S) and north-central Salta and Jujuy provinces, to 45° S latitude south of Deseado river in Santa Cruz province. In north and northwest Argentina, *C. musculus* is predicted in high and contiguous patches. In combina-

tion, the predicted distribution encompassed several phytogeographic units, included in two major Domains: the Chacoan Domain and the Andean-Patagonic Domain. The predicted *C. musculus* distribution also includes Uruguay, western Bolivia and Peru, and several sites in Paraguay.

In *C. musculus*, the confusion matrix with 11 control points was accurate overall (score 90.13). Only one control point was unclassified and 7% of pseudo-absence classes were classified as presence (likely over-prediction). Threshold for pixel inclusion in presence class was 0.95.

O. flavescens had a higher number of presence sites to characterize the habitat but was also the widest distributed. It covered from 22°4' S in the north to 40° 30' in the south. *Oligoryzomys flavescens*' distribution extended to the north of Santa Cruz province on the Atlantic coast. It included Chaco, El Espinal and Pampean phytogeographic provinces; El Monte in the Chacoan Domain, and only a small band of Patagonic province in the Andean-Patagonic Domain. The estimated area also included Uruguay, and southern Paraguay and Brazil.

Table 1

Percentage of variability explained in environmental variables for PCA components

	Total variability (%)				
	PC 1	PC 2	PC 3	PC 4	PC 5
Rainfall	99.702	0.213	0.029	0.025	0.009
NDVI	99.719	0.106	0.070	0.022	0.015
LST	99.970	0.020	0.002	0.001	0.001

Table 2

Pair Separation (least to most) by Jeffries-Matusita test for 7 variables

Pair	
Absence south and absence center	0.31402102
Presence <i>O. flavescens</i> and presence <i>C. musculus</i>	1.52877895
Absence center and presence <i>O. flavescens</i>	1.97692013
Absence south and presence <i>O. longicaudatus</i>	1.97913876
Absence south and presence <i>C. musculus</i>	1.98041215
Presence <i>O. flavescens</i> and presence <i>O. longicaudatus</i>	1.99841922
Absence center and presence <i>C. musculus</i>	1.99888092
Presence <i>C. musculus</i> and presence <i>O. longicaudatus</i>	1.99892012

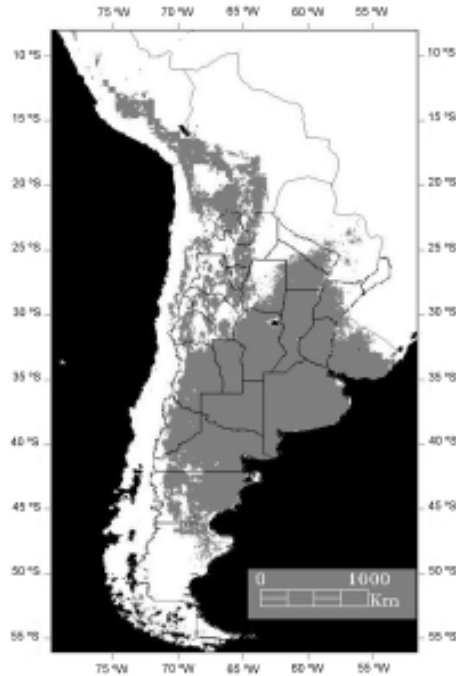


Fig. 1. Estimated geographic distributions for *Calomys musculus* in Southern America. Areas predicted by model appear in gray.

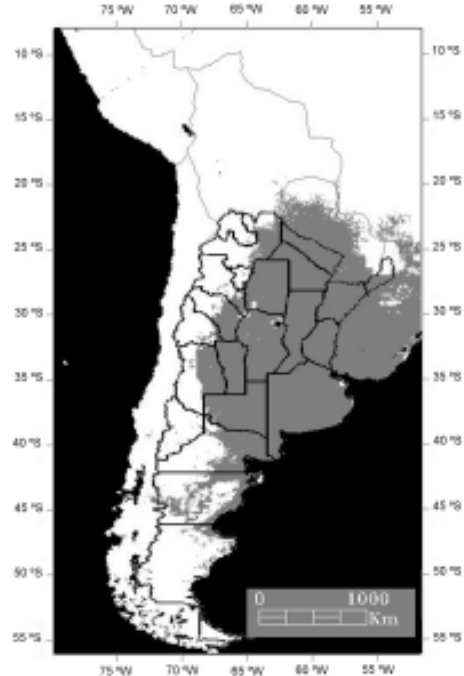


Fig. 2. Estimated geographic distributions for *Oligoryzomys flavescens* in Southern America. Areas predicted by model appear in gray.

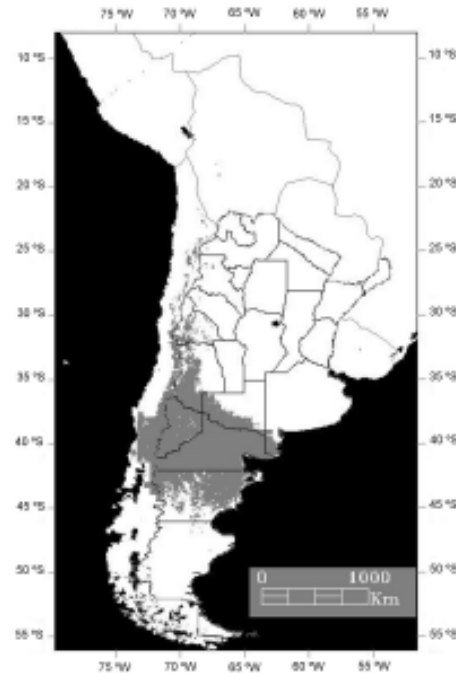


Fig. 3. Estimated geographic distributions for *Oligoryzomys longicaudatus* in Southern America. Areas predicted by model appear in gray.

A strict limit of similarity among the pixels analyzed was used (Threshold=0.99), resulting in a 95% overall classification accuracy. Most errors observed were commission errors (3.5% of pseudo-absence class classified as presence).

In *O. longicaudatus* the map predicted a more restricted distribution than in the former species. The distribution occurred in the east Andean zone of the Patagonic forest, from San Juan (30°) to the center of Chubut (44°) provinces, and it extended to the Atlantic Ocean in Río Negro and Chubut provinces. The map did not predict the presence of *O. longicaudatus* in the north of Argentina (Salta and Jujuy). The *O. longicaudatus* distributions include a portion of the Patagonic province in the

Andean-Patagonic Domain, and a portion of El Monte region in de Chacoan Domain.

In *O. longicaudatus*, few points of control were taken because of the low number of presence sites. In Chile, the potential distribution registered was between 33° and 44° S, and was extended in discontinued form to 22° at North. The overall accuracy was 95.9 % with Argentinean control points correctly classified but one assigned to pseudo absence class in Chile but only 2% incorrectly in pseudo absence class. The threshold used for the classification was 0.95.

DISCUSSION

This work was based on a combination of field data of species occurrence and environmental data collected by satellite remote sensing. The model is based on the species' fundamental niche with factors controlling distributions (Grinnell, 1917a, b; MacArthur, 1972). In the Grinnell (1917b) and MacArthur (1972) multidimensional ecological/environmental space concept, the ecological niche of a species can be defined as the intersection of ecological conditions within which it can maintain populations without immigration. This is a habitat or distribution concept. The approach we used herein for mapping rodent distributions cannot identify the variables that best predict areas of apparent suitability. However, the distribution maps do show large areas of suitable habitats for the species with the variables used. Previous works (Crespo, 1966; Crespo et al., 1970; Bonaventura and Kravetz, 1989; Paterson et al., 1990; Kelt, 1996; Monjeau et al., 1997; Castellarini and Polop, 2002; Castellarini et al., 2002; Pardiñas et al., 2003) suggested that rainfall, temperature, and vegetation are important ecological variables for the distribution of Argentinean rodents. Accurate knowledge of these variables in relation to the distribution and abundance of the rodents is imperative for a better mapping of the species in the future. A better understanding of these ecological factors might enhance our ability to predict how the distribution of rodent species might be affected in the light of the current environmental changes in the region.

Several factors require these distribution maps to be interpreted with caution. First, the original resolution of climatic and vegetation data is quite coarse. Even though we carefully chose the pixels adjacent to presence data (excluding pixels with water or great changes in the digital numbers values compared with its neighbor) to increase the Training site size, this procedure could produce some biases on the resulting map. On a fine scale at sub-regional or local level the situation will be different. The density of the required information is high and remote sensing based on mapping approaches has to include additional knowledge from field investigations, ecological information and a new generation of high-resolution sensors.

We give the overall performance of classifications even knowing they do not provide an effective means for identifying the best model (Anderson et al., 2003). We prefer to point out the correct classification of control points and small commission errors, suggesting little over-prediction of presence data. It could give an idea of the accuracy of the classification. Furthermore, if populations in other parts of the species range occupy environmental conditions outside those typified by the present sample, the exclusion of records from those distributional areas may have led to an underestimation of the species' niche in the examined environmental dimensions (Anderson, 2003). Moreover, only moderate numbers of places for species occurrence were used as training sites. Given these limitations, we compared the predictive maps with data from literature for species occurrence that were not used as training sites in our study. Despite these caveats and possible sources of error, the predictive maps yielded a realistic prediction of the species' potential distribution. In the *C. musculus*, *O. flavescens* and *O. longicaudatus* maps, the high overall accuracy (90.1, 95.0 and 97.4 respectively) indicated high predictive values.

Olrog and Lucero (1981) indicated the Colorado river was the southern distributional edge of *C. musculus*, and Redford and Eisenberg (1992) cited the southern limit of the species

as near the Negro river in Río Negro province. However, Thomas (1927) and Hershkovitz (1962) had already recorded the species in Patagonia. Saba et al. (1995) registered *C. musculus* in Puerto Madryn sandbank, and Massoia and Pardiñas (1994) extended the distribution to the southwest of Santa Cruz Province. Moreover, Pardiñas et al. (2003) registered 14 occurrence sites of *Calomys* sp. from raptor pellet material in Patagonia not used as training sites in our study. These authors listed the specimens as *Calomys* sp., but suggested referring them to *C. musculus* in accordance with Puerto Madryn specimens collected previously (Salazar-Bravo et al., 2001). Our *C. musculus* distribution map (Fig. 1) predicted these occurrences, and its presence in sites such as Punta Delgada in Península Valdez (42°46'13"S; 63°38'25"W) where it was recently registered by Pardiñas et al. (2003). Our predictive map extended the *C. musculus* distribution edge further than the Negro river, inhabiting extremely heterogeneous and complex geographical areas.

In northern Argentina Thomas (1913) and Cabrera (1961) registered *C. musculus* in Jujuy, Salta and Catamarca, and Olog and Lucero (1981) considered the species present in Salta and Jujuy, and in all Formosa province. But, Mares et al. (1981, 1989), and Ojeda and Mares (1989) did not register the species in Salta and Jujuy Provinces, and Pardiñas and Teta (in press) did not register *C. musculus* presence in Formosa province. Our study predicted its presence only in some parts of Formosa, Salta and Jujuy Provinces. On the other hand, our map predicted *C. musculus* in Tucumán province, not used as a training site in our study, where the species has been captured by Barquez et al. (1991). Moreover, the estimated area of our map also includes Uruguay, and western Bolivia and Peru, where *C. musculus* has not been recorded. Uruguay has similar environmental condition as the pampean region in Argentina. Thus, the absence of this species in Uruguay may be related to historical and ecological factors that are not taken into account in our approach. The predicted presence of *C. musculus* in

Paraguay is corroborated by William et al. (1997), who captured eight specimens in Toledo, Loma Plata and Monte Palma localities. Moreover, the Bolivia presence is corroborated by *C. musculus* specimens captured in Tarija (Salazar-Bravo et al., 2001). Its presence needs to be confirmed in Peru .

Our results predict the presence of *O. flavescens* from -23° to -47° latitude, to the east of the 67° W meridian, extending the southern edge as a thin border on the Atlantic Ocean coast up to the north of Santa Cruz province. The distribution of *O. flavescens* encompasses large variation in climate, soil, and vegetation variability. *Oligoryzomys flavescens*' predictive distribution map agreed with occurrence sites not used as training sites in our study (Thomas, 1927; Hershkovitz, 1962; Saba et al., 1995; Monjeau et al., 1997; Pardiñas et al., 2003). The distribution map also predicts *O. flavescens* in the Chacoan region, including Formosa province and east of Salta province, but Pardiñas and Teta (in press), and Mares et al. (1989) did not register the species in these provinces.

The estimated distribution of *O. flavescens* also included Uruguay and southern Brazil, where the presence of this rodent was mentioned by Andrades-Miranda et al. (2001), Becker and Vieira (2002), and Marinho et al. (2002), and the South of Paraguay, where its presence needs to be confirmed. Delfraro et al. (2003) showed that *O. flavescens* captures in the southern areas of Uruguay could be the host for a pathogenic hantavirus called Central Plata.

Even though the potential distributions of *O. flavescens* and *C. musculus* greatly overlapped, the areas of high support for the respective predicted distributions was not the same (Figs. 1 and 2). The distribution of these species does not fit the distribution of phytogeographic units. This is likely due to the great plasticity in the distributional behavior of these species, as they appear to be greatly influenced by anthropogenic modifications (Pardiñas, 1999; Pardiñas et al., 2000; Pardiñas et al., 2004). The high training site numbers that characterized these species habitats could di-

minish the classification accuracy because of the high training site variability.

Previous studies (Olrog and Lucero, 1981; Redford and Eisenberg, 1992) have recognized *O. longicaudatus* along an extensive geographical range in the west of Argentina from Salta in the north to Santa Cruz and Tierra del Fuego in the south. Pearson (1983), Carleton and Musser (1989), and Monjeau et al. (1998) considered *O. longicaudatus* as ranging in the west, from southern Mendoza (32° S) to northern Santa Cruz (48° S) provinces, associated with *Nothofagus* forests as well as the ecotone between these forests and the Patagonian steppe. Recently, populations from southern Argentina and Chile have been considered as *O. longicaudatus* (Galliari et al., 1996). All *O. longicaudatus* sites cited by Pardiñas et al. (2003) and Monjeau et al. (1997) have been predicted by our distribution map. Out of 28 occurrence sites listed by Palma et al. (2005), only the north Pacific coast (La Silla, Fray Jorge, Quebrada del Tigre and San Antonio) are not included in our map (Fig. 3). Tiranti (1988) also reported *O. longicaudatus* from owl pellets in Curacó and Lihuel Calel departments (La Pampa province) near the north edge of our distribution map. On the other hand, Monjeau et al. (1997) did not register *O. longicaudatus* specimens in nine study sites in Patagonia steppe: our map predicted the presence in two of these sites: 15 km at Mencué northeast (Río Negro province) (40° 21' S; 69° 31' W), and 100 km at Dolavon west (Chubut) (43° 17' S; 67° 04' W).

The Orán Hantavirus strain was isolated from putative *O. longicaudatus* in northern Argentina. However, a number of authors suggested that this *Oligoryzomys* belongs to a distinct species (Capllonch et al., 1997; Díaz, 1997; Levis et al., 1998; Massoia, 1998; Calderón et al., 1999; Enria et al., 2000; Ortiz and Pardiñas, 2001). Phylogenetic studies supported by analysis of restriction sites of mitochondrial DNA (Gonzalez Ittig et al., 2002) and partial sequences of cytochrome b (Myers et al., 1995) concluded that specimens from northern Argentina showed differences from those in Patagonia, a conclusion also reached by Palma

et al. (2005). Espinosa and Reig (1991) distinguished between karyotyped specimens of Tucumán Province from *O. longicaudatus* of Chile and south of Argentina. Specimens from Bolivia ascribed as *O. longicaudatus* were then identified as *O. andinus*, *O. destructor* or as undetermined species of the “*flavescens* complex” (Carleton and Musser, 1989).

The absence of potential habitats beyond 48°S registered in our map agrees with Gallardo and Palma (1990) and Steppan (1995), who suggested separation between *O. longicaudatus* (38° S to 48° S) and *O. magellanicus* (48° to Tierra del Fuego). However, Palma et al. (2005) refers *O. magellanicus* to synonymy with *O. longicaudatus*, thus enlarging the range of this species at least as far as latitude 51°S in both Argentina and Chile. These authors concluded that the phylogenetic relationship of *O. longicaudatus* in Chile and nearby areas in Argentina confirms the existence of a single species, suggesting strong gene flow among populations that would account for the genetic uniformity of population along their range of distribution.

Our predictive maps showed large areas of apparent suitability in which none of the rodent species was recorded, either due to them not actually occurring there or in which no information is yet available on these areas. This is a feature of many prediction maps in which species do not always occupy habitats that are suitable for them or are not always found even when they do occur (Rogers et al., 1996). Moreover, the use of different trapping methods by different collectors and time of collection may determine the absence or presence of a species in a given area (Gebre-Michael et al., 2004).

However, the maps proposed here afford several advantages. Clearly, objective modeling of a species' geographic distribution is an important improvement over subjective, broad-stroke shaded outline maps. First, the predictive maps incorporate geographically explicit predictions of potential distribution into the test. In addition, although fine-resolution base environmental data are always desirable, the development of modeling techniques that provide

general distributional hypotheses using the relatively coarse environmental data currently available is important (Anderson and Martinez-Meyer, 2004). Second, the validity of the predictive map can be appreciated when localities of previous records of the studied species, not used as training sites or used as control sites, overlay in the map. In this approach, environmental factors, criteria and analytical techniques are explicit and can be easily verified. Hence, we can temporally fit data in more precise distribution maps.

Future research should continue to evaluate these approaches with other *C. musculus*, *O. flavescens* and *O. longicaudatus* occurrence records, as well as with other species and their necessary environmental related data requirements.

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APPENDIX 1

Presence and control sites of *Oligoryzomys flavescens* expressed as Latitude and Longitude in centesimal degrees.

PRESENCE SITES

Locality	Province/Country	Latitude	Longitude
Abasto	Buenos Aires	-34.98	-58.10
Alcira Gigena	Córdoba	-32.77	-64.35
Alcorta	Santa Fe	-33.51	-61.67
Aparados da Serra	Brasil	-29.17	-50.09
Bartolomé Bavio	Buenos Aires	-35.08	-57.90
Belén de Escobar	Buenos Aires	-34.37	-58.80
Bengolea	Córdoba	-33.03	-66.67
Berisso	Buenos Aires	-33.23	-59.20
Berna	Santa Fe	-29.27	-59.86
Campo de Mayo	Buenos Aires	-34.55	-58.70
Castelli	Buenos Aires	-36.10	-57.80
Chascomus	Buenos Aires	-35.57	-58.02
Chillar	Buenos Aires	-37.30	-59.98
Chucul	Córdoba	-33.02	-64.16
City Bell	Buenos Aires	-34.87	-58.05
Coronel Vidal	Buenos Aires	-37.45	-57.73
Cruz del Eje	Córdoba	-30.73	-64.82
Dolores	Buenos Aires	-36.32	-57.07
Dudignac	Buenos Aires	-35.65	-60.70
El Rastreador	Buenos Aires	-33.68	-63.53
Ensenada	Buenos Aires	-34.87	-57.90
Fighiera	Santa Fe	-33.22	-60.47
Garin	Buenos Aires	-34.42	-58.73
General Belgrano	Buenos Aires	-36.77	-58.05
Isla Lechiguana	Buenos Aires	-33.48	-60.02
Ingeniero Maschwitz	Buenos Aires	-34.38	-58.73
Santa Catarina	Brasil	-36.77	-58.50
Lisandro Olmos	Buenos Aires	-35.00	-58.03
La Balandra	Buenos Aires	-34.81	-58.03
La Plata	Buenos Aires	-34.96	-57.93
La Plata	Buenos Aires	-34.92	-57.95
Laguna Larga	Córdoba	-31.77	-63.82
Longchamps	Buenos Aires	-34.87	-58.38
Los Conquistadores	Entre Ríos	-30.60	-58.45
Los Hornos	Buenos Aires	-34.88	-58.92
Los Pozos	Córdoba	-30.19	-64.09
Maciel	Santa Fe	-32.47	-60.88
Mar Chiquita	Buenos Aires	-37.66	-57.28
Máximo paz	Santa Fe	-33.53	-60.90
Melo	Córdoba	-34.35	-63.43
Nono	Córdoba	-31.28	-65.00
Oliveros	Santa Fe	-32.60	-60.86
Orán	Salta	-23.13	-64.33
Pampa de Achala	Córdoba	-31.63	-64.83
Pampa de San Luis	Córdoba	-31.33	-64.76
Punta Valdes	Uruguay	-33.40	-50.00
Quintao	Brasil	-30.33	-50.27
Ranelagh	Buenos Aires	-34.29	-58.17
Río Segundo	Córdoba	-31.63	-63.93
Río Tercero	Córdoba	-32.18	-64.10
Río Oro	Chaco	-26.81	-58.96
Rosario	Santa Fe	-32.95	-60.65

Rota do Sol	Brasil	-29.37	-50.18
Rota do Sol	Brasil	-29.32	-50.20
Rota do Sol	Brasil	-29.50	-50.10
San Nicolás	Buenos Aires	-33.35	-60.15
San Vicente	Buenos Aires	-35.02	-58.42
San Miguel del Monte	Buenos Aires	-35.42	-58.82
Tainhas	Brasil	-29.27	-50.30
Uranga	Santa Fe	-33.28	-60.68
Villa de las Rosas	Córdoba	-31.33	-65.02
Villa Cacique	Buenos Aires	-37.66	-59.28
Villa Dolores	Córdoba	-31.95	-65.20
Villa Paranacito	Entre Ríos	-33.72	-58.67
Yacanto	Córdoba	-32.02	-64.27
Zárate	Buenos Aires	-34.03	-59.01

CONTROL SITES

Locality	Province/Country	Latitude	Longitude
Balcarce	Buenos Aires	-37.87	-58.25
Chanqueadas	Brasil	-29.95	-51.52
Cosquín	Córdoba	-31.23	-64.45
Florencio Varela	Buenos Aires	-34.82	-58.28
Juan B. Molina	Santa Fe	-33.48	-60.50
Las Flores	Buenos Aires	-36.02	-59.10
Magdalena	Buenos Aires	-36.10	-57.52
Nonoaí	Brasil	-27.42	-53.07
Pergamino	Buenos Aires	-33.93	-60.49
Rojas	Buenos Aires	-34.20	-60.73
San Pedro	Buenos Aires	-33.48	-59.68
Villa de María	Córdoba	-29.90	-63.73

APPENDIX 2

Presence and control sites of *Calomys musculus*, expressed as Latitude and Longitude in centesimal degrees.

PRESENCE SITES

Locality	Province/Country	Latitude	Longitude
Abasto	Buenos Aires	-34.98	-58.10
Alcorta	Santa Fe	-33.51	-61.67
Bartolomé Bavio	Buenos Aires	-35.08	-57.90
Belén de Escobar	Buenos Aires	-34.37	-58.80
Bengolea	Córdoba	-33.03	-66.67
Castelli	Buenos Aires	-36.10	-57.80
Chascomus	Buenos Aires	-35.57	-58.02
Chillar	Buenos Aires	-37.30	-59.98
Chucul	Córdoba	-33.02	-64.16
City Bell	Buenos Aires	-34.87	-58.05
Cosquín	Córdoba	-31.23	-64.45
Cruz del Eje	Córdoba	-30.73	-64.82
Dolores	Buenos Aires	-36.32	-57.67
Dudignac	Buenos Aires	-35.65	-60.70
El Rastreador	Córdoba	-33.68	-63.53
Fighiera	Santa Fe	-33.22	-60.47

Gigena	Córdoba	-32.76	-64.35
General Belgrano	Buenos Aires	-36.76	-58.50
Hernando	Córdoba	-32.43	-63.73
Juan B. Molina	Santa Fe	-33.48	-60.50
La Plata	Buenos Aires	-34.91	-57.95
Laguna Larga	Buenos Aires	-31.77	-63.82
Los Conquistadores	Entre Ríos	-30.60	-58.45
Los Hornos	Buenos Aires	-34.88	-58.91
Los Toldos	Buenos Aires	-35.00	-61.03
Marcos Juárez	Córdoba	-32.68	-66.03
Máximo paz	Santa Fe	-33.53	-60.90
Melo	Córdoba	-34.35	-63.43
Olavarría	Buenos Aires	-36.88	-60.03
Oliveros	Santa Fe	-32.60	-60.86
Pergamino	Buenos Aires	-33.93	-60.49
Puerto Madryn	Chubut	-42.77	-65.03
Ranchos	Buenos Aires	-35.52	-58.03
Rastreador	Córdoba	-33.68	-63.53
Río Tercero	Córdoba	-32.18	-64.10
Roque Perez	Buenos Aires	-35.34	-59.33
San Miguel Monte	Buenos Aires	-35.35	-58.82
San Nicolás	Buenos Aires	-33.35	-60.15
San Pedro	Buenos Aires	-33.48	-59.68
San Vicente	Buenos Aires	-31.02	-58.35
Uranga	Santa Fe	-33.28	-60.68
Villa Constitución	Santa Fe	-35.93	-66.18
Viamonte	Córdoba	-33.75	-63.10
Villa de María	Córdoba	-29.90	-63.73
Villa Dolores	Córdoba	-31.95	-65.20

CONTROL SITES

Locality	Province/Country	Latitude	Longitude
Berisso	Buenos Aires	-33.23	-59.20
Coronel Vidal	Buenos Aires	-37.45	-57.73
Florencio Varela	Buenos Aires	-34.82	-58.28
Lisandro Olmos	Buenos Aires	-35.00	-58.03
Maciel	Santa Fe	-32.47	-60.88
Pampa Achal	Córdoba	-31.63	-64.83
Rojas	Buenos Aires	-34.20	-60.73
Tandil	Buenos Aires	-37.31	-59.13
Zárate	Buenos Aires	-34.03	-59.01
Maimara	Jujuy	-23.622	-65.41
San S. de Jujuy	Jujuy	-24.196	-65.294

APPENDIX 3

Presence and control sites of *Oligoryzomys longicaudatus* expressed as Latitude and Longitude in centesimal degrees.

PRESENCE SITES

Locality	Province/Country	Latitude	Longitude
Bariloche	Río Negro	-41.13	-71.45
Cholila	Chubut	-42.51	-71.46
El Bolsón	Río Negro	-41.97	-71.52
El Cóndor	Río Negro	-41.06	-71.07
El Hoyo	Chubut	-42.03	-71.44
El Huecu	Neuquén	-37.60	-70.60
Epuyen	Chubut	-42.23	-71.37
Estancia María Sofía	Río Negro	-40.22	-70.05
Junin de los Andes	Neuquén	-39.27	-71.83
Lago Futalaufquen	Chubut	-42.32	-71.22
Lago Puelo	Chubut	-42.02	-71.05
Nahuel pan	Chubut	-41.00	-71.05
Neltume	Chile	-39.22	-72.23
Neuquén	Neuquén	-38.96	-68.06
Paillaco	Chile	-40.08	-72.91
Parque Los Alerces	Chubut	-42.87	-71.77
Rinquilon	Neuquén	-38.35	-70.60
Valdivia	Chile	-30.63	-70.58
Paraje Contra	Neuquén	-39.78	-71.37
Las Coloradas	Neuquén	-39.55	-70.92
Esquel	Chubut	-42.90	-71.32
Hilario Ascasubi	Buenos Aires	-39,375	-62,652

CONTROL SITES

Locality	Province/Country	Latitude	Longitude
El Prado	Chile	-35.63	-71.88
Lago Rivadavia	Chubut	-42.05	-71.05
Puerto Blest	Chubut	-41.01	-71.29
Villa la Angostura	Neuquén	-40.75	-71.58
Chos Malal	Neuquén	-37.32	-70.17