Predicting the Potential Geographical Distribution of *Rhodnius neglectus* (Hemiptera, Reduviidae) Based on Ecological Niche Modeling

RODRIGO GURGEL-GONÇALVES¹,²,³ AND CÉSAR AUGUSTO CUBA CUBA¹


ABSTRACT  *Rhodnius neglectus* is frequently found in palm trees and bird nests in sylvatic environments. However, adult specimens infected by *Trypanosoma cruzi* have been invading houses in central Brazil. Analyzing and predicting the geographical distribution of this species may improve vector surveillance strategies for Chagas disease. Ecological niche modeling using the genetic algorithm for rule-set production (GARP) was applied to predict the geographical distribution of *R. neglectus* from occurrence records and a set of 23 predictor variables (e.g., temperature, precipitation, altitude, and vegetation). Additionally, the geographical distribution of *R. neglectus* was compared with the geographical distribution of four species of palm trees and two species of birds from the study region. The models were able to predict, with high probability, the occurrence of *R. neglectus* as a regular (although nonendemic) species of the Cerrado biome in central Brazil. Caatinga, Amazonian savanna, Pantanal, and the Bolivian Chaco appear as areas with lower probabilities of potential occurrence for the species. A great overlap was observed between the distribution of *R. neglectus*, palm trees (*Acrcomia aculeata* and *Syagrus oleracea*), and birds (*Phacellodomus ruber* and *Pseudoseisura cristata*). By including new records for *R. neglectus* (from both sylvatic and domestic environments), our study showed a distribution increase toward the west and northeast areas of Brazil in the “diagonal of open/dry ecoregions of South America”. These results should aid Chagas disease vector surveillance programs, given that household invasion by *Rhodnius* species maintains the risk of disease transmission and limits control strategies.

KEY WORDS  *Rhodnius neglectus*, genetic algorithm for rule-set production, geographical distribution, Cerrado, Caatinga

*Rhodnius neglectus* (Lent) (Hemiptera, Reduviidae, Triatominae) inhabits various types of palm trees in Brazil, including *Attalea, Acrcomia, Mauritia, Oenocarpus*, and *Syagrus* (Barretto et al. 1969, Diotaiuti and Dias 1984, Carcavallo et al. 1998, Gurgel-Gonçalves et al. 2004a, Abad-Franch et al. 2009); the species is also found in bird nests (Furnariidae) (Barretto and Carvalheiro 1968) and in mammal refugia such as *Didelphis* and plays an important role in the maintenance of *Trypanosoma cruzi* transmission in the wild (Gurgel-Gonçalves et al. 2004b). However, adult specimens have been invading houses in central Brazil (Gurgel-Gonçalves et al. 2008). Household infestation (with adventitious bugs occasionally establishing breeding colonies) has been reported in the Brazilian states of Goiás, Minas Gerais, and São Paulo (Silveira et al. 1984, Silva et al. 2003). *R. neglectus* is currently the second most common triatomine species infesting artificial environments in the state of Goiás, and >4,500 *R. neglectus* specimens (~1% infected with *T. cruzi*) were collected over 2 yr (Oliveira and Silva 2007), maintaining the risk of Chagas disease transmission in central Brazil.

The geographical distribution of *R. neglectus* including four Brazilian states (Goiás, Minas Gerais, São Paulo, and Mato Grosso) was described by Lent and Wygodzinsky (1979). Using the domestic infestation data obtained from the Brazilian Chagas Disease Control Program between 1975 and 1983, Silveira et al. (1984) had listed 12 states where *R. neglectus* was found, although only 8 states were cited by Galvão et al. (2003). According to the distribution map of triatomines of the genus *Rhodnius* (Carcavallo et al. 1999), *R. neglectus* is the most widespread species in Brazil, occurring from sea level to >1,000 m in altitude and ranging from 3° to 25° south latitude. However, such distribution may present problems because of possible misidentification of *R. neglectus*. This species belongs to the *R. prolixus* complex that contains several morphologically similar species such as *R. nasutus*, *R. prolixus*, and *R. robustus* (Barrett 1991). The relationship between geographical distribution and environmental

¹ Laboratório de Parasitologia Médica e Biologia de Vetores, Faculdade de Medicina, Área de Patologia, Universidade de Brasília, Asa Norte, CEP 70.910–900 Distrito Federal, Brazil.
² Laboratório de Zoologia, Universidade Católica de Brasília, Q5 07 Lote 01 EPTC Bloco M, sala 331, CEP 72030-170 Distrito Federal, Brazil.
³ Corresponding author, e-mail: rgurgel@uch.br.
variables (e.g., temperature, precipitation, and altitude) was presented in a qualitative way for some triatomine species (Carcavallo et al. 1999). Finally, further studies have analyzed the influences of environmental variables on triatomine distribution (Costa et al. 2002, Gorla 2002, Rodrigues and Gorla 2004, López-Cárdenas et al. 2005, Sandoval-Ruiz et al. 2008).

Various methods have been used to predict species potential distribution using ecological niche modeling (ENM) based on occurrence data points and environmental variables, showing generally good results (see references in Tsoar et al. 2007). ENM may be particularly significant in vector studies, suggesting potential areas of vector occurrence, and consequently, risk areas of pathogen transmission (Peterson 2006). This approach has been used to study the potential distribution of vectors such as mosquitoes, ticks, sandflies (Herbreteau et al. 2005), and triatomines (Costa et al. 2002, Peterson et al. 2002, López-Cárdenas et al. 2005, Sandoval-Ruiz et al. 2008).

Among the ENM methods developed, the genetic algorithm for rule-set production (GARP) (Stockwell and Peters 1999) has proven especially useful in predicting species’ potential distributions under a wide variety of situations (Anderson et al. 2003 and references therein). GARP includes several distinct algorithms in an iterative approach. Briefly, the algorithms relate the environmental conditions (e.g., temperature, precipitation, altitude, and vegetation) of recorded occurrence points of the species with the environmental conditions of points sampled randomly from the study region, developing a set of rules that better explains the factors associated with the species presence. As a result, potential distribution maps of the species are generated (Peterson et al. 2002, 2004; Sweeney et al. 2006). ENM has also been applied to differentiate Triatoma brasiliensis populations in northeastern Brazil (Costa et al. 2002), to examine the relationships between host distribution (Neotoma spp.) and vectors (Triatoma proctata group) in Mexico (Peterson et al. 2002) and to analyze the geographical distribution of three triatomine species (Triatoma barberi, T. dimidiata, and Mecus pallidipennis) in the Mexican state of Puebla (Sandoval-Ruiz et al. 2008).

Our field observations suggest that the geographical distribution of R. neglectus in Brazil may be wider than the one suggested by Carcavallo et al. (1999) and Galvão et al. (2003). Thus, the aims of this study were (1) updating known geographical distribution of R. neglectus including new occurrence records for this species in Brazil and (2) predicting potential geographical distribution of this species using GARP from occurrence records and a set of 23 environmental variables. Additionally, the geographical distribution of R. neglectus was compared with that of palm trees and birds from the study region.

Materials and Methods

Occurrence Records and Distribution Ranges of Rhodnius neglectus, Palm Trees, and Birds. The occurrence records of R. neglectus were obtained from (1) distribution of triatomines captured in human environment by the Brazilian Chagas Disease Control Program in the period of 1975/83 (Silveira et al. 1984) and from 2002/2007 surveys carried out in entomology laboratories of the ‘Secretarias Estaduais de Saúde’ of Brazil (n = 349 records), (2) records on sylvatic environment of R. neglectus in Brazil (Barretto and Carvalheiro 1968, Diotaüti and Dias 1984, Bento et al. 1992, Teixeira et al. 2001, Emperaire and Romana 2006) (n = 15), and (3) sampling points of R. neglectus in palm trees (Mauritia flexuosa) in Brazil georeferenced between 2003 and 2007 (n = 181). Sources 1 and 2 gave only names of municipalities. Geographical coordinates of the municipality administrative center were obtained from the Brazilian Institute of Geography and Statistics (IBGE; http://www.ibge.gov.br) database. The distribution range (species’ occurrence limits) of R. neglectus was gathered by linking extreme occurrence records (in sylvatic and domestic environment) and compared with the one previously recorded by Carcavallo et al. (1999).

Geographical distribution maps of palm trees (Acrocomia aculeata, Attalea speciosa, Mauritia flexuosa, and Syagrus oleracea) were obtained in Lorenzo et al. (2004) and Henderson et al. (1995); for furnarid birds (Phacellodomus ruber and Pseudoseisura cristata), we used the distribution maps presented by Ridgely et al. (2005). The distribution range of these species were overlaid with the occurrence records of R. neglectus. Palm trees and birds species were both selected based on occurrence records and blood meal sources of R. neglectus in sylvatic environment (Diotaüti and Dias 1984, Carvalho et al. 1998, Gurgel-Gonçalves et al. 2004a, Emperaire and Romana 2006, Gurgel-Gonçalves and Cuba 2007). All maps were created and edited in the software ARC VIEW (version 3.2).

ENM. Twenty-three variables were used to generate models using DesktopGarp application (version 1.1.6). The altitude and climatic variables were obtained from the Worldclim project database (Hijmans et al. 2005) available at http://www.worldclim.org/. The environmental database used in GARP analyses covers all the Brazilian territory and some South American countries (Bolivia, Paraguay, Peru, and part of Argentina) showing a spatial resolution of 2.5’ (5 by 5 km). The climatic data averaged over the period 1961–1990 including data layers summarizing annual trends (e.g., mean annual temperature, annual precipitation), seasonality (e.g., annual range in temperature and precipitation), and extreme or limiting environmental factors (e.g., temperature of the coldest and warmest month and precipitation of the wet and dry quarters). The data layers were generated through interpolation of average monthly climate data from weather stations (see Hijmans et al. 2005 for details). Additionally, we used remotely sensed images, including monthly composite normalized difference indices (NDVs) from 1982 to 1992 based on data from the advanced very high resolution radiometer (AVHRR) sensor. Only occurrence records of R. neglectus in palm trees (n = 181, corresponding to 34 unique points) were used to generate predictive models. The species identi-
Identification in such areas was based on morphometric (Gurgel-Gonçalves et al. 2008) and molecular parameters (R.G.G., unpublished data). This procedure avoided the use of uncorrected occurrence records caused by misidentification of related species of *Rhodnius* (*R. neglectus*, *R. nasutus*, *R. prolixus*, and *R. robustus*), whose natural distribution ranges often overlap partially.

GARP works in an iterative process of rule selection, evaluation, testing, and incorporation or rejection, dividing occurrence records into training points (used to generate the model) and test points (for model evaluation). A method is chosen from a set of possibilities (logistic regression, bioclimatic rules) applied to the training data. Predictive accuracy is evaluated using 1,250 points resampled randomly considering the environmental characteristics of test points compared with another 1,250 points sampled randomly from the study region (Tsoar et al. 2007).

All analyses were carried out using the following software parameters: 50% of points to generate and 50% of points to test the model, 100 runs, and 0.01 convergence limit; 1,000 iterations and all rules (atomic, range, negated range, and logistic regression) were used. The best subset was used to select only 10 best models attributing 5% omission error (percentage of occurrence points outside the predicted area) and 40% commission error (percentage of the predicted area that exceeds the recorded occurrence). The selection of such parameter added a component of conservatism in the predictions of GARP that otherwise could extrapolate too much of the potential areas. By using only the models in the best subset selection, we tried to optimize our results with respect to omission/commission relationships (see Anderson et al. 2003); best models were consistently found at low levels of omission and moderate-to-high commission values. The $\chi^2$ statistics were used to compare the success observed in predicting distributions of test points with those expected under random models. Additionally, model quality was tested by the independent sets of points (50%) set aside before GARP modeling. The 10 best models generated by GARP were imported into ARC VIEW (version 3.2) and summed using the Map Calculator function to generate a single distribution map with a ranking of probability of occurrence.

**Results**

The distribution of *R. neglectus* occurrence records in sylvatic and domestic environment shows that the
species is widespread in Brazil (Fig. 1) and occurs within 2–23° S latitude and 36–59° W longitude, from sea level to 1,200 m.a.s.l. R. neglectus occurred in the Brazilian Cerrado biome and transitional areas (ecotones) in Caatinga (western areas of Bahia state), Pantanal (Mato Grosso do Sul state), and Amazon (northern areas of Mato Grosso and Tocantins states). Therefore, R. neglectus is a regular (although not endemic) species of the Cerrado biome.

The 10 best models resulting from ecological niche analysis presented \( \chi^2 \) values that ranged from 62.3 to 102.7 and were all statistically significant \( (P < 0.001) \). The average of the commissionerror for these models was 4.6. Furthermore, the average omission error was 4.9. Based on the random 50% resampling, in which one half the data are set aside to provide an independent test of model quality, the 10 best-subset GARP models for R. neglectus were also statistically significant \( (\text{average } \chi^2 = 36.4, P < 0.001) \). The sum of the 10 best models of potential distribution showed high probability of occurrence of R. neglectus in central Brazil, mainly in Tocantins, Maranhão (south), Piauí (south-central), Bahia (west), Goiás, Mato Grosso (south-central), Rondônia (southwest), and São Paulo (northwest) states. The map also indicated areas with potential occurrence of the species in other Brazilian states and northeastern Bolivia (Fig. 2).

By comparing distribution ranges based on point-occurrence in sylvatic and domestic environment and the recorded distribution of R. neglectus in Brazil (Carcavallo et al. 1999), two differences in the species geographical distribution can be clearly visualized. First, an increase in western distribution, mainly in areas of Mato Grosso state. Second, an increase in northeastern distribution, mainly in Bahia and Pernambuco states (Fig. 3). The increase in western distribution was confirmed by our sylvatic records in the extreme west portion of Mato Grosso state. The increase in northeast distribution, however, requires future study because the only reliable occurrence record of R. neglectus in the northeast region is from municipality of Curacá, northeastern Bahia (Emperaire and Ramaña 2006). Also, when the prediction maps are compared with the occurrence maps it was observed that the GARP models did not perform well in the south of R. neglectus distribution, mainly considering southwest São Paulo, north of Paraná and Mato Grosso do Sul states (Figs. 1 and 2).
Finally, overlap between the distribution of *R. neglectus*, palm trees (Figs. 4 and 5) and furnarid birds (Fig. 6) was observed, showing that biotic interactions may also contribute in the analysis of triatomine species distribution patterns. The largest areas of overlap between *R. neglectus* occurrence records and the distribution of palm trees and birds were observed for *Acrocomia aculeata/Syagrus oleracea* and *Phacellodinus ruber/Pseudoseisura cristata*, respectively.

**Discussion**

The results established potential areas of *R. neglectus* occurrence in South America using ENM based on environmental variables such as altitude, temperature, precipitation, and NDVI. Some studies evaluated the influence of climatic factors on triatomine distribution and abundance (Carcavallo 1999, Costa et al. 2002, Rodriguero and Gorla 2004) and showed temperature and precipitation limits where the species may occur. High population densities of triatomines are associated with high temperatures and prolonged dry seasons (Carcavallo 1999). According to Gorla (2002), temperature is a good indicator of *T. infestans* geographical distribution in South America. Implications for vector surveillance of Chagas disease can be obtained from these studies. Abad-Franch and Monteiro (2007) suggested that triatomine household infestation is restricted to Amazon driest regions, because populations adapted to extreme humid microhabitats have limited ability to colonize artificial environments. Moreover, all *Rhodnius* species with ability to colonize artificial environments (mainly *R. prolixus* but also *R. neglectus* and *R. nasutus*) derive from ancestral lineages that probably adapted to arid and semi-arid climates long before human beings reach America. In this sense, risk maps showing the vectors synanthropic potential could be produced based on climatological data and consequently become an important tool for planning the vector surveillance strategies. Besides, the influence of global climatic changes may be evaluated in the future using these models to study its consequences in the distribution patterns of such insects, including *R. neglectus*.

The vegetation indices were also important variables to predict the potential geographical distribution of *R. neglectus*. In previous comparative testing with and without NDVI, we observed that the models with NDVI presented higher values of $\chi^2$ and lower values of omission and commission. The NDVI is commonly used for the study of vector distribution (Herbreteau et al. 2005) because it is a variable that integrates effects of temperature, precipitation, and land cover. Compared with other studied variables (air temperature, surface temperature, infrared radiation, and vapor pressure deficit), this index better explained the *T. infestans* geographical distribution in South America (Gorla 2002).

The interaction between *R. neglectus* and some palm tree species may also explain the distribution patterns observed. The presence of *Mauritia flexuosa* palm trees ecotopes is one of the most important indicators of *R. neglectus* occurrence in the Cerrado biome (Gurgel-Gonçalves et al. 2003, 2004a). However, ecological niche modeling of *R. neglectus* did not show potential areas of the species occurrence in the Amazon basin, suggesting that this palm tree would not be a good ecological indicator of *R. neglectus* outside the Cerrado biome. In fact, other palm tree species are considered habitats of *R. neglectus* in Brazil (Carcavallo et al. 1998). The overlap between occurrence records of *R. neglectus* obtained from the current study and distribution ranges of these palm trees (Figs. 4 and 5) indicated that *Syagrus oleracea* and *Acrocomia aculeata* (open/dry species) also promote the maintenance of *R. neglectus* populations in the Cerrado biome. However, palm trees such as *Attalea speciosa* promotes the occurrence of *R. neglectus* outside the limits of this biome, mainly in Cerrado-Amazon and Cerrado-Caatinga transitional areas.

The presence of Cerrado patches in Caatinga and Amazon (Prance 1982), and *R. neglectus* occurrence in...
transitional areas may also support the potential geographical distribution shown in this study. Transitional areas are mosaics of two or three types of vegetation that can be observed in the limits of Cerrado with other biomes, including intermediate vegetation (e.g., *Attalea speciosa* palm forests).

Several lines of evidence suggest an Amazonian origin of the tribe Rhodniini (see Abad-Franch and Monteiro 2007). Some *Rhodnius* lineages dispersed toward presently arid or semiarid ecoregions. In some cases, these ancestral dispersing populations established ecological associations with dry forest palm species (e.g., *Fig. 4.* Overlapping between *R. neglectus* occurrence records (black circles) and the distribution range of dry palm tree species in Brazil.

Fig. 4. Overlapping between *R. neglectus* occurrence records (black circles) and the distribution range of dry palm tree species in Brazil.

Fig. 5. Overlapping between *R. neglectus* occurrence records (black circles) and the distribution range of wet palm tree species in Brazil.
Copernicia prunifera—R. nasutus, Acrocomia aculeata—R. neglectus). The evidence of a “savanna corridor” or a “diagonal of open/dry formations” formed by Chaco-Cerrado-Caatinga biogeographical provinces (Prado and Gibbs 1993, Morrone 2006) may have promoted R. neglectus dispersal over the Cerrado province and occasionally over the Caatinga of northeast Brazil. Thus, the biogeographical hypothesis would be that the R. neglectus distribution follows the diagonal of open/dry formations. The potential distribution presented in our study is in accordance with the latest hypothesis. Although niche modeling indicates the Cerrado as the main area for R. neglectus occurrence, it also suggests that Caatinga, Bolivian Chaco and Chiquitania dry forests are suitable regions for species occurrence. A wider sampling in these regions may confirm predicted areas and reinforce this hypothesis. The biogeographical pattern described above is not in accordance with the one presented by de Paula et al. (2006), that suggested that R. neglectus is restricted to Serra do Mar and Serra da Mantiqueira mountain systems in Brazilian Atlantic Forest. Also, no occurrence records of R. neglectus in either sylvatic or domestic environments in this ecoregion were recorded and we hypothesize that these mountain systems are geographical barriers for R. neglectus dispersal.

Psammolestes and Rhodnius species are ornithophilous and have substances secreted during the oviposition that adhere the eggs to the substrate (Barata 1998). Such mechanism may facilitate passive dispersal and promote the geographical distribution expansion of these triatomines because birds have ability of movement and are able to migrate. R. neglectus is frequently found in bird nests of the family Furnariidae such as Phacellodomus ruber (Gurgel-Gonçalves et al. 2004a, Gurgel-Gonçalves and Cuba 2007) and Pseudoseisura cristata (Emperaire and Romaña 2006). When comparing the occurrence records of R. neglectus observed in this study with the geographical distribution of those species of birds (Fig. 6), a significant overlap area is observed. This coincidence suggests that passive dispersal by birds may be an important dispersal mechanisms for R. neglectus, supporting the potential geographical distribution from west to northeast Brazil and consequently the biogeographical hypothesis of distribution along the “diagonal of open/dry ecoregions of South America.”

ENM generates geographical distribution models of species, presenting great accuracy and sensibility (Anderson et al. 2003, Tsoar et al. 2007). This approach has been applied to studies on vectors (Costa et al. 2002; Peterson et al. 2002, 2004; López-Cárdenas et al. 2005; Sweeney et al. 2006; Sandoval-Ruiz et al. 2008) contributing to an epidemiological study of tropical diseases (Peterson 2006). Our work has updated the alti-latitudinal distribution of R. neglectus based on new records of the species in sylvatic and domestic environments. We also presented the potential geographical distribution models of the triatomine, confirming the R. neglectus distribution in Cerrado and indicating that Caatinga, Amazonian savanna, Pantanal, and Bolivian Chaco areas also present favorable environmental conditions for the species occurrence. Additionally, the predicted geographic distribution area of R. neglectus in southwest Brazil would be greater if reliable records of these regions were used. Our reliable records of R. neglectus (from palm trees and identified using morphometric and molecular methods) did not include areas of south Brazil, where

![Fig. 6. Overlapping between R. neglectus occurrence records (black circles) and distribution range of furnarid birds species in Brazil.](https://academic.oup.com/jme/article-abstract/46/4/952/940132/fig6)
R. neglectus traditionally occur. Such potential areas should be investigated in future studies to broadly compare the realized distribution with the one predicted by the model. Some of these areas may have been occupied by similar species (e.g., R. nasutus in Caatinga) or represent regions in which R. neglectus could not disperse or even became extinct. Thus, ENM may be a useful tool to study biogeographical, ecological, and evolutionary aspects of the species (Anderson et al. 2003).

Beyond abiotic variables, the interaction between R. neglectus and some birds and palm trees species may also explain the distribution patterns of this triatomine species, considering that the results showed an increase of the distribution in west and northeast Brazil. These results should aid Chagas disease vector surveillance programs, given that household invasion by Rhodnius species maintains disease transmission risk and limits control strategies.

Acknowledgments

We thank R. B. Machado for provision of the database compiled for analysis using GARP; K. Schmidt for assistance in earlier methodological analysis; F. Oliveira Alves for great fieldwork assistance; C. E. Tosta, D. E. Gorla, F. Abad-Franch, F. Monteiro, G. Costa, and R. Constantino for suggestions on an preliminary version of this manuscript; and the workers of the Brazilian Chagas Disease Control Program for providing the list of municipalities with R. neglectus occurrence. Field surveys were financed by FAP-DF and CNPq (Brazil). Grant PPSUS/2004 193.000.036/2005.

References Cited


Received 15 August 2008; accepted 26 October 2008.