

MODELING HANTAVIRUS RESERVOIR SPECIES DOMINANCE IN HIGH SEROPREVALENCE AREAS ON THE AZUERO PENINSULA OF PANAMA

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Abstract. Habitat fragmentation commonly influences distribution of zoonotic disease reservoirs. In Panama, populations of rodent hosts of hantaviruses are favored by small habitat fragments isolated by agricultural lands. We expected a similar relationship between landscape characteristics and host distribution at fine geographical scales in southern Panama. The relative abundance of *Zygodontomys brevicauda*, the primary host for “Calabazo” virus, and other rodents was assessed at 24 sites within the Azuero Peninsula. We used satellite imagery to produce several spatial variables that described landscape; however, only slope was consistently related to abundances of the two most dominant rodent species. Using regression, we constructed a spatial model of areas of *Z. brevicauda* dominance, which in turn relates to higher infection rates. The model predicts highest abundances of *Z. brevicauda* in flat areas, where humans also dominate. These predictions have important ecological and conservation implications that associate diversity loss, topography, and human land use.

INTRODUCTION

Generalist species are able to survive in an extremely wide array of small patches of forest as well as in human dominated ecosystems. Numerous studies have shown a strong correlation between generalist rodent species and infectious diseases carried by them. Such is the case for hantavirus pulmonary syndrome (HPS) outbreaks in Europe, Asia, and North and South America.^{1–4} As a consequence, various spatial approaches have been used in epizootiological studies to predict the distribution of disease reservoirs (species that carry infectious agents) and to identify landscape attributes correlated with infection rates.⁵ However, most studies that attempt to predict reservoir distribution of other infectious diseases (e.g., Chagas,⁶ malaria,⁷ hantaviruses,^{5,8}) are based on presence-absence or density models for a particular host species, using approaches such as GARP (genetic algorithm for rule-set production) or others that include neural networks, ordination and classification methods, and Bayesian models.^{9–11}

While GARP and other techniques can potentially produce an output of probabilistic spatial models of species occurrence, most studies disregard the relative dominance of the species within a community in favor of predicting particular species occurrence. Rather than focus on presence of a species, we used a multiple regression approach to geographically predict areas of dominance (as relative abundance) of an endemic “Calabazo” hantavirus reservoir, *Zygodontomys brevicauda* (short-tailed cane mouse).

Modeling the distribution of a particular species is difficult in many tropical areas because of constant changes in land use. Furthermore, the complexity of human land use that produces a mosaic of various successional stages and patches of forests results in rodent communities being dominated by different generalist species such as *Sigmodon hispidus*, *Z. brevicauda*, and *Oligoryzomys fulvescens* as confirmed by research in Venezuela,¹² United States,¹³ Paraguay,¹⁴ and Costa Rica.¹⁵ Species distributed within countryside scenarios

are physiologically and behaviorally similar in traits, including reproduction, foraging habits, and tolerance to human settlements.¹⁵ Moreover, often the ancestors of such species are grassland inhabitants and also carriers of different human pathogens.

In Panama, HPS was first documented in December 1999,^{16,17} and since then, > 78 human cases have been detected in the Azuero Peninsula, with sporadic cases still appearing (B. Armien and others, unpublished data). Since the first outbreak, three new hantaviruses have been described: HPS-causing Choclo virus with *Oligoryzomys fulvescens* as the primary reservoir, Rio Segundo virus with *Reithrodontomys mexicanus* as primary reservoir,¹⁸ and Calabazo virus, associated with *Z. brevicauda*.¹⁶ Because *Z. brevicauda* has been involved in Calabazo hantavirus transmission to humans in Panama,¹⁷ we concentrated on *Z. brevicauda* as the focus species of our study.

We hypothesized that relative abundance of *Z. brevicauda* is positively related to those landscape characteristics that are relatively common in human dominated habitats, such as increased edge densities, flatter topography, and greater number of isolated forest fragments. Furthermore, we expected that if there were a relationship between the host’s relative abundance and particular landscape characteristics, that relationship should not vary with scale of analysis.

MATERIALS AND METHODS

Study area and trapping. The study area was located in the southern part of Azuero Peninsula, in southwestern Panama (80.59° W, 70.67° N; Figure 1). Azuero Peninsula is a mostly transformed agricultural landscape with low human density and scattered remnants of tropical dry forests. The native vegetation consists predominantly of deciduous trees with some perennial and succulent species, including mangrove swamps near the coast, while grasslands include several introduced pasture grasses.¹⁹ Most of the country has a hot and humid tropical climate, with cooler temperatures at higher elevations. Mean annual rainfall is least along the central Pacific coast, where rainfall is ~1,200 mm/yr.²⁰ On the Azuero Peninsula, the climate is extremely arid during the dry season

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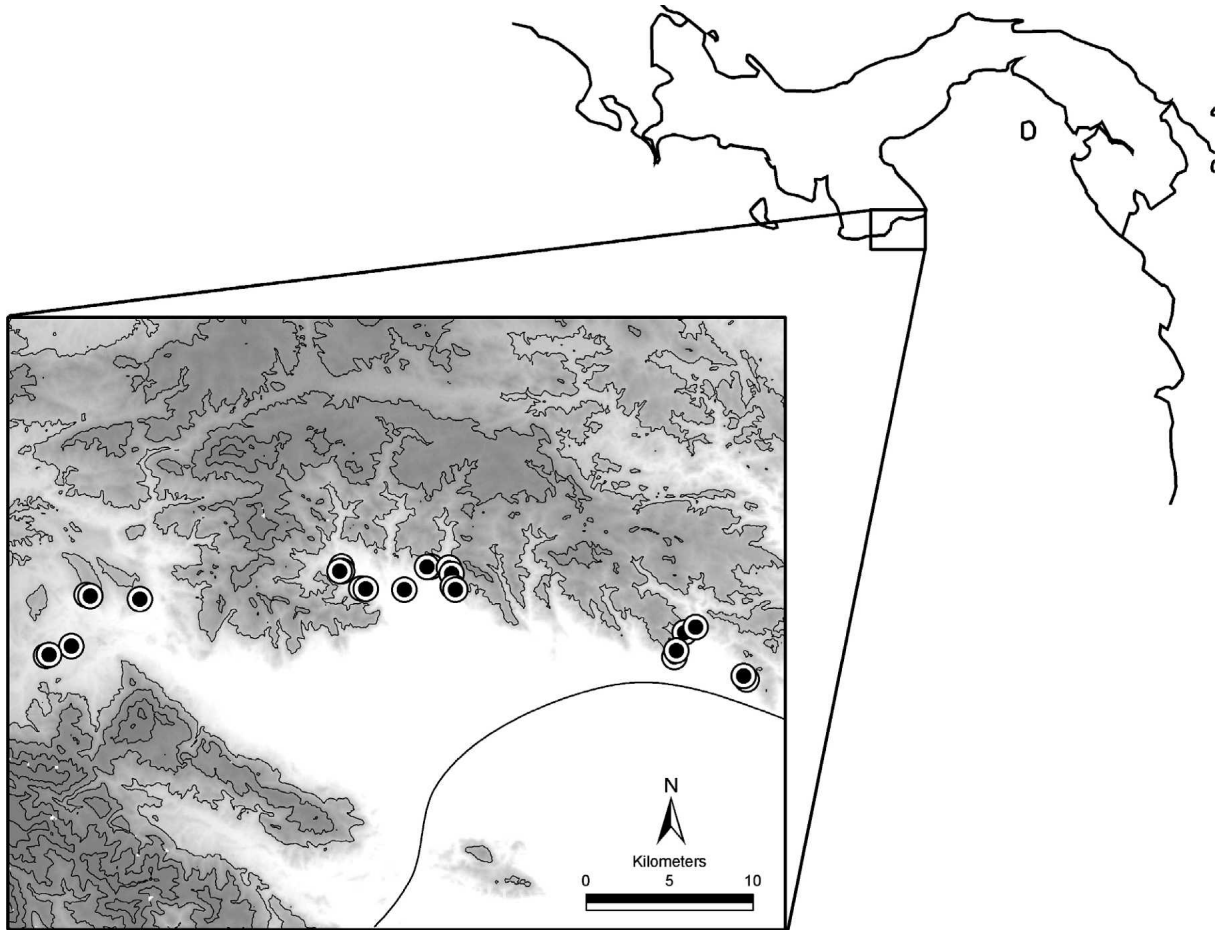


FIGURE 1. Location of study sites in south central Panama with a digital elevation model as a background. Shaded contours start at 200 m above sea level.

(January to April), and several weeks can go by with no rain at all. Topographically, altitude in the study area varies from sea level to > 1,500 m, with highest elevations and mountainous terrain concentrated along the western side of the peninsula, where terrain is generally steep and broken with slope gradients commonly above 45° .

To prevent spatial autocorrelation among sites in landscape analysis and control for factors such as altitude, we selected 16 of 24 sites that shared similar environmental conditions and were distributed along an east–west axis in the southern part of the peninsula (Figure 1). From eight pairs of sites geographically close to each other, we randomly selected one site from each pair and used those sites for post hoc model validation. All selected sites were forest edges that we defined as an abrupt transition between two relatively homogeneous ecosystems very common in human dominated tropical areas: human-generated pastures and primary or secondary tropical forests. At each site, we established one 60×60 -m trapping grid, containing 49 Sherman traps ($8 \times 8 \times 23$ cm; H. B. Sherman Traps, Tallahassee, FL) in a 7×7 design, each trap set 10 m apart, with the central trap line centered on the edge of the forest. The traps were baited with peanut butter and seeds. Each site was sampled for three consecutive nights in June 2003, and all mammals captured were measured, ear-tagged, and released at the capture site.

Variable selection. Given the limited number of sites, a

careful exploratory selection process was used to identify predictor geographical variables that would most likely reflect the processes that influence the dominance of *Z. brevicauda* in the rodent community. We focused on topography and landscape fragmentation characteristics as the main variables, partially, because of the limited availability of digital spatial information for southern Panama. Because the sites did not vary greatly in elevation, a raster layer of slope was derived from the ~90-m resolution digital elevation model distributed by USGS as the Shuttle Radar Topography Mission (SRTM) Elevation Dataset. Landscape metrics were produced from a layer derived from a SPOT image (Satellite Pour l'Observation de la Terre, designed and operated by the Center National d'Etudes Spatiales), the image being the best freely available data distributed by NIMA (National Imagery and Mapping Agency, USA). Using supervised classification, we classified the panchromatic 10-m SPOT image into forested and non-forested areas (Figure 2). Although we did not perform a quantitative assessment of the accuracy of the classification, a qualitative examination based on the senior author's field notes matched very well with predicted ground conditions.

To obtain measures of landscape characteristics (including quantification of characteristics that are relatively common in human dominated habitats, such as increased edge densities and number of isolated fragments), subsequent to classifica-

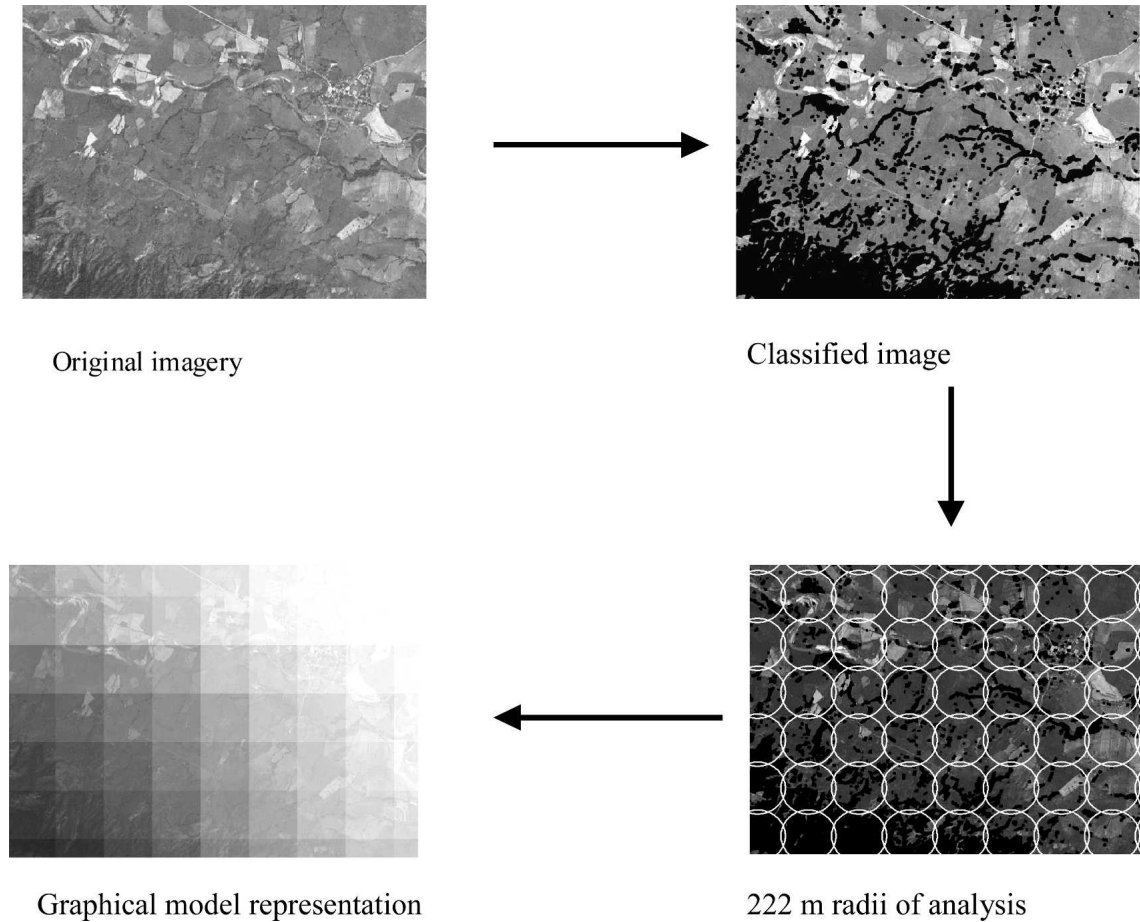


FIGURE 2. Steps in preparation of satellite imagery for use in analyses and modeling.

tion, we used the Patch Analyst ArcView extension²¹ for all trapping sites at three different scales (analysis radii of 222, 500, and 1,000 m). The first analysis radius is based on dispersal distances calculated from field data (222 m was the maximum distance of individual recapture in this study). For each trapping site, we obtained 13 variables describing landscape configuration characteristics that were reduced through principal component analysis (PCA) to three main factors that explained > 79% of variance at all three scales (Tables 1

and 2). While PCA factors can make interpretation of results more difficult, they conveniently summarize different variables produced by the Patch Analyst extension.

Model development. To produce a spatial model that would allow a representation of dominance for each species in a rodent community, we used a multiple linear regression model. All four variables (three principal factors from landscape metrics PCA and average slope for the site at scale of analysis) were checked for normality using Kolmogorov-

TABLE 1
Eigenvalues table and component matrix for the first three factors from PCA for each radius of analysis

| Landscape characteristics | Radius of analyses | | | | | | | | |
|---|--------------------|--------|--------|--------|--------|--------|--------|--------|--------|
| | 1 | 2 | 3 | 1 | 2 | 3 | 1 | 2 | 3 |
| Number of patches | -0.596 | 0.617 | -0.413 | 0.093 | 0.894 | 0.112 | -0.510 | 0.697 | 0.350 |
| Mean patch size | 0.796 | 0.210 | 0.538 | 0.774 | -0.581 | -0.027 | 0.919 | 0.054 | -0.287 |
| Median patch size | 0.902 | 0.054 | -0.210 | 0.148 | -0.382 | 0.545 | 0.524 | -0.010 | -0.656 |
| Patch size coefficient of variance | -0.516 | 0.704 | 0.164 | 0.786 | 0.111 | -0.361 | 0.647 | -0.047 | 0.628 |
| Patch size SD | 0.025 | 0.307 | 0.806 | 0.820 | -0.372 | -0.306 | 0.910 | -0.058 | 0.204 |
| Total edge | -0.129 | 0.949 | -0.194 | 0.778 | 0.542 | 0.178 | 0.159 | 0.934 | 0.142 |
| Edge density | -0.129 | 0.949 | -0.194 | 0.778 | 0.542 | 0.178 | 0.159 | 0.934 | 0.142 |
| Mean patch edge | 0.960 | 0.201 | 0.158 | 0.850 | -0.415 | 0.236 | 0.896 | 0.182 | -0.365 |
| Mean shape index | 0.896 | 0.267 | -0.137 | 0.855 | -0.110 | 0.212 | 0.191 | 0.736 | -0.403 |
| Area weighted mean shape index | 0.800 | 0.461 | -0.164 | 0.940 | 0.036 | 0.021 | 0.801 | -0.002 | 0.569 |
| Mean perimeter-area ratio | -0.208 | -0.041 | 0.730 | 0.272 | 0.157 | -0.878 | -0.553 | 0.445 | 0.006 |
| Mean patch fractal dimension | -0.068 | -0.041 | 0.266 | -0.134 | 0.005 | 0.819 | -0.097 | -0.466 | 0.233 |
| Area weighted mean patch size fract. dimen. | 0.230 | -0.300 | -0.860 | 0.538 | 0.314 | 0.252 | 0.197 | -0.016 | 0.774 |

TABLE 2
All three factors explain > 79% total variance in all 13 landscape characteristic variables

| PCA factor | Radius of analysis | | | | | | | | |
|------------|--------------------|-------|-------|-------|-------|-------|---------|-------|-------|
| | 222 m | | | 500 m | | | 1,000 m | | |
| | Total | % Var | Cum % | Total | % Var | Cum % | Total | % Var | Cum % |
| 1 | 4.57 | 35.14 | 35.14 | 5.85 | 44.98 | 44.98 | 4.51 | 34.70 | 34.70 |
| 2 | 3.29 | 25.33 | 60.46 | 2.33 | 17.92 | 62.90 | 3.23 | 24.84 | 59.55 |
| 3 | 2.67 | 20.53 | 80.99 | 2.20 | 16.95 | 79.85 | 2.39 | 18.37 | 77.91 |

Smirnov tests²² ($P > 0.05$), and whereas correlation analyses revealed some positive and negative relations between variables, none of the collinearity statistics were high enough to warrant exclusion of any one variable from the complete model. A sensibility analysis of the regression model (using Cook's distance [D]) indicated the influence or contribution of each site to the parameters of the model. We calculated Cook's distances for both the model with all 24 sites and with the 16 selected sites.²³ The models, after removal of one, three, and five sites with the highest D values, were compared with each other to test the sensibility.

To further the use of final geographic models and explore consequences for human-rodent interactions, we included human population density data from the Center for International Earth Science Information Network at Columbia University (<http://www.ciesin.org/>), quantifying the relationship between topography and human habitation.

RESULTS

Community structure and dominance. A total of 204 individuals belonging to five rodent species were sampled. The species trapped were *Liomys adspersus*, *Origoryzomys talamancae*, *Peromyscus semiespinosus*, *Sigmodon hispidus*, and *Zygodontomys brevicauda*. Overall, the community was dominated by *Z. brevicauda* (52.45%), followed by *L. adspersus* (34.80%) and *S. hispidus* (8.8%). There was an inverse abundance relationship between *Z. brevicauda* and *L. adspersus*, that is, where one of the two species was dominant, the abundance of the other was diminished, whereas in most of the sites, *Z. brevicauda* was the species that dominated the community (Figure 3). The Hill's diversity number N_2 (recip-

rocal Simpson index) showed variation between sites, the index ranging from 1 to 3.3 in the most diverse sites. Variation was also found in evenness of the reciprocal Simpson index between sites ranging from 0 to 1.

Landscape analyses. Initially, the proportions of *Z. brevicauda*, *L. adspersus*, and *S. hispidus* individuals within the rodent community at 16 different sites were used as dependent variables in a multiple linear regressions:

$$Y = X_1 + X_2 (\text{mean \% slope}) + X_3 (\text{PCA factor 1}) + X_4 (\text{PCA factor 2}) + X_5 (\text{PCA factor 3}) + e_{ij}$$

In all cases, slope was considered as mean slope for area of analysis based on a 90-m resolution digital elevation model. The first PCA factor was highly correlated with all three measures of landscape pattern: patch size, amount of edge, and shape of patches, whereas the second PCA factor was highly correlated with both amount and density of edges. Various measures of patch size were most strongly related to PCA factor 3. The third PCA factor correlates with different secondary measures, such as fractal dimensions or patch size standard deviation, depending on scale of analysis (Tables 1 and 2).

For the initial analyses, we did not consider forward or backward stepwise regression to evaluate individual variable contributions (Table 3), whereas sufficient abundance data for all sites existed only for *Z. brevicauda*, *L. adspersus*, and *S. hispidus*. After the development of complete regression models, we used the data from the remaining eight sites to validate the models. Regression models were only significantly correlated to the actual relative abundance for *Z. brevicauda* at 1,000 m and *L. adspersus* at 500 and 1,000 m, whereas there was no model that was significantly correlated

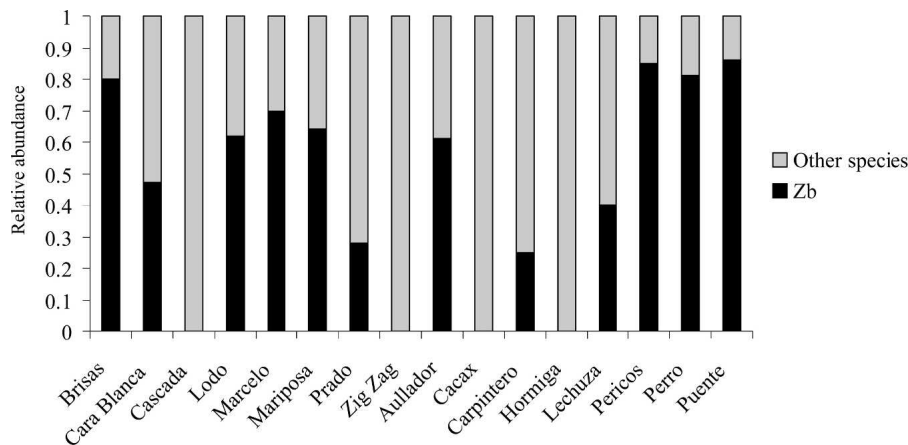


FIGURE 3. Proportion of *Z. brevicauda* individuals captured at each site.

TABLE 3
Multiple linear regression parameters relating landscape characteristics to relative abundance of four rodent species

| Species and scale of analysis | R adj | df | Sig | Constant | % Slope | PCA1 | PCA2 | PCA3 |
|--------------------------------|--------|----|-------|------------|---------|--------|--------|--------|
| <i>Zygodontomys brevicauda</i> | | | | | | | | |
| 222 m | 0.660 | 4 | 0.002 | Y = 0.990 | -0.032 | 0.039 | -0.054 | 0.081 |
| 500 m | 0.663 | 4 | 0.002 | Y = 1.013 | -0.034 | -0.036 | -0.115 | -0.067 |
| 1,000 m | 0.621 | 4 | 0.004 | Y = 1.020 | -0.038 | 0.069 | -0.033 | -0.033 |
| <i>Liomys adspersus</i> | | | | | | | | |
| 222 m | 0.605 | 4 | 0.005 | Y = -0.108 | 0.032 | -0.005 | 0.102 | -0.109 |
| 500 m | 0.640 | 4 | 0.003 | Y = -0.143 | 0.035 | 0.085 | 0.115 | 0.104 |
| 1,000 m | 0.508 | 4 | 0.017 | Y = -0.137 | 0.038 | -0.054 | 0.050 | 0.032 |
| <i>Oryzomys talamancae</i> | | | | | | | | |
| 222 m | -0.001 | 4 | 0.450 | Y = 0.018 | 0.0 | -0.007 | 0.005 | 0.016 |
| 500 m | 0.541 | 4 | 0.012 | Y = 0.014 | 0.0 | 0.007 | 0.0 | -0.027 |
| 1,000 m | -0.079 | 4 | 0.593 | Y = 0.011 | 0.0 | 0.008 | 0.003 | 0.015 |
| <i>Sigmodon hispidus</i> | | | | | | | | |
| 222 m | -0.031 | 4 | 0.503 | Y = 0.089 | 0 | -0.023 | -0.049 | -0.017 |
| 500 m | 0.055 | 4 | 0.357 | Y = 0.105 | -0.001 | -0.059 | 0.007 | 0.020 |
| 1,000 m | -0.027 | 4 | 0.496 | Y = 0.106 | -0.001 | -0.043 | -0.015 | -0.030 |

with *S. hispidus* relative abundance (Table 4). Because the sum of predicted abundances for *Z. brevicauda* and *L. adspersus* was 90% of total, we focused on these two species for subsequent analyses, where a backward stepwise regression identified slope as the single most important variable in all cases. Geographical representations of the abundances for *Z. brevicauda* and *L. adspersus* are based on these models.

There was an apparent difference between the scales of analyses (expressed as a radius), with the 1,000-m scale producing significant regression models for *L. adspersus* and *Z. brevicauda*. Furthermore, partial regression plots revealed slope as the variable that is significantly negatively correlated with *Z. brevicauda* relative abundance within the rodent communities at the three scales and positively correlated with *L. adspersus* abundance (Figure 4). While principal factors of landscape characteristic analyses helped to explain additional variation, there were no significant trends between scales that were apparent from partial regression plots. Based on subsequent application of the spatial model to Azuero Peninsula, the model revealed a large area near the coast where *Z. brevicauda* is expected to dominate the rodent community (Figure 5). That area is tied to higher human activity, which was confirmed when topographic characteristics were compared with data on human population densities (Figure 6).

The regression model, which includes all 24 sites, exhibited

similar patterns and significance as the model using 16 sites at three different distances. The sensitivity analyses for all the regression models did not detect particular sites that could affect the models' structure and significance. The highest Cook's distances detected for a particular site were $D = 0.24$ for 222 m, $D = 0.39$ for 500 m, and $D = 0.12$ for 1,000 m.

DISCUSSION

The community structure of small mammals associated with human settlements can be extremely important from an epidemiologic perspective. This significance is increased if the dominant species is a primary reservoir for an infectious disease because dominance of a reservoir in a rural landscape can achieve complex epidemiologic scenarios that may increase risk of disease to humans. That is the case for *Z. brevicauda*, which is the most common species captured in our human impacted sites. Modeling its marked dominance in an endemic hantavirus area offers a significant tool toward understanding disease dynamics and predicting high risk areas for humans. *Z. brevicauda* has been reported repeatedly to dominate human altered landscapes in low diversity areas in

TABLE 4
Correlation between predicted values of abundance at analyzed sites and those at eight sites used for validation

| | Radius of analysis | | |
|---------------------------|--------------------|--------|---------|
| | 222 m | 500 m | 1,000 m |
| <i>Z. brevicauda</i> | | | |
| Pearson correlation | 0.155 | 0.348 | 0.708 |
| Significance (two-tailed) | 0.714 | 0.398 | 0.049* |
| <i>L. adspersus</i> | | | |
| Pearson correlation | 0.245 | 0.765 | 0.890 |
| Significance (two-tailed) | 0.558 | 0.027* | 0.003† |
| <i>S. hispidus</i> | | | |
| Pearson correlation | 0.059 | 0.116 | 0.026 |
| Significance (two-tailed) | 0.889 | 0.785 | 0.951 |

* Correlation is significant at the 0.05 level (two-tailed).
† Correlation is significant at the 0.01 level (two-tailed).

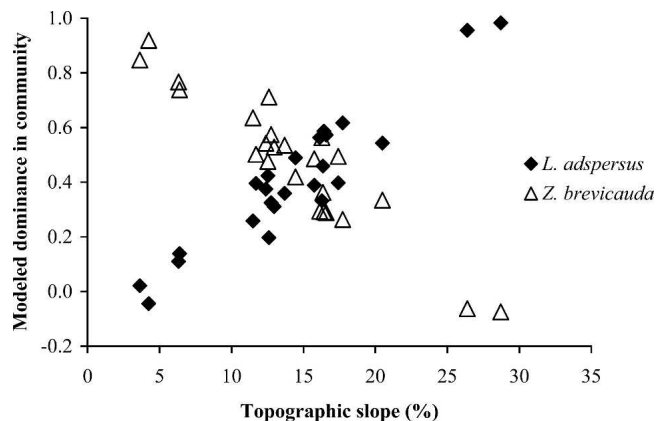


FIGURE 4. Relationships between modeled dominance in the rodent community (*L. adspersus* and *Z. brevicauda*) and topographic slope at study sites (%).

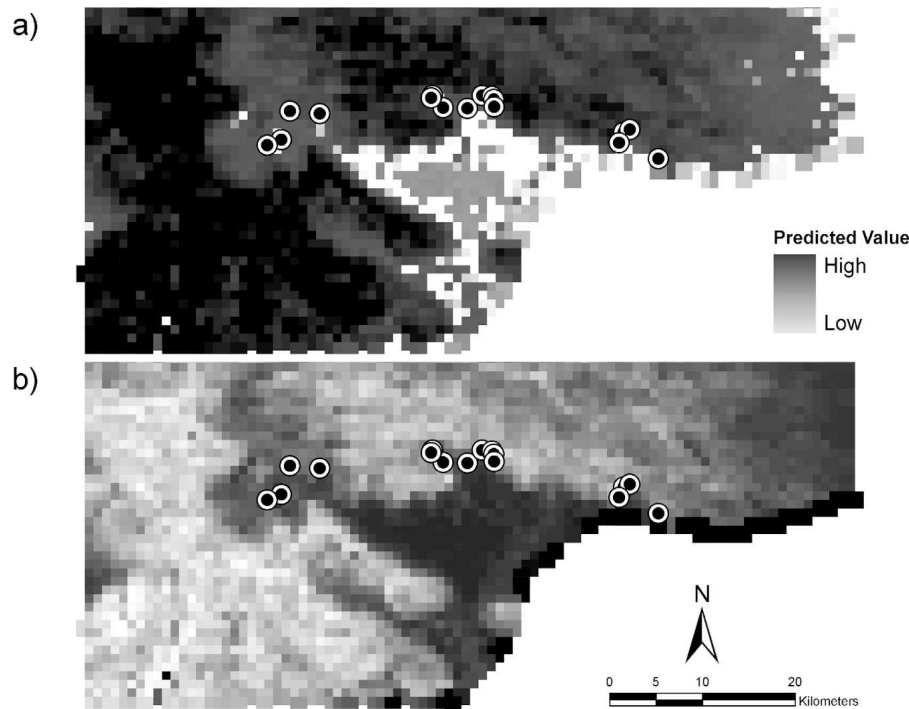


FIGURE 5. The spatial representation of community dominance model for (A) *L. adspersus* and (B) *Z. brevicauda* for Azuero Peninsula, Panama. Markers indicate the location of study sites. In both images individual pixels are 1×1 km.

Costa Rica,¹⁵ Panama,⁴ and Venezuela,¹² and has quickly become a public health concern.

In this study, we focused only in the response of a community of small mammals to different landscape features and further analyses should be implemented to relate reservoir total abundances and hantavirus infection rates to enhance outbreak forecasts. Despite the limitations of our analysis, it seems that dominance of *Z. brevicauda* populations is limited by topography at the landscape scale and perhaps interspecific competition at the local scale.

Human development in the Azuero Peninsula is more prevailing in flat areas (Figure 6), in which crop production is easier to accomplish; therefore, it is not a surprise that gen-

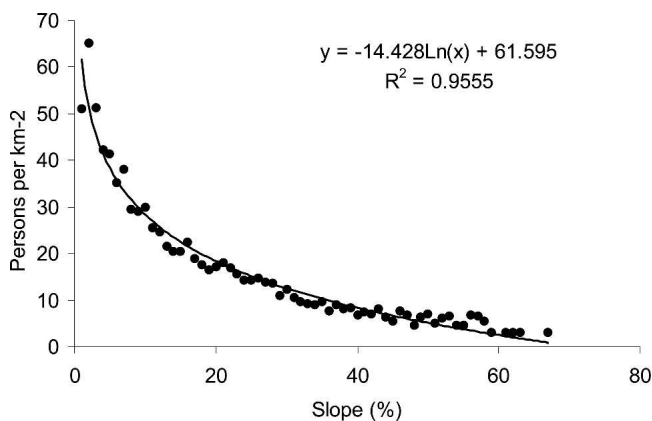


FIGURE 6. Relationship between human population density and topographic slope for southern Panama. Population density data obtained from Center for International Earth Science Information Network at Columbia University, New York.

eralist species such as *Z. brevicauda*, associated with rice production (a common crop in the Peninsula), show a marked tendency to dominate these flat lands (Figure 5). However, *Z. brevicauda* dominance is not related to the amount of deforested land (incorporated in PCA analysis) at spatial scales that we measured, which suggests a more complex relationship between its abundance and perceived habitat available. Our results could indicate more complex interactions between landscape fragmentation, environmental characteristics (such as availability of foraging resources for rodents), and *Z. brevicauda* dominance. It is possible that our analysis scale failed to associate landscape fragmentation at the appropriate level for *Z. brevicauda* or that the classification of landscape into forested and deforested zones was overly simplistic. In other words, *Z. brevicauda* might be associated with specific vegetation structure or may depend on specific plant species, especially because all sites sampled were located in edges of small patches of forest in which secondary vegetation was dominant. Furthermore, we did not analyze *Z. brevicauda* dominance in terms of population structure and dynamics, therefore ignoring the consequences of landscape variability for persistence. Nevertheless, topography expressed as slope showed the strongest correlation with *Z. brevicauda* dominance and, whereas landscape fragmentation characteristics added to the predictive power of regression, they did not significantly improve it.

One of the factors that did not explain *Z. brevicauda* dominance as expected was related to the presence of edges and its derivatives (e.g., edge densities, total edge). This has been suggested frequently as an important determinant of biogeographical patterns for mammal communities.²⁴ Furthermore, patch size and shape complexity were not as significant as expected, and they did not correlate with *Z. brevicauda* domi-

nance. It is possible that our scale of analysis captures a landscape that is already heavily fragmented and variation in *Z. brevicauda* dominance can only be observed when fragments are fairly large. On the other hand, we feel that our scale of analyses properly reflects the landscape perceived by *Z. brevicauda* as indicated by home range estimations using diffusion constants.²⁵ Other studies have shown that habitat preferences for generalist species are not only a function of a patch size, isolation, and shape, but also there are behavioral traits that allow generalist to dominate.^{26,27}

To improve on our modeling effort, a more detailed analysis of vegetation type, including plant species information, as well as information on cleared lands, such as land use (cattle grazing versus different types of cultivars), should be collected. This type of information is more difficult to derive from satellite imagery and requires meticulous field validation. Dominance of *Z. brevicauda* could be related to various factors stemming from rice and corn cultivation, time of harvest, or season. However, when coupled with tools like Arcview and remote sensed imagery, a better understanding of *Z. brevicauda* dominance in the community may be possible. Remarkably, entire sites were either dominated by *Z. brevicauda* or by *L. adspersus*, and both species comprised nearly 90% of individuals in the community. Thus, from a health risk management perspective, it would be beneficial to further study what factors besides topography increase abundances of *L. adspersus*. Artificially increasing *L. adspersus* populations could in turn reduce *Z. brevicauda* populations and consequently infection rates. In addition, translocation experiments could also improve the understanding of topography as a factor in *Z. brevicauda* dominance and its inverse relation with *L. adspersus*.

Our approach and findings should be relevant to a number of other tropical regions, particularly if the infection is endemic and if it is driven by the combination of reservoir dominance, topography, and a landscape matrix dominated by small patches of forest. Spatial models that incorporate landscape structure and population response to landscape change may not be effective if the scale of analyses is not appropriate.²⁸ We recognize that extrapolating findings across spatial scales can lead to erroneous conclusions; however, we believe that in this case, the predictive map can provide at least a starting point for further studies and aid in efforts to manage and control hantavirus outbreaks. Furthermore, our predicted abundance of hantavirus host corresponds well with areas of high incidence of human cases of HPS.¹⁷ This type of predictions are especially important for areas such as Azuero Peninsula, where 74% of HPS cases in Panama were registered (B. Armien and others, unpublished data).

We analyzed *Z. brevicauda* distribution in detail using patches in the landscape; however, other species of rodents such as *Oligoryzomys fulvescens* should also be studied, because this species is also a reservoir for hantavirus pulmonary syndrome in Panama, and its abundance is closely related to human settlements and croplands. Other descriptive variables may explain its distributions among human settlements and may not necessarily relate to topography. Our results make important contributions to the understanding of community ecology in a hantavirus endemic area in human dominated landscapes, typically species-poor communities and strengthen the multidisciplinary approach to the understanding of infectious disease. Such contributions should lead to increased

conservation measures in tropical areas while at the same time preventing disease outbreaks.

Received August 23, 2005. Accepted for publication February 17, 2006.

Acknowledgments: The authors thank A. Townsend Peterson for helpful suggestions and comments and J. Cook, E. S. Loker, R. Parmenter, and H. Samaniego who reviewed an earlier version of this manuscript. The authors thank an anonymous reviewer who provided insightful comments. We also thank A. Armien, E. Broce, and other Instituto Conmemorativo Gorgas staff for general support, and A. McKency, M. Ávila, O. Vargas, N. Ríos, F. Crespo, E. Valdez, M. Hudson, and R. Jiménez for field assistance. We are grateful for all support provided by the Ministry of Health of Panama.

Financial support: The fieldwork was funded by NSF Dissertation Improvement Grant 3-25471-3100 and DARPA grant #066000.

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