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RESEARCH PAPER

Land cover associated with hantavirus presence in Paraguay

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ABSTRACT

Aims Hantaviruses are zoonotic, aetiological agents maintained by rodents of the family Muridae. The occurrence of hantavirus in rodent hosts has been correlated to a number of climatic and environmental factors, including landscape structure. To date, most of these correlative studies have been conducted at moderate to fine spatial resolution. Our aim is to determine whether land cover classes defined at a mapping resolution of 1 km^2 are associated with rodents with antibodies to hantavirus in Paraguay.

Location The Republic of Paraguay.

Methods A total of 362 rodents from 10 species known to host hantaviruses were tested for the presence of hantavirus antibodies, resulting in 27 seropositive individuals. This data base was then combined with a map of six land cover types derived from coarse resolution remote sensing data to create a series of contingency tables, which were used to relate serostatus to land cover type using nonparametric tests of proportions and qualitative comparison of observed and expected values.

Results There was a significant difference in habitat association between seropositive and seronegative rodents when species were pooled. Seropositive rodents were found with disproportionately high frequency in areas where human disturbance in the form of intensive and mosaic agricultural landscapes was present.

Main conclusions Human-disturbed land cover classes have a detectable relationship to the hantavirus serostatus of host population rodents when observed at coarse spatial resolutions. Although coarse-grained analysis does not lead to any conclusions as to why agricultural land cover is more likely to harbour seropositive rodents, the relationship between them could form the basis for a monitoring system designed to relate land cover change to potential viral outbreaks in rodents and humans.

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Keywords
Geospatial analysis, GIS, hantavirus, land cover, remote sensing, rodents, rodent habitat.

INTRODUCTION

Hantaviruses are zoonotic, host-specific RNA viruses that persistently infect rodents of the family Muridae (Schmaljohn & Hjelle, 1997). Hantaviruses are known to cause two often fatal diseases in humans. In North and Latin America, they are associated most closely with hantavirus pulmonary syndrome (HPS), an acute respiratory illness fatal in 30–50% of cases (Butler & Peters, 1994). In 1995, an outbreak of HPS occurred in the Chaco region of northwestern Paraguay, where 17 confirmed cases were reported in Departamento Boquerón (Williams *et al*., 1997; Yahnke *et al.*, 2001). Additional HPS cases were reported in Paraguay in 2000, 2001, and 2004. Subsequent analysis has shown that hantaviruses are endemic to both of Paraguay's principal ecological regions (Chaco, Interior Atlantic Forest), with as many as five strains of hantavirus circulating (Chu *et al*., 2003).

The emergence of hantavirus illness as a threat to human health has led to a number of studies aimed at understanding the influence of environmental factors on the presence and persistence of hantaviruses in rodent populations. In North America,

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hantavirus presence in rodents has been correlated with weather and climate factors, particularly with precipitation anomalies associated with the El Niño/Southern Oscillation (ENSO) phenomenon (Engelthaler *et al.*, 1999). Topography (altitude and aspect), habitat, and vegetation vigour have also been associated with viral presence (Mills *et al.*, 1997; Boone *et al.*, 2000). Langlois *et al.* (2001) noted that, in addition to climatic and environmental factors, there is a strong link between landscape structure and the occurrence of hantaviruses in Canada. Langlois *et al.* hypothesized that landscape changes result in fragmentation of the host rodent habitat. This landscape fragmentation affects the movement of rodents through the landscape, increasing interspecific contact and competition, and increasing the probability of virus transfer from infected to non-infected members of the host population. Based on their results, Langlois *et al.* recommended that epidemiological models make use of the spatial structure of the host population, as inferred from landscape structure.

The importance of monitoring viral activity and predicting the potential for viral emergence into human populations has resulted in the increasing use of spatial data and geospatial analysis technologies to model the relationship between landscape factors and hantavirus dynamics. Geospatial analysis of viral activity has generally involved the use of remote sensing imagery and other spatial data, analysed within a geographic information system (GIS) framework (see Boone *et al.*, 2000). Most studies to date that have evaluated the relationship between landscape structure, environmental factors, and hantavirus dynamics using GIS have done so over a relatively limited geographic extent, using either aerial photos or moderate resolution remote sensing data (e.g. Landsat TM/ETM+) as their principal data source (Glass *et al.*, 2000; Langlois *et al.*, 2001). Fewer studies have attempted to relate viral activity to the landscape at larger spatial extents using coarser resolution data; however, there are some notable advantages to utilizing this type of remote sensing data. These advantages include: (1) a better understanding of the macroecology of the virus–host-landscape system, and (2) the potential for exploiting the synoptic coverage and overpass frequency of coarse resolution operational sensors (e.g. SPOT-VGT, AVHRR) for regional or countrywide monitoring of landscape conditions conducive to viral outbreaks.

In this paper, we evaluate the coarse resolution relationship between human land cover disturbance and seropositivity rates among rodents known as reservoirs for hantavirus. In particular, we will address two research questions: (1) are there detectable regional-scale relationships between land cover type and hantavirus prevalence, and can these relationships be observed using coarse resolution spatial data; and (2) is anthropogenic disturbance associated with viral presence at this coarse spatial grain?

METHODS

Land cover mapping

Land cover data were derived from a map of South America produced as part of the Global Land Cover 2000 (GLC2000) project of the European Commission's Global Vegetation Monitoring (GVM) unit (Eva *et al.*, 2002). The GLC2000 land cover map was assembled from a variety of remote sensing data sources, depending on the type of land cover being mapped. Humid forest cover was classified using unsupervised ISODATA classification (Richards & Jia, 1999) applied to a data mosaic obtained from the Along Track Scanning Radiometer (ATSR) instrument on board the ERS-2 satellite. The remaining non-humid forest vegetation was classified using data from the SPOT-VGT instrument using a combination of visual interpretation and machine processing (Eva *et al.*, 2002). Class accuracy was determined using input from a variety of regional expert sources (see Eva *et al.*, 2002 for details). The resulting map depicts land cover over the entire South American continent at 1 km^2 spatial resolution. Classes were defined at two nested levels of detail, a global legend designed to be compatible with other GLC2000 products (Bartholomé & Belward, 2005), and a regional legend that resolves global land cover into more detailed categories. The data we obtained were mapped initially using the more detailed regional land cover categories. To simplify the analysis, we recoded the original 13 regional land cover categories into seven global classes using the GLC2000 published guidelines (Eva *et al*, 2002; Bartholomé & Belward, 2005, see Table 2). Of the seven recoded classes, two were forested, two were dominated by herbaceous or woody shrub vegetation, two were defined by anthropogenic use (mosaic and intensive agriculture), and one was a water class where no trapping occurred. Because water is not a habitat for the host rodents, this cover type was dropped from further analysis.

The difference in time between the date of field data collection (May 1996–August 1998) and the acquisition dates of the satellite data used to assemble the land cover map (1999–2001) was a cause for concern, because rapid land cover change throughout Paraguay might result in a rodent trapping site being assigned to an incorrect land cover class. To minimize these errors, we examined each of the field data collection sites using false colour composite Landsat Thematic Mapper images obtained as nearly as possible to the time of the field trapping. Areas that showed obvious signs of land cover change (e.g. deforestation, cropping, etc.) were recoded manually to their correct cover type. This re-analysis resulted in changes to the land cover map at three sites: Mbaracayu (15), Ape Aime (26), and Estancia San Jose (27) (see Fig. 1; numbers refer to mapped locations). For each of these three sites, the Landsat TM data used to correct land cover were obtained no more than 3 months from the time trapping occurred.

Small mammal and seroprevalence data

The rodents used in this study were obtained from an inventory of small mammals conducted in Paraguay from May 1996 to September 1998 (Chu *et al.*, 2003). In total, 362 small mammals were collected at 15 sites representing six of Paraguay's seven major ecosystems distributed throughout both the Chaco and the Interior Atlantic Forest (Esser, 1982; see Fig. 1). The sample sites are well distributed among the various natural and anthropogenically disturbed land cover classes (Fig. 1). Closed and open deciduous forest areas occurred mainly in the Atlantic

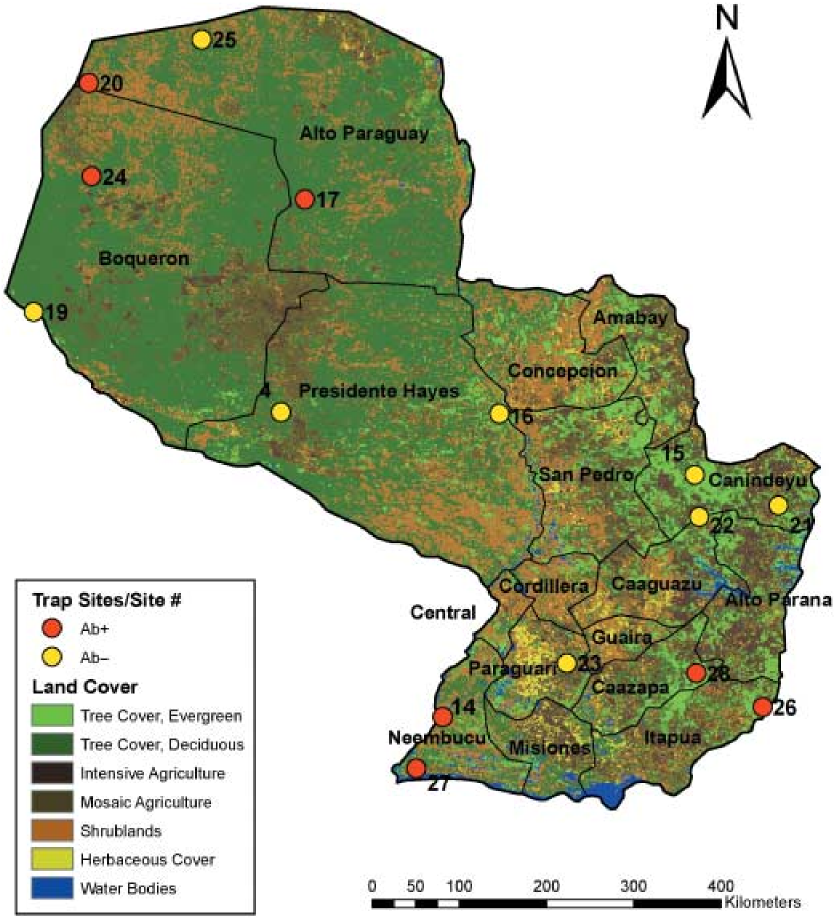

Figure 1 Map of Paraguay showing locations of trapping sites and land cover classes. See Table 1 for names of the trapping sites.

Forest regions of eastern Paraguay, whereas scrub savanna and thorn forest regions were located mainly in the Chaco. Agricultural sites are found throughout the country, with intensive agriculture found mainly in the Chaco, and mosaic agriculture occurring mainly in eastern Paraguay.

Captured rodents were prepared as standard museum specimens, and will be deposited in the mammal collections of the Museum of Texas Tech University and the Museo Nacional de Historia Natural del Paraguay. Tissue samples are deposited in the frozen tissue collections of the Museum of Texas Tech University.

Tissue from each of the 362 rodents was tested for the presence of hantavirus antibodies using immunoflourescent antibody (IFA) assays (Chu *et al.*, 2003). Of the 362 tested, 27 individual rodents yielded positive IFA results. A positive IFA result indicates that the animal is seropositive; that is, it has been exposed to hantavirus, but may or may not have virus still present in its system. Given the relatively short life spans of the host species (generally less than 2 years, see Nowak & Paradiso 1983; Emmons, 1990) and their restricted activity space (generally much less than 1 km^2: the spatial grain of this study, see Anderson, 1970; Kelt & VanVuren, 1999), it is reasonable to assume that any seropositive rodents were exposed to the virus within a short time of being trapped and near the trapping site. Therefore, we can assume further that seropositive rodents were exposed to the virus within the same land cover in which they were trapped, rather than migrating into the land cover type associated with the trap site after being exposed elsewhere. The complete trapping data set, including number, species, and serostatus of each of the rodents from each of the 15 sites, is summarized in Table 1.

Categorical data analysis

We used the national boundaries coverage supplied by ESRI with the ArcView GIS software to extract Paraguay from the full South American land cover data set. The six-class land cover data set was merged with the field data using the ArcView GIS. A summary table was then generated with the following information about each of the 362 rodents in the data base: trapping location, genus, species, antibody status (seropositive or negative), and the land cover class where the rodent was trapped. This summary table was used to generate a series of contingency tables categorizing each rodent by antibody status and habitat type. The contingency tables were then used to perform a series of nonparametric categorical data analyses (Selvin, 1998; Higgins, 2004) to test for significant relationships between land cover class and the frequency of seropositivity. All the statistical analysis reported here was conducted using the R statistical programming environment (Venables *et al.*, 2005), and the StatXact software package, version 5 (Cytel Software Company, 2001).

Table 1 Summary of trapping sites and number of rodents trapped at each site. Site number refers to numbered locations in Fig. 1. Numbers in parentheses are seropositive individuals at each site or for each species

Site Number	Site Name	*Akodon azarae*	*A. montensis*	*Bibimys chacoensis*	*Graomys griseoflavus*	*Holochilus chacarius*	*Nectomys squamipes*	*Oligoryzomys chacoensis*	*O. fornesi*	*O. nigripes*	*Oryzomys* sp.	Total
4	Estancia Sombrero					1						1
14	Estancia Yacaré	7 (1)	4			25 (1)			2	1	3	40 (3)
15	Reserva Mbaracayú		5				1					6
16	Estancia Loma Porá	4				10		1	1			16
17	Laguna Placenta				6	6 (2)		4				16 (2)
19	Pedro P. Peña				2							2
20	Parque Cué				28 (2)							28 (2)
21	Itabó		7							5		12
22	Estancia Golondrina		1			1			2	2		6
23	Parque Nacional Ybycuí		3				3			3		9
24	Parque Nacional Tte. Enciso				21 (1)							21 (1)
25	Palmar de las Islas				13							13
26	Ape Aimé		51 (5)	1			5 (1)			12 (2)		76 (8)
27	Estancia San José		1			2			2 (1)	6	8	19 (1)
28	Estancia Parabel		60 (6)	4 (1)			5 (1)		5	5	18 (2)	97 (10)
Total		11 (1)	132 (11)	5 (1)	70 (3)	45 (3)	14 (2)	6 (1)	12 (1)	34 (2)	33 (2)	362 (27)

Table 2 Global (generalized) land cover classes used in this study along with the regional land cover categories that compose the global classes; adapted from Eva *et al.* (2002)

Global land cover classes	Regional land cover classes
Evergreen tree cover	Closed evergreen tropical forest
	Open evergreen tropical forest
Deciduous tree cover	Closed deciduous forest
	Semi deciduous transition forest
Mosaic agriculture	Mosaic agriculture/degraded forest
Intensive agriculture	Intensive agriculture
Herbaceous cover	Shrub savanna
	Open steppe grasslands
	Periodically flooded grasslands
Shrub cover	Closed shrublands
	Open shrublands
	Periodically flooded shrublands
Water	Water

RESULTS AND DISCUSSION

Tabulation of the frequency of habitat occupation for each rodent species (Table 3) shows considerable interspecific variation in rodent habitat association. Expected values (calculated as the product of the row and column sums divided by N) for many of the species/land cover class combinations were low, precluding the use of a chi-square (χ^2) test or other quantitative categorical analysis method to assess the significance of deviations between observed and expected frequencies for individual rodent species (the χ^2 test is invalid if any expected value is less than 1.0 or if 20% of the expected values are less than 5, see Bradley *et al.*, 1979). However, simple comparison of the observed vs. expected values allow some qualitative conclusions to be drawn. One species, *Akodon montensis*, accounted for over one-third of all the trapped rodents. This species shows a marked preference for intensive and mosaic agriculture sites, as well as evergreen tree cover, presumably its natural habitat. Observed frequency for *A. montensis* is nearly double that expected in areas dominated by anthropogenically disturbed land cover types (Table 3). *Akodon montensis* is proportionately under-represented in the herbaceous, shrub, and deciduous tree cover classes.

Graomys griseoflavus, the next most common species after *A. montensis*, occurs most frequently in areas of shrubland and deciduous forest, and is nearly absent from the anthropogenically disturbed cover types such as mosaic and intensive agriculture areas. *Holochilus chacarius* is also well represented in the data base, and like *G. griseoflavus* is associated primarily with either sparse herbaceous or shrub areas. One individual of *H. chacarius* was trapped in an anthropogenically disturbed area. Of the three species of *Oligoryzomys* present in the data set, *O. nigripes* appears more commonly in mosaic agriculture and evergreen forest. The other two species of *Oligoryzomys* (*O. fornesi* and *O. chacoensis*) are not present in sufficient numbers in the sample data to evaluate their habitat preference. The *Oryzomys* (not yet identified to species) is mainly associated with intensive agriculture, but occurs in all cover types.

To assess the relationship between land cover and serostatus in the sample of trapped rodents, each rodent in the data set was coded as either seropositive or seronegative, according to the results of the IFA test. A contingency table relating rodent serostatus to land cover class was generated (Table 4), and χ^2 analysis performed on the data. Results indicate a significant relationship between land cover class and serostatus ($\chi^2 = 27.02$, d.f. = 5, $P < 0.001$). Categorical analysis of the observed and expected values for each combination of land cover class and serostatus shows that observed values of seropositives exceed expected values in the intensive and mosaic agriculture categories, a pattern suggesting that seropositive rodents are more likely to be found on anthropogenically disturbed land cover. In contrast, observed seropositive values are less than or nearly the same as their expected values for the four land cover categories not defined in terms of human disturbance.

Table 3 Contingency table of rodents trapped by land cover class. Values in parentheses are the expected values for each species/land cover class combination, calculated as row marginal × column marginal/total

	Land cover class						
Species	Evergreen tree cover	Deciduous tree cover	Intensive agriculture	Mosaic agriculture	Herbaceous cover	Shrub land	Total
Akodon azarae	4 (2.32)	1 (1.08)	0 (2.02)	0 (1.99)	3 (0.94)	3 (2.62)	11
A. montensis	37 (28.13)	0 (13.15)	50 (24.48)	39 (24.11)	1 (11.33)	5 (31.79)	132
Bibimys chacoensis	0 (1.06)	0 (0.49)	1 (0.92)	1 (0.91)	2 (0.42)	1 (1.19)	5
Graomys griseoflavus	0 (14.08)	15 (6.92)	0 (12.88)	4 (12.69)	4 (5.96)	47 (16.74)	70
Holochilus chacarius	10 (9.52)	6 (4.45)	1 (8.28)	0 (8.16)	8 (3.83)	20 (10.75)	45
Nectomys squamipes	4 (2.56)	1 (1.38)	2 (2.58)	4 (2.54)	2 (1.19)	1 (3.35)	14
Oligoryzomys chacoensis	0 (1.23)	5 (0.59)	0 (1.10)	0 (1.09)	0 (0.51)	1 (1.43)	6
O. fornesi	2 (2.54)	0 (1.19)	0 (2.21)	1 (2.18)	5 (1.02)	4 (2.87)	12
O. nigripes	13 (7.19)	4 (3.36)	3 (6.26)	11 (6.16)	0 (2.90)	3 (8.13)	34
Oryzomys sp.	5 (7.19)	4 (3.36)	10 (6.26)	6 (6.16)	6 (2.90)	2 (8.13)	33
Total	75	36	67	66	31	87	362

Table 4 Contingency test and χ^2 statistic for serostatus of all rodents in the data base by land cover category. Numbers in parentheses are expected values

Sersostatus	Evergreen tree cover	Deciduous tree cover	Intensive agriculture	Mosaic agriculture	Herbaceous cover	Shrub land	Total
Seropositive	0 (5.59)	1 (2.67)	11 (4.97)	9 (4.92)	5 (2.31)	1 (6.48)	27
Seronegative	75 (69.40)	35 (33.31)	56 (62.03)	57 (61.08)	26 (28.68)	86 (80.51)	335
Total	75	36	67	66	31	87	362
χ^2 (d.f.)	27.02 (5)						
P-value	< 0.001						

Table 5 Tabulation of species vs. antibody status for each of the six land cover types (Ab+ indicates seropostives, Ab– indicates seronegatives). Dashed line in cell indicates that the species did not occur in that land cover type and was not included in the statistical test. Dashed line in *P*-value cell indicates cover type with no seropositive rodents present and for which no exact test could be conducted. The *P*-value represents the probability calculated using Fisher's exact test. Note that there are no odds ratios associated with an exact test on a contingency table greater than 2 × 2

	Evergreen tree cover		Deciduous tree cover		Intensive agriculture		Mosaic agriculture		Herbaceous cover		Shrub land	
Species	Ab+	Ab–	Ab+	Ab–	Ab+	Ab–	Ab+	Ab–	Ab+	Ab–	Ab+	Ab–
Akodon azarae	0	4	0	1	—	—	—	—	1	2	0	3
Akodon montensis	0	37	—	—	6	44	5	34	0	1	1	5
Bibimys chacoensis	—	—	—	—	0	1	0	1	1	1	0	1
Graomys griseoflavus	—	—	0	15	—	—	1	3	2	2	0	47
Holochilus chacarius	0	10	1	5	1	0	—	—	0	8	0	20
Nectomys squamipes	0	4	0	1	1	1	1	3	0	2	0	1
Oligoryzomys chacoensis	—	—	0	5	—	—	—	—	—	—	0	1
O. fornesi	0	2	—	—	—	—	0	1	1	4	0	4
O. nigripes	0	13	0	4	0	3	2	9	—	—	0	3
Oligoryzomys sp.	0	5	0	4	3	7	0	6	0	6	0	2
P-value	—		0.583		0.087		0.663		0.141		0.237	

Results from χ^2 analysis on Table 4 support both our research hypotheses: that there are regional scale relationships between hantavirus occurrence and land cover, and that agricultural landscapes are more likely to harbour seropositive rodents. However, there are two factors that may confound these results. First, the proportions of captured rodent species are not balanced. More than one-third of the sample consists of a single species, *A. montensis*, which was encountered most abundantly in agricultural habitats (see Table 3). If *A. montensis* also had a disproportionate tendency to be seropositive, then its higher numbers in agricultural areas might create the appearance that agriculture (or human disturbance in general) is related to hantavirus antibody prevalence when, in fact, the relationship may be due to some other cause.

The second potential confounding factor is the geographic distribution of the sampling sites (Fig. 1). Of the 15 trapping sites, only seven yielded seropositive rodents (Table 1). If a large number of positives were from a single site that was also highly disturbed by agriculture, this could skew the proportionality tests and lead to the conclusion that agricultural land cover is associated with increased frequency of hantavirus antibody presence, when in fact the cause is some other factor specific to that one site.

To test for the effect of unbalanced numbers of species in the trapping samples, we created contingency tables of species against antibody status for each of the six cover types (Table 5). Of the six cover types, evergreen tree cover harboured no seropositive rodents and was excluded from further consideration. Contingency tables from the remaining five cover types were tested for across-species variations in antibody presence using a form of Fisher's exact test that allows for contingency tables with rank greater than 2 × 2 (Clarkson *et al.*, 1993). Fisher's exact test was applied using a two-tailed test of significance. Use of Fisher's exact test instead of the more familiar χ^2-test was necessitated by the low observed values in several cells of the contingency tables. In each of the five contingency tables, *P*-values indicate no significant deviation from a uniform distribution of seropositive and seronegative rodents by species. Based on this result, there is no evidence to suggest that numerical predominance of any species, particularly *A. montensis*, results in a significantly larger proportion of seropositive rodents within any cover type.

To determine if there were significant associations between disturbed land cover and antibody presence across the six sites where rodents with hantavirus antibody were trapped, we used

Table 6 Results of Mantel–Haenszel test on binary data from the six sites where seropositive rodents were found. Pooled P-value is significant

	Antibody Status	
Disturbance State	Ab+	Ab–
Estancia Parabel		
Disturbed	9	50
Undisturbed	1	37
Estancia Yacare		
Disturbed	2	5
Undisturbed	1	32
Estancia San Jose		
Disturbed	1	3
Undisturbed	0	15
P.N. Tte Enciso		
Disturbed	0	1
Undisturbed	1	19
Laguna Placenta		
Disturbed	1	3
Undisturbed	1	11
Ape Aime		
Disturbed	8	48
Undisturbed	0	20
Parque Cue		
Disturbed	2	8
Undisturbed	0	12
Pooled Odds Ratio	9.21	
Pooled P-value	0.0002	
Monte Carlo on pooled P-value	0.83	

the exact form of the Mantel–Haenszel test (Higgins, 2004). The Mantel–Haenszel test is essentially a form of Fisher's exact test where the odds ratios are pooled over multiple test strata and the significance of the test is calculated for all strata. The Mantel–Haenzsel test requires that each stratum be represented by a 2×2 contingency table. We recoded the land cover data into two categories: undisturbed, formed by combining the evergreen forest, deciduous forest, herbaceous, and shrubland classes; and disturbed, formed by combining the agricultural classes. For our analysis, each of the seven sites with antibody present were treated as a stratum. A one-tailed test of significance was used.

The pooled results of this test yielded a significant common odds ratio, indicating an association between human disturbance and antibody presence (Table 6). The P-value for the pooled common odds ratio was significant ($P = 0.0002$), a result consistent with the hypothesis that the proportion of seropositive rodents in disturbed areas was higher than would be expected by chance. It is possible that this result might have occurred because of an exceptionally strong response at one or two sites, rather than a uniform effect across all seven sites where seropositive rodents were trapped. To test for this possibility, we used a two-tailed Monte-Carlo simulation (10,000 iterations) to test for the homogeneity of the odds ratios across all seven sites. The resulting P-value was not significant ($P = 0.83$), indicating that the proportion of rodents in each cell of the 2×2 contingency tables is statistically similar at each site, although the magnitude of the values varied considerably. These results support the hypothesis that antibody-positive rodents are more likely to be associated with human-disturbed land cover, regardless of the geographic location of the site.

CONCLUSIONS

We have hypothesized that there is a positive relationship between agricultural land cover disturbance and hantavirus in rodents in Paraguay, and that this relationship is detectable using coarse spatial resolution remote sensing data. Our findings support both of these hypotheses. The majority of the seropositive rodents (20 of 27) were trapped in agricultural areas (Table 4). Of the remaining seven positives, all but one occurred in areas dominated by shrubs or herbaceous vegetation. The land cover classes associated with the presence of hantavirus are notable for greater spatial diversity and internal complexity than the closed canopy forest types (Forman, 1997). This observation suggests that land cover structure and human impact might both be implicated in producing conditions susceptible to the presence of infected host animals. Thus, our analysis suggests two conclusions:

(**1**) land cover plays a role in the prevalence of positive cases, with agricultural land cover associated with a greater presence of seropositive rodents; and

(**2**) human disturbance matters in the distribution of rodents that are or have been exposed to hantavirus.

Because agriculture is a common form of human land cover alteration, these two conclusions are no doubt interrelated.

This study does not permit more detailed analysis of the reasons why agricultural landscapes are more likely to harbour antibody positive rodents. However, because agriculture is often associated with changes in landscape structure, we can speculate on the reasons why a coarse scale relationship between cover type and antibody status is observable. Clearly, the scale of landscape change relevant to rodents is much too fine to be evaluated meaningfully using the remote sensing data utilized here. However, we can surmise that certain land cover classes, especially those characterized by human disturbance, are associated with a higher likelihood of fine-scale habitat alteration. That is, landscape change relevant to the rodents that host hantavirus occurs at extremely fine *grain*, but the *extent* of the disturbance can be quite large — large enough, in fact, to differentiate the disturbed area as a discrete land cover category at a mapping resolution of 1 km^2. At a finer spatial scale, alteration of habitat within the agricultural areas increases the likelihood that a rodent will be exposed to hantavirus during its lifetime. Although the exact mechanism of interspecific transmission of hantavirus is not known, one possibility is transmission from infected to non-infected rodents through encounters between individuals as they compete for territory and resources. If a region of potential rodent habitat is disturbed, for example by replacing relatively homogeneous extents of the original land cover with a more patchy mosaic of agricultural cover, this could serve to increase these encounters as individuals compete for smaller areas of desirable territory (Langlois *et al.*, 2001). There is some evidence to suggest that environmental stresses might increase susceptibility to infection in hantavirus hosts in urban areas (Klein *et al.*, 2002). Rodents in agriculturally altered environments might also undergo physiological stress reactions that render them more susceptible to infection. Further studies at finer spatial scales are needed to understand fully why agriculture or other anthropogenic disturbance is associated with higher rates of viral presence in host rodents.

In addition to contributing to a basic understanding of the ecology of hantaviruses (and perhaps zoonotic aetiological agents in general), our results also have important implications for the use of geospatial analysis technologies for predicting the presence of hantaviruses in rodent communities and in humans. Our results suggest that monitoring efforts for detecting hantavirus outbreaks should concentrate on areas of human landscape disturbance, especially agricultural areas. Our results further show that coarse resolution remote sensor data can be a valuable tool for monitoring land cover changes likely to be associated with the presence of hantavirus. We could envision a multiresolution monitoring system in which regional or national scale observations from coarse spatial resolution sensors such as AVHRR or SPOT-VGT might be used along with climate and environmental data to identify areas where land cover change creates potential 'hotspots' of viral activity (*sensu* Niklasson *et al.*, 1992). Once identified, these hotspots could then be more closely monitored using higher resolution remote sensing instruments or perhaps by ground level surveillance. When environmental, climatic, and landscape conditions indicate heightened susceptibility to viral activity, local public health organizations could be alerted. Such a monitoring system would be particularly valuable in developing countries such as Paraguay, where hantavirus illnesses are a significant public health threat.

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