Journal of Mammalogy, 89(3):684–690, 2008

EPIDEMIOLOGICAL CONSIDERATIONS OF RODENT COMMUNITY COMPOSITION IN FRAGMENTED LANDSCAPES IN PANAMA

Gerardo Suzán,* Anibal Armién, James N. Mills, Erika Marcé, Gerardo Ceballos, Mario Ávila, Jorge Salazar-Bravo, Luis Ruedas, Blas Armién, and Terry L. Yates

Museum of Southwestern Biology and Department of Biology, University of New Mexico, Albuquerque, NM 87131-0001, USA (GS, EM, TLY)
Instituto Conmemorativo GORGAS, Avenida Justo Arosemena y Calle 35, P.O. Box 6991, Zona 5, Ciudad de Panamá, 53706-1102 Panamá (AA, MA)
Division of Viral and Rickettsial Diseases, Centers for Disease Control and Prevention, Atlanta, GA 30333, USA (JNM)
Instituto de Ecología, Universidad Nacional Autónoma de México, Apartado Postal 70-275, Ciudad Universitaria CP. 04510, México, Distrito Federal, México (GC)
Department of Biological Sciences, Texas Tech University, Lubbock, TX 79409-3131, USA (JS-B)
Department of Biology and Museum of Vertebrate Biology, Portland State University, Science Building, Portland, OR 97207-0751, USA (LR)
Department of Pathobiological Sciences, School of Veterinary Medicine, University of Wisconsin–Madison, 2015 Linden Drive, Madison, WI 53706-1494, USA (BA)

We predicted that more-fragmented habitats are associated with lower diversity of small mammals and higher densities of populations of rodents that are hosts of hantaviruses. We compared diversity and distribution of small mammals that are either hosts or nonhosts of hantaviruses in 6 Panamanian national parks and adjacent areas with varying degree of human impacts. We sampled forest, edge, and anthropogenically disturbed habitats. The generalist rodents *Oligoryzomys fulvescens* (reservoir of Choclo virus) and *Zygodontomys brevicauda* (reservoir of Calabazo virus) were more abundant in disturbed habitats, especially in smaller and more isolated patches, where population density and diversity of other rodent species was lowest. In contrast, these 2 species had lower abundances in larger forested areas with more nonreservoir species of small mammals. Our results suggest that the change in the natural environment resulting from tropical deforestation is increasing the abundance and distribution of species that are reservoirs for hantaviruses. Therefore, it is likely that forest fragmentation has contributed to recent outbreaks of hantavirus pulmonary syndrome in tropical areas. Conservation of natural resources becomes all the more imperative, not only for protecting fauna and flora but also for human health.

Key words: diversity loss, emerging diseases, generalist rodents, habitat fragmentation, hantavirus reservoirs, Panama

Tropical forests have been dramatically reduced by human activities worldwide in the last 3 decades and the ecological, epidemiological, and social consequences of such large-scale transformation are still unpredictable. Millions of hectares of tropical forest are destroyed annually. Between 1980 and 1990, 40% of the world's tropical forest was converted into permanent agriculture, cattle ranching, or other uses (Hughes et al. 1997; Kremen et al. 2000). Extensive global habitat destruction has created a complex array of land cover, fragmenting species distributions, altering the composition of natural communities, and changing biotic interactions such as predation, mutualism, competition, and infectious diseases (Ceballos and Ehrlich 2002; McNaughton 1993).

Increases in the geographic distribution and size of human populations and anthropogenic changes such as deforestation, land conversion, agricultural intensification, and introduction of livestock and exotic species might influence community structure and species composition, and consequently, the dynamics of infectious diseases. In the case of small mammal communities, a generalized outcome of habitat destruction and fragmentation is the simplification of communities, which tend to be dominated by generalist species. These generalists tend to

---

* *Correspondent: gerardosuz@gmail.com*

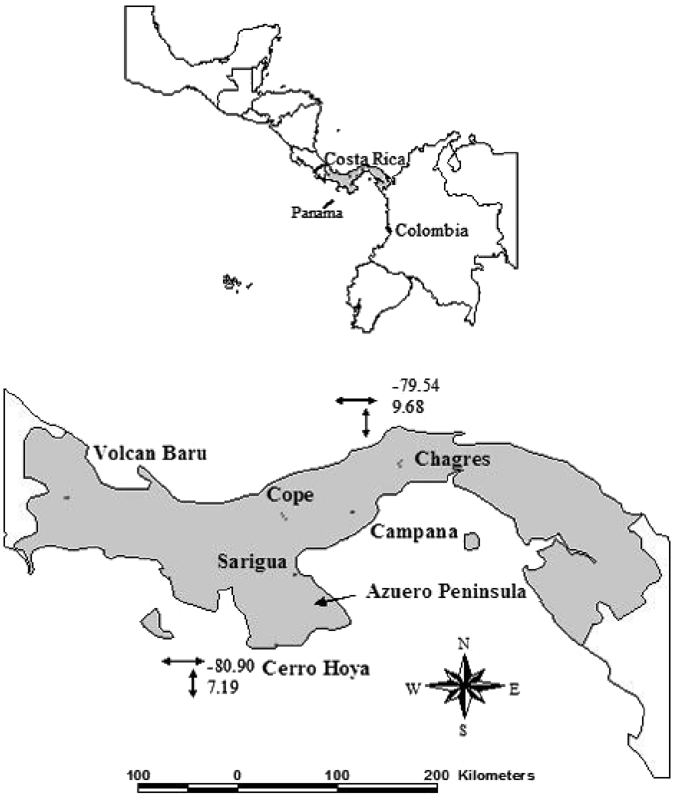

FIG. 1.—Location of the 6 national parks in central and western Panama used as small mammal study sites, June 2001 and November 2002.

TABLE 1.—Environmental characteristics of 6 national parks in Panama used as study sites. The parks were selected to represent the environmental heterogeneity of the country, from tropical dry forests to rain forests, across elevational gradients, and from relatively small to large protected areas.

Park	Elevation category (m)	Fragment size (ha)	Protected area (ha)
Chagres National Park	<300	>5	129,000
Sarigua National Park	<300	<5	8,000
Cope (Omar Torrijos) National Park	300–800	>5	6,000
Cerro Hoya National Park	300–800	<5	32,000
Volcan Baru National Park	>800	>5	207,000
Campana National Park	>800	<5	4,800

have a high adaptability to a wide range of habitats. In contrast, specialist species, which are highly adapted to live in a narrowly defined habitat, are prone to become endangered because of the extensive habitat destruction and agricultural and urban development. Studies in Costa Rica (Daily et al. 2003), Venezuela (Utrera et al. 2000), the United States (Diffendorfer et al. 1995), and Paraguay (Yahnke et al. 2001), among other places, have shown that human-induced habitat loss results in limited or decreasing populations of specialist forest species and favors those species that tolerate human activities. These generalist species flourish in agricultural plots, small remnants of native vegetation, and even in human settlements. Generalist species are often involved in the transmission of pathogens to humans, including arenaviruses such as Lassa fever and the South American hemorrhagic fevers, parvovirus, toxoplasma, and rabies, among others (Childs et al. 1995; Deem et al. 2001; Suzán and Ceballos 2005).

Hantaviruses are hosted by a great variety of species of rodents in the family Cricetidae in Europe, Asia, and the Americas. Hantaviruses are transmitted to humans by inhalation of the aerosolized virus in rodent urine, feces, and saliva or by direct contact such as bites (Tsai 1987). Hantaviruses cause hemorrhagic fever with renal syndrome in Asia and Europe and hantavirus pulmonary syndrome in the Americas. Although incidence of hantavirus pulmonary syndrome in the United States is low, with only 416 reported cases since 1993, mortality is as high as 35% (Centers for Disease Control and Prevention 2007). Hantavirus pulmonary syndrome in humans has been reported throughout North, Central, and South America (Williams et al. 1997) and recently specifically in Panama where 79 human cases have been detected and sporadic cases still occur (B. Armién, in litt.).

After the 1st cases of hantavirus pulmonary syndrome in Panama in 2000, 2 new hantaviruses were identified: Choclo virus causes hantavirus pulmonary syndrome and is associated with the pygmy rice rat (*Oligoryzomys fulvescens*) as its host, and Calabazo virus, which is not known to cause hantavirus pulmonary syndrome, and is associated with the short-tailed cane mouse (*Zygodontomys brevicauda*—Bayard et al. 2004; Vincent et al. 2000). Based on the information already available, we hypothesized that both habitat fragmentation and loss of diversity resulting from human activities favors the distribution of these hantavirus reservoir species and the potential risk of hantavirus pulmonary syndrome outbreaks in Panama. To test this hypothesis, we compared communities of small mammals in different habitats with varying degrees of anthropogenic fragmentation, including forest, edges, and pastures, in 6 national parks and surrounding areas in Panama. We expected to find less-diverse small mammal assemblages numerically dominated by hantavirus host species in the more degraded habitats.

MATERIALS AND METHODS

Study area and sampling design.—We selected 6 national parks distributed in several biomes throughout Panama (Fig. 1; Table 1). At each park, we choose 3 types of habitat: forest—pristine areas inside mature forest; disturbed—anthropogenically disturbed habitats, specifically pastures and agricultural fields outside the boundaries of the forest fragment; and edge—relatively abrupt transitions between forest and disturbed habitats. Edge sites were located at the border of forest fragments. We compared small mammal communities and their species composition, richness, evenness, and relative abundance with site characteristics such as fragmentation and elevation. The 3 habitat types were included in the analyses.

In each park we established a 10 × 10 grid in a forest, a disturbed area, and an edge. Each grid was sampled using 100 Sherman live traps (8 × 8 × 23 cm; H. B. Sherman Traps, Inc.,

TABLE 2.—Species identity and total number of captured individuals by habitat type. Species are classified by habitat association (specialist or generalist) and whether the species have been reported as reservoirs, hosts, potential host, or nonhosts in Panama.

Species	Forest	Edge	Disturbed	Habitat specialist/generalist	Hantavirus reservoir/host/nonhost
Didelphis marsupialis	1			Forest generalist	Nonhost
Heteromys desmarestianus	18			Forest specialist	Nonhost
Marmosa mexicana	1			Forest specialist	Nonhost
Marmosa robinsoni	1			Forest specialist	Nonhost
Sigmodontomys alfari	2			Forest specialist	Potential host
Oryzomys bolivaris	8	1		Forest specialist	Potential host
Peromyscus mexicanus	26	13		Forest generalist	Host (unknown hantavirus)
Reithrodontomys mexicanus	13	6	1	Forest generalist	Host (Rio Segundo virus)
Reithrodontomys creper	3	2		Forest generalist	Host (unknown hantavirus)
Oryzomys talamancae	3	2	1	Forest generalist	Potential host
Melanomys caliginosus	2	2		Forest generalist	Potential host
Oryzomys albigularis	3	4	1	Forest generalist	Potential host
Liomys adspersus	14	10	22	Generalist	Nonhost
Proechimys semispinosus	2	5		Forest specialist	Nonhost
Scotinomys xerampelinus	5	11	3	Forest generalist	Host (unknown hantavirus)
Zygodontomys brevicauda	1	3	4	Generalist	Reservoir (Calabazo virus)
Mus musculus			3	Generalist	Nonhost
Sigmodon hispidus		3	9	Generalist	Potential reservoir
Oligoryzomys fulvescens		7	10	Generalist	Reservoir (Choclo virus)
Reithrodontomys sumichrasti		9		Specialist	Host (unknown hantavirus)
Tylomys watsoni		1		Specialist	Potential host
Oligoryzomys vegetus		1		Specialist	Potential host

Tallahassee, Florida), with traps set at 10-m intervals and baited with peanut butter and oats. In edges, the middle trap line was centered on, and parallel to, the edge of the forest. Each site was sampled for 3 consecutive nights during each of 2 sampling periods (June 2001 and November 2002). Thus, a total of 18 grids were established (6 parks × 3 habitat types). In each park there was a total of 1,800 trap-nights including 600 trap-nights per habitat.

All small mammals were identified to species and sex and weighed. The project was approved by the University of New Mexico Animal Care and Use Committee (protocol 20014), and meets the guidelines approved by the American Society of Mammalogists (Gannon et al. 2007). All animals were treated in a humane manner. Voucher specimens were deposited at the Museum of Southwestern Biology, University of New Mexico.

Data analysis.—We considered 2 categories of fragment size for forested areas: isolated fragments of <5 ha and fragments > 5 ha and connected to other forested areas (Table 1). Elevation was classified in 3 categories: <300 m, 300–800 m, and >800 m. Two parks were included in each elevation category (Table 1). An analysis of variance (ANOVA) was used to test for differences in species diversity and richness among sites. Statistical significance was set at $P < 0.05$.

Species richness, species composition, and diversity of small mammals at all sites were determined. Species diversity was calculated by using N_2 of Hill ($N_2 = 1/\Sigma\, p_i^2$, where p_i is the proportion of species i in the community—Hill 1973). Evenness ($E = N_2/S$, where $S =$ total number of species—Krebs 1999) was calculated as the relative distribution of individuals among the species present in the community. To assess the relation between hantavirus reservoirs and species diversity, we selected the 2 hantavirus reservoirs found in the Peninsula de Azuero (*O. fulvescens* and *Z. brevicauda*, hosts for Choclo and Calabazo viruses, respectively; Fig. 1). We compared the dependent variable (combined total captures of *O. fulvescens* and *Z. brevicauda*) with explanatory variables including species diversity, habitat type, elevation, and fragment size using ANOVA. Statistical significance was set at $P < 0.05$. Analyses were done using SYSTAT 9 (Systat Software Inc., San Jose, California), and SPSS 12 (SPSS Inc., Chicago, Illinois).

Cluster analyses for species distributions were performed based on the Sorensen index, measured as percent of dissimilarity (PD) $= (1 - 2W/(A + B)$, where W is the sum of shared abundances and A and B are the sums of abundances in individual sample units—McCune and Mefford 1999). Finally, the Jaccard similarity index (*J*—Jaccard 1912) was used to quantify the similarity of species composition among habitat types (forest, edges, and disturbed habitats). The Sorensen index and Jaccard index are quantitative and qualitative indices, respectively, and were used to compare the degree of similarity between samples, both within and between plots. Only rodents were considered in all statistical analyses.

RESULTS

Community composition and structure.—A total of 237 individuals belonging to 22 species, including 3 marsupials and 19 rodent species, were captured during 2 sampling periods in 6 National Parks (Table 2). Of these species, 6 such as *Heteromys desmarestianus* and *Sigmodontomys alfari* are considered forest specialists, 8 such as *Peromyscus mexicanus* and *Reithrodontomys mexicanus* are forest generalists, and 5 such as *O. fulvescens* and *Z. brevicauda* are generalists.

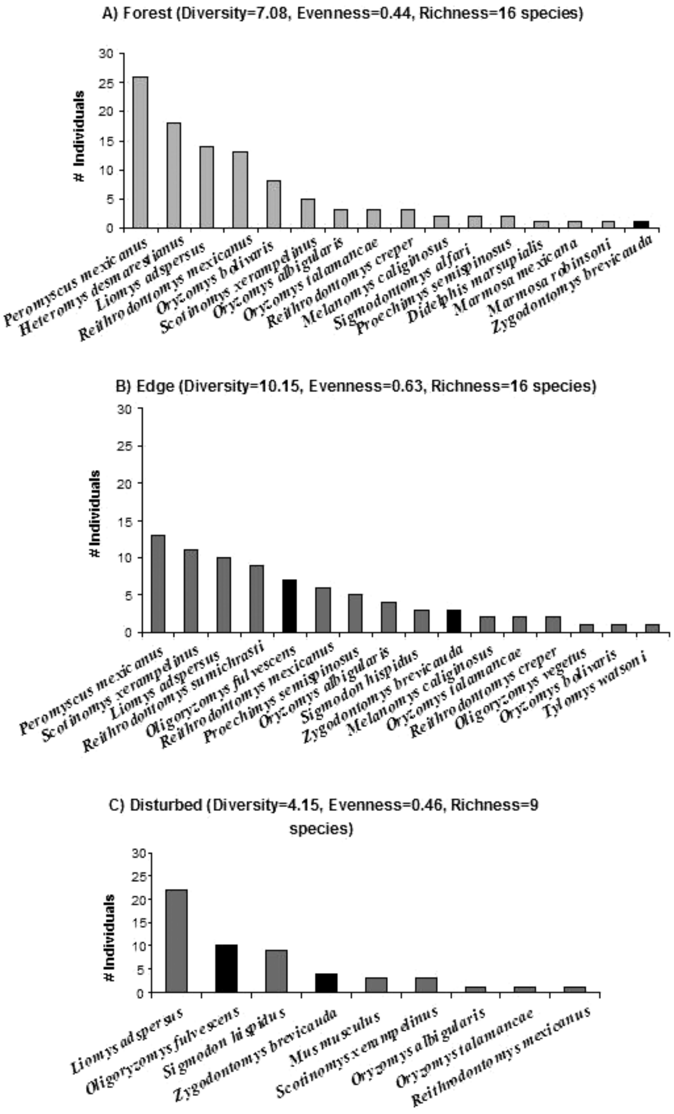

FIG. 2.—Species composition of small mammal communities in the 3 habitat types in our study. Diversity (Hill's N_2), evenness, and species richness are provided for each habitat type. Bars in black represent the relative abundance of the hantavirus reservoirs.

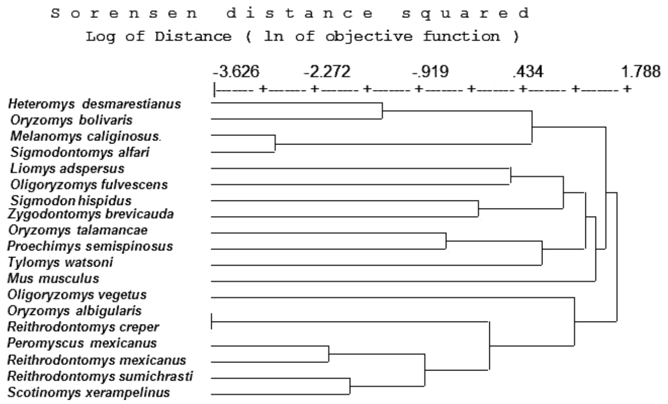

FIG. 3.—Cluster analysis using Sorensen distance (measured as percent dissimilarity, which assesses relative presence/absence and is most influenced by rare taxa). An asterisk (*) indicates generalist species, including the hantavirus reservoirs *Oligoryzomys fulvescens* and *Zygodontomys brevicauda*. A dot (•) indicates species that have been reported with hantavirus antibodies in other regions in Panama.

As we expected, there were differences in small mammal composition and abundances among habitats, with higher species diversity and higher numbers of specialist species in forest habitats. Differences among habitat types in total abundances were not statistically significant (1-way ANOVA, $F = 0.55$, *d.f.* = 2, 13, $P = 0.58$); however, most individuals (103, 43%, 16 species) were trapped in forested areas, followed by edge habitats (80, 34%, 16 species), and disturbed habitats (54, 23%, 9 species). A large number of species (13, 59%) tended to occur in both forest and forest edges, whereas 3 species (13%) tended to occur in both edges and disturbed habitats, including *O. fulvescens*, the reservoir for Choclo virus. The introduced *Mus musculus* was exclusively found in disturbed habitats. Forest habitats included more specialist species, whereas generalist species were distributed in edges and pastures (Table 2). Although overall abundance of small mammals was greatest in forest, species diversity was greatest in edge habitat (Fig. 2). Average species richness and diversity of small mammals were lower in disturbed habitats ($\bar{X} = 2.16$, $SE = 0.4$, and $\bar{X} = 1.81$, $SE = 0.3$, respectively) than in edges ($\bar{X} = 3.50$, $SE = 0.72$, and $\bar{X} = 2.76$, $SE = 0.45$, respectively) and forested areas ($\bar{X} = 3.00$, $SE = 1.00$, and $\bar{X} = 2.14$, $SE = 0.55$, respectively). Diversity as measured by Hill's N_2 was not statistically different among categories of elevation ($F = 0.45$, *d.f.* = 2, 13 $P = 0.67$). We predicted and confirmed that the size of forest fragments is relevant to species diversity. The 3 smaller habitat fragments in forested areas (<5 ha) had significantly fewer species ($\bar{X} = 3.77$) than did larger (>5-ha) fragments ($\bar{X} = 2.00$; 1-way ANOVA, $F = 6.00$, *d.f.* = 1, 14 $P = 0.026$).

Abundance of hantavirus reservoirs.—As expected, both hantavirus reservoirs (*O. fulvescens* and *Z. brevicauda*) were more common in both disturbed habitats and edge habitats than in forest (Fig. 2). Forested areas had much lower abundances of *O. fulvescens* and *Z. brevicauda* (species combined; $\bar{X} = 0.16$ individuals/site, $SD = 0.40$) than edges ($\bar{X} = 1.66$ individuals/site, $SD = 1.63$) or pastures ($\bar{X} = 2.33$ individuals/site, $SD = 2.73$). Regardless of elevation, trapping sites in smaller fragments in forested edges and disturbed areas had significantly higher combined abundances of *O. fulvescens* and *Z. brevicauda* than did sites in larger fragments (0.77 individuals/site versus 0.10 individuals/site, respectively; $F = 8.67$, *d.f.* = 1, 16, $P = 0.01$). There were no statistical differences in the combined abundances of *O. fulvescens* and *Z. brevicauda* among the 3 categories of elevation ($F = 0.69$, *d.f.* = 2, 15, $P = 0.51$).

Clustering of species by Sorensen distances grouped *O. fulvescens* and *Z. brevicauda* with other generalist species. A 2nd cluster grouped species that have been reported with hantavirus antibodies in other regions in Panama where Río Segundo virus is endemic (Salazar-Bravo et al. 2004; Fig. 3). The small mammal community of the forests was more similar to that of edges (Jaccard similarity index, $J = 0.54$) than to that of disturbed areas ($J = 0.11$). Higher similarities in species composition were also found between edges and disturbed areas ($J = 0.42$). Species composition in all disturbed sites was similar. Finally, when projecting their distribution and abundance at a coarse scale, the proportion of the total small mammal assemblage composed of the 2 species of hantavirus reservoir was relatively high in the 2 parks on the Azuero Peninsula, where most cases of hantavirus pulmonary syndrome have been reported (Fig. 4).

DISCUSSION

Tropical forests have been dramatically transformed into pastures and croplands at a worldwide scale in recent decades. The ecological, epidemiological, and social consequences of the massive transformation are still unpredictable. Our data support the hypothesis that higher species diversity of small mammals in neotropical forests (and possibly in other tropical regions) is associated with lower abundances of some hantavirus reservoir species. Our results clearly indicate that habitat fragmentation and conversion of natural habitats to pastures and agriculture has favored rodent species that are hantavirus reservoirs, such as *O. fulvescens* and *Z. brevicauda*, across a gradient of habitats. These species are more abundant in the seminatural matrix where more human activities occur and have likely played a role in the recent outbreaks of hantavirus pulmonary syndrome in Panama.

Although a buffering role of biodiversity against the incidence and spread of disease has been demonstrated by theoretical and empirical studies, little is known about the role of biological diversity in directly transmitted diseases. It has been proposed that greater diversity of plant communities would increase resistance to invasion by nonnative plants (diversity-invasibility hypothesis), and that a greater diversity would decrease the severity of plant disease (diversity-disease hypothesis—Elton 1958). Recently, it has been suggested that higher species diversity in vertebrate communities reduces the incidence of Lyme disease, an indirectly transmitted diseases (the dilution-effect hypothesis of Ostfeld and Keesing [2000]). Our results suggest that the change in the natural environment resulting from tropical deforestation is increasing the abundance and local distribution of rodent species that are reservoirs for hantaviruses, which are viruses transmitted directly to humans.

Our results on patterns of species abundance and distribution are a convincing example that rodent species that are hantavirus reservoirs are more abundant in sites with higher isolation and fragmentation resulting from human activities. Our results show clearly that these rodent hantavirus reservoir species are more abundant where habitat fragmentation and human settlements are persistent. Overgrazing and expansion of agriculture also may have contributed to the increased abundance and distribution of the most generalist species of sigmodontine rodents in other countries. These include some species of *Calomys* and *Oligoryzomys* in South America and *Zygodontomys*, *Sigmodon*, and *Oligoryzomys* in Central America (Daily et al. 2003; Utrera et al. 2000). Paleontological studies have suggested that environmental deterioration due to the expansion of farming has favored an increase in population densities of rodents, including hantavirus reservoirs in Chile, for hundreds of years (Pardiñas et al. 2000).

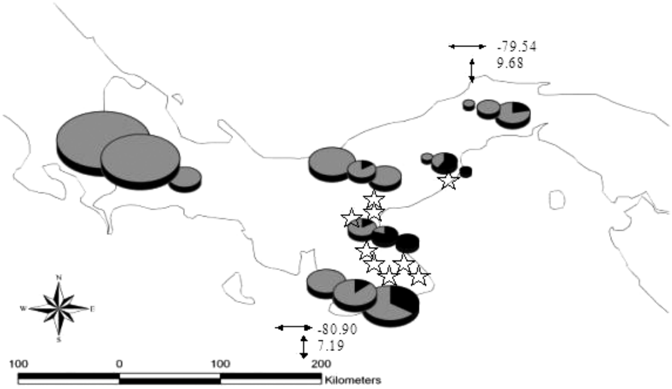

FIG. 4.—Spatial projection of combined relative abundance of *Oligoryzomys fulvescens* and *Zygodontomys brevicauda*. Size of each pie chart is proportional to the number of individuals captured. Proportions of captures consisting of *O. fulvescens* and *Z. brevicauda* are indicated in black; other species are indicated in gray. Stars represent areas where cases of hantavirus pulmonary syndrome in humans are reported.

Similarity indices and cluster analyses can be important indicators of ecological relationships among hosts in the ecology of infectious diseases. Our results showing that prevalence of reservoir species also is enhanced in small mammal communities in degraded lands with low biodiversity are supported by additional empirical and experimental studies (Peixoto and Abramson 2006; Ruedas et al. 2004; Suzán et al. 2006). However, this is the 1st time this issue has been addressed in terms of the services provided by high-biodiversity small mammal communities, and 1 of few examples available about the links among diversity of small mammals, diseases affecting humans, and ecosystem services.

Although little is known about the mechanisms underlying the changes in rodent community structure in perturbed landscapes, habitat loss has been shown to alter species interactions, resulting from the reduction in the number of specialists and the increase in generalist species (Taylor and Merriam 1996). Generalist species are able to survive in a wide array of small patches of forest as well as in human-dominated ecosystems. Ecological consequences of the increase in abundance of generalist species may include restructuring food webs and endangering endemic fauna (Kruuk and Snell 1981). Our results showed that many species were absent or present in low numbers in the altered landscape. Undoubtedly, if tropical forest cover further declines, extinction of specialist species will likely occur, with important consequences for ecosystem function and for human health (Ceballos and Ehrlich 2002).

Panama has undergone severe loss of biodiversity over the last 50 years. Dramatic habitat transformation has occurred due to shifting cultivation and cattle raising (Fischer and Vasseur 2000). This has led to agricultural areas dominating the landscape and has greatly changed the composition of small mammal communities. The remaining communities of rodents in the altered landscapes are often generalist species that are able to survive in small patches of forest or in human-dominated ecosystems. Understanding the dynamics, distribution, and structure of mammal assemblages in the major biomes of Panama also will help to understand the distribution of hantavirus and areas of major epidemiological risk. Because habitat fragmentation and loss of diversity are global concerns, the basic conclusions of our study may apply to other infectious diseases in several geographical regions or habitat types. The association of biodiversity and risk of disease is an additional factor contributing to the importance of conservation of natural resources.

Tropical deforestation is responsible for many extinctions of species, and despite conservation efforts, rates of deforestation and conversion to agriculture remain high. If this pace continues, we expect to see an increase in both distribution and abundance of rodent hosts of hantaviruses as well as other zoonotic diseases in tropical areas, with unknown epidemiological consequences.

RESUMEN

En este trabajo hicimos la predicción de que los hábitats más fragmentados están asociados con una menor diversidad de pequeños mamíferos y una mayor densidad de los hospederos de hantavirus. Para probar esta hipótesis, comparamos la diversidad y distribución de pequeños mamíferos en 6 parques nacionales y áreas adyacentes en Panamá con diferente grado de intervención humana. Se muestreó el bosque, borde y hábitats perturbados por actividades antropogénicas. Los roedores generalistas *Oligoryzomys fulvescens* (reservorio del virus Choclo) y *Zygodontomys brevicauda* (reservorio del virus Calabazo) fueron más abundantes en hábitats perturbados. Contrariamente, fue en éste tipo de hábitat donde la densidad y diversidad de otras especies de roedores fue menor. En contraste, los parches de mayor área tuvieron mayor diversidad de especies de pequeños mamíferos y menor abundancia de *O. fulvescens* y *Z. brevicauda*. Estos resultados sugieren que el cambio en los ambientes naturales debido a la deforestación en los trópicos, aumenta la abundancia y distribución de especies que son reservorias para hantavirus. Debido a esto, pensamos que la fragmentación de hábitats ha contribuido en recientes brotes del sindrome pulmonar hantavirus en Panamá. La conservación de los recursos naturales es imperativa no sólo con el fin de protejer a la flora y fauna, sino a la salud humana.

ACKNOWLEDGMENTS

This research was supported by Instituto Conmemmorativo Gorgas, American Society of Mammalogists, and Latin American and Iberian Institute, University of New Mexico. We thank Instituto Conmemmorativo GORGAS personnel for splendid field assistance, serological analyses, and general support. We especially thank H. Suzán-Azpiri for statistical analyses and O. Vargas, N. Ríos, E. Broce, F. Crespo, C. Falcón, K. Gelusso, J. M. Pascale, and H. Padmanaba for field assistance. We are grateful for all support provided by the Ministry of Health of Panama. We thank Chilean International Collaboration in Infectious Disease Research grant for providing some supplies and T. Giermakowski, J. Cook, R. Parmenter, and E. S. Loker, who reviewed an earlier version of this manuscript.

LITERATURE CITED

BAYARD, V., ET AL. 2004. Outbreak of hantavirus pulmonary syndrome, Los Santos, Panama, 1999–2000. Emerging Infectious Diseases 10:1635–1642.

CEBALLOS, G., AND P. R. EHRLICH. 2002. Mammal population losses and the extinction crisis. Science 296:904–907.

CENTERS FOR DISEASE CONTROL AND PREVENTION. 2007. Case information: hantavirus pulmonary syndrome case count and descriptive statistics. http://www.cdc.gov/ncidod/diseases/hanta/hps/noframes/caseinfo.htm. Accessed January 2007.

CHILDS, J. E., J. N. MILLS, AND G. E. GLASS. 1995. Rodent-borne hemorrhagic-fever viruses—a special risk for mammalogists. Journal of Mammalogy 76:664–680.

DAILY, G. C., G. CEBALLOS, J. PACHECO, G. SUZAN, AND A. SANCHEZ-AZOFEIFA. 2003. Countryside biogeography of neotropical mammals: conservation opportunities in agricultural landscapes of Costa Rica. Conservation Biology 17:1814–1826.

DEEM, S. L., W. B. KARESH, AND W. WEISMAN. 2001. Putting theory into practice: wildlife health in conservation. Conservation Biology 15:1224–1233.

DIFFENDORFER, J. E., M. S. GAINES, AND R. D. HOLT. 1995. Habitat fragmentation and movements of 3 small mammals (*Sigmodon*, *Microtus*, and *Peromyscus*). Ecology 76:827–839.

ELTON, C. 1958. The ecology of invasions of plants and animals. Methuen, London, United Kingdom.

FISCHER, A., AND L. VASSEUR. 2000. The crisis in shifting cultivation practices and the promise of agroforestry: a review of the Panamanian experience. Biodiversity and Conservation 9:739–756.

GANNON, W. L., R. S. SIKES, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 88:809–823.

HILL, M. O. 1973. Diversity and evenness—unifying notation and its consequences. Ecology 54:427–432.

HUGHES, J. B., G. C. DAILY, AND P. R. EHRLICH. 1997. Population diversity: its extent and extinction. Science 278:689–692.

JACCARD, P. 1912. The distribution of flora in the alpine zone. New Phytologist 11:37–50.

KREBS, J. C. 1999. Ecological methodology. 2nd ed. Addison-Wesley Educational Publisher, Inc., Menlo Park, California.

KREMEN, C., ET AL. 2000. Economic incentives for rain forest conservation across scales. Science 288:1828–1832.

KRUUK, H., AND H. SNELL. 1981. Prey selection by feral dogs from a population of marine iguanas (*Amblyrhynchus cristatus*). Journal of Applied Ecology 18:197–204.

MCCUNE, B., AND M. J. MEFFORD. 1999. PC-ORD. Multivariate analysis of ecological data, version 4.10. MjM Software Design, Gleneden Beach, Oregon.

MCNAUGHTON, S. J. 1993. Biodiversity and function of grazing systems. Pp. 361–383 in Biodiversity and ecosystem function (E.-D. Schulze and H. A Mooney, eds.). Springer-Verlag, Berlin, Germany.

OSTFELD, R., AND F. KEESING. 2000. The function of biodiversity in the ecology of vector-borne zoonotic diseases. Canadian Journal of Zoology 78:2061–2078.

PARDIÑAS, U. F. J., G. J. MOREIRA, C. M. GARCIA-ESPONDA, AND L. J. M. DE SANTIS. 2000. Environmental deterioration and micromammals during the Holocene in northeastern Patagonian steppe (Argentina). Revista Chilena de Historia Natural 73:9–21.

Peixoto, I. D., and G. Abramson. 2006. The effect of biodiversity on the hantavirus epizootic. Ecology 87:873–879.

Ruedas, L. A., et al. 2004. Community ecology of small mammal populations in Panama following an outbreak of hantavirus pulmonary syndrome. Journal of Vector Ecology 29:177–191.

Salazar-Bravo, J., et al. 2004. Serosurvey of wild rodents for hantaviruses in Panama, 2000–2002. Journal of Wildlife Diseases 40:103–109.

Suzán, G., and G. Ceballos. 2005. The role of feral mammals on wildlife infectious disease prevalence in two nature reserves within Mexico City limits. Journal of Zoo and Wildlife Medicine 36:479–484.

Suzán, G., J. T. Giermakowski, E. Marce, H. Suzán-Azpiri, B. Armien, and T. L. Yates. 2006. Modeling hantavirus reservoir species dominance in high seroprevalence areas on the Azuero Peninsula of Panama. American Journal of Tropical Medicine and Hygiene 74:1103–1110.

Taylor, P. D., and G. Merriam. 1996. Habitat fragmentation and parasitism of a forest damselfly. Landscape Ecology 11:181–189.

Tsai, T. F. 1987. Hemorragic fever with renal syndrome: mode of transmision to humans. Laboratory Animal Science 37:428–430.

Utrera, A., et al. 2000. Small mammals in agricultural areas of the western llanos of Venezuela: community structure, habitat associations, and relative densities. Journal of Mammalogy 81: 536–548.

Vincent, M. J., et al. 2000. Hantavirus pulmonary syndrome in Panama: identification of novel hantaviruses and their likely reservoirs. Virology 277:14–19.

Williams, R. J., et al. 1997. An outbreak of hantavirus pulmonary syndrome in western Paraguay. American Journal of Tropical Medicine and Hygiene 57:274–282.

Yahnke, C. J., P. L. Meserve, T. G. Ksiazek, and J. N. Mills. 2001. Patterns of infection with Laguna Negra virus in wild populations of *Calomys laucha* in the central Paraguayan Chaco. American Journal of Tropical Medicine and Hygiene 65:768–776.

Submitted 13 January 2007. Accepted 12 September 2007.

Associate Editor was John A. Yunger.