Hantavirus Infection and Habitat Associations among Rodent Populations in Agroecosystems of Panama: Implications for Human Disease Risk

Aníbal G. Armínio,* Blas Armínio, Frederick Koster, Juan M. Pascale, Mario Avila, Pablo González, Manuel de la Cruz, Yenatze Zaldívar, Yaxedis Mendoza, Fernando Gracia, Brian Hjelle, Sang-Hoon Lee, Terry L. Yates, and Jorge Salazar-Bravo

Department of Population Medicine, College of Veterinary Medicine, University of Minnesota, Twin Cities, St. Paul, MN, USA; Instituto Comunitario de Ortuño, Gtavas de Estudios de la Salud, Panama City, Panama; Ministry of Health, Panama Province, Panama; Lellosse Respirometry Research Institute, Albuquerque, New Mexico; Hospital Santo Tomas, Panama City, Panama; Department of Pathology, School of Medicine, University of New Mexico, Albuquerque, New Mexico; Division of Epidemiology and Biostatistics, Department of Internal Medicine, University of New Mexico, Albuquerque, New Mexico; Texas A&M University, College Station, Texas

Abstract. Hantavirus cardiopulmonary syndrome (HCPS), which is caused by infection with Choclo virus, is uncommon in Panama, yet seropositivity among rural residents is as high as 60%. To clarify the environmental risk factors involving rodent-to-human transmission, we tested sera from 3,067 rodents captured over a five-year period for antibodies against recombinant N protein of hantavirus by enzyme immunoassay and strip immunoblot. Among 220 seropositive rodents, Oligoryzomys fulvescens, the reservoir of Choclo virus, had the highest overall seroprevalence (23.5%); more abundant rodents (Zygopodomys brevicauda and Sigmodon hispidus) had lower seroprevalences. In the mixed (combined modern and traditional) productive agroecosystem, the highest seroprevalence was among O. fulvescens captured in residences and in crops grown within 40 meters of a residence, with significantly lower seroprevalence in adjacent pasture and non-productive vegetation. Thus, crop habitats may serve as refuge for invasion into adjacent human residences and suggests several interventions to reduce human infection.

INTRODUCTION

Hantavirus cardiopulmonary syndrome (HCPS) is an acute and often fatal febrile disease caused by enveloped, segmented, negative-strand RNA viruses of the family Bunyaviridae and genus Hantavirus. This syndrome is characterized by increased vascular permeability, hypotension, interstitial pneumonitis, and acute cardiac dysfunction. Since the first description of HCPS in the southwestern United States in 1993, novel New World hantaviruses and their specific rodent reservoirs have been documented in most regions of the Americas.

Each hantavirus is typically associated with a single species of murid rodent host in which it establishes a chronic infection that involves shedding of the infectious virus in bodily secretions and excretions. Studies in rodent models suggest that hantaviruses may be transmitted principally among rodents by saliva or saliva aerosols. Direct bloodborne transmission by biting and fighting may be an important mode of infection. It is believed to be transmitted to humans by inhalation of aerosolized virus in association with rodent excreta. Person-to-person transmission has been described only for Andes virus, and there is no evidence for person-to-person transmission in Panama. Peridomestic environments with active rodent infestations may present the greatest risk for human infection. Risk of transmission to persons is largely defined by the rodent reservoirs' geographic distributions, although within these regions, risk also varies with the ecology of the rodent species and human contact within their habitats.

In Central America, HCPS was first reported in the Azuero Peninsula of Panama. In the HCPS outbreak of 1999–2000, a novel human-pathogenic hantavirus (Choclo virus) and its rodent reservoir (Oligoryzomys fulvescens) were identified in peridomestic environments. In the investigation, differences were found in small mammal community structure between case sites and a control site, suggesting that human activities coupled with environmental factors may have combined to cause an increased risk of HCPS to residents in the Azuero Peninsula. From six reservoir species identified in Panama, geographic focus of hantavirus infection in rodents was evident, with Choclo and Calabazo viruses circulating in rodent populations in the Azuero Peninsula. The short-tailed cane mouse (Zygopodomys brevicauda), the host of Calabazo virus, was found to be the most abundant rodent and the dominant species on the flat land of Azuero Peninsula.

In Panama, all HCPS appears to be caused by Choclo virus with only 108 cases and 22 deaths (21.0%) reported to the present (Armínio B, unpublished data). In contrast to most hantavirus-endemic regions, however, a high prevalence of antibody to hantavirus (up to 60%) is found in residents of the endemic agricultural region of central Panama (Armínio B, unpublished data). Similar to other America hantaviruses, transmission of Choclo virus appears to be predominantly in peridomestic habitats. The high seroprevalence of hantavirus antibody in rodents as well as humans permits a more detailed examination of microhabitats within the peridomestic area where infected rodents and humans interact. We hypothesize that in agroecosystems in Panama, specific rodent microhabitats near human habitation provide high-risk sites for human infection. This study focuses on habitat associations of hantavirus-infected rodents, a longitudinal study and climate-driven fluctuations in rodent and human infections are presented elsewhere.

MATERIALS AND METHODS

Trapping and study sites. Our sampling was conducted in 35 localities in central section of western Panama (Figure 1). There is a rainy season from May through December and a dry season from January through April. The lowlands of central-western Panama are heavily populated and much of the original deciduous forest has been converted to an
agroecosystem. Small fragments of secondary dry deciduous forests exist primarily in the lowlands, large areas of evergreen forests predominate in higher elevations, and mangrove vegetation is locally abundant along the coast.

In the agroecosystems of central-western Panama, 60% of the land area is covered by agricultural vegetation located on flat to sloping topography with good to poor quality soils. Productive systems in Panama are defined in terms of land use, topography, and relative density of native second-growth vegetation cover (Figure 1) as one of two categories according to agricultural intensification. The predominant category is the mixed productive system (MPS) (combined modern and traditional productive systems) characterized by small to large scale mechanized agriculture on lowland with small to large scale irrigation system, semi-extensive livestock grazing and less than 10% of native shrub and mature second-growth vegetation cover. Human habitations are closely adjacent to subsistence as well as mechanized cropland (Figure 1). The second category is the traditional productive system (TPS) located on predominantly sloped topography with extensive livestock grazing, subsistence agriculture, and 10-40% covered with native shrub and mature second-growth vegetation on the remaining fragments.

Within these two categories of productive systems, we trapped rodents in two distinct environments, defined as domestic and peridomestic habitats. The domestic habitat included the area of family activities within (intradomestic) and outside (paradomestic) the habitation, and extended in general up to 40 meters from the perimeter of the residence. The paradomestic microhabitat is defined as the areas immediately outside human habitation that include patios and ornamental gardens, wees, subsistence crops plantation (corn, sugar cane, vegetables) and livestock barns. Occasionally small areas of mechanized plantations were located in the paradomestic area. The peridomestic habitat is defined as the area of human activity more than 40 meters from the perimeter of residences and consisted of small to large scale mechanized plantations of rice, corn, sugar cane, vegetables, cultivated wood, cultivated grass, native grassland (e.g., Hyparrhenia rufa) used for cattle, as well as small fragments of subsistence cultivation.
Small-mammal sampling. Sherman live traps (model LEATDG; H. B. Sherman Traps, Inc., Tallahassee, FL) were set from January 2002 through December 2006 in 35 localities of central-western Panama, with 79.0% of the trapping effort concentrated on the Azuero Peninsula. Traps were baited with a mixture of crunchy peanut butter and cracked corn, or a combination of rolled oats, birdseed, maltose, and vanilla extract. Grids of 100 traps (10 columns by 10 rows per site at 10-meter intervals) were established in microhabitats (i.e., vegetation, crop of the season, human habitation) in domestic and peridomestic areas. In 1.3% of the trapping effort, 100 traps were randomly placed in some domestic and peridomestic areas. Trapping in each site was conducted for three consecutive nights during the dry and wet seasons throughout the five years of the study. A total of 80.9% (61,405) of the trapping effort was concentrated in the MPS, whereas 19.1% (14,528) was performed in the TPS. Description of the microhabitats was consistently recorded.

Mammals were handled according to recommendations by Mills and others.28 Blood was obtained from the retro-orbital sinus using heparinized capillary tubes. The animals were killed with inhaled methoxyflurane (Pitman-Moore, Mundelein, IL). Individual field catalog numbers were assigned to each animal. Data collected for all individuals captured included trap location, weight, and standard body measurements (length of body, tail, hind foot, and ear). Data on sex and reproductive condition were determined based on the position and type of external reproductive structures and vaginal wall. Females were classified as pregnant or non-pregnant. The approximate age of each animal was estimated based on body measurements, body condition, and reproductive condition. Rodents were identified in the field using existing keys.31,32 For the known reservoir species (Oligoryzomys fulvescens, Zygodontomys brevicauda, and Sigmodon hispidus), individuals were assigned to body mass classes chosen to correspond to subjective mature ages based on standardized field data.

For O. fulvescens, the body mass classes were juvenile (class 1, 6.0-8.9 grams; class II, 8.9-9.8 grams; class III, 10.9-11.9 grams; class IV, 12.0-13.9 grams; class V, 14.0-15.9 grams; class VI, 16.0-17.9 grams; class VII, ≥ 18.0 grams). For Z. brevicauda, the body mass classes were juvenile (class I, 6.0-8.9 grams; class II, 9.0-11.9 grams; class III, 12.0-14.9 grams; class IV, 15.0-15.9 grams; class V, 16.0-17.9 grams; class VI, 18.0-19.9 grams; class VII, ≥ 20.0 grams). For S. hispidus, the body mass classes were juvenile (class I, 4.0-5.9 grams; class II, 6.0-7.9 grams; class III, 8.0-9.9 grams; class IV, 10.0-11.9 grams; class V, 12.0-13.9 grams; class VI, 14.0-15.9 grams; class VII, ≥ 16.0 grams).

Serologic analysis. Animals were tested by strip immunoblot for IgG containing a recombinant N protein of the CC106 strain of Sin Nombre virus and used as described.33 Seropositivity was confirmed by reverse transcription-polymerase chain reaction (RT-PCR) and sequencing of amplifiers from RNA tissue extracts of 10 seropositive O. fulvescens and 14 seropositive Z. brevicauda specimens, as Choclo and Cabaña viruses, respectively.

Data analyses. Data were transferred from field collection forms to a database (Epi Info Version 6.04d, Centers for Disease Control and Prevention, Atlanta, GA) for statistical analyses using Stata/IC Statistical Software Version 12.0, 2011 (StataCorp Ltd, College Station, TX). One-way analysis of variance (ANOVA) and Tukey's multiple comparison tests were performed to determine differences in the percentage of positive samples between traps. To account for small expected values of categorical data, we used Fisher's exact test and corresponding exact P values. The observed outcomes are assumed to be independent because captured mammals were not released; thus, we do not have a chance to capture the same amphidinids again. There may be a certain probability that we still have some correlation between observations caused by transmission. However, we did not perform statistical tests accounting for correlation between individual observations assuming independence for simplicity. We performed comparison studies for proportions (with 95% confidence intervals [CIs]) to examine if we can detect a statistically significant difference with a 5% significance level in the detection of antibodies against hantavirus and in the following pairs of comparisons: same species among habitat and microhabitat (i.e., MPS versus TPS, or domestic versus peridomestic or, intradomestic versus paramural or, among vegetation categories of the peridomestic or peridomestic habitats); among opossum species in a single habitat or microhabitat; and among rodent sex, age, and wound status. The statistical significance level has been adjusted for multiple comparisons based on Bonferroni correction when we interpreted our results.

RESULTS

Small-mammal community structure and distribution. During 5 years of trapping, 75,933 effective trap-nights yielded 3,446 individuals belonging to 14 species in 4 rodent families: Muridae, Cricetidae, Heteromyidae, and Echimyidae. Zygodontomys brevicauda (56.0%), S. hispidus (21.3%), Lomas adspersus (11.7%), and O. fulvescens (9.3%), the reservoir of Choclo virus, were the most abundant species. The remaining 10 species represented 1.7% of all individuals trapped (Supplementary Table 3, available online at www.jahid.org). Thirteen species were found in the MPS whereas 9 species were found in the TPS. In the MPS, 13 species were captured, with Z. brevicauda (45.9%), S. hispidus (11.9%), the reservoir of a novel hantavirus, and O. fulvescens (10.9%) as the dominant species, with a relative abundance in the MPS of 47 individuals/100 trap-nights. In the MPS sites, the relative abundance was 3.8% of individuals/100 trap-nights. The dominant species were S. hispidus and L. adspersus (51.3% and 38.6%, respectively), and Z. brevicauda and O. fulvescens represented 7.0% and 1.1%, respectively (Supplementary Table 3).
Prevalence of hantavirus antibodies and rodent habitat association. Among 3,367 (89%) individuals tested for hantavirus antibodies only three species contained all seropositive rodents (Table 1). *Oligoryzomys fulvescens* the fourth most common rodent in both the MPS and TPS, had the highest percentage of positive individuals (73.5%) compared with 7.8% of *Z. brevicauda*, the most abundant rodent in the MPS and the reservoir of Caluahoto virus, and 3.4% of *S. hispidus*, the most common rodent in the TPS and the reservoir of a novel hantavirus (*S. hispidus* associated hantavirus). Virtually all of the antibody-positive *O. fulvescens* (67 of 68) and *Z. brevicauda* (12 of 17) were captured in the MPS. In contrast, more seropositive *S. hispidus* were captured in the TPS than in the MPS (odds ratio [OR] = 4.92, 95% CI = 1.82–15.42, *P* = 0.0006).

The proportion of seropositive *O. fulvescens* was high in the domestic and peridomestic habitats (18.6% and 27.1%, respectively) (Figure 2). The relative abundance of *O. fulvescens* was greater in the domestic habitat than in the peridomestic habitat, possibly increasing the risk of human contact with Coio-infected rodents in the home (Figure 2). *Oligoryzomys fulvescens* was more likely to be seropositive than *Z. brevicauda* in peridomestic (OR = 4.24, 95% CI = 0.83–2.44, *P* = 0.0001) and domestic (OR = 2.85, 95% CI = 1.39–5.82, *P* = 0.0020) habitats. Both *Oligoryzomys fulvescens* and *Z. brevicauda* were found commonly inside houses but *O. fulvescens* was more likely to be seropositive (42.9%) inside human habitats (Figure 3).

Comparison of rodent seropositivity in different peridomestic microenvironments (pasture, crops, weeds, and ornamental garden) showed low seropositivity among *O. fulvescens* in pasture (9%), weeds (11%) and ornamental garden (16%) but high seropositivity in adjacent crops (80%), comparable to the high seropositivity of capybara in the habitations (42%) (Figure 3). Density is also a critical factor, reflecting relative abundance of captured rodents; 61.1% (11 of 18) of all antibody-positive *O. fulvescens* in the peridomestic area were captured in ornamental gardens. In contrast to seropositive *O. fulvescens* in certain microenvironments, the seropositivity for *Z. brevicauda* was the same across all microenvironments (Figure 3).

In the peridomestic habitats more distant from the habitations, the proportion of antibody-positive *O. fulvescens* was almost as high as some domestic habitats, with 15.6% in pasture, 28.9% in secondary vegetation, and 32.2% in crops (Supplementary Table 4, available online at www.elah.org). The proportion of seropositive *O. fulvescens* varied from 28.0% in rice to 42.9% in corn (Figure 4), and relative abundance was comparable among each crop, suggesting that *O. fulvescens* had no strong preference for any one crop in spite of its common name, rice rat.

**Antibody prevalence in relation to sex, mass class, and wound status.** The prevalence of hantavirus antibody was significantly higher in male rodents than in female rodents for *O. fulvescens* (*P* = 0.010, by Fisher's exact test) and *Z. brevicauda* (*P* = 0.0001, by Fisher's exact test) but not for *S. hispidus* (Table 2). Seropositive individuals were more frequently adults among *O. fulvescens* (*P* = 0.0046, by Fisher's exact test) and *Z. brevicauda* (*P* < 0.0001, by Fisher's exact test). The prevalence of hantavirus antibody was significantly higher in wounded than unwounded males rodents for both **Table 1**

| Table 1 | Percentage of *Oligoryzomys fulvescens* (O), *Zygodontomyx brevicauda* (Z) and *Sigmodon hispidus* (S) with antibodies against hantavirus captured in agroecosystems in central-western Panama, 2000–2006*
<table>
<thead>
<tr>
<th>Species</th>
<th>Mixed productive system, % (95% CI)</th>
<th>Traditional productive system, % (95% CI)</th>
<th>Total % positive (95% CI)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>O. fulvescens</em></td>
<td>23.4 (13/57)</td>
<td>16.7 (1/6)</td>
<td>23.5 (6/26)</td>
</tr>
<tr>
<td><em>Z. brevicauda</em></td>
<td>7.9 (12/152)</td>
<td>2.9 (1/35)</td>
<td>7.8 (129/1,663)</td>
</tr>
<tr>
<td><em>S. hispidus</em></td>
<td>1.4 (4/296)</td>
<td>6.7 (17/253)</td>
<td>2.4 (23/609)</td>
</tr>
<tr>
<td>Other species††</td>
<td>0 (0/23)</td>
<td>0 (0/23)</td>
<td>0 (0/464)</td>
</tr>
<tr>
<td>No. positive animals of total tested††</td>
<td>7.9 (20/255)</td>
<td>3.7 (7/191)</td>
<td>7.2 (220/3,067)</td>
</tr>
<tr>
<td>No. species positive</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% Species positive</td>
<td>23.4 (13/57)</td>
<td>16.7 (1/6)</td>
<td>23.5 (6/26)</td>
</tr>
</tbody>
</table>

* Fisher's exact test was used to estimate the P value. **Percentage of individuals with antibodies against hantavirus seropositive.**

---

1. *O. fulvescens* vs. *Z. brevicauda* OR = 1.21, 95% CI = 0.46–3.14, *P* = 0.69; mixed productive system vs. traditional productive system (OR = 3.52, 95% CI = 1.07–11.63, *P* = 0.032; *Z. brevicauda* vs. *S. hispidus* OR = 1.21, 95% CI = 0.46–3.14, *P* = 0.69; mixed productive system vs. traditional productive system (OR = 3.52, 95% CI = 1.07–11.63, *P* = 0.032).

2. *O. fulvescens* vs. *Z. brevicauda* OR = 1.21, 95% CI = 0.46–3.14, *P* = 0.69; mixed productive system vs. traditional productive system (OR = 3.52, 95% CI = 1.07–11.63, *P* = 0.032).

3. *O. fulvescens* vs. *Z. brevicauda* OR = 1.21, 95% CI = 0.46–3.14, *P* = 0.69; mixed productive system vs. traditional productive system (OR = 3.52, 95% CI = 1.07–11.63, *P* = 0.032).

4. *O. fulvescens* vs. *Z. brevicauda* OR = 1.21, 95% CI = 0.46–3.14, *P* = 0.69; mixed productive system vs. traditional productive system (OR = 3.52, 95% CI = 1.07–11.63, *P* = 0.032).
HANTAVIRUS-POSITIVE RODENT SEROPREVALENCE IN PANAMA.

![Image](image.png)

**Figure 3.** Percentage of individuals with antibodies against hantavirus nucleocapsid and relative abundance of rodents captured (individuals/100 traps night) for *Oligoryzomys fulvescens (O)*, *Zygodontomys brevicauda*, and *Sigmodon hispidus (Sh)* by crop (Corn [C], Rice [R], and Others [O]) in peri-domestic area in agroecosystems in central-western Panama, 2002-2006. Numbers above each column indicate numbers of individuals tested.

**Figure 4.** Percentage of individuals with antibodies against hantavirus nucleocapsid and relative abundance of rodents captured (individuals/100 traps night) for *Oligoryzomys fulvescens (O)*, *Zygodontomys brevicauda*, and *Sigmodon hispidus (Sh)* by crop (Corn [C], Rice [R], and Others [O]) in peri-domestic area in agroecosystems in central-western Panama, 2002-2006. Numbers above each column indicate numbers of individuals tested.

O. fulvescens (P = 0.0005, by Fisher’s exact test) and Z. brevicauda (P = 0.9004, by Fisher’s exact test). Wounding correlated with larger body mass among wounded males for both species (Supplementary Figure S5, available online at www.ajtmh.org).

**DIFFUSION**

This study confirms previous findings of evidence of hantavirus infection among rodents in central-western Panama. As a consequence of our larger data set and more detailed analysis, a better understanding of the ecology of the reservoir species with implication for human disease risk emerge. Greater numbers of captures found higher seroprevalence than previously reported and increased our ability to correlate seroprevalence with favored habitats. The overall seroprevalence of 23.5% among *O. fulvescens* host for the human pathogen Chocho virus, is higher than that reported for most pathogenic hantaviruses in Central and South America. The high rodent seroprevalence to Sin Nombre virus in western North America is contrasted to the low human seroprevalence of less than 1%. Only the high Calomys laevis rodent and human seroprevalences caused by Laguna Negra virus in western Paraguay, where peridomestic infection and MPS predominate, approaches that documented in Panama. Because human seroprevalence on the Azuero Peninsula is high, ranging from 16% to 60%, we sought to explain this observations by examining in detail the habitat preferences of seropositive rodents (Armien B, unpublished data).

In spite of multiple hantaviruses in Panama, human infection appears to be exclusively caused by Chocho virus. First, in all acute-phase human sera from HCPS patients tested to date for viral genome by RT-PCR, only Chocho virus sequences have been found (Pascale JM, unpublished data). Second, all positive serum samples from persons without a history of HCPS contained Chocho virus-neutralizing activity when tested for hantavirus antibody by neutralization inhibition assays (Koster E, unpublished data). Although we cannot rule out human infection with Calabazo virus transmitted from its *Z. brevicauda* host for the purposes of this study, the only rodent of medical interest is *O. fulvescens*.

The rodent and human seroprevalence data used two assays: an enzyme-linked immunosorbent assay and a strip immunoblot. These binding assays have shown a concordance of 98.0% in human samples from Panama (Pascale JM and Quiroz E, unpublished data). The enzyme-linked immunosorbent assay and the strip immunoblot used Sin Nombre virus nucleocapsid antigen, which is cross-reactive with antibodies to all known sigmodontine-borne hantaviruses in the Americas. However, these methods do not identify the viral strain. Preliminary sequencing of 600 base pairs by RT-PCR amplifiers from tissue RNA from seropositive *S. hisatus* specimens indicates that these viruses are not closely related, but additional characterization is required.

Earlier comparisons of small-mammal assemblages showed the highest small-mammal diversity in natural ecosystems and the highest abundance in human-altered ecosystems. Our data support the notion that Chocho, Calabazo and *S. hisatus*-associated hantaviruses are concentrated on the human-dominated habitats, whereas other hantaviruses such as the *Pomona* and *Retobus* spp.-associated hantaviruses appeared to be restricted to the tropical upland natural forests of the extreme western region of Panama (Volcan Baru in Chiriqui Province). Furthermore, *Z. brevicauda*, the host of Calabazo virus, was the only reservoir species consistently present and the most abundant reservoir in agroecosystems from the extreme west to the extreme east of the Isthmus of Panama (Armien B, unpublished data). In central-western Panama, *O. fulvescens* and *Z. brevicauda* were consistently found in the MPS but were uncommon in TPS (Table 1). In contrast, *S. hisatus* was more common and more often seropositive in the TPS than in the MPS.

Our data is consistent with the hypothesis that increased rodent density and competition is a cause of increased seroprevalence. For *O. fulvescens* and *Z. brevicauda*, but not *S. hisatus*, antibody prevalence was associated with sex, wounding, and body weight, a surrogate for age, agreeing with multiple studies on rodent reservoirs of American hantavirus. Although aggressive encounters among adult males may
account for much of the transmission within rodent populations. Thus, other aspects such as social behaviors and habitat features have also been proposed as additional factors influencing transmission.

Risk to humans is a function of frequency of seropositivity and relative abundance in habitats frequented by persons. Crops within 40 meters of a residence contained the highest percentage of seropositive *O. fuscusculus* compared with pastures and other vegetation types in paradoxic environments (Figure 2). However, because of increased relative abundance, greater numbers of seropositive *O. fuscusculus* were captured in ornamental gardens. Seropositive rice rats (*O. fuscusculus*) were more common in the traditional (non-mechanized) mixed cultivation of corn and vegetables (42.9%, 12 of 28) than in the mechanized monocultures of rice (17.4%, 4 of 23) (Armien A, unpublished data). However, crops within 40 meters of residences may have special significance because the nocturnal foraging distance for these rodents was 20-40 meters as determined by radiotelemetry in one of our intensively surveyed sites (Armien B, unpublished data). Thus, during the post-harvest dry season when seed availability was reduced in the field, rodent foraging near residences would not require long-distance travel to reach intra-habitat foods. Long-term data from marketcrupe studies may help clarify the relationship between antibody prevalence, rodent community structure, density, and home range for paradoxic environments.

The physical relationship between crops and ornamental gardens near human residences may have public health implications. Thus, one potential intervention may be relocating crops away from residences, locating short grass near residences, and identifying the plans in ornamental gardens that attract *O. fuscusculus*. Further studies will examine food storage and preparation in and near residences. In a future contribution, detailed analyses of seasonal assessment of human and rodent seroprevalence by site, habitat, season, and year will clarify the dynamic relationship between human and rodent seroconversions in the same communities.

<table>
<thead>
<tr>
<th></th>
<th><em>O. fuscusculus</em></th>
<th><em>Z. beevoria</em></th>
<th><em>S. darcyi</em></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Characteristics</strong></td>
<td><strong>% (Gibson) (%)</strong></td>
<td><strong>OR (95% CI)</strong></td>
<td><strong>P</strong></td>
</tr>
<tr>
<td><strong>Sex</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male</td>
<td>29.3 (48/164)</td>
<td>2.18 (1.16-4.18)</td>
<td>0.0017</td>
</tr>
<tr>
<td>Female</td>
<td>16.0 (18/113)</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td><strong>Weight</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Juvemile-</td>
<td>3.1 (14/164)</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Adult-</td>
<td>3.1 (150/164)</td>
<td>2.00 (1.51-5.79)</td>
<td>0.0006</td>
</tr>
<tr>
<td>Wound-</td>
<td>39.5 (100/256)</td>
<td>3.00 (1.50-5.56)</td>
<td>0.0003</td>
</tr>
<tr>
<td>Yes</td>
<td>21.4 (22/107)</td>
<td>1.85 (0.84/1.299)</td>
<td>1</td>
</tr>
<tr>
<td>Male</td>
<td>48.1 (251/52)</td>
<td>3.56 (1.65-7.75)</td>
<td>0.0005</td>
</tr>
<tr>
<td>No</td>
<td>20.3 (201/112)</td>
<td>1.52 (0.38-5.20)</td>
<td>0.3337</td>
</tr>
<tr>
<td><strong>Female</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Yes</td>
<td>14.7 (14/95)</td>
<td>2.95 (0.03-26.5)</td>
<td>1</td>
</tr>
<tr>
<td>No</td>
<td>14.7 (14/95)</td>
<td>2.95 (0.03-26.5)</td>
<td>1</td>
</tr>
</tbody>
</table>

* Fisher's exact test was used to estimate the P value. % = percentage of individuals with antibodies against hantavirus. OR = odds of infection that were antibody reactive to hantavirus. n = no. of mice for each category.

Acknowledgments: We thank the International Centers for Infectious Diseases Research (ICIDR) program of the National Institutes of Health, Ministry of Health, the University of New Mexico, the Gorgias Memorial Institute of Studies of Health, the Panamanian Institute of Livestock and Agricultural Research, and the National Environmental Authority for their support. We also thank persons from the community, several state organizations, the rodent ecology team of the Ministry of Health, and especially Dr. Emilio Rebeiro, Dr. Carlos Pleguez, Omar Vargas, Francisco Crespo, and Nelson Rico for support during fieldwork. The ELISA reagents were provided by the Special Pathogen Branch, Divison of Viral and Rickettsial Diseases, Centers for Disease Control and Prevention (Atlanta, GA).

We dedicate this paper to the memory of Jerry L Yates.

Financial support: This study was supported by an Opportunity Pool award and supplement from the International Centers for Infectious Diseases Research program of the National Institutes of Health (U19 AI45452); funds from the Instituto Conmemorativo Gorgas de Estudios de la Salud, Hantavirus Research Project No. 04-09-0075-08; the Ministry of Health, Panama; and the Secretaria Nacional de Ciencia y Tecnología, Innovation and Technology Program no. P06-089, Panama.

Authors' addresses: Anibal G. Armien, Department of Population Medicine, College of Veterinary Medicine, University of Minnesota, Saint Paul, MN 55108, E-mail: armien000@umn.edu, Blas Armien, Juan M. Pascal, Paul Gonzalez, Manual de la Cruz, Yamiel Zaldivar, and Yashei Mendez, Instituto Conmemorativo Gorgas de Estudios de la Salud, Avenida Justo Arrieta, Apartado 6991, zona 5, Panama, E-mail: barrion@orgas.gob, Mario Avila, Instituto Conmemorativo Gorgas de Estudios de la Salud, Avenida Justo Arrieta, Apartado 6991, zona 5, Panama, Ministry of Health, Herrera Province, Panama, Fredrick Koster, Lovelace Respiratory Research Institute, Albuquerque, NM 87108, Fernando Garcia, Hospital Santo Tomas, Panama City, Panama, Brian Hjelle, SOM Pathology Department, 08 4640, University of New Mexico Health Sciences Center, Albuquerque, NM 87131, 0001, Sung-Joon Lee, Department of Internal Medicine, MSC 10 555, University of New Mexico Health Sciences Center, Albuquerque, NM 87131-0001, Jorge Solano Bravo, Center for Epidemiology and Zooparasites, Department of Biological Sciences, Texas Tech University, Lubbock, TX 79409.

Reprint requests: Blas Armien, Instituto Conmemorativo Gorgas de Estudios de la Salud, Avenida Justo Arrien, Apartado 6991, zona 5, Panama, E-mail: barrion@orgas.gob, Panama.

REFERENCES


