

SPATIAL CLUSTERING OF MURID RODENTS INFECTED WITH HANTAVIRUSES: IMPLICATIONS FROM META-ANALYSES

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Abstract. We applied a rigorous, quantitative methodology to the analysis of local-scale spatial clustering of multiple murid mice (brush mice, *Peromyscus boylii*; deer mice, *P. maniculatus*; piñon mice, *P. truei*; western harvest mice, *Reithrodontomys megalotis*) infected or uninfected with hantaviruses. Rodents were sampled longitudinally from 1994 to 2001 on 23 trapping webs at 10 locations in the southwestern United States. This study provided an opportunity to apply meta-analysis techniques to an important ecological question. There were sufficient captures by species on 199 occasions (three consecutive nights) to compare general use of space using multi-response permutation procedures (MRPP). The MRPP results were then used in meta-analyses by species to determine if overall effects of spatial clustering of hantavirus-infected mice as well as categorical effects (elevation, season, site, and state) were present. Based on MRPP analyses, overall spatial clustering of hantavirus-infected mice was most pronounced for brush mice, followed by the deer mouse. Meta-analyses indicated significant overall effects of spatial clustering and varying categorical effects (elevation, season, site, state) of infected mice for each species compared. The overlapping space use by rodents might be an important factor affecting the local transmission of several hantaviruses.

Key words: *Bunyaviridae*; *El Moro Canyon virus*; *hantaviruses*; *Limestone Canyon virus*; *meta-analysis*; *MRPP*; *Muridae*; *Peromyscus*; *Reithrodontomys*; *Sin Nombre virus*; *space use*.

INTRODUCTION

The spatial clustering of disease occurrence or pathogen transmission has been well documented. Recent examples include bluetongue viruses (Ward et al. 1996) and contagious bovine pleuropneumonia (Giovannini et al. 2000) in livestock, leptospirosis (Ward 2002) and rabies among dogs (Laurenson et al. 1997), Lassa virus in small mammals (Demby et al. 2001), and rat bites (i.e., potential transmission of many zoonoses; Childs et al. 1998), Lyme disease (Kitron and Kazmierczak 1997), and visceral leishmaniasis (Werneck et al. 2002) in humans. Therefore, the use of space by hosts of pathogens is an important principle in the epidemiology

of many infectious diseases, at both the regional and local levels.

To date, at least 39 hantaviruses have been recognized worldwide, typically each with a single primary host (sensu Calisher et al. 2003). Questions have been asked about why and by what route animals are infected with a hantavirus (Shope 1999). Earlier work indicated that hantaviruses are contracted by their rodent hosts through passage of virus in urine or saliva, via bite wounds during fighting (Glass et al. 1988), contact with virus-contaminated nest material, or contact with aerosolized virus in closed spaces (Gavrilovskaya et al. 1990). More recently, secondary mechanisms, such as close associations during communal nesting and behavioral mechanisms during the breeding season, were proposed (Mills et al. 1999a, Douglass et al. 2001, Escutenaire et al. 2002). Regardless of route, each mode of transmission requires rodents to be in direct or indirect contact with other rodents, necessitating that they share space. Therefore, hantavirus-infected rodents might be expected to be more spatially clustered with one another than would uninfected rodents.

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Mills et al. (1997) observed focality in the distribution of seropositive deer mice on a regional scale. However, in brush mice (*Peromyscus boylii*) distinct clusters of Limestone Canyon virus (LSCV; Sanchez et al. 2001) infection, apparently associated with preferred microhabitat, have been observed at the local level (Abbott et al. 1999, Kuenzi et al. 1999, Mills et al. 1999a). The presence and number of antibody-positive brush mice are not evenly distributed at some study sites (Kuenzi et al. 1999). For example, during periods of high population density, antibody-positive brush mice occupied scattered chaparral habitats of sites in central Arizona and moved freely between trapping locations; however, during periods of low population densities, antibody-positive brush mice withdrew to a few, distinct refugia (Abbott et al. 1999). Although several species of *Peromyscus* were captured in both vegetation associations (semidesert grassland and oak riparian) within a select study site in southern Arizona, all but one of the antibody-positive mice were captured in oak riparian vegetation, and the majority were trapped in one portion of one trapping area (Kuenzi et al. 1999). Similarly, Otteson et al. (1996) found that deer mice infected with Sin Nombre virus (SNV), an etiologic agent of hantavirus pulmonary syndrome, were confined to small foci at their study sites in California and Nevada.

The apparent spatial clustering of rodents infected with a hantavirus has been observed in several previous studies (Otteson et al. 1996, Abbott et al. 1999, Kuenzi et al. 1999, Mills et al. 1999a). However, only Escutenaire et al. (2002) have attempted to address this issue (based on habitat association) in a quantitative manner at the local level. New tools, including spatial statistics methods, enable researchers to address the spatial aspects of diseases more thoroughly and less subjectively than simple descriptions (Chaput et al. 2002). We applied a rigorous, quantitative methodology to the analysis of local-scale spatial clustering of multiple murid mice infected with one or another hantavirus.

Meta-analysis, the statistical synthesis of research results from a set of primary studies, has recently been introduced to ecology (Gurevitch et al. 1992). A feature that is characteristic of meta-analysis data sets is that the data have at least two sources of variation: (1) within-study sampling error, and (2) between-study variance (Gurevitch and Hedges 1999). Problems associated with the application of meta-analytic methods in the ecological discipline are poor reporting of data (Gurevitch et al. 1992, Gurevitch and Hedges 1999), and publication bias of results that are statistically significant (Gurevitch and Hedges 1999). Our study may be unique in that data from all study sites used in analyses were sampled during the same general time frame and all researchers used nearly identical methodology, yielding a unique opportunity to conduct ecological meta-analyses without many of the typical problems.

Our objective was to determine quantitatively, the difference in the general space use/clustering of hantavirus-infected and uninfected murid rodents of the same species. Analyses were conducted for four murid rodent species commonly observed to have antibody to one or another hantavirus in the southwestern United States. These species included brush mice associated with LSCV, deer mice associated with SNV (Childs et al. 1994), piñon mice (*P. truei*; possibly associated with SNV), and western harvest mice (*Reithrodontomys megalotis*; associated with El Moro Canyon virus; ELMCV; [Hjelle et al. 1994]). The SNV infections in piñon mice may represent a "spill-over" effect (i.e., interspecific transmission). Additionally, meta-analyses were conducted among all study sites to determine whether an overall effect was present among study sites, states, elevation, seasons, and species. The techniques employed in this study may have applications for future studies of the spatial aspects of the transmission mechanisms of rodent-borne viruses among natural populations of reservoir species.

METHODS

We conducted longitudinal studies of rodents and hantaviruses from 1994 to 2001. The general field (mark-recapture) methodology and study site descriptions are available elsewhere (Abbott et al. 1999, Calisher et al. 1999, 2001, Kuenzi et al. 1999, Mills et al. 1999b, Parmenter et al. 1999). Data are presented from study sites (23 trapping webs) at 10 geographically distinct locations in three states (Arizona, Colorado, and New Mexico; Fig. 1). These study sites included Limestone Canyon (LC1, LS1, and LS2; Yavapai County) and Walnut Creek (WCA and WCW) from central Arizona; Santa Rita (SR2, SR3, and SR4; Pima County) from southern Arizona; Hesperus (HA and HB; La Plata County), Molina (MA and MB; Mesa County), and Pinon Canyon Maneuver Site (MRC; Las Animas County) from Colorado; and Navajo (N1 and N2; McKinley County), Placitas (P1, P2, and P3; Sandoval County), Sevilleta (S1, S2, and S3; Socorro County), and Zuni (Z1 and Z2; McKinley County) from New Mexico. Rodents were live-trapped monthly in Arizona and New Mexico and every six weeks when weather permitted in Colorado. Typically, each study site was sampled for three consecutive nights during a primary sampling session. Workers at each "sister" site followed the same general protocols throughout these studies (Mills et al. 1999b).

There is little doubt that live-trapping has some limitations in determining the general space use, microhabitat selection (Douglass 1989), movement (Desy et al. 1989), and home range sizes (Bergstrom 1988, Drickamer et al. 1999) of rodents. The size of lifetime ranges of rodents may be considerably larger than short-term home ranges and may therefore be underestimated on small trapping areas (Rajska-Jurgiel 2001). However, many workers have used live-trapping

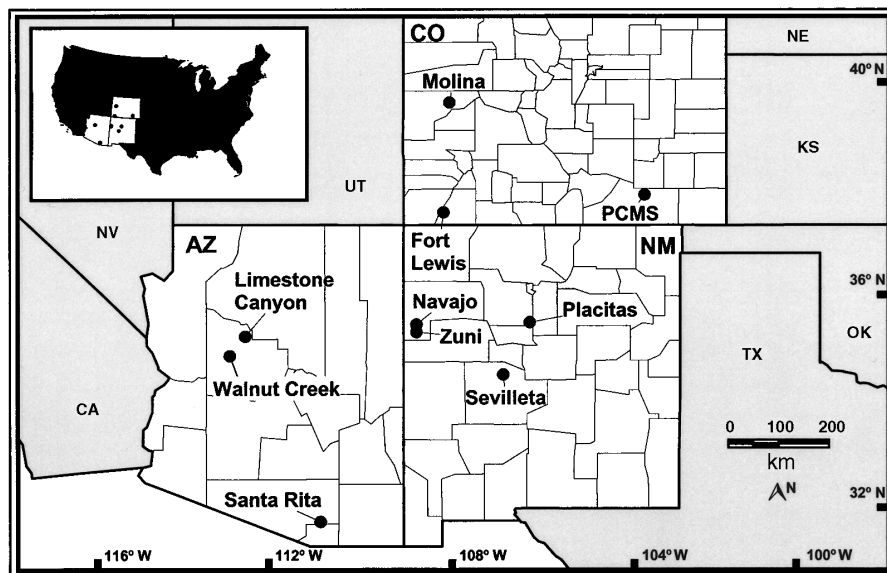


FIG. 1. Locations of study sites in Arizona, Colorado, and New Mexico in the southwestern United States, 1994–2001.

data as a method to evaluate space use (i.e., Bowers 1995, Atanassov 2000), movements (i.e., Andersen et al. 2000), and home range sizes (i.e., Bond and Wolff 1999, Atanassov 2000). The intent of this study was to detect spatial clustering of trap locations by utilizing the same trapping configurations across all study sites.

The trapping web design (Anderson et al. 1983) has been found to be superior to many other methods of population density estimation (Parmenter et al. 2003) and was utilized at all study sites analyzed in this paper. The size and configuration of these webs have been described elsewhere (Mills et al. 1999b). Each trap station was given a set of Cartesian coordinates (i.e., the origin of the web was $X = 0$ and $Y = 0$) for spatial analyses. For spatial analyses it was assumed that: (1) trap stations included in the trapping webs were sufficient to describe the general space use of the rodents captured, and (2) biases in captures of rodents were equal between the groups that we analyzed.

Spatial analyses for detection of rodent clustering within groups (i.e., mice infected with a hantavirus) were conducted with multi-response permutation procedures (MRPP; Zimmerman et al. 1985, Mielke 1991) for each species separately. The purpose of MRPP is to identify concentration within a priori groups without dependence on parametric assumptions, such as normality or homogeneity of variances under the alternative hypothesis (Zimmerman et al. 1985). Statistical programs are available online for MRPP and BLOSSOM.^{11,12}

In the MRPP analyses, mice infected with a hantavirus were considered the single group; however, un-

infected mice were included in the analyses as “background,” against which infected mice could be tested (i.e., synonymous with the EXCESS option in program BLOSSOM; Cade and Richards 2001). For example, if 30 captures (10 infected and 20 uninfected) were recorded during a trapping session, the excess group (the 20 captures of uninfected mice) would be treated as the remaining part of the population of 30 captures (see Mielke and Berry 2001). Two dimensions of capture location (i.e., X and Y of a plane) were used in all analyses. The MRPP procedure (Zimmerman et al. 1985, Mielke 1991) produces Δ observed (i.e., a measure of the average distance between all pairs of locations at which mice infected with a hantavirus were captured), Δ expected (i.e., a measure of the expected distance based on locations at which all mice [background] were captured), as well as the P values associated with these Δ observed and Δ expected comparisons. MRPP analyses were conducted for each trapping session when at least four captures of mice infected with a hantavirus (i.e., a minimum of two individuals) and a minimum of six total captures were recorded.

The means (of Δ observed and of Δ expected) and variance produced from our MRPP analyses were used in meta-analyses, conducted with MetaWin 2.0 (Rosenberg et al. 2000), to calculate effect sizes (Hedges’ d ; i.e., a standardized mean difference multiplied by a correction factor for small sample sizes; see Hedges and Olkin 1985:81, Rosenberg et al. 2000). Fixed-effect meta-analytic models were employed. Fixed-effect models assume that all studies with similar enough characteristics share a common effect size, and estimates differ by sampling error only (see Gurevitch and Hedges 1999 and citations therein). Considering our

¹¹ <http://www.stat.colostate.edu/~mielke/permute.html>

¹² <http://www.fort.usgs.gov/products/software/blossom.asp>

desire to address categorical variables (e.g., elevation, season; Gurevitch and Hedges 1999) and the very similar methodologies employed among all studies, we believe that the fixed-effect model is appropriate.

For each species, an overall mean effect size (\bar{E}) and bootstrap confidence intervals were computed based on the effect sizes (d) weighted by their associated variances (Hedges and Olkin 1985, Rosenberg et al. 2000). Comparisons were considered significant when 95% bootstrap (based on 9999 iterations) confidence intervals were negative and did not bracket zero. In addition, a test for homogeneity of effect sizes (Q_T , Hedges and Olkin 1985, Rosenberg et al. 2000) was computed for each species. A significant Q_T is an indication that observed variance among effect sizes is greater than expected from sampling error (Rosenberg et al. 2000). Fail-safe calculations were also tabulated by the method of Rosenthal (1979). A fail-safe number is the quantity of nonsignificant, missing, or unpublished studies that would need to be included in an analysis in order to alter the results from significance to nonsignificance (Hedges and Olkin 1985, Rosenberg et al. 2000).

For the four rodent species (brush mice, deer mice, piñon mice, and western harvest mice), categorical meta-analyses were conducted using state, site, season, and elevation variables. Categorical results included an overall mean effect size (\bar{E} ; a weighted average for each category type) and confidence intervals for each category. Therefore, data from the three states and 23 trapping webs surveyed in this study were analyzed individually and combined. Seasons were winter (January–March), spring (April–June), summer (July–September), and fall (October–December). Elevation categories were <1500 m, 1501–1700 m, 1701–1900 m, 1901–2100 m, 2101–2300 m, and >2300 m.

RESULTS

More than 600 000 trap nights were conducted on 23 trapping webs in three states over eight years. As noted in the methods, MRPP tests were only conducted on occasions where a minimum of four captures of infected mice and six total captures were recorded. Additionally, a few sampling occasions were omitted from analyses because of occasional coding discrepancies from some sites. Therefore, during many occasions and at some sites (i.e., control sites), few or no tests could be conducted. This minimum criterion for analyses of all captures (i.e., first captures and recaptures of individuals from a primary trapping session) allowed for 138 tests (549 total trapping sessions) of brush mice from sites LC1, LS1, LS2, P3, SR2, SR3, SR4, WCA and WCW; 49 tests (507 total trapping sessions) of deer mice from sites HA, HB, MA, MB, MRC, N1, N2, Z1, and Z2; 7 tests (187 total trapping sessions) of piñon mice from sites LS2, MB, N1; and 5 tests (230 total trapping sessions) of western harvest mice from MRC, S1, WCW, and Z2 (Table 1). Results were considered statistically significant if $P < 0.05$.

When statistically significant clustering of infected rodents was detected, sample sizes varied greatly, and multifold differences were routinely observed (Table 1). We observed no association between sample size and the ability to detect spatial clustering. For example, statistically significant ($P < 0.05$) clustering of infected brush mice was observed at the central Arizona site WCW when samples sizes ranged from 23 total captures (4 infected and 19 uninfected) to 166 total captures (13 infected and 153 uninfected). Similarly, for infected deer mice in Colorado at site HA, statistically significant clustering ranged from 6 total captures (4 infected and 2 uninfected) to 66 total captures (12 infected and 54 uninfected). Although total captures do not reflect true density, they provide an estimate of the relative population size.

Statistically significant heterogeneity may not be unexpected, considering the exceptionally large sample sizes for brush mice and deer mice. Increased heterogeneity was highly correlated with increased sample sizes (overall $R = 0.97$; Tables 2–5). Nonetheless, the overall mean effect size (\bar{E}) was significant for all species, indicating that hantavirus-infected mice tend to cluster more than their uninfected cohorts (Tables 2–5). Rosenthal's (1979) fail-safe method indicated that >1000, >1000, >90, and >10 nonsignificant trapping sessions (for brush mice, deer mice, piñon mice, and western harvest mice, respectively) would need to be added to these meta-analyses in order to change the results from significance to nonsignificance (see Hedges and Olkin 1985, Rosenberg et al. 2000).

For infected brush mice, statistically significant spatial clustering was observed at three of six study sites where this species was captured in sufficient numbers for analysis (Table 2). Results from three of six study sites and one of two states were significant for deer mice (Table 3). For piñon mice, sample sizes were insufficient to conduct tests for state or site categorical effects (Table 4). For western harvest mice, results from one of two states were significant (Table 5).

Analyses of spatial clustering were significant for one of two elevation categories and three of four seasons for infected brush mice (Table 2). For infected deer mice, clustering during the spring was significant; the sample size for the winter comparison was insufficient (Table 3). All elevation categories <2300 m yielded significant spatial clustering for deer mice (Table 3). One analysis of season (spring) was significant for piñon mice (Table 4). For infected western harvest mice, significant clustering was noted for the winter and spring seasons (Table 5). Elevation categories were not testable for piñon mice and western harvest mice (Tables 4 and 5).

DISCUSSION

The analysis of disease clusters has received considerable attention within the field of public health (Lawson 2001). Many researchers have documented

TABLE 1. Spatial analyses (from program MRPP [Zimmerman et al. 1985, Mielke 1991]) of four murid rodent species based on all captures within a primary trapping session of mice infected with a hantavirus vs. all mice captured from study sites in the southwestern United States, 1994–2001.

Species	Sessions	$n+$	$n-$	N †	Δ observed	Δ expected	Δ difference	Standardized difference	Avg. (P)§
Brush mouse‡ (<i>Peromyscus boylii</i>)	43 (S)	6.9 (0.5)	48.1 (5.4)	54.9 (5.6)	45.8 (2.9)	93.3 (2.2)	-47.5	-2.91	0.012 (0.002)
	95 (NS)	9.7 (0.8)	44.7 (3.5)	54.4 (4.1)	94.5 (1.7)	94.0 (1.4)	0.5	0.001	0.472 (0.027)
	138 (C)	8.8 (0.6)	45.8 (2.9)	54.6 (3.3)	79.3 (2.4)	93.8 (1.2)	-14.5	-0.91	0.329 (0.026)
Deer mouse (<i>Peromyscus maniculatus</i>)	10 (S)	9.0 (1.3)	28.8 (5.9)	37.8 (6.9)	53.3 (4.4)	82.3 (2.5)	-29.0	-2.18	0.026 (0.004)
	39 (NS)	8.9 (1.0)	26.7 (3.3)	35.6 (3.9)	73.5 (3.2)	79.6 (1.9)	-6.1	-0.31	0.436 (0.050)
	49 (C)	9.0 (0.8)	27.1 (2.8)	36.1 (3.4)	69.3 (2.9)	80.2 (1.6)	-10.9	-0.69	0.353 (0.046)
Piñon mouse (<i>Peromyscus truei</i>)	4 (S)	5.8 (1.1)	15.5 (5.3)	21.3 (6.3)	38.6 (7.1)	73.1 (7.9)	-34.5	-2.33	0.022 (0.008)
	3 (NS)	4.3 (0.3)	13.7 (6.9)	18.0 (6.8)	65.0 (5.5)	68.1 (4.0)	-3.1	-0.10	0.443 (0.091)
	7 (C)	5.1 (0.7)	14.7 (3.9)	19.9 (4.3)	50.0 (6.9)	71.0 (4.6)	-21.0	-1.37	0.202 (0.091)
Western harvest mouse (<i>Reithrodontomys megalotis</i>)	2 (S)	5.0 (0.0)	7.5 (6.5)	12.5 (6.5)	35.4 (6.8)	62.7 (23.5)	-27.3	-1.43	0.022 (0.016)
	3 (NS)	5.0 (0.6)	5.3 (1.2)	10.3 (1.5)	42.0 (11.5)	60.0 (14.8)	-18.0	-0.47	0.319 (0.128)
	5 (C)	5.0 (0.3)	6.2 (2.2)	11.2 (2.3)	39.4 (6.9)	61.1 (11.0)	-21.7	-0.85	0.200 (0.101)

Notes: Results are pooled and summarized by species and categorized as statistically significant (S, $P < 0.05$), nonsignificant (NS, $P > 0.05$), and combined S + NS (C). Averages of the number of captures of mice infected ($n+$) or uninfected ($n-$) with a hantavirus, total captures (N), Δ observed (a MRPP measure of the average distance between all pairs of locations at which mice infected with a hantavirus were captured), Δ expected (a measure of the expected distance based on locations at which all mice were captured), Δ difference (Δ expected - Δ observed), standardized differences (Hedges' d), along with the standard error (in parentheses) are shown.

† Combined totals may not add to variable totals due to rounding error.

‡ Study sites included LC1, LS1, LS2, P3, SR2, SR3, SR4, WCA, and WCW for brush mice; HA, HB, MA, MB, MRC, N1, N2, Z1, and Z2 for deer mice; LS2, MB, and N1 for piñon mice; and MRC, S1, WCW, and Z2 for western harvest mice.

§ The average P value among all sessions.

the spatial clustering of disease occurrence or transmission (e.g., Ward et al. 1996, Kitron and Kazmierczak 1997, Laurenson et al. 1997, Giovannini et al. 2000, Demby et al. 2001, Ward 2002, Werneck et al. 2002). Our results are consistent with previous observations, but extend the use of quantitative spatial analyses to rodent hosts of hantaviruses.

From MRPP analyses, we observed no discernible association of population size and within-species clustering of individuals of the four rodent species infected with one or another hantavirus (Table 1). Previous data have suggested contrasting trends. First, during periods of low population densities, antibody-positive brush mice have been observed to withdraw to a few, distinct refuges (Abbott et al. 1999). As expected, we observed spatial clustering of infected brush mice during periods of low population densities; however, significance was also found with multifold increases in sample size as compared to the smallest statistically significant sample size. Second, anecdotal evidence from Colorado sites suggested that deer mice infected with SNV tend to show a clustered spatial pattern during periods of high population density. However, in this study, clustering was also shown during sampling occasions when small

sample sizes (i.e., six) were observed in Colorado. The occurrence of such conflicting observations emphasizes the need for data collection over long periods across large spatial scales, and for the application of objective, quantitative spatial analyses. Nonetheless, there are limitations to our results. For example, it was assumed that biases in captures of rodents were equal between the groups that we analyzed. However, for several hantaviruses, adult male rodents have been observed to be more commonly infected. Also, capture biases could have been present for select age classes or gender classes.

Many researchers have demonstrated that territories or mutually exclusive home ranges are common in *Peromyscus* species (reviewed by Wolff 1989). Wolff et al. (1983) and Wolff (1985) experimentally tested for territoriality in white-footed mice (*P. leucopus*) and deer mice using behavioral trials (reviewed by Wolff 1989). During periods of low (<25 mice/ha) population densities, individuals of the same sex typically maintained exclusive home ranges (Wolff 1985); however, during periods of high population densities (>25 mice/ha; Wolff et al. 1983), home range overlap, increased aggression, and territorial defense were observed

TABLE 2. Meta-analyses of the spatial distributions of brush mice (*Peromyscus boylii*) based on all captures within a primary trapping occasion of brush mice infected with Limestone Canyon virus vs. all brush mice captured from study sites in the southwestern United States, 1994–2001.

Categorical variables†	<i>n</i>	Q_T	<i>P</i>	\bar{E}	Bootstrap CI
Individual sites					
LC1	21	346.64	<0.00000	-0.65	-1.43 to 0.08
LS1	38	278.24	<0.00000	-0.93	-1.33 to -0.53
LS2	34	546.46	<0.00000	-0.26	-0.85 to 0.31
SR2	2	2.49	0.11400	-0.88	-1.86 to -0.37
WCA	21	117.80	<0.00000	0.02	-0.26 to 0.30
WCW	19	196.55	<0.00000	-2.02	-2.71 to -1.36
All Arizona					
Elevation					
<1500 m	4	13.44	0.00376	-0.67	-1.86 to 0.32
1501–1700 m	133	1827.71	<0.00000	-0.54	-0.81 to -0.29
Season					
Winter	29	301.46	<0.00000	-0.62	-1.21 to -0.18
Spring	39	704.40	<0.00000	-0.73	-1.28 to -0.18
Summer	39	432.50	<0.00000	-0.48	-0.96 to -0.05
Fall	31	382.27	<0.00000	-0.27	-0.85 to 0.12
Overall	138	1844.76	<0.00000	-0.55	-0.82 to -0.30

Notes: Results are summarized by site, state, elevation, season, and the overall effect. Number of trapping sessions (*n*; *df* = *n* - 1), heterogeneity (Q_T , for categorical data and for total), heterogeneity probability (*P*), mean effect sizes (\bar{E}), and 95% bootstrap confidence intervals (bootstrap CI) are listed.

† Comparisons with less than two studies are not shown. Therefore, the number of studies for each categorical variable may not add to the overall total.

TABLE 3. Meta-analyses of the spatial distributions of deer mice (*Peromyscus maniculatus*) based on all captures within a primary trapping occasion of deer mice infected with Sin Nombre virus vs. all deer mice captured from study sites in the southwestern United States, 1994–2001.

Categorical variables†	<i>n</i>	Q_T	<i>P</i>	\bar{E}	Bootstrap CI
Individual sites					
HA	10	141.68	<0.00000	-0.15	-1.36 to 0.69
HB	16	98.76	<0.00000	0.02	-0.45 to 0.45
MA	8	61.35	<0.00000	-1.53	-2.20 to -0.63
MB	5	12.05	0.01702	-1.01	-1.61 to -0.43
N1	5	3.35	0.50066	-0.94	-1.37 to -0.63
Z2	2	5.07	0.02437	-0.45	-1.30 to 0.12
State					
Colorado	40	412.32	<0.00000	-0.40	-0.85 to 0.01
New Mexico	9	21.03	0.00706	-0.77	-1.30 to -0.30
Elevation (m)					
1901–2100	16	99.86	<0.00000	-1.16	-1.65 to -0.62
2101–2300	6	6.11	0.29502	-1.09	-1.57 to -0.71
>2300	26	241.67	<0.00000	-0.04	-0.53 to 0.39
Season					
Winter	N/A				
Spring	17	100.02	<0.00000	-0.58	-1.05 to -0.14
Summer	21	244.81	<0.00000	-0.45	-1.15 to 0.19
Fall	10	83.74	<0.00000	-0.17	-1.34 to 0.51
Overall	49	437.54	<0.00000	-0.44	-0.84 to -0.08

Notes: Results are summarized by site, state, elevation, season, and the overall effect. Number of trapping sessions (*n*; *df* = *n* - 1), heterogeneity (Q_T , for categorical data and for total), heterogeneity probability (*P*), effect sizes (\bar{E}), and 95% bootstrap confidence intervals (Bootstrap CI) are listed.

† Comparisons with less than two studies are not shown. Therefore, the number of studies for each categorical variable may not add to the overall total.

TABLE 4. Meta-analyses of the spatial distributions of piñon mice (*Peromyscus truei*) based on all captures within a primary trapping occasion of piñon mice infected with Sin Nombre virus (or a Sin Nombre-like virus) vs. all piñon mice captured from study sites in the southwestern United States, 1994–2001.

Categorical variables†	<i>n</i>	Q_T	<i>P</i>	\bar{E}	Bootstrap CI
Season					
Winter	3	7.55	0.02296	-0.51	-1.87 to 0.31
Spring	3	16.87	<0.00000	-1.98	-3.31 to -0.32
Summer	N/A				
Fall	N/A				
Overall	7	35.53	<0.00000	-1.35	-2.40 to -0.40

Notes: Results are summarized by season and the overall effect. Sample sizes were not sufficient to test for site, state, and elevation effects. Number of trapping sessions (*n*; *df* = *n* - 1), heterogeneity (Q_T , for categorical data and for total), heterogeneity probability (*P*), effect sizes (\bar{E}), and 95% bootstrap confidence intervals (Bootstrap CI) are listed.

† Comparisons with less than two studies are not shown. Therefore, the number of studies for each categorical variable may not add to the overall total.

(Wolff 1985). Notably, increasing population densities have been implicated in enhanced rates of transmission of several wildlife diseases (see Mills et al. 1999a, Cully and Williams 2001).

The recognition of a significant biological association among disease and environmental variables has provided a means to understanding the distribution of disease agents (Hess et al. 2002). Climatic events are well known to have drastic effects on densities of small-mammal populations (Lima et al. 1999, Yates et al. 2002, Calisher et al., *in press*). For example, Morrison et al. (2002) noted that with the exception of one species, rodents in select study sites of southern Arizona responded numerically to increased rainfall. Furthermore, meteorological events, such as increased precipitation, could cluster food resources into select locations or microhabitats. Clustering of food resources could, therefore, be a facet of the transmission of hantaviruses, as it could force animals that might normally not cluster to cluster in space.

In light of the forgoing, spatial clustering of hantavirus-infected mice under conditions of high vs. low population densities may have different explanations. During periods of high population densities, infected mice are likely to transmit a hantavirus to their closest neighbors via frequent aggressive encounters, creating spatial clusters of infected mice. Periods of low population density are generally associated with periods of unfavorable environmental conditions (e.g., drought). Under such conditions, clustering of infected mice may be because those mice that are most likely to be infected (older, larger, dominant mice [Mills et al. 1997, Abbott et al. 1999, Calisher et al. 1999, Mills et al. 1999a, Douglass et al. 2001, Calisher et al. 2002]), will be occupying the few remaining pockets of optimal habitat for the species in question.

Statistically significant spatial clustering of infected mice was detected in three seasons (winter, spring, and summer) for brush mice (Table 2). This association was only observed during the spring for deer mice, during

TABLE 5. Meta-analyses of the spatial distributions of western harvest mice (*Reithrodontomys megalotis*) based on all captures within a primary trapping occasion of mice infected with El Moro Canyon virus vs. all western harvest mice captured from study sites in the southwestern United States, 1994–2001.

Categorical variables†	<i>n</i>	Q_T	<i>P</i>	\bar{E}	Bootstrap CI
State					
Colorado	2	4.58	0.03236	-1.55	-2.59 to -0.86
New Mexico	2	1.63	0.20222	-0.27	-0.81 to 0.26
Season					
Winter	2	0.40	0.52752	-0.55	-0.81 to -0.27
Spring	2	4.58	0.03236	-1.55	-2.59 to -0.86
Summer	N/A				
Fall	N/A				
Overall	5	12.12	0.01648	-0.82	-1.73 to -0.16

Notes: Results are summarized by state, season, and the overall effect. Sample sizes were not sufficient to test for site and elevation effects. Number of trapping sessions (*n*; *df* = *n* - 1), heterogeneity (Q_T , for categorical data and for total), heterogeneity probability (*P*), effect sizes (\bar{E}), and 95% bootstrap confidence intervals (Bootstrap CI) are listed.

† Comparisons with less than two studies are not shown. Therefore, the number of studies for each categorical variable may not add to the overall total.

the spring for piñon mice, and during the winter and spring for western harvest mice (Tables 3–5). Communal nesting of mice during the winter months has been hypothesized as a potential means of transmission for hantaviruses (Mills et al. 1999a, Shope 1999). Seasonal comparisons of two species (insufficient data for deer mice) provide some support for this idea (Tables 2–5). However, the failure of high-elevation (>2300 m) SNV-infected deer mice at HA and HB (those that might maintain communal groups for the longest period, i.e., even in the spring) to yield significant results fails to support this view (Table 3).

Our results suggest that home ranges of hantavirus-infected mice may overlap more due to the closer spatial proximity between individuals; e.g., infected brush mice were on average 14.5 m closer in space (see Table 1). The closer spatial associations of hantavirus-infected individuals may be explained by the fact that certain rodent species, e.g., *P. leucopus* (Wolff and Lundy 1985), tolerate familiar relatives more than they do unfamiliar nonrelatives. In a Colorado study, Root et al. (2004) found evidence that hantavirus-infected deer mice were more related to one another than were seronegative mice at one of two trapping sites. Understanding the spatial clustering of rodents may also be related to pre- and postmating associations. For example, Wolff et al. (1988) noted that select pairs of related (first-order relatives) white-footed mice had overlapping home ranges during the breeding season. Furthermore, communally nesting deer mice and white-footed mice have been shown to commonly be close relatives (Wolff 1994). Thus, the tolerance of relatives and their common space use could reduce the transmission of hantaviruses if related individuals fight less frequently; however, it could enhance transmission because related rodents might share space and come into contact (through huddling, mutual grooming, or other social interactions) more often than would unrelated mice.

The interspecific similarities of these results (i.e., overall significant effects for each species) support the idea that overlapping use of space by the hosts of LSCV, SNV, and ELMCV is an important factor in their transmissions (Tables 2–5). Nonetheless, there remains the possibility that we neglected to study an unidentified but important variable (e.g., relative degree of mammalian diversity, disturbance, habitat quality, climate, or weather), inclusion of which may have yielded different interspecific results. Unfortunately, the majority of these data are not presently available. Thus, it is possible that more pronounced interspecific differences might occur—undetected differences that might indicate somewhat different mechanisms of transmission of these three hantaviruses.

To date, all credible methods that have been proposed as transmission mechanisms of hantaviruses necessitate that rodents directly or indirectly share space. Furthermore, intense space sharing might promote ag-

gressive encounters among individual mice. Aggressive encounters are thought to be an important facet of the transmission of LSCV among brush mice (Abbott et al. 1999, Mills et al. 1999a), and to a lesser extent, of SNV among deer mice (Calisher et al. 1999, Mills et al. 1999a). Considering that brush mice yielded the vast majority of the significant spatial clustering of infected individuals, the clumped spatial pattern of infected brush mice lends support to a hypothesis that more chance encounters between individuals of this species provide more opportunities for fighting. This may indicate an enzootic cycle of LSCV in populations of brush mice. However, the strong association between antibody and the prevalence of wounds in brush mice (K.D. Abbott, *unpublished data*) tends to support an epizootic cycle of LSCV. The uneven seasonality of associations for deer mice may indicate that this species is more likely to become infected with SNV during particular seasons (e.g., spring), thereby indicating a more epizootic cycle of SNV in populations of deer mice (Table 3).

Both standard meta-analyses and fail-safe methods clearly support the observation of significant spatial clustering of four species of hantavirus-infected rodents. Spatial clustering of these four rodent species may very well be a factor in the transmission of hantaviruses for which they serve as hosts. However, the mechanisms of transmission of these distinct viruses may be equally distinct. Therefore, the differences we observed between species may relate to intersite or interspecies differences in social structure or behavior, characteristics that could influence the transmission of hantaviruses (Mills et al. 1999a). This emphasizes the need for longitudinal research over large geographic scales and the use of additional variables (e.g., meteorological data, dispersal distances, and home range overlap) in future research. This study may have applications for future studies of the spatial dynamics of pathogen transmission over small-scale areas.

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