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RELATIONSHIPS OF DEER MOUSE MOVEMENT, VEGETATIVE STRUCTURE, AND PREVALENCE OF INFECTION WITH SIN NOMBRE VIRUS

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ABSTRACT: The effects of vegetative structure on movement of deer mice (*Peromyscus maniculatus*) were examined in two distinct vegetation associations, one near Hesperus and the other near Molina in western Colorado (USA) from June–October 1994 to October 1998. We monitored movement by live-trapping small mammals within Gambel's oak/mixed-grass (Hesperus) and sage brush/juniper (Molina) vegetation types. Vegetative structure differed between the sites with Molina having more cover provided by shrubs and Hesperus having more cover provided by forbs. Adult male deer mice moved greater distances at Hesperus than at Molina. Sub-adult males tended to move greater distances than did adult females. Relative abundances of deer mice tended to differ by season, but the average relative abundance of deer mice was greater at Molina. Long-term prevalence of infection with SNV was greater at Hesperus and was greatest in adult males at Hesperus (36.1%). Adult males at Molina exhibited a prevalence of infection with SNV of 25.0%. Infection with SNV was highly associated with scars or wounds for adult male, adult female, and juvenile male deer mice at Hesperus, but only for adult female deer mice at Molina. The presence of scars or wounds tended to be associated with greater age, but male deer mice at Hesperus were more likely to have wounds than female deer mice of the same age class. A similar pattern, excluding juveniles, was observed at Molina. Intraspecific interactions and environmentally elicited long-distance movements of deer mice may play a role in prevalence of infection with SNV in these animals.

Key words: Hantavirus, mouse movement, *Peromyscus maniculatus,* Sin Nombre virus, vegetative structure.

INTRODUCTION

In 1993 several human infections caused by Sin Nombre virus (SNV; family Bunyaviridae, genus *Hantavirus*) were reported near the Four Corners region of the southwestern United States, the majority were fatal. Eventually, this newly recognized illness was termed hantavirus pulmonary syndrome (HPS; Butler and Peters, 1994; Elliott et al., 1994). Deer mice (*Peromyscus maniculatus*) are the primary hosts of SNV (Childs et al., 1994; Mills et al., 1997). A national serosurvey has shown that deer mice infected with SNV occur in nearly every state within the range of the species but that there are differences in prevalence of infection among populations on a broad geographic scale (sensu Mills et al., 1997). However, we know nothing about differences in prevalence of infection among populations of the same species across habitat types within a defined geographic area (Mills et al., 1997). Mills et al. (1997) determined that the lowest overall prevalence of infection was found at altitudinal and climatic extremes (i.e., desert and alpine tundra), but no discernible pattern in the geographic distribution of infected animals was observed. Thus, a principal question about SNV ecology is why prevalences of infection are greater in some habitats than in others even though the two have similar climates and altitudes. The answer undoubtedly is multifaceted, but this paper provides one possible explanation.

Hantaviruses are thought to be contracted by their rodent hosts through passage of urine or saliva via bite wounds during fighting (Glass et al., 1988) or possibly by direct contact with rodents that are virus carriers, contact with their nest material, blood, urine, saliva, or contact with aerosolized virus in closed spaces (Gavrilovskaya et al., 1990). Infectious virus may be shed for the life of the host (Mills et al.,

1999). Bite wounds and antibody prevalence appear to be more common in males for many species of rodents (Mills et al., 1992, 1997; Abbott et al., 1999). This association is predominantly in males in the oldest age and heaviest body mass classes (Mills et al., 1994). It has been suggested that infections of several rodent viruses are acquired through horizontal transmission (Mills et al., 1999) and intraspecific interactions among adult males, which have been documented for several decades (Anderson, 1989), appear to be important mechanisms of such transmission events (Mills et al., 1994, 1999). One might assume that population structure within a habitat mosaic could play a significant role in the spatial distribution of hantavirus infection in local populations of reservoir species (Glass et al., 1998) and, therefore, it would be expected that increasing population densities would result in increased rodent-to-rodent contact, a greater number of potential virus-transmission events, and a higher overall incidence and cumulative prevalence of infection within host populations (Mills et al., 1999). This clearly is not always the case (Douglass et al., 1996; Mills et al., 1997; Boone et al., 1998) because population trends are not always clearly associated with periods of virus transmission (Childs et al., 1987).

An increased prevalence of infection of the arenavirus Junin virus in male rodents may be due to their greater movements and a greater level of agonistic behavior, when compared to that of females (Mills et al., 1992). Further, differences in movement between habitat types may contribute to increased prevalence of infection with SNV among different deer mice communities because movements of greater distances, relative to areas where movements are short, should increase the number of chance encounters with conspecifics, thus the potential for intraspecific interactions. Longer movements may increase the probability that mice moving long distances become infected with SNV.

Differential movements by the same species in different habitat types are often dictated by vegetative structure (Gates, 1991; Root et al., 1998). Therefore, we investigated the influence of vegetative structure in two distinct habitat types in western Colorado on the movement of deer mice. Our objective was to quantify small mammal movement in both study sites and to relate this information to differences in the prevalence of SNV infection of deer mice at these sites.

MATERIALS AND METHODS

Study sites

Study sites were established near Hesperus (La Plata County, Colorado; 37°13′30.9″N, 108°10′51.1″W) and Molina (Mesa County, Colorado; 39°09′45.8″N, 108°03′18.4″W). These sites were in close proximity to the residences of human HPS cases. See Calisher et al. (1999) for a detailed summary of the natural history of these areas.

Two trapping webs (Anderson et al., 1983) were established at each location. Each replicate was located a minimum of 500 m from the other and either a road or irrigation ditch separated each pair of webs. Our webs were modified to 12 trap-lines and 12 trap-stations per trap-line. Trapping webs of this design are centered on a single trap-station in the center of the web. Twelve, 100-m trap-lines radiated from the central trap-station at 30° angles from one another. On each trap-line, the first four trap-stations were spaced 5 m apart, the other eight trap-stations 10 m apart. A single Sherman non-folding, aluminum live trap (8 by 9 by 23 cm; H. B. Sherman Trap Co., Tallahassee, Florida, USA) was placed at each trap-station. Traps were baited with a mixture of rolled oats, cracked corn, and peanut butter and were sampled for two, usually three consecutive nights. Logistical constraints occasionally dictated two nights of sampling during the beginning of this study but sampling for three nights was initiated at the same time for both sites.

Small mammal sampling.

Rodents were sampled each six weeks from June 1994 (Hesperus) and October 1994 (Molina) to October 1998, as weather permitted. Small mammal processing was conducted according to protocols and methods for trapping and sampling small mammals for virological testing (Mills et al., 1995). Briefly, we took morphological measurements, scar and wound assessments, and blood samples, then attached individually numbered ear tags to newly captured mice. Mice from only one web at each

study site were bled until we confirmed that we were not impacting the survival of the mice (Calisher et al., 1999). Mice at both webs were bled beginning in the fall of 1996.

Movements of deer mice were monitored by live-trapping individuals throughout the course of each sampling period. During trapping sessions, the ear tag number and trap-station of each captured mouse were recorded. Each time an individual was captured on a consecutive night, its movement distance was tabulated. We defined movement distance as the straight-line distance from one trap-site to another trap-site during a 24 hr period. This distance was assessed with the aid of a scaled map that replicated our study sites. Therefore, the distances we report are the minimum distances moved by individuals. Data were analyzed with a two sample *t*-test. Analyses were conducted with SAS (SAS Institute, 1988). Deer mice were assigned to three categories based on body mass, which can be used as an indicator of relative age of rodents (Mills et al., 1997). Mass classes for *P. maniculatus* were I (adult), ≥18.7 g; II (sub-adult), 15.8–18.6 g; and III (juvenile), ≤15.7 g. These mass classes are similar to others that have been tabulated and used for *P. maniculatus* (Fairbairn, 1977; Mills et al., 1997). Enumeration was used to tabulate the minimum number alive (MNA) to estimate relative abundances (Krebs, 1966), and to calculate the minimum number infected (MNI; see Abbott et al., 1999).

Antibody assays

Enzyme-linked immunosorbent assay (EIA) for IgG antibody to Sin Nombre virus of *P. maniculatus* was done by the method of Feldmann et al. (1993).

Vegetation sampling methods

Vegetation was surveyed during July 1998 using the line-intercept technique (Canfield, 1941). This method estimates cover, which provides more precise data about the actual structure of vegetation than does density (Gysel and Lyon, 1980), and has been considered to be of more ecological significance (Daubenmire, 1968). Five randomly placed 50 m line transects were sampled on each study site. A random number generator was used to produce a random trap-station starting point and a random azimuth for the transect to follow. Hence, the vegetative structure was studied on a habitat level because microhabitat effects are poor predictors of habitat use compared to macrohabitat effects (Morris, 1987; Jorgensen, 1996). Dominant vegetative species were noted and cover provided by shrubs, forbs, grasses, and trees were tabulated. These data were analyzed with a one-way analysis of variance (ANOVA) with sampling error. Analyses were conducted with SAS (SAS Institute, 1988).

TABLE 1. Movement of *Peromyscus maniculatus* sampled within Gambel's oak/mixed-grass (Hesperus) and sage brush/juniper (Molina) vegetation types in western Colorado, 1994–1998.[a]

P. maniculatus	Mass class	Study site: Hesperus	Study site: Molina	SE	*P*
Males	I	42.7	27.4	2.1	<0.01
	II	36.0	30.6	2.6	>0.10
	III	16.7	28.6	3.4	>0.05
Females	I	25.1	25.7	2.5	>0.10
	II	28.6	22.6	2.4	>0.10
	III	16.1	22.9	2.9	>0.10

[a] Mean movement reported in meters.

RESULTS

In 33,640 trap-nights during June–October 1994 to October 1998, we captured 1,052 individual deer mice. We tabulated 723 movements from 533 individual deer mice during this period.

Differential movement effects were detected for adult male *P. maniculatus*. Males tended to move greater distances within the Hesperus study plots, as compared to the Molina study plots ($P < 0.01$, Table 1). All other age and sex classes failed to show this effect. However, subadult males from both study sites tended to move greater distances than did adult females.

From 1994 to 1998, the mean (±SD) minimum number alive was 20.5 ± 12.1/web/trapping session (range, 4 to 56) deer mice at Molina while at Hesperus there was an average of 14.5 ± 7.6/web/trapping session (range, 1 to 37) deer mice. Table 2 provides a seasonal summary of these captures. However, the prevalence of antibody to SNV during this time period was 23% (48/209) for Hesperus males, 10.1% (28/278) for Hesperus females, 15% (37/247) for Molina males, and 7.1% (23/326) for Molina females (Table 3). Adult males at Hesperus represented the group with

TABLE 2. Summary of seasonal relative abundance (MNA), number of infected individuals (MNI), and prevalence of SNV infection (%) in western Colorado, 1994–1998.

		Study site[a]					
		Hesperus			Molina[b]		
Year	Season	MNA	MNI	%	MNA	MNI	%
1994	Spring	12.0 ± 4.2	2.5	23.0			
	Summer	30.2 ± 5.5	4.5	14.8			
	Fall	9.2 ± 3.9	1.0	10.8	10.5 ± 0.7	0	0
1995	Spring	4.8 ± 2.8	1.5	31.5	9.0 ± 2.7	1.5	26.6
	Summer	14.5 ± 5.8	1.5	10.3	30.0 ± 11.5	6.0	20.0
	Fall	15.5 ± 1.5	1.5	10.0	47.2 ± 7.5	2.0	4.2
1996	Spring	9.5 ± 3.6	0	0	25.0 ± 3.3	5.0	20.0
	Summer	19.5 ± 5.0	0	0	10.7 ± 5.3	1.5	13.9
	Fall	9.5 ± 6.3	0.0 ± 0.0	0	12.0 ± 8.4	0.0 ± 0.0	0
1997	Spring	3.8 ± 2.7	1.2 ± 1.5	33.3	4.5 ± 1.0	0.3 ± 0.5	5.5
	Summer	12.5 ± 5.0	1.0 ± 2.0	8.0	11.7 ± 8.1	0.3 ± 0.5	2.1
	Fall	9.5 ± 6.3	1.5 ± 2.1	15.7	31.0 ± 2.8	1.0 ± 1.4	3.2
1998	Spring	18.7 ± 6.0	3.7 ± 3.8	19.7	29.5 ± 0.7	5.5 ± 7.7	18.6
	Summer	26.2 ± 3.1	5.0 ± 3.1	19.0	23.7 ± 5.4	2.5 ± 1.9	10.5
	Fall	22.5 ± 2.1	6.5 ± 4.9	28.8	21.5 ± 2.1	3.0 ± 2.8	13.9

[a] Standard deviations for the minimum number infected are not reported until subjects at both webs at each study site were bled.
[b] Sampling began at Molina during the fall of 1994.

the highest prevalence of infection 36.1% (30/83). This was >11% higher than the next highest group, Molina adult males at 25.0% (28/112) prevalence of infection (Table 3). The number of seropositive mice was associated with animals having scars or wounds for adult male ($\chi^2 = 4.55$, $P < 0.05$, 1 df), adult female ($\chi^2 = 9.42$, $P < 0.05$, 1 df), and juvenile male ($\chi^2 = 16.5$, $P < 0.05$, 1 df) deer mice at Hesperus. At Molina, only in adult female deer mice was this significant ($\chi^2 = 9.29$, $P < 0.05$, 1 df). At Hesperus, scars were documented on 30 (33%) of 89 adult males, 17 (22.7%) of 75 sub-adult males, seven (10.4%) of 67 juvenile males, 34 (20.6%) of 165 adult females, four (8.5%) of 47 sub-adult females, and four (4.8%) of 83 juvenile females. Scars were present on 34 (31.2%) of 109 adult males, 21 (21.6%) of 97 sub-adult males, one (2.1%) of 47 juvenile males, 29 (25.9%) of 112 adult females, nine (19.5%) of 86 sub-adult females, and six (4.1%) of 145 juvenile females at the Molina sites.

At Hesperus, vegetation consisted pri-

TABLE 3. Sex, age distribution, and numbers of deer mice infected (+) or uninfected (−) with Sin Nombre virus and prevalence of infection (%), western Colorado, 1994–1998.[a]

	Hesperus						Molina					
	Males			Females			Males			Females		
Mass class	+	−	%	+	−	%	+	−	%	+	−	%
I (Adults)	30	53	36.1	21	142	12.8	28	84	25.0	19	97	16.3
II (Sub-adults)	15	49	23.4	3	40	6.9	9	76	10.5	0	99	0.0
III (Juveniles)	3	59	4.8	4	68	5.5	0	50	0.0	4	107	3.6
Totals	48	161	22.9	28	250	10.0	37	210	14.9	23	303	7.0

[a] Totals do not exactly match the totals in the text because all individuals were not bled during every sampling period.

TABLE 4. Percent cover of vegetation at Hesperus and Molina study sites in western Colorado.

Vegetative growth form	Study site		SE	*P*
	Hesperus	Molina		
Shrub[a]	3.2	48.3	2.8	<0.01
Forb	28.1	5.1	1.2	<0.01
Grass	29.6	24.7	1.4	>0.10
Tree	18.3	11.3	2.1	>0.10

[a] Percent cover from 50 m transects.

marily of Gambel's oak (*Quercus gambeli*), ponderosa pine (*Pinus ponderosa*), fringed sage (*Artemisia frigida*), western wheatgrass (*Agropyron smithii*), Idaho fescue (*Festuca idahoensis*), timothy (*Phleum pratense*), tailcup lupine (*Lupinus caudatus*), and western yarrow (*Achillea millefolium*). At Molina, study site vegetation consisted primarily of pinon pine (*Pinus edulis*), Rocky Mountain juniper (*Juniperus scopulorum*), big sagebrush (*Artemisia tridentata*), Parry's rabbitbrush (*Chrysothamnus paryii*), cheatgrass (*Bromus tectorum*), and western wheat grass.

Shrub cover was greater at the Molina study sites ($P < 0.01$) than at the Hesperus sites (Table 4). At Hesperus, forb cover was greater ($P < 0.01$) than at the Molina sites (Table 4). No differences ($P > 0.10$) were noted for grass and tree cover between study sites (Table 4).

DISCUSSION

Vegetative cover and species composition differed between the two habitats surveyed in this study. The observed differences in shrub cover characterize a high structural vegetative contrast. Additionally, shrubs on these study sites appeared to be a perennial feature of the landscape, particularly when compared to the many, mostly annual, forbs and grasses observed. Characteristics of vegetation are known to influence patterns of distribution, abundance, outcome of competition (Rosenzweig and Winakur, 1969), and movement for some species of small mammals (Jorgensen et al., 1995; Root, 1997).

The cover provided by shrubs was relatively homogenous at both Molina sites. The shrub cover at the Hesperus sites was very limited and patchy, although an occasional low growing *Q. gambeli* provided cover that was similar (low and thick) to the shrub cover (primarily *A. tridentata*) observed at the Molina study sites. Notably, conspicuously shorter movement distances have been documented for *Peromyscus* spp. living in areas with dense cover when compared to animals living in areas with less cover (sensu Stickel, 1968).

Additionally, predation risk may affect foraging behavior (Pierce et al., 1992) and in turn may help structure communities of prey when risk differs among habitats (Kotler, 1984). Habitats with homogenous cover (Molina) provide small mammals the opportunity to move short distances among foraging patches (i.e., shrub to shrub movement). However, habitats with patchy cover (Hesperus) may force an animal to move long distances to a new foraging patch after the resources of the initial patch have been exhausted (Table 1; Table 4). Unfortunately, the importance of movement (distance and/or frequency) has been ignored in most population studies (Briese and Smith, 1974).

The long-term associations of relative abundance and prevalence of infection with SNV reported here appear to be similar to those found in other studies (Douglass et al., 1996; Mills et al., 1997; Boone et al., 1998). Molina sites averaged 20.5 ± 12.1 deer mice per trapping session while Hesperus only averaged 14.5 ± 7.6 deer mice per trapping session (Table 2). Relative abundances varied by season (Table 2) but this is not unusual because periodic fluctuations seem to be common among the small mammals of temperate regions (Krebs, 1966) and are often correlated with food production (Wolff, 1996). However, the prevalences of infection with SNV during this time period were only 14.9% and 7.0% for Molina males and females, respectively, but were 22.9% for Hesperus males and 10.0% for Hesperus

females (Table 3). Table 2 provides a summary of the prevalences of infection with SNV and the MNI by site, year, and season. Notably, the long-term antibody prevalences at Hesperus were higher than at Molina (Table 3) even though we failed to detect an infected mouse at Hesperus over the entire year of 1996 (Table 2). Also, a greater number of infected adult males were detected at Hesperus than at Molina even though more adult males were captured at Molina. A greater prevalence of infection where mice are less abundant is contrary to expectation because hantaviruses are transmitted rodent to rodent by close contact (Glass et al., 1988; Gavrilovskaya et al., 1990). Typically, in an area with a greater abundance of deer mice, more chance encounters should occur (Mills et al., 1997) and increasing numbers of mice should become infected with SNV. However, if movements in selected areas of high deer mouse abundance tend to be more abbreviated, fewer encounters with conspecifics may occur than in areas where movement distances are longer. This may be especially true in areas of high productivity or homogenous vegetative structure. For example, *Peromyscus* living in areas where food was abundant were documented to travel shorter distances than did mice living where food was not as available (Linduska, 1942). Conversely, in areas of low productivity or patchy vegetative structure, deer mice may move greater distances, thereby potentially encountering more conspecifics. Further, good foraging patches (sustenance and predation avoidance) may be limited, such that an individual deer mouse is more likely to come into contact with another deer mouse when it reaches the next foraging patch. The latter may be a function of competition or predation pressure (Pierce et al., 1992) because excessive movement increases exposure to predators as well as the probability of death on unfamiliar terrain (Metzgar, 1967). Spatial and temporal habitat variability may create dynamic mosaics on which behavioral strategies evolve and are expressed (Anderson, 1989).

A difference in movement was observed between the Molina and Hesperus study sites for adult male deer mice. Also, subadult males tended to move greater distances than did adult females. Notably, excluding juveniles, each age and sex class which moved greater distances had a higher prevalence of SNV infection. These differences in movement may be dependent on vegetative structure which may affect various age and sex classes uniquely. For example, Hall and Morrison (1997) reported that male piñon mice (*Peromyscus truei*) had larger home ranges than females. They further indicated that female *P. truei* were associated with different habitat characteristics than males at den sites, perhaps related to reproductive constraints on females. All mass classes of male and female deer mice at Molina moved similar distances. However, adult male and female deer mice clearly had greater prevalences of infection with SNV when compared to other mass classes in their respective sex class (Table 3). This indicates that age is also an important aspect of SNV infection, especially in males (Abbott et al., 1999; Mills et al., 1999). It is reiterated, however, that the only mass class of mice that moved significantly greater distances than its respective counterpart were adult male deer mice at Hesperus when compared to adult male deer mice at Molina. Also, a large difference (11.1%) in prevalence of infection with SNV was noted between adult male deer mice (Table 3). Sub-adult males at Hesperus moved greater distances and had a greater prevalence of infection with SNV than sub-adult males at Molina. However, the difference in movement was not statistically significant. Dispersal by the sub-adult males may have affected their movements (Fairbairn, 1978). Therefore, we draw no conclusions from this comparison. Deer mouse abundance was lower at Hesperus, but except for adult females, all age and sex classes exhibited a higher prevalence of infection with SNV

at the Hesperus sites when compared to their counterparts at Molina. The exception of adult female deer mice represents a difference of only 3.5%. We conclude that research concerning intraspecific interactions and deer mouse movement in varying vegetative structures may be an important aspect of SNV transmission among its vertebrate host. Replicated, comparative studies are needed to collaborate and investigate the generality of this phenomenon.

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