

## ANTIBODY TO SIN NOMBRE VIRUS IN RODENTS ASSOCIATED WITH PERIDOMESTIC HABITATS IN WEST CENTRAL MONTANA

AMY J. KUENZI, RICHARD J. DOUGLASS, DON WHITE, JR., CLIFFORD W. BOND, AND JAMES N. MILLS

*Department of Biology, Montana Tech of the University of Montana, Butte Montana; School of Forestry Resources, The University of Arkansas-Monticello, Monticello, Arkansas; Department of Microbiology, Montana State University, Bozeman, Montana; Special Pathogens Branch, Division of Viral and Rickettsial Diseases, National Center for Infectious Diseases, Centers for Disease Control and Prevention, Atlanta, Georgia*

**Abstract.** Most human cases of hantavirus pulmonary syndrome are acquired in the peridomestic environment, yet studies of the ecology and infection dynamics in the reservoir host, the deer mouse (*Peromyscus maniculatus*), have focused on sylvan populations. We describe a 2.5-year study of hantavirus infection in rodents associated with peridomestic habitats in west central Montana. Antibodies reactive with Sin Nombre virus (SNV) were found in five species. Overall SNV antibody prevalence was highest among deer mice (25% of individuals tested). As has been demonstrated for sylvan populations, the antibody-positive component of the deer mouse population consisted of a higher proportion of adults and males. However, the prevalence of antibodies to SNV was higher in this study than has been reported in most sylvan studies. The average monthly proportion of deer mouse blood samples with antibodies to SNV ranged from approximately 20% to 25% and was highest in the late spring/early summer. The higher SNV antibody prevalence in peridomestic compared with sylvan settings may be related to behavioral differences and/or potentially longer survival of the virus deposited inside buildings. Peridomestic settings presented higher concentrations of virus and may present a higher risk of human infection than do sylvan settings.

### INTRODUCTION

Hantaviruses are rodent-borne pathogens that produce chronic persistent infections in their reservoir hosts. Prior to 1993, only two hantaviruses had been described in North America, Prospect Hill and Seoul virus.<sup>1,2</sup> In 1993, an outbreak of a respiratory illness of unknown etiology in the Four Corners region of the southwestern United States led to the isolation and identification of Sin Nombre virus (SNV) and to the description of hantavirus pulmonary syndrome (HPS).<sup>3</sup> The primary reservoir of SNV was determined to be the deer mouse (*Peromyscus maniculatus*).<sup>4</sup>

Recognition of HPS increased interest in the ecology of reservoir hosts, and a series of cross-sectional and longitudinal studies<sup>5-8</sup> were initiated to describe the extent of hantavirus infection in North American reservoir species and to increase understanding of reservoir ecology and host-virus dynamics.<sup>9</sup> These studies were largely restricted to wild populations in natural environments. Most human cases of HPS are likely acquired in peridomestic settings, including human dwellings, out-buildings, corrals, and ranch yards.<sup>10</sup> Although the dynamics of natural populations likely influence the numbers and behavior of peridomestic deer mice, the specific factors of human and rodent behavior that lead to peridomestic exposure can be elucidated only through studies in the specific environment of exposure.<sup>11</sup>

Unfortunately, little work has been done in this area. Bennett and others<sup>12</sup> collected rodents from various habitat types in southern California, including urban-suburban and rural residential areas. The prevalence of antibodies to hantavirus in deer mice from these areas was 11.6%. High antibody prevalences to SNV among some rodent populations associated with peridomestic situations have previously been reported<sup>5,13</sup> (Ksiazek TG and others, unpublished data). These higher prevalences were thought to be related to the fact that sampling was conducted at specific sites where human exposure had occurred. Jay and others<sup>5</sup> reported an overall prevalence of 27% for deer mice trapped at sites near human cases of HPS in California. Zeitz and others<sup>13</sup> examined

prevalence of hantavirus antibodies in *Peromyscus* spp. in and around HPS case households and near and far control households in the southwestern United States following the 1993 outbreak. Prevalence around these dwellings ranged from 27.5% to 32.5%, with no significant difference between case and control households. Nevertheless, all control homes were located within a clearly defined epidemic area. The prevalence of antibodies to hantavirus in deer mice captured inside homes in a nonoutbreak area in Montana was somewhat lower at 20%.<sup>14</sup> In Argentina, Calderón and others<sup>15</sup> sampled rodents associated with peridomestic settings and found antibody reactive to SNV in six species. Prevalence differed with species and province but ranged from 0% to 12%. None of these studies examined population and prevalence dynamics over extended periods. Long-term studies of peridomestic populations of host species are needed to elucidate the dynamics of hantavirus infection in these host populations.

This study was initiated to determine prevalence of hantavirus infection in rodents associated with peridomestic habitats in west central Montana. None of our study sites were associated with human cases of HPS. Our specific objectives were to identify infected species, describe the characteristics of infected individuals, assess temporal and intra-specific variation in prevalence of infection, and compare these characteristics with those of sylvan populations in the same geographic areas.

### MATERIALS AND METHODS

**Study sites.** We established three study sites, one located near Anaconda (Silver Bow County, Montana), one near Butte (Silver Bow County, Montana), and one near Cascade (Cascade County, Montana). All three sites were cattle ranches, and each included the following features: homes, yards, driveways, fence lines, grassy/weedy fields, and out-buildings including barns, workshops, and garages. The out-buildings present at each site were not abandoned buildings;

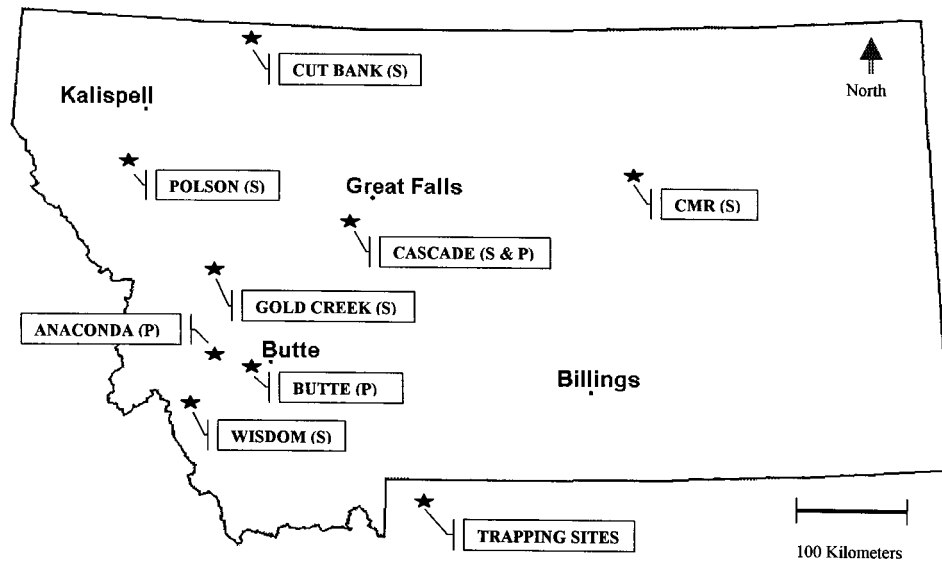


FIGURE 1. Location of six sylvan (S) and 3 peridomestic (P) small mammal trapping sites in Montana.

TABLE 1

Overall prevalence of antibodies to Sin Nombre virus among wild rodents at 3 study sites in west-central Montana, October 1996–August 1999

Family/species	Site	No. individuals trapped* (total captures)	Hantavirus antibody		
			Number tested	Number positive	Percent positive
<b>Sciuridae</b>					
<i>Tamias amoenus</i>	Anaconda	133 (194)	109	1	0.9
	Butte	63 (83)	50	6	12.0
	All sites combined	196 (277)	159	7	4.4
<i>Spermophilus lateralis</i>	Anaconda	12 (17)	8	0	0.0
	Butte	29 (34)	15	1	6.7
	All sites combined	41 (51)	23	1	4.3
<i>Spermophilus richardsonii</i>	Cascade	1 (1)	1	0	0.0
<b>Muridae</b>					
<i>Peromyscus maniculatus</i>	Anaconda	1,132 (2,571)	1,020	237	23.2
	Butte	705 (1,497)	652	188	28.8
	Cascade	348 (503)	331	65	19.6
	All sites combined	2,185 (4,571)	2,003	490	24.5
<i>Neotoma cinerea</i>	Butte	12 (13)	6	0	0.0
	Cascade	2 (4)	2	0	0.0
	All sites combined	14 (17)	8	0	0.0
<i>Mus musculus</i>	Anaconda	48 (73)	34	0	0.0
	Butte	27 (38)	21	0	0.0
	All sites combined	75 (111)	55	0	0.0
<i>Clethrionomys gapperi</i>	Anaconda	29 (35)	23	1	4.3
	Cascade	1 (1)	1	0	0.0
	All sites combined	30 (36)	24	1	4.2
<i>Microtus longicaudus</i>	Anaconda	4 (4)	3	0	0.0
	Butte	6 (9)	5	0	0.0
	All sites combined	10 (13)	8	0	0.0
<i>Microtus pennsylvanicus</i>	Anaconda	72 (84)	52	3	5.8
	Butte	110 (115)	57	6	10.5
	Cascade	28 (31)	26	5	19.2
	All sites combined	210 (230)	135	14	10.4
<b>Zapodidae</b>					
<i>Zapus princeps</i>	Butte	16 (16)	16	0	0.0
<b>TOTAL</b>					
	Anaconda	1,430 (2,978)	1,249	242	19.4
	Butte	968 (1,805)	822	201	24.5
	Cascade	380 (540)	361	70	19.4
	All sites combined	2,778 (5,323)	2,432	513	21.1

\* Number individuals trapped includes new individuals that were found dead in traps.

most buildings on these ranches were used by people on a daily basis. Buildings not used daily were generally storage buildings that were entered on an irregular basis. Characteristics of these peridomestic populations were compared with those of sylvan populations on 18 mark-recapture grids located at six different sites in western and central Montana (Figure 1). One of these sites was located approximately 1.5 km from the Cascade study site. These grids and populations are described in detail by Douglass and others.<sup>7</sup>

**Rodent collection.** We captured rodents in non-folding aluminum Sherman live traps (8 × 9 × 23 cm; H.B. Sherman Trap Co., Tallahassee, FL). At all three peridomestic sites, traps were set inside of buildings, around the perimeter of buildings, and in outside areas up to 150 m away from buildings. The number of traps used varied with site. At the Anaconda site, approximately 78% of 225 traps were set in outside areas, 9% around building perimeters, and 13% in buildings used daily. At the Butte site, approximately 40% of 177 traps were set outside, 12% around building perimeters, 37% in buildings used daily, and 11% in buildings used on an irregular basis. At the Cascade site, approximately 21% of 70 traps were set outside, 58% in buildings used daily, and 21% in buildings used irregularly. The number and placement of traps at each site remained constant throughout the study.

Sampling began in November 1996 at the Anaconda and Cascade sites and in February 1997 at the Butte site and continued through August 1999. Traps were baited with peanut butter and oatmeal, provided with polyester bedding, and set for three consecutive nights once a month. We followed the safety recommendations provided by Mills and others<sup>16,17</sup> during all sampling procedures. Each morning, all captured rodents were transported to a central site for processing. We recorded species, body mass, sex, reproductive condition (males: testes scrotal or abdominal; females: nonperforate, perforate, pregnant, and/or lactating), presence of scars or wounds, and location of capture. We inferred age for *P. maniculatus* based on the following weight categories: < 14 grams were considered juveniles, 14–17 grams were sub-adults, and > 17grams were adults.<sup>18</sup> Rodents were then ear-tagged with metal fingerling tags. The enumeration technique<sup>19</sup> was used to determine the minimum number of *P. maniculatus* alive during each month.

**Blood sampling and antibody testing.** Blood samples were collected from the retro-orbital sinus of each animal by using a heparinized capillary tube and were stored on dry ice until transferred to -70°C freezers for storage. Between April 1997 and August 1997, rodents were sampled for three consecutive nights twice a month at the Anaconda and Butte site. All captured rodents were processed as described above, but blood samples were taken only from individuals captured during the first trapping session of the month. Serologic testing was conducted at Montana State University (Bozeman, MT). Samples of whole blood were tested for antibody reactive with SNV recombinant nucleocapsid protein by an enzyme-linked immunosorbent assay according to standardized protocols.<sup>20</sup> This assay will detect, but not distinguish among, infections by all known North American hantaviruses. In addition, the assay was devised to detect only IgG, not IgM antibody.

TABLE 2  
Percentage of antibody-positive and antibody-negative deer mice by age, presence or absence of wounds and capture site. Number of individuals are shown in parentheses

Characteristic	Anaconda		P**	Butte		P**	Cascade		P**
	Positive	Negative		Positive	Negative		Positive	Negative	
<b>Sex</b>									
% Male (No.)	62.9 (149/237)	48.4 (379/783)	<0.0001	62.2 (117/188)	50.9 (236/463)	0.0115	56.9 (37/65)	53.9 (144/267)	0.7677
% Female (No.)	37.1 (88/237)	51.6 (404/783)		37.8 (71/188)	49.1 (227/463)		43.1 (28/65)	46.1 (123/267)	
<b>Age</b>									
Juvenile	10.1 (14/139)	8.1 (56/689)	<0.0001	8.5 (11/129)	17.6 (75/427)	<0.0001	20.0 (10/50)	5.0 (13/258)	<0.0001
Sub-adult	11.5 (16/139)	33.1 (228/689)		22.5 (29/129)	43.3 (185/427)		10.0 (5/50)	31.8 (82/258)	
Adult	78.4 (109/139)	58.5 (405/689)		69.0 (89/129)	39.1 (167/427)		70.0 (35/50)	63.2 (163/258)	
<b>Scars</b>									
Yes	28.3 (36/127)	11.8 (82/697)	<0.0001	22.2 (24/108)	10.3 (44/429)	0.0015	22.0 (11/50)	23.4 (62/265)	0.9746
No	71.7 (91/127)	88.2 (615/697)		77.8 (84/108)	89.7 (385/429)		78.0 (39/50)	76.6 (203/265)	

\* P associated with chi-square values with Yate's correction and 1 degree of freedom for sex and scar comparisons. P associated with chi-square values and 2 degrees of freedom for age comparisons.

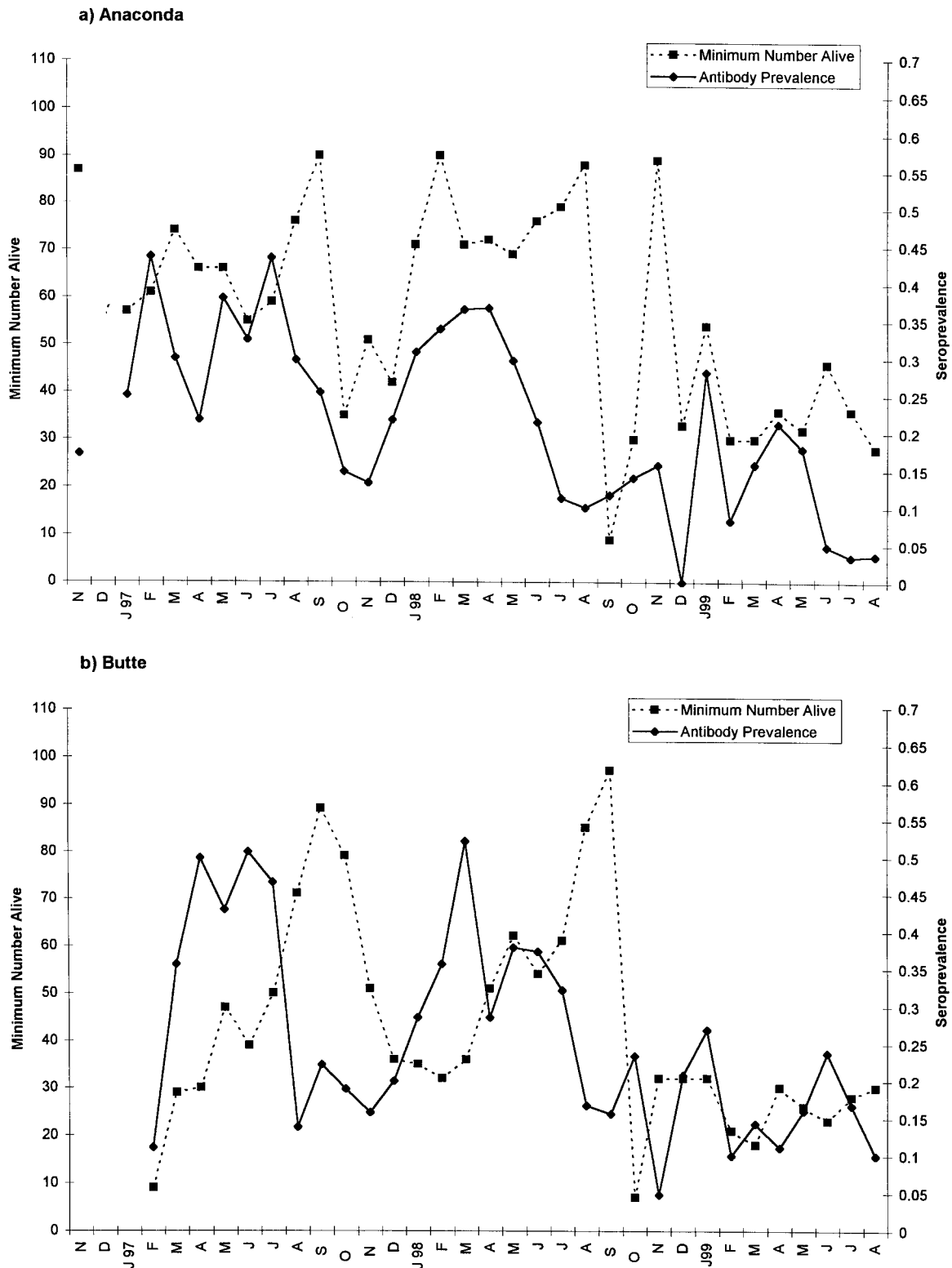


FIGURE 2. Trends in population size and antibody prevalence for deer mice at 3 study sites in west-central Montana from November 1996–August 1999.

**Statistical analysis.** Statistical analysis was performed using JMP (SAS Institute, Inc., Cary, NC). All continuous variables used in parametric tests were normally distributed and exhibited appropriate homogeneity of variances.

RESULTS

**Species captured.** Between October 1996 and August 1999, 2,778 rodents were captured 5,323 times and 2,432

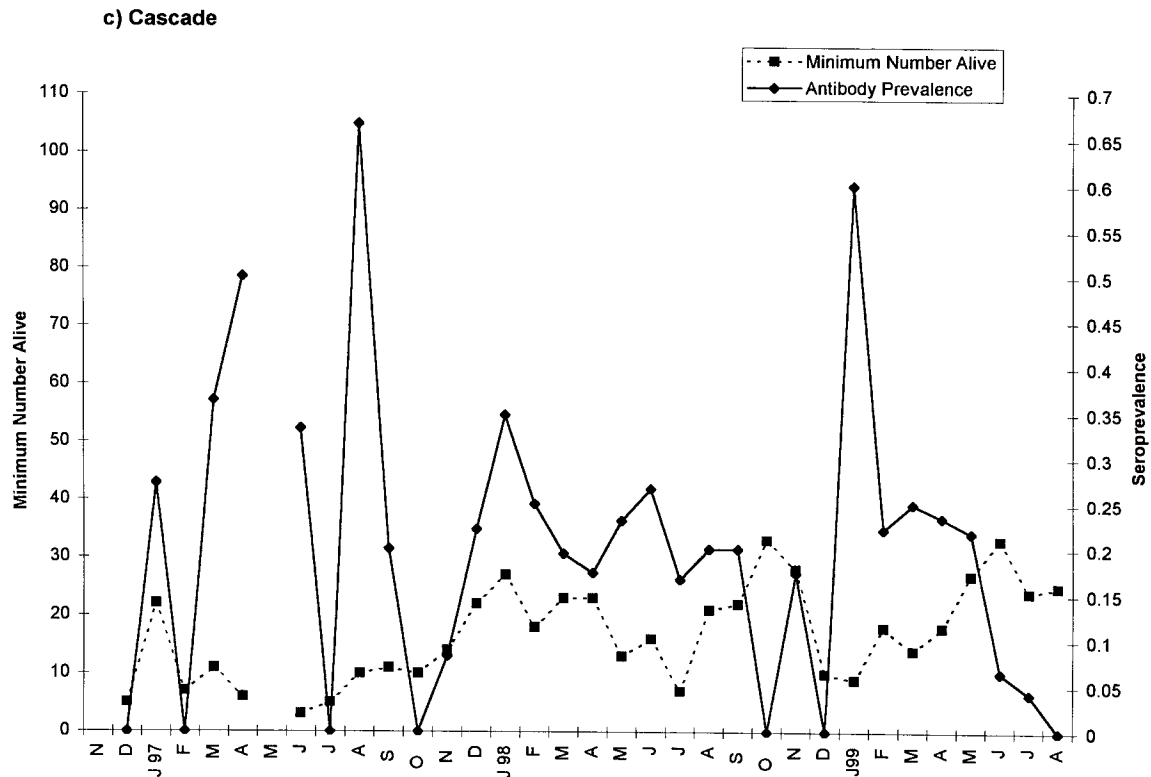


FIGURE 2. Continued.

blood samples were obtained from all sites combined (Table 1). The deer mouse (*P. maniculatus*) was the most common species captured overall and at each of the individual study sites. The only other species captured at all three study sites was the meadow vole (*Microtus pennsylvanicus*). Yellow-pine chipmunks (*Tamias amoenus*) were relatively common at Anaconda (9.3%) and Butte (6.5%), but were not captured at Cascade. Other species captured infrequently (< 3%) at one or more sites included house mice (*Mus musculus*), golden-mantled ground squirrels (*Spermophilus lateralis*), bushy-tailed wood rats (*Neotoma cinerea*), southern red-backed voles (*Clethrionomys gapperi*), long-tailed voles (*Microtus longicaudus*), western jumping mice (*Zapus princeps*), and Richardson's ground squirrels (*Spermophilus richardsonii*).

At Anaconda most rodent captures (88%) occurred in outside areas. Captures in frequently used buildings accounted for 8% of all captures, while 4% of all captures came from around the perimeter of buildings. Outside locations accounted for 44% of the rodent captures at the Butte study site. Captures in buildings used daily made up 23% of total captures while captures in buildings used irregularly accounted for 17%. The remaining captures at this site came from around the perimeter of buildings. At Cascade, 37% of captures occurred outside, 42% in frequently used buildings, and 21% in buildings used irregularly.

**Prevalence of antibody.** Of 1,249 rodents tested from Anaconda, 242 (19.4%) had antibodies reactive with SNV (Table 1). At the Butte site, we found 201 (24.5%) positive animals among 822 rodents. At Cascade, 70 (19.4%) of 361 rodents tested positive for antibodies.

Two species in the family Sciuridae had antibodies reac-

tive with SNV, *T. amoenus* and *S. lateralis* (Table 1). The majority of antibody-positive *T. amoenus* (6 of 7) came from the Butte site, where prevalence was 12.0%. Only one (0.9%) of 109 *T. amoenus* were antibody positive at Anaconda. One individual *S. lateralis* was found to be SNV antibody positive at the Butte site. None of the *S. lateralis* tested at the Anaconda site had antibodies reactive with SNV.

In the family Muridae, three species had antibodies reactive with SNV: *P. maniculatus*, *C. gapperi*, and *M. pennsylvanicus* (Table 1). Antibody prevalence was highest among deer mice for which nearly 25% of individuals tested were antibody-positive. Among study sites, SNV antibody prevalences ranged from 19.6% (65 of 331) at Cascade to 28.8% (188 of 652) at Butte. Antibody prevalences for *C. gapperi* ranged from 0% at Cascade to 4.3% (1 of 23) at Anaconda. *M. pennsylvanicus* had an overall prevalence of 10.4% (14 of 135), with the highest SNV antibody prevalence being found at the Cascade site (19.2%).

**Characteristics of infected deer mice.** Antibody-positive deer mice were more likely to be male than female and were predominately adults (Table 2). The ratio of male to female among antibody positive deer mice was significantly higher than that among the total sample and significantly more adults were antibody positive than would be expected from the distribution of age classes among the total samples at both the Anaconda and Butte study sites. The ratio of male to female among antibody positive mice did not differ from that of antibody negative mice at Cascade.

Antibody-positive deer mice were more likely to have wounds than antibody-negative individuals (Table 2). The frequency of scars among antibody positive mice was sig-

nificantly higher than that among the total sample at both the Anaconda and Butte study sites. Since antibody to SNV and scars both accumulate with age, the greater prevalence of antibody in animals with scars could be due to the correlation of both of these variables with age. To test for this, we also examined the frequency ratio of scars among antibody positive males within each age class. Adult antibody-positive mice were found to have a significantly higher frequency of scars (30.4 % [65 of 214]) than antibody-negative adults (17.9 % [132 of 738]) ( $\chi^2 = 15.01$ , degrees of freedom [df] = 1,  $P = 0.0001$ ). There were no significant differences in the frequency of scars between antibody-positive (12.2 % [5 of 41] with scars) and antibody-negative subadults (9.5% [47 of 496]) ( $\chi^2 = 0.085$ , df = 1,  $P = 0.771$ ) or antibody-positive (0% [0 of 25]) and antibody-negative juveniles (5.5% [8 of 145]) ( $\chi^2 = 0.479$ , df = 1,  $P = 0.0489$ ).

**Deer mouse population and antibody-prevalence dynamics.** There was an overall trend for deer mouse numbers to peak in late summer and early fall and then decrease over the winter at all sites (Figures 2A–C and 3A). At Cascade and Anaconda, however, numbers increased in January 1998 and remained high over that winter. The monthly prevalence of SNV antibody among deer mice at each of the three study sites ranged from 0% to approximately 70% (Figures 2A–C). Average prevalences of antibody to SNV over the course of the study were 21.6 % (SD = 11.86, n = 31) at Anaconda, 25.5% (SD = 13.4, n = 31) at Butte, and 20.9% (SD = 16.8, n = 31) at Cascade. Antibody prevalence began increasing in late winter and early spring, and was generally highest during January through June before descending sharply in the fall (Figures 2A–C and 3A) as the breeding season ended (Figure 4A).

**Comparisons with sylvan populations.** Deer mouse numbers and antibody prevalence in sylvan populations in Montana showed a similar pattern to that from our peridomestic populations (Figure 3B). Prevalence of infection began increasing in late winter and early spring, and was generally highest during March through June before descending sharply in the fall as the breeding season ended and uninfected juveniles began to enter the trappable population. (Figure 4B). The percentage of males in breeding condition showed a similar seasonal pattern between sylvan and peridomestic populations with peaks usually occurring in February or March (Figures 4A and B). The highest percentages of females in breeding condition occurred in June for both peridomestic and sylvan populations.

Overall, the prevalence of antibody to SNV in deer mice was significantly higher at the peridomestic study sites compared with those in sylvan areas (Table 3). In addition, the average monthly prevalence was significantly higher at the peridomestic sites. Peridomestic populations consisted of a higher proportion of deer mice compared with other species of rodents. These differences were apparent when comparing across all study sites as well as when restricting comparisons to the Cascade site, where peridomestic and sylvan sampling sites were very close (Table 3). Sex and age ratios of captured deer mice, however, did not differ between the peridomestic populations and sylvan populations at all trapping sites. The percentage of adults in the population that had scars was higher for the peridomestic population at Cascade but this finding was not consistent across all study sites.

## DISCUSSION

Most field studies of hantaviruses and their rodent hosts in the United States have been conducted in sylvan populations. Ours is the first long-term study of prevalence of hantavirus infection among rodents in peridomestic settings. We found antibodies to a hantavirus in three murid rodent species and two species of sciurids within peridomestic environments in Montana. Hantavirus infection in sylvan populations of murid rodents has been found to be common in many regions throughout the United States,<sup>5,7,12,21–23</sup> and in peridomestic environments in the United States<sup>5,12,13</sup> and Argentina.<sup>15</sup> Infection in other rodent families is believed to be due to spillover, possibly during times of high rodent population density and or increased interspecific contact.<sup>22</sup>

Of five species positive for antibodies to hantaviruses, only deer mice were commonly captured inside buildings including houses at all three study sites. Others have documented *Peromyscus* frequently invading rural housing.<sup>24</sup> We also occasionally captured three other antibody-positive species, the meadow vole, yellow-pine chipmunk, and golden-mantled ground squirrel, inside ranch buildings other than homes. The red-backed vole was captured only outside. One other species commonly associated with peridomestic environments is *M. musculus*.<sup>12,15</sup> This species was rare at our study sites in Montana and no antibody-positive individuals were captured. Hantavirus antigens (Puumala-like virus) have been detected in house mice from Serbia and Yugoslavia,<sup>25</sup> but infection of house mice with SNV or other American hantaviruses is rare.<sup>4,5,12,21</sup> (Ksiazek TG and others, unpublished data).

The overall prevalence of antibodies reactive with SNV antigen among deer mice from peridomestic environments in Montana ranged from 19.6% to 28.8%. Prevalence for all sites combined was 24.5%. These hantavirus antibody prevalences are higher than those of deer mice from urban-suburban and rural residential areas in southern California,<sup>12</sup> but slightly lower than those found by Zeitz and others<sup>13</sup> in their case-control study following the original HPS outbreak in the Four Corners region of the southwestern United States. Our hantavirus antibody prevalences are also slightly lower than those from deer mice trapped at sites near human cases of HPS in California, where prevalence was close to 27%.<sup>5</sup>

However, the prevalences we obtained are much higher than the overall prevalence reported for sylvan populations of deer mice in Montana during the same period, as well as sylvan populations in numerous other areas of the United States.<sup>5,6,12,22,24,26–28</sup> Although they did not focus on the peridomestic environment, Otteson and others<sup>21</sup> also documented a higher SNV antibody prevalence among rodents trapped near buildings. At one of their study sites in Nevada, all antibody-positive animals were captured within a 100-m radius of ranch buildings. These results suggest that higher antibody prevalences observed when sampling at peridomestic case sites<sup>5</sup> may not necessarily represent site-specific associations resulting in human disease. Instead, they may reflect a broader pattern of higher prevalences in peridomestic environments, regardless of human cases. Additional comparisons of sylvan and peridomestic prevalences in other geographic areas are needed to confirm this pattern.

Hantavirus antibody-positive deer mice in peridomestic

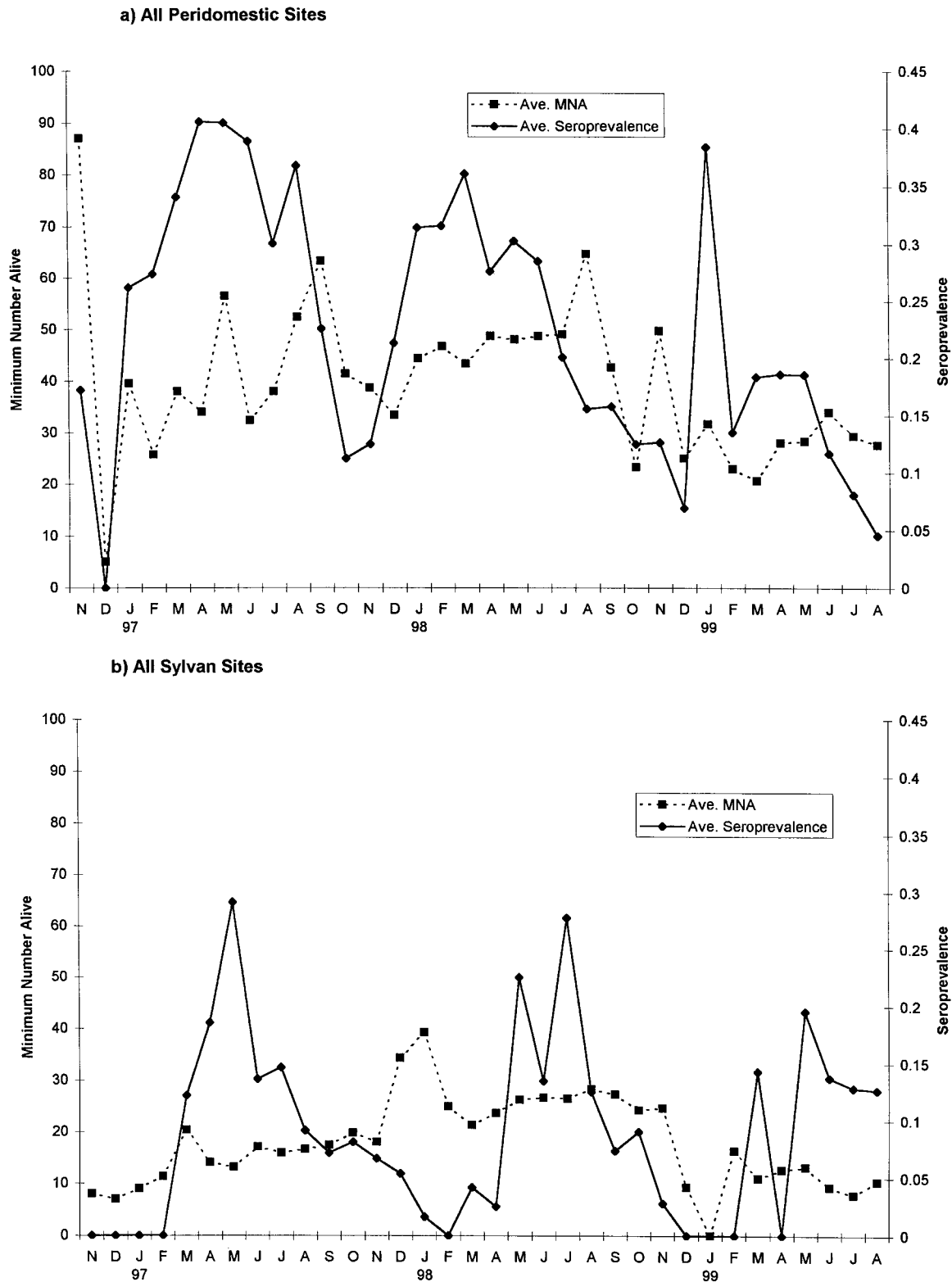


FIGURE 3. Average trends in population size and antibody prevalence. a) Data averaged from 3 peridomestic sites. b) Data averaged from 6 sylvan study sites during the months of May through October. Data averaged from 1 study site (Cascade) during November through April.

environments within Montana were more likely to be male than female and were predominately adults. These findings support those from sylvan populations.<sup>11,22,24</sup> Since a higher proportion of males are infected than females, a male-biased

sex ratio would lead to higher overall prevalence. Thus, differences in population demographics could explain why peridomestic populations have a higher seroprevalence compared with sylvan populations. However, we found no dif-

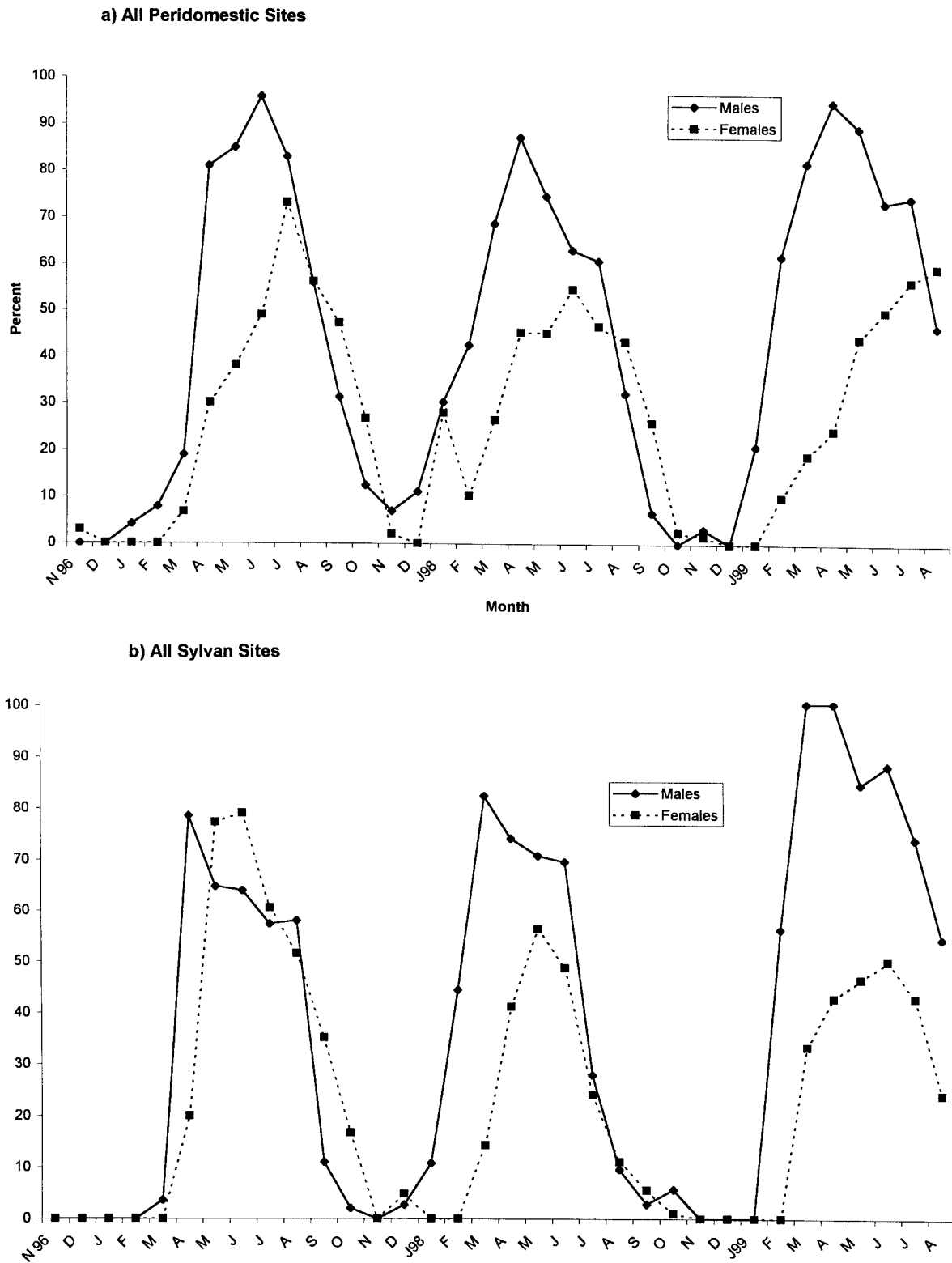


FIGURE 4. Percentage of male and female deer mice that were reproductively active by month. a) Data from 3 peridomestic study sites in west-central Montana were combined. b) Data from May through October is combined from 18 grids from 6 sylvan study sites. Data from November through April is combined from 3 grids at 1 sylvan study site (Cascade).



TABLE 3

Comparison of peridomestic deer mouse populations with sylvan deer mouse populations in Montana from October 1996–August 1999. Cascade peridomestic and sylvan sampling sites were separated by ~1500 meters

Characteristic	All peridomestic sites	All sylvan sites	<i>P</i> -value‡	Cascade peridomestic	Cascade sylvan	<i>P</i> -value‡
Overall SNV Antibody Prevalence*	24.5 (490/2,003)	16.54 (302/1,845)	<0.0001	19.6 (65/331)	7.1 (33/465)	<0.0001
Average Monthly Prevalence†	22.3 ± 11.2 (34)	9.72 ± 8.10 (31)	<0.0001	20.9 ± 16.8 (31)	8.49 ± 9.09 (31)	0.0006
Sex Ratio (Males: Females)*	1:0.89 (1,062:941)	1:0.89 (980:865)	0.9782	1:0.83 (181:150)	1:0.72 (271:194)	0.3487
Age Ratio (Adults: Subadults: Juveniles)*	1:0.6:0.2 (968:545:179)	1:0.5:0.2 (943:477:196)	0.1438	1:0.44:0.12 (198:87:23)	1:0.38:0.15 (220:84:34)	0.3783
% of adults with scars*	20.6 (197/952)	24.4 (211/863)	0.063	25.8 (51/198)	12.7 (43/338)	0.0002
% of population consisting of deer mice*	78.7 (2,185/2,778)	74.3 (1,874/2,522)	0.0002	91.6 (348/380)	73.7 (481/653)	<0.0001

\* Number of individuals shown in parentheses.

† Number of months shown in parentheses.

‡ *P* associated with chi-square values with Yates' correction and 1 degree of freedom for overall prevalence, Sex ratio, % of adults with scars, % of population consisting of deer mice comparisons. *P* associated with chi-square values and 2 degrees of freedom for age ratio comparisons. *P* associated with student's *t*-test for average monthly prevalence comparisons.

ference in sex or age structure when comparing the two types of populations.

Several studies of sylvan deer mouse populations<sup>12,22,27</sup> (Douglass RJ and others, unpublished data) have reported a higher prevalence of wounds or scars among infected individuals, indicating fighting as a likely mode of transmission between infected and non-infected individuals. We found no difference in the ratio of scars between antibody-positive and antibody-negative juvenile or subadults. However, adult antibody-positive mice did have a higher ratio of scars to no scars than did antibody-negative adults. The proportion of the population that had scars was higher among the peridomestic population than among the sylvan population at Cascade suggesting increased encounters between individuals in peridomestic populations. However, these percentages were similar between peridomestic and sylvan populations across all study sites combined.

The prevalence of antibody to hantavirus varied considerably within sites by month for both peridomestic and sylvan populations in western and central Montana. Prevalence began increasing in winter and peaked in spring or early summer. Cases of human infection in the Four Corners region of the United States show a spring-summer pattern of seasonality<sup>29,30</sup> and peaks of seroprevalence in sylvan populations of deer mice have been documented as occurring in mid to late summer in Nevada<sup>23</sup>, and in the spring in Colorado.<sup>27</sup>

In summary, we found many similarities between peridomestic and sylvan deer mouse populations in terms of characteristics of infected mice and prevalence dynamics. However, prevalence of infection was found to be higher among peridomestic populations. There are several possible reasons for this observation. First, home range size in peridomestic settings may differ from those in sylvan populations. Overlapping home ranges could lead to increased encounters and potential virus transmission events between rodents and smaller home range size could lead to a concentration of urine and feces within the home range. Second, movements inside of buildings are restricted, also leading to the concentration of urine and feces within specific areas. Finally, virus shed in peridomestic environments, especially inside of buildings, may persist longer than in outdoor environments, where infectious aerosols would be quickly dissipated and virus would be quickly inactivated by ultraviolet light.

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**Authors' addresses:** Amy J. Kuenzi and Richard J. Douglass, Department of Biology, Montana Tech of the University of Montana, Butte, MT 59701. Don White, Jr., School of Forestry Resources, The University of Arkansas-Monticello, Monticello, AR 71656. Clifford W. Bond, Department of Microbiology, Montana State University, Bozeman, MT 59717-3520. James N. Mills, Special Pathogens Branch, Division of Viral and Rickettsial Diseases, National Center for Infectious Diseases, Centers for Disease Control and Prevention, 1600 Clifton Road, Atlanta, GA 30333.

**Reprint requests:** Amy J. Kuenzi or Richard J. Douglass, Department of Biology, Montana Tech of the University of Montana, Butte, MT 59701.

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