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DO UNUSUAL SITE-SPECIFIC POPULATION DYNAMICS OF RODENT RESERVOIRS PROVIDE CLUES TO THE NATURAL HISTORY OF HANTAVIRUSES?

Charles H. Calisher,^{1,6} James N. Mills,² William P. Sweeney,^{1,3} Jerry R. Choate,⁴ Daniel E. Sharp,⁵ K. Max Canestorp,⁵ and Barry J. Beaty¹

¹ Arthropod-borne and Infectious Diseases Laboratory, Foothills Campus, Colorado State University, Fort Collins, Colorado 80523, USA

² Division of Viral and Rickettsial Diseases, National Center for Infectious Diseases, Centers for Disease Control and Prevention, MS/G14, 1600 Clifton Road, N.E., Atlanta, Georgia 30333, USA

³ Present address: Muñiz Engineering, Inc., 16903 Buccaneer Lane, Suite 200, Houston, Texas 77058, USA

⁴ Sternberg Museum of Natural History, Fort Hays State University, Hays, Kansas 67601-4099, USA

⁵ U.S. Fish and Wildlife Service, Colorado Fish and Wildlife Assistance Office, 755 Parfet St., Suite 496, Lakewood, Colorado 80215, USA

⁶ Corresponding author (e-mail: calisher@promedmail.org)

ABSTRACT: Between January 1995 and November 1997, longitudinal mark-recapture studies of rodent hosts of hantaviruses in a disturbed microhabitat within a shortgrass prairie ecosystem in southeastern Colorado (USA) were conducted. The site was distinguished by edaphic and floristic characteristics unique to this area and associated with historical land use patterns, as well as the year-around availability of water from a functioning windmill. Populations of two common rodent species that are hosts for hantaviruses, *Peromyscus maniculatus* and *Reithrodontomys megalotis*, had unusually rapid turnover, a younger age structure, and a much lower prevalence of antibody to Sin Nombre virus than did populations at nearby sites in more typical shortgrass prairie and canyon habitats. Based on these findings, we suggest that a stable resident population of the reservoir is critical to the maintenance of hantaviruses at a given site, and we hypothesize that long-lived, persistently infected rodents are the principal transseasonal reservoir of hantaviruses.

Key words: El Moro Canyon virus, habitat, hantaviruses, *Peromyscus maniculatus*, *Reithrodontomys megalotis*, rodents, shortgrass prairie, Sin Nombre virus, virus.

INTRODUCTION

In late spring 1993, the first cases of hantavirus pulmonary syndrome were detected in humans in the Four Corners area of the southwestern USA. These infections had been caused by a newly recognized virus of the family Bunyaviridae, genus *Hantavirus*, Sin Nombre virus (SNV; Ksiazek et al., 1995). Succeeding investigations showed that the principal host of this virus is the deer mouse, *Peromyscus maniculatus* (Childs et al., 1994).

Intensive investigations of wild rodent populations in the Americas revealed additional hantaviruses. In the USA alone, the following viruses and their rodent hosts have been found: Black Creek Canal and Muleshoe viruses in hispid cotton rats (*Sigmodon hispidus*) in Florida and Texas, respectively; New York virus in white-footed mice (*Peromyscus leucopus*) in New York; Bayou virus in rice rats (*Oryzomys palustris*) in Louisiana, Georgia and South

Carolina; Bloodland Lake virus in prairie voles (*Microtus ochrogaster*) in Missouri; Isla Vista virus in California voles (*Microtus californicus*) in California; and El Moro Canyon virus in western harvest mice (*Reithrodontomys megalotis*) essentially throughout its range. It is likely that more hantaviruses will be found in other murid rodent species. In all, these findings have demonstrated a close association (suggesting a long-term relationship) between each hantavirus and a particular rodent host species (Morzunov et al., 1998).

In the specific host, hantaviruses establish a chronic infection that involves persistent or sporadic shedding of infectious virus in bodily secretions and excretions for many months, probably for the life of the host (Lee et al., 1981; Yanagihara, 1990; Hutchinson et al., 1998). Numerous studies have demonstrated an age-related prevalence of antibody, often favoring males (Glass et al., 1988; Childs et al.,

1994; Mills et al., 1997; Calisher et al., 1999), indicating that virus is maintained in reservoir populations via horizontal transmission, perhaps most frequently through aggressive encounters among adult males. Populations consisting of older individuals may have much higher prevalences of infection than populations comprising mostly young mice. It has been hypothesized that transseasonal maintenance of hantaviruses in reservoir populations in temperate environments occurs via long-lived resident animals, which maintain infection from the previous season and reintroduce virus to susceptible animals each spring (Abbott, et al., 1999; Calisher et al., 1999; Mills et al., 1999a).

The foregoing hypothesis implies that a stable, resident reservoir population is required for the maintenance of infection with a hantavirus at a given site. Thus, it may be predicted that a reservoir population with a consistently young age structure, maintained by a high rate of population turnover, should demonstrate a relatively low rate of hantavirus infection, or may not support hantavirus infection at all. These conditions of high population turnover might be found in marginal populations at the periphery of a host species range, at locations of suboptimal habitat within the species range, or in areas where unusually intense predation or competition contribute to a rapid loss of resident individuals.

Since 1995, we have been conducting mark-recapture studies of rodent populations at four specific sites in a shortgrass prairie ecosystem in southeastern Colorado. The rodent assemblages at the sites include two species that are common hantavirus reservoirs in the area, *P. maniculatus* and *R. megalotis*. A third potential host species, *S. hispidus*, is present at some of the sites and, although known to host hantaviruses in the southern USA, has not been shown to host a hantavirus in Colorado.

In the current study, we investigated population and community dynamics with-

in a rodent assemblage occurring in a disturbed microhabitat. We demonstrated that populations of two common hantavirus reservoir species at this site undergo increased rates of population turnover relative to nearby populations in more natural, less disturbed habitats. We used these natural experimental conditions to test the hypothesis that reservoir populations experiencing a high rate of population turnover will not support the maintenance of hantaviruses.

MATERIALS AND METHODS

Description of study site

The Piñon Canyon Maneuver Site (PCMS), Las Animas County, southeastern Colorado, comprising more than 1,040 km², is managed by the Directorate of Environmental Compliance and Management, Fort Carson, Colorado. Prior to its acquisition by the U.S. Army in 1983, the area was regularly grazed by domestic and wild ungulates and small populations of humans had resided there since it was pioneered in the late 1870's. The nearest towns are more than 30 miles distant. Complete descriptions of this tract (Shaw et al., 1989; U.S. Department of the Army, 1980; Andersen et al., 1989) have characterized the area as follows: "Climate is classified as dry continental and elevation ranges from 1,300 to 1,700 m. Topography consists of broad, moderately sloping uplands bordered by the Purgatoire River Canyon on the east, limestone hills on the west, and a basaltic hogback on the south. Vegetation is dominated by shortgrass prairie and pinyon pine (*Pinus edulis*)-juniper (*Juniperus monosperma*) woodland" (Costello, 1954). The pinyon-juniper plant association is concentrated along the Purgatoire River Canyon and its side canyons, in the limestone hills, and on parts of the basaltic hogback.

Located at 37°31'32.7" North latitude, 103°53'54.5" West longitude, 1,560 m altitude, our 107 m × 107 m fenced study site (Fig. 1) is comprised of deep Wiley loam derived from Eolian silt and sand from sedimentary rock. Although it apparently is recovering some 12 yr after the last cattle were present, this site is severely disturbed from decades of vegetation and water utilization, hoof compaction, and loafing by cattle.

Floral composition was assessed by an ocular estimate based on past line intercept studies. Observations of floral composition at the windmill and at other trapping sites were made a total of three times, in spring, early summer,

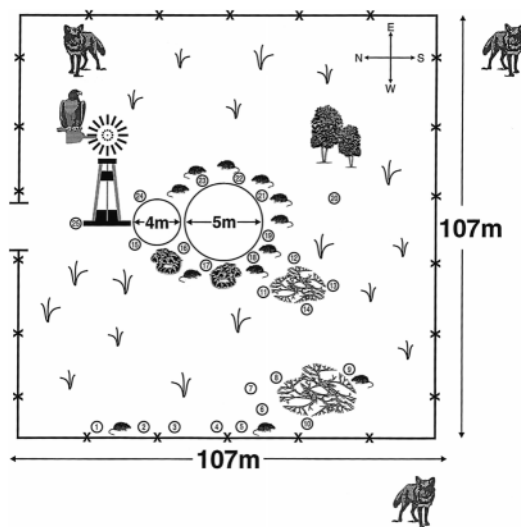


FIGURE 1. Schematic diagram of a windmill site at Piñon Canyon Maneuver Site, southeastern Colorado. Encircled numbers indicate trap locations.

and fall 1998. Observations were made on transects running approximately north, south, east, and west from the fenced area for distance of at least 750 m outside the fenced area. Inside the fenced area, surrounding the windmill, the ground cover is comprised of about 10% grasses, 20% shrubs, and 70% forbs; outside the fenced area the ground cover is predominantly native grasses (approximately 40%), shrubs (50%), and forbs (10%). The following species were identified: *Populus deltoides monilifera* (plains cottonwood), *Ceratoides lanata* (common winterfat), *Gutierrezia sarothrae* (broom snakeweed), *Descurainia pinnata* (pinnate tansymustard), *Kochia scoparia* (kochia), *Lactuca serriola* (prickly lettuce), *Sphaeralcea coccinea* (scarlet globemallow), *Linum lewisii* (Lewis flax), *Marrubium vulgare* (common horehound), *Astragalus missouriensis* (Missouri milkvetch), *Brassicaceae* sp. (flaxseed), *Bromus japonicus* (Japanese brome), *Agropyron smithii* (western wheatgrass), *Sporobolus cryptandrus* (sand dropseed), *Bouteloua gracilis* (blue grama), *Hordeum pusillum* (little barley), *Bouteloua curtipendula* (sideoats grama), and *Opuntia polyacantha* variety, *polyacantha* (plains prickly pear) in proportions ranging from "trace" to about 30% of all vegetation.

To compare the structure and dynamics of the small mammal communities with those in more natural, less perturbed habitats, we chose three sites where longitudinal studies are being conducted by mark-recapture. These sites are about 13 km from the windmill in the interior of a canyon (site A, a web array comprising 145

traps) and 15 km from the windmill at the mouth of that canyon (site B, a grid array comprising 75 traps); site C (a web array comprising 145 traps) is a shortgrass prairie habitat about 8 km from the windmill site. At the canyon sites, the soils range from sandstone-derived slopes to sandy loam flat areas. Water there was intermittently and focally available. Summarizing the floral composition at these canyon sites: slopes—10% bare ground, flora comprised of 45% grasses, 15% shrubs, 35% forbs, 5% cacti and no trees; flats—10% bare ground, flora comprised of 30% grasses, 15% shrubs, 50% forbs, 5% cacti, and no trees. At the shortgrass prairie site, which is a typical limestone breaks habitat, bare ground represented 30% of the area and the flora was comprised of 60% grasses, 10% shrubs, and 30% forbs.

The Fort Carson authorities have made concentrated efforts to protect, maintain, and improve wildlife habitat, archaeological sites, roads, and facilities, and have continued to maintain in good repair many windmills, formerly used to provide water for cattle and now used for that same purpose for wildlife.

In contrast to conditions in the surrounding habitat or at the nearby web sites, we observed that abundant green vegetation was present at the windmill site year-round, even in dry, cold, winter months. Such conditions might contribute to a greater carrying capacity for rodent populations by providing consistent shelter, nitrogen-rich green foliage, and relatively abundant fruits and seeds. These characteristics would directly benefit herbivorous and granivorous small mammals and would indirectly benefit insectivorous species by supporting greater densities of arthropods.

Small mammal trapping and processing

For 1 to 3 nights approximately every 6 wks between January 1995 and November 1997, we placed 25 traps in an irregular pattern at the windmill site (Fig. 1). A 7.6 cm × 8.9 cm × 22.9 cm Sherman trap (H. B. Sherman Traps, Inc., Tallahassee, Florida, USA) was placed at each of 25 locations near where rodents were likely to forage; i.e., bordering two circular stock tanks, one about 4 m in diameter and the other about 5 m in diameter, which provide a continuous source of water for the local fauna, next to brush piles, and in short or tall grass. The location of each trap was marked with a construction flag.

Trapping and processing rodents followed methods recommended by the Centers for Disease Control and Prevention (CDC; Mills et al., 1995). Traps were baited with a mixture of

cracked corn, rolled oats, and peanut butter (3:1:0.5). They were opened in late afternoon of the first day and, because we did not observe the presence of diurnal rodents, were allowed to remain open throughout the trapping period. When temperatures were expected to be $<5^{\circ}\text{C}$, three nonabsorbent polyfill balls were placed in each trap to provide insulating material. Early on the mornings following each night of trapping, traps containing animals were collected, labeled as to trap station, placed in plastic 130 l bags, and returned to a central processing area. There, each trapped animal was ear-tagged and processed according to methods published previously (Mills et al., 1999b). After being processed, rodents were returned to the exact locations from which they were collected. A clean, baited, and opened trap was used to replace the potentially contaminated trap.

Mammals were identified with standard reference sources (Armstrong, 1972; Fitzgerald et al., 1994). The following data were recorded: sequential accession number; date processed; species; total length, length of tail, length of right hind foot, length of ear, weight, stage (young, subadult, or adult estimated from body weights using the values of Fitzgerald, et al., 1994); whether the animal was newly captured, was a recapture (not captured within the previous 3 days), was a repeater (captured within the previous 3 days), or was dead.

Weight classes were defined for deer mice as 11 to 15 gm = young, 16 to 23 gm = subadult, and 24 to 33 gm = adult and for western harvest mice as 5 to 7 gm = young, 8 to 11 gm = subadult, and 12 to 16 gm = adult.

Sampling was conducted for one to (usually) three nights each 6 wks between January 1995 and November 1997, depending on weather and site conditions. In 1995, we trapped the nights of 19 to 20 January, 1 to 3 March, 18 to 20 April, 3 to 5 October, and 13 to 15 November (total 337 trap-nights). In 1996, we trapped the nights of 16 to 17 January, 3 to 5 March, 9 to 11 April, 22 to 24 May, 30 June to 2 July, 20 to 21 August, 24 to 25 September, and 5 to 6 November (total 483 trap-nights). In 1997, we trapped the nights of 28 to 30 January, 11 to 13 March, 20 to 21 April, 3 to 4 June, 15 to 16 July, 19 to 20 August, and 21 November (367 trap-nights). The canyon (sites A and B) and shortgrass prairie (site C) areas used for comparison were trapped simultaneously with the windmill site. In 1998, the windmill was non-functional from at least April until late summer. When we visited the site 1 to 2 September 1998, we found few signs of green forage and the soil was denuded and compacted. Rodent burrows had been abandoned, and we observed

TABLE 1. Frequency of recapture [number of individual rodents recaptured/total number of individual rodents captured (percent of individuals recaptured)] for three rodent species captured at four sites in southeastern Colorado, January 1995 to June 1997.^a

Site	Deer mice	Western harvest mice	Hispid cotton rats
Windmill	6/28 (21)	6/28 (21)	13/44 (29)
Site A	83/131 (63)	52/146 (36)	53/84 (63)
Site B	97/201 (48)	34/99 (34)	47/78 (60)
Site C	26/56 (56)	44/58 (76)	0/0

^a Chi-square analysis across three sites for three species: ($\chi^2 = 18.76$, 3 df, $P < 0.003$; $\chi^2 = 37.11$, 3 df, $P < 0.001$; $\chi^2 = 14.60$, 2 df, $P = 0.007$).

no evidence of raptors, coyotes, or rattlesnakes; nonetheless, we set out traps there for 2 nights.

Blood samples were transported to the Fort Collins laboratory, where they were stored in a mechanical freezer (-75°C) until they were tested for IgG antibody to Sin Nombre virus by a published method (Feldmann et al., 1993). Data were entered and analyzed using EPI-5 (Dean et al., 1990).

RESULTS

Capture and recapture frequencies

During the nearly 3 yr study at the windmill site, 143 individual rodents were captured (*P. maniculatus*, *P. leucopus* [white-footed mouse], *R. megalotis*, *S. hispidus*, *Dipodomys ordii* [Ord's kangaroo rat], *Mus musculus* [house mouse], *Neotoma mexicana* [Mexican wood rat], *Onychomys leucogaster* [northern grasshopper mouse], and *Perognathus flavus* [silky pocket mouse]), of which 100 deer mice, western harvest mice and hispid cotton rats were recaptured at least once, some as often as five times (Table 1). Twenty-eight deer mice were captured between January 1995 and April 1997; six (21%) were recaptured. Twenty-eight western harvest mice were captured between January 1995 and June 1997; six (21%) were recaptured. Forty-four hispid cotton rats (*S. hispidus*) were captured between October 1995 and November 1997; 13 (29%) were recaptured. At sites A and B (canyon and canyon mouth habitats), we recaptured, respectively, 63% and 48% of deer mice, 36% and 34% of western harvest

TABLE 2. Distribution by weight (age) class for deer mice, western harvest mice, and hispid cotton rats at the windmill site as compared to three other trapping sites in southeastern Colorado.^a

Weight class	Windmill	Site A	Site B	Site C
Deer mice ^b				
11–15 g	24 (51)	8 (3)	18 (4)	11 (18)
16–23 g	23 (49)	217 (71)	279 (66)	46 (77)
24–33 g	0	80 (26)	123 (29)	3 (5)
Western harvest mice ^c				
5–7 g	23 (68)	14 (4)	2 (2)	32 (31)
8–11 g	11 (32)	229 (67)	61 (59)	71 (69)
12–16 g	0	96 (28)	41 (39)	0
Hispid cotton rats ^d				
0–50 g	2 (3)	15 (9)	17 (13)	0
51–150 g	55 (71)	116 (67)	99 (73)	0
151–300 g	20 (26)	41 (24)	20 (15)	0

^a Numbers provided are numbers of captures and percentages (in parentheses) of the total captures at each site. All tests were 2×3 contingency tables except windmill site vs. Site C for western harvest mice, which was a 2×2 table. P = significance of chi-square analysis testing the null hypothesis that the age distribution of mice at the windmill site is the same as that at each of the other sites. df = degrees of freedom.

^b For sites A, B, C: $\chi^2 = 120$, 2 df, $P < 0.0001$; $\chi^2 = 119$, 2 df, $P < 0.001$; $\chi^2 = 14$, 2 df, $P < 0.001$.

^c For sites A, B, C: $\chi^2 = 137$, 2 df, $P < 0.0001$; $\chi^2 = 78$, 2 df, $P < 0.001$; $\chi^2 = 13$, 1 df, $P < 0.001$.

^d For sites A, B: $\chi^2 = 3$, 2 df, $P = 0.21$; $\chi^2 = 9$, 2 df, $P = 0.01$.

mice, and 63% and 60% of hispid cotton rats. At site C (shortgrass prairie), where hispid cotton rats did not occur, we recaptured 56% of deer mice and 76% of western harvest mice. When compared to the other three local trapping sites (antibody to Sin Nombre virus detected in rodents at all three sites), recapture frequencies for *P. maniculatus*, *R. megalotis*, and *S. hispidus* were always much lower at the windmill site. Contingency table analysis demonstrated significantly different recapture frequencies among sites for the three species (Table 1).

Age structure, population densities

When analyzed by weight for relative age estimation (Table 2), deer mice and western harvest mice in the smallest weight class were captured significantly more frequently at the windmill than at other sites (Table 2). The weight distribution of hispid cotton rats at the windmill site was similar to that at site A, but had fewer smaller and more larger individuals than did site C.

In 1996, hispid cotton rat populations at the windmill site underwent an abrupt irruption, while numbers of other species

declined (Fig. 2). In August 1996, hispid cotton rats represented 83% of the rodents captured at the windmill site. This proportion, in comparison with the proportions of hispid cotton rats at two other sites at PCMS, is shown in Figure 3. Whereas the populations of these rats fluctuated seasonally at all sites, hispid cotton rats became the dominant rodent only at the windmill site.

Antibody to Sin Nombre virus

An adult female western harvest mouse was the only rodent at the windmill site with IgG antibody to SNV, probably a result of infection with El Moro Canyon virus. This animal had antibody (titer 1,600) when it was first captured on 2 March 1995 and (3,200) when captured on 18 April 1995. None of 28 deer mice at this site had such antibody. In contrast, between January 1995 and November 1997 at sites A and B, which are similar, the two sites about 13 and 15 km from the windmill site, mean prevalence of antibody to SNV in adult deer mice was 15% (124/853); (Yates corrected Chi-square 5.82, $P = 0.016$), and in western harvest mice 13.3% (72/542; Yates corrected Chi-square

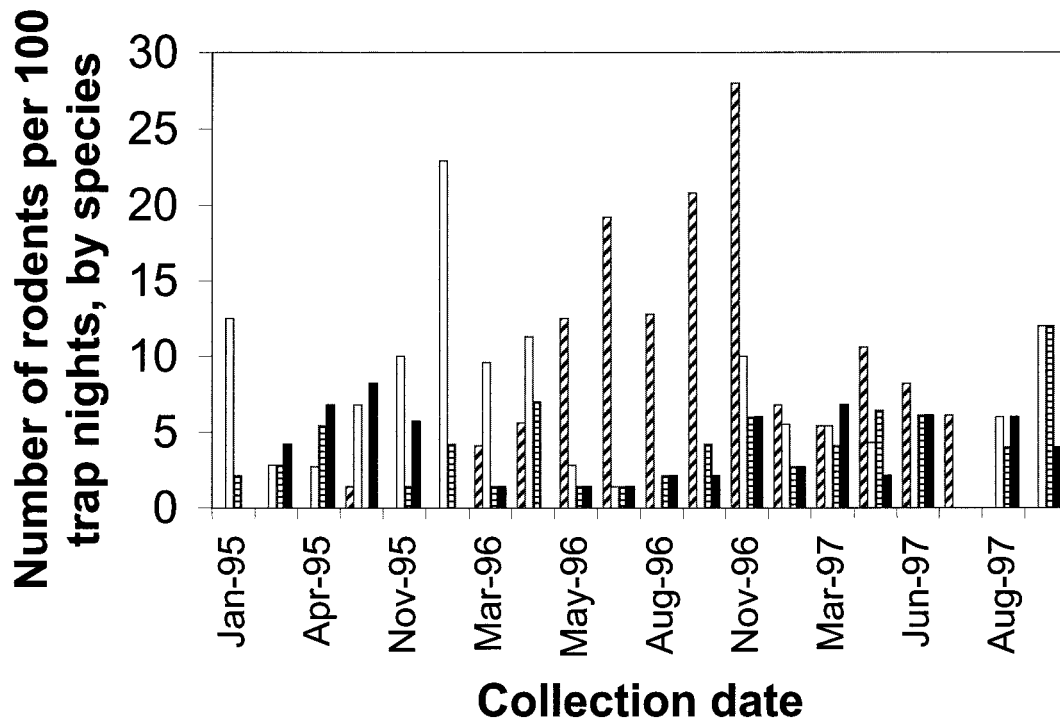


FIGURE 2. Graphic representation of rodent collections at a windmill site, southeastern Colorado, by date of collection, number of rodents per 100 trap nights, and species. *Sigmodon hispidus* (hatched), *Peromyscus maniculatus* (white), *Reithrodontomys megalotis* (ladder), all other species (black).

11.85, $P = <0.001$). At site C, 1/28 deer mice, 7/78 piñon mice (*P. truei*), and 5/28 western harvest mice had antibody to SNV.

DISCUSSION

The results of our study corroborate the hypothesis that hantaviruses are maintained in reservoir populations by trans-seasonal persistence of chronically infected individuals in stable, resident populations. A logical prediction derived from this hypothesis (that reservoir populations with a young age structure and a high rate of turnover will not support infection with a hantavirus) was supported by data accrued by collections at the windmill site, which is within the range of at least two common mammalian species that serve as reservoirs for hantaviruses.

The factors limiting the establishment of the hantavirus reservoir populations at the windmill site are several but common for disturbed habitats. One factor could have

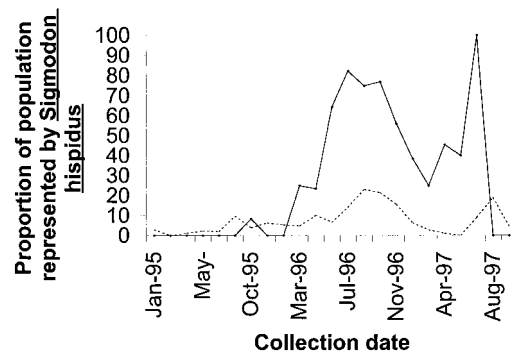


FIGURE 3. Graphic representation of comparison of proportion of rodent population represented by hispid cotton rats (*Sigmodon hispidus*) at a windmill site and at two other sites (data pooled) at Piñon Canyon Maneuver Site. Solid line represents mean proportion of hispid cotton rats at the windmill site; dotted line represents proportion of hispid cotton rats at other Piñon Canyon Maneuver Site locations.

been interspecific competition. Precipitous fluctuations of hispid cotton rat populations on the southern Great Plains are well known (Flehart et al., 1972). The population of hispid cotton rats at the windmill site underwent an abrupt expansion during the second year of this study. Increases in the hispid cotton rat population were accompanied by decreases in populations of deer mice and western harvest mice. Because the rapid turnover in populations of deer mice and western harvest mice was observed prior to the increases in hispid cotton rat populations, it is unlikely that the latter event was the cause of the rapid turnover and low prevalence of infection in the hantavirus reservoir species at the windmill. Nevertheless, that 76% of western harvest mice were recaptured at site C, where there were no hispid cotton rats, and 21%, 36%, and 34% recaptured at the windmill site and at sites A and B, where there were hispid cotton rats, confounds these considerations, at least in regard to western harvest mice.

A second possibility is that the windmill site represented a sub-optimal habitat that would not support resident populations of deer mice or western harvest mice, and that captured animals were dispersing transients. Evidence for this explanation is seen in the apparent unwillingness of dispersing young to establish territories near the windmill, as demonstrated by low recapture rates. Some critical element provided by typical grass-dominated, short-grass prairie, may have been absent from the compacted-soil, forb-dominated environment of the windmill site and the exotic plants found there may have been noxious and may not have provided adequate cover and food resources.

Finally, it is possible that dispersing young attempted to establish territories, but were quickly eliminated by predators. Thus the windmill site may have represented a dispersal sink where available territory was continuously opened by the removal of temporary residents by predators. Indeed, except for early September 1998,

whenever we visited the windmill site, we observed predators. These included one or more of many coyotes (*Canis latrans*), prairie rattlesnakes (*Crotalus viridis viridis*), and many raptors, including many red-tailed hawks (*Buteo jamaicensis*), and northern harriers (*Circus cyaneus*). Badgers (*Taxidea taxus*) and swift foxes (*Vulpes velox*) infrequently have been observed by others (M. Canestorp and D. Sharp, pers. comm.) at this site. Only rarely did we observe predators, mostly coyotes, at site A and never at sites B or C, even though these sites were visited with the same frequency as was the windmill site.

Studies have demonstrated that hantavirus infections in reservoir populations can be focal, and prevalences may range from 0% to 60% on a regional scale (Kaufman et al., 1994; Mills et al. 1997; Glass et al. 1998). Such focality of infection has not been adequately explained, but has been thought to be due to local extinction, probably due to "bottle-neck effect" when local reservoir populations experience very low population densities. Infection is likely to be reintroduced eventually through infected immigrants or expansion of populations so that they become contiguous with neighboring populations (Mills et al., 1999a).

The conditions described at the windmill site (a disturbed habitat) offer an alternative mechanism for the existence of populations of common reservoir species that remain free of hantavirus infection. Although infected transients occasionally may be found in the population, permanent reintroductions of hantaviruses into reservoir populations at the windmill site are unlikely to be maintained, even when population densities may be relatively high, because long-lived residents, which may be necessary to insure transseasonal maintenance of virus, are absent from the population.

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