

MICROHABITAT USE BY DEER MICE IN RESPONSE TO FLUCTUATIONS IN PINYON MOUSE ABUNDANCE

Jeffrey B. Doty, Arthropod-borne and Infectious Diseases Laboratory, Department of Microbiology, Immunology and Pathology, College of Veterinary Medicine and Biomedical Sciences, Colorado State University, Fort Collins, CO 80523

Charles H. Calisher, Arthropod-borne and Infectious Diseases Laboratory, Department of Microbiology, Immunology and Pathology, College of Veterinary Medicine and Biomedical Sciences, Colorado State University, Fort Collins, CO 80523

J. Jeffrey Root, Arthropod-borne and Infectious Diseases Laboratory, Department of Microbiology, Immunology and Pathology, College of Veterinary Medicine and Biomedical Sciences, Colorado State University, Fort Collins, CO 80523¹

Barry J. Beaty, Arthropod-borne and Infectious Diseases Laboratory, Department of Microbiology, Immunology and Pathology, College of Veterinary Medicine and Biomedical Sciences, Colorado State University, Fort Collins, CO 80523

ABSTRACT

We captured deer mice (*Peromyscus maniculatus*) and pinyon mice (*Peromyscus truei*) from October 1994 to October 2005 in an area of sympatry near Molina, west-central Colorado. We examined relative abundances and microhabitat use of these rodents in an area dominated by two major vegetation types: sagebrush (*Artemisia* spp.) and pinyon-juniper (*Pinus edulis-Juniperus* spp.). This was conducted to assess changes in microhabitat use over time and how these changes relate to the relative abundances of these rodents. Pinyon mouse captures were associated with pinyon-juniper habitat during every year of the study, whereas deer mouse captures were associated with sagebrush habitat during some years but not specifically associated with either habitat type during other years. Generally, when pinyon mouse abundance was relatively low, deer mice were not specifically associated with either habitat. Notably, when deer mouse abundance was relatively low, we captured pinyon mice in sagebrush habitat more often than in years of high deer mouse abundance. Our data suggested that fluctuations in relative abundance in one of these sympatric peromyscine rodents affect microhabitat use of the congener.

Key words: deer mouse, habitat, rodents, *Peromyscus maniculatus*, *Peromyscus truei*, pinyon mouse

INTRODUCTION

The concept that differences in microhabitat utilization may allow closely related species to occur sympatrically has been extensively studied for rodents within the genus *Peromyscus* (Geluso 1971, Holbrook 1978, Kantak 1983, Ribble and Samson 1987, Etheredge et al. 1989, Kalcounis-Rüppell and Millar 2002). Certain studies have focused entirely on both the deer mouse (*P. maniculatus*) and the pinyon mouse (*P. truei*; Douglas 1969, Hammond and Yensen 1982). These investigators found

that differences in activity patterns and availability of space and food allowed these rodents to coexist over broad portions of their ranges.

Differences in microhabitat utilization can be attributed to numerous factors. Kantak (1983) found that foraging habitat and nest location preferences accounted for differences in habitat selection by deer mice and white-footed mice (*P. leucopus*) in a laboratory setting. Holbrook (1978) suggested that the size of food items, vegetation complexity, multidimensional use of space, i.e., arboreal vs. terrestrial, and competitive interactions can affect microhabitat utilization of deer mice, pinyon

Current Address:

¹National Wildlife Research Center, 4101 La Porte Avenue, Fort Collins, Colorado 80521

mice, brush mice (*P. boylii*) and rock mice (*P. nasutus*) in New Mexico.

Pinyon mice range from southwest Oregon to southern Wyoming, western Kansas and north central Texas in the U.S., south to Baja California and central Mexico (Fitzgerald et al. 1994). Many studies have suggested that pinyon mice are limited to pinyon-juniper or other woodland habitats. On the other hand, deer mice are typically found in relatively open habitats, such as sagebrush, but as generalists they are not limited to a particular habitat type (Douglas 1969, Holbrook 1978, Hammond and Yensen 1982, Ribble and Samson 1987).

Deer mice are the most widely distributed native small mammal in North America (Fitzgerald et al. 1994). They invade human habitations when given the opportunity (Kuenzi et al. 2001) and are the principal rodent host of Sin Nombre virus (SNV, family *Bunyaviridae*, genus *Hantavirus*), the etiologic agent of hantavirus pulmonary syndrome (Childs et al. 1994) and therefore, are of public health and epidemiologic interest.

Since 1994, we have been conducting longitudinal studies of rodents in western Colorado for epidemiologic purposes. A report of the early years of our work has been published (Calisher et al. 1999) along with other reports such as understanding the relationships of deer mouse movement, vegetative structures, and prevalence of infection with SNV; analyses of gene flow among deer mice; genetic relatedness of deer mice; and spatial clustering of murid rodents infected with hantaviruses (Root et al. 1999, Root et al. 2003, Root et al. 2004, Root et al. 2005).

Incidental to our principal studies of deer mice, we have regularly captured pinyon mice, which also are natural hosts for SNV. The longitudinal studies presented us with an opportunity to examine data regarding the microhabitat associations of these rodents, as well as fluctuations in their populations.

We were not able to find detailed, published reports of the effects of changes in microhabitat use and how interspecific

interactions as they relate to fluctuations in population sizes of the congeners might affect such changes. Thus, we evaluated distributions of pinyon mice and deer mice at sites where both occur. To assess impacts of interspecific interactions on microhabitat use, we studied the microhabitat associations of deer mice and pinyon mice and compared these associations to fluctuations in the relative abundances of these rodents.

METHODS

The study site was located in west-central Colorado near Molina (N 39° 09' 45.8" latitude, W 108° 03' 18.4" longitude, altitude 1951 m). A description of the study site has been published previously (Calisher et al. 1999). The area generally is characterized by sagebrush (*Artemisia* spp.), juniper (*Juniperus* spp.), pinyon pine (*Pinus edulis*), and rabbitbrush (*Chrysothamnus* spp.). Annual precipitation averaged 20.1 cm $\pm$ 9.8 s for the 11 years of this study.

We used two trapping webs > 500 m apart and separated by a ditch periodically filled for irrigation that likely does not limit the dispersion of rodents. Livestock had not grazed this area for several years prior to this study. Web A was comprised principally of sagebrush and bare ground with interspersed grasses and forbs. This vegetation type was typical of the area and occurred primarily in the central and northern portion this web. The eastern portion of web A slopes down toward a pasture grazed by livestock that is characterized by pinyon pines and junipers with sparse undergrowth among rocks and juniper deadfall. The southern and western edges of web A were comprised of pinyon-juniper woodland. Web B is essentially flat, with pinyon, juniper, and sagebrush scattered throughout but with less sagebrush and more juniper than at web A.

Each web consisted of 145 trap stations arranged in 12 lines of 12 traps each, radiating from a single trap station at the center of the web, with lines being 30° apart (Mills et al. 1999). We spaced the first four trap stations in each line at 5-m intervals and the next eight trap stations at 10-m intervals. One 18-x 19-x 23-cm non-folding Sherman

live-trap (H. B. Sherman Traps, Inc., Tallahassee, FL) was placed at each trap station and baited with a mixture of rolled oats, cracked corn, and peanut butter. Traps were checked for three or rarely two ($n = 6$) consecutive nights during each trapping session ($n = 54$).

Rodents were trapped at 6-week intervals from October 1994 through October 2005; however, trapping efforts typically ceased from November through March. Data from 1994 were not included in these analyses because trapping did not begin until October of that year; therefore, data for these analyses begins in May 1995.

Trapped rodents were anesthetized with isoflurane, measured, bled from the retro-orbital plexus for SNV antibody testing, marked with individually numbered stainless steel ear tags, and released at the exact site of capture. Processing was conducted according to published protocols (Mills et al. 1995) and approved by the Colorado State University Animal Care and Use Committee.

We categorized microhabitats of trap stations as "tree" or "non-tree" (generally shrub). A trap station was considered as belonging to the "tree" category if there was the trunk of a live tree or there was canopy (> 2.5 m in height) within 5 m of the trap station. If there were no trees or canopy within 5 m of the trap station, it was considered "non-tree." In the trap-dense center of the web (the central trap plus the first four trap stations in each line), a single tree could affect classification of several trap stations. To promote independence of observations in this area, the first and third trap stations on odd numbered lines and the first three trap stations on even numbered lines were removed from these analyses (Root et al. 2001). This effectively increased the distance between trap stations in this area. In total, we used 230 of 290 trap stations (2 webs) for the microhabitat analyses.

Data were grouped by year and analyzed by Yate's corrected Chi square tests (Sokal and Rohlf 1995) for significant associations between captures of rodents and microhabitat categories. To contrast changes

in microhabitat associations and population fluctuations, we compared the results to mean annual relative abundances of rodents. To estimate relative abundances, the minimum number alive (MNA; Chitty and Phipps 1966) was tabulated for each species and each sampling period and a mean MNA was calculated for each year of the study. The MNA provides a reliable estimate of population size and typically within 10 percent of the actual number of animals if trapability is high (Hilborn et al. 1976). A t -test was performed to test the hypothesis that pinyon mouse abundance would be lower during years when deer mice used the available habitats at random than during years when deer mice were associated with non-tree (sagebrush) habitat (Sokal and Rohlf 1995).

RESULTS

During 41,210 trap-nights 3562 peromyscine rodent captures were recorded; deer mice = 2486, pinyon mice = 1076. Yearly mean MNA for both rodents appear in Table 1. Pinyon mouse MNA (mean = 16.6 ± 7.1) was lowest from 1997-2000, whereas deer mouse MNA (mean = 30.5 ± 18.7) was lowest from 2000-2003.

Of the 230 trap stations used in these analyses, deer mice or pinyon mice were captured in 229 during the 11-year study. Of the 229 trap stations, 77 (33.6%) captured rodents were of a single *Peromyscus* spp. That is, only deer mice were captured in 73 trap stations, and only pinyon mice were captured in four trap stations. At one time or another both rodents were captured in the remaining 152 trap stations.

Of the 230 trap stations, 116 (50.4%) were in the non-tree category and 114 (49.6%) were in the tree category. Generally, the non-tree category trap stations were associated with sagebrush (< 10 were associated with bare-ground or herbaceous cover). Over the 11-year observation period, pinyon mouse captures tended to be associated with trees more than the null hypothesis predicts ($\chi^2 = 57.4$, $P < 0.0001$, $df = 1$). We captured deer mice at tree and non-tree microhabitats with equal

Table 1. Annual habitat associations of pinyon mice and deer mice, near Molina, Colorado, with Yates' corrected Chi-square (χ^2) and P -values, as well as the minimum number alive (MNA) are reported. When no association to either habitat type was detected, habitat use was considered random.

Year	Pinyon mouse habitat	χ^2, P	Pinyon mouse mean MNA	Deer mouse habitat	χ^2, P	Deer mouse mean MNA
1995	Pinyon-juniper	41.9, <0.0001	17.33	Sagebrush	12.4, 0.0004	49.83
1996	Pinyon-juniper	60.8, <0.0001	19.60	Sagebrush	8.4, 0.0037	31.60
1997	Pinyon-juniper	31.1, <0.0001	9.40	Random	0.6, 0.417	25.20
1998	Pinyon-juniper	37.7, <0.0001	16.00	Random	1.74, 0.187	50.00
1999	Pinyon-juniper	4.3, 0.039	3.00	Random	0.01, 0.92	25.50
2000	Pinyon-juniper	11.9, 0.0006	11.75	Sagebrush	7.0, 0.0083	12.50
2001	Pinyon-juniper	31.3, <0.0001	20.20	Sagebrush	10.1, 0.0015	13.60
2002	Pinyon-juniper	52.2, <0.0001	17.50	Random	1.9, 0.16	17.67
2003	Pinyon-juniper	46.2, <0.0001	23.50	Sagebrush	4.1, 0.042	13.25
2004	Pinyon-juniper	42.1, <0.0001	27.40	Sagebrush	6.0, 0.014	66.00
2005	Pinyon-juniper	7.4, 0.006	3.50	Random	0.12, 0.731	21.50

probability ($\chi^2 = 2.3$, $P = 0.126$, $df = 1$).

On an annual basis, captures of pinyon mice tended to be associated with trees more than expected for each year (Table 1). In partial contrast, deer mice tended to be associated with non-tree sites more than expected in 6 of 11 study years (1995, 1996, 2000, 2001, 2003, and 2004). Captures of deer mice did not differ significantly from the expected in 1997-1999, 2002, and 2005 (Table 1). The t -test showed that the pinyon mouse MNA was significantly lower ($t = 2.70$, $df = 7$, $P = 0.031$) during years when deer mice used the habitat at random than when deer mice were associated with non-tree or sagebrush habitat.

Although pinyon mice were associated with trees during each year of this study, higher percentages of pinyon mice were captured in the non-tree trap stations during 2000 (32.4%) and 2001 (26.1%), when the deer mouse MNA (12.5 and 13.6, respectively) was the lowest of the 11-year study period. The mean percentage of pinyon mice captured in non-tree trap stations was 13.7 ± 9.6 percent.

DISCUSSION

Habitat associations of deer mice and pinyon mice have been well documented by Douglas (1969), Holbrook (1978), Hammond and Yensen (1982), Ribble and Samson (1987). Our observations concur with theirs. Pinyon mice were associated

with pinyon-juniper habitat during each year of this study. Deer mice were associated with sagebrush habitats during some years and were not associated specifically with either pinyon-juniper or sagebrush habitat type during other years, supporting the concept that they are habitat generalists.

Adaptation to a suitable and particular habitat type may provide a competitive advantage to one congener. Adaptive features, such as longer tails and larger feet, likely allow pinyon mice to better exploit the arboreal resources available in the pinyon-juniper habitat (Horner 1954). Moreover, use and avoidance of microhabitats by peromyscine rodents is likely related to many factors, including foraging strategies, vegetation composition and complexity, differential nest site availability, and competitive interactions. The effects of interspecific and competitive interactions on microhabitat use are not well documented and require further investigations to elucidate these variables.

During 4 of 5 years when pinyon mouse abundance was low (1997-2000 and 2005), deer mice were not specifically associated with the sagebrush habitat (1997-1999 and 2005). Pinyon mouse MNA was significantly lower during years when deer mice used the habitat at random than they were during years when deer mice were specifically associated with the sagebrush habitat. Thus, when abundance of pinyon mice was low,

deer mice could exploit the tree habitat more effectively. Notably, Holbrook (1978) found that 50 percent of deer mouse captures were made in grass or sagebrush habitats. However, during one year of her study, when three other peromyscines (pinyon mice, brush mice, and rock mice) were essentially absent from the area, nearly 80 percent of deer mouse captures were from habitats primarily utilized by the other three peromyscine rodents.

In 2000, when pinyon mouse abundance was still relatively low, deer mouse abundance was the lowest of the study period. Therefore, it is not surprising that deer mice again would be associated with sagebrush habitat. The driest 12-month period of the study occurred between September 2001 and August 2002, during which only 9.7 cm of precipitation was recorded compared to an average of $20.1 \text{ cm} \pm 9.8 \text{ s}$ for the study period. During the summer of 2002 deer mouse abundance was relatively low, but they were not specifically associated with either habitat type; however, pinyon mouse abundance was relatively high. During that year deer mice may have been searching for alternative, more reliable sources of food, including juniper berries and pinyon nuts. Pinyon nut abundance was not formally assessed and we rarely observed pinyon nuts on trees or on the ground.

It is notable that when deer mouse abundance was at its lowest (2000-2001), more pinyon mice were captured in the sagebrush habitats. This suggests that when deer mouse abundance was low, pinyon mice exploited sagebrush habitat more effectively.

The use of capture data is likely not the best way to assess microhabitat use, as compared with other techniques, such as radio-telemetry (Douglass 1989). Obviously, we baited traps to lure animals to them, a recognized study bias. However, this study showed changes in microhabitat use over a long period of time without the use of expensive radio-telemetry equipment.

In summary, pinyon mice were associated with pinyon-juniper habitat

during each year of this study and deer mice were typically associated with sagebrush habitat, except during years when pinyon mouse abundance was low. During these time periods deer mice were not associated with either habitat type and they appeared to use these habitats at random. Although pinyon mice were specifically associated with pinyon-juniper habitat, when relative abundance of deer mice was low, more pinyon mice were captured in the sagebrush than during years of high relative abundance of deer mice. We have presented data suggesting that changes in relative abundance in one of these sympatric peromyscine rodents may affect the microhabitat use of the congener.

ACKNOWLEDGEMENTS

The authors thank the many students and others from Colorado State University who provided enthusiastic assistance in accomplishing these field studies. In addition, we thank Ms Robin Carns, Mesa County Health Department, Grand Junction, Colorado, Dr. Tony Schountz, Mesa State College, Grand Junction, Colorado, and his students Ms Marcia Patterson-Hernandez, Mr. Louis Starzel, Jr., Ms Emily Kampf, and Ms Jodi Grewell for their assistance. We also thank Mr. Jim zumBrunner for providing statistical advice. Funding for this work was provided by the National Institutes of Health contract A125489 and the U.S. Centers for Disease Control and Prevention, Atlanta, GA, under cooperative agreement No. U50/ccu809862-03, for which we are grateful.

LITERATURE CITED

- Calisher, C. H., W. Sweeney, J. N. Mills, and B. J. Beaty. 1999. Natural history of Sin Nombre virus in western Colorado. *Emerging Infectious Diseases* 5:126-134.
- Childs, J. E., T. G. Ksiazek, C. F. Spiropoulou, J. W. Krebs, S. Morzunov, G. O. Maupin, K. L. Gage, P. E. Rollin, J. Sarisky, R. E. Ensore, J. K. Frey, C. J. Peters, and S. T. Nichol. 1994. Serologic and genetic identification of

- Peromyscus maniculatus* as the primary rodent reservoir for a new hantavirus in the southwestern United States. *Journal of Infectious Diseases* 169:1271-1280.
- Chitty, D., and E. Phipps. 1966. Seasonal changes in survival in mixed populations of two species of vole. *Journal of Animal Ecology* 35:313-331.
- Douglas, C. L. 1969. Comparative ecology of pinyon mice and deer mice in Mesa Verde National Park, Colorado. University of Kansas Publications 18:421-504.
- Douglass, R. J. 1989. The use of radio-telemetry to evaluate microhabitat selection by deer mice. *Journal of Mammalogy* 70:645-652.
- Etheredge, D. R., M. D. Engstrom, and R. C. Stone, Jr. 1989. Habitat discrimination between sympatric populations of *Peromyscus attwateri* and *Peromyscus pectoralis* in west-central Texas. *Journal of Mammalogy* 70:300-307.
- Fitzgerald, J. P., C. A. Meaney, and D. M. Armstrong. 1994. *Mammals of Colorado*. University Press of Colorado, Niwot. 467 pp.
- Geluso, K. N. 1971. Habitat distribution of *Peromyscus* in the Black Mesa region of Oklahoma. *Journal of Mammalogy* 52:605-607.
- Hammond, D. B., and E. Yensen. 1982. Differential microhabitat utilization in *Peromyscus truei* and *Peromyscus maniculatus* in the Owyhee Mountains, Idaho. *Journal of the Idaho Academy of Sciences* 18:49-54.
- Hilborn, R., J. A. Redfield, and C. J. Krebs. 1976. On the reliability of enumeration for mark and recapture census of voles. *Canadian Journal of Zoology* 54:1019-1024.
- Holbrook, S. J. 1978. Habitat relationships and coexistence of four sympatric species of *Peromyscus* in northwestern New Mexico. *Journal of Mammalogy* 59:18-26.
- Horner, B. E. 1954. Arboreal adaptations of *Peromyscus* with special reference to the use of the tail. *Contributions from the Laboratory of Vertebrate Biology, University of Michigan*, 61:1-84.
- Kalcounis-Rüppell, M. C., and J. S. Millar. 2002. Partitioning of space, food, and time by synoptic *Peromyscus boylii* and *P. californicus*. *Journal of Mammalogy* 83:614-625.
- Kantak, G. E. 1983. Behavioral, seed preference and habitat selection experiments with two sympatric *Peromyscus* species. *American Midland Naturalist* 109:246-252.
- Kuenzi, A. J., R. J. Douglass, D. White, C. W. Bond, and J. N. Mills. 2001. Antibody to Sin Nombre virus in rodents associated with peridomestic habitats in west central Montana. *American Journal of Tropical Medicine and Hygiene* 64:137-146.
- Mills, J. N., J. E. Childs, T. G. Ksiazek, C. J. Peters, and W. M. Velleca. 1995. Methods for trapping and sampling small mammals for virologic testing. U. S. Centers for Disease Control and Prevention, Atlanta, GA. 61 pp.
- Mills, J. N., T. L. Yates, T. G. Ksiazek, C. J. Peters, and J. E. Childs. 1999. Long-term studies of hantavirus reservoir populations in the southwestern United States: rationale, potential, and methods. *Emerging Infectious Diseases* 5:95-101.
- Ribble, D. O., and F. B. Samson. 1987. Microhabitat associations of small mammals in southeastern Colorado, with special emphasis on *Peromyscus* (Rodentia). *Southwestern Naturalist* 32:291-303.
- Root, J. J., W. C. Black, IV, C. H. Calisher, K. R. Wilson, and B. J. Beaty. 2004. Genetic relatedness of deer mice (*Peromyscus maniculatus*) infected with Sin Nombre virus. *Vector Borne and Zoonotic Diseases* 4:149-157.
- Root, J. J., W. C. Black, C. H. Calisher, K. R. Wilson, R. S. Mackie, T. Schountz, J. N. Mills, and B. J. Beaty. 2003. Analyses of gene flow among populations of deer

- mice (*Peromyscus maniculatus*) at sites near hantavirus pulmonary syndrome case-patient residences. *Journal of Wildlife Diseases* 39:287-298.
- Root, J. J., C.H. Calisher, and B. J. Beaty. 1999. Relationships of deer mouse movement, vegetative structure, and prevalence of infection with Sin Nombre virus. *Journal of Wildlife Diseases* 35: 311-318.
- Root, J. J., C. H. Calisher, and B. J. Beaty. 2001. Microhabitat partitioning by two chipmunk species (*Tamias*) in western Colorado. *Western North American Naturalist* 61:114-118.
- Root, J. J., K. R. Wilson, C. H. Calisher, K. D. Wagoner, K. D. Abbott, T. L. Yates, A. J. Kuenzi, M. L. Morrison, J. N. Mills, and B. J. Beaty. 2005. Spatial clustering of murid rodents infected with hantaviruses: implications from meta-analyses. *Ecological Applications* 15:565-574.
- Sokal, R.R., and F.J. Rohlf. 1995. *Biometry*, 3rd ed. W. H. Freeman and Co., New York. 887 pp.

Received 22 August 2006

Accepted 13 December 2006