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DEER MOUSE (*PEROMYSCUS MANICULATUS*) HOME-RANGE SIZE AND FIDELITY IN SAGE-STEPPE HABITAT

B.A. Wood¹, L. Cao², and M.D. Dearing^{1,3}

ABSTRACT.—Within a species, home-range size can vary due to factors such as sex, mass, age, and breeding condition of individuals as well as habitat type, food availability, population density, and season. The objectives of this study were to estimate home ranges of deer mice (*Peromyscus maniculatus*) in sage-steppe habitat and to test the hypothesis that several factors (sex, mass, reproductive status, and seasonality) affect home-range size. We also tested the hypothesis that deer mice exhibit home-range fidelity over time. Passive integrated transponder (PIT) technology was used to estimate home ranges in June and September 2006. Home-range estimates varied from 360 m² to 5868 m² (65 individuals, 753 observations). Home-range size increased by approximately 60% from June to September. Besides seasonality, none of the other predictors of home range were informative in explaining the variation in home range. Deer mice recaptured in September (3 months after initial capture) had high fidelity in home-range use (42.1% [SE = 8.4%] overlap with 74.1% [SE = 8.7%] area conserved; $n = 9$). All animals for which home range was estimated in both seasons retained some fraction of their June home range in September. Results support the use of combined location data collected over long periods, such as weeks or months, to estimate home range for deer mice. The results have implications for deer mouse–pathogen ecology, particularly with respect to modeling transmission of Sin Nombre virus—a pathogen that is directly transmitted by deer mice.

Key words: deer mice, home range, minimum convex polygon, passive integrated transponder (PIT) tags, site fidelity.

Home range is the area an animal travels for normal activities, including food gathering, mating, and caring for young (Burt 1943). Within a species, home-range size can vary due to factors such as sex, mass, age, and breeding condition of individuals, as well as habitat type, food availability, population density, and season (Burt 1943, Stickel 1968, Loretto and Vieira 2005). Hence, home-range size can vary considerably both within and between populations. Despite the fact that home range is critical in understanding animal ecology and population dynamics, information on home range is lacking for many species or species in particular habitats.

The deer mouse (*Peromyscus maniculatus*) is the most widespread and common small mammal in North America (Baker 1968, Fitzgerald et al. 1994). Despite numerous home-range studies of the deer mouse (Blair 1940, 1942, 1943, Storer et al. 1944, Williams 1955, Merritt and Merritt 1978, O'Farrell 1978, Feldhamer 1979, Taitt 1981, Wolff 1985, Ribble and Millar 1996, Douglass et al. 2006), few are set in the sage-juniper habitat (Juelson 1966, O'Farrell 1978, Feldhamer 1979). Movement behavior of the deer mouse in sage-juniper habitat is of interest

because the deer mouse is the primary host for Sin Nombre virus (SNV; Childs et al. 1994). This pathogen can lead to hantavirus cardiopulmonary syndrome, a disease with high mortality in humans (Elliott et al. 1994). The prevalence of SNV in sagebrush habitat is relatively high, reaching nearly 40% at some sites (Mills et al. 1997, Douglass et al. 2001, Mackelprang et al. 2001, Lehmer et al. 2008). Hence, estimates of the home-range size and factors that govern home-range size are of particular concern to disease ecologists attempting to understand SNV transmission among deer mice.

Our first objective in this study was to obtain a current estimate of deer mouse home-range size in the sage-juniper habitat. The 3 previous studies conducted in this habitat are at least 30 years old (Juelson 1966, O'Farrell 1978, Feldhamer 1979). Considerable anthropogenic alterations to this ecosystem have occurred over the past 3 decades, warranting a recent study (Lehmer et al. 2008).

Our second objective was to investigate determinants of home range. Based on deer mouse ecology, we hypothesized that home range would change with season, body size,

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reproductive status, and sex. The mating system of deer mice is promiscuous, including both polygyny and polyandry (Birdsall and Nash 1973, Ribble and Millar 1996). Home range of females is determined by availability of food and shelter needed to successfully raise offspring, whereas home range of males is dependent upon access to mates (Frank and Heske 1992). Previous studies of deer mice have reported that home range is larger for males than females (Blair 1940, 1942, 1943, Storer et al. 1944, Williams 1955, Merritt and Merritt 1978, O'Farrell 1978, Ribble and Millar 1996). Thus, we predicted that estimated home range would be larger for males.

Home-range size is often positively correlated with body size, at least at the interspecific level (McNab 1963, Lindstedt et al. 1986, Swihart et al. 1988, du Toit 1990, Ottaviani et al. 2006); however, this relationship is not always present at the intraspecific level (Saunders and McLeod 1999, Dahle et al. 2006). For deer mice, juveniles have smaller home ranges than adults (Blair 1942, Storer et al. 1944, Williams 1955). Given that mass increases with age and determines the energetic requirements of an individual, we predicted that larger deer mice would have larger home ranges than smaller individuals.

Breeding condition might also have an effect on home range size. For female deer mice, home range reportedly increased at the onset of reproductive activity (O'Farrell 1978). Given the promiscuous mating system of this species, we predicted that individuals currently in breeding condition and in search of mates will have larger home ranges than nonbreeding individuals. Moreover, we predicted that home-range size would decrease from spring to fall for both sexes due to a decrease in breeding activity and nightly temperatures.

Our last objective was to investigate fidelity of home-range use. *Peromyscus* species are reported to have high home-range fidelity (Blair 1943, Stickel 1968, Ribble et al. 2002). In fact, home-range fidelity is often cited as the justification for collecting home-range data over long periods (i.e., weeks to months; Ribble et al. 2002). Despite this fundamental assumption for home-range estimation, to our knowledge quantitative information on home-range fidelity for deer mice is not present in the literature. Therefore, we tested the assumption that those deer mice remaining on the study

site over a 3-month period exhibit high home-range fidelity.

METHODS

Mark and Recapture

Deer mice were captured and marked at a site in the West Tintic Mountains, Juab County, Utah. Nocturnal rodents at this site have been sampled twice a year since 2002 as part of a larger multisite project (Previtali et al. 2010). Vegetation at the site is dominated by big sagebrush (*Artemisia tridentata*) and Utah juniper (*Juniperus osteosperma*).

Trapping was conducted 19–23 June and 15–17 September 2006, during the new moon. Rodents were captured using Sherman traps (H.B. Sherman Traps, Tallahassee, FL) arranged in a web configuration of twelve 100-m transects covering 3.14 ha (Mills et al. 1999). One hundred forty-eight trap locations were set each night for 5 nights in June and 3 nights in September. Two traps were set at each trap location in June, and one trap was set at each location in September. Each trap was baited with oats and peanut butter, and provisioned with batting for nest material. Traps were set each evening at dusk and checked the following morning at sunrise. Each deer mouse captured was marked with a unique eartag (1005-1, National Band and Tag Co., Newport, KY) and a unique PIT tag (TX1400ST, BioMark, Inc., Boise, ID). PIT tags were injected subcutaneously in the interscapular area and pushed laterally away from the injection site to minimize possible loss of the tag through the injection hole. We recorded body mass, sex, and breeding condition. Male mice were considered to be reproductively active if scrotal, and female mice were considered breeding if lactating or pregnant. Following processing, mice were released at the location of capture. All personnel followed precautions for working with animals potentially infected with hantavirus (Mills et al. 1995), and procedures were approved by the Institutional Animal Care and Use Committee at the University of Utah (IACUC #05-03011).

PIT-tag Monitoring

We documented the movement of deer mice using PIT-tag monitoring stations that consisted of foraging arenas coupled to PIT-tag readers. Foraging arenas are designed to simulate foraging opportunities in nature; foragers are

predicted to leave the arena when the rate of return is lower than the average rate of return elsewhere (Brown et al. 1994). When the day-trapping sessions ended, foraging arenas were placed at 49 locations on the inner portion of the trapping web (approximately 1.1 ha). Each arena consisted of 1 L of fine-grain sand (Jurassic Playsand, Salt Lake City, UT) mixed with 3 g of certified weed-free millet in a round plastic tray (diameter 26.7 cm, depth 3.8 cm) with a spray-foam ring that acted as a ramp into the tray. Millet comprised 0.03% of the volume in these foraging arenas; thus deer mice had to invest time and effort to harvest the seed from the sand just as they do in pockets of naturally deposited seeds at the base of shrubs. Furthermore, the maximum gain (under benign environmental conditions) for any one animal was <60% of daily intake; thus individuals had to also forage elsewhere (based on metabolic demands given in Nestler et al. 1996). The initial stocking density ($3 \text{ g} \cdot \text{L}^{-1}$) was determined in preliminary trials where we varied initial densities to determine a minimum density that attracted foragers to the trays. Millet seeds are comparable in size to seeds that occur naturally in the Great Basin (Crist and Friese 1993). Deer mice and other nocturnal rodents on the site did not completely deplete the foraging arenas of all seeds (average amount of millet remaining in the morning: June, 0.05 g; September, 0.22 g), indicating that they must have foraged elsewhere.

All 49 foraging arenas were set out each night in the same location for 6 consecutive nights in June and September (Wood 2007). The spatial arrangement was 4 foraging arenas along each of the 12 trapping transects, spaced 15 m apart, and 1 arena at the center point of the trapping web. The locations of the PIT stations were not identical to the trapping stations (traps were 5 m apart for the first 20 m from the center of the web and 10 m apart subsequently). Arenas were closed with lids each morning just after sunrise. Shortly thereafter, each arena was sifted and restocked with 3.00 g of millet and 1 L sand and kept closed until evening. The first night was a discovery night where presence of animals was not monitored. During the subsequent 5 nights, we set out monitoring equipment consisting of 12 PIT-tag readers (FS2001FR-ISO, Destron, South St. Paul, MN) and rotated the equipment through each of the 49 foraging-arena locations. PIT-tag readers consisted of a circular

antenna, a data logger, and a 14.1 V battery (MU-1SLDG Gel Star deep cycle, Standard Battery, Inc., Salt Lake City, UT). The antenna was placed beneath the tray, and the battery and antenna were attached to the data logger. Date, time, and PIT-tag number of marked individuals visiting the foraging tray was recorded in the data logger.

One PIT-tag monitoring station was present on each of the 12 transects for the first 4 nights. On the fifth night, a PIT-tag monitoring station was located at the center point of the trapping web, in addition to locations where the battery, antenna, or data logger had previously failed during the first 4 nights. Each morning, data were downloaded from each data logger onto a computer. Location and animal ID files were then combined to calculate home-range estimates.

Home-range Estimation

Home-range size was estimated using the 100% minimum convex polygon (MCP) method (Jennrich and Turner 1969) with Hawth's analysis tools (Hawthorne Beyer, www.spatial-ecology.com) in ArcGIS 9.0 (Environmental Systems Research Institute, Redlands, CA). We selected the MCP because it was more appropriate for our data than other methods, such as kernel density estimates (Ribble et al. 2002). MCP home range was determined for each mouse that met the following criteria: (a) visited 5 or more unique PIT-tag monitoring stations and (b) had <50% of the PIT-tag locations on the outer ring of the area monitored (Taitt 1981). We assumed that if an individual had more than 50% of their PIT-tag locations on the outer edge of the area monitored, the majority of their home range may lie outside of the observed area; thus the calculated home range would be an underestimate of the actual home range. If an animal met the above criteria, home range was calculated from the PIT-tag locations as well as from the locations at which the animals were trapped. Thus, the minimum number of locations used to estimate home range was 6.

We determined whether the unequal spacing between monitoring stations as a result of the web configuration had an effect on home-range size. Stations in the center of the web are closer together than those further from the center. For each home range, we estimated the distance from the centroid of the home range to the center of the trapping web and compared this

distance to home-range size with a regression analysis. If the clustering of stations in the center of the web enhanced home-range size then we predicted that home-range size would significantly decrease with increasing distance from the center of the web.

Factors Governing Home-range Size

General linear models (GLMs) were used to determine if sex, mass, breeding condition, or all possible interactions explained home-range size for June and September separately. Backward stepwise elimination was used to generate the most parsimonious model for variation in home-range size. For positively skewed continuous variables, a square-root transformation was used to normalize the distribution for analysis. All statistical analyses were conducted with Systat 10 (Systat Software, Inc., www.systat.com).

Home-range estimates were conducted in both June and September (representing spring and fall, respectively) to determine if there were seasonal effects on home-range size. Seasonal differences in home-range estimates were compared for all individuals using an ANOVA and for individuals that had home-range estimates in both June and September using a paired *t* test.

Home-range Fidelity

For individuals with home-range estimates in both seasons, 2 measurements were calculated to estimate home-range fidelity. First, percent overlap, or the percentage of home range that remained constant for an individual mouse from June to September, was calculated using the following expression (Bernstein et al. 2007):

$$\left[\frac{\text{Area}_{\text{Overlap}}}{\text{Area}_{\text{June}} + \text{Area}_{\text{September}} - \text{Area}_{\text{Overlap}}} \right] \times 100.$$

Second, the degree of home range conserved across seasons, or the percentage of the June home range that is conserved in September for an individual, was calculated using the following expression:

$$\left(\frac{\text{Area}_{\text{Overlap}}}{\text{Area}_{\text{June}}} \right) \times 100.$$

These 2 measures differ in that the percent overlap represents the area used by an individual that remained constant across both seasons, whereas the percent conserved represents the area of the initial home range observed in June that remained constant across both seasons.

RESULTS

Home-range Estimation

A total of 65 home ranges were calculated from 753 observations for both June and September combined. Overall, the average number of locations used to estimate home range was 11.6, with a range of 6–26 locations. Estimates of home range for June ranged from 360 to 3798 m² based on 6–18 trap and PIT-tag locations (*n* = 31). In September, home ranges varied from 556 to 5868 m² based on 6–26 trap and PIT-tag locations (*n* = 34). Individuals with an estimated home range did not differ from individuals for which a home range could not be estimated in terms of proportion of males to females (June: $\chi^2 = 0.58$, *P* = 0.45; September: $\chi^2 = 0.02$, *P* = 0.90), proportion of breeding to nonbreeding individuals (June: $\chi^2 = 0.007$, *P* = 0.94; September: Fisher's exact test, *P* = 1.00), and body mass (June: $F_{1,268} = 0.16$, *P* = 0.90; September: $F_{1,143} = 1.34$, *P* = 0.25).

In both months, there was no significant relationship between home-range size and distance from the centroid of the home range to the center of the trapping web (June: $R^2 = 0.01$, *P* = 0.25; September: $R^2 = 0$, *P* = 0.39).

Factors Governing Home-range Size

In both June and September, none of the factors examined (i.e., sex, mass, breeding condition, or interactions) explained home-range size. Females tended to have larger home-range estimates than males in June, and body mass had a positive relationship to home-range size in September. However, neither of these relationships were significant (June: $F_{1,29} = 3.06$, *P* = 0.09; September: $R^2 = 0.07$, *P* = 0.07).

Seasonality appeared to affect home-range size. Home ranges expanded from June to September. At the population level, the mean home-range size for September was approximately 60% larger than for June ($F_{1,63} = 11.41$, *P* = 0.001; Fig. 1a). However, there was not a significant difference in home-range size for the 9 individuals with home-range estimates in both seasons (paired $t_8 = 1.93$, *P* = 0.09; Fig. 1b), although home ranges in September were approximately 40% larger than those in June.

Home-range Fidelity

The majority of deer mice trapped in June (*n* = 271) were not recaptured in September

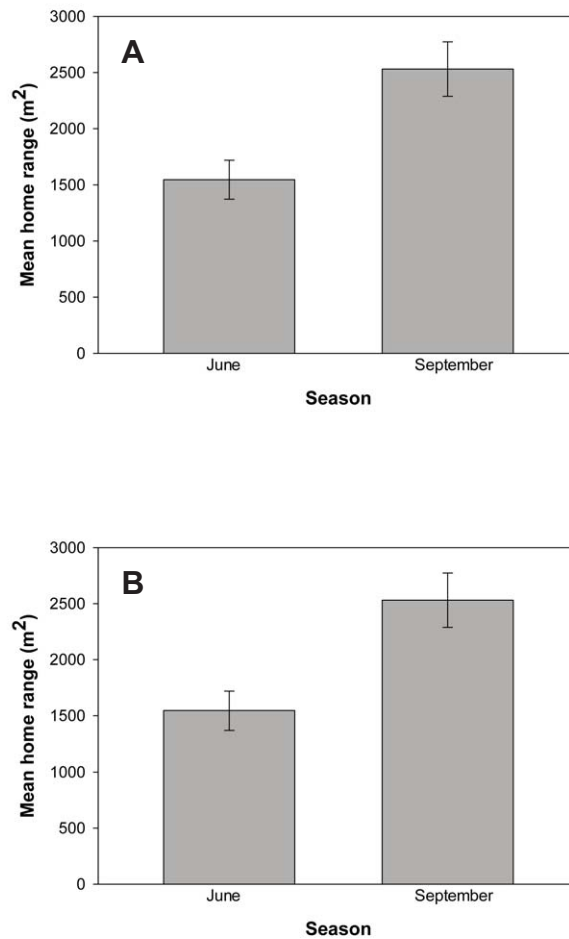


Fig. 1. Seasonal difference in average home-range size for (A) all individuals with home-range estimates ($P = 0.001$) and (B) individuals with home-range estimates in both June and September 2006 (paired t test: $P = 0.09$). Error bars represent standard error.

(79%). Similarly, of the 31 deer mice for which home ranges were estimated in June, the majority of these were not recaptured on the trapping web in September (68%). Of the 31 deer mice with June home ranges, there was no difference in sex or age of those recaptured or not recaptured in September (Fisher's exact tests: age, $P = 1.0$; sex, $P = 0.45$). We cannot determine whether the absence of deer mice in September is the result of emigration or mortality and therefore cannot assess site fidelity in these individuals. Thus, fidelity estimations are restricted to the 10 deer mice with home ranges in June that were recaptured in September. Of these deer mice, 9 individuals had sufficient data for calculation of home

ranges. These 9 deer mice exhibited high home-range fidelity. The mean percent overlap of the home range was 42.1% (SE = 8.4%) and the area conserved was 74.1% (SE = 8.7%; Fig. 2). One individual died in a trap, so we were unable to calculate a September home range for this individual; however, the location of the trap was within this animal's home range from June.

DISCUSSION

The objective of this study was to document the space use of deer mice in sage-steppe habitat, to identify factors that contribute to variation in home-range estimates, and to quantify home-range fidelity. We found that home-range

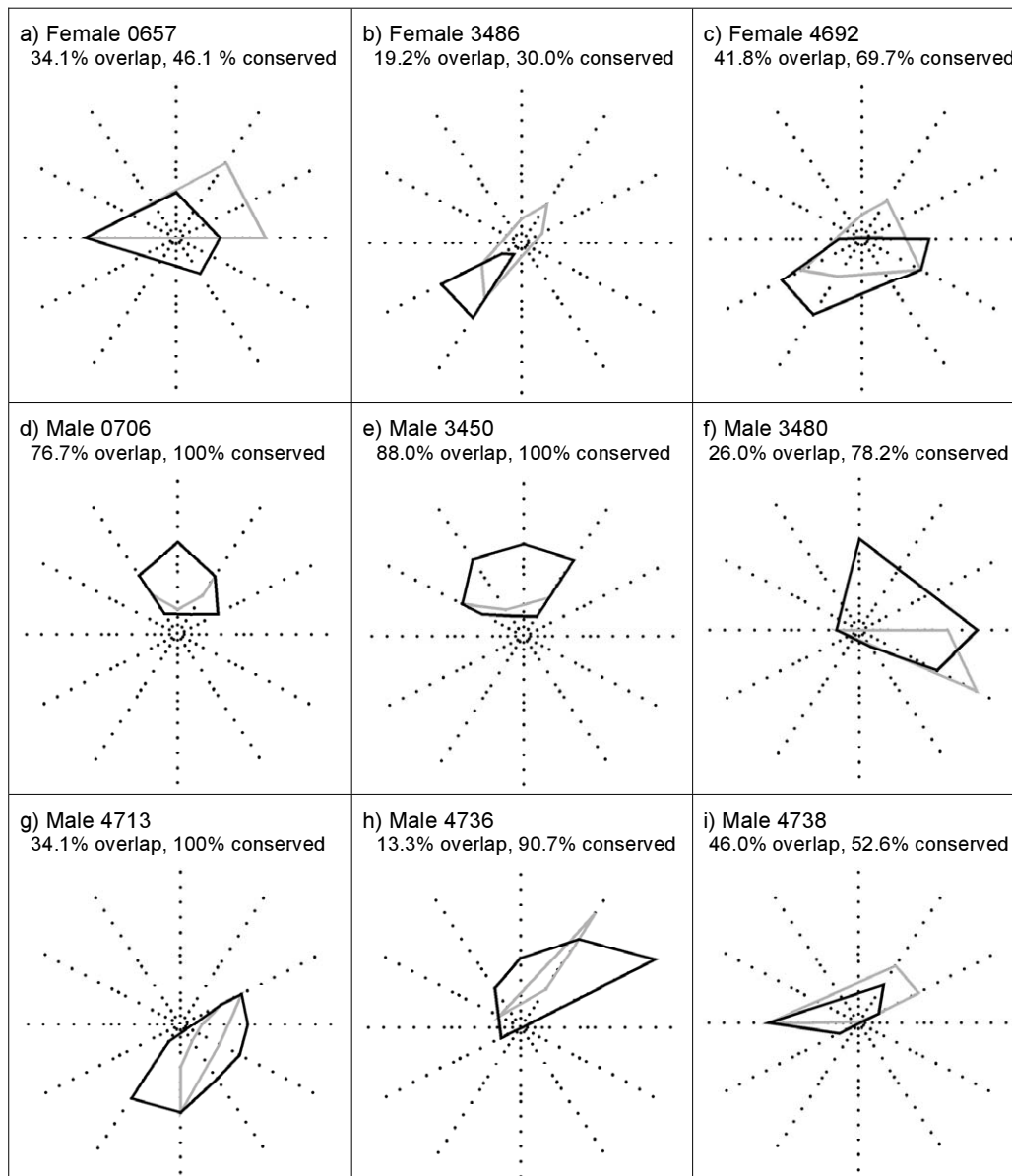


Fig. 2: Home-range fidelity (percent overlap and percent conserved) for the 9 individuals with home-range estimates in both June (gray) and September (black). Dots represent the trap and/or PIT-tag reader locations.

size varied by sampling period but that none of the other factors examined in this study accounted for variation in home-range estimates. To our knowledge, this is the first study to provide quantitative estimates of home-range fidelity in deer mice. This study adds to the limited number of studies that have estimated home range of deer mice in the sagebrush

habitat of the Great Basin desert (Juelson 1966, O'Farrell 1978, Feldhamer 1979).

Comparison of Home Range to Other Studies

The home-range estimates reported in this study are on the lower end of values previously reported for deer mice in this habitat (O'Farrell 1978, Feldhamer 1979) but are most comparable

to those reported by Juelson (1966). Comparisons of home ranges across studies are intrinsically difficult given the variety of methods employed in trapping and calculating home ranges. However, we suggest that the values reported herein are reflective of space use of animals at the time. In our study, we were able to generate enough fixes to calculate home range in relatively short periods of 9 or 11 days. Home ranges of individuals in this study would have been larger if the data were compiled across seasons (Fig. 2). In addition, it is possible that the home-range sizes recorded in this study represent the low end of the range for deer mice at these sites. The density of rodents, including deer mice, in 2006 was the highest recorded for this site across 8 years of sampling (>50 deer mice \cdot ha $^{-1}$). As home ranges often contract under high-density conditions (Erlinge et al. 1990, Ribble et al. 2002), the ranges reported herein may be smaller than those in years of low animal densities.

The lack of correlation between home-range size and distance from the home-range centroid to the center of the trapping web suggests that the unequal distances separating PIT-tag monitoring stations did not affect home-range size. This finding is relevant given the number of small mammal studies that utilize a web design where traps are not equidistantly spaced (Mills et al. 1999).

Factors Governing Home-range Size

That none of the factors examined in this study significantly explained home-range size was surprising considering the wealth of literature reporting differences in home-range size for deer mice based on sex and age, including differences in mass and breeding condition (Blair 1940, 1942, 1943, Storer et al. 1944, Williams 1955, Merritt and Merritt 1978, O'Farrell 1978, Ribble and Millar 1996). Although our sample sizes were large ($n > 30$), especially for a home-range study at a single site and within a given sampling period, the models were unable to detect significant differences among study factors. The order-of-magnitude range in home-range sizes measured within a sampling period could necessitate the collection of larger sample sizes for statistical significance.

We do not think that our inability to find significant factors was due to the exclusion of animals with $>50\%$ of their recorded locations

on the edge of the monitored area. First, the inclusion of these animals would have resulted in the addition of individuals with smaller home-range sizes, thereby increasing the variation in home-range size and reducing the ability to find significant factors. Second, other studies typically take into account edge effects and exclude individuals on the edge of the grid because much of their home range occurs in an area that is not measured (Taitt 1981).

The lack of a difference in the home-range size of males and females during this study yields interesting implications for understanding the transmission of SNV. Typically, more males are infected with SNV than females (Mills et al. 1997, Calisher et al. 2005), and this bias holds true for the site used in this home-range study (Pearce-Duvel et al. 2006, Lehmer et al. 2007). The difference in prevalence between the sexes is still not understood. However, for another rodent-virus system, the higher prevalence in males is speculated to be due to the increased degree of movements and number of aggressive contacts (Mills et al. 1992). The data from our study suggests that males and females had equal home-range sizes, with any difference being females having larger home-range sizes. Thus, the role of home range in SNV transmission warrants further investigation.

Home-range size increased significantly from June to September. This result is similar to previously reported deer mice home ranges in June and September in sagebrush habitat (O'Farrell 1978). The observed seasonal differences in home range in this study could be due to a variety of factors, including age, resource availability, and abundance of deer mice. Additionally, by September, the majority of the population were adults (estimated from body mass), which is the demographic typically with the largest home ranges (Blair 1942, Storer et al. 1944, Williams 1955). Thus, the increase in home-range size may be due in part to age, which is linked to season.

Home-range Fidelity

Two-thirds of the deer mice for which home ranges were determined in June were not present on the study site 3 months later in September. We do not know whether these animals died or emigrated from the site. The average life span estimated from deer mice mortality in this area is 65 days for females

and 90 days for males, respectively (Adler et al. 2008). Thus, it is possible that many of these mice died. However, we were not monitoring long-distance emigration from the site, so it is also possible that some of these deer mice left the area.

For the animals that remained on the study site, the relatively high fidelity to home range observed across seasons supports the idea that once a deer mouse establishes a home range, the individual can maintain the same general area for an extended period (Blair 1943, Storer et al. 1944, Stickel 1968). All of the individuals that remained on the study site maintained a portion of their June home range (i.e., no remaining individual completely abandoned its June home range). This finding is important to studies collecting home-range fixes over long periods, such as weeks to months, because such studies assume that animals do not greatly alter home range over time. The minor shifts in home range observed for each individual are likely due to a combination of factors, including changes in population dynamics, resource abundance, and seasonality (Blair 1940, Stickel 1968). Additionally, deer mice that were present on the site in both seasons, but for which we were unable to estimate home range ($n = 38$), used similar regions of the area monitored by trap and/or PIT-tag stations. This similar utilization of space, although not quantifiable, again suggests that deer mice have relatively high fidelity to home range.

This fidelity of space use over long stretches of time has interesting implications for the ecology of deer mice, particularly with respect to the spread of directly transmitted pathogens such as SNV. Models of pathogen transmission often assume homogenous mixing of individuals. However, the high site fidelity of deer mice may result in "hot spots," where pathogens may persist in particular locations because deer mice are not mixing homogeneously across a landscape.

Home-range Estimation with PIT-tag Technology

In this study, we used relatively new PIT-tag technology to generate home-range data over reasonably short windows of time. Although radiotelemetry is the preferred technology among many mammalogists for estimating home ranges, PIT-tag technology does offer some advantages. First, the PIT-tag method allows for a

large proportion of a population to be monitored, meaning the number of individuals for which home-range data can be collected is relatively high. In this study, 31 and 34 home-range estimates were determined over 11- or 9-night periods in June and September, respectively. Compared to other studies, this is a large sample size for a short sampling period (Blair 1943, Feldhamer 1979, Ribble et al. 2002). Second, this method allows movement data to be collected for both adult and juvenile animals. Unlike radiotelemetry, the weight of the tracking device is minimal compared to body mass (PIT-tag is <1% of deer mouse body mass), thus creating no restrictions on the size or age class of individuals studied. Third, this method allows for individuals to be free ranging. Similar to radio-telemetry and GPS tracking, marked individuals are able to go about normal activities and are able to visit more than one PIT-tag monitoring station per night. Fourth, this method is only moderately labor intensive. Once equipment is present on the site, the amount of time per day to restock seeds and to rotate and set up the PIT-tag equipment is minimal compared to the amount of time it would take to bait and check traps or to triangulate locations of mice during the night. Lastly, PIT-tag readers record other ecological information such as the length of time an individual spends at the foraging area as well as number of individuals that are present at the reader.

One potential drawback of using PIT-tag technology is the pantry effect created by the use of seeds in the foraging arena and its effect on home-range size. This method requires some form of enticement to draw animals to the PIT-tag readers, which clearly impacts their use of space. Taitt (1981) demonstrated that deer mice decrease their home-range size in the presence of additional food resources. However, other studies have demonstrated that the addition of a food resource did not have an effect on deer mouse home-range size (Metzgar 1973, Wolff 1985). Nonetheless, we attempted to minimize the pantry effect by providing a type of enticement (seed) that naturally occurs in the diet. This resource was presented in minimal quantities and in a matrix (sand) that forced the animal to actively forage. Also, the foraging arenas present a more natural foraging situation than a trap because the arenas are open to the environment and thus animals are subject to predation and competition.

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