Genetic relatedness and spatial associations of dusky-footed woodrats (*Neotoma fuscipes*)

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We studied the association between space sharing and kinship in a solitary rodent, the dusky-footed woodrat (*Neotoma fuscipes*). Genetic relatedness was inversely correlated with geographic distance for female woodrats but not for males, a pattern consistent with female philopatry and male dispersal. However, some female neighbors were unrelated, suggesting the possibility of female dispersal. Relatedness of female dyads was positively correlated with overlap of their home ranges and core areas, indicating that females were more likely to share space with relatives, whereas males showed no correlation between relatedness and the sharing of either home ranges or core areas. However, some females that shared space were not close relatives, and some closely related males shared space. House sharing was exhibited both by close relatives and by distantly related or unrelated woodrats, and was not correlated with relatedness. The kin structuring we describe likely resulted from a pattern of female philopatry and male dispersal, but also may have resulted from kin-directed behaviors by females.

Key words: dusky-footed woodrat, kinship, *Neotoma fuscipes*, philopatry, Sierra Nevada, space sharing

Most mammals are characterized by female philopatry (Greenwood 1980; Johnson and Gaines 1990), and this pattern, by generating spatial clusters of closely related females, is considered a central feature promoting the evolution of sociality in mammals (Lutermann et al. 2006; Silk 2007). Following kin selection theory, individuals are expected to tolerate their kin more than nonkin and can gain fitness benefits from spatial associations with related individuals (Hamilton 1964; Maynard Smith 1964). However, kin interactions can render costs as well (Griffin and West 2002; Hamilton 1964). If the fitness costs associated with kin interactions outweigh the benefits, then closely related individuals may avoid each other or disperse from their natal home ranges (Hamilton 1964; Wade and Breden 1987). Hence, although many studies have demonstrated close spatial associations among kin (Balloux et al. 1998; Boellstorff and Owings 1995; Cutrera et al. 2005; Ishibashi et al. 1997; Moyer et al. 2006; Surridge et al. 1999) and fitness-enhancing benefits that can promote sociality (Davis 1984; Lambin and Krebs 1993; Moses and Millar 1994; Ylönen et al. 1990), some studies find little or no evidence of such spatial patterns (Burton and Krebs 2003; Schaeff et al. 1999) or their associated benefits (Boonstra and Hogg 1988; Dalton 2000; Kawata 1987).

Recent research has focused on solitary species, which can promote an understanding of the early stages of sociality (Cutrera et al. 2005; Kays et al. 2000; Maher 2009; McEachern et al. 2007). We studied the association between

resource sharing and kinship in a solitary, nocturnal rodent, the dusky-footed woodrat (*Neotoma fuscipes*). We focused on space as a resource because the sharing of space among closely related females can influence home-range placement and access to limiting resources (Carpenter and MacMillen 1976; McLoughlin et al. 2000), and can have significant effects on reproductive success and survival (Moses and Millar 1994). Thus, space sharing may be an important initial step leading to the evolution of more complex forms of mammalian sociality. Further, dusky-footed woodrats build, maintain, and defend from conspecifics large stick houses, a potentially limiting resource (Carraway and Verts 1991; Innes et al. 2007) and are classified as solitary breeders and parental-care providers. Despite their territorial and solitary nature, dusky-footed woodrats demonstrate a substantial degree of space-use overlap both within and between sexes (Cranford 1977; Innes et al. 2009; Lynch et al. 1994; Sakai and Noon 1997), as well as sharing of houses (Innes et al. 2009; Lynch et al. 1994; McEachern et al. 2007). Consequently, opportunities for social interactions arise from overlapping space use, particularly among close relatives such as adult females and their philopatric daughters.

We capitalized on the availability of detailed spatial information on a population of dusky-footed woodrats (Innes et al. 2009) to evaluate the relationship between spatial organization and relatedness. Because female philopatry and male-biased dispersal are common in solitary mammals (Waser and Jones 1983), we predicted that females, but not males, would display a negative relationship between genetic relatedness and geographic distance at a local scale. Space sharing among relatives might result from the spatial proximity caused by philopatry, and also from the preferential treatment of relatives because of kin selection. Hence, we predicted that females that overlapped in home-range, core-area, and house occupancy would be more closely related than females that did not share these spatial resources.

MATERIALS AND METHODS

We studied dusky-footed woodrats from May to October 2004 at 2 study sites located 1.2 km apart in mixed-conifer forest in the Plumas National Forest near Quincy, Plumas County, California (121°N, 39°W). Study sites 1 and 2 were 6.2 and 3.7 ha in size and located at 1,750 and 1,450 m elevation, respectively. We trapped dusky-footed woodrats at each site by setting 4 Sherman live traps (7.6 × 9.5 × 30.5 cm; H. B. Sherman Traps, Inc., Tallahassee, Florida) at the base of each house for 4 consecutive nights in late spring (May–June) and late summer (August–September) and intermittently as needed at occupied houses to monitor reproductive status of individuals. Traps were set at all houses within each study site, and also at all houses within 3 home-range diameters (approximately 180 m—Cranford 1977; Lynch et al. 1994; Sakai and Noon 1997) of each study site, in order to ensure that all woodrats potentially influencing the spatial organization were identified (Innes et al. 2009). Traps were baited with

raw oats and sunflower seeds coated with peanut butter. Traps were opened at dusk and checked at dawn. Synthetic batting was provided for thermal insulation. At 1st capture, woodrats were ear-tagged (Monel #1005-1; National Band and Tag Co., Newport, Kentucky), sexed, weighed, and aged, and a small amount of ear tissue was removed using sterile surgical scissors. Ear tissue was placed in 95% ethanol and transferred to −20°C in the laboratory for storage. Age was estimated based on a combination of body mass (adult: ≥170 g, juvenile: <170 g), pelage (adult: brown, juvenile: gray or intermediate), and reproductive status (adult female: pregnant–lactating, adult male: scrotal, juvenile: nonreproductive—Innes et al. 2007). Adult woodrats were further classified as residents or nonresidents; adult woodrats qualified as residents if the animal was captured or radiolocated repeatedly at the same house or set of houses within the study area prior to 1 August (McEachern et al. 2007). We believe we captured all woodrats resident in our 2 study sites (Innes et al. 2009). Radiocollars were fitted to all adult resident woodrats (Innes et al. 2009). All handling procedures were approved by the University of California Davis Animal Use and Care Administrative Advisory Committee, and met guidelines recommended by the American Society of Mammalogists (Sikes et al. 2011).

Because individual woodrats at our study sites were often captured at multiple houses (Innes et al. 2009), geographic distances between individuals were calculated by averaging the number of captures at each house to obtain a single weighted-average location for each woodrat. Weighted-average locations were calculated using Universal Transverse Mercator coordinates; prior to analyses, the Universal Transverse Mercator coordinates for each house were accurately determined (≤1 m) using a Trimble global positioning system unit (GeoExplorer and GeoXT; Trimble Navigation, Ltd., Sunnyvale, California). The standard Euclidean distances between all pairs of adult woodrats within each study site were then calculated based on these weighted-average locations (McEachern et al. 2007).

Radiocollared woodrats were tracked for a mean of 109 days (range = 44–162 days). We determined nocturnal locations via radiotelemetry triangulation 20–30 times per month, and we determined diurnal occupation of houses via radiotelemetry homing 12 times per month (Innes et al. 2009). We used the minimum convex polygon method to estimate 95% minimum convex polygon home ranges and 50% minimum convex polygon core areas, and we calculated an index of overlap (OI—Minta 1992) for all pairs of adult residents (Innes et al. 2009). We used diurnal radiolocations to determine house sharing (either simultaneous or nonsimultaneous) and successive occupancy for all radiocollared woodrats.

The DNA was extracted from ear tissue using Qiagen DNeasy tissue kits (Qiagen Inc., Valencia, California). DNA at 8 polymorphic microsatellite loci (Nfu1, Nfu2, Nfu3, Nfu5, Nma10, Nma15, Ppa1, and Pml1 [Castleberry et al. 2000; Chirhart et al. 2000; Matocq 2001; Wooten et al. 1999]) was extracted and amplified following the protocols described in

McEachern et al. (2007). We used GENEPOP 3.4 (Raymond and Rousset 1995) to estimate the observed and expected heterozygosities, deviations from Hardy–Weinberg equilibrium, and linkage disequilibrium for each locus and the population as a whole, with significance levels set at $\alpha = 0.05$ and adjusted for multiple comparisons using the sequential Bonferroni correction. We used ML-RELATE (Kalinowski et al. 2006), which uses MonteCarlo randomizations (Guo and Thompson 1992) to test for heterozygote deficiencies, and the U-statistic (Raymond and Rousett 1995) to detect null alleles. Loci that had a Bonferroni-corrected 1-tailed P-value of <0.05 were classified as having null alleles (Wagner et al. 2006).

We calculated a maximum-likelihood estimate of pairwise genetic relatedness between all pairs of woodrats, both resident and nonresident, at each site using the program ML-RELATE. This method was chosen because maximum-likelihood estimates of relatedness generally are more accurate than other estimators (Milligan 2003). ML-RELATE implements the maximum-likelihood approach developed by Kalinowski and Taper (2006) to accommodate for the presence of any null alleles, which improves estimates compared with ignoring the presence of null alleles or discarding the affected loci (Wagner et al. 2006).

ML-RELATE calculates Wright's (1922) coefficient of relatedness (r), so the degree of relatedness between individuals is on an absolute scale (0–1), not a relative scale as with other programs (e.g., KINSHIP—Queller and Goodnight 1989). Relatedness values were compiled into a matrix in ML-RELATE, with values of expected relatedness ranging from 0 (unrelated individuals) to 0.5 (e.g., mother–offspring or full siblings). To determine the relationship between pairwise relatedness and geographic distance, we imported matrices of pairwise relatedness estimates obtained in ML-RELATE into GENALEX 6.1 (Peakall and Smoose 2006). Mantel tests of correlations between geographic distance and pairwise relatedness (r) were estimated by sex for each site using 9,999 permutations.

Using data from Innes et al. (2009), we calculated the median home-range overlap for same-sex dyads (male–male dyads: median OI = 0.30, range = <0.01–0.82, $n = 21$; female–female dyads: median OI = 0.21, range = 0.02–0.77, $n = 22$) and categorized home-range overlap for each dyad as high (OI ≥ the median), low (median > OI > 0), or no overlap (OI = 0). Mantel tests of correlations between home-range overlap categories and relatedness (r) were estimated by sex for each site using 9,999 permutations using the software program GENALEX 6.1 (Peakall and Smoose 2006). For core areas, we categorized overlap as overlapping (OI > 0) or not overlapping (OI = 0) and used Mantel tests of correlations as described for home-range overlap. To determine if same-sex dyads that shared a house were closely related, we evaluated r for those dyads that shared a house and those that did not. Mantel tests of correlations between house sharing categories and r were estimated by sex using 9,999 permutations. House sharing may be simultaneous (woodrats occupy a house at the same time),

nonsimultaneous (woodrats alternate occupancy of a house), or successive (Innes et al. 2009). However, because of small sample sizes, we combined all in 1 category, sharing.

RESULTS

We captured 17 adult female woodrats (9 residents and 8 nonresidents), 5 adult males (all residents), and 27 juveniles (12 females and 15 males) at study site 1, and we captured 7 adult females (6 residents and 1 nonresident), 11 adult males (7 residents and 4 nonresidents), and 18 juveniles (8 females and 10 males) at study site 2. Density of all woodrats was 6.3 individuals/ha at site 1 and 5.2 individuals/ha at site 2.

Allele counts for the 8 loci ranged from 6 to 12 alleles across sites ($\bar{X} = 7.6$). Observed heterozygosities per locus averaged 0.74 (range = 0.50–0.94) at site 1 and 0.75 (range = 0.40–0.86) at study site 2 (Table 1). Significant deviations from Hardy–Weinberg equilibrium were observed at 1 of the 8 loci (but only at site 2) when testing at the population level after Bonferroni adjustment for multiple tests (Table 1). When analyzed by individual loci across all populations, there were 2 cases of linkage disequilibrium detected between loci Nma10 and Nma15 and loci Nma10 and Ppa1. When analyzed by individual loci at the population level, only 1 pair (loci Nma10 and Nma15) was out of equilibrium in both populations. Other loci deviated from linkage equilibrium but not consistently between sites. Linkage disequilibrium was observed between loci Nfu3 and Pml1 and loci Nfu5 and Pml1 at site 1, and loci Nma10 and Ppa1 at site 2. Deviations from Hardy–Weinberg equilibrium and linkage disequilibrium in our data may be due to a variety of factors, including nonrandom mating, presence of null alleles, drift, or selection for loci linked to a neutral marker (Lowe et al. 2004). The deviations we observed may be due to population substructure because relatives appear to be clustered within our population (see below).

We calculated r for all pairs of woodrats at each study site. Relatedness values ranged from 0 to 0.76 ($\bar{X} = 0.08 \pm 0.004$ SE, $n = 1,176$ pairwise comparisons) at study site 1 and 0 to 0.84 ($\bar{X} = 0.08 \pm 0.006$ SE, $n = 630$ pairwise comparisons) at study site 2. The average value of relatedness ($\bar{X} \pm SE$) for mother–offspring pairs as identified using captures of juveniles at the houses(s) of adult females was 0.47 ± 0.03 (95% confidence interval [95% CI] = 0.40–0.53) at site 1 and 0.39 ± 0.05 (95% CI = 0.28–0.50) at site 2, which were consistent with the expected value of 0.5.

As expected, the Mantel tests revealed a significant negative relationship between genetic relatedness and geographic distance in pairs of adult resident females at site 1, with a trend toward a significant relationship at site 2 (Table 2), indicating that related females were more likely to reside in proximity. A similar pattern was shown for all adult females (Table 2). However, R^2-values were small, indicating a relatively weak relationship between spatial distance and genetic relatedness (Fig. 1). As expected, there were no significant relationships found in adult males, either for residents or all adults (Table 2).

TABLE 1.—Microsatellite loci used to investigate relatedness in dusky-footed woodrats (*Neotoma fuscipes*) at 2 study sites in Plumas National Forest, California, from May to October 2004. Data include resident and nonresident adult and juvenile dusky-footed woodrats captured at each site. An asterisk (*) indicates significant deviation from Hardy–Weinberg equilibrium for the hypothesis of heterozygote deficiency.

Locus	Repeat motif	Allele size (base pairs)	n Site 1	Site 2	No. alleles Site 1	Site 2	H_O Site 1	Site 2	H_E Site 1	Site 2
Nfu1	$(CA)_{28}$	154–164	48	35	7	6	0.73	0.83	0.70	0.79
Nfu2	$(CA)_{32}$	256–303	49	36	8	10	0.94	0.81	0.86	0.81
Nfu3	$(GC)_5(CA)_{21}$	200–207	49	36	6	6	0.76	0.86	0.77	0.75
Nfu5	$(CA)_{23}$	111–143	48	36	9	7	0.77	0.69	0.80	0.73
Nma10	$(CCT)_2(CT)_{21}(CA)_{25}$	206–252	48	36	11	12	0.58	0.81	0.78	0.79
Nma15	$(CA)_{19}$	139–147	49	36	7	6	0.90	0.80	0.82	0.80
Ppa1	$(AC)_{24}$	180–196	49	36	6	8	0.76	0.78	0.67	0.78
Pml1	$(CA)_{18}$	169–196	48	35	6	7	0.50	0.40	0.70	0.71*

Mantel tests for correlation between relatedness and home-range overlap revealed a significant positive relationship at both study sites, indicating that females that shared a high portion of their home ranges were more closely related (Table 3). At study site 2, all female dyads that shared a high portion of their home ranges were close relatives (i.e., $r \geq 0.25$), but at study site 1, only 2 of 7 such dyads were close relatives. Female dyads that shared low or no portions of their home ranges showed very low levels of relatedness. Although males often exhibited substantial home-range overlap and 2 dyads comprised close relatives, we did not find a significant relationship between home-range overlap and relatedness for males at either site (Table 3). None of the male dyads at study site 1 that shared a high portion of their home ranges were closely related, whereas 2 of 9 such dyads at study site 2 were closely related.

Sharing of core areas showed a similar pattern as for sharing of home ranges. Females at site 1 that shared their core areas were significantly more related than were those that did not, and females at site 2 showed a trend toward such a relationship (Table 4). Males showed no significant relationship between relatedness and core-area overlap (Table 4).

We observed no apparent pattern with respect to relatedness among same-sex dyads that shared houses; some house sharers were closely related, whereas others were not. With data combined across study sites, mean relatedness values ranged from 0 to 0.25 (mean $r = 0.10 \pm 0.05$ *SE*, $n = 5$) for all female dyads that shared houses, and from 0 to 0.55 (mean $r = 0.22 \pm 0.14$ *SE*, $n = 4$) for all male dyads that shared houses. Simultaneous sharing might be more likely to occur between close relatives than nonsimultaneous sharing, which may merely reflect a brief visit during an exploratory excursion. However, we recorded 1 instance of simultaneous sharing and these individuals were not closely related ($r = 0.12$). Mantel tests revealed that relatedness of female house sharers was not significantly different from nonsharers at site 2 ($P = 0.551$, $n = 15$), but showed a trend toward a significant difference at site 1 ($P = 0.088$, $n = 36$), with sharers being more related. Relatedness of males that shared houses at site 2 showed a trend toward a significant difference from nonsharers ($P = 0.093$, $n = 21$); no males shared houses at site 1. We note that our sample sizes were small for all tests. In some cases, a high degree of home-range overlap, rather than relatedness, appeared to influence house sharing among same-sex dyads. Mantel tests revealed that with increased home-range overlap, there was an increased probability of house sharing among female dyads at site 1 ($P = 0.024$), but not site 2 ($P = 0.282$).

TABLE 2.—Mantel tests of correlations between geographic distance and pairwise relatedness (r—Kalinowski et al. 2006) by study site and dyad category for resident adult and all adult (resident and nonresident) dusky-footed woodrats (*Neotoma fuscipes*) in Plumas National Forest, California, from May to October 2004. An asterisk (*) indicates statistical significance.

	Dyad category	Site	No. pairs	R^2	Mantel P-value
Resident adults	Female–female	1	36	0.150	0.005*
		2	15	0.278	0.075
	Male–male	1	10	0.279	0.961
		2	21	0.054	0.166
All adults	Female–female	1	136	0.048	0.005*
		2	21	0.145	0.060
	Male–male	1	10	0.279	0.961
		2	55	0.007	0.258
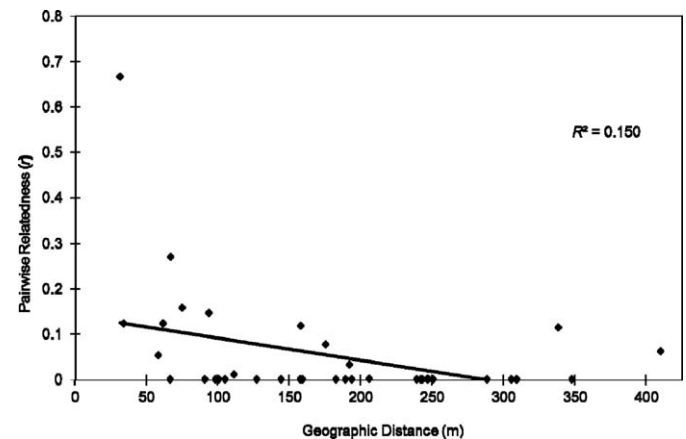
FIG. 1.—Linear relationship between geographic distance and pairwise relatedness in resident adult female dusky-footed woodrats (*Neotoma fuscipes*) at study site 1 in 2004, illustrating the high degree of variability in the relationship.

TABLE 3.—Mean pairwise relatedness (*r*—Kalinowski et al. 2006) by dyad category and study site for resident adult dusky-footed woodrats (*Neotoma fuscipes*) with overlapping home ranges in Plumas National Forest, California, from May to October 2004. Overlap category indicates whether the overlap index (OI) was greater (High) or less (Low) than the median value. No overlap indicates that OI $= 0$. An asterisk (*) indicates statistical significance.

Dyad category	Site	Overlap category	No. dyads	OI $\bar{X} \pm SE$	OI Range (minimum–maximum)	Mean pairwise relatedness $\bar{X} \pm SE$	Mean pairwise relatedness Range (minimum–maximum)	R^2	Mantel *P*-value
Female–female	1	High	7	0.45 ± 0.06	0.22–0.71	0.20 ± 0.08	0–0.67	0.285	0.003*
		Low	6	0.10 ± 0.03	0.02–0.15	0.03 ± 0.02	0–0.15		
		No overlap	23	0	0	0.02 ± 0.01	0–0.12		
	2	High	5	0.45 ± 0.10	0.14–0.77	0.42 ± 0.06	0.25–0.56	0.626	0.006*
		Low	4	0.06 ± 0.02	0.02–0.09	0.04 ± 0.04	0–0.14		
		No overlap	6	0	0	0.04 ± 0.03	0–0.16		
Male–male	1	High	2	0.47 ± 0.29	0.18–0.75	0.07 ± 0.07	0–0.13	0.085	0.931
		Low	2	0.09 ± 0.08	0.01–0.18	0.01 ± 0.01	0–0.01		
		No overlap	6	0	0	0.11 ± 0.04	0–0.24		
	2	High	9	0.54 ± 0.15	0.36–0.82	0.13 ± 0.18	0–0.55	0.049	0.176
		Low	8	0.14 ± 0.10	0.002–0.30	0.12 ± 0.19	0–0.50		
		No overlap	4	0	0	0 ± 0	0–0		

DISCUSSION

Genetic relatedness is inversely related to geographic distance for female dusky-footed woodrats but not for males, a pattern consistent with female philopatry and male dispersal. Female philopatry and male-biased dispersal is typical of highly social mammals (Eisenberg 1977; Waser and Jones 1983), and also is shown in less social and solitary species (Kitchen et al. 2005; Moyer et al. 2006; Ratnayeke et al. 2002; van Staaden et al. 1994). However, small R^2-values for female woodrats in our study indicate that not all neighboring resident females were related, suggesting that some females are not philopatric and do disperse from their natal areas. Female philopatry in woodrats may be influenced by density. Other studies of *Neotoma* found evidence of a matrilineal structure that was weak or nonexistent at high (35–40 woodrats/ha) and low (1 or 2 woodrats/ha) densities, but more pronounced at intermediate densities (11 woodrats/ha—Matocq and Lacey 2004; McEachern et al. 2007). This pattern might be expected if very low densities preclude the accumulation of kin clusters and very high densities break down kin clusters due to increased local resource competition (Armitage 1975; Hamilton 1996;

McEachern et al. 2007). Our results are consistent with this pattern; we observed a relatively weak matrilineal structure at woodrat densities that were low to intermediate (5 or 6 woodrats/ha) compared with those reported elsewhere.

In our study area, sharing of home ranges was common among woodrats, but sharing of core areas was more restricted: 52% of same-sex dyads overlapped home ranges, but of those only 30% overlapped core areas (Innes et al. 2009). Despite small sample sizes, we detected correlations between genetic relatedness of females and overlap of home ranges and core areas, indicating that females were more likely to share their home ranges and core areas with relatives. This relationship was especially pronounced for close relatives, which often showed a high degree of home-range sharing, suggesting that mothers may allow their mature daughters to remain in their natal home ranges. However, some females that shared a high portion of their home ranges were not close relatives, and some closely related males shared home ranges. Hence, although our results indicate a general pattern of female philopatry and male dispersal, that pattern is not absolute.

TABLE 4.—Mean pairwise relatedness (*r*—Kalinowski et al. 2006) by dyad category and study site for resident adult dusky-footed woodrats (*Neotoma fuscipes*) with overlapping core areas in Plumas National Forest, California, from May to October 2004. Overlap category indicates whether the dyad overlapped or not. No overlap indicates that the overlap index (OI) $= 0$. An asterisk (*) indicates statistical significance.

Dyad category	Site	Overlap category	No. dyads	OI $\bar{X} \pm SE$	OI Range (minimum–maximum)	Mean pairwise relatedness $\bar{X} \pm SE$	Mean pairwise relatedness Range (minimum–maximum)	R^2	Mantel *P*-value
Female–female	1	Overlap	4	0.22 ± 0.13	0.04–0.60	0.24 ± 0.15	0–0.67	0.283	0.008*
		No overlap	32	0	0	0.03 ± 0.01	0–0.27		
	2	Overlap	3	0.32 ± 0.14	0.05–0.52	0.37 ± 0.10	0.25–0.56	0.255	0.100
		No overlap	12	0	0	0.12 ± 0.05	0–0.50		
Male–male	1	Overlap	1	0.06	0.06	0	0	0.104	—
		No overlap	9	0	0	0.09 ± 0.03	0–0.24		
	2	Overlap	9	0.21 ± 0.06	0.02–0.45	0.13 ± 0.07	0–0.55	0.014	0.223
		No overlap	12	0	0	0.08 ± 0.05	0–0.50		

Philopatry in rodents may be influenced by ecological conditions, such as population turnover, that create opportunities for local settlement (Solomon 2003). A high degree of home-range sharing by close relatives was more common for females at study site 2 (100%) than at study site 1 (29%), with a similar relationship for males at study site 2 (22%) compared with study site 1 (0%), suggesting higher levels of philopatry by both sexes at site 2. Relatives may live near each other not because they are attracted to kin or benefit from interacting with them, but because they settle in the 1st available territory they encounter, which happens to be near the natal range (Peacock and Smith 1997; Waser and Jones 1983). During the subsequent year (2005), we recaptured 22% of 49 woodrats at study site 1 and 14% of 36 woodrats at study site 2 (R. Innes, in litt.), suggesting the possibility of higher turnover at study site 2, where home-range sharing was more common. However, the difference was not significant ($\chi^2 = 0.995$, $P = 0.318$).

Woodrat houses are an essential resource for survival and reproduction (Atsatt and Ingram 1983; Innes et al. 2007; Vestal 1938), likely explaining why woodrats maintain near-exclusive use of houses (Innes et al. 2009). We expected that the uncommon occurrences of same-sex house sharing would involve relatives because of the benefits of kin selection. Our results did not support that expectation; house sharing was exhibited both by close relatives and by distant relatives or unrelated woodrats, suggesting that relatedness was not the only factor influencing house sharing. In some mammals, an increased probability of nest sharing coincides with increasing range overlap (Michener 1983). At one of our study sites, house sharing was associated with greater home-range overlap, suggesting the importance of proximity. However, some houses were shared by woodrats that normally were distant from one another, and such incidents may have resulted from exploratory excursions to assess resources (Johnson 1989).

In summary, our results show that kin structure was present, although relatively weak, among female woodrats but not among males. This structure may have resulted primarily from a pattern of female philopatry and male dispersal, although we found some evidence for female dispersal and male philopatry. Moreover, the degree of philopatry may be influenced by population turnover. The kin structure we described also could have resulted from kin-directed behaviors; we identified several pairs of closely related females that exhibited extensive home-range overlap, suggesting a surprising degree of tolerance by a species considered to be territorial. Closely related females in close proximity could benefit from cooperative behaviors such as tail-rattling, which may serve as an alarm signal, or allogrooming (Wallen 1977). Woodrats might also benefit via a reduction in the cost of home-range defense (Hamilton 1964).

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