

Genetic relatedness and space use in a behaviorally flexible species of marmot, the woodchuck (*Marmota monax*)

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Abstract Solitary species show several patterns of space use and relatedness. Individuals may associate randomly or may live near female or male kin, often as a result of natal philopatry or dispersal patterns. Although usually described as solitary or asocial, woodchucks (*Marmota monax*) are behaviorally flexible marmots that exhibit greater sociality in some populations than others. I examined relationships between kinship, geographic distance, and home range overlap, as well as dispersal and philopatry, to determine the extent to which kin associated spatially. I used a combination of microsatellite DNA analysis, long-term behavioral observations, and radiotelemetry to test predictions that females, but not males, would associate with kin. Indeed, woodchucks lived closer and shared a greater proportion of their home range with more closely related animals. Overlap of females' and males' home ranges was positively correlated with kinship, and male–female dyads shared more area with closer kin. Most juveniles delayed dispersal beyond their first summer. Females often remained philopatric and settled near their natal range. Although males often dispersed as yearlings, some males also established territories within or immediately adjacent to their natal home ranges. A combination of factors can explain these spatial patterns, including high population density associated with the study site's location within a suburban environment, high dispersal costs, and abundant food. Thus, despite their asocial and solitary reputation, woodchucks displayed spatial patterns seen in other, more social species of ground-dwelling sciurids.

Keywords Home range overlap · Natal philopatry · Kinship · Spatial organization

Introduction

Many models of mammalian social behavior describe the formation of kin clusters as an initial step in developing sociality (Armitage 1981; Michener 1983; Waser and Jones 1983; Perrin and Lehmann 2001). Typically, females display natal philopatry, which can produce groups of female kin and set the stage for increased rates of amicable interactions favored by kin selection (Greenwood 1980; Armitage 1981, 1999). Kin selection also may favor joint territorial defense and cooperative breeding (Michener 1983; Solomon and Getz 1997).

Recent studies, however, have exposed greater diversity in mammalian dispersal patterns and the structure of social groups. For example, genetic work has revealed no sex bias in dispersal (e.g., Blundell et al. 2002; Fredsted et al. 2007) and many cases of female-biased dispersal (see Munshi-South 2008). Moreover, social groups may not consist of kin, highlighting the fact that processes other than kin selection can favor group formation (Blundell et al. 2004; Hare and Murie 2007). Even among kin-structured groups, philopatry and limited dispersal may increase competition among relatives, negating the beneficial effects of kin selection, and researchers increasingly are examining both cooperative and competitive interactions (Griffin and West 2002; West et al. 2002).

Nevertheless, kin selection probably plays a large role in the development of many mammalian social groups. Numerous studies of social mammals, including rodents, have documented that females live near kin (e.g., Vestal and McCarley 1984; van Staaden et al. 1994; Armitage 1996a).

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More recently, however, researchers have focused greater attention on solitary species, which can provide insights into the early stages of sociality (Kays et al. 2000; Cutrera et al. 2005; McEachern et al. 2007). In some solitary species, kin share more space or live closer to each other (e.g., raccoons, *Procyon lotor*, Ratnayeke et al. 2002; gerbils, *Meriones tamariscinus*, Tchabovsky and Bazykin 2004; black bears, *Ursus americanus*, Moyer et al. 2006), whereas in other species or populations, they do not (black bears, Schenk et al. 1998; snowshoe hares, *Lepus americanus*, Burton and Krebs 2003) or only females demonstrate such patterns (brown bears, *Ursus arctos*, Støen et al. 2005; dusky footed woodrats, *Neotoma fuscipes*, McEachern et al. 2007; black bears, Costello et al. 2008). Even among solitary species, such spatial organization may result from natal philopatry or settlement in nearby vacant ranges (Waser and Jones 1983), which in turn depends on ecological conditions such as population density, food resources, and risk of dispersal (Solomon 2003).

Woodchucks (*Marmota monax*) belong to a group of social ground-dwelling sciurids, the marmots, yet woodchucks are considered solitary, aggressive, and the least social species (Bronson 1964; Armitage 1999; Blumstein and Armitage 1999). In most marmots, individuals postpone dispersal at least 1 year and sometimes more than 3 years (Blumstein and Armitage 1999). Depending on the species, males all may disperse (e.g., yellow-bellied marmots, *Marmota flaviventris*, Armitage 2000), some females also disperse (Armitage 2000), or males may postpone dispersal longer than females (Arnold and Dittami 1997). Both sexes of woodchucks have been reported to disperse as juveniles from their natal range (DeVos and Gillespie 1960; Bronson 1963; Snyder 1976), which could preclude relationships between kinship and space use patterns. However, in this behaviorally flexible species, individuals in some populations delay dispersal or show natal philopatry (Meier 1992; Swihart 1992; Maher 2006), which could lead to formation of kin clusters. No one has undertaken a detailed study of genetic relatedness in woodchucks to determine if kin associate spatially. Woodchucks are believed to represent the ancestral condition in marmots (Kruckenhauser et al. 1999; Steppan et al. 1999); thus, they typically represent the prototype ancestral species in models of sociality (Blumstein and Armitage 1998, 1999). However, their flexibility can provide insights into how sociality may have evolved in this taxon.

To better understand the dynamics of spatial patterns and kin structure in solitary mammals, I estimated genetic relatedness using microsatellite markers and examined its relationship to space use in woodchucks. Specifically, I examined spatial proximity and home range overlap, and I documented the extent of natal philopatry and dispersal in both males and females. Because I previously had observed

natal philopatry among females in this population (Maher 2006), I expected that females would live closer to kin and share more home range area with more closely related females, but that males would not exhibit these same patterns.

Materials and methods

Study species and population

Woodchucks are moderately sized (2–5 kg), semifossorial ground squirrels that occupy the widest geographic range of any marmot, extending across northern Canada southward across the eastern USA to the southeastern states (Armitage 2003). Because of their broad range, hibernation patterns vary; however, in northern areas, adult males generally emerge from hibernation in late February to early March, followed by adult females 2–3 weeks later (Ferron 1996; Maher 2006). Juveniles first appear aboveground around 30 days of age (Hamilton 1934; Grizzell 1955), and they may disperse in their first summer or delay dispersal until their second active season (Bronson 1963; Meier 1992; Swihart 1992; Maher 2006). Some juveniles remain philopatric throughout their lifetimes, i.e., they settle within the natal range or less than one home range diameter (195 m) from that natal range (Maher 2006). Adults immerse in late summer, whereas juveniles remain active until early to mid October (Maher 2006). Woodchucks purportedly live 5–6 years (Hamilton 1934; Grizzell 1955), but long-term studies are lacking. The longest lived male and female in the study population were at least 10 and 12 years old, respectively (C. Maher, unpublished data).

Woodchucks are considered solitary, i.e., adults typically live alone and do not demonstrate coordinated activity with other woodchucks (Bronson 1963; Ferron and Ouellet 1989; Meier 1992). Once an animal establishes a home range, usually as a yearling or adult, it typically remains there until its death or disappearance, presumably because it died. I rarely observed adults relocating to a new home range in the study population (C. Maher, unpublished data). Within the home range, woodchucks use more than one burrow system, which may contain multiple entrances either conspicuously identified by large amounts of excavated soil or hidden in the vegetation and used as escape routes (Hamilton 1934; Ferron and Ouellet 1989; Swihart 1992). During the breeding season, males and females may occasionally share burrows (Swihart 1992), and some evidence suggests that woodchucks may hibernate together, at least in the same burrow system (Ferron 1996). Mothers and their juvenile offspring use the same burrows initially. Juveniles move further from the natal burrow as summer progresses, at times occupy-

ing different burrows than their mothers (Meier 1992; Swihart 1992).

Woodchucks are assumed to be polygynous (Meier 1992; Allainé 2000). However, this conclusion is based largely on studies of spatial overlap of home ranges rather than on behavioral observations or genetic analyses, and future work is needed to confirm the mating system.

The study population was located at Gilsland Farm Sanctuary in Falmouth, Maine (43°42' N, 70°14' W). This 24-ha wildlife preserve is surrounded by the Presumpscot River estuary, U.S. Rt. 1, and housing subdivisions. Woodchucks hibernate in mixed hardwood-coniferous forest that borders three large (6, 3.5, and 2.5 ha) meadows, which woodchucks use after snowmelt when burrows no longer are flooded. They also occupy areas around the Maine Audubon Society's administrative buildings and an adjacent apple orchard. Topography includes gently rolling hills with sandy soils, and elevation ranges from 0 to 10 m. Vegetation increases in height as the growing season progresses, which precludes observations in some parts of the study site. However, in mid to late summer, plants overgrow each other such that their weight reduces vegetation height. Furthermore, property managers commence mowing some of the meadows in late summer, improving visibility.

Since 2002, population density averaged 1.7 animals/ha and remained relatively stable over time (C. Maher, unpublished data). Based on total counts, population size was 30–35 adults and yearlings, and juveniles increased the population by 30–45 animals each summer when they first emerged. Sex ratios for adults and yearlings were nearly 1:1 (C. Maher, unpublished data).

Field methods

Field assistants and I commenced trapping woodchucks when animals first emerged each spring. During daylight hours, we captured woodchucks in Tomahawk live traps (Tomahawk Live Trap, Tomahawk, WI, USA; 81×25×30 cm) baited with peanut butter and fresh apples, which we monitored hourly. Each animal was transferred to a cloth handling bag and subsequently weighed (adults to the nearest 0.25 kg, juveniles to the nearest 0.05 kg) using a Pesola spring scale, then sexed using anogenital distance, descended testes (males in spring only), or distended nipples indicating lactation (females in summer only). Juveniles were readily distinguishable by size and weight, being smaller and lighter than adults throughout the first summer (Maher 2006). To obtain DNA, I wore vinyl gloves and pulled approximately 75–100 hairs from the woodchuck's hindquarters, placing hairs in a self-sealing paper envelope. Hair samples were stored in the lab until they were processed, and storage time averaged 3 years. I

applied a unique dye mark to the animal's back and hindquarters, using hair dye (Clairol Balsam Color, Clairol, Stamford, CT, USA) and a small artist's brush. Such marks remained until the animals molted in summer, at which point we attempted to recapture them to reapply marks. Finally, I attached numbered, metal ear tags (National Band and Tag Company, Newport, KY, USA, Size 3) in each ear and then released the animal at its capture location. A subset of juveniles (one in 2002, six in 2005, six in 2006) received implanted radiotransmitters (Telonics, Mesa, AZ, USA, IMP-300 L) equipped with a mortality-motion sensor. Surgical procedures followed Van Vuren (1989).

Spatial patterns

In this paper, I used data gathered during March 2002–October 2006 and restricted home range analyses to adults and yearlings, excluding juveniles because they typically shared their mothers' home ranges during the first summer or disappeared, at which point I often did not know if they died or dispersed (see below). During that time, my assistants and I logged over 4,200 person-hours in the field. To obtain data on animals' locations, we patrolled the property in search of animals active aboveground. We followed a haphazard schedule and walked the entire property at least once daily. Typically, we censused most areas three to six times within a 6-h period although the frequency of surveys depended upon the number of woodchucks seen and the number of focal samples recorded. Upon sighting an animal, we determined its identity using dye marks, color patterns (some animals were melanistic), and unique markings such as scars. We then noted its location with respect to the nearest burrow for which we had previously obtained Global Positioning System (GPS) coordinates within 0.1 m using Trimble GeoExplorer handheld GPS units (Trimble Navigation, Sunnyvale, CA, USA). Once the animal moved belowground or away from the area, we measured distance from its initial location to the burrow, to the nearest 1 m. We also used a LA12-Q portable receiver (AVM Instrument, Colfax, CA, USA) and H antenna (Telonics) to radiotrack woodchucks 1–5 days/week until transmitters shut down over winter to conserve battery life or the battery died. To maintain statistical independence of locations, we took positions >8 h apart (Swihart et al. 1988), and we obtained an average of 32 positions per animal. All locations were recorded using UTM coordinates.

I calculated home range areas with Animal Movement Extension (Hooge and Eichenlaub 1997) in ArcView 3.3 (ESRI, Redlands, CA, USA), using the fixed kernel method to obtain 95% and 50% utilization distributions (Worton 1989). To calculate spatial proximity, I used ArcGIS 9.1 (ESRI) to determine the geographic center of each animal's

95% home range. I then used ArcGIS 9.1 to calculate distance between geographic centers for each pair of animals present each year. To measure amount of home range overlap, I used the Intersect tool in ArcGIS 9.1 to overlay 95% and 50% (core) home ranges for pairs of woodchucks present each year. I then used Calculate Area to measure the area of overlap. I only included animals that were likely to use the same area, i.e., they were present at the same time. Furthermore, I compared dyads that coexisted during the entire season, e.g., I did not include yearlings that disappeared early in the season and thus may have dispersed. In Microsoft Excel, I calculated percentage of overlap for each pair of home ranges by dividing the area of overlap by each animal's home range area. Thus, for each pair of animals, I obtained two values since amount of overlap may differ depending on the size of their home ranges (e.g., a male may have a larger home range than a female, so his percentage of overlap with a female could be lower than her overlap with his home range). To obtain one value for each dyad, I calculated a coefficient of overlap (Cole 1949; Wronski and Apio 2006): $2(\text{overlap}_{12})(\text{Area}_1)/(\text{Area}_1 + \text{Area}_2)$, where overlap is the proportion of overlap between the dyad, and area is each animal's home range size. Nearest neighbor distances were determined by examining the distance to the centers of 95% home ranges for a woodchuck's four closest neighbors.

Genetic relationships

I extracted genomic DNA from ten hairs per individual using the Chelex-100 method (Walsh et al. 1991; Richlen and Barber 2005). Some animals, especially adults, were repeatedly trapped in successive years, and I processed the most recent hair sample. Extractions remained frozen at -20°C and were used within 3 months of being processed. All extracts amplified successfully for the loci used.

Microsatellites are short tandem repeats of one to five nucleotides, dispersed randomly throughout the genome (Goossens et al. 1996). Microsatellite DNA is the preferred genetic marker used in field studies of relatedness, partly due to high mutation rates and patterns of Mendelian inheritance (Hughes 1998). Seven microsatellite loci amplified consistently, could be scored reliably, and exhibited variation in woodchucks: *BIBL-1*, *BIBL-4*, *BIBL-18*, *BIBL-25* isolated from alpine marmots (Goossens et al. 1998), *MS41*, *MS47* also from alpine marmots (Hanslik and Kruckenhauser 2000; da Silva et al. 2003), and *GS22* isolated from Columbian ground squirrels, *Spermophilus columbianus* (Stevens et al. 1997). I amplified DNA in a $25\ \mu\text{l}$ reaction mixture containing $0.5\ \mu\text{M}$ of each primer, $200\ \mu\text{M}$ dNTPs, $100\ \mu\text{M}$ fluorescent dNTPs, $1\times$ Taq buffer, $2.5\ \text{mM}$ MgCl_2 , $5\ \text{ng}$ BSA, and $0.5\ \text{U}$ DyNAzyme EXT Taq polymerase (New England Biolabs, Ipswich, MA,

USA). I used a programmable thermal cycler (PTC-100 Peltier Thermal Cycler or PTC-200, MJ Research, Waltham, MA, USA) under the following conditions: for *BIBL-1*, *BIBL-4*, and *BIBL-25*: initial denaturation at 94°C for 2 min, then a stepdown protocol with denaturation at 94°C for 30 s, annealing at $60\text{--}55^{\circ}\text{C}$ for 20 s in -0.5° increments followed by extension at 72°C for 30 s, then 30 cycles of denaturation at 94°C for 30 s, annealing at 56°C for 20 s, and extension at 72°C for 30 s, and concluding with a final extension at 72°C for 15 min. For *BIBL-18*, I modified the program such that I ran 25 cycles at an annealing temperature of 56.5°C . For *GS22*, I used the following program: denaturation at 92°C for 2 min, a stepdown protocol of denaturation at 92°C for 30 s, annealing at $65\text{--}55^{\circ}\text{C}$ in -1.0°C increments for 20 s, and extension at 72°C for 30 s, followed by 30 cycles of denaturation at 92°C for 30 s, annealing at 57.5°C for 20 s, and extension at 72°C for 30 s, with a final extension at 72°C for 15 min. For *MS47*, I modified the previous program, using a range of annealing temperatures of $60\text{--}50^{\circ}\text{C}$ and a lower annealing temperature of 49°C for 30 cycles. For *MS41*, I further modified the *MS47* program, using an annealing temperature of 50°C for 25 cycles.

I verified PCR amplification by examining samples on agarose gels. Samples were analyzed at the University of Maine DNA Sequencing Facility, where they were run on an ABI 3730 capillary sequencer (Applied Biosystems, Foster City, CA, USA). I used GENEMAPPER 4.0 software (Applied Biosystems) to determine allele sizes.

Allelic dropout may occur when researchers sample DNA noninvasively (Broquet and Petit 2004). I retyped 36 homozygous samples and calculated a dropout frequency of 0.0101 (Broquet and Petit 2004).

I examined loci for departures from Hardy–Weinberg equilibrium and for linkage disequilibrium between locus pairs using the web version of GENEPOP (Raymond and Rousset 1995), and the probability of null alleles was estimated using CERVUS 3.0 (Kalinowski et al. 2007). Estimates of genetic relatedness can be calculated in several ways, and each method has advantages and disadvantages with no single estimator outperforming others (Van de Castele et al. 2001; Csillery et al. 2006). I chose the most widely used genetic estimator (van Horn et al. 2008), *R*, a regression-based estimator developed by Queller and Goodnight (1989), to estimate genetic relatedness between woodchuck pairs, and I used RELATEDNESS 5.0 to calculate these values. This software uses allele frequencies in the population and each animal's genotype to calculate a coefficient that measures the degree to which two individuals share alleles by descent (Queller and Goodnight 1989). Relatedness estimates range from -1 to 1 . Positive values indicate that two individuals are more related than expected by chance, i.e., they share more alleles that are identical by

descent, whereas negative values indicate that pairs of animals are less related than expected by chance (Kitchen et al. 2005). Relatedness values are estimates and can be quite variable (Queller and Goodnight 1989; van Horn et al. 2008); nevertheless, the expected value for full siblings or mother–offspring is 0.5, and this value should lie within a distribution that has a mean of 0.5 if the population is in Hardy–Weinberg equilibrium (Moyer et al. 2006). Because I observed this population for many years, I could verify all mother–offspring and grandmother–grandoffspring estimates using pedigrees (van Horn et al. 2008).

Statistical analyses

For spatial data, I calculated spatial proximity and home range overlap for each pair of animals each year. Because some pairs were present in multiple years, I then calculated a mean value for those pairs. I used the Mantel Z test (Mantel 1967) to compare matrices of genetic relatedness and geographic distance or coefficients of overlap. I ran 9,999 random permutations of the matrices, and significance was determined by comparing the distribution of these Z statistics to the observed value (Burton and Krebs 2003).

To further examine patterns between genetic and geographic distances in males and females, I performed spatial autocorrelation analyses in GENALEX 6.1 (Peakall and Smouse 2006). ArcGIS 9.1 calculated the geographic centers of each animal's 95% home range. GENALEX software then determined genetic and geographic distances for each pair of animals and calculated an autocorrelation coefficient (r) for each distance interval specified. I initially examined the data at distances of 10–250 m. I presented results using 25-m intervals because this distance provided sufficient sample sizes in each category without losing the ability to detect genetic structure (Peakall et al. 2003; Walker et al. 2008b). To test for statistical significance, the software ran 999 permutations to generate probabilities of randomly obtaining a value \geq observed r . If $p \leq 0.05$, then the null hypothesis of no spatial genetic structure can be rejected (Peakall et al. 2003). GENALEX also ran 1,000 bootstraps to generate 95% confidence intervals. If the confidence interval does not include 0, then again, the null hypothesis of no spatial genetic structure can be rejected (Peakall et al. 2003). Bootstrap tests are considered more conservative because bootstrap errors can be larger than permutational errors at small sample sizes, such that we cannot reject the null hypothesis (Peakall et al. 2003). Bootstrap testing was used to determine if r values differed between males and females; nonoverlapping error bars indicate statistical significance (Peakall et al. 2003).

To determine if dispersal was sex-biased, I conducted genetic assignment tests using the frequencies-based method

(Paetkau et al. 1995) in GENECLASS2 (Piry et al. 2004). The program used Monte Carlo resampling methods (Paetkau et al. 2004) to calculate the probability that an individual originated from the population in which it was sampled, comparing likelihoods to a simulated population of 10,000 individuals. I tested for a sex bias in assignment probabilities by running 10,000 permutations in RESAMPLING STATS 3.

Throughout the paper, I reported means \pm SE. Additional parametric and nonparametric statistics were performed in JMP 5.1 (SAS Institute 2004), and significance levels were $\alpha < 0.05$.

Results

Microsatellite DNA analyses

Among the seven loci, variation ranged from two to seven alleles per locus, $H_O = 0.24–0.84$ and $H_E = 0.48–0.80$, with a mean of 0.58 (Table 1). After sequential Bonferroni correction for multiple comparisons, no loci consistently departed significantly from Hardy–Weinberg equilibrium across all years ($p > 0.002$). One locus, *BIBL-25*, deviated in some years, but not all. One explanation for such departures is null alleles. Based on behavioral observations, I knew mother–offspring relationships, and thus, I compared genotypes of all known mother–offspring pairs (83 pairs from 30 litters) but detected no evidence of null alleles at these loci. CERVUS also indicated a low probability (-0.2077) of null alleles at this locus. Furthermore, behavioral observations indicated that many animals in the population were related (e.g., uncle–niece), and inbreeding also could lead to departures from Hardy–Weinberg equilibrium (Hartl and Clark 1997; Cutrera et al. 2005). Inbreeding should lead to deviations among multiple loci (Cutrera et al. 2005), but most loci did not depart from Hardy–Weinberg equilibrium. For these reasons, I included data from all seven loci across all years in the analyses.

Table 1 Characteristics of microsatellite loci used to estimate relatedness in woodchucks

Locus	No. of alleles	Size range (bp)	H_O	H_E
BIBL-1	3	95–103	0.61	0.48
BIBL-4	5	176–184	0.35	0.54
BIBL-18	4	131–137	0.60	0.60
BIBL-25	6	135–149	0.24	0.48
MS41	5	177–197	0.74	0.70
MS47	7	168–190	0.84	0.80
GS22	2	163–167	0.56	0.50

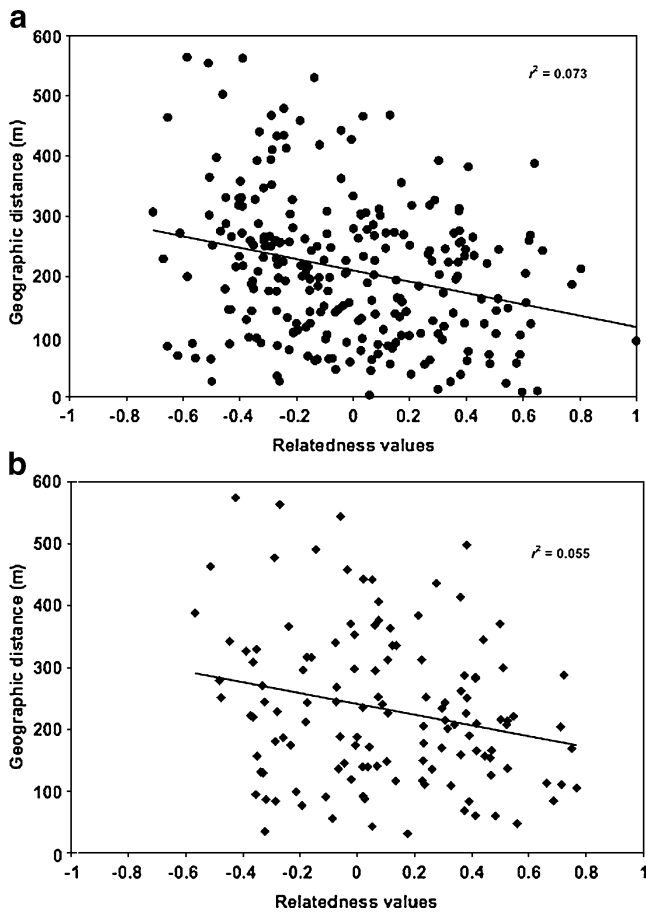


Fig. 1 Relationship between geographic distance and kinship in woodchucks for **a** female–female and **b** male–male pairs analyzed separately

Mean relatedness, R , for all known mother–offspring pairs was 0.38 ± 0.027 ($N=66$ pairs), which was significantly lower than the expected average of 0.5 if the population was in Hardy–Weinberg equilibrium ($t_{65}=-4.33$, $p<0.0001$) (Girman et al. 1997; Kays et al. 2000). The mean relatedness estimate between mother–offspring pairs was significantly higher than the mean relatedness estimate for randomly selected pairs in the population (0.045 ± 0.05 ; $t_{68.8}=5.22$, $p<0.0001$). Some relatedness values may be underestimated in this population, perhaps due to higher than expected numbers of close relatives (Kays et al. 2000). Although relatedness estimates may be lower than predicted, they still can be useful for examining relatedness when comparing individuals within the same population (de Ruiter and Geffen 1998). Furthermore, any patterns based on kinship represent conservative results.

Geographic distance and relatedness

For both sexes combined, geographic distance was negatively related to kinship, i.e., more closely related animals lived closer to each other (Mantel $Z=332,668$, $\rho=-0.20$, $p=0.0001$,

$N=1128$ pairwise comparisons). Furthermore, when I analyzed each sex separately, female kin lived closer to each other (Mantel $Z=223,632$, $\rho=-0.26$, $p<0.0001$, $N=351$ pairwise comparisons; Fig. 1a), as did male kin (Mantel $Z=448,862$, $\rho=-0.20$, $p=0.0002$, $N=253$ pairwise comparisons; Fig. 1b).

Results from spatial autocorrelation analyses indicated significant positive autocorrelation for females only at 25 m ($p=0.014$); values were not significant at greater distances (Fig. 2a). Males showed significant positive spatial relationships at 100 m ($p=0.044$), but the value at 175 m was statistically not significant ($p=0.063$; Fig. 2b). Males and females did not differ significantly from each other at any distance, as indicated by overlapping bootstrap error bars.

Home range overlap and relatedness

On average, females shared $5.2 \pm 0.86\%$ of their larger (95%) home ranges and $1.47 \pm 0.35\%$ of their core (50%)

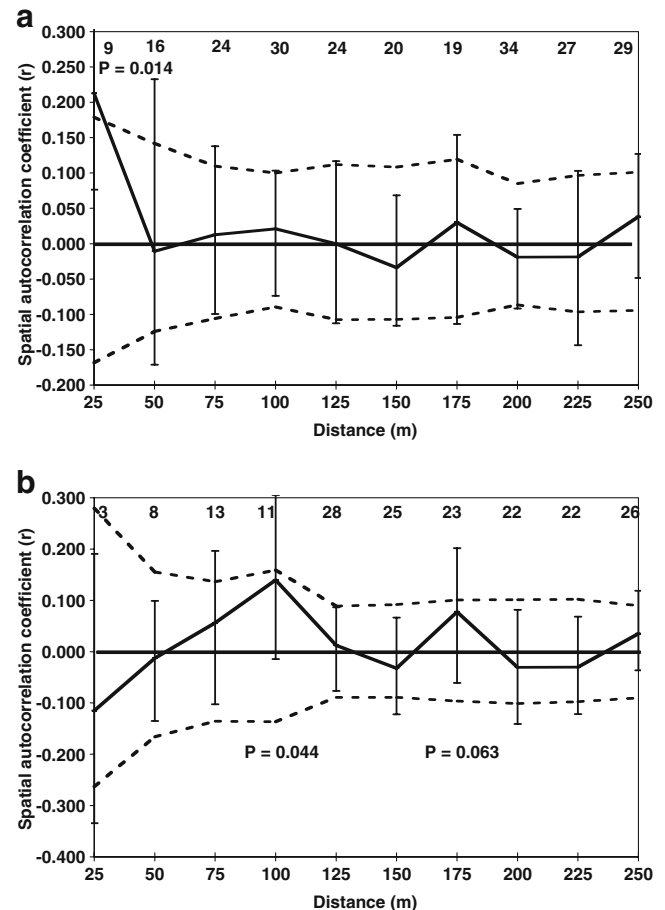


Fig. 2 Correlograms indicating spatial correlations (r) for microsatellite markers and geographic distance for woodchuck **a** females and **b** males. Sample sizes for each distance class are indicated at the top of each graph. Dashed lines delineate 95% permuted confidence intervals about the null hypothesis of no genetic structure, error bars represent bootstrapped 95% confidence intervals about r , and p values represent results from 999 permutations

ranges with other females ($N=26$ females). Males shared $13.9\pm 1.93\%$ of their larger home ranges and $2.79\pm 0.68\%$ of their core ranges with other males ($N=22$ males). Intrasexual overlap of 95% home ranges was significantly higher for males than females ($t_{29,2}=-4.11$, $p=0.0003$); however, intrasexual overlap did not differ by sex for core ranges ($t_{31,6}=-1.73$, $p=0.093$). Female–male overlap averaged $18.56\pm 1.74\%$ of 95% home ranges and $5.66\pm 0.92\%$ of core home ranges, whereas male–female overlap averaged $4.89\pm 0.88\%$ of larger home ranges and $1.80\pm 0.50\%$ of core ranges. Intersexual overlap was significantly higher for females than males for both 95% and 50% home ranges (95%: $t_{36,5}=6.99$, $p<0.0001$; 50%: $t_{37,9}=3.68$, $p=0.0007$).

For all dyads combined, the amount of home range overlap increased with increasing relatedness, for both 95% ranges (Mantel $Z=406,187,364$, $\rho=0.18$, $p=0.0001$, $N=1125$ pairwise comparisons) and 50% ranges (Mantel $Z=406,187,027$, $\rho=0.10$, $p=0.0001$, $N=1125$ pairwise comparisons). Similarly, females shared greater amounts of their home ranges with more closely related females (95% range: Mantel $Z=91,816,692$, $\rho=0.20$, $p=0.0001$, $N=503$ pairwise comparisons; 50% range: Mantel $Z=91,816,620$, $\rho=0.18$, $p=0.0001$, $N=503$ pairwise comparisons). Males showed significant, but weaker, relationships between amount of overlap and kinship (95% range: Mantel $Z=114,770,233$, $\rho=0.11$, $p=0.0001$, $N=254$ pairwise comparisons; 50% range: Mantel $Z=114,770,138$, $\rho=0.012$, $p=0.0001$, $N=254$ pairwise comparisons). Among intersexual dyads, woodchucks shared more home range overlap with more closely related individuals, but the relationship was stronger for 95% ranges (Mantel $Z=255,236,244$, $\rho=0.13$, $p=0.0001$, $N=368$ pairwise comparisons) than for core ranges (Mantel $Z=256,134,945$, $\rho=0.073$, $p=0.0001$, $N=368$ pairwise comparisons).

Dispersal and philopatry

From 2002 to 2006, I trapped 48 juvenile females and 62 juvenile males. Of those trapped, 54.8% of males and 54.2% of females remained within their natal range through their first season, i.e., they were philopatric. Males and females then differed in the percentages that dispersed or remained philopatric as adults (G test: $G_1^2=9.53$, $p=0.002$). Of the philopatric animals, 35.3% of males subsequently were known to disperse as yearlings, i.e., they moved more than one home range diameter (Maher 2006) from their natal range and were resighted or killed elsewhere, 26.5% remained philopatric as adults, and the fates of 35.3% were unknown. In contrast, only 7.7% of philopatric females were known to disperse as yearlings. Among females that did not disperse after the first year, 65.4% remained philopatric and, as adults, established home ranges within or adjacent to their natal range. Thus, more females became resident than males (Fisher's exact test: $df=1$, $p=0.0023$).

Of these 17 females that became resident, only one first reproduced as a yearling; eight females weaned their first litters as 2 year olds, and three females did not successfully produce young until ages 3, 4, and 5 years, respectively. Fates of 26.9% of philopatric females were unknown after their first hibernation.

Genetic assignment probabilities indicated that most (90.5%) woodchucks could be assigned to the study population. Nonetheless, several animals, including four females and two males, appeared to originate from outside the sampled area. In four cases (three females, one male), the animals lived at the edges of the study site and may have moved from the surrounding neighborhoods. The second male, an adult with distinctively lighter pelage than the resident woodchucks, suddenly appeared in mid-summer and probably was relocated by a homeowner who trapped him and released him on the site. Randomization tests indicated that males and females did not differ in genetic assignment scores, suggesting no sex bias in dispersal (resampling stats, $p=0.50$).

Nearly half of the trapped juveniles disappeared and were never seen again, so their fates were unknown; they may have dispersed or they may have died. To better track movements, I implanted radiotransmitters into 13 juveniles during this period, and only two of those animals, both males, dispersed from their natal ranges as yearlings. One juvenile male died over winter, hibernating at the edge of his natal range. The ten surviving philopatric woodchucks included five females and five males.

As expected, woodchucks that were philopatric moved significantly shorter distances (66.4 ± 10.4 m, $N=23$) from their natal range compared to dispersing animals (559.3 ± 101.6 m, $N=9$; Mann–Whitney test: $Z=4.32$, $p<0.0001$). Furthermore, philopatric animals were more closely related to their nearest neighbors ($r=0.19\pm 0.034$, $N=26$) than dispersers were ($r=-0.026\pm 0.046$, $N=14$; Mann–Whitney test: $Z=-3.36$, $p=0.0008$).

Discussion

Woodchucks in this population lived near kin and overlapped spatially to a greater extent with closer relatives. These general patterns held for both males and females, but the sexes differed to some degree. Female kin showed positive spatial structure at shorter distances of 25 m, whereas male kin showed positive associations at larger distances of 100 m and to some extent at 175 m. Both females and males shared a greater amount of both 95% and core home ranges with more closely related animals, although the relationship was stronger for females. Two processes could explain these results: natal philopatry and settlement in nearby vacant territories (Waser and Jones 1983).

Natal philopatry could produce the kinship patterns observed in this population. Over 50% of juveniles remained in their natal ranges through their first summer. Between 2002 and 2006, no animals were known to disperse before their first hibernation, but these data are biased because numerous juveniles disappeared and may have dispersed or died. Among juveniles that received radiotransmitters, 77% remained philopatric and established territories within or adjacent to their natal ranges. Although these data also are somewhat biased because juveniles had to grow large enough to accommodate implanted transmitters, usually by August, and again, some juveniles may have dispersed before then, they suggest that both sexes are philopatric as juveniles, creating opportunity for the formation of kin clusters. Furthermore, philopatric woodchucks were more closely related to their nearest neighbors compared to dispersing animals. However, females exhibited positive genetic structure at smaller distances of 25 m, whereas males exhibited positive genetic structure at distances of 100 and 175 m.

After their first year, most (65%) philopatric females continued to reside in or near their natal range and thus remained near kin. Among mammals, females tend to disperse shorter distances, if they disperse at all (Greenwood 1980; Waser and Jones 1983); female woodchucks followed this pattern. Although woodchucks display intra-sexual territoriality (Maher 2004), mothers may allow daughters to remain within the natal territory. At least two females chased adult daughters occasionally but did not exclude them from the territory. I did not observe reproduction in these daughters; the exceptions occurred when one mother did not produce a litter, and in that same year, her 5-year-old daughter weaned pups. In a second case, a female's daughter weaned her first surviving litter at age 4 years, when she shifted her home range and did not overlap extensively with her mother. Although these daughters may have produced pups that I never observed, they lived in areas that my field assistants and I observed intensively, so we were unlikely to miss newly emerged juveniles. Such tolerance and range overlap between parents and offspring also occur, as does reproductive suppression, among other solitary species (Waser and Jones 1983). Furthermore, reproductive suppression occurs widely in marmots, regardless of social system (Armitage 1996b; Allainé 2000).

Results indicating that females lived near kin and shared more of their home range with their closer relatives were not surprising since similar patterns have been reported in many species, including less social or solitary species (Vestal and McCarley 1984; van Staaden et al. 1994; Ratnayeke et al. 2002; Kitchen et al. 2005; Støen et al. 2005; Moyer et al. 2006; McEachern et al. 2007). However, finding such patterns among males was more unexpected.

Fewer studies have described males associating with kin although male philopatry and spatial proximity have been reported in greater white-tailed shrews, *Crocidura russula* (Balloux et al. 1998), swift foxes, *Vulpes velox* (Kitchen et al. 2005), raccoons (Ratnayeke et al. 2002), and southern hairy-nosed wombats, *Lasiiorhinus latifrons* (Walker et al. 2008b). In a coastal population of river otters, *Lontra canadensis*, males dispersed shorter distances than females (Blundell et al. 2002). Like females, woodchuck males lived closer to more closely related male kin. Male pairs showed significant positive spatial genetic structure at 100 m, with similar results approaching statistical significance at 175 m. Results at shorter distances were not statistically significant although sample sizes were limited. Since more males dispersed than females, they potentially would settle farther from female kin but could associate with male kin across these greater distances. Indeed, 25% of males remained near their natal home ranges such that they, too, lived near kin. Males also might disperse together and establish territories near each other. I did not observe males dispersing with male relatives. However, I knew of two separate cases, in different years, where a homeowner trapped and killed a brother and sister at the same location within a short period of time, anecdotally suggesting that siblings traveled together. Animal movements provide another explanation for the patterns observed in this population.

Kin may live adjacent to each other not because of natal philopatry but because they settle in the first vacant territory they encounter, which happens to be near the natal range (Waser and Jones 1983; Peacock and Smith 1997; Armitage 2000). The distribution of territories suggests such movements occur in this population. Woodchucks may live several years (Hamilton 1934; Grizzell 1955). In some years, territories become vacant, presumably due to the owner's death, and yearlings born nearby may fill such vacancies. However, the same individual can occupy a territory for several years. Turnover in male and female territories averaged $0.23 \pm 0.029/\text{year}$ and $0.15 \pm 0.034/\text{year}$, respectively. Thus, in any given year, a potential disperser may not encounter a nearby vacant territory. The animal then must decide whether to disperse further or to remain in the natal range.

The decision to disperse or to remain at home represents a complex interplay of costs and benefits associated with each option (Koenig et al. 1992; Solomon 2003; Lacey and Sherman 2007). Certainly, dispersal can be risky. Of woodchucks known to disperse in this population ($N=9$), 67% died from car collisions or homeowners killing them. Philopatry offers some protection although even philopatric animals died from encounters with vehicles or predators. Furthermore, the study site afforded the animals good habitat and abundant food resources in addition to

familiarity with the area, including locations of burrows for refuge (Waser and Jones 1983; Jacquot and Solomon 1997).

Opportunities for successful dispersal may be limited. As a wildlife sanctuary, the study site represents an island of excellent habitat surrounded by a sea of developed suburbia. Furthermore, at a density of 1.7/ha, this woodchuck population falls near the upper end of densities reported in the literature (Maher 2006). Under conditions of habitat saturation, when offspring may be unable to disperse successfully, parents may tolerate kin nearby (Waser and Jones 1983). When southern hairy-nosed wombats experienced habitat fragmentation and higher population densities, females did not disperse as they typically do in other populations, and they preferred to associate with female kin vs. nonkin (Walker et al. 2008a). Similarly, both male and female prairie voles (*Microtus ochrogaster*) became more philopatric under conditions of experimentally higher population density, reflecting greater habitat saturation (Lucia et al. 2008). Food availability in this woodchuck population may reduce competition such that mothers and fathers pay relatively low costs to allowing offspring to remain in the natal range. Indeed, in years with greater food abundance, more juveniles remained philopatric (C. Maher, unpublished data). Some of the highest densities of woodchucks and the area where mothers tolerated their adult daughters occurred in an apple orchard that produced abundant quantities of fruit in most years, a resource that could not be defended effectively but that could be shared (Waser and Jones 1983).

In addition to sharing food resources, such kinship patterns may lead to other positive as well as negative consequences. Woodchucks, like other ground-dwelling sciurids, produce alarm calls that could warn kin of potential predators (Barash 1989). Nonetheless, offspring may pay a cost for being allowed to remain in the form of reproductive suppression. Some woodchucks may disperse to avoid reproductive suppression by either males or females. In yellow-bellied marmots, females face relatively low dispersal costs and have high rates of survival (Van Vuren and Armitage 1994), so by dispersing, they can avoid competition with related females (Armitage 1996b). Among alpine marmots, however, dispersal costs can be

higher (Hacklander et al. 2003) although animals in some populations may have little chance of successfully breeding in their natal range and still disperse (Allainé 2000). Future research could examine the interplay between costs of dispersal and costs of reproductive competition, documenting the extent to which reproductive suppression occurs in woodchucks and how it varies with population density and food resources.

Another possible consequence of living near kin is inbreeding. Male–female pairs shared more home range area when they were more closely related. The extent to which males mate with close relatives will be investigated further; however, anecdotal evidence suggests that uncle–niece matings occur. I also have observed sons courting mothers, brothers courting sisters, and grandsons courting grandmothers although I have not observed copulations, which generally occur below ground. Inbreeding may occur in this population, as it does in other natural populations, with apparently limited consequences (Waser and Jones 1983; Blumstein and Armitage 1999). I did not examine inbreeding depression directly; however, I found little obvious, morphological evidence of inbreeding depression. Over the past 10 years, I have seen two cases of dental malocclusion in yearlings. I have not observed this phenomenon in juveniles, however, and I do not know if these animals were born in the population or emigrated from the surrounding area. Other marmots may breed with close relatives and suffer no apparent ill effects (Blumstein and Armitage 1999) although yellow-bellied marmots showed reduced survival of inbred vs. outbred young (Armitage 2004).

Among the marmots, woodchucks in this population most closely resemble yellow-bellied marmots in their patterns of space use and kinship. Female yellow-bellied marmots share home ranges with related females; most males and 50% of females wait to disperse as yearlings; and females may suppress reproduction in subordinates (Armitage 1999; Blumstein and Armitage 1999). However, unlike yellow-bellied marmots, some woodchuck males in this population remained philopatric as adults. Males and females face different costs and benefits to dispersal and philopatry (Greenwood 1980; Van Vuren and Armitage 1994). Perhaps

Table 2 Summary of statistically significant correlations (r or ρ) between geographic distance and genetic relatedness for solitary species

Species	Correlation	Reference
Raccoon (<i>Procyon lotor</i>)	0.29	Ratnayeke et al. 2002
Brown bear (<i>Ursus arctos</i>)	−0.206	Støen et al. 2005
Black bear (<i>Ursus americanus</i>)	−0.08	Costello et al. 2008
	−0.231 to −0.444	Moyer et al. 2006
Talar tuco-tuco (<i>Ctenomys talarum</i>)	−0.331, −0.692	Cutrerera et al. 2005
Dusky footed woodrat (<i>Neotoma fuscipes</i>)	−0.356	McEachern et al. 2007
Woodchuck (<i>Marmota monax</i>)	−0.20, −0.26	This study

dispersal costs are higher for woodchuck males in this population compared to others, especially given its location in a suburban setting where animals may be killed by vehicles, domestic dogs, and homeowners, and where males may not find vacant territories due to lack of suitable habitat in a housing subdivision. In addition, resource availability at the study site may reduce competition sufficiently that males can remain near kin. Alternatively, turnover among males may open up territories and allow kin to settle near their natal ranges. Among yellow-bellied marmots, territorial males remain resident for 2.39 years (Armitage 2004), whereas in this woodchuck population, the average residency for territorial males was 4.64 ± 0.69 years ($N=11$ males). Females were similar to males, remaining in a territory for 4.73 ± 0.64 years ($N=15$ females), which is also higher than the average residency for yellow-bellied marmots, where females average 3.26 years (Armitage 1986). Therefore, woodchucks, once they establish a territory, retain it longer. In yellow-bellied marmots, vacancies usually occur because of overwinter mortality (Armitage 1991). Yellow-bellied marmots generally occupy less hospitable environments than woodchucks do (Armitage 2000), which could lead to higher turnover rates in territories. In contrast, woodchuck territories are more stable, and males may have fewer opportunities to secure a territory in any given year. Habitat saturation, food availability, and dispersal costs all may contribute to a male's decision to remain closer to the natal range.

To conclude, woodchucks resemble some other solitary species in that kin, particularly females, live near each other (Table 2), and they share more home range area. Such proximity creates the potential for increased tolerance and higher rates of amicable interactions although it also may increase competition among kin, and future work will examine interactions among kin. Thus, some solitary species provide evidence for relationships between kinship and spatial patterns, supporting some models of mammalian social evolution (Armitage 1981; Michener 1983; Waser and Jones 1983). Under different ecological conditions, however, social organization may vary (Lott 1991). Woodchucks in this population, characterized by relatively high population density, abundant resources, and high dispersal costs, associated with kin. Yet, different ecological conditions can alter the costs and benefits of dispersal and philopatry (Koenig et al. 1992), and solitary species, including woodchucks, may display behavioral flexibility that leads to different types of social organization (Ratnayeke et al. 2002; Maher 2006; McEachern et al. 2007). Historically overlooked, researchers increasingly are turning their attention to solitary species for insights into the evolution of social behavior. So far, many such species are offering up such insights, particularly into the early stages of sociality where kin associate spatially.

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