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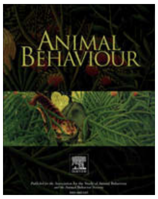

Another genetically promiscuous ‘polygynous’ mammal: mating system variation in *Neotoma fuscipes*

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Polygyny is widely thought to be the dominant mating system in mammals. However, more recent genetic work casts doubt on this view. Variation in mating systems has been found in both males and females within and across mammalian species. The causes and consequences of mating system variation have important implications for understanding the population and evolutionary dynamics of species. To better understand mating system variation, both in mammals and more generally, this study analyses genetic mating system variation in dusky-footed woodrats, *Neotoma fuscipes*. Contrary to expectation, there was little support for polygyny at the genetic level. Instead, the study populations were characterized by promiscuity and monogamy, in both males and females. At higher densities, variance in the numbers of mates and offspring were higher in breeding males than in females, as is often observed. However, this trend was reversed in low-density, coniferous forest habitat. Model selection revealed that the best model of successfully mated pairs includes population density, operational sex ratio and individual pairwise distances as predictors. Higher densities coupled with male-biased sex ratios appear to decrease the probability of mating and decrease opportunities for polygamy, particularly in females. Although woodrats display sexual size dimorphism, male body size had no detectable effect on mating success. This study questions the prevalence of polygyny in mammals and demonstrates the need for more detailed, genetic investigations of mating systems. Future studies are needed to explore the complex interactions among mating system determinants and test hypotheses of sex-specific mating system variation.

Patterns of mating influence the amount of genetic variation, strength of sexual selection and overall rate of evolution in populations (Wright 1951; Bush et al. 1977; Emlen & Oring 1977; Bessa-Gomes et al. 2004). One evolutionarily important contrast is the distinction between polygyny and promiscuity. Polygyny, a mating system in which single males monopolize and exclusively mate with multiple females, has very different population genetic consequences than a promiscuous mating system, defined as a mating system in which both males and females mate nonexclusively with multiple partners in a breeding season. A strictly polygynous mating system increases genetic relatedness within groups, reduces the effective population size (N_e), and increases genetic differentiation among groups relative to monogamous or promiscuous mating systems. These differences have important implications for our understanding of how mating system variation influences population viability and evolution via kin and sexual selection (Sugg et al. 1996; Parker & Waite 1997).

Given its evolutionary importance, the empirical literature on mating system variation (MSV) is highly incomplete. Observational studies of mating systems have often focused on males (Clutton-Brock 1989; Shuster & Wade 2003), in particular, their ability to monopolize and control access to multiple resources and mates under variable environmental conditions. While such studies have significantly advanced our understanding of mating systems, revealing their inherent flexibility both temporally and spatially, within and among species, there is a relative lack of data from cryptic, solitary mammals that are difficult to study observationally. In addition, the female perspective has often been overshadowed by a male-dominated focus, resulting in a relative paucity of information on the determinants of female MSV and mating success (Clutton-Brock 1989; Wolff & Macdonald 2004).

Despite these gaps in knowledge, the idea that polygyny is the predominant mating system in mammals continues to pervade the literature (Krebs & Davies 1993; Birkhead 2000; Storz et al. 2001; Eberle & Kappeler 2004). It remains unclear whether this idea will

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hold once females are fully integrated into mating system theory and a more complete inventory of species is considered. Clutton-Brock (1989) noted the lack of data on females and on solitary mammals, which make up a large portion of mammalian species. Cryptic, solitary females may be more difficult to monopolize than social gregarious ones, and recent studies have pointed out the ways in which females, solitary or gregarious, can benefit from mating with multiple partners (Soltis & McElreath 2001; Wolff & Macdonald 2004). Thus, a more thorough investigation of mating systems with detailed genetic data on both male and female mating success could reveal that promiscuity is more common in mammals than previously thought. Indeed, behavioural ecologists studying solitary rodents have long suspected that promiscuity characterizes the mating systems of their subjects (Waterman 2007), but the genetic evidence to support this claim has been sparse. More evidence is mounting, however, with a recent review suggesting that promiscuous mating in mammals is quite common, occurring in 133 species, 33 families and 9 orders (Wolff & Macdonald 2004).

To generate a better understanding of MSV in females and the extent to which polygyny characterizes mammalian mating systems, we used spatial and genetic data to investigate male and female mating behaviour in the dusky-footed woodrat, *Neotoma fuscipes*. Dusky-footed woodrats are solitary, nocturnal rodents (200–350 g) that build conspicuous stick houses in the coastal and mountainous regions of northern California. Male-biased dispersal coupled with spatial clusters of related females, or matrilines, are thought to generate a predominantly polygynous mating system in the genus *Neotoma* (Kelly 1989). However, monogamy, promiscuity and polyandry have been reported anecdotally (Linsdale & Tevis 1951; Kelly 1989). Observational studies of woodrats suggest that females tend to mate with spatially proximate males that overlap in home range. However, the extent to which observational studies reliably predict MSV in *N. fuscipes* has not been verified with genetic data.

To test for ecological and demographic correlates of MSV in woodrats, we studied woodrats in three distinct habitats that supported different spatial distributions, densities and sex ratios. Specifically, we examined the degree to which differences in these variables affect the number of mates with which individuals successfully breed, from both the male and female perspectives. Using a maximum likelihood model selection approach and following Emlen & Oring's (1977) ecological framework, we tested the general prediction that clumped spatial distributions, increased population densities and biased sex ratios increase frequencies of polygamous matings (polygyny, promiscuity, polyandry). We also examined the extent to which body mass, often considered an important determinant of male mating success because of its influence on intrasexual competition and sexual selection (Ribble 1992; Solomon 1993; Eberle & Kappeler 2004), predicted mated pairs.

METHODS

Operational Definitions

The extreme flexibility of mating systems both within and among species has generated varied definitions of mating systems. To avoid confusion, we provide operational definitions of the mating system terms we apply to dusky-footed woodrats in this study. Our definitions are based on the number of mating partners per male and female per breeding season, and are generally consistent with the definitions proposed by Krebs & Davies (1993).

Mating

We classified mated pairs based on the production of viable offspring, detected by live trapping and parentage confirmed with genetic data. Individuals that may have copulated but did not successfully produce viable offspring were classified as nonbreeders having zero mates.

Genetic mating system

Characterization of the mating system based on molecular analysis of parentage of offspring representing successful fertilization.

Social mating system

Characterization of the mating system based on observations of spatial relationships (e.g. home range overlap) among males and females during the breeding season, and during courtship and copulations.

Polygyny

Males monopolize and exclusively mate with multiple females. Females mate with only one male.

Polyandry

Females monopolize and exclusively mate with multiple males. Males mate with only one female.

Promiscuity

Members of both sex mate nonexclusively with multiple partners during a breeding season, without the formation of stable pair bonds. Our use of the term promiscuity does not assume random mating or lack of mate choice.

Monogamy

A single male and a single female mate exclusively during a breeding season. In woodrats, monogamy does not involve stable pair bonds or paternal care.

Polygamy

A general term for any mating system that involves either sex mating with multiple partners (e.g. polygyny, polyandry, polygynandry, promiscuity).

Study Populations

Two populations of dusky-footed woodrats from three habitats in northern California were studied June 1999 through September 2002. The primary study area was located on the northeastern shore of Eagle Lake in Lassen County, California, U.S.A. (40°37′N, 120°43′W) and spanned two habitat types, mixed-coniferous forest and juniper woodland. In 2002, an additional study site was established at the Quail Ridge Reserve in Napa County, California (38°29′N, 122°9′W) in oak woodland habitat. See McEachern et al. (2006, 2007) for more detailed descriptions of the study areas and plant communities in each habitat.

Spatial Dynamics

Woodrat houses within each study area were located, marked with metal tagging, and mapped using a Trimble GPS unit (Trimble Navigation Ltd, Sunnyvale, CA, U.S.A.). Houses were inspected each year for signs of woodrat occupancy (e.g. fresh plant clippings, fresh droppings, lack of spider webs and debris blocking entryways). Regardless of occupancy status, all woodrat houses were live-trapped June–October 1999, May–October 2000, April–September 2001, and May–August 2002 at Eagle Lake and January–August 2002 at Quail Ridge. One to two extra-long Sherman traps baited with oats were set outside each house over the course of multiple trapping sessions. Trapping sessions ranged in length from 2–6 nights, depending on weather conditions. Each house was live-trapped during at least two trapping sessions for a total of 6–10 trap nights per year per house. Time between consecutive trapping sessions at a given house ranged from 4–8 weeks. Captured individuals were transferred to a canvas handling bag, then marked with numbered metal eartags, weighed, sexed and released at their point of capture. Small snips of ear tissue were collected from all newly captured individuals and stored at −20 °C for subsequent genetic analyses. Our methods were approved under University of California Davis IACUC animal care protocol 9095. Live trapping was approved by the California Department of Fish and Game under permit number SC-004206.

Weighted-average locations for all woodrats in a given year were calculated in metres using house UTM (Universal Transverse Mercator) coordinates, with averages weighted by the number of captures per trap location. Nearest potential mate (NPM) distance, defined as the distance to the nearest opposite-sex adult, was calculated using standard Euclidean distances between all adult woodrats within the same subpopulation and year. Spatial and demographic data were used to calculate population density, defined as the number of woodrats per hectare, and the operational sex ratio (OSR), expressed as the proportion of adult males in the adult population in a given year and habitat.

Genetic and Parentage Analyses

Ten microsatellite loci were used to analyse parentage of detected offspring. Details on extraction method, microsatellite primer sequences and PCR conditions are reported in McEachern et al. (2007). PCR products were run on manual 5.5% polyacrylamide gels, scanned in a Molecular Dynamics FluorImager 595 (Amersham Biosciences, Inc., Sunnyvale, CA, U.S.A.: www.amershambiosciences.com) and visualized using ImageQuant 5.2 software (Amersham Biosciences, Inc.). A portion of samples was analysed multiple times on different gels to confirm allele scores. This portion ranged from 20–98% (mean 60%) of the samples, depending on the variability of the locus. The programs FSTAT 2.9.2 (Goudet 1995) and GENEPOP 3.4 (Rousset & Raymond 1995) were used to calculate allele frequencies and test for Hardy–Weinberg equilibrium and linkage disequilibrium.

To reconstruct mating relationships in woodrats, parentage analysis was conducted using CERVUS 2.0 (Marshall et al. 1998). This program uses a maximum likelihood approach to assign the most-likely parents to offspring given the allele frequencies of the reference population. Critical values of delta, a measure of the difference in maximum likelihoods between alternative models, were estimated at 80% confidence levels. Simulations consisted of 1000 iterations and assumed a 1% typing error rate. The number of candidate parents in each simulation varied by year and habitat (Table 1). All adult individuals within a given year and habitat were included in the pool of candidate parents. Candidate mothers were evaluated first and the results cross-checked with trap data; in many cases juveniles were caught at the same time and location as adult females, indicating a probable mother–offspring pair. Candidate fathers were then evaluated assuming a known mother. In cases where paternity remained unresolved at Eagle Lake, we expanded the pool of candidate fathers to include adult males from both habitats and males from the previous year (since breeding can begin as early as January or February).

Table 1
Numbers of offspring and candidate parents included in parentage analysis of woodrats by year and habitat at Eagle Lake and Quail Ridge, California, U.S.A.

Habitat	Year	Offspring	Candidate mothers	Candidate fathers	Mean PIC
Coniferous forest (EL)	2000	10	5	10	0.644
	2001	5	2	3	0.636
Juniper woodland (EL)	1999	9	14	12	0.572
	2000	16	13	14	0.644
	2001	7	12	7	0.636
	2002	10	4	13	0.623
Oak woodland (QR)	2002	17	20	11	0.752

PIC refers to the polymorphic information content of the 10 microsatellite loci (averaged over all loci).

Model Selection

To statistically evaluate predictors of genetic mating system variation and reproductive success in woodrats, we used a model selection approach whereby the maximum log-likelihoods of alternative models and their associated hypotheses were simultaneously compared (Burnham & Anderson 2002). The relative support for each model was evaluated using the Akaike information criterion corrected for small sample size ($\mathrm{AIC_c}$), defined as:

$$\mathrm{AIC_c} = -2\log\mathcal{L} + 2\frac{pn}{n-p-1},$$

where $\log\mathcal{L}$ is the log-likelihood of the maximum likelihood fit model, p is the number of parameters and n is the sample size (Burnham & Anderson 2002). The minimum $\mathrm{AIC_c}$ score represents the best fit to the observed data taking into account model complexity, but the absolute difference in scores contains information, in addition to the rank order. Therefore, we also calculated Akaike weights, w_i for each model i, which estimate the probability that a given model is the best model within a given set of alternatives (Burnham & Anderson 2002). The weight of any model x is given by:

$$w_x = \frac{\exp(-\frac{1}{2}\Delta_x)}{\sum_j \exp(-\frac{1}{2}\Delta_j)},$$

where $\varDelta_x = \mathrm{AIC}_x - \mathrm{AIC_{min}}$, the difference between the AIC of model x and the smallest AIC in the set of compared models. For the best-fitting model with the smallest AIC, $\varDelta = 0$. These weights are numbers between zero and one that estimate the relative likelihoods of each model being the best model in the set. These relative weights can be read as weights of evidence in support of each model. Unlike the common alternative Bayesian information criterion (BIC), AIC does not assume that the true model is present in the set of considered models. It instead attempts to estimate the model that comes closest to the truth (Shao 1997).

Alternative models were fit to the observed data using R's glm command (2008, R Development Core Team, The R Foundation for Statistical Computing, Vienna, Austria). All models assumed binomial outcome distributions, following the logic that opposite-sex interactions can result in one of two possible outcomes: successful mating or no successful mating. Each row of observed data corresponded to a putative female–male pair. All possible pairs in a given habitat and year were included in the analysis. Males and females not in the same habitat were not considered, and it turns out that no pairings between individuals from different habitats were found in the data. This resulted in 539 pairings to analyse.

We then used other variables to predict which pairs within a habitat actually mated. Therefore, the models were multiple logistic regressions with observed mating for a given pair being the 0/1 dependent variable. Habitat population density, habitat operational sex ratio (OSR, calculated as the proportion of adult males in the total adult population), pairwise Euclidean distances between the female and male, and male body mass (as a proxy of male competitive ability) were included as predictor variables predicting successfully mated pairs.

Model Hypotheses

By constructing models containing these factors, we were able to evaluate five general hypotheses: (1) mating is random and none of these factors predicts mated pairs, (2) mating is influenced by density, (3) mating is influenced by operational sex ratio, (4) mating is influenced by pairwise distance, (5) mating is influenced by male body mass. To accommodate the possibility that any one of these factors could mask the effects of another, our analysis included the possibility that these predictor variables work together and interact in nonadditive ways. For example, pairwise distance may interact with any effects of competition, such that large males obtain matings over large distances whereas small males do not. A large number of different interaction effects are plausible a priori, and we know of no consensus in the literature to help us narrow them down. Thus we considered all plausible combinations of interaction terms, generating a total of 19 alternative, nested models. Our aim was to test the five hypotheses above by seeing which of the four single factors appear repeatedly in high-ranking models, and explore the nature of interactions among factors. If no interaction terms reoccur across high-ranking models, we can conclude that additional measurement and modelling will be needed to verify them. If instead one or more interaction terms reoccur in the best models, we can conclude that these dependent relationships were important in our populations.

RESULTS

Spatial Dynamics

In all, 156 woodrats (107 Eagle Lake and 49 Quail Ridge) were live-trapped over the course of the study. This number is a good estimate of the actual number of woodrats present at each study site based on inspections of woodrat houses; locations where woodrats were not caught showed no signs of house occupancy. In contrast, houses with obvious signs of use (e.g. fresh plant clippings and fresh faecal pellets) yielded consistent captures. There was no indication that woodrats avoided live-traps, as most individuals were captured multiple times, often at the same location.

Densities of woodrats varied both by habitat and by year (Table 2), with very low densities at Eagle Lake compared to Quail Ridge and other previously studied woodrat populations showing densities as high as 22 woodrats/ha (Lynch et al. 1994; Vreeland & Tietje 1999). Within the Eagle Lake population, juniper woodland habitat supported higher densities of woodrats than coniferous forest habitat. However, in both habitats, densities declined considerably over the course of the study.

Nearest potential mate (NPM) distances also differed between habitats. Mean NPM distances were smallest in oak woodland (high density), largest in coniferous forest (low density) and intermediate in juniper woodland (low–intermediate density). Significant differences were detected between habitats and years ($F_{6,72} = 6.68$, $P < 0.0001$; Table 2).

Table 2
Habitat types and associated woodrat densities (individuals/hectare), mean nearest potential mate distances (NPM, expressed in metres with standard errors in parentheses) and operational sex ratios (OSR, expressed as proportion of the adult population that is male) at Eagle Lake and Quail Ridge, California, U.S.A.

Habitat	Year	Density	Mean NPM distance	OSR
Coniferous forest	2000	0.9	157.0 (25.7)	0.44
	2001	0.5	186.6 (44.5)	0.67
Juniper woodland	1999	2.8	62.9 (29.9)	0.46
	2000	1.7	74.2 (31.4)	0.32
	2001	1.2	96.1 (30.4)	0.33
	2002	0.7	111.7 (40.6)	0.43
Oak woodland	2002	11.3	20.1 (29.0)	0.35

Genetic and Parentage Analysis

Of the 10 microsatellite loci sampled, the range for the number of alleles per locus was 2–17 (mean 7.5) in the Eagle Lake population and 9–17 (mean 11.3) in the Quail Ridge population. There was no significant evidence for deviations from Hardy–Weinberg equilibrium, null alleles or linkage disequilibrium at any of the 10 loci sampled. Maternity was assigned for 91% of offspring at the 80% confidence level. Paternity was assigned for 77% of offspring at both the 80% and 95% confidence levels. Proportions of maternities and paternities assigned varied by habitat with a lower proportion of maternities assigned in coniferous forest habitat than in juniper or oak woodland

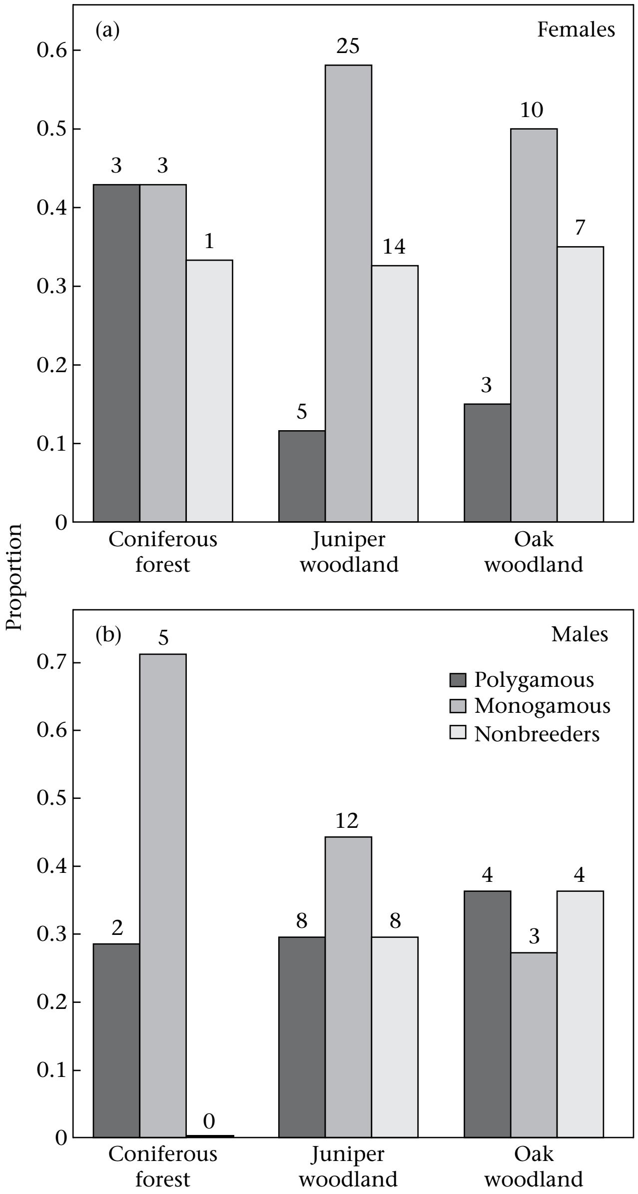

Figure 1. Proportions of adult females (a) and males (b) that successfully mated polygamously, monogamously or with zero partners in coniferous forest, juniper woodland and oak woodland habitats. Sample sizes are indicated above each bar.

habitats. Parentage assignment was more successful in the Quail Ridge population, having both higher mean PIC (polymorphic information content) and higher mean exclusionary power than the Eagle Lake population.

Mating System Variation and Reproductive Success

Pooling across habitats and years, 54% of adult females were monogamous, 15% were polygamous, and 31% failed to produce detectable offspring. Differences in these estimates by habitat are shown in Fig. 1. Polyandry was not detected among any of the polygamous females. The proportion of females mating with multiple partners (polygamy) within a breeding season was highest in low-density coniferous forest habitat (43%). The proportion of females mating with a single partner (monogamy) was highest in juniper woodland habitat (58%), followed by oak woodland (50%) and coniferous forest (43%) habitats. For females that successfully produced offspring, the mean number of mates ranged from 1.2 to 1.7 and mean number of offspring ranged from 1.3 to 2.3 (Table 3). Multiple paternity was detected in 4 of 12 multiple-offspring litters.

The same analysis in males revealed that across habitats and years, 43% of males were monogamous, 30% were polygamous, and 26% failed to produce detectable offspring (see Fig. 1 for estimates by habitat). Over the 4-year study, only 4 of 14 polygamous males could be classified as polygynous and these occurred in juniper woodland and oak woodland habitats. Contrary to females, the highest proportion of males mating with multiple partners was found in the higher-density oak woodland habitat (36%) and juniper woodland habitat (33%), while the lowest proportion occurred in low-density coniferous forest habitat (25%). Coniferous forest also supported the highest proportion of monogamous males (75%). After excluding males that did not successfully breed, mean number of mates ranged from 1.3 to 2.3 and mean number of offspring ranged from 1.9 to 2.4 (Table 3).

Model selection involved the analysis of 539 potential male–female pairs and revealed that inclusion of a three-way interaction between density, pairwise distance and OSR produces the best-fit model, with an Akaike weight of 0.403 (Table 4). Two additional models, containing pairs of two-way interactions between OSR, density and distance, received the next highest support, with Akaike weights of 0.243 and 0.207. A fourth model with a weight of 0.125 contained all three two-way interactions between OSR, density and distance. Together these four models accounted for 0.978 of the weight evidence. No model containing male body mass as a predictor received a weight greater than 0.001.

Parameter estimates of the top four models are shown in Table 5, with quadratic approximate standard errors in parentheses. All main effects of the best-fit model, except distance, had positive effects on mating probabilities. However the two-way interaction between sex ratio and density was negative, indicating that when both OSR and densities are high, the number of mated pairs in a population decreases.

DISCUSSION

Genetic Mating System

Our genetic reconstruction of mating relationships shows that promiscuity occurred in all three habitats. Both males and females mated with multiple partners. However, a substantial number of individuals in each habitat were monogamous, an unexpected result based on previous studies suggesting a predominantly polygynous mating system within the genus (Linsdale & Tevis 1951; Kelly 1989). Our results provide little support for polygyny in *N. fuscipes*. Many of the females involved in seemingly polygynous matings had multiple partners, and multiple sires were detected within litters, indicating that males were not successfully defending or monopolizing access to females during the breeding season.

Table 3
Mean numbers of mates and offspring in male and female dusky-footed woodrats at Eagle Lake and Quail Ridge, California, U.S.A.

Habitat	Sex	Mean (SD) no. mates	Mean (SD) no. offspring
Coniferous forest (EL)	Female	1.7 (0.90)	2.3 (1.90)
	Male	1.3 (0.24)	1.9 (0.14)
Juniper woodland (EL)	Female	1.2 (0.15)	1.4 (0.54)
	Male	1.8 (2.03)	2.2 (3.81)
Oak woodland (QR)	Female	1.2 (0.19)	1.3 (0.40)
	Male	2.3 (2.24)	2.4 (2.29)
All habitats	Female	1.2 (0.28)	1.5 (0.75)
	Male	1.8 (1.68)	2.1 (2.55)

Evidence for a promiscuous mating system and multiple paternity has been shown in a genetic study of the closely related *Neotoma macrotis* (Matocq & Lacey 2004). Genetic evidence also suggests that promiscuity is the dominant mating system in the bushy-tailed woodrat, *Neotoma cinerea* (Topping & Millar 1999). Thus, the available genetic data indicate that promiscuity is the more common mating system in *Neotoma*, not polygyny. On a larger scale, these studies and others (Wolff & Macdonald 2004; Waterman 2007) raise questions about the extent to which polygyny dominates mammalian mating systems in general. Additional genetic studies that characterize mating systems from both the male and female perspectives are needed to re-evaluate this idea across mammalian taxa.

Genetic monogamy occurred frequently in all three habitats, however, there was no indication that social monogamy, as found in species like the California mouse, *Peromyscus californicus* (Ribble 1991) and elephant-shrew, *Elephantulus rufescens* (Rathbun 1979), occurs in woodrats. Although males and females are known to overlap in home range and interact socially, breeding adults do not maintain long-term, exclusive pair bonds (Linsdale & Tevis 1951; Wallen 1977; Kelly 1989). Moreover, there is no indication that males provide any parental care. Thus, monogamy in woodrats appears to be a strictly genetic phenomenon. Our results suggest that woodrats are promiscuous when opportunities arise, but monogamy will occur when environmental and social conditions limit the frequency or success of promiscuous interactions.

Table 4
Models predicting mated pairs sorted by AIC$_c$ and model weight

Model structure	No. parameters	AIC$_c$	Weight
*O***N***D*	8	340.2	0.403
*O***N*+*N***D*	6	341.3	0.243
*O***N*+*O***D*	6	341.6	0.207
*O***N*+*O***D*+*N***D*	7	342.6	0.125
*O***N*	4	346.3	0.019
*O***N**BM	8	351.7	0.001
*O***N***D**BM	16	352.1	0.001
*N***D*	4	352.6	<0.001
*O***D*+*N***D*	6	352.8	<0.001
*N***D**BM	8	357.0	<0.001
N	2	358.4	<0.001
Intercept only	1	361.6	<0.001
*N**BM	4	361.9	<0.001
BM	2	362.3	<0.001
D	2	362.7	<0.001
O	2	363.6	<0.001
*O***D*	4	364.1	<0.001
*D**BM	4	365.4	<0.001
*O**BM	4	366.2	<0.001

Interactions are indicated with asterisks and also imply all simpler terms in a factorial design. For example, *O***N* implies the main effects *O* + *N*. BM refers to male body mass, *O* is the operational sex ratio expressed as the proportion of males in the population, *N* is density (woodrats/ha), and *D* is distance (m).

Table 5
Maximum-likelihood parameter estimates for the top four Akaike-weighted models, from Table 4

Model structure	Intercept (SE)	O (SE)	N (SE)	D (SE)	O^*N (SE)	O^*D (SE)	N^*D (SE)	O^*N^*D (SE)
O^*N^*D	−4.353 (2.267)	9.864 (6.144)	4.144 (1.325)	0.003 (0.006)	−11.877 (3.723)	−0.012 (0.017)	−0.009 (0.004)	0.024 (0.012)
O^*N+N^*D	−3.157 (1.040)	6.334 (2.725)	2.029 (0.562)	−0.002 (0.001)	−5.935 (1.607)		−0.0004 (0.004)	
O^*N+O^*D	−1.802 (1.750)	3.056 (4.641)	1.960 (0.569)	−0.007 (0.005)	−5.890 (1.600)	0.012 (0.012)		
$O^*N+O^*D+N^*D$	−1.943 (1.751)	3.108 (4.615)	1.899 (0.576)	−0.005 (0.005)	−5.592 (1.637)	0.010 (0.012)	−0.0004 (0.0004)	

O is the operational sex ratio expressed as the proportion of males in the population, N is density (woodrats/ha), and D is distance (m). Standard errors are indicated in parentheses.

Determinants of Mating System Variation

While a positive relationship between polygamy and population density was apparent in males, this relationship was not apparent in females, where polygamy was highest in low-density, coniferous forest habitat (Fig. 1). As expected, the variances in number of mates and offspring tended to be higher in males than in females. However, this pattern was reversed in low-density coniferous forest habitat, where females were more variable both in numbers of mates and numbers of offspring. These results could reflect a real difference in how males and females respond to changes in density. However additional data, especially from low-density populations, are needed to confirm this possibility.

Given that mating system variation (MSV) can be influenced by many demographic and environmental variables that can also interact with one another, it is perhaps not surprising that our analysis supports some interactions, in addition to large main effects. Thus, the idea that mating system variation in woodrats is random (Hypothesis 1) is not supported: the intercept, or random, model did not do a good job of predicting mated pairs (Table 4). In agreement with Emlen & Oring's (1977) framework, density and OSR (Hypotheses 2 and 3) do matter. Their main effects were positive, as expected. Based on parameter estimates (Table 5), OSR (O) and density (N), in particular, appeared to have the strongest main effects on mating. Distance (Hypothesis 4) only mattered in interaction, as the estimates of its main effect were all very small. Thus, the predictions that small spatial scales (Hypothesis 4) and large male body size (Hypothesis 5) increase polygamy are the only ones not supported by the main effects analysis.

There was also evidence of complex interactions. The interaction between OSR and density had a strongly negative effect on multiple mating (Table 5, column O^*N). Thus, in these data, when both density and OSR were high (there were both a lot of males and a lot of males relative to females) the probability of multiple mating decreased. In other words, having many males around does not necessarily increase opportunities for polygamy, particularly in females. However, in our data, when density was lowest and OSR highest (i.e. coniferous forest habitat), the proportion of polygamous females was also highest.

One possible explanation for this trend is that high population densities lead to more competition and mating interference than do lower-density populations with fewer males. Dusky-footed woodrats are territorial, so it makes sense that when there are enough males in a population, they can restrict each other's movements and access to mates. However, even in our highest-density population (Quail Ridge), some females successfully mated with multiple partners. This result suggests that males are not guarding mates directly. Indeed, adult males and females maintain and defend individual core areas and are not known to share houses. However, males can control space around females and presumably restrict mating access indirectly. This phenomenon may explain why females did not experience an increase in polygamy in a higher-density habitat containing more males.

Although spatial relationships are often used to predict mating systems in mammals, our results indicate that pairwise distance (D) had a relatively small effect on mating probability. In the best-AIC model, the effect of distance on mating probability was slightly positive, indicating a higher probability of mating when mates are further apart (i.e. less likely to overlap in home range). In all three cases the magnitude of the distance effect was close to zero, with relatively large standard errors. Thus, distance appears to be important only as it interacts with OSR and density. The two-way interaction between density and distance (N^*D) was consistently negative, indicating that matings tend to remain more local in densely populated habitats, but that individuals mate with increasingly more distant individuals in sparsely populated habitats. Similar results have been found in banner-tailed kangaroo rats, *Dipodomys spectabilis*, another solitary rodent (Randall 1991). We did not venture this prediction a priori, although in hindsight, it appears obvious: when there are fewer individuals to encounter, individuals must travel further to find mates. We found the interactions O^*D, N^*D and O^*N^*D, with their large standard errors, to be harder to understand. Understanding the precise nature of the three-way interaction, in particular, will require additional theorizing and empirical validation.

Similarly, we did not detect a strong relationship between male body size (Hypothesis 5) and mating success in woodrats. Body size is often considered a determinant of male reproductive success. Several studies support this notion (Ribble 1992; Solomon 1993; Eberle & Kappeler 2004). However, Topping & Millar (1999) found no evidence for a correlation between large body size and reproductive success in bushy-tailed woodrats. These results are somewhat surprising given that both *N. fuscipes* and *N. cinerea* are sexually dimorphic in body size. This may reflect a conflict between male–male competition, generating selection for larger male body size, and female choice, reflecting selection for multiple-male mating and thereby diluting the strength of selection on large male body size. Additionally, the relationship between male body mass and mating success may depend upon local relative body mass, rather than the simple linear relationship we modelled here.

Our study of genetic mating system variation in woodrats presents limitations that deserve careful consideration when interpreting results. Our characterization of the mating system is based on genetic parentage analysis of observed offspring and our definition of mating does not include unsuccessful mating attempts (i.e. those that did not produce viable, weaned offspring). Thus, we do not attempt to characterize the social mating systems of our study populations, and our methods are likely to underestimate the number of social mating partners in both males and females. Detailed home range data would have yielded additional information on male–female social interactions, however, a persistent population decline at Eagle Lake prevented us from pursuing this option. Home range data collected for a subset of woodrats in 2000 revealed a negative correlation between home range overlap and pairwise distance (correlation coefficient = −0.844, 95% confidence interval = −0.971, −0.345) (McEachern 2005). Thus, we opted to use pairwise distance, rather than home range overlap, in our mating system models because these data were readily available. Both types of data yield useful but different information, and ideally both would be included as model predictors of mated pairs.

However, for the limited home range data available, previous analyses suggest that home range overlap is a poor predictor of successfully mated pairs in our study populations (McEachern 2005).

Conclusions

This study does not support previous observational work suggesting a predominantly polygynous mating system in woodrats (Linsdale & Tevis 1951; Kelly 1989), but it does support the conclusion that woodrats are promiscuous, with a portion of males and females mating with multiple partners during a breeding season and evidence for multiple paternity within litters. This study also reveals that many individuals are facultatively monogamous, even when the environmental potential for polygamy is high.

Discrepancies between the social and genetic mating systems of species are not surprising given that they describe different yet equally important aspects of the mating system, one focusing on courtship and social interactions and the other on the genetic outcomes of those interactions. The concern, however, is the effect this discrepancy has on our theoretical understanding of mating system variation and the determinants of reproductive success. Our study cautions that the determinants of female mating system variation may differ from male mating system variation, especially with respect to how the sexes respond to changes in population density. Genetic studies of mating system variation from additional species, addressing both the male and female perspectives, are needed to understand how demographic and environmental variables influence the evolutionary dynamics of mating systems.

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