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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