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Multiple paternities increase genetic diversity of offspring in Brandt's voles

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ABSTRACT

Mating system and philopatry influence the genetic structure of a social group in mammals. Brandt's vole (*Lasiopodomys brandtii*) lives in social groups year-round and has male biased dispersal, which makes the vole a model system for studies of genetic consequences of mating system and philopatry. This study aimed to test the hypotheses that: (1) multiple paternity (MP) would exist in Brandt's voles, enhance offspring genetic diversity and reduce genetic relatedness between littermates; (2) promiscuity would occur in this species in that males and females mate with multiple partners; and (3) plural breeders of a social group would be genetically related because of philopatry of female juveniles in Brandt's voles. Paternity analysis indicated that MP occurred in 11 (46%) of 24 social groups examined and that promiscuity existed in this species. Multiple paternity litters had twice the offspring genetic diversity and half the average within-litter genetic relatedness of single paternity litters. We also found plural breeding females in six social groups. Average pairwise genetic relatedness of plural breeders ranged from 0.41 to 0.72 in four social groups, suggesting first-order kinship. Future studies need to investigate effects of reproductive skew and MP on population genetic structure of Brandt's voles.

1. Introduction

Genetic consequences of social behavior are critical to understanding social organizations of rodents. Mating systems and philopatry of females are the two main factors influencing genetic structure of a social group in mammals. A common social system among murid rodents, especially the arvicolines, is for females to be territorial and males to have large home ranges that overlap those of several females as well as several other males (Wolff, 1985). However, exceptions exist such as in prairie voles (*Microtus ochrogaster*), in which a pair of bonded male and female shares a home range (Getz et al., 1993; Ophir et al., 2008). Mating systems are frequently flexible ranging from monogamy to polygyny and promiscuity, often within the same species (McEachern et al., 2009; Solomon and Keane, 2007; Waterman, 2007). Multi-male mating appears also to be relatively common in the murid rodents, particularly the arvicolines (Solomon and Keane, 2007; Boonstra et al., 1993b; Gordon et al., 1998; Solomon et al., 2004; Borkowska et al., 2009). Multiple paternity (MP—multiple males siring a litter) has many direct and indirect benefits including increased offspring genetic diversity (Wolff and Macdonald, 2004; Reynolds, 1996) and effective population sizes (Karl, 2008), which may subsequently enhance survival of offspring (Yasui, 1998).

Kinship plays a major role in the evolution of group living (Griffin and West, 2003; Hamilton, 1964). Philopatry of juveniles, particularly female pups, is the proximate cause of social group formation in rodents (Lacey and Sherman, 2007; Nunes, 2007; Solomon, 2003). Natal dispersal is typically male biased in mammals; more male juveniles disperse from their natal habitat to a new one than do female juveniles (Greenwood, 1980). Daughters remain in their natal groups, delay sexual maturity, and assist in care of offspring of parents or siblings (i.e., alloparental care). As a result, female group mates may be kin (e.g., mother–daughter and siblings). Kinship enhances the fitness of social group members through either direct or indirect benefits of group living (Griffin and West, 2003; Hamilton, 1964; Lacey and Sherman, 2007). Direct benefits can include increased female reproductive success owing to cooperative breeding or alloparental care (Hamilton, 1964; Lacey and

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Sherman, 2007; Solomon and Getz, 1997). Meanwhile, philopatric, non-breeding kin gain inclusive fitness by helping nurse and protect offspring of their parents or siblings (Hamilton, 1964; Lacey and Sherman, 2007; Solomon and Getz, 1997). Despite reproductive skew, daughters or subordinate kin may have opportunities to breed even with mothers present (Clutton-Brock, 1998; Emlen et al., 1998; Keller and Reeve, 1994). Therefore, social groups can have more than one breeding female (plural breeders; Solomon and Getz, 1997; Solomon and Keane, 2007). It is plausible to hypothesize that females, including plural breeders, of a social group are first-order or second-order kin (Hamilton, 1964; Solomon and Keane, 2007).

Brandt's voles (*Lasiopodomys brandtii*) live in groups, each of which occupies a burrow system conspicuously visible due to connected burrows and runways (Zhong et al., 2007; Formozov, 1966). A social group consists of up to 20 individuals of both sexes at a sex ratio of 1:1 and mixed ages with six to seven adult males (Zhong et al., 2007); thus, multi-male mating seems likely. Juvenile males disperse prior to reaching sexual maturity. Although plural breeders have been found in the same social group (Zhong et al., 2007), kinship of these plural breeders has not been quantified with genetic methods in Brandt's voles. As part of a long-term study of rodent social behavior, herein we used Brandt's voles as a model system to test three hypotheses regarding genetic consequences of MP and philopatry of females. We tested the hypotheses that: (1) MP would exist in Brandt's voles, enhance offspring genetic diversity, and reduce genetic relatedness between littermates; (2) promiscuity would occur in this species in that males and females will mate with multiple partners; and (3) plural breeders of a social group would be kin because of philopatry of female juveniles in Brandt's voles. We expected that MP would be common in the litters of Brandt's voles and that genetic diversity of offspring sired by two or more males would be greater than that of offspring sired by a single male. We also predicted that genetic relatedness coefficients between plural female breeders of Brandt's voles would be greater than 0.25.

2. Materials and methods

2.1. Study area

The study site was located in Maodeng Ranch about 30 km east of Xilinhot, Inner Mongolia, China (N44°9′, E116°24′) and was in typical steppe habitat at an elevation of 1400 m. Habitat consisted of a relatively monotypic grassland dominated by the needlegrass *Stipa krylovii*. *Stipa krylovii* was 5–10 cm tall, grew in clumps, and composed >90% of the vegetation, providing very little cover. The vegetation was relatively sparse with about 50% of the bare ground exposed. Voles could be observed running on the soil surface from a distance of 10 m.

2.2. Field collection

We identified 20 burrow systems and placed approximately 20–25 snap traps baited with peanuts at burrow entrances of each system in July 2007. We checked snap traps hourly from dawn to dusk, removing captured voles from traps and re-setting the traps. Trapping lasted for about 48 h for a burrow system. We concluded that all voles of a social group were captured if no voles were captured in the last 12 h (Wang et al., 2003; Zhong et al., 2007). For each captured vole, we recorded colony number, sex, body mass, body length, and length of testes and seminal vesicles for males or numbers of embryos and placental scars on each side of the uterine horns for females. We collected tissue samples from captured voles for population genetic analysis using microsatellite markers. From adults, we collected a small piece of the liver. For embryos, we extracted each embryo from the maternal uterine horns of each pregnant female, placed the embryos on a clean (DNA free) surface, removed carefully the embryonic sac and placenta, measured the crown-rump length, and then collected body tissue from each embryo. Tissue samples were placed individually in small centrifuge tubes with 75% alcohol until extraction. We did not collect tissue samples of captured males except for seven adult male voles. Our trapping and handling of Brandt's voles in the field were approved by the Institutional Animal Use and Care Committee of the Institute of Zoology, Chinese Academy of Sciences.

2.3. Microsatellite amplification and genotyping

Genomic DNA was extracted from tissue samples following the procedure described by Sambrook and Russell (2001) with some modifications. Quality and quantity of DNA samples were estimated with 2% agarose gel electrophoresis using ethidium bromide to stain DNA on the gel for visualization. We used microsatellite DNA markers for nine loci to genotype pregnant females, adult males, and embryos. Primers for microsatellite markers BVM01, BVM02, BVM03, BVM04, BVM05, BVM06, BVM08, BVM09, and BVM11 were developed for Brandt's voles by Wang and Shi (2007). The forward primer oligonucleotides of each microsatellite marker was labeled with one of three colors according to the nucleotide size range of each marker: green (HEX) for BVM01, BVM04, and BVM11, blue (FAM) for BVM02, BVM03, and BVM05, and yellow (TAMRA) for BVM06, BVM08, and BVM09. All nine loci were amplified separately for each sample using polymerase chain reaction (PCR) with conditions optimized using a touchdown protocol on a Thermo Hybaid thermal cycler (Fisher Scientific, Pittsburgh, PA, USA). Amplification of each locus was conducted in a 10-μl reaction volume containing approximately 50 ng genomic DNA, 5 μl Premix Taq (TaKaRa Bio Company, Madison, WI, USA), and 0.5 μM of paired primers. The PCR protocol was as follows: initial denaturation at 95 °C for 5 min and 35 cycles of 94 °C for 15 s, annealing temperature for 30 s, and a final extension step at 72 °C for 10 min. Annealing temperature for each marker ranged from 48 to 67 °C (Wang and Shi, 2007). Amplified fragments were resolved on an ABI 3700 automated sequencer (Applied Biosystems, Foster City, CA, USA) with a GS 400 ROX ladder that is able to distinguish between a single base pair difference, using the software Genescan® Version 3.7 (Applied Biosystems). Each vole sample was genotyped independently by two different observers. If the genotypes of a vole from two observers differed, genotyping was repeated until a consensus was reached.

2.4. Statistical analyses

Hardy–Weinberg equilibrium (HWE) was tested for each locus using the program FSTAT 1.2 (Goudet, 1995). Linkage disequilibrium (LD) was tested for each pair of loci using the program GENEPOP 3.4 with the Markov chain option (Raymond and Rousset, 1995). We used Bonferroni correction for multiple comparisons with a nominal significance level of 0.05. We calculated mean number of alleles per locus, allele frequencies, Shannon's information index, and expected heterozygosities using the program GENALEX 6 (Peakall and Smouse, 2006). We tested for the presence of null alleles, short allele dominance, and typing error using the program MICRO-CHECKER (Van Oosterhout et al., 2004). A simulation study shows that the presence of null alleles in frequency less than 0.2 does not cause any significant bias or error in parentage analysis (Dakin and Avise, 2004). Therefore, we included microsatellite loci of null allele frequency less than 0.1 in our analysis.

We used the program GERUD 2.0 (Jones, 2005) to determine minimum number of fathers to explain the progeny array of each litter with the mother known and to reconstruct genotypes of putative fathers. When more than one genotype was identified for a

putative father, we used priority scores to choose the most likely genotype for the putative father (Jones, 2005). We also conducted a paternity analysis to assign the most likely father(s) to a litter with our seven genotyped male adults as candidate fathers using the program CERVUS 3.0 (Marshall et al., 1998). We assumed that proportion of candidate fathers sampled was 0.1, proportion of loci typed 0.99, proportion of loci mistyped 0.001, and error rate in likelihood calculations 0.001. We ran the simulations 10,000 times and only considered a paternity assignment at a strict confidence level of 95%. We also calculated exclusion probabilities and probabilities of identity using CERVUS. With GENALEX 6.0, we calculated mean Queller and Goodnight (QG) relatedness coefficient (Queller and Goodnight, 1989) within a litter with the five loci that were in HWE and linkage equilibrium (LE). We chose the bootstrap option to calculate mean QG relatedness coefficients and their 95% confidence intervals (CI) by litter with 1000 iterations. The bootstrap procedure randomly resamples allele frequencies from observed allele frequencies at each locus of the whole population studied (Peakall and Smouse, 2006). We also calculated pairwise QG relatedness coefficients between plural breeders of a colony. Means were reported as mean ± standard error (SE).

3. Results

We captured 27 pregnant females from 20 colonies. Litter sizes ranged from three to nine embryos ($\bar{x} = 7.1 \pm 0.25$). Numbers of embryos in left uterine horns (3.7 ± 0.31) and right horns (3.4 ± 0.24) did not differ (paired $t = 1.71$, $d.f. = 26$, $P = 0.32$). Embryos were large enough to provide uncontaminated tissue samples for DNA extractions with an average crown-rump length of 14.6 ± 1.12 mm.

We typed 227 samples at nine microsatellite loci for 27 pregnant females, 193 embryos, and seven adult males. The corroboration rate of repeated genotyping of a sample was over 99%. Locus BVM11 was eliminated from genetic analysis because of difficulties with scoring alleles. Among the eight loci tested, only BVM01, BVM05, BVM06, BVM08, and BVM09 were in HWE and LE. Numbers of alleles per locus ranged from two to eight (4.4 ± 1.03; Table 1). Average observed heterozygosity of five loci was 0.47. MICRO-CHECKER did not detect any typing error and small allele dominance in all eight alleles. Null allele frequencies of BVM01, BVM02, BVM03, BVM04, BVM05, and BVM06 ranged from −0.04 to 0.02, and those of BVM08 and BVM09 were 0.05 and 0.07, respectively. Loci BVM08 and BVM09 were also included in our genetic analysis because of low null allele frequency (<0.1). Three pregnant female samples were excluded from paternity analysis: the female July-3-300M and her litter because of failures to genotype her at the locus BVM08 even with 3 repetitions; the female July-2-272M and her litter July-2-272 because of their identical genotypes at all five loci; and the female July-28-14M and her litter because of the genotype mismatches between mother and two embryos at the locus BVM06.

Table 1
Number of alleles per locus (*Na*), observed heterozygocity (*Ho*) and expected heterozygocity (*He*) of Brandt's vole samples collected in Inner Mongolia, China, July 2007.

Locus	*N*	*Na*	*Ho*	*He*
BVM01	227	4.000	0.485	0.452
BVM05	227	8.000	0.564	0.614
BVM06	227	5.000	0.648	0.676
BVM08	226	3.000	0.456	0.527
BVM09	227	2.000	0.128	0.127

Eleven (46%) of the 24 tested litters had a minimum of two sires indicating MP (Table 2). Average number of alleles per locus (*Na*), expected heterozygosity (*He*), and Shannon's information index (*I*) were greater in MP litters than SP litters (*Na*: $t = 4.59$, $d.f. = 22$, $P < 0.001$; *He*: $t = 2.43$, $d.f. = 22$, $P = 0.02$; and *I*: $t = 2.9$, $d.f. = 22$, $P = 0.008$). Therefore, MP mechanistically increased offspring genetic diversity.

Bootstrap mean relatedness coefficients within litters ranged from 0.04 to 0.81. Bootstrap mean relatedness did not differ from zero in six litters with bootstrap 95% CI's including zero, but differed significantly from zero in the remaining 21 litters with bootstrap 95% CI's excluding zero. Average genetic relatedness of MP litters was 0.23 ± 0.15, but 0.51 ± 0.20 in single paternity (SP) litters ($t = 3.33$. $d.f. = 22$, $P = 0.001$). Average relatedness of the 27 litters was 0.38 ± 0.04 indicating that embryos within a litter were either half-siblings (relatedness = 0.25) or full siblings (relatedness = 0.5 or 1.0).

We captured two or more pregnant females in each of six social groups. In two of the six groups, putative fathers shared iden-

Table 2
Multiple paternity in Brandt's voles collected in Inner Mongolia, China, July 2007.

Mother ID	Litter Size	Inferred number of paternal alleles at each locus					Minimum number of fathers
		BVM01	BVM05	BVM06	BVM08	BVM09	
July-1-40M	8	1	2	3	2	2	2
July-1-56M	6	1	1	2	1	2	1
July-1-136M	8	1	2	3	2	2	2
July-1-149M	8	2	2	2	2	2	1
July-1-186M	9	1	1	2	2	2	1
July-2-234M	6	1	2	1	1	2	1
July-2-259M	8	3	3	3	2	2	2
July-2-261M	6	1	2	1	1	2	1
July-2-296M	7	2	2	3	2	2	2
July-3-301M	7	2	2	2	1	1	1
July-4-302M	8	3	2	3	2	2	2
July-21-1M	8	4	3	2	2	2	2
July-21-2M	8	2	2	2	1	1	1
July-21-3M	7	3	3	2	1	2	2
July-21-4M	6	3	2	4	1	2	2
July-21-5M	8	2	2	2	1	1	1
July-24-6M	8	3	3	2	3	2	2
July-24-7M	8	2	2	2	3	2	2
July-24-8M	6	2	2	2	1	2	1
July-24-9M	3	1	3	2	1	2	2
July-28-10M	7	1	2	2	1	2	1
July-28-11M	8	1	2	2	2	1	1
July-28-12M	6	1	2	2	2	2	1
July-28-13M	7	1	2	2	2	1	1

Table 3
Inferred genotypes of putative fathers in two social groups of Brandt's voles collected in Inner Mongolia, China, July 2007.

Group ID	Mother ID	Inferred genotype of putative fathers				
		BVM01	BVM05	BVM06	BVM08	BVM09
July-21-G16	July-21-2M	163/167	176/182	205/213	221/221	177/177
	July-21-5M	163/167	176/182	205/213	221/221	177/177
July-28-G6	July-28-11M	163/163	176/182	197/213	239/241	177/177
	July-28-13M	163/163	176/182	197/213	239/241	177/177

tical genotypes (Table 3). The probability of identify was 0.003 suggesting that three of 1000 randomly selected individuals may share identical genotypes characterized by the 5 loci. Furthermore, CERVUS assigned the male (ID 126) to be the sires of the litters of females July-1-149M and July-2-259M in group 4 at the 95% confidence level. The combined exclusion probability of the five loci was 0.79 with mother genotype known. The observed genotype of male 126 matched with that of the putative father of the two litters. Therefore, male and female Brandt's voles mated with multiple individuals of the opposite sex.

Average pairwise relatedness coefficients of plural breeders in two social groups were −0.12 and −0.46. Breeding females of negative relatedness coefficients were unlikely to be related; however, average pairwise relatedness coefficients of plural breeders in the remaining four social groups ranged from 0.41 to 0.72. Therefore, plural breeders of the four social groups were either mother–daughter pairs or full-sisters.

4. Discussion

We found MP in 11 (46%) of 24 tested litters (Table 2). Multiple paternity increased offspring genetic diversity and reduced within-litter genetic relatedness by 50% relative to that in SP litters. Promiscuity may exist in Brandt's voles; however future studies of variation in the mating systems of Brandt's voles are needed. Six of 20 social groups had plural breeders with two to three pregnant females captured per group. Plural breeders in four of the six social groups were first-order kin. Therefore, our results support the hypotheses regarding promiscuity (Tables 2 and 3) and kinship of plural breeders in Brandt's voles.

Multiple paternity existed in Brandt's voles. Two or more males sired a litter (Table 2). Multiple paternity has been found in many mammals, including murid rodents (Boonstra et al., 1993a; Crawford et al., 2008; Nielsen and Nielsen, 2007; Wolff and Macdonald, 2004; Shurtliff et al., 2005; Solomon et al., 2004; Baker et al., 1999). Several hypotheses have been proposed to explain multi-male mating, including sib competition, increased genetic diversity, infanticide avoidance, female's giving in to male harassment, etc. (Karl, 2008; Reynolds, 1996; Wolff and Macdonald, 2004; Ridley, 1993; Loman et al., 1988). Our results demonstrate that MP increases the genetic diversity of offspring (Solomon and Keane, 2007), which may in turn improve survival and reproductive success of offspring (Yasui, 1998). However, demographic benefits of mating with multiple males remain unanswered in the arvicolines (Solomon et al., 2004). High population densities may further limit male dispersal due to increased aggression of territory holders and habitat saturation (Hestbeck, 1988; Nunes, 2007; Solomon and Getz, 1997). Consequently, more male juveniles remain at natal sites at high densities than at low densities, and dominant males may no longer be able to guard their mates on territories due to increased male–male competition and increased costs of mate guarding and defense. Therefore, MP may be more common at high densities than at low densities. Future studies need to assess the roles of MP in shaping population genetic structure of Brandt's voles.

Philopatry of female offspring results in kinship among group mates, particularly females (Solomon, 2003; Blumstein and Armitage, 1998; Solomon and Getz, 1997; Lacey and Sherman, 2007). Living in groups benefits social rodents in resource acquisition and defense, defense against predation, and adaptation to cold (Ebensperger, 2001). In cooperative breeders, daughters remain at their natal nests, give up breeding opportunities, and provide alloparental care of kin (Solomon and Getz, 1997). Socially infertile individuals share ½ of genes with their mothers or full siblings; thus, non-breeding kin gain inclusive fitness through their contributions to the reproductive success of breeding kin (Hamilton, 1964; Oli and Armitage, 2003). Ylonen et al. (1990) found that high genetic relatedness increased survival and population growth rates of bank voles (*Clethrionomys glareolus*). In four of the six social groups with plural breeders in this study, breeding females were either first-order or second-order kin, suggesting that daughters remained at the natal sites. Therefore, female kin of a social group may share reproductive opportunities in Brandt's voles. However, it is unknown whether reproductive opportunities are skewed in favor of dominants in Brandt's voles as shown in the meerkat (*Suricata suricatta*; Griffin et al., 2003). Both ecological and genetic data are needed to assess reproductive skew among female kin to better understand benefits of philopatry of females in social rodents.

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