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J C. Cawford
Eastern Illinois University

Zhiwei Liu
Eastern Illinois University, zliu@eiu.edu

T A. Nelson
Eastern Illinois University

C K. Nielsen
Southern Illinois University Carbondale

C K. Bloomquist
Southern Illinois University Carbondale

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MICROSATELLITE ANALYSIS OF MATING AND KINSHIP IN BEAVERS (*CASTOR CANADENSIS*)

JOANNE C. CRAWFORD,* ZHIWEI LIU, THOMAS A. NELSON, CLAYTON K. NIELSEN, AND CRAIG K. BLOOMQUIST

Department of Biological Sciences, Eastern Illinois University, Charleston, IL 61920, USA (JCC, ZL, TAN)
Cooperative Wildlife Research Laboratory, Southern Illinois University, Carbondale, IL 62901, USA (CKN, CKB)

Monogamy is rare among mammals and molecular investigations have revealed that many socially monogamous species participate in extrapair mating. The North American beaver (*Castor canadensis*) is a socially monogamous species that exhibits classic monogamous behavior, generally living in discrete colonies composed of a mated pair and their offspring. We examined genetic relationships within and among beaver colonies for 2 populations in Illinois to investigate average relatedness within colonies, occurrences of extrapair mating within or between colonies, and the influence of geographic distance on intercolony relatedness. Seven microsatellite loci developed for the beaver were used to estimate relatedness and parentage for 55 beavers in central Illinois and 72 beavers in southern Illinois. Average within-colony relatedness varied widely in both populations, ranging from 0.04 to 0.64 in central Illinois and from 0.16 to 0.41 in southern Illinois. Colonies were composed primarily of 1st- and 2nd-order relatives, but included unrelated individuals. Paternity analysis revealed that 5 (56%) of 9 litters had been sired by ≥ 2 males. Extrapair mating frequently occurred between members of neighboring colonies in southern Illinois. In contrast to long-held views that beavers are genetically monogamous and colonies are typically 1st-order relatives, we documented a wide range of relationships among colony members and multiple paternity in >50% of litters.

Key words: beaver, *Castor canadensis*, colony, microsatellite, multiple paternity, relatedness

The study of mating systems is central to understanding population dynamics and conservation biology, and molecular studies of parentage have become commonplace in wildlife research (Jones and Arden 2003). A growing body of literature suggests that for many species social monogamy does not equate to genetic monogamy, and extrapair matings are not rare (Birkhead and Møller 1995; Westneat and Sherman 1997). Monogamy generally refers to a mating system in which a mated pair remains together for ≥ 1 breeding season (Kleiman 1977; Reichard 2003). The North American beaver (*Castor canadensis*) has typically been described as a socially monogamous species, living in discrete colonies that consist of an adult male and female, young of the year, and juveniles from the previous breeding season (Bradt 1938; Busher et al. 1983; Sun 2003; Svendsen 1980).

Beavers exhibit many of the behaviors considered characteristic of monogamous mating systems (Kleiman 1977), including long-term pair-bonding, biparental care, and territorial defense by both adults (Busher et al. 1983; Sharpe and

Rosell 2003; Svendsen 1980, 1989). Furthermore, analysis of anal gland secretion compounds used in territorial scent-marking has revealed similar chemical composition among individuals from the same colony (Sun and Müller-Schwarze 1998). Other monogamous rodents, such as the California mouse (*Peromyscus californicus*) and the prairie vole (*Microtus ochrogaster*), also form long-term pair-bonds and, like beavers, exhibit many behavioral characteristics associated with a monogamous mating system (Lonstein and De Vries 2000).

Biparental care can be an important component of monogamy and is often observed in beavers (Sharpe and Rosell 2003; Sun 2003; Svendsen 1989). Kleiman (1977) contends that the need for food resources for offspring is sufficiently high to require male participation in food acquisition. In beavers, adult males and females participate in dam and lodge construction, food acquisition, and territorial defense (Sharpe and Rosell 2003; Sun 2003; Svendsen 1989). Offspring typically disperse at 2–3 years of age (Sun et. al. 2000; Svendsen 1980; Van Deelen and Pletscher 1996). Accordingly, both parents must remain with the family long enough to provide for the young. However, because pair-bonds between adults may last only 2–3 years (Svendsen 1989), it is probable that some colonies contain half-siblings and any subsequent adult males tolerate unrelated subadults. Therefore, deviations from monogamy can only be investigated within the same

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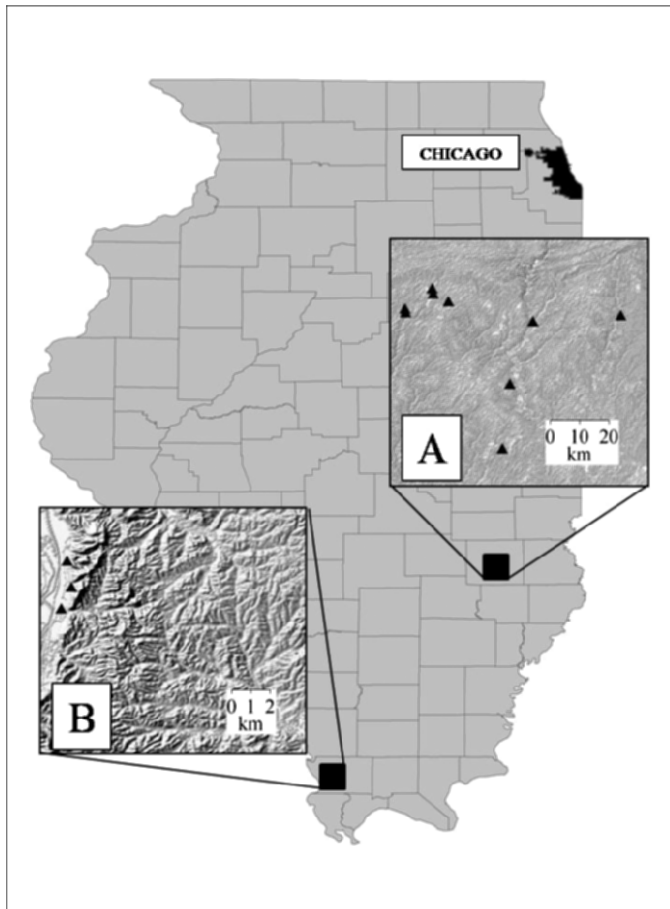* Correspondent: crawford.joanne@gmail.com

FIG. 1.—Locations of beaver (*Castor canadensis*) colonies in A) central and B) southern Illinois. Triangles within each nested figure denote locations of colonies at each study site.

breeding season unless the duration of a pair-bond is known a priori.

Monogamous pairings appear to be the dominant pattern in beavers, yet colony composition does deviate from that expected pattern. Some studies have reported colonies with ≥3 adults present and it is thought that "extra" adults are older offspring that have not dispersed (Busher et al. 1983; McTaggart and Nelson 2003; Müller-Schwarze and Schulte 1999). A few studies have found >1 lactating or pregnant females in a colony (Bergerud and Miller 1977; Busher et al. 1983; Wheatley 1993). These findings raise questions about the reported social organization and assumed familial relationships of individual beavers living in a colony.

Despite these occassional deviations, members of beaver colonies usually are assumed to be 1st-order relatives. However, to date no genetic studies have been conducted to investigate parentage or kinship within beaver colonies. Given the rarity of monogamy among mammals, the beaver offers an opportunity to investigate the social and environmental factors under which monogamy is favored. In this study, we used microsatellite loci to describe genetic relationships within and among beaver colonies in 2 disparate populations in Illinois. Specifically, we examined average relatedness among colony

members, occurrence of extrapair matings within or between colonies, and influence of geographic distance on relatedness.

MATERIALS AND METHODS

Study area.—Our research was conducted at 2 study areas in Illinois during 2005–2007 (Fig. 1). Beavers were trapped in central Illinois within the Embarras River watershed during September–March of each study year. Habitat on this study area consisted of linear streams in Coles and Cumberland counties. Beavers were open to harvest in central Illinois and colony density was estimated at 0.40 colonies/km of stream (Cox 2005).

Beavers also were trapped in southern Illinois in the Union County Conservation Area during September–March of each study year. This 2,510-ha refuge is managed by the Illinois Department of Natural Resources as a wetland complex consisting of interconnected wetlands, including 3 large lakes. Beavers were not open to harvest on the Union County Conservation Area; colony density was estimated at 3.3 colonies/km^2.

Sample collection.—Beavers were trapped using Conibear 330 traps (Fleming Outdoors, Remer, Alabama) placed around active lodges. Trappers attempted to remove all colony members over a 2-week period. The location of each lodge trapped was recorded in Universal Transverse Mercator coordinates. All lodges were separated by >1 km and data on home ranges from animals trapped at lodges in southern Illinois over a 2-year period confirmed that these lodges were in fact distinct colonies. Sex of the animals was determined by dissection, and animals were weighed and categorized as young (McTaggart and Nelson 2003). A small section of muscle tissue from each animal was removed using a biopsy punch and stored in 95% ethanol or aluminum foil at −20°C. Tissues were collected from pregnant females and their fetuses when possible.

During the 2005–2006 trapping season, additional animals were livetrapped using cable snares (McNew et al. 2007) following protocols approved by Eastern Illinois University's Institutional Animal Care and Use Committee (protocol 06-001), Southern Illinois University Carbondale's Institutional Animal Care and Use Committee (protocol 01-020), and consistent with recommendations of the American Society of Mammalogists' Animal Care and Use Committee (Gannon et al. 2007). Snared beavers were immobilized with an intramuscular injection of ketamine hydrochloride (10 mg/kg) and xylazine hydrochloride (1 mg/kg) in a 9:1 mix (6–12 mg/kg) to facilitate handling (McNew et al. 2007; McNew and Woolf 2005). Beavers were anesthetized, weighed, and sex was determined by palpation (Osborn 1955). A 2-mm biopsy punch of ear tissue was collected for genetic analysis. Sex was later confirmed using the SRY molecular marker (Kühn et al. 2002). All DNA samples used in this study were archived at Eastern Illinois University.

Microsatellite analysis.—DNA was extracted using a DNeasy Extraction Kit (Qiagen, Inc., Valencia, California) and amplified using a PTC-100 thermocycler (MJ Research, Inc., Waltham, Massachusetts). Polymerase chain reactions

were carried out separately in 25-μl volumes for each of 7 microsatellite loci (*Cca8*, *Cca9*, *Cca10*, *Cca13*, *Cca15*, *Cca18*, and *Cca19*) as described by Crawford et al., in press. Forward primers for each locus were labeled with Well-Red fluorescent tags D3 or D4 (Sigma-Aldrich, St. Louis, Missouri). Reactions included 50–100 ng DNA, 1X polymerase chain reaction buffer, 200 μM each deoxynucleoside triphosphate, 0.3 μM each primer, 3.5 mM MgCl$_2$, and 1 U *Taq* polymerase. Amplifications consisted of an initial 5-min denaturation at 95°C, followed by 36 cycles at 95°C for 30 s, 30 s at the locus-specific annealing temperature (Crawford et al., in press), extension for 2 min at 72°C, and a final extension step at 72°C for 1 h. Polymerase chain reaction products were screened by capillary electrophoresis and scored using Fragment Analysis on a CEQ8800 automated sequencer (Beckman Coulter, Fullerton, California).

Statistical analysis.—Deviations from Hardy–Weinberg equilibrium and the presence of null alleles were tested in both populations using CERVUS software version 3.0 (Marshall et al. 1998). Linkage disequilibrium tests with Bonferroni correction were conducted using GENEPOP version 3.4 (Raymond and Rousset 1995). For both populations, the average relatedness (*R*) within each colony was calculated with jackknife resampling over all loci using the computer program Relatedness 5.0.8 (Queller and Goodnight 1989). For colonies containing ≥3 young, we calculated average relatedness among young within each colony. The average relatedness of adult females within colonies also was calculated to examine female philopatry. The likelihood-based software Kinship version 1.3.1 (Goodnight and Queller 1999) was used to test hypotheses of kinship among colonies. This software tests the likelihood ratio of a primary hypothesis of relatedness (such as full siblings) over the null hypothesis of nonrelatedness for all pairs. Statistical confidence was tested at the 95% and 99% levels using 9,999 simulated pairs for each hypothesis. A primary hypothesis of relatedness was accepted if the likelihood ratio exceeded that required for confidence at the 95% level.

We attempted to assign parentage to all fetal samples, young, yearlings, and subadults within colonies; however, candidate parents could not be identified for several individuals. In total, we examined the occurrence of extrapair mating in 7 litters (6 fetal and 1 young) from southern Illinois and 2 litters (young) from central Illinois. For males, extrapair mating was identified when a male sired the offspring of >1 female in the same breeding season. Extrapair mating was identified for females that produced offspring sired by >1 male within the same litter. Parentage was assigned by a likelihood approach using CERVUS. This program assigns parentage by calculating Δ, the difference in likelihood scores between the most-likely parent and the 2nd-most-likely parent. The cutoff in Δ scores for candidate parents is determined for both the 80% and 95% levels of confidence after a parentage simulation. CERVUS is appropriate for this study for several reasons. As with all genetic analyses, scoring errors, mutation, and null alleles can reduce the statistical confidence in parentage and kinship assignments (Jones and Arden 2003; Pemberton et al. 1995).

Marshall et al. (1998) included corrections for null alleles, scoring errors, and mutations in CERVUS, whereas other potentially useful programs do not accommodate these types of error consistently (Jones and Arden 2003). The statistical confidence in assignments also is more robust because the program calculates an expected distribution of Δ based on a simulated data set. A critical value of Δ is established so that the significance of Δ values calculated from the study population can be determined (Jones and Arden 2003; Marshall et al. 1998).

Critical values of Δ were determined separately from 10,000 simulations for maternity, paternity, and parental pairs in each population. Simulations allowed for a genotyping error of 0.02 estimated from mother–fetal pairs. Sampling efficiencies were based on estimates of the percentage of beavers trapped within a colony relative to the estimated size of the colony. In central Illinois, an average of 3.8 beavers/colony was trapped, yet previous estimates of colony size averaged 5.6 beavers. Therefore, we used a conservative sampling efficiency of 50%. In southern Illinois, the average colony size (9.0) in this study was in good agreement with colony estimates from previous studies. Still, we used a conservative sampling efficiency here of 80%. These conservative sampling efficiencies require higher Δ values when determining confidence of parentage assignments, reducing the risk of incorrect assignments. Occurrences of extrapair mating within the same litter and breeding season were investigated using CERVUS and confirmed, when possible, by examining allelic variation among offspring. Percentages and means ± 1 *SE* are reported throughout the text.

The computer program SPAGeDi version 1.2 (Hardy and Vekemans 2002) was used to examine the relationship between geographic distance and genetic relatedness. SPAGeDi calculates pairwise relatedness (*R*) according to Queller and Goodnight (1989) and regresses these values against pairwise, straight-line distances between individuals. Numerical resampling is performed to assess the significance of the regression. Because the program permutes spatial locations, the regression analysis is equivalent to performing a Mantel test (Hardy and Vekemans 2002). We calculated pairwise *R*-values for all pairs within populations and used Universal Transverse Mercator coordinates of colony locations to calculate pairwise distance between individuals.

RESULTS

Fifty-five beavers were trapped from central Illinois and 72 from southern Illinois. Colonies in central Illinois contained a mean of 3.8 ± 2.4 beavers/colony (*n* = 46 in 12 colonies), whereas colonies in southern Illinois averaged 9.0 ± 2.0 beavers/colony (*n* = 27 in 3 colonies). Each colony in southern Illinois had ≥1 pregnant female, providing an additional 22 fetal samples from 6 litters. The remaining 32 beavers (9 from central Illinois and 23 from southern Illinois) were livetrapped, but were not part of colonies that were sampled completely. These animals were genotyped and included in regression

TABLE 1.—Microsatellite loci used to examine relatedness in central Illinois (CI) and southern Illinois (SI) populations of *Castor canadensis*, 2005–2007.

Locus	No. alleles (CI)	No. alleles (SI)
Cca8	9	7
Cca9	8	9
Cca10	15	12
Cca13	4	5
Cca15	4	5
Cca18	3	3
Cca19	10	8

TABLE 2.—Average relatedness values (Queller and Goodnight 1989) for age and sex classes within beaver colonies in central and southern Illinois, 2005–2007.

	Average pairwise relatedness ($R \pm 1\ SE$)	No. pairwise comparisons (no. colonies)
All members		
Central Illinois	0.33 ± 0.19	97 (12)
Southern Illinois	0.24 ± 0.14	420 (3)
Fetal littermates		
Southern Illinois	0.45 ± 0.13	33 (3)
Young		
Central Illinois	0.50 ± 0.19	19 (6)
Adult females		
Central Illinois	0.55	1 (1)
Southern Illinois	0.45 ± 0.09	30 (3)
Adult males		
Southern Illinois	0.03 ± 0.31	10 (3)

analysis, but were omitted from further colony kinship analyses. All microsatellite loci were moderately polymorphic in both populations and none was identified as linked after Bonferroni correction at $\alpha = 0.05$ (Table 1). However, *Cca8* and *Cca10* deviated significantly from Hardy–Weinberg equilibrium because of an excess of heterozygotes.

Colony kinship.—Colonies in both study areas varied widely in average relatedness (Table 2), ranging from 0.04 to 0.64 in central Illinois and from 0.16 to 0.41 in southern Illinois. Of 6 fetal litters collected in southern Illinois, 2 (33%) were composed of half-siblings, although the most-likely fathers could not be identified. In central Illinois, young occupying the same colony were identified as full-siblings in 4 (67%) of 6 colonies with *R*-values near 0.50. In the 4 largest colonies (≥7 individuals), adult females were shown to be 1st-order relatives; however, mother–daughter pairs could not be distinguished from full-sibling pairs because all shared 1 allele at each locus. Our sample included 3 colonies with ≥2 adult males. In each case, these males were either unrelated to each other or 2nd-order relatives.

Parentage assignments.—Microsatellite loci showed moderate levels of polymorphism in both populations, giving a combined total exclusionary power of 0.987 for the 1st parent and 0.917 for the 2nd parent in central Illinois and 0.990 and 0.933, respectively, in southern Illinois. In central Illinois, CERVUS identified ≥1 parent with 95% confidence in 23 (74%) of 31 young, yearlings, and subadults, including parental pairs (16%) for 3 young. Because of these results, extrapair mating could only be assessed for 2 litters. CERVUS identified a colony in which 1 male sired the young of 2 females. Allele counts and likelihood analysis of 3 young from another colony also showed extrapair mating, with 2 young being full-siblings and the other a half-sibling.

In southern Illinois, 16 (61%) of 26 offspring (from 7 litters) were assigned to 10 parental pairs and extrapair mating was assessed for all litters. All fetal specimens were correctly assigned to their mothers with 95% confidence, but only 5 father–offspring pairs could be identified with 95% confidence. When relaxing the confidence level to 80%, 6 males were identified as the sires of 13 (59%) of 22 fetuses. Males from different colonies were identified as the most-likely fathers for 6 (46%) of these 13 fetuses. As noted above, 2 litters were shown to contain half-siblings. This was supported by allele counts; 4 paternal alleles were detected among fetuses,

indicating that the litter had been sired by ≥2 males. All young and yearlings ($n = 4$) were assigned to 1 or both parents. A half-sibling pair was found occupying the paternal colony of 1 of the young, whereas the most-likely mother of both young occupied a separate colony with another mate. This male was identified as the sire of the 2-year-old offspring still occupying the natal colony, as well as the sire of her current unborn litter. None of the adult females from the paternal colony were identified as possible mothers of these young. Furthermore, the 2nd-most-likely parental pair also was from a different colony and was not identified as likely parents for the young's half-sibling. In total, we found 3 occurrences of within-season extrapair mating and 7 instances of intercolony mating in southern Illinois. When combining results from both study areas, a total of 5 (56%) of 9 litters showed evidence of within-season extrapair mating.

Spatiogenetic analysis.—We found no relationship between relatedness and distance between colonies in central Illinois ($n = 1,380$ pairs, $r^2 = 0.001$, $P = 0.283$). Pairwise distances ranged from 1 to 68 km. Genetic relatedness also was not correlated significantly with distance in southern Illinois ($n = 2,120$, $r^2 = 0.002$, $P = 0.06$). Distance between individuals spanned a smaller range here, with pairwise distances from 1 to 5 km.

DISCUSSION

We designed this study to examine the degree to which beavers fit the model of monogamy, living in discrete, 1st-order family groups. Indeed, several empirical studies on behavior, dispersal, and pheromones support the view that this species is genetically monogamous (Sun 2003). However, our genetic analyses indicate that beavers are not always genetically monogamous and colonies are not necessarily discrete family groups.

Colonies in both populations showed a wide range of relatedness, including unrelated groups, as well as combinations of 1st- and 2nd-order relatives. Only 1 of 12 colonies in

central Illinois contained a mated adult pair and their 2 offspring, although failure to detect other such single-family colonies may have been due in part to incomplete sampling. McTaggart and Nelson (2003) reported that colonies averaged 5.6 beavers in our central Illinois study area 4 years earlier. Because we averaged 3.8 beavers/colony in this area, we believe that some colonies were not trapped completely, explaining why some parents remained unidentified. As a result, our data may underestimate the number of single-family colonies.

The 4 large colonies were composed of extended relatives and 3 of these colonies contained >1 pregnant female. Although female beavers can become sexually mature by their 2nd year, reproduction among subadults is thought to be suppressed by the presence of dominant adults in the den (Brooks et al. 1980; McTaggart and Nelson 2003). Sterilization of either adult in a colony has been shown to inhibit colony reproduction, suggesting that 1 or both dominant adults may prevent mating by subordinates, either through behavior or physiology (Brooks et al. 1980). McTaggart and Nelson (2003) reported 3 colonies in central Illinois in which ovulation had occured in subordinate females when the pregnant adult female had been removed >2 weeks earlier. In contrast, subadult females that were trapped within a week of the removal of the pregnant female had yet to ovulate. Despite these findings, several studies have documented the presence of >1 pregnant or lactating female within a colony (Bergerud and Miller 1977; Busher et al. 1983; Wheatley 1993). It is possible that the ability of the dominant pair to restrict matings by other colony members may be limited in large colonies, which could explain our findings of multiple pregnant females within a colony.

Adult females within the same colony were always identified as 1st-order relatives, whereas adult males always were unrelated mates of females in the colony. Furthermore, the largest colonies sometimes contained several related adult females who had reproduced. Estimates of natal dispersal rates between sexes vary among studies. In southern Illinois, McNew and Woolf (2005) observed nearly equal dispersal rates between the sexes, but juvenile males were more likely to disperse than juvenile females in central Illinois (Cleere 2005; Havens 2006). Natal dispersal may be delayed in high density beaver populations (Brooks et al. 1980; Havens 2006; Müller-Schwarze and Shulte 1999), and delayed dispersal has been documented repeatedly in telemetry studies in our study areas (C. K. Bloomquist, in litt.; Cleere 2005; Havens 2006; McNew and Woolf 2005.). In addition, demographic studies showed that 43% of colonies in central Illinois contained >2 adults and all 8 colonies trapped out in southern Illinois contained >2 adults, further suggesting that delayed natal dispersal, particularly by females, may account for our genetic results (C. K. Bloomquist, in litt.; McTaggart and Nelson 2003).

We identified 3 (20%) of 15 colonies that contained ≥1 individual who was unrelated to others; 2 of these were young. Beavers use anal gland secretions to mark their territory and aggressively defend these against intruders (Rosell and Bjørkøyli 2002; Sun 2003). However, members of neighboring colonies may be tolerated. For example, Eurasian beavers (C.

fiber) spend less time investigating and respond less aggressively to neighbors' scent-mounds than to strangers' scent-mounds (Rosell and Bjørkøyli 2002). At high densities, dispersing individuals from neighboring colonies may reside periodically in nonnatal colonies before establishing breeding territories (Svendsen 1980). Busher et al. (1983) observed frequent intercolony movement of subadults and adults of both sexes in a dense population in Nevada, whereas Sun et al. (2000) frequently observed natal or secondary adult dispersals to neighboring sites in an unharvested New York population. We speculate that unrelated colony members in our study areas may be dispersers or, in the case of young, orphans.

Extrapair matings occurred in >50% of litters and these were often the result of matings with neighbors. Although mated pairs usually share parental duties, cooperative activities may afford either parent opportunities to seek additional mates (Emlen and Oring 1977). Our results suggest that outbreeding is common in beavers; matings between neighbors are fairly common, but mated pairs within a colony are not close relatives. Although beaver colonies may inhabit several lodges, home-range and movement data from both areas confirm that colonies in our study were discrete (C. K. Bloomquist, in litt.; Havens 2006), with mating between members of neighboring colonies reflecting intercolony mating rather than mating between members of the same colony occupying separate lodges. By accepting mates from outside of their colony, females may avoid inbreeding depression and secure additional resources for their offspring. We observed that young born to parents from neighboring colonies resided periodically in either parent's colony and this may effectively double their territory and resources. This sharing may be facilitated by the fact that beavers recognize the secretions of close relatives and respond less aggressively to these than to those of unrelated strangers (Sun and Müller-Schwarze 1997, 1998). High population density, restricted habitat, and mild winters in central and southern Illinois may increase winter movements, female philopatry, and the duration of the dispersal season, increasing the likelihood of extrapair and intercolony matings (McNew and Woolf 2005; Sun 2003).

Geographic distance was not a significant predictor of average relatedness among individuals in either population. Previous studies reporting fewer aggressive interactions between neighboring colonies led us to hypothesize that adjacent colonies may be more closely related than distant ones (Rosell and Bjørkøyli 2002; Sun et al. 2000; Svendsen 1980). In central Illinois, the longest pairwise distance between colonies in our study area was nearly 70 km. Hence, our large-scale, coarse-grain sampling scheme did not provide data for a series of neighboring colonies, and we may have missed fine-scale patterns of intercolony relatedness. Nonetheless, in central Illinois, the median natal dispersal distance among juveniles is 12.2 km, indicating that offspring do not necessarily establish territories near their parents, but routinely disperse considerable distances before settling (Havens 2006). Other studies of natal dispersal have also reported that beavers typically disperse considerable distances from the natal colony (Sun et al. 2000; Van Deelen and Pletscher 1996), suggesting that beaver

populations should be characterized by a high amount of gene flow rather than local genetic structuring.

In southern Illinois, where dispersal distances are shorter ($\bar{X} = 5.9$ km—McNew and Woolf 2005), we found a weak relationship ($P = 0.06$) between pairwise distances and relatedness for neighboring colonies. Although this association was not statistically significant, our mating studies suggest that neighboring colonies do contain related individuals. This sampling area was considerably smaller than that of central Illinois, with the longest pairwise distance between colonies at 4.3 km. McNew and Woolf (2005) reported a mean dispersal distance among juveniles of only 5.9 km in the population at the Union County Conservation Area. Therefore, it is speculative but consistent with these data to suggest that the long, linear stream habitats of central Illinois may facilitate longer dispersal distances and more genetic mixing. In contrast, the interconnected wetland complexes of southern Illinois are associated with shorter dispersal distances and more genetic relatedness among adjacent colonies.

This study is the 1st molecular investigation of mating and kinship in beavers. In contrast to long-held views that beavers are genetically monogamous and colonies are typically 1st-order relatives, we documented a wide range of relationships among colony members and multiple paternity in >50% of litters. This was most evident in large colonies containing several breeding adults. Extrapair mating primarily has been reported in socially monogamous birds (Birkhead and Møller 1995). In contrast, multiple paternity is rarely reported in monogamous rodents. Genetic investigations have revealed extrapair paternity in the prairie vole (*M. ochrogaster*—Solomon et al. 2004) and the common mole-rat (*Cryptomys hottentotus hottentotus*—Bishop et al. 2004), but have not found deviations from monogamy in the oldfield mouse (*Peromyscus polionotus*—Foltz 1981), California mouse (*P. californicus*—Ribble 2003), and Malagasy giant jumping rat (*Hypogeomys antimena*—Sommer and Tichy 1999). Deviations from a monogamous mating system may be more likely under high population densities. In the monogamous Ethiopian wolf (*Canis simensis*) extrapack mating (and associated multiple paternity) has been observed in packs where natal dispersal was low and inbreeding potential was high because of high population density (Sillero-Zubiri et al. 1996). The high ecological densities of beaver populations in Illinois may allow for similar patterns of intercolony and extrapair mating; however, additional research is needed to describe more fully the environmental factors that may influence mating system and spatial genetic patterns in beavers.

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