GENETIC POPULATION STRUCTURE WITHIN AND BETWEEN BEAVER (CASTOR CANADENSIS) POPULATIONS IN ILLINOIS

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Mating behavior and social structure can influence genetic structure within and between populations, yet most studies focus on highly kin-structured, polygynous species. The North American beaver (Castor canadensis) is socially monogamous; however, examination of recent genetic data suggests that this species may be opportunistically promiscuous. We used 7 microsatellite loci to quantify genetic structure within and between 2 beaver populations in Illinois. An analysis of molecular variance revealed significant genetic subdivision among breeding groups in southern Illinois ($F_{ST} = 0.086, P < 0.001$), whereas regional genetic subdivision was evident in central Illinois ($F_{ST} = 0.037, P < 0.001$). Overall $F_{ST}$ between populations also was significant ($0.068 \pm 0.012 \text{ SE}, P < 0.001$). Bayesian clustering assigned individuals from the 2 geographic sampling regions into 2 distinct genetic clusters with 70% of individuals assigned to 1 of the 2 clusters. Migration between populations was low at 0.16 individuals/generation (confidence interval = 0.0079–0.33). Estimates of population subdivision, cluster analysis, and dispersal indicate that these populations are genetically distinct, but are connected by infrequent dispersal.

Key words: Bayesian clustering analysis, beaver, Castor canadensis, dispersal, $F_{ST}$, genetic structure

Mammalian mating systems and social structure are of particular interest to researchers because of the important role they play in evolution (Sugg et al. 1996). Consequently, the field of population genetics has adopted a “social structure” approach, in which breeding units represent a distinct level in hierarchical population studies (Chesser 1991; Clutton-Brock 1989; Storz 1999; Sugg et al. 1996). This social structure subdivides mammalian populations into partially isolated breeding groups in which gene flow may be limited and the effective population size of local demes is reduced (Chesser et al. 1993; Clutton-Brock 1989). For example, polygynous species with sex-biased dispersal, such as black-tailed prairie dogs (Cynomys ludovicianus), exhibit considerable genetic structuring within and between populations with $F_{ST}$ values as high as 0.22 between groups (Chesser 1983; Dobson et al. 1998; Roach et al. 2001). Although patterns of genetic population structure in highly kin-structured, polygynous species have received considerable attention, few studies have investigated genetic structure in pair-bonded, socially monogamous mammals (Balloux et al. 1998; Fredsted et al. 2007).

The North American beaver (Castor canadensis) represents an ideal organism with which to investigate genetic population structure because beavers exhibit flexibility in their mating behavior and social system. Several studies of 2 beaver populations in Illinois reveal marked differences in colony composition, dispersal, and mating behavior between populations (Bloomquist 2007; Cleere 2005; Crawford et al. 2008; Havens 2006, McNew and Woolf 2005). Beavers traditionally have been considered monogamous based on behavior and colony composition (Sun 2003). However, examination of recent genetic data suggests that beavers are not always genetically monogamous and will adopt a promiscuous mating strategy when extra mates are available (Crawford et al. 2008). Although beavers mate with individuals other than their pair-bonded mate, extrapair mating is not restricted to mating within the colony; rather, numerous occurrences of intercolony...
extrapair mating have been observed (Crawford et al. 2008). Despite reports of nearly equal dispersal rate and distance between the sexes (Bloomquist 2007; Havens 2006; McNew and Woolf 2005; Sun et al. 2000), genetic kinship analysis has indicated female philopatry in colonies from 1 of our study populations (Crawford et al. 2008). Such sex-biased philopatry can result in high genetic subdivision between breeding groups, because females within colonies will be more closely related to each other than they are to females from other colonies (Storz 1999). In beaver colonies, where even philopatric females mate with multiple males, this subdivision should be reduced when intercolony mating occurs (Crawford et al. 2008). Although strongly polygynous species with sex-biased dispersal may be expected to exhibit subdivision among breeding groups (Chesser 1983; Storz 1999), less is known regarding expectations of genetic structure among breeding groups of pair-bonding, yet promiscuous mammals. Given this socially monogamous, yet genetically promiscuous structure, we asked where beaver populations would lie in the continuum of genetic population structure, from strictly monogamous to fully polygynous kin-structured populations.

A 2nd aim of this paper was to investigate genetic differentiation between partially isolated beaver populations in Illinois. Genetic differentiation can be a useful measure of movement between populations and may be applied to studies investigating dispersal, population isolation, and patterns of colonization (Bohonak 1999). However, estimates of differentiation, such as $F_{ST}$ (Weir and Cockerham 1984), may be less informative than more recently developed techniques, and assumptions of equilibrium may be violated in small populations that have undergone demographic perturbations (Pearse and Crandall 2004). Bayesian clustering analysis can be used to define populations based on genotypes (rather than geographic demarcations) and can be useful in assigning biologically appropriate management units (Pearse and Crandall 2004).

The well-documented ecology and social structure of beavers, and particularly that of our 2 study populations, allows us to assess aspects of genetic structure within and between populations. In central Illinois, where beaver colonies are typically composed of 1st-order relatives and dispersal is nearly equal between the sexes (Crawford et al. 2008; Havens 2006), genetic subdivision is expected to follow an isolation-by-distance model, with subdivision increasing with increasing distance between colonies (Wright 1965). Alternatively, the southern Illinois population is characterized by large colonies composed of 1st- and 2nd-order relatives, female philopatry, and a promiscuous mating system (Bloomquist 2007; Crawford et al. 2008). Because intercolony mating is also common in this population (Crawford et al. 2008), we expect subdivision to be limited among colonies. Finally, average natal dispersal distance in our 2 populations shows wide variation between study sites and years, but is typically $<30$ km (Bloomquist 2007; Cleere 2005; Havens 2006; McNew and Woolf 2005). Consequently, we expect that central and southern Illinois will be genetically distinct because dispersal between distant populations should be rare.

**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. Colonies in central Illinois were located in 2nd-, 3rd-, and 4th-order streams within the Embarras River watershed (Havens 2006). Beavers were open to harvest in central Illinois and colony density was estimated at 0.4 colonies/km of stream (Cox 2005). Throughout, we use the term “colony” to denote a group of beavers living in the same lodge or lodges. A colony was not necessarily composed of related individuals, as we have previously observed (Crawford et al. 2008).

In southern Illinois, beavers also were trapped during September–March of each study year from the Union County Conservation Area, a waterfowl refuge along the Mississippi River. 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 Union County Conservation Area; colony density was estimated at 3.3 colonies/km² (Bloomquist 2007).

**Sample collection.**—Beavers 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 HCl (10 mg/kg) and xylazine hydrochloride HCl (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, categorized as young (<2 years), subadults (2–3 years), or adults (>3 years) based on body mass (McTaggart and Nelson 2003), and sex was determined by palpation (Osborn 1955). A biopsy punch of ear tissue was collected and stored in 95% ethanol or aluminum foil at −20°C. Sex was later confirmed by molecular sex diagnosis using the SRY marker located on the Y-chromosome (Kühn et al. 2002). Additional tissue samples were collected from removal-trapped beavers harvested during the 2005–2006 and 2006–2007 Illinois furbearer harvest seasons at both study locations. These beavers also were assigned to age classes based on mass, and sex was determined by dissection. Fetal tissue samples were collected and stored from females in southern Illinois.

**Microsatellite analyses.**—DNA was extracted from beavers in central ($n = 55$) and southern Illinois ($n = 72$, including 22 fetal samples) using a DNeasy Extraction Kit (Qiagen, Inc., Valencia, California). Microsatellite analysis was conducted for 7 loci (Cca8, Cca9, Cca10, Cca13, Cca15, Cca18, and Cca19) following the protocol described by Crawford et al. (2007). Forward primers for each locus were labeled with Well-Red fluorescent tags D3 or D4 (Sigma-Aldrich, St. Louis, Missouri).
and alleles were scored on a CEQ8800 (Beckman-Coulter, Fullerton, California) using Fragment Analysis software provided by the manufacturer. Genotyping accuracy was confirmed by mother–fetal allele matches and by running 10% of our samples ≥ 3 times.

**Genetic differentiation within populations.**—We used GENEPOP 3.4 (Raymond and Rousset 1995) to conduct Fisher’s exact tests of Hardy–Weinberg equilibrium across all loci within each population using the Markov chain method (Guo and Thompson 1992). Significance of multiple tests was assessed after \( P \)-values were adjusted using a sequential Bonferroni correction as described by Rice (1989), where \( k \) was defined as the number of microsatellite loci. To assess genetic structure within populations, we conducted analyses of molecular variance (AMOVAs) using Arlequin version 2.0 software (Schneider et al. 2000). These tests calculate fixation indices \((F_{ST})\) analogous to Wright’s \( F \)-statistics (Wright 1965), which allowed us to investigate hierarchical population structure by differentiating variation between groups versus variation within each group (Excoffier et al. 1992). Differentiation between the sexes was tested using both adult and subadult samples within each population because individuals classified as subadults may represent offspring that have delayed dispersal and therefore are still capable of dispersing in the future (Bloomquist 2007; Havens 2006). AMOVAs also were conducted for age classes (adults, subadults, young, and fetal samples where available) within both populations.

Colonies in southern Illinois were typically larger \((\bar{X} = 9.0 \pm 2.0 \text{ beavers/colony}, \text{excluding fetal samples})\) than those in central Illinois \((\bar{X} = 3.8 \pm 2.4 \text{ beavers/colony})\) and contained numerous breeding adults (Crawford et al. 2008). Therefore, in southern Illinois, we had the opportunity to test for genetic subdivision among the 3 colonies sampled \((n = 27 \text{ individuals})\) using an AMOVA. In contrast, colonies from central Illinois were composed of only a few individuals representing a single family or unrelated group and this small sample size prohibited \( F_{ST} \) analysis among colonies. These colonies were sampled over 3 counties, a larger geographic area compared to the sampling scheme used in southern Illinois, and there was some question whether population substructure was present at the regional scale. We tested for genetic subdivision by grouping 55 individuals from 12 colonies into 1 of 3 geographic regions in central Illinois based on global positioning system trap locations (Mattoon, Toledo, and Charleston; Fig. 1). For all AMOVAs, observed \( F_{ST} \) was compared to those derived from 10,000 permutations to assess significance at the \( \alpha = 0.05 \) level.

**Genetic differentiation between populations.**—GENEPOL was used to determine differences in allele frequencies between populations using Fisher’s exact tests. Significance of multiple tests was assessed in the manner described above for within-population tests. The program SPAGeDi version 1.2 (Hardy and Vekemans 2002) was used to calculate \( F_{ST} \) as described by Weir and Cockerham (1984) and significant \( P \)-values were determined by permutation tests.

**Bayesian analysis of population structure.**—To further assess genetic differentiation within and between the central and southern Illinois populations, we conducted a Bayesian clustering analysis using the program STRUCTURE (Pritchard et al. 2000). This program uses multilocus genotypes to assign fractions of each individual’s genetic ancestry into genetic clusters based on a predefined number of \( K \) clusters. This approach requires that allele frequencies within each cluster are in Hardy–Weinberg equilibrium and that loci are not linked. We estimated \( K \) using the Monte Carlo Markov chain approach for each \( K \) after a burn-in period of 50,000 and a run length of 100,000 iterations. The posterior log-likelihood of \( K \) was estimated for \( K = 1–8 \) genetic clusters with 5 independent runs at each \( K \). For each run, we chose the admixture model of ancestry and specified that allele frequencies were correlated. We did not include prior population information in the model when assigning individuals to clusters. We estimated the true number of genetic clusters by calculating \( \Delta K \) as described by Evanno et al. (2005). Individuals were then assigned to a single cluster if their membership coefficient in that cluster was \( \geq 0.80 \).

**Dispersal between populations.**—Recent dispersal between central and southern Illinois populations was inferred using a Bayesian approach in BAYESASS+ (Wilson and Rannala 2003). This method uses multilocus genotypes to assign
expected heterozygosity ($H_e$), expected heterozygosity ($H_e$), and associated $P$-values for beaver (*Castor canadensis*) populations in central and southern Illinois, 2005–2007. Asterisks (*) indicate significant deviation from Hardy–Weinberg equilibrium after Bonferroni correction at $\alpha = 0.05$.

<table>
<thead>
<tr>
<th>Population/locus</th>
<th>$A$</th>
<th>$H_e$</th>
<th>$H_o$</th>
<th>$P$</th>
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</thead>
<tbody>
<tr>
<td><strong>Central Illinois</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cca8</td>
<td>9</td>
<td>0.740</td>
<td>0.750</td>
<td>0.068</td>
</tr>
<tr>
<td>Cca9</td>
<td>8</td>
<td>0.727</td>
<td>0.707</td>
<td>0.533</td>
</tr>
<tr>
<td>Cca10</td>
<td>15</td>
<td>0.764</td>
<td>0.818</td>
<td>0.021</td>
</tr>
<tr>
<td>Cca13</td>
<td>4</td>
<td>0.389</td>
<td>0.350</td>
<td>1.000</td>
</tr>
<tr>
<td>Cca15</td>
<td>4</td>
<td>0.655</td>
<td>0.630</td>
<td>0.297</td>
</tr>
<tr>
<td>Cca18</td>
<td>3</td>
<td>0.527</td>
<td>0.504</td>
<td>0.570</td>
</tr>
<tr>
<td>Cca19</td>
<td>10</td>
<td>0.788</td>
<td>0.837</td>
<td>0.093</td>
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<tr>
<td><strong>Overall</strong></td>
<td></td>
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<td>0.065</td>
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<td><strong>Southern Illinois</strong></td>
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<tr>
<td>Cca8</td>
<td>7</td>
<td>0.886</td>
<td>0.842</td>
<td>0.001*</td>
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<tr>
<td>Cca9</td>
<td>9</td>
<td>0.806</td>
<td>0.772</td>
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<tr>
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<td>0.002*</td>
</tr>
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<td>Cca13</td>
<td>5</td>
<td>0.542</td>
<td>0.522</td>
<td>0.978</td>
</tr>
<tr>
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<td>5</td>
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<td>0.476</td>
<td>0.113</td>
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<tr>
<td>Cca18</td>
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<td>0.498</td>
<td>0.528</td>
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<tr>
<td>Cca19</td>
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<td>0.817</td>
<td>0.731</td>
<td>0.441</td>
</tr>
<tr>
<td><strong>Overall</strong></td>
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<td>0.001*</td>
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Genetic differentiation between populations.—Central and southern Illinois populations differed significantly in allele frequencies at 6 of 7 loci ($P < 0.001$), with locus Cca18 being the single exception ($P = 0.772$). Locus Cca18 was not significantly different from 0 between populations ($F_{ST} = −0.008$, $P = 0.250$). All other $F_{ST}$ values for single loci were significantly different from 0 and ranged from 0.052 to 0.15 ($P < 0.001$). The overall $F_{ST}$ value ($0.068 \pm 0.012$ SE) between populations was significantly different from 0 ($P < 0.001$).

Bayesian population structure.—The $\Delta K$ calculations were highest when only 2 genetically distinct clusters were identified ($\Delta K = 2$ was 377), whereas estimates for all other values of $K$ were <15. These clusters corresponded to the central and southern Illinois sampling areas. Membership coefficients assigning individuals to 1 of the 2 clusters were high, with a mean of 0.82 ($SD = 0.17$). Seventy-four (70%) of 105 individuals were assigned to 1 of the 2 clusters, and 71 (98%) of these individuals were assigned to the cluster identified with their geographic origin. One beaver from central Illinois was assigned to the southern Illinois cluster, and 2 individuals from southern Illinois were assigned to the central Illinois cluster. Seventeen (31%) of 55 beavers from the central Illinois population and 14 (28%) of 50 beavers from southern Illinois were shown to be of mixed ancestry.

DISCUSSION

Few genetic surveys have been conducted to compare local differences within populations of socially monogamous mammals. In this study, central and southern Illinois beaver populations represented very different demographic and social systems. The central Illinois population reflected the social structure typically associated with beavers, that of small colonies composed of single-family groups (Sun 2003), whereas the southern Illinois population was composed of large colonies with multiple breeding adults (Crawford et al. 2008). The differences in social structure may be due largely to differences in environment. Although colony size may be constrained and intercolony interactions restricted on streams and rivers in central Illinois (Havens 2006), beavers inhabiting the lakes of southern Illinois are free to interact with members of nearby colonies. Beavers in linear habitats, such as in central Illinois, defend a linear home range, whereas beavers inhabiting lakes are less able to mark and defend the nonlinear lacustrine environment. In addition, larger colony size in the unharvested southern Illinois population provided the opportunity for increased interactions at this study site.
These ecological differences between the central and southern Illinois populations clearly have genetic consequences. Contrary to our prediction that southern Illinois colonies would exhibit low $F_{ST}$ values due to promiscuous intercolony mating, we documented a moderate level of subdivision, with an $F_{ST}$ value of nearly 9%. Despite previous studies based on radiomarked individuals indicating approximately equal dispersal between the sexes (Bloomquist 2007; McNew and Woolf 2005), adult females within colonies in southern Illinois were often 1st-order relatives, suggesting female philopatry (Crawford et al. 2008). Under such a scenario, we might expect $F_{ST}$ values to be similar to those of polygynous species with female philopatry. Highly kin-structured mammals such as black-tailed prairie dogs (C. ludovicianus—Chesser 1983, Dobson et al. 1998) and red howler monkeys (Alouatta seniculus—Pope 1998) show between-group $F_{ST}$ values ranging from 0.142 to 0.227. However, Schwartz and Armitage (1980) found that yellow-bellied marmots (Marmota flaviventris), despite moderate female philopatry, had enough dispersal of both sexes between colonies to limit genetic structuring, resulting in an estimate of between-colony $F_{ST}$ (0.07) that was similar to that observed in this study. Although it appeared that females remained in their natal colonies in southern Illinois, leading to moderate subdivision, parentage analysis also indicated recent intercolony mating and a promiscuous mating system (Crawford et al. 2008). Therefore, gene flow between colonies was maintained despite the fact that these colonies functioned primarily as distinct breeding units.

Individual beaver colonies in central Illinois were too small to conduct tests of among-colony genetic subdivision, so the colonies were grouped into 3 local clusters that showed low levels of among-cluster genetic subdivision. This result is consistent with reports that beavers in this region disperse on average 12.2 km from their natal colony (Havens 2006). The observed $F_{ST}$ was similar to that found in other studies of local population subdivision, such as yellow-pine chipmunks (Tamias amoenus; $F_{ST} = 0.019–0.036$—Shulte-Hostedde et al. 2001) and Columbian ground squirrels (Spermophilus columbianus; $F_{ST} = 0.026$—Dobson 1994).

Bayesian clustering methods can be important in assigning populations to genetically distinct groups for wildlife management and conservation, and can provide a more complete picture of genetic differences compared to a designation of populations based on geography alone (Pearse and Crandall 2004). This is especially true when identifying cryptic genetic subdivision within populations, as has been observed in Scandinavian lynx (Lynx lynx—Ruessen et al. 2003) and coyotes (Canis latrans—Sacks et al. 2005). Although traditional $F$-statistics can be an important measure of genetic variation in populations and can be used to estimate inbreeding within a population or differentiate between populations, $F$-statistics represent only 1 measure of population differentiation (Neigel 2002; Pearse and Crandall 2004). Still, $F$-statistics are commonly employed in population genetics and are readily comparable among studies (Neigel 2002). Given the geographic distance between beaver populations in central and southern Illinois (>200 km) coupled with the known mean dispersal distances of beavers (generally <30 km), we expected $F_{ST}$ estimates to reflect a moderate level of population subdivision between the 2 populations. Both overall and single-locus $F_{ST}$ values indicated moderate levels of genetic differentiation between central and southern Illinois beaver populations (Wright 1978). Significant differences in allelic distribution also illustrated that both populations contained unique alleles at all but 1 locus.

Although the relationship is difficult to assess, there is some consensus that $F_{ST}$ values and dispersal ability are negatively correlated (Bohonak 1999; Neigel 2002). Using microsatellite markers, researchers found that monogamous greater white-toothed shrews (Crocidura russula) exhibited $F_{ST}$ values between populations that mirrored the estimate found in this study at 5–6% (Balloux et al. 1998). Sommer (2003) showed significant $F_{ST}$ differences among fragmented populations of Malagasy giant jumping rats (Hypogeomys antimena). She found that differences in $F_{ST}$ values were evident for coding versus noncoding DNA, and values were much lower for coding major histocompatibility complex genes (0.02) than noncoding mitochondrial DNA (0.77). These differences were expected because mitochondrial DNA mutates faster than nuclear genes (Sommer 2003), and they also illustrate that meaningful comparison of $F_{ST}$ values across studies should be based on similar genes and gene regions. We expected to find significant genetic differences between the central and southern Illinois beaver populations, in part because they were separated by >200 km. Bayesian cluster analysis and low-to-moderate estimates of recent dispersal support this conclusion. Despite evidence for occasional long-distance dispersal in beavers (Havens 2006), average dispersal distances in both populations in this study were too short to allow for frequent immigration (Havens 2006; McNew and Woolf 2005). The relatively low but significant $F_{ST}$ value of 0.068, along with estimated dispersal and distinct genotypic clustering between populations, indicated limited subdivision. However, our analysis suggests that infrequent dispersal between these 2 populations has occurred. Beavers are known to be abundant within major river systems between the central and southern Illinois study sites (Woolf et al. 2003), and it is likely that these 2 populations were part of a metapopulation inhabiting the southern portion of the state. Our inability to sample connecting populations may have led to incorrect conclusions regarding mixed ancestry and gene flow between central and southern Illinois.

The use of genetic descriptors other than $F$-statistics has become more common in recent years as statistical and computational power increases (Pearse and Crandall 2004). Our study demonstrates significant population subdivision between central and southern Illinois beaver populations, and the techniques we used can be useful in wildlife management to designate biologically appropriate management units. Despite relatively recent reintroductions of beavers to Illinois (Pietsch 1956), both populations showed moderate levels of genetic variation in microsatellite loci and our study suggests that limited dispersal occurs between these populations. This indicates that these aquatic furbears are capable of long-distance dispersal, a phenomenon that has been seldom
observed in traditional radiotelemetry studies of dispersal. To
our knowledge, only 2 studies have reported dispersal distances
of >50 km. Beer (1955) reported a distance of 82 km, and
Havens (2006) observed 1 beaver from central Illinois
dispersing 286 km downstream. Given that our study
populations were approximately 240 km apart, it appears that
long-distance dispersal between central and southern Illinois
can occur but likely is rare. Future studies that include
mitochondrial DNA may allow us to infer patterns of
recolonization and phylogeography throughout the state.

ACKNOWLEDGMENTS

We thank R. Havens, R. Boeser, M. Bloomquist, E. Hillard, A.
Nollman, and L. Hall for invaluable field assistance and comments on
the project. Thanks to G. Fritz, E. Latch, M. Matocq, A. Runck, and K.
Miller for their helpful advice and comments on this manuscript. We
are grateful for comments provided by 2 anonymous reviewers that
greatly improved the final manuscript. Funding was provided through
the Graduate School at Eastern Illinois University, the Illinois
Department of Natural Resources via Federal Aid in Wildlife
Restoration Project W-135-R, and the Cooperative Wildlife Research
Laboratory, Department of Zoology, and Graduate School at Southern
Illinois University Carbondale.

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Associate Editor was Mark S. Hafner.