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# Long-term pair bonding and genetic evidence for monogamy among urban coyotes (*Canis latrans*)

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Coyotes (*Canis latrans*) occur across North America in many types of ecosystems, including urban areas, yet certain aspects of coyote behavior remain obscure. Previous observational studies have provided evidence that coyotes are socially monogamous; however, the degree to which coyotes exhibit genetic monogamy has not previously been determined. We used radiotelemetry and genetic techniques to determine the mating system of an urban coyote population. We obtained samples from 236 coyotes captured during 2000–2006 in the Greater Chicago Metropolitan Area of Illinois. Individuals were genotyped using 12 polymorphic microsatellite markers. Among 18 litters comprising 96 offspring, we found no evidence of polygamy, and detected a single instance of a double litter (pups from different parents sharing the same den). The 2 mated pairs that contributed to the double litter had not interbred. However, the relatedness values shared between 1 mated pair and the pups that were not their offspring suggested that they were closely related, possibly as cousins or grandparents/grandoffspring. Across all radiocollared mated pairs, mean home range overlap for the male and female was 80.1% ($SD$ = 13.4). Among 7 mated pairs, 3 of which were radiotracked over multiple years, there was no evidence of mate abandonment and multiyear monogamy was maintained. Despite the high food resources available and high population density, urban coyotes display no variability in their monogamous mating system.

Key words: *Canis latrans*, coyote, den sharing, double litter, microsatellites, monogamy, parentage, urban wildlife


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Social monogamy is the rarest form of breeding system among mammals, estimated to occur in only 3–5% of mammalian taxa, yet is the most common breeding system among canids (Kleiman 1977). Furthermore, many canids have been described as ''obligate monogamists,'' meaning that the success of a litter is dependent on the cooperation of both parents (Kleiman 1977). Canid species reinforce social monogamy with behaviors such as continual proximity of the pair during estrus, displayed mating preferences, absence of unrelated adult conspecifics in the home range of the breeding pair, and breeding by only 1 pair in the social group (Kleiman 1977).

Extra-pair copulations (EPCs) have been discovered in every canid mating system that has been investigated genetically, regardless that social monogamy was the observed norm. Indeed, some researchers have predicted that EPCs would be discovered in any canid species investigated genetically (Sillero-Zubiri et al. 1996). A population of island foxes (*Urocyon littoralis*) was reported to practice monogamy, polyandry, and polygyny (Roemer et al. 2001), whereas the bat-eared fox (*Otocyon megalotis*), the Ethiopian wolf (*Canis simensis*), and the African wild dog (*Lycaon pictus*) were reported to have engaged in EPCs (Girman et al. 1997; Gottelli et al. 1994; Wright et al. 2010). Mating tactics for some canid species may be influenced by environmental factors. For example, swift foxes (*Vulpes velox*) and gray foxes (*U. cinereoargenteus*) were thought to have monogamous mated pair systems, but were shown through genetic analysis to be polygamous in high-density populations (Kitchen et al. 2006; Weston Glenn et al. 2009). Density and territory size can be indicative of resource abundance, which has been suggested as being a motivating factor of EPCs for other canid species. For example, Zabel and Taggart (1989) suggested that red foxes (*V. vulpes*) are usually monogamous, but cross a polygyny threshold when presented with an abundance of resources. The polygyny threshold is reached when a female mates with an already paired male and

experiences reproductive success that is equal to or greater than a female that pairs with an as-yet unpaired male. A study of urban red foxes reported further support for polygynous behavior (Baker et al. 2004), and a study of arctic foxes (*Alopex lagopus*) reported a parallel behavior, a switch from monogamy to polyandry when resources were high (Carmichael et al. 2007). Another potential factor influencing EPCs is shrinking habitat, which can lead to a smaller mate pool. Sillero-Zubiri et al. (1996) suggested that EPCs in a declining population of the endangered Ethiopian wolf may be a strategy to avoid inbreeding and increase the genetic diversity within each litter. Social structure may also influence mating systems. A cross-species analysis by Cohas and Allainé (2009) suggested that social structure may be a strong predictor for EPCs, because EPC rates for family-living and solitary species were higher than those for pair-living species.

Multiple lines of evidence support social monogamy in coyotes, including such behaviors as mated pairs defending their territory jointly, exhibiting an approximately 20-min postcopulatory tie, and participating in group howls (Andelt 1985). Coyotes have an unusually long proestrus period, which is strongly associated with pair bonding in canids (Asa 1997). Coyotes tend to have large litters and their offspring have long dependency periods, during which both parents tend the pups and defend the den (Bekoff 1977). Additionally, nursing females rely on the male for provisioning and territory defense (Sacks and Neale 2001). Mated pairs display fidelity until 1 mate dies, and they do not often ''divorce'' (Sheldon 1992, but see Andelt 1985). Behavioral studies have shown that mated pairs maintain a bond across years, producing a litter annually (Bekoff and Gese 2003). Additionally, sexual dimorphism is minimal in coyotes (Bekoff 1977), which is typical of monogamous species (Kleiman 1977).

Although there is strong evidence for social monogamy in coyotes, extra-pair mating behaviors have been reported, such as 2 reported observations of a female mating with multiple males in 1 estrus cycle (Cadieux 1983; Gese et al. 1996), and reports of males provisioning breeding females at 2 separate dens (Crabtree and Varley 1995; Gese et al. 1996; Parker 1995; Way et al. 2001). These reports bring into question the monogamous behavior of coyotes, which has heretofore not been investigated genetically.

Coyotes have become a common presence in urban areas across North America. This study focuses on a population of coyotes adapted to the urban landscape of the Chicago metropolitan area. A diet analysis of coyotes in the study area revealed a reliance on a variety of natural foods (Morey et al. 2007). The main contributing factor to coyote mortality was vehicular collisions, which caused 62% of the deaths of study animals (Gehrt and Riley 2010). Annual adult survival rates ranged from 0.48 to 0.83 (both sexes combined; Gehrt and Riley 2010), which is higher than adult survival rates reported for exploited populations (e.g., 0.38—Roy and Dorrance 1985).

Although several canid species are known to inhabit urban areas (e.g., kit foxes, red foxes, and coyotes—Baker and Harris 2007; Cypher 1993; Grinder and Krausman 2001), few studies have assessed how urbanization may affect mating systems of these species (Baker et al. 2004). Coyotes in urban landscapes generally exhibit small territory size and higher local densities relative to those in rural areas (Atwood et al. 2004; Fedriani et al. 2001; Gehrt and Riley 2010). These are indicators of high resource availability. In the study area for this research paper, coyote population density is high and ranges from 2 to 6 individuals per $km^2$ (Gehrt and Riley 2010). Additionally, the coyotes in this study area form packs and retain nonbreeders within the territory of the mated pair (Hennessy 2007), which has been reported to be an indicator of high resource availability among other canids, notably red fox (von Schantz 1984). Given these indicators, it is likely that coyotes in this study area experience near-optimal conditions for reproduction, which make them ideal for studying the limits of monogamy. Because other canid species deviate from monogamous arrangements when experiencing high resource availability, we expect urban coyotes to do the same. Previous studies of this coyote population have shown that territory boundaries abut one another and mature transient coyotes roam across many territories (Gehrt et al. 2009). Presumably, the high density of the coyote population provides ample opportunity for EPCs. Additionally, the prevalent social structure in this study area of pack-living coyotes (as opposed to pair-living) indicates that EPCs would be expected (Cohas and Allainé 2009). Our primary objective was to test the prediction that coyotes would exhibit complex breeding systems in high-resource, densely populated urban areas. Additionally, we investigated other aspects of coyote mating structure that we encountered; notably double litters (wherein 1 litter comprises pups from 2 mothers) and the behavior of coyotes after the death of a mate.

## Materials and Methods

*Study area.*—Fieldwork was conducted in portions of the following counties of northeastern Illinois: Cook, Kane, Dupage, and McHenry. These counties are part of the Greater Chicago Metropolitan Area, which is home to approximately 9.7 million people (United States Census Bureau 2008), and is the 3rd largest metropolitan area in the United States. The majority of the area has been heavily fragmented by roads and urban development, although small patches of eastern tallgrass prairie, open oak stands, and a few scattered wetlands remain (Fig. 1; Greenberg 2002). The study area comprised the following land use types: commercial/industrial (43%), residential (20%), agriculture (14%), undeveloped (13%), and other (10%—Gehrt et al. 2009).

*Sample collection.*—Coyotes were captured with padded foothold traps or with cable restraint devices during 2000–2006 as part of a larger study of coyote ecology in the Chicago region (Gehrt et al. 2009). Captured adult coyotes were transported in handling cages to a laboratory for processing, where they were immobilized with an intramuscular injection of Telazol (Lin et al. 1993; Fort Dodge Animal Health, Fort Dodge, Iowa). During late spring each year, coyote pups were

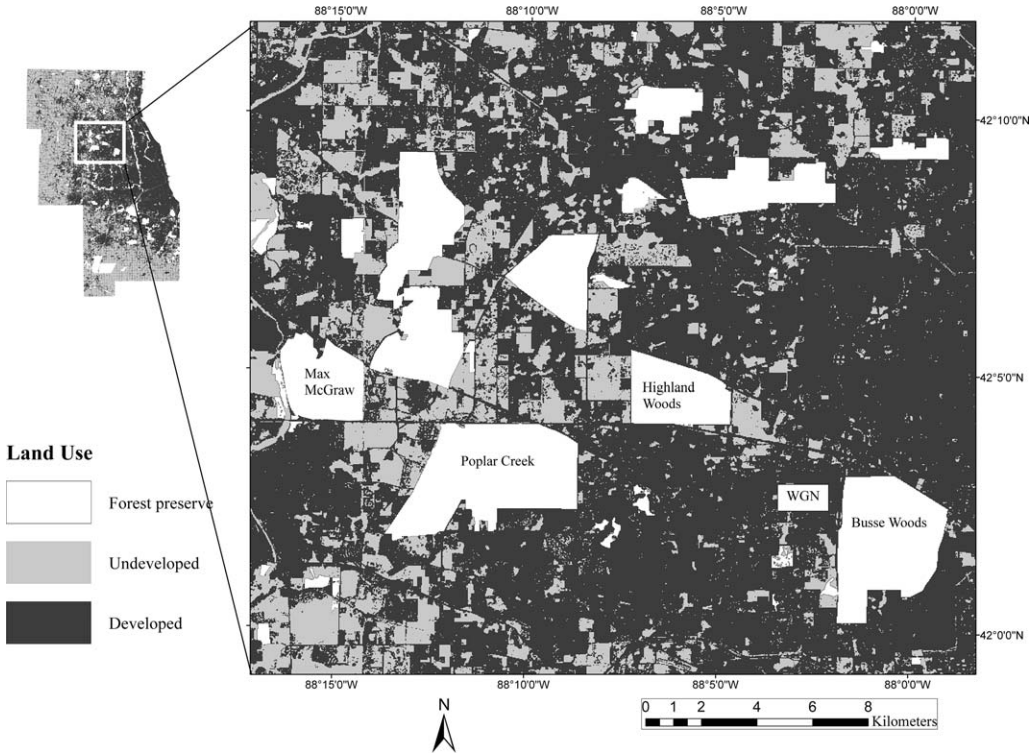


**Fig. 1.**—Study area in the Greater Chicago Metropolitan Area, with labels on the major trapping areas. Genetic samples from coyotes (*Canis latrans*) were collected from 2000 to 2006.

excavated from dens and restrained by hand without chemical immobilization. Age was estimated on the basis of size, weight, and incisor wear (Parks 1979). Reproductive condition of adults was estimated by the size of testes or condition of teats. All animals were assumed to have been born in April or early May (Bekoff 1977). The term ''pup'' refers to coyotes that are less than 1 year old, ''yearling'' refers to coyotes that are 1 to 2 years old, and ''adult'' refers to coyotes that are older than 2 years of age. Each captured individual was assigned a unique alphanumeric identification that included a reference to the trap location. Pups older than 5 months, yearlings, and adults were ear-tagged in both ears and fitted with radiocollars (Advanced Telemetry Systems, Isanti, Minnesota). Subcutaneous transponder chips (AVID Marketing Inc., Norco, California) were implanted under the dermis of the scruff of pups younger than 5 months to provide identification upon recapture.

Blood samples were drawn using a sterile needle and syringe and were deposited in serum-separating tubes for the purposes of disease analysis; after centrifuging, the plasma was removed and the remaining blood product was kept in frozen storage (−20°C) until deoxyribonucleic acid (DNA) extraction. Tissue samples were collected opportunistically from road-killed and nuisance coyotes that had been euthanized by Cook County wildlife officials and stored in sealed bags in frozen storage (−20°C). In some instances, hair bulbs instead of blood samples were obtained from pups, due to small veins, and these were also kept in frozen storage (−20°C). Coyotes were released at the capture location. Capture and handling protocols were approved by the Institutional Animal Care and Use Committee at The Ohio State University, protocol number 2003R0061. Research adhered to the guidelines of the American Society of Mammalogists for the use of wild mammals in research (Sikes et al. 2011).

*Genetic methods.*—Blood and tissue samples were extracted using a standard phenol–chloroform procedure (Sambrook et al. 1989). Hair bulb samples were processed using Qiagen QIAamp Mini DNA Kit (Qiagen, Los Angeles, California). We used 12 domestic dog (*C. lupus familiaris*) microsatellite markers that amplified in coyotes (annealing temperature was 56°C except where noted in brackets: CXX109 [59°C], CXX123, CXX204 [59°C], CXX213, CXX225, CXX250—Ostrander et al. 1993; CXX172 [52°C]—Roy et al. 1994; FH2328 [52°C], FH2380 [52°C]—Breen et al. 2001; FH2161 [52°C], FH2054, FH2088—Francisco et al. 1996). Polymerase chain reactions (PCRs) were carried out in 12.5-µl reaction volumes containing 40 ng of DNA, 0.2 mM dinucleotide triphosphate, 8 pmol of primer, 0.5 U of *Taq* polymerase, 1× reaction buffer, and 1.6–2.0 mM $MgCl_2$. Reactions were performed in a BioRad iCycler (Bio-Rad Laboratories, Hercules, California) with the following profile: initial denaturation step 94°C (2 min) followed by 35 cycles of denaturation at 94°C (1 min), annealing temperature (45 s), and an extension at 72°C (1 min), followed by a 10-min extension of 72°C. Amplified products were sized on a Beckman-Coulter CEQ 8000XL automated capillary electrophoresis system (Beckman-Coulter, Inc., Fullerton, California), along with a 400-base-pair internal size standard.

Microsatellite alleles were scored using Genetic Analysis System Software (version 8.0, Beckman-Coulter, Inc., Fullerton, California).

We validated the consistency and accuracy of allele calls for all markers and individuals in 4 ways. First, known first-order relative pairs (2 mother–offspring pairs) were used to optimize PCR conditions and to confirm allele calls for all loci. Second, fragment sizes for each individual, locus, and allele were graphed to compare bin assignments. Fragments that were on the margins of each bin were reanalyzed. Third, we amplified and reran approximately 20% of the total sample set to clarify ambiguous signals, and to ensure precision through duplication. Finally, we used MICROCHECKER (van Oosterhout et al. 2004) to survey the loci for evidence of scoring errors, large allele dropout, and null alleles (Bruford and Wayne 1993; DeWoody et al. 2006).

*Statistical analysis.*—We used the program FSTAT (version 2.9.3.2; Goudet 2001) to calculate expected and observed heterozygosity, number of alleles, and $F_{IT}$ at each locus, all of which were performed on the adult population only (Weir and Cockerham 1984). If pups and yearlings were included in the calculation of *F*-statistics, the inbreeding coefficient could be inflated. We used the Weir and Cockerham (1984) method with jackknifing over loci to obtain the *F*-statistics for the population. We used GENEPOP (version 4.1; Rousset 2008) and FSTAT (version 2.9.3.2; Goudet 2001) to determine whether the population was in Hardy–Weinberg equilibrium and the loci in linkage equilibrium. To mitigate for multiple comparisons, we applied Bonferroni corrections post hoc (Rice 1989). Allele frequencies, parental exclusionary power, polymorphic information content, and probability of identity were determined by CERVUS (version 3.0.3; Marshall et al. 1998).

Genotypes of pups and candidate parents were sorted by year. We included all biologically possible parents in the analysis; i.e., a pup born in 2000 could have been a parent in 2001 (Mengel 1971). Likewise, a yearling caught early in 2001 was most likely a pup in 2000 and was included in the cohort of pups for the previous year. Parentage analysis was not limited by territory usage, because coyotes are capable of making long-distance forays, which may not be evidenced by radiotelemetry data. We defined a ''litter'' as 3 or more pups in the same den. Genotype data and relatedness information (see below) were used to investigate the parentage of litters, and to confirm that all the pups in a litter came from the same 2 parents. In cases where only 1 parent and $\geq$3 offspring were sampled, the unsampled parent was identified by excluding the alleles in the genotypes of the offspring that came from the known parent (genotype reconstruction). In these cases, the unsampled parent was given a unique combination of name (UF/M, for unidentified female/male) and number so that the reconstructed genotype could be included in the pool of potential parents for other offspring. In the situations for which neither parent was sampled, we confirmed that there were no more than 4 alleles at each locus for the litter, as this is the maximum that 2 heterozygous parents could pass on to their offspring. No reconstruction was performed in these situations.

Genotypes of pups were matched with parents using the programs CERVUS and PASOS (version 1.0; Duchesne et al. 2005). The program CERVUS allocates parents to offspring using a likelihood-based approach and calculates statistical significance on the basis of the difference in the logarithm of the likelihood ratio scores of candidate parents. The program PASOS calculates likelihood of parent assignment using the same method, but was designed to identify parents in open systems. To this end, PASOS estimates the number of uncollected parents and includes reconstructed genotypes in the allocation procedure. Both programs allow for genotyping errors. Results from PASOS and CERVUS were compared for agreement.

Relatedness for all coyotes in the population was determined using KINGROUP (version 2.9; Konovalov et al. 2004). This program uses population allele frequencies and genotypes of the individuals to calculate the likelihood that the shared alleles of the 2 individuals are identical by descent, which results in a relatedness ratio referred to as Grafen's relatedness coefficient (*r*). KINGROUP allows the user to set $r_m$ and $r_p$, which define the probabilities that individuals share an allele by direct descent from their mother or father, respectively. We set the primary hypothetical $r_m$ and $r_p$ values at 0.5, as this is the relatedness coefficient expected between first-order relatives such as parents and offspring or full siblings. The program ran a simulation on the basis of allelic frequencies and hypothesized relationships, which was repeated 10,000 times to provide a distribution of likelihoods and determined a significance level at 0.001. We ran similar tests with both $r_m$ and $r_p$ set at 0.25. These tests were performed to test the likelihood that 2 individuals would be related as second-order relatives (e.g., half-siblings, cousins, or grandparents/grandoffspring). Manual checks of all genotypes for likely relatives were completed to verify that parentage assignments and subsequent KINGROUP analyses agreed. In addition, we used the program KINSHIP (Goodnight and Queller 1999) to estimate *r*-values between individuals. First- and second-order relationships were evaluated at the same *r*-values as used in KINGROUP.

*Spatial analyses.*—Radiocollared coyotes were located by triangulation with a truck-mounted Yagi antenna and receiver (Advanced Telemetry Systems, Isanti, Minnesota). Tracking shifts at 1–2-h intervals were conducted 5–10 times per month. Radiotelemetry locations were recorded as universal transverse Mercator coordinates and imported into ArcGIS (ver. 3.2, ESRI; Environmental Systems Research Institute, Inc., Redlands, California). Ninety-five percent minimum convex polygons (MCPs) were constructed for each radiocollared member of a mated pair. MCPs were preferred to fixed-kernel polygons because they do not extend home ranges beyond known locations with probability zones (Seaman and Powell 1996; Worton 1989). For more detailed radiotelemetry and home range estimation methods used in this project, see Gehrt et al. (2009). Percent overlap of MCP areas was determined using the Geoprocessing feature in ArcGIS with the following formula (Atwood and Weeks 2003): $([\text{area}_{AB}/\text{home range}_A][\text{area}_{AB}/\text{home range}_B])^{0.5}$. When 2 individuals exhibited at

least 30% overlap between their home ranges, they were considered to be interacting in some way, either as pack members or as putative members of a mated pair, depending on their age, sex, and behavior (Andelt 1985; Patterson and Messier 2001). Radiotelemetry was fundamental to identifying potential mated pairs in the sample before genetic analysis, and to locate den sites.

## Results

*Genetic analysis.*—We obtained viable genetic samples from 236 individual coyotes during 2000–2006. The majority of animals ($n = 225$) were genotyped at all 12 loci, but some were not ($n = 11$), due to low concentrations of DNA in hair extractions. Individuals genotyped at less than 10 loci were not included in the analysis.

The program FSTAT calculated a $F_{IT}$ score of 0.020 ($SE = \pm 0.013$). Using CERVUS, average expected heterozygosity was 0.691 and average observed heterozygosity was 0.697 (Table 1). Locus CXX204 was the least polymorphic locus, but it was retained because it amplified samples reliably. In addition, it exhibited the highest exclusionary power (Table 1). Using GENEPOP, we found that the population was in Hardy–Weinberg equilibrium (when the $H_0$: heterozygote deficient; $P = 0.53$). A total of 44 marker pairs was significant for linkage disequilibrium after Bonferroni corrections, from both FSTAT and GENEPOP analyses. However, previous genomic mapping studies have shown that 16 of these significant pairs are in different linkage groups and are not physically linked (Mellersh et al. 1997, 2000; Neff et al. 1999, Richman et al. 2001, vonHoldt et al. 2010). In addition, studies by vonHoldt et al. (2010) and Sacks et al. (2004) reported a high number of significant linkage disequilibrium values for marker pairs in their studies of wolf and coyote populations. They attributed these results to population substructure and nonrandom mating. This is a likely scenario for the coyotes in our landscape. The coyote packs are mostly comprised of family members in this landscape (Hennessy 2007), which could mimic signatures of population structure across the sampled area. Therefore, we did not remove any markers from the study on the basis of linkage disequilibrium. Analysis with MICRO-CHECKER found no evidence of large allele dropout or null alleles, and CERVUS showed null allele frequencies to be <3% (Table 1). The results from CERVUS and PASOS were in agreement. Using CERVUS, total exclusionary power with 1 and 2 parent(s) in the sample respectively was 0.658 and 0.502. Probability of correct allocation was estimated by PASOS at 0.938, and the total estimate of uncollected parents was 16.

*Monogamy analysis.*—One hundred forty-eight of the captured coyotes were radiocollared. Seven mated pairs were identified on the basis of high home range overlap of 2 adult coyotes of the opposite sex. Genetic analysis of the offspring (see below) in the parentally attended dens confirmed that the 7 mated pairs had bred. Percent overlap of mates ranged from 55.3 to 99.6 (Table 2; see also Fig. 2), with a mean of 80.1 ($SD \pm 13.4$). Relatedness values of the mated pairs were generally low ($r = -0.14$ to 0.06); however, 1 mated pair exhibited a higher value ($r = 0.26$; Table 2), suggesting that these 2 mates were potentially related.

**Table 1.**—Microsatellite statistics (CERVUS 3.0.3; Marshall et al. 1998) for 225 coyotes (*Canis latrans*) from the Greater Chicago Metropolitan Area (2000–2006). All were genotyped at 12 microsatellite loci. Number of alleles ($k$), observed and expected heterozygosity ($H_o$ and $H_e$, respectively), polymorphic information content (PIC), total exclusionary power with 1 parent (Excl(1)) and 2 parents (Excl(2)), and the null allele frequency (NF) were calculated for the coyotes sampled, excluding pups to avoid inflating the exclusionary power of the loci.

| Locus | $k$ | $H_o$ | $H_e$ | PIC | Excl(1) | Excl(2) | NF |
|---|---|---|---|---|---|---|---|
| C109 | 8 | 0.816 | 0.831 | 0.807 | 0.514 | 0.342 | +0.0097 |
| C123 | 7 | 0.715 | 0.703 | 0.649 | 0.717 | 0.549 | −0.0088 |
| C172 | 6 | 0.544 | 0.537 | 0.489 | 0.845 | 0.692 | −0.0174 |
| C204 | 3 | 0.232 | 0.220 | 0.198 | 0.976 | 0.900 | −0.0299 |
| C213 | 8 | 0.746 | 0.695 | 0.662 | 0.701 | 0.517 | −0.0369 |
| C225 | 10 | 0.623 | 0.652 | 0.626 | 0.735 | 0.547 | +0.0266 |
| C250 | 10 | 0.776 | 0.808 | 0.785 | 0.543 | 0.366 | +0.0264 |
| FH2328 | 18 | 0.868 | 0.890 | 0.879 | 0.363 | 0.221 | +0.0120 |
| FH2161 | 14 | 0.846 | 0.867 | 0.851 | 0.428 | 0.270 | +0.0114 |
| FH2380 | 4 | 0.636 | 0.584 | 0.496 | 0.825 | 0.703 | −0.0456 |
| FH2054 | 12 | 0.724 | 0.695 | 0.642 | 0.718 | 0.550 | −0.0214 |
| FH2088 | 10 | 0.838 | 0.811 | 0.788 | 0.536 | 0.361 | −0.0163 |
| Average | 9.17 | 0.697 | 0.691 | 0.656 | 0.658 | 0.502 | |

We genotyped 18 litters across 6 years to determine if mated pairs were monogamous. The litters ranged in size from 3 to 10 pups ($\bar{X} = 5.0$, $SD \pm 2.2$), which included 96 pups overall (Table 3). Parentage analysis using CERVUS, PASOS, and KINGROUP revealed that 9 litters had both parents in the sample, 6 litters had 1 parent in the sample, and 2 litters had neither parent in the sample. Additionally, 1 litter was a double litter, with 2 pups from an identified mated pair and 3 pups from 2 unidentified parents. There was no evidence of an extra parent in any litter; that is, the genotypes of all offspring in every litter could be attributed to 2 parents only (with the exception of the double litter, see below). We did not detect evidence of extra-pair mating, either as polyandry or polygyny. Polyandry, if it had occurred, would have been revealed if any offspring in a litter had the same mother as its siblings but a different father. Polygyny, if it had occurred, would have manifested as 2 litters with the same father but with 2 different mothers, most likely in 2 separate dens.

*Double-litter analysis.*—A double litter is a litter that comprises offspring from 2 noninterbreeding mated pairs. One litter, sampled 28 May 2002, appeared to have no discernable differences upon capture; the appearance and weights of the pups were similar (female PC59: 1.3 kg, female PC60: 1.6 kg, female PC61: 1.6 kg, male PC62: 1.3 kg, female PC63: 1.1 kg). However, parentage analysis of the pups in the double litter revealed that there were 2 separate mated pairs involved. The double litter consisted of 5 pups, 2 of which (PC59 and PC63) were offspring from a sampled mated pair (female PC4 and male PC10), and the remaining 3 pups (PC60, PC61, PC62) were offspring from 2 unidentified parents. The $r$-values

**Table 2.**—Home range sharing of coyote (*Canis latrans*) mated pairs in the Greater Chicago Metropolitan Area using minimum convex polygon overlap. All mated pairs included in this table were confirmed by genetic analysis as parents of the offspring at the dens that they attended. Grafen's relatedness coefficient ($r_{xy}$) indicates how closely related mates are to each other ($-1 > r_{xy} > 1$; with 1 being a complete match at all alleles, 0 being unrelated, and negative values being more unrelated than expected by chance).

| Pairing (male + female) | Year | $r_{xy}$ | No. locations (male) | No. locations (female) | % Overlap |
|---|---|---|---|---|---|
| PC10 + PC4 | 2000 | −0.04 | 122 | 185 | 99.57 |
| PC10 + PC4 | 2001 | | 242 | 251 | 87.52 |
| PC10 + PC4 | 2002 | | 448 | 681 | 83.18 |
| WGN14 + WGN13 | 2000 | 0.04 | 65 | 66 | 88.62 |
| MM42 + MM38 | 2001 | 0.26 | 44 | 121 | 59.91 |
| MM42 + MM38 | 2002 | | 575 | 650 | 76.95 |
| PC21 + PC125 | 2005 | −0.14 | 147 | 157 | 85.17 |
| HW88 + HW111 | 2004 | −0.10 | 189 | 296 | 89.12 |
| MM53 + MM113 | 2004 | −0.10 | 125 | 137 | 55.29 |
| WGN115 + WGN1 | 2004 | 0.06 | 222 | 202 | 79.15 |
| WGN115 + WGN1 | 2005 | | 147 | 144 | 66.12 |
| WGN115 + WGN1 | 2006 | | 73 | 65 | 90.57 |

between PC4 and pups PC60, PC61, and PC62 (0.43, 0.17, 0.30; $P < 0.05$) and the *r*-values between the same pups and PC10 (0.15, 0.39, 0.26; $P < 0.05$) were at a level that indicated that the coyotes were relatives, possibly 2nd-order relatives such as cousins or grandparent/grandoffspring. The *r*-values between those 3 pups and the other 2 pups, PC59 and PC63, ranged from 0.30 to 0.51 ($P < 0.05$).

*Behavior following the death of a mate.*—Over the period of the study, there were no instances of divorce as defined by Sheldon (1992). However, we did identify 3 mated pairs (MM42 and MM38; PC4 and PC10; HW88 and HW111) that dissolved due to the death of the male. The female responses differed. In December 2002, male MM42 died presumably due to mange-related exposure, and his mate MM38 dispersed from their territory later that month. When male PC10 died in September 2002, his mate PC4 dispersed 5 months later. Male HW88 was killed in a vehicle collision in July 2004, and his mate, HW111, maintained the home range and successfully mated the following year with an unsampled male.

## Discussion

Our results confirm that the mated pairs in our study area were genetically monogamous, despite the optimal food resources and high coyote density in this landscape. This indicates that the social mechanisms that coyotes use to enforce monogamy (e.g., mate-guarding and territory defense) are successful. It may also be the case that coyotes do not regularly attempt EPCs, whereby the previously reported incidents in the literature were anecdotal occurrences. Studies of other canid species that revealed EPCs within a dominantly

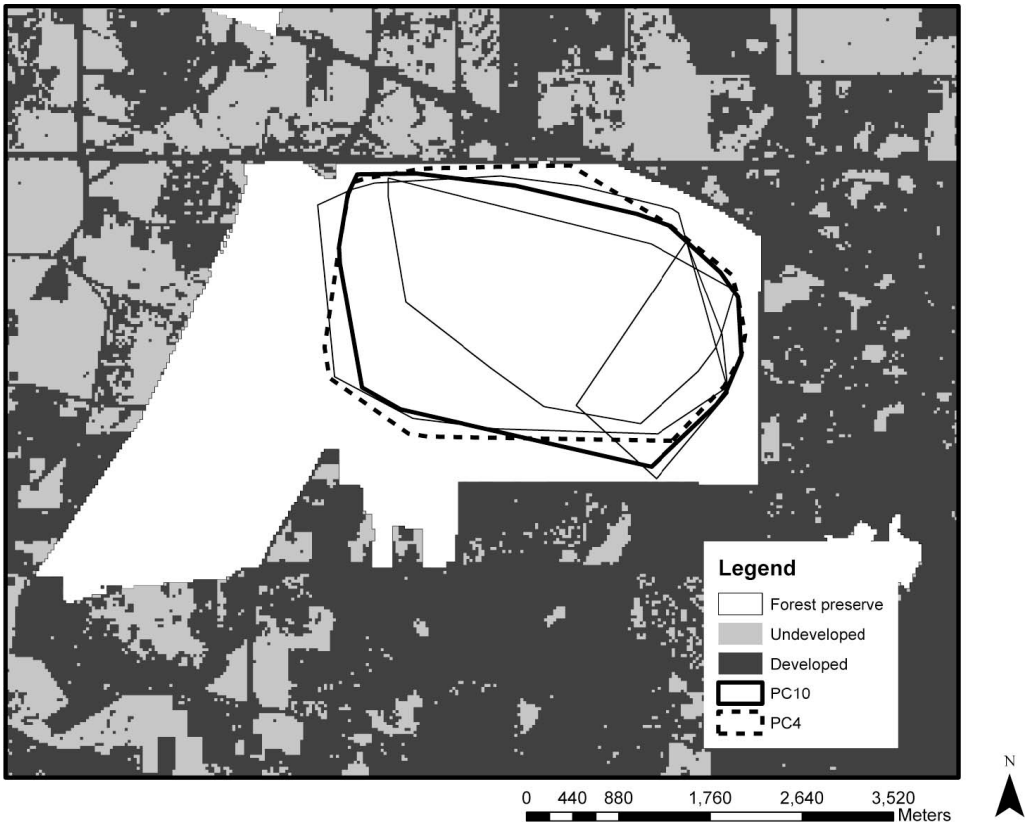


**Fig. 2.**—Overlap of 95% minimum convex polygon (MCP) home ranges of radiocollared coyotes (*Canis latrans*) in 2001 representing mated pairs PC10 and PC4 (in bold) and other coyotes in the Poplar Creek Forest Preserve in Cook County, Illinois. The annual overlap percentage exhibited by the mated pair in this figure is 87.52%.

monogamous social structure suggested explanations such as high resource density (Weston Glenn et al. 2009; Zabel and Taggart 1989), high population density (Kamler et al. 2004), and inbreeding avoidance (Sillero-Zubiri et al. 1996). Because breeding coyotes can be pair-living or pack-living, a species-wide prediction of EPC occurrence on the basis of social structure is not advisable. However, most of our coyote pairs existed as part of a pack, which would increase the likelihood of EPCs, according to Cohas and Allainé (2009), and yet we found none. However, Dobson et al. (2010) suggested that no single factor, or set of factors, can explain the variation of mating systems across animal species. The discovery of the mated pair that appeared to be related ($r = 0.26$) may reveal that the urban coyotes' breeding strategy may not be sufficient to completely avoid mating between relatives. The long-term pair bonds exhibited in this study population may indicate that the resources in this landscape are abundant enough to support adults and offspring year after year, yet not abundant enough for the coyotes to cross the polygyny threshold. It is also possible that this species, unlike certain fox species, would not cross the polygyny threshold, regardless of resource abundance.

To our knowledge, no study has genetically confirmed long-term pair bonding for alpha pairs of coyotes. Continuing radiotelemetry data, field observations, and genetic analyses have confirmed that the WGN pair (1 and 115) and the PC pair (21 and 125) continued their pair bonds through 2007–2010, extending their relationships to at least 8 years. The high levels of home range overlap shared by the male and female of each mated pair indicate high levels of interaction (Fig. 2).

Although double litters are fairly common according to observational studies of coyotes (Andrews and Boggess 1978; Camenzind 1978; Crabtree and Varley 1995; Nellis and Keith 1976), this is the 1st study that provides genetic evidence of den sharing. It has been assumed in previous studies that the mated pairs that contribute pups to the double litter are closely related, which is supported in this study by the *r*-values shared between one mated pair and the pups from the other (unsampled) mated pair. Subordinate coyotes are often present at dens and act as alloparents to the offspring of the alpha pair. However, alpha female coyotes are known to discourage mating attempts of subordinate females using behavioral actions, and there are physiological phenomena that suppress breeding conditions in beta females (Allen et al. 1987; Asa 1997; Moehlman and Hofer 1997). Double litters that are noted in the literature were classified on the basis of litter size (Baker et al. 1998; Gier 1975), breeding adult presence at the den (Andrews and Boggess 1978; Baker et al. 1998; Camenzind 1978), and perceived differences between ages of the pups (Nellis and Keith 1976). Due to wide variation in coyote litter size and pup size (Bekoff and Gese 2003), it is possible that some, if not all, cases of presumed double litters were misidentified, and were actually litters comprised entirely of offspring from 1 mated pair.

The rate of double litters that we found in our sample was comparable with previous coyote studies. On the basis of size difference in pups, Nellis and Keith (1976) determined that 3 litters of 29 that were excavated from dens were double litters, which resulted in a rate of 10.3%. Our estimate of the prevalence of double litters (1 of 18, or 5.6%) is similar to the rate of 5.0% determined through the observational records of Crabtree and Varley (1995), who undertook an intensive 6-year study of 18 coyote packs in Yellowstone National Park. On the basis of our radiotelemetry data, we know that the double litter of 5 pups was tended by the pair of identified parents (PC4 and PC10). Because neither member of the 2nd mated pair was radiocollared, it is unknown whether they were present at the den. On the basis of other observational studies of den-sharing coyotes, it is likely that the unidentified mated pair was tending the pups jointly with PC4 and PC10 (Camenzind 1978; Crabtree and Varley 1995). The *r*-values between the identified mother (PC4) and her offspring (PC59 and PC63) with the 3 other pups (PC60, PC61, and PC62) indicated that the coyotes sharing the den may have been an extended family. As grown offspring often remain on their parents' territory (Allen et al. 1987), it is possible that the unsampled mother is the daughter of PC4, or vice-versa. The relationship between 2 sets of parents that contribute to a double litter, in addition to preceding social behavior, requires further investigation.

In a study of red fox social groups in the city of Bristol, United Kingdom, Baker et al. (1998) investigated double litters wherein the 2 mothers that contributed to the litter were positively identified as the alpha female and her adult subdominant daughter. The minimum frequency for breeding success by each subdominant female was 0.21, but this was likely an underestimate, because the identification of double-litters was based on number of cubs present in the den. As we found in our study, a small double litter could easily escape the notice of wildlife researchers. The relatively low rates of double litters expressed in the Baker et al. (1998) study and in our own suggest that the potential for breeding concurrently with the alpha pair is not a strong motivator for subdominants to remain on their parents' territory. Instead, the inclusive fitness that full siblings confer through alloparental behaviors, whereby they increase their younger siblings' survival, may be more beneficial, as the proportion of genes shared between full siblings is often higher than those shared between parents and their offspring (Asa and Valdespino 1998). As these benefits between siblings would be decreased if they were less related (i.e., if their mothers were not monogamous), the cost of EPCs to alpha pairs may be the potential loss of alloparental assistance from their previous offspring (Moehlman 1987). With several pairs of eyes in a coyote pack, and considering the long postcopulatory tie, monogamy may therefore be a product of kin selection (Eberhard 1975).

Studying urban coyote pairs over several years gave us unique insight into pair behavior, including the response of a coyote to the death of its mate. Previous research has posited that the sex that is more likely to exhibit adult dispersal, such as that that happens after the loss of a mate, would likely be the sex that exhibits higher rates of natal dispersal (Kitchen et al. 2005). The swift foxes in the Kitchen et al. (2005) study

**Table 3.**—Coyote (*Canis latrans*) pups from 16 litters were genotyped at 12 microsatellite loci and compared with adult coyotes in the Greater Chicago Metropolitan Area from 2000 to 2006. Here are parental results for 79 pups with parents, singly and as a pair, on the basis of CERVUS analysis (LOD = logarithm of the odds). In the Parents column, any parent marked UM/UF (unidentified male/female) followed by a number is a genotype that was constructed by allelic exclusion of the pups with the identified parent, and was included in the population as a candidate parent for following years. Mismatched loci (ML) and confidence levels (Cf) are included for reference with codes as follows: * = strict alpha value (0.05); + = relaxed alpha value (0.20); − = unresolved assignment; blank = no assignment. The *P*-value for the offspring–parent relationship test in KINGROUP is also displayed for each pup–parent pair (KGROUP *P*-value).

| Year | Den site | Pup ID | Dam ID | ML | LOD score | Cf | KGROUP *P*-value | Sire ID | ML | LOD score | Cf | KGROUP *P*-value | Trio LOD | Cf |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2000 | MM | 11 | UF2 | 0 | 7.99E+00 | * | <0.01 | 9 | 1 | 1.64E+00 | − | <0.01 | 1.24E+01 | + |
| | | 20 | UF2 | 1 | 2.17E+00 | − | <0.01 | 9 | 1 | −4.66E−01 | | 0.04 | 4.66E+00 | − |
| | | 22 | UF2 | 0 | −6.56E−01 | | 0.22 | 9 | 0 | 7.92E+00 | * | <0.01 | 8.96E+00 | + |
| | | 23 | UF2 | 0 | 4.83E+00 | + | 0.01 | 9 | 1 | 2.02E+00 | − | 0.01 | 1.06E+01 | * |
| | | 37 | UF2 | 1 | 6.44E−01 | − | 0.03 | 9 | 0 | 9.68E+00 | * | <0.01 | 1.42E+01 | * |
| 2001 | MM | 39 | 38 | 0 | 6.39E+00 | * | <0.01 | 42 | 0 | 1.01E+01 | * | <0.01 | 1.87E+01 | * |
| | | 40 | 38 | 0 | 7.15E+00 | * | <0.01 | 42 | 0 | 1.17E+01 | * | <0.01 | 2.28E+01 | * |
| | | 41 | 38 | 0 | 7.18E+00 | * | <0.01 | 42 | 0 | 8.96E+00 | + | <0.01 | 1.86E+01 | * |
| 2002 | HW | 56 | 49 | 0 | 4.47E+00 | + | <0.01 | UM3 | 0 | 1.25E+01 | − | <0.01 | 2.08E+01 | + |
| | | 57 | 49 | 0 | 7.46E+00 | * | <0.01 | UM3 | 0 | 1.14E+01 | * | <0.01 | 2.29E+01 | * |
| | | 58 | 49 | 1 | 3.01E+00 | + | <0.01 | UM3 | 0 | 7.96E+00 | − | <0.01 | 1.49E+01 | − |
| | BW | 64 | UF4 | 0 | 3.48E+00 | + | 0.03 | 32 | 0 | 6.68E+00 | * | <0.01 | 1.26E+01 | * |
| | | 65 | UF4 | 0 | 3.74E+00 | + | 0.02 | 32 | 0 | 5.74E+00 | * | <0.01 | 1.08E+01 | * |
| | | 66 | UF4 | 0 | 5.88E+00 | * | <0.01 | 32 | 0 | 7.52E+00 | * | <0.01 | 1.64E+01 | * |
| | | 67 | UF4 | 0 | 4.73E+00 | + | <0.01 | 32 | 0 | 4.99E+00 | + | <0.01 | 1.22E+01 | * |
| | | 68 | UF4 | 1 | 2.07E+00 | − | <0.01 | 32 | 0 | 5.61E+00 | * | <0.01 | 7.30E+00 | − |
| | | 69 | UF4 | 0 | 5.17E+00 | + | <0.01 | 32 | 0 | 6.16E+00 | * | <0.01 | 1.49E+01 | * |
| | | 70 | UF4 | 0 | 4.98E+00 | + | <0.01 | 32 | 0 | 8.53E+00 | * | <0.01 | 1.59E+01 | * |
| | | 71 | UF4 | 0 | 6.34E+00 | * | <0.01 | 32 | 0 | 4.02E+00 | + | <0.01 | 1.27E+01 | + |
| | | 72 | UF4 | 0 | 5.53E+00 | * | <0.01 | 32 | 0 | 5.97E+00 | + | <0.01 | 1.30E+01 | + |
| | | 76 | UF4 | 0 | 6.03E+00 | * | <0.01 | 32 | 0 | 4.85E+00 | + | <0.01 | 1.47E+01 | * |
| | PC | 59 | 10 | 0 | 8.65E+00 | + | 0.01 | 4 | 0 | 4.94E+00 | − | <0.01 | 1.70E+01 | − |
| | | 63 | 10 | 0 | 8.57E+00 | * | <0.01 | 4 | 1 | 4.40E+00 | | <0.01 | 1.31E+01 | − |
| 2004 | MM | 154 | 113 | 0 | 8.00E+00 | * | <0.01 | 53 | 0 | 6.67E+00 | * | <0.01 | 1.94E+01 | * |
| | | 156 | 113 | 0 | 5.12E+00 | + | <0.01 | 53 | 0 | 5.46E+00 | * | <0.01 | 1.19E+01 | * |
| | | 157 | 113 | 0 | 6.29E+00 | * | <0.01 | 53 | 0 | 5.97E+00 | * | <0.01 | 1.31E+01 | * |
| | HW | 136 | 111 | 1 | −5.68E−01 | | 0.03 | 88 | 0 | 3.94E+00 | | 0.01 | 4.15E+00 | − |
| | | 138 | 111 | 0 | 4.74E+00 | − | <0.01 | 88 | 0 | 6.67E+00 | + | <0.01 | 1.59E+01 | * |
| | | 139 | 111 | 0 | 3.76E+00 | − | 0.02 | 88 | 0 | 8.65E+00 | − | <0.01 | 1.78E+01 | − |
| | | 140 | 111 | 1 | −6.08E−01 | | 0.02 | 88 | 1 | 9.25E−01 | | 0.01 | 7.27E+00 | − |
| | | 141 | 111 | 0 | 4.27E+00 | + | <0.01 | 88 | 1 | −1.80E+00 | | 0.09 | 1.40E+00 | |
| | | 143 | 111 | 1 | −1.50E+00 | | 0.07 | 88 | 0 | 3.02E+00 | | 0.03 | 2.76E−01 | |
| | BW | 178 | UF12 | 0 | 4.90E+00 | + | 0.02 | 182 | 0 | 1.16E+01 | * | <0.01 | 2.15E+01 | * |
| | | 179 | UF12 | 0 | 5.60E+00 | * | 0.01 | 182 | 0 | 1.09E+01 | * | <0.01 | 2.12E+01 | * |
| | | 183 | UF12 | 0 | 4.79E+00 | + | <0.01 | 182 | 0 | 7.25E+00 | * | <0.01 | 1.56E+01 | * |
| | PC | 127 | 125 | 0 | 5.18E+00 | + | 0.01 | 21 | 0 | 6.99E+00 | * | <0.01 | 1.62E+01 | * |
| | | 128 | 125 | 1 | 3.31E+00 | − | <0.01 | 21 | 1 | −3.80E+00 | | 0.21 | 6.02E+00 | − |
| | | 130 | 125 | 2 | −6.55E+00 | | 0.30 | 21 | 0 | 5.79E+00 | − | <0.01 | 1.59E+00 | |
| | | 131 | 125 | 0 | 6.58E+00 | * | <0.01 | 21 | 0 | 3.69E+00 | − | <0.01 | 1.46E+01 | * |
| | | 132 | 125 | 1 | 3.36E+00 | + | <0.01 | 21 | 0 | 3.06E+00 | − | 0.01 | 1.05E+01 | + |
| | WGN | 145 | 1 | 0 | 8.03E+00 | * | <0.01 | 115 | 0 | 5.96E+00 | | <0.01 | 1.66E+01 | − |
| | | 147 | 1 | 1 | 2.23E+00 | − | <0.01 | 115 | 0 | 3.03E+00 | | <0.01 | 7.12E+00 | − |
| | | 148 | 1 | 0 | 1.22E+01 | * | <0.01 | 115 | 0 | 4.75E−01 | | 0.11 | 1.12E+01 | |
| | | 150 | 1 | 0 | 9.87E+00 | * | <0.01 | 115 | 0 | 4.72E+00 | | <0.01 | 1.77E+01 | − |
| | | 151 | 1 | 0 | 9.12E+00 | * | <0.01 | 115 | 0 | 5.49E+00 | | <0.01 | 1.82E+01 | * |
| 2005 | HW | 197 | 111 | 0 | 3.63E+00 | − | 0.03 | UM11 | 0 | 8.11E+00 | + | <0.01 | 1.63E+01 | − |
| | | 198 | 111 | 0 | 3.18E+00 | | 0.01 | UM11 | 0 | 9.81E+00 | * | <0.01 | 1.79E+01 | + |
| | | 200 | 111 | 0 | 5.41E+00 | − | <0.01 | UM11 | 0 | 7.95E+00 | * | <0.01 | 1.76E+01 | + |
| | | 202 | 111 | 0 | 3.81E+00 | + | 0.01 | UM11 | 0 | 8.23E+00 | * | <0.01 | 1.60E+01 | − |
| | | 203 | 111 | 0 | 2.44E+00 | − | 0.06 | UM11 | 0 | 1.03E+01 | * | <0.01 | 1.71E+01 | − |
| | BW | 215 | UF12 | 0 | 3.32E+00 | + | 0.04 | 182 | 0 | 5.73E+00 | * | <0.01 | 1.09E+01 | * |
| | | 216 | UF12 | 1 | 8.59E−01 | | <0.01 | 182 | 0 | 5.76E+00 | * | <0.01 | 6.66E+00 | − |
| | | 217 | UF12 | 2 | −3.04E+00 | | 0.08 | 182 | 0 | 8.53E+00 | * | <0.01 | 8.31E+00 | − |
| | | 218 | UF12 | 1 | 6.52E−01 | | 0.03 | 182 | 0 | 9.74E+00 | + | <0.01 | 1.28E+01 | − |
| | | 219 | UF12 | 2 | −4.42E+00 | | 0.02 | 182 | 0 | 7.58E+00 | * | <0.01 | 1.95E+00 | |
| | | 220 | UF12 | 2 | −2.34E+00 | | 0.01 | 182 | 0 | 6.16E+00 | * | <0.01 | 6.19E+00 | |

**Table 3.**—Continued.

| Year | Den site | Pup ID | Dam ID | ML | LOD score | Cf | KGROUP *P*-value | Sire ID | ML | LOD score | Cf | KGROUP *P*-value | Trio LOD | Cf |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 221 | UF12 | 0 | 3.16E+00 | | 0.01 | 182 | 0 | 6.84E+00 | * | <0.01 | 1.47E+01 | − |
| | | 223 | UF12 | 0 | 3.13E+00 | | 0.01 | 182 | 0 | 7.15E+00 | * | <0.01 | 1.49E+01 | − |
| | | 224 | UF12 | 0 | 2.33E+00 | − | 0.03 | 182 | 0 | 6.39E+00 | + | <0.01 | 1.05E+01 | − |
| | | 225 | UF12 | 0 | 2.30E+00 | − | 0.06 | 182 | 0 | 7.27E+00 | + | <0.01 | 1.44E+01 | − |
| | PC | 210 | 125 | 0 | 7.66E+00 | | <0.01 | 21 | 0 | 3.10E+00 | − | 0.02 | 1.46E+01 | + |
| | | 211 | 125 | 0 | 8.02E+00 | + | <0.01 | 21 | 0 | 3.52E+00 | | 0.02 | 1.68E+01 | + |
| | | 212 | 125 | 0 | 4.44E+00 | | <0.01 | 21 | 0 | 4.43E+00 | + | 0.01 | 9.78E+00 | − |
| | | 213 | 125 | 0 | 9.21E+00 | − | <0.01 | 21 | 0 | 7.93E+00 | + | 0.02 | 1.79E+01 | − |
| | | 214 | 125 | 0 | 5.80E+00 | * | <0.01 | 21 | 0 | 5.17E+00 | | <0.01 | 1.40E+01 | − |
| | WGN | 226 | 1 | 0 | 6.60E+00 | | <0.01 | 115 | 0 | 4.86E+00 | | <0.01 | 1.61E+01 | + |
| | | 227 | 1 | 0 | 3.85E+00 | | 0.02 | 115 | 0 | 5.02E+00 | | <0.01 | 1.13E+01 | |
| | | 233 | 1 | 0 | 8.21E+00 | + | <0.01 | 115 | 0 | 2.83E+00 | | 0.01 | 1.40E+01 | − |
| 2006 | PC | 253 | 125 | 0 | 4.07E+00 | | 0.01 | 21 | 0 | 6.23E+00 | + | <0.01 | 1.46E+01 | * |
| | | 254 | 125 | 0 | 3.40E+00 | − | 0.03 | 21 | 0 | 7.19E+00 | − | <0.01 | 1.46E+01 | * |
| | | 255 | 125 | 0 | 9.13E+00 | − | <0.01 | 21 | 0 | 2.21E+00 | | 0.03 | 1.59E+01 | − |
| | | 256 | 125 | 0 | 7.35E+00 | | <0.01 | 21 | 0 | 3.57E+00 | − | 0.02 | 1.54E+01 | + |
| | | 257 | 125 | 0 | 1.03E+01 | + | <0.01 | 21 | 0 | 2.32E+00 | | 0.06 | 1.81E+01 | − |
| | | 258 | 125 | 0 | 8.28E+00 | + | <0.01 | 21 | 0 | 5.22E+00 | | <0.01 | 1.93E+01 | + |
| | | 259 | 125 | 1 | −1.25E−01 | | 0.02 | 21 | 1 | −1.41E+00 | | 0.03 | 4.30E+00 | |
| | WGN | 263 | 1 | 0 | 6.14E+00 | | <0.01 | 115 | 0 | 7.83E+00 | + | <0.01 | 1.68E+01 | |
| | | 264 | 1 | 0 | 7.24E+00 | − | <0.01 | 115 | 0 | 3.78E+00 | | 0.01 | 7.75E+00 | |
| | | 265 | 1 | 0 | 9.23E+00 | + | <0.01 | 115 | 0 | 5.51E+00 | | <0.01 | 1.73E+01 | − |
| | | 266 | 1 | 0 | 7.13E+00 | − | <0.01 | 115 | 0 | 1.88E+00 | | 0.01 | 7.70E+00 | |

of home range maintenance in response to the death of a mate revealed that a species-wide tendency toward juvenile male dispersal was mirrored by a strong bias for adult females to retain their home range, in contrast to 50% adult male emigration. As natal dispersal in coyotes is not correlated to sex (Harrison et al. 1991), it is not surprising that 1 female dispersed immediately and 2 females stayed through the whelping period and then dispersed. What may also be of interest is the timing of the death of the mate in relation to dispersal, as a female coyote that is still raising young may be more motivated to maintain her home range (as in the case of PC4 and HW111), whereas a coyote with independent offspring (as in the case of MM38 in the month of December) may be more likely to disperse. A study of mated females that had lost their mate reported that females with pups will not abandon their litter upon the death of their mate, but will instead expend more energy to compensate for the loss of the other parent (Sacks and Neale 2001). In that population of coyotes in an undeveloped landscape, the loss of paternal care resulted in underweight pups and the females' loss of future reproductive opportunities. We were not able to determine the effect of the death of a parent on the pups' health, but we confirmed that HW111 maintained her territory and mated in the following year, producing a litter of 5 pups.

In conclusion, our results show that urban coyotes maintain long-term monogamous bonds, despite abundant food resources and a dense population. Considering that canid social groups display a high degree of intraspecific flexibility (Andelt 1985; Moehlman and Hofer 1997), similar studies should be conducted in different regions and landscape types. The occurrence of double litters may be related to factors such as prey abundance, landscape saturation, or scarcity of den sites; future studies are needed to address these interesting behaviors. Further investigation is also recommended to determine the relationships between the mated pairs that share dens, and to parse out the conditions that lead to den-sharing behavior.

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