GENETIC DETERMINANTS OF RACCOON SOCIAL BEHAVIOR IN A HIGHLY URBANIZED ENVIRONMENT

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ABSTRACT

Raccoons (*Procyon lotor*) are one of the most ubiquitous mammals in North America, yet the details of their social behavior remain enigmatic. Recent research, however, suggests that raccoons possess a more complex social system than previously believed (Prange and Gehrt unpublished data). Raccoons carry a wide variety of zoonotic diseases, including rabies, that are transmitted through close contact. Therefore, a more complete understanding of raccoon social behavior, or interaction rate, is helpful in modeling disease transmission rates. Additionally, the emerging social associations among raccoons afford us a unique opportunity to examine which mechanism(s) is (are) responsible for their complex and selective sociality.

I examined the extent to which social associations among adult raccoons can be attributed to their degree of relatedness. I examine five predictions that pertain to this objective: 1) related individuals share greater proportions of their home ranges than unrelated individuals, 2) related individuals exhibit a negative correlation between relatedness and geographic distance between activity centroids, 3) related dyads contact each other more frequently than unrelated dyads, 4) related individuals have consistently higher rates of contact than unrelated dyads, and 5) related individuals den share more often than unrelated individuals. Captured adult raccoons (*n*=42; 20M, 22F) were sampled for genetic analysis and fitted with proximity detecting radio collars. Proximity detectors allow for the collection of spatial data via traditional VHF radio telemetry.

Additionally, proximity detectors record when two or more individuals come within approximately 1m of each other. A series of randomization tests were used to analyze social data in conjunction with relatedness values. Highly related dyads did not share greater home range overlap, live in closer proximity, or have higher contact rates than unrelated individuals (all $P > 0.156$). Male-male pairs had more stable associations than female-female or male-female dyads (Prange and Gehrt, unpublished data) throughout the year, but relatedness was not greater among consistently social pairs than seasonally social pairs. I found that relatedness is not the main factor driving social associations among raccoons. I suggest that a high-density population and abundant, highly concentrated resources, such as occurred at my study site, are more likely the factors responsible for raccoon social tolerance.

Another aspect of raccoon biology that is poorly understood is their mating behavior. Raccoons reportedly engage in a polygynous or promiscuous system depending on the synchronicity of estrus periods, and such systems are facilitated by the formation of male coalitions. However, these assertions are based solely on denning associations and coarse-grained radio-telemetry studies. Although denning associations are often used as a surrogate for matings, no studies have determined if instances of co-denning result in progeny. Moreover, no studies have examined the relatedness among male coalition members, or the mating success of coalition members versus solitary males. To answer these questions, I addressed three specific objectives: 1) determine the mating system for a high-density population of raccoons, 2) describe the social associations (spatial relationships, contact rates, and denning associations) for identified

parents, and 3) determine if instances of multiple paternity are reserved for coalition members.

I captured 44 juveniles within an area where adult raccoons had been monitored extensively using proximity detecting radio collars. All adults and juveniles were genotyped using 16 highly variable microsatellite loci. Based on analysis of littermates, I found a high rate of multiple paternity (83.3%) and evidence for a promiscuous breeding system as both males and females bred with multiple mates. Females often exhibited the greatest spatial overlap and highest contact rates with males that sired their litters. Males, however, associated with many females other than those whose litters they sired. Male coalition members did not sire the majority of assigned young. Overall, I found a low percentage of parental assignment, but twice as many resident females were assigned parentage than resident males. Similar results were observed in another study on raccoon multiple paternity, and this may be an indication of male roaming behavior in raccoons. Of the four parental dyads, none were recorded to share dens during winter. Although den sharing occurred throughout the winter, the incidence of den sharing increased markedly during the peak of the mating season. These results suggest that although denning associations increase during the mating period, den sharing may not be a common mating strategy, or reserved solely for mating associations.

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CHAPTER 1

INTRODUCTION

As the human population continues to grow through the 21st century, more wildlife habitat is juxtaposed with human dominated environments. As wildlife and humans occupy similar space, instances of human-wildlife conflict become increasingly important, especially when zoonotic diseases are present. Raccoons (*Procyon lotor*) present multiple threats to human health in the form of rabies, *Baylisascaris procyonis*, and leptospirosis, among others (Jackson et al. 1993, Rupprecht and Smith 1994, Page et al. 1999). Despite myriad investigations of raccoons, the details of how this animal transmits and spreads diseases across geographic areas remain largely unknown due to the secretive, nocturnal interactions between conspecifics.

It is necessary to better understand the social associations between raccoons so that the spread of infectious diseases may be curtailed, yet of equal importance is uncovering the mechanisms that allowed raccoon social behavior to emerge. Sociality and cooperation among individuals have principally arisen through three main selective processes; kin selection (Hamilton 1964), reciprocal altruism (Trivers 1971), and mutualism (Connor 1981) have each been cited as the driving forces behind social formations in various species. While reciprocal altruism and mutualism both deal with cooperation among unrelated individuals, only kin selection describes the degree of sociality among closely related individuals. Therefore, the first step in understanding the mechanism driving a species' social system is to determine if close associations are reserved for related individuals.

High relatedness among individuals is commonly cited as the force responsible for social interactions among highly social carnivores. Hamilton (1964) theorized that individuals should tolerate and share resources with kin due to the indirect fitness gained by the survival of individuals with similar genetic information (i.e., closely related kin). Numerous studies have substantiated this logic, showing that related individuals often form spatially condensed clusters and that the geographic distance between activity centroids of individuals decreases as relatedness increases (Ralls et al. 2001, Kitchen et al. 2005, Støen 2005, Moyer et al. 2006). Kin-based groups are also common among many canids (wolves [*Canis lupus*]; Lehman et al. 1992, African wild dogs [*Lycaon pictus*]; McNutt 1996, swift foxes [*Vulpes velox*]; Kitchen et al. 2005, and San Joaquin kit foxes [*Vulpes macrotis mutica*]; Ralls et al. 2001), whereas groups of highly related females are reported for lions (*Panthero leo*; Packer et al. 1991), coatis (*Nasua narica*; Gompper et al. 1998), and kinkajous (*Potos flavus*; Kays et al. 2000).

Mutualism, or the cooperation of individuals to benefit both members, has also been used to explain the social interactions of carnivores. Within Carnivora, lions (Packer et al. 1991), hyenas (*Crocuta* spp.; Van Horn et al. 2004, Wagner et al. 2007), wolves (Vucetich et al. 2004), coastal river otters (*Lontra canadensis*; Blundell et al. 2004), male kinkajous (Kays et al. 2000), and dwarf mongooses (*Helogale parvula*; Creel and Waser 1993) have all demonstrated cooperation among non-kin. Investigations into brown bear (*Ursus arctos*) and black bear (*Ursus americanus*) spatial distribution revealed that these typically solitary and territorial carnivores modify those behaviors in response to superrich food sources (Egbert and Stokes 1976, Rogers 1987). But these studies did not address whether animals that foraged communally at superrich food sources were genetically related.

With respect to raccoons, Ratnayeke et al. (2002) examined home range overlap and genetic relatedness of females in a low-density population in rural Tennessee. Using random amplification of polymorphic DNA (RAPD) molecular markers Ratnayeke et al. (2002) found that female raccoons follow a general trend of increasing relatedness as distance between home ranges decreases, but acknowledged several aberrant cases, suggesting that relatedness was not a prerequisite for sharing home ranges. Unfortunately, they did not equip male raccoons with radio collars and therefore could not examine what role relatedness plays in the social associations of males, or male-female associations.

To date, no studies have examined the role relatedness plays in raccoon social interactions. In order to gain insight on the social behavior, and therefore possible implications for disease transmission, we must understand how this nocturnal, semi-arboreal species interacts with conspecifics. Here, I examine the genetic relatedness of male and female raccoons within a forest preserve in the northwestern suburbs of Chicago, Illinois. Using 16 highly polymorphic microsatellites I estimate relatedness between individuals. I then overlay relatedness onto home range overlap values and contact rates for raccoons (Prange and Gehrt unpublished data). The reported social complexity of raccoons inhabiting this urban area provides us with a unique opportunity to examine which behavioral mechanisms are responsible for their newly documented sociality. Additionally, by understanding the role of relatedness in social behavior we will be able to create management policies based on sound biological principles. These results will be a valuable asset to behavioral ecologists, wildlife managers and public health officials alike.

Literature Review

Morphology

Raccoons are classified as medium-sized nocturnal carnivores. Their body mass typically averages between 4 and 9 kg (Gehrt 2003), but varies among geographic regions and seasons. Males are heavier and larger than females but no forms of pelage dimorphism occur between the sexes. Records of the smallest raccoons exist in southern climates during the winter months, where average weights were 2.4 and 2.0 kg for males and females respectively (Goldman, 1950, Ritke and Kennedy 1988). Raccoons occupying more northern climates tend to be larger. Average weights of male and female raccoons in Illinois were 7.6 kg and 6.4 kg, respectively, during winter (Sanderson 1987). Body length co-varies with mass across a latitudinal gradient.

Raccoons are in the order Carnivora and, along with the other characteristics of this order, they have well developed canines (Feldhamer et al. 1999), and reasonably well developed carnassial teeth. Their total dentition formula is I: 3/3, C: 1/1, P: 4/4, M: 2/2 = 40 total adult teeth. Raccoons have deciduous teeth; the emergence and wear of adult teeth are the generally accepted methods for aging individuals (Grau et al. 1970). The oldest raccoon recorded in captivity was 17 years (Garrett and Goertz 1975) and the oldest recorded in the wild was approximately 13 years old based on livetrapping data

(Johnson 1970). These ages may not be representative of most raccoons which often have high mortality rates due to hunting, dangers associated with dispersal, disease, and extreme winter conditions in northern latitudes. Sanderson (1951) calculated that population turn over in Missouri is every 7.4 years.

Ecology

The raccoon is one of the most adaptable mammals in the world. Historically it was found only in the New World, ranging from the southern Canadian border to Mexico and from the eastern seaboard to the west coast (Gehrt 2003). Today the raccoon is one of the most ubiquitous animals in North America. They can survive in rural, suburban, and even highly urbanized areas (Shinner and Cauley 1974, Rosatte and MacInnes 1989, Prange et. al. 2003). New populations of raccoons have been established in Central Europe, Japan and several islands off the U.S. west coast (Lutz 1984, Hartman and Eastman 1999, Asano 2003).

Raccoon populations increased in modern times and Sanderson (1987) estimated that populations in the U.S. were 15 to 20 times larger in 1980 than in 1930. This increase was probably due to reduced hunting, decline in pelt price and expansion of suburban areas. Raccoons attain their highest densities in suburban areas where refuse and supplemental feedings can boost fecundity and survival (Prange et al. 2003). Lower densities in rural areas are the result of several mortality factors. In rural environments, hunting, trapping, disease, predation, and vehicle-related mortalities all resulted in reduced survivorship. In suburban Illinois, disease and vehicle-related deaths were the only reported sources of mortality (Prange et al. 2003).

Disease plays a large role in the mortality of raccoons and is an important aspect of their ecology. Raccoons are known to carry a wide array of diseases and parasites, many of which can be transmitted to humans and/or their pets (Gehrt 2003). Perhaps the most important of these zoonotic pathogens is raccoon rabies, which was mostly confined to Georgia and Florida until it was introduced to Virginia in 1980, likely via a shipment of raccoons from the southern enzootic area (Jenkins et al. 1998). Since that introduction, the disease has moved rapidly across the eastern seaboard, migrating westward at approximately 25-60 km/yr (Krebs et al. 2002). Other zoonoses exist, such as *Baylisascaris procyonis*, the raccoon roundworm, which is a debilitating disease in humans. Canine distemper may be the pathogen that plays the greatest role in regulating raccoon populations, and several studies have documented its presence in raccoon populations.

Chamberlain et al. (1999) found that 16% (*n* = 69) of known mortalities were due to natural causes in Mississippi (disease and one case of predation). Hoff et al. (1974) described the prevalence of canine distemper in Sarasota County, Florida during 1972 and 1973. In this case 114 clinically sick raccoons were captured and tested or destroyed, of which 54% had significant titers. In New Jersey, 17 distemper epizootics affecting raccoons occurred from 1977 to 1991 (Roscoe 1993). Schinner and Cauley (1974) cited canine distemper as an important mortality factor for urban raccoons in Cincinnati, Ohio, second only to mauling by dogs.

Predation in natural populations is not regarded as a factor that significantly impacts raccoon mortality or survivorship (Gehrt 2003). In Mississippi, Chamberlain et al. (1999) reported the cause-specific mortality for rural raccoons from 1991 to 1997. Of

69 reported known mortalities only one death was attributed to predation. Gehrt and Fritzell (1999a) reported that 5 out of 23 raccoon deaths were from predation in south Texas. While the overwhelming majority of raccoon survivorship studies reported few predation events on raccoons, one study conducted on an island reported that coyotes (*Canis latrans*) frequently consumed raccoons (O'Connell et al.1992). When predation events do occur the predator is often coyotes, but alligators (*Alligator mississippiensis*), owls (various species), and red foxes (*Vulpes vulpes*) have also been reported (Stains 1956, Johnson 1970, Kaufman 1982, Shoop and Ruckdeschel 1990).

Despite their classification in the order Carnivora, raccoons are highly omnivorous. Their diet is often representative of the habitat where they reside and what resources are available to them. Raccoons inhabiting aquatic areas often consume fish, crayfish, salamanders, insects, and eggs of waterfowl (Gehrt 2003). Raccoons are also often cited as the top predator of song bird, waterfowl, and turtle nests (Rogers and Caro 1998, Marchand et al. 2002). Soft mast such as berries and hard mast such as acorns are consumed by raccoons when seasonally available (Stains 1956). Most people living in developed areas today are aware that suburban and urban raccoons consume human refuse whenever available. Raccoons living near humans also take advantage of seed and suet left for birds, fish-stocked garden ponds, and food left on porches for outdoor cats (personal observation).

Raccoons living in developed environments also take advantage of human domiciles for den sites. Investigations into nuisance denning behavior have shown that raccoons choose human-made structures for denning even when suitable trees are nearby, and even after individuals are removed from homes. Two months post-partum, 59% (*n*=

46) of females removed from human-made structures were again located in homes, and one year after removal 80% (*n* =10) were back in human-made structures (O'Donnell and DeNicola 2006). Raccoons have been reported using tree dens, ground dens, and even rock outcrop dens in more natural environments (Rabinowitz and Pelton 1986, Gehrt et al. 1990).

Tree cavities were used most commonly by raccoons in eastern Kansas (Gehrt et al. 1990). Raccoons displayed preferences for sycamore (*Plantanus occidentalis)* and cottonwood (*Populus deltoides)*, as they denned in those species 28 and 52% of the time respectively, despite the fact that those species only made up 1-3% of the forest stand. Rabinowitz and Pelton (1986) studied seasonal variation of den sites in Tennessee. Females denned in tree cavities significantly more often in the spring and summer months when rearing litters, and used rock dens significantly more in the winter months. Males did not show such seasonal variation for day bed selection. Both studies documented that den sites are frequently used more than once, and by more than one individual.

Reproduction

Most matings occur between February and March, with some variation among locations (Gehrt 2003). Ovulation is spontaneous and females may come into a second estrus period later in the year if their first mating proved unsuccessful or if they lost their first litter shortly after birth (Sanderson and Nalbandov 1973). Ovulation is suppressed during lactation (Sanderson and Nalbandov 1973). Gestation lasts approximately 63 days, ranging from 54 to 70 days. The number of young per litter is usually 3 or 4 and parturition typically occurs in April, varying with location (Gehrt 2003).

Sanderson and Nalbandov (1973) found the peak of the mating season in Illinois to be early February, and that juvenile males reached sexual maturity 3 to 4 months after adult males, which reduces their opportunity to mate with females during the first estrous period. However, this late development enables juvenile males to breed with females in their second estrus period, when adult males who were capable of breeding earlier in the year have little or no motile semen left in their epididymis.

Raccoons bear altricial young and females raise the litter without any male contribution (Gehrt 2003). Postpartum females show a reduction in nocturnal activity patterns (Schneider et al. 1971, Hauver et al. unpublished data) and reduce home range as they return to the den site frequently each night to care for their young. Young began to travel with their mother at approximately 72 days in Texas (Gehrt and Fritzell 1998a) and 63 days in Illinois (personal observation). While there is some variation in dissolution of familial bonds, it seems that most young maintain fairly close ties to their mother until her next estrous period (Schneider et al. 1971, Gehrt and Fritzell 1998b).

Social Structure and Behavior

Raccoon dispersal is male biased. Eighty percent of marked male juveniles dispersed by their first mating season in Texas (Gehrt and Fritzell 1998a). Recent research has suggested that male coalitions of two to four individuals are formed and maintained for extensive periods. Males from a coalition had home ranges that overlapped 80-92%, whereas non-coalition males had 0-14% home range overlap (Gehrt and Fritzell 1998b). Gehrt and Fritzell (1999b) suggested that these male-male groups could be the byproduct of higher densities, whereas strict territoriality occurs in extremely low density areas (Fritzell 1978). If dominant males gain access to only one female at a time they risk relatively little by associating with subordinates. Subordinates, on the other hand, are likely to gain access to females unattended by the dominant breeding male. Gehrt and Fritzell (1999b) found evidence for a system of breeding dominance as one male from each social group consorted with females on more days than all other males combined. Additionally, they found a positive relationship between length of estrus and number of consortships for females. Thus, synchronicity and length of estrus shifts the breeding structure from polygynous to promiscuous (Gehrt and Fritzell 1999b).

Although males in moderate to high-density areas are known to form coalitions, females are still described as solitary and having little association with adult conspecifics. Home range overlap between females has been documented, but encounters between females are thought to be infrequent (Gehrt 2003). The occasional reports of female-female tolerance that do occur are often cited as the result of genetic relatedness (Ratnayeke et al. 2002, Gehrt and Fritzell 1998b). Consistent with this claim, females do maintain some degree of home range overlap with female kin; however, not all instances of female-female home range overlap involved close kin (Ratnayeke et al. 2002).
No molecular genetic studies have been conducted to examine the relationship between home range overlap and male relatedness. Barash (1974) placed wild-caught male raccoons of unknown relatedness into "neutral" enclosures to observe resultant social interactions. He found that all pairs trapped within 5 km of each often assumed dominance/subordinate roles, but pairs trapped over 5 km apart did not assume hierarchal roles and often fought or displayed other agonistic behaviors. What role kinship plays on these types of recognition and aggressive behaviors remains to be seen.

Genetics

The relatedness of males within coalitions and the role familial ties play in sociality have not been thoroughly investigated in raccoons. Several studies of proteomic genetic similarity conducted in the 1980's led to the conclusion that raccoons from various areas are highly genetically similar (Beck and Kennedy 1980, Dew and Kennedy 1980, Hamilton and Kennedy 1987). But these types of investigations fail to reveal relatedness of individuals. Since the advent of microsatellite marker technology, myriad investigations into bird relatedness and behavior have been conducted. Mammalian studies in this area have lagged (Hughes 1998), but in recent years researchers have begun to adopt this powerful technique.

Negative associations between pairwise relatedness values and geographic distance between home ranges have been reported for Florida black bear (*Ursus americanus floridanus*) and brown bears (Moyer et al. 2006, Støen et al. 2005). Arctic foxes (*Alopex lagopus*) in Norway were found to be more closely related to neighboring foxes than non-neighboring foxes (Strand et al. 2000). Similarly, Ralls et al. (2001) found a similar relationship where neighboring San Joaquin kit foxes (*Vulpes macrotis mutica*) were usually highly related. All of these investigations used microsatellite analysis and improved our understanding of observational studies.

Despite the paucity of investigations of raccoon relatedness, genetic studies have been carried out on two other procyonids, the coati and the kinkajou. Coatis are a social omnivore whose females live in all-female groups (called bands); males are solitary, but maintain home ranges that encompass their natal band as well as a few other males (Gompper et al. 1998). Using fingerprinting technology, Gompper et al. (1998) found that females display high degrees of inter-band relatedness and low degrees of intra-band relatedness, although a few inter-band dyads (8.1%) were found to be only slightly related. Males whose home ranges overlapped were found to be more closely related than males with non-overlapping home ranges.

Kinkajous were once thought to be solitary and asocial but recent studies have documented a fission-fusion social formation where individuals congregate to feed and sleep (Kays and Gittleman 2001; Kays 1999). These social groups generally consist of one adult female, two adult males, one subadult, and one juvenile (Kays et al. 2000). Microsatellite analysis found these groups to resemble family units because the subadult and juvenile were closely related to the adult female and one of the adult males. However, the two adult males were not closely related to each other or to the adult female. Kays et al. (2000) also found that males were more closely related to neighboring males than neighboring females, suggesting that females of the species disperse. These studies on Procyonids reveal the usefulness of molecular techniques in delineating social systems in this behaviorally flexible and intriguing taxonomic family.

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CHAPTER 2

GENETIC DETERMINATS OF RACCOON SOCIAL BEHAVIOR IN A HIGHLY URBANIZED ENVIRONMENT

Mammalian social behavior is variable in its complexity and distribution among species. While the vast majority of mammals are considered solitary (Eisenberg 1981), advances in technology have enabled more accurate classification of species that are neither solitary nor gregarious (Rood 1989, Waser et al. 1994, Gehrt and Fritzell 1998a, Kays et al. 2000); those whose behavior places them in the midst of a sociality spectrum. The evolution of highly gregarious behavior in some species and less sociality in others is often attributed to relatedness. Indeed, many studies have proven that spatial overlap (coati [*Nasua narica*]; Gompper et al. 1998, kit foxes[*Vulpes macrotis*]; Ralls et al. 2001, swift foxes [*Vulpes velox*]; Kitchen et al. 2005, white-tailed deer [*Odcoileus virginianus*]; Comer et al. 2005, Florida black bears [*Ursus americanus floridanus*]; Moyer et al. 2006), grooming (baboons [*Papio cynocephalus*]; Silk et al. 2006), and other amicable behaviors (kinkajou [*Potos flavus*]; Kays et al. 2000, Japanese macaques [*Macaca fuscata*]; Chapais et al. 2001) occur primarily between kin. While relatedness is often the reason cited for the formation of associations, other motives have been proposed.

By-product mutualism, or pseudo-reciprocity (Connor 1986), is a commonly reported mechanism by which social associations arise. It is so prevalent because cooperation often forms around behaviors that are preformed even if the individual is solitary (i.e. hunting, sequestering mates, etc.), but often greater efficiency is garnered by dyad or group formation. Within Carnivora, lions (*Panthero leo*; Packer et al. 1991), African wild dogs (*Lycaon pictus*; McNutt 1996), hyenas (*Crocuta* spp.; Van Horn et al. 2004, Wagner et al. 2007), wolves (*Canis lupus*; Vucetich et al. 2004), coastal river otters (*Lontra canadensis*; Blundell et al. 2004), male kinkajous (*Potos flavus*; Kays et al. 2000), and dwarf mongooses (*Helogale parvula*; Creel and Waser 1993) have all demonstrated mutualistic cooperation among non-kin.

One member of Carnivora for whom the mechanisms responsible for their complex and facultative sociality have not been identified, is the raccoon (*Procyon lotor*). Raccoons are a nocturnal, semi-arboreal, mid-sized mammal that inhabits much of North America. They are an intelligent species (Davis 1984, reviewed by Gehrt 2003) capable of neighbor recognition (Barash 1974) and attain their highest densities in urban environments (Schinner and Cauley 1974, Riley et al. 1998, Prange et al. 2003) that often contain superabundant food resources. Raccoons are extensively studied due to their importance as transmitters of zoonotic diseases (Hoff et al. 1974, Rupprecht and Smith 1994, Page et al. 1999, Krebs et al. 2002), as nest predators (Fritzell 1978a) and as furbearers (Sanderson 1951, Chamberlain et al. 1999). Yet their social behavior remains largely a mystery. Raccoons are often described as solitary and intolerant of conspecifics (Bissonnette and Csech 1938, Fritzell 1978b), but instances of group foraging (Sharp and Sharp 1956), extended familial bonds (Gehrt and Fritzell 1998b), den cohabitation (Mech and Turkowski 1966, Gehrt and Fritzell 1998b), and male coalition formation (Gehrt and Fritzell 1999, Chamberlain and Leopold 2002, Prange and Gehrt unpublished data) have been documented. It is currently unknown how relatedness affects the variation in social associations observed among raccoons.

Ratnayeke et al. (2002) found that female raccoons were philopatric in Tennessee, whereby related females shared greater proportions of their home ranges and lived in closer proximity to one another than unrelated females. However, that study lacked a fine-grain focus on social behavior, which is often necessary to describe subtle associations, as only spatial structure, and not direct interactions, was used to quantify the degree of sociality between raccoons. Additionally, Ratnayeke et al. (2002) only radio collared females, which left out the notably complex interactions among male raccoons. Therefore, much information about raccoon social behavior and organization remains unknown, and further investigation is warranted.

A recent study (Prange and Gehrt, unpublished data) examined the frequency and duration of interactions between free-ranging raccoons such that a more complete picture of social behavior could be identified. They found a surprisingly high number of interactions between many pairs as 12,577 contacts between 32 raccoons were recorded during the first 11 weeks of study alone. Of 473 dyads, 304 exhibited at least one contact, with the average contact rate being 0.4 contacts/day (range: 0-22.5) for an average of 1.5 minutes/day (range: 0-150.8). This wide range in observed contact rate and duration of contact between individuals was suggested to be the result of a high-density environment and kin-directed associations.

Prange and Gehrt (unpublished data) also identified four male coalitions based on high contact rates and spatial overlap, of which two were comprised of a sole dyad of similar age. They theorized that these male-male (MM) dyads could be the result of extended sibling bonds. Over one year, 19 male-female (MF) dyads were identified as having a significantly higher contact rate than expected from a randomized distribution. In all cases the female was as old, or older, than the male of the pair, suggesting extended familial bonds. Nine female-female (FF) dyads exhibited a higher rate of contact than expected. One specific FF pair was comprised of females from age class IV (5-7 years) and I (yearling), and they were initially captured together in the same trap. This dyad produced the 4th highest contact rate and 3rd longest duration of all dyads recorded, which lends support to their suggestion of extended familial bonds, as this appeared to be a case of a mother-daughter relationship.

While much speculation has been made, no investigation has attempted to answer what role genetic relatedness plays in the complex social behavior of raccoons. Therefore the overall objective of this paper is to determine if relatedness explains the variation of social interactions between raccoons. I anticipated that relatedness would have a strong bearing on the spatial and behavioral associations between females due to the philopatric nature of female raccoons (Ratnayeke et al. 2002, Gehrt and Fritzell 1998b). Yet this trend should not continue for associations between males due to the system of male-biased dispersal (Stuewer 1943, Urban 1970, Gehrt and Fritzell 1998a). Additionally, males and females with high degrees of contact and home range overlap should be restricted to non-kin who associate for breeding purposes, or in the instances of older females and younger male associations, relatedness may be high due to extended familial bonds (Gehrt and Fritzell 1998b). I addressed the following questions related to my overall objective: 1) Do closely related individuals share a greater proportion of their home ranges than those that are unrelated? 2) Is the degree of relatedness inversely correlated with the geographic distance between average locations of dyads? 3) Do closely related individuals contact each other more frequently than unrelated individuals? 4) Does relatedness explain the persistence of high contact rates throughout multiple seasons? 5) Are the instances of same-sex den cohabitation between adult raccoons dependent upon genetic similarity?

METHODS

Study Area

I conducted fieldwork on a portion of the Ned Brown Forest Preserve in northeastern Illinois from March 2004 through July 2006. The 1,499 ha Preserve is surrounded by suburban development and is located approximately 30 km northwest of Chicago. Dwyer et al. (1985) estimated that over 1.5 million visitors attended the park annually (1985), and it is believed that at least as many visitors attended the park during the fieldwork period (Chris Anchor, pers. comm.). The preserve consisted of 51% woodlands, 19% wetlands (including open water), 18% tall grasses, and 12% mowed lawns, picnic shelters and roads. The preserve was primarily used for picnicking; garbage receptacles were uncovered which gave raccoons easy access to refuse for the 8 months of the year that the preserve was open to the public (April to November). Field work was concentrated in a smaller section of this preserve, Busse Woods, which was bounded to the north and east by 4-lane, high-volume highways and to the south and west by a large lake, creating a geographically isolated section of parkland. Despite sectioning of the park, raccoons were able to leave, and few individuals moved back and forth into surrounding park land or suburban developments.

Trapping and Capture

A 20-ha section of woods was designated as the core trapping area and efforts were made to capture all resident raccoons within this area. Thirty-two box traps (Tomahawk Live Trap Co., Tomahawk, Wisconsin) were set in places thought to maximize raccoon capture success (e.g., along creeks, near snags, etc.). Traps were baited with commercial brand cat food, checked daily between 0700 and 1200, and maintained during May 2004. During the third week of May, 12 additional traps were placed outside the periphery of the 20-ha core to ensure all resident animals had been captured.

All unmarked raccoons were sedated with an intramuscular injection of Telazol (Fort Dodge Laboratories, Fort Dodge, Iowa, USA; Gehrt et al. 2001). Immobilized raccoons were sexed, weighed, and marked with individually numbered ear tags (Monel #3, National Brand and Tag Company, Newport, Kentucky, USA). Adults were distinguished from juveniles by tooth wear (Grau et al. 1970) and reproductive condition (Sanderson and Nalbandov 1973), whereas adults were assigned to multi-year age classes by tooth wear (Fritzell 1878b, Gehrt and Fritzell 1998b, Prange et al. 2003). Each age class encompasses approximately 14-28 months (Class I: 0-14, Class II: 15-38, Class III: 39-57, Class IV: 58-86, Class V: >86), which does not allow for discerning the precise year of birth (Grau et al. 1970). Previously marked individuals were released without handling. All individuals were processed in accordance with The Ohio State University's Animal Care and Use Protocols (ILACUC#2003R0062).

Genetics

Blood samples were collected from captured individuals and taken to the Brookfield Zoo (Brookfield, Illinois) for processing. DNA was extracted using standard phenol-chloroform techniques (Sambrook et al. 1989), and amplified with polymerase chain reaction (PCR) using an iCycler (Bio-Rad Laboratories, Hercules, California). Sixteen independent and highly variable microsatellite loci were employed from multiple published libraries. One locus, G10X, was obtained from black bears (*Ursus americanus*; Paetkau et al 1995); two loci, PFL9 and PFL11 (Kays et al. 2000), were cloned from kinkajous. All other primers were developed specifically for use in raccoons (P140, P161 (Van Den Bussche unpublished data), PLO-M2, PLO-M3, PLO2-14, PL0-M15, PLO-M17, PLO-M20, PLO3-71, PLO2-117, PLO3-117, PLO3-86, PLO2-123 (Cullingham et al. 2006)). PCR reactions equaled a total volume of 12.5 µL with 1.25 µL of 10% 10X buffer (ProMega Corp.), 0.5 units *Taq* (Flexi-go), 0.2 mM dNTP, 8pmol primer, and 30-50 ng DNA. $MgCl_2$ was adjusted to optimize reactions, with concentrations ranging between 1.6 and 2.4 mM (Table 2.1). After PCR products were visually checked by running samples through a 1.5% agarose gel, successful reactions were sized by a Beckman-Coulter CEQ 8000XL automated capillary genotyping system (Beckman-Coulter, Inc., Fullerton, California). Fragments were analyzed using Genetic Analysis System Software, version 8.0 (Beckman-Coulter, Inc., Fullerton, California). Automated allele calls were visually assessed by graphing the distribution of fragment size and locating natural breaks, or bins, in the distribution. Samples were re-run as positive controls to ensure consistent allele calling, and allele calls were used to construct individual genotypes.

Number of alleles per locus and allelic frequencies were calculated using the program Microsatellite toolkit (Park 2001). The program Microchecker screened the data for evidence of scoring errors, large allele drop out, and null alleles (Van Oosterhout et al. 2004). Results were screened for linkage disequilibrium and deviations from Hardy-Weinberg equilibrium (HWE) using Genepop (Raymond and Rouset 1995), and CERVUS (Marshall et al. 1998). Relatedness (r) was calculated using a log-likelihood ratio generated by the program Kinship 1.2 (Queller and Goodnight 1999). Relatedness ranges on a scale from -1 to 1, with a zero value indicating that the pair of individuals is approximately as related as expected by chance alone, given the allelic frequencies in the population. Positive relatedness values represent individuals that are more genetically similar; parents have a hypothetical r of 0.5 with their offspring and half-siblings have a hypothetical r of 0.25 with each other. I obtained raccoon blood samples of 2 known mother-offspring pairs from a separate study within the Chicago metropolitan area and examined those samples to determine if relatedness values varied widely from theoretical values.

Spatial Distribution

All adults processed were fitted with proximity detectors (Sirtrack Ltd., New Zealand) equipped with VHF radios to obtain estimates of locations and home ranges. Locations of individual raccoons were obtained by triangulation of ≥2 bearings from a truck-mounted 3-element antenna. Nocturnal locations were obtained minimally once per week for each individual, once per hour for five hours beginning after sunset. Visual observations of any radio collared raccoon were opportunistically recorded, but with no more than one location per hour included in seasonal home range estimates. Diurnal locations were often obtained daily either by triangulation from a vehicle, or by homing in on signals with a hand held antenna and receiver. Error polygons for locations were always less than 5.0 ha, and usually considerably lower. Telemetry error, the average distance between the estimated and true location, averaged 25.5 m (SD = 30.2 m) for 300 bearings from 10 test collars.

Seasonal home ranges were created using a minimum of 30 total locations, with no more than 15 locations being diurnal. Seasons were defined as summer (June - August), fall (September - November), winter (December - February), and spring (March - May), based on change in climate and biological factors associated with raccoon reproductive behavior (Prange et al. 2004). Winter home ranges were not calculated due to the inactivity of raccoons during cold months, (Prange et al. 2004) however, contact rates (*see Contacts*) were still available and therefore analyzed.

Fixed-kernel home ranges and core use areas (95% and 50% contours, respectively) were created using the Animal Movements extension in ArcView GIS 3.3 (Hooge and Eichenlaub 1997). Home range overlap between dyad members was calculated using Neil's Utility extension in ArcView GIS 3.3 as:

$$\text{Coefficient of overlap} = 2(\text{Overlap Area}_{1,2}) / (\text{Area}_1 + \text{Area}_2).$$

Distance between centroids, or the average easting and northing coordinates for an individual within a season (Moyer et al. 2006), was also calculated using the Neil's Utility extension in ArcView GIS 3.3.

Contacts

Proximity detectors were also equipped with a UHF emitter and receiver which provided the capability to record when two or more individuals "contacted" each other.

A contact was defined as when two or more individuals came within one meter of each other. The collars also recorded the date and time contact was initiated, the duration of the contact (in seconds), and the identification number of the contacted collar. Data were stored in the collar's internal memory until subsequent downloading via interface and portable computer, which was attempted every 3 months. For a more detailed description of the proximity detectors see Prange et al. (2006). Contact rates, persistence of contact rates throughout the year, and contacts indicative of den sharing were identified by Prange and Gehrt (unpublished data).

Data analysis

I used one-tailed permutation tests to assess the predictions that relatedness within FF dyads was higher than within MM dyads and MF dyads. I used permutation tests rather than conventional two-sample tests (e.g., Mann-Whitney *U*-test) to compensate for the interdependence of relatedness estimates within the matrix of all possible dyadic comparisons. Each relatedness value is calculated by comparing the genotypes of two individuals at a time and the likelihood of obtaining that degree of similarity given the allelic frequencies within the population. Therefore, each individual is included in more than one comparison and lack independence. Using the program R (R development core team 2005), I conducted permutation tests that calculated the difference between population values, and then pooled the populations and sub-sample the pooled values 1,000 times to determine if the observed values are different than a random reshuffling of the data. *P*-values were calculated by the number of permuted differences that exceed the original difference, divided by the number of total permutations.

I tested the prediction that positively related dyads would be more socially connected than negatively related dyads. To do so, I used three surrogates of sociality: percent home range overlap, distance between centroids, and contact rate. Prior analyses revealed that home ranges and contact rates varied significantly by dyad type and season (Prange and Gehrt unpublished data). Thus, for each measure of sociality, I conducted the analysis within a dyad type and season. Analysis consisted of a series of non-parametric correlations. For same sex dyads (MM and FF) I compared each symmetric relatedness matrix (within season and dyad type) to the corresponding symmetric matrix of percent home range overlap (first at the 95, then the 50% level), distances between centroids, and contact rates using Mantel tests in PC-ORD (McCune and Mefford 1999).

Mantel tests require the matrices to be symmetrical, yet the number of females and males included in a season were not equal and thus created asymmetrical matrices. Therefore, partial Mantel tests were used to examine the relationship between relatedness and home range overlap for MF pairs. A partial Mantel test uses 3 matrices; in this case, one for relatedness (of all possible dyads), one for social distance (either home range overlap, core area overlap, distance between centroids, or contact rates of all possible dyads), and the final matrix is used to indicate which cells are to be used in the correlation analysis (a 1 is placed in cells that correspond to a MF dyad in the first two matrices while a 0 indicates either a MM or FF dyad that is of no interest in this analysis). All Partial Mantel tests were run with the software ZT (Bonnett and Van de Peer 2002).

For any comparisons with a small sample size (≤ 7), the total number of possible permutations were less than 10,000, therefore the one of the matrices was permuted as many times as unique permutations were possible (i.e., for $n = 6$, permutations = 720). If the sample size was greater than seven, 10,000 permutations were used as a sub-sample of the total number of possible permutations. All tests were one-tailed in the direction of the corresponding hypothesis.

In addition to these analyses, Prange and Gehrt (unpublished data) determined which dyads contacted each other more frequently than expected, indicating a social bond. Dyads with significantly more contacts per day than expected were identified as those who exhibited contact rates ≥ to those with a probability of occurrence ≤ 0.05 based on the expected Poisson distribution curve. Overall deviation from the expected distribution of contact rates for dyad types (MM, FF, and MF) was analyzed with a χ^2 test. Dyads with significant contact rates were examined closely to determine if relatedness had a bearing on the persistence of high contact rates. Finally, I examined the relatedness values for dyads that shared dens to determine if den sharing among same-sex dyads was reserved for related individuals.

RESULTS

Trapping and Capture

52 raccoons were captured during the initial trapping period; 42 (20 M, 22 F) of these were identified as adults and processed as described above. The majority of these captures were made within the first two weeks of trapping. Only three other individuals were captured during the third week, when traps were added outside the periphery of the core trapping area. No unmarked individuals were captured during the final week of trapping. This capture history coupled with observations from nightly telemetry rounds suggested that most, if not all, adults within the core were radio collared by the end of May 2004.

Genetics

Blood samples were collected from all but one individual of the 42 adults processed in May 2004. I obtained relatedness estimates for 861 unique dyads (190 MM, 253 FF, 418 MF) from these samples. One individual was genotyped at 15 loci; all others were genotyped using 16 loci. The mean number of alleles per locus was 10.6 (range 4-24) and the mean observed heterozygosity was 0.74 (range 0.49-0.92, Table 2.1). No evidence of scoring errors, large allele drop out or null alleles were found. Exact tests showed that three of 16 loci deviated from Hardy-Weinberg equilibrium (Table 2.1); there was a deficiency in the number of observed heterozygotes in each case. One locus (PLO3-117) was noted to be sex-linked (Cullingham et al. 2006), but inclusion of this loci changed all relatedness values equitably among sampled individuals and was therefore kept in the analysis. The deviation from HWE may be due to violation of the assumptions of random mating and a large population. Deviations from HWE at multiple loci can be an indication of population substructure, where there may be an overrepresentation of closely related or inbred family groups (Marshall et al. 1998, Kitchen et al. 2005). No deviation from HWE or linkage disequilibrium was found for these 3 suspect loci in 2 previous studies (Cullingham et al. 2006, Roy Nielsen and Nielsen 2007) which employed the same loci. Both studies were conducted in areas >125 times the size of my trapping area, with nearly double the sample size. Additionally, the 2 sets of known mother-offspring processed for this study produced *r* values similar to 0.5 (0.47 and 0.54), lending credibility to my relatedness estimates. Therefore, I proceeded with all 16 loci in my analysis.

Relatedness within dyad types

Relatedness values varied widely within, as well as among dyad groups (Figure 2.1). Mean genetic relatedness was -0.026 (range: -0.28-0.46), 0.002 (range: -0.30-0.72), and -0.012 (range: -0.284, 0.606) for MM, FF, and MF dyads respectively. Relatedness was significantly higher within FF dyads than MM dyads ($T = 0.89$, *d.f.* = 1, P=0.002), or MF dyads ($T = -9.68$, *d.f.* = 1, $P = 0.03$). Additionally, relatedness tended to be lower within MM dyads than within MF dyads ($T = 0.89$, *d.f.* = 1, P=0.05), although this failed to reach statistical significance with the necessary family-wise error Bonferroni correction ($P = 0.048$)

Relatedness and spatial distribution

I obtained 6,314 locations for 42 radio collared raccoons. Of these, 19 raccoons survived and were equipped with functioning radio collars intact for the duration of study. Therefore, the number of home ranges obtained varied by season; 31 in summer 2004 (13M, 18 F), 29 in fall 2004 (14M, 15F), 26 in spring 2005 (10M, 16F), 22 in summer 2005 (9M, 13F), and 21 in fall 2005 (8M, 13F). Home ranges were smaller for females than males for spring and summer in both years (summer 2004: $H = 4.502$, *d.f.* = 1, $P = 0.03$; spring 2005: $H = 15.625$, *d.f.* = 1, $P = 0.00007$; summer 2005: $H = 6.957$, *d.f.* = 1, $P = 0.008$), but there was no significant difference between female and male home range size during fall of either year (2004: $H = 0.55$, *d.f.* = 1, $P = 0.458$; 2005: $H = 0.131$, *d.f.* = 1, $P = 0.717$; Table 2.2).

Home range overlap (95% contours) and relatedness for FF dyads correlated for 3 of the 5 seasons investigated (summer 2004: $r = 0.197$, $P = 0.036$; summer 2005: $r = 0.370$, $P = 0.006$; fall 2005: $r = 0.274$, $P = 0.031$; Table 2.3). Additionally, relatedness and home range overlap tended to correlate for FF dyads during spring 2005 (*r* = 0.148, *P* = 0.089). MM dyads exhibited a correlation between home range overlap and relatedness for only 1 season (summer 04: *r* = 0.236, *P* = 0.021; all other *P* ≥ 0.232; Table 2.3). MF relatedness correlated with home range overlap for summer 2004 (*r* = 0.178, *P* = 0.002) and fall 2005 (*r* = 0.179, *P* = 0.028; Table 2.3).

I found no relationship between core area overlap (50% contours) and relatedness (*r* range = -0.108 - 0.14, *P* range = 0.124 - 0.434; Table 2.4) for FF dyads. MM dyads, however, exhibited a significant correlation between core area overlap and relatedness for summer 2004 (*r* = 0.211, *P* = 0.039), and approached, but did not obtain significance (*r* = 0.186, *P* = 0.048) for fall 2004, when Bonferroni correction was applied (*P* = 0.045). Relatedness and core area overlap did not correlate for MM dyads during any other season (*r* range = -0.06 - 0.06, *P* range = 0.312 - 0.413; Table 2.4). Relatedness and core area overlap correlated for MF dyads during summer 2004 (*r* = 0.093, *P* = 0.044), but not for any other season (all other *r* ≤ 0.006, all other *P* ≥ 0.311). Distance between centroids was not correlated with genetic relatedness for any dyad type during any season (Table 2.5), but ranged widely (Table 2.6).

Relatedness and contacts

When examining the contact rates between related and unrelated individuals I found that close encounters did not correlate with relatedness for any dyad type in any season (all P-values ≥0.111; Table 2.7), except MM dyads during fall 2004 (*r* = -0.566, *P* = 0.007). Highly social dyads were not often comprised of positively related individuals. In fact, MM dyads with significant rates of contact were typically unrelated. Of the 11 MM dyads with high contact rates, 8 were negatively related (72.7%, Table 2.8).

Relatedness was not a precursor to high contact rates between FF dyads either as nearly half (4/9, 44.4%, Table 2.9) of the most social dyads were negatively related. Similarly for MF pairs, nearly half (9/19, 47.3%, Table 2.10) of the most social dyads were negatively related.

Relatedness and persistent contact

Social associations between individuals lasted longer for MM dyads than FF or MF dyads. Of 11 MM dyads that had higher contact rates than expected, 8 (72.7%) exhibited significant contact rates during all seasons during which data were available (Table 2.8). By contrast, none of the 9 FF dyads (Table 2.9; Fisher's exact test: P = 0.0014, two-tailed) or 19 MF dyads (Table 2.10; $P = 2.8\times10^{-5}$) were consistently significantly social for every season for which data were available. Five of the eight (62.5%) MM dyads with high contact rates for more than one season were negatively related. FF dyads had higher contact rates than expected for more than one season only twice, and both of those dyads were negatively related. Eight MF dyads had higher contact rates than expected for more than one season and seven (87.5%) of those were positively related. All of the seven positively related MF dyads with high contact rates occurred between females that were as old, or older, than the male involved, and six of these seven dyads contained the same two females.

Relatedness and den sharing

Den sharing was not confined to highly related dyads, or in the case of MF den sharing in winter, restricted to unrelated dyads. Of 34 MF dyads that shared dens throughout the year, 18 dyads were negatively related (52.9%). These 34 dyads denned together a total of 219 times, of which 98 (44.7%) instances were between negatively related dyads. Specifically during the breeding season (winter), 17 of 31 MF dyads that denned together were negatively related (54.8%). Yet the majority of den sharing instances were between positively related individuals (98/173, 56.6%). The majority of MM dyads (13/19, 68.4%) and instances of den sharing (182/317, 57.4%) among MM dyads were between negatively related dyads. Conversely, the majority of FF dyads (6/11, 54.5%) and instances of den sharing among FF dyads (33/57, 57.8%) were between positively related dyads.

DISCUSSION

My study is the first to use both fine-scale proximity detecting and genetic technologies to elucidate the role of relatedness in social behavior for any species. Additionally, this study is the first to examine the role of relatedness in sociality for an urban raccoon population, as well as the first that addresses relatedness and sociality for MM and MF associations of raccoons in any environment. While the density estimate for my study population was high and the home ranges were small, these parameters are both within the normal range reported for raccoons (Gehrt 2003). Conclusions from this study may therefore be applicable to various raccoon populations, but specifically those inhabiting urban environments.

My results confirmed some previously held notions of raccoon behavior, but more often revealed an unexpected layer of social complexity. I found evidence for a system of female based philopatry in that FF dyads were more closely related on average than MM or MF dyads. Also, because MF dyads were more closely related than MM dyads, it appears that males disperse into new areas for mating opportunities. Indeed, several telemetry studies found evidence for male dispersal (Schneider et al. 1971, Fritzell 1978, Gehrt and Fritzell 1998b), and those findings were corroborated by Ratnayeke et al.'s (2002) genetic investigation. That investigation also found that FF dyads were more genetically similar than MM or MF dyads, and that MF dyads were more closely related than MM dyads.

Ratnayeke et al. (2002) found positive correlations between percent home range overlap and relatedness, and an inverse relationship between distance between harmonic centers of activity and relatedness for FF dyads. I report similar findings for FF pairs, as females exhibited, or tended towards, significance in the correlations between their relatedness and home range overlap for 4 of 5 seasons. However, I did not observe a significant inverse relationship between relatedness and distance between centroids. Although home range overlap and relatedness correlated for FF dyads during several seasons in this study, these were weak connections and many unrelated individuals shared space.

Unrelated females not only shared space, but also contacted each other, maintained high rates of contact, and shared dens together. It was expected, due to the reported philopatric nature of female raccoons (Gehrt and Fritzell 1998b, Ratnayeke et al. 2002), that social associations would be greatest among related females. However, relatedness and contact rate did not correlate for FF dyads. Additionally, the FF dyad that recorded the 4th highest contact rate and 3rd longest duration of any dyad type and consisted of an older female and yearling female caught in the same trap together that were presumed to be a mother-offspring pair, were not first order relatives ($r = 0.11$). Moreover, of the two FF dyads that had high contact rates for more than one season, both were negatively related. Finally, while most den sharing instances occurred between related females, den sharing was not uncommon between unrelated females. Clearly, relatedness is not the major factor driving social associations among female raccoons in this urban environment.

The frequent associations between unrelated individuals may be due to two factors, which are not necessarily mutually exclusive. First, raccoons at my study site exhibited a high rate of multiple paternity (Chapter 3). High rates of multiple paternity dilute the relatedness among littermates (Van Horn et al. 2004) as they are only half as closely related as full siblings. Even though relatedness values are lowered, familiarity, which can lead to strong associations (Chapais et al. 2001, Wahaj et al. 2004, Silk et al. 2006), remains just as high. Therefore, social associations can arise between individuals with low relatedness, yet high familiarity. Second, low densities and large home ranges may be coupled with low rates of association among adult raccoons (Fritzell 1978, Johnson 1970). These findings are similar to those reported by Roy Nielsen and Nielsen (2007), who failed to find a correlation between relatedness and distance between initial trap location of raccoons in southern Illinois: their study site had an 83.3% rate of multiple paternity and an extremely high density (1 raccoon/0.6ha). Therefore, tolerance and social associations among female raccoons may depend on space and resource availability, rather than relatedness.

Males are known to be the dispersing sex of raccoons (Stuewer 1943, Urban 1970, Gehrt and Fritzell 1998a), therefore it was anticipated that relatedness would not affect the sociality of adult male raccoons. However, 2 of the 3 measures of sociality (home range overlap and contact rates) correlated with relatedness for MM dyads during 1 of 5 seasons. Relatedness correlated positively with increasing home range overlap (at

95 and 50% contours), yet exhibited a strong inverse relationship with contact rate for MM dyads. It is known that that home range overlap and contact rate correlate, but the correlation is weak and home range overlap often fails to identify high rates of contact (Prange and Gehrt, unpublished data). Therefore, it is not wholly surprising that differing trends were observed when examining the effect of relatedness on various indicators of sociality. Relatedness played a much smaller role in MM than FF associations as evidenced by these opposing trends and the fact that such correlations were significant for only 1 of 5 seasons. These generalities could indicate an underlying importance for relatedness in female spatial distribution, even when densities are high and space is limited, that is not expressed in male spatial distribution. In fact, many studies on carnivores, as well as other taxa, have demonstrated that relatedness plays a greater role in the acquisition of home range for females than males (Rogers 1987, Gompper et al. 1998, Van Horn et al. 2004, Moyer et al. 2006, Silk et al. 2006).

Why males form group associations still remains under investigation. Male coalitions among carnivores are often found to occur between two unrelated individuals (Packer et al. 1991, Kays et al. 2000, Blundell et al. 2004, Wagner et al. 2007) or three or more related individuals. This was also the case in my study population. Prange and Gehrt (unpublished data) identified four distinct male groups within the study area that were largely spatially distinct; members within groups had high overlap of their core areas and demonstrated high rates of contact. Two of the four groups were comprised of sole dyads, one group was comprised of three males, and the last included four individuals. Prange and Gehrt (unpublished data) suggested that the two groups composed of a single dyad could be siblings, due to their similarity in age. Yet the only group that contained related individuals was the largest group of four. Group four was the only group where consortship was not recorded for every member of the group (Chapter 3), as one male failed to consort, or den share, with any female. This supports the theory that male raccoon coalitions form for mate sequestering opportunities. Small coalitions of males share mating opportunities more equitably than large coalitions of related individuals (Packer et al. 1991). While my study did not examine the mating success of male coalition members, the only instance of relatedness occurred within the largest group; equal mating access is less likely to occur between 4 as it is between 2 individuals.

It is often noted in literature that the only associations between adult male and female raccoons occurs for mating purposes (Gehrt and Fritzell 1999, Gehrt 2003). Therefore, the positive correlations between relatedness and home range overlap (at 95 and 50% contours) for MF dyads was unanticipated. Retention of familial bonds has been reported (Gehrt and Fritzell 1998b) and it is interesting to note that all of the significant associations within MF dyads occurred between a female and a younger or as young male. In this study we found that the majority (10/19) of MF associations occurred within positively related dyads. Yet, of these 10 dyads, only 3 were closer than 2nd order relatives, and only one was a 1st order relationship. Roy Nielsen and Nielsen (2007) found that the average relatedness value between mated raccoons was low, yet the value could be as high as 0.11. Therefore, many of the positively related dyads in my study may still have been associating for mating opportunities.

Although relatedness between mated raccoon pairs has never been observed to extend higher than the 3rd order relation (Roy Nielsen and Nielsen 2007, Chapter 3), the correlation between space use and relatedness found in this study indicates that highly related males and females live in close proximity. This close proximity of relatives may explain why females mate multiply (Roy Nielsen and Nielsen 2007, Chapter 3) and associate with younger males. Multiple mating may reduce the chance that a litter is sired exclusively by a closely related male. Associations between older females and younger males (which occurred in this study) may reduce the chances that a female will mate with her father. This tactic may expose females to mating with their sons, but because mothers provide the sole investment in litter rearing (Gehrt 2003), it is feasible that a female could distinguish her son with certainty, but not her father. Additionally, because the majority of male raccoons are known to disperse (Stuewer 1943, Urban 1970, Gehrt and Fritzell 1998a), the likelihood of mating with a son is reduced.

My results indicate that genetic relatedness cannot solely explain the formation and variation in social associations of adult raccoons. These results offer evidence that relatedness may be responsible for underlying association patterns, yet it is not the ultimate factor influencing sociality. How these patterns of association compare in rural areas are unknown and worth further investigation. Perhaps in low density environments with limited food resources, relatedness plays a much greater role in the formation and maintenance of social associations than what was observed here. Although raccoons are classically defined as solitary and intolerant of conspecifics, defense of space or resources in a high-density environment with superabundant food, would likely be disadvantageous. The benefits, however, of social tolerance (i.e. sharing home ranges and food sources) in such an environment could be great. Raccoons are well known for their highly adaptable nature, and are expert exploiters of their environment. That flexibility may be the key to their social tolerance, and in turn, their successful expansion into urbanized systems.

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TABLES AND FIGURES

Locus	Annealing temp (°C)	$MgCl_2$ (mM)	Number of alleles	H_e	H_o	*P*-value
M2	56	2.4	12	0.860	0.825	0.822
M3	56	2.4	7	0.765	0.873	0.125
M14	68	1.6	18	0.878	0.857	0.373
M15	56	2.4	12	0.859	0.778	0.267
M17	56	1.6	8	0.780	0.714	0.535
M20	56	2.4	12	0.863	0.794	0.001
M71	56	2.4	12	0.767	0.714	0.158
M117	56	2.0	18	0.880	0.841	0.145
M117X	64	2.0	7	0.770	0.429	0.000
M86	56	2.0	24	0.901	0.921	0.013
M123	68	2.4	12	0.866	0.825	0.813
G10C	56	2.4	4	0.414	0.492	0.401
P140	52	1.6	8	0.754	0.698	0.107
P161	68	2.4	8	0.491	0.508	0.822
PFL9	54	2.0	10	0.828	0.794	0.183
PFL11	62	1.6	15	0.873	0.810	0.098

Table 2.1. Annealing temperature (°C), concentration of Mg Cl_2 (mM), number of alleles, expected and observed heterozygosity by locus.

	Summer 2004		Fall 2004		Spring 2005		Summer 2005		Fall 2005	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Male	48.5	14.8	58.4	47.2	66.9	22.5	69.5	22.6	55.2	51.5
Female	44.0	52.6	46.5	28.1	16.9	15.2	43.1	18.4	44.4	16.4

Table 2.2. Mean (standard deviation) 95% fixed-kernel home range area (ha) for male and female adult raccoons by season in Busse Woods in northeastern Illinois from summer 2004 through fall 2005.

	MM			FF			MF		
	N	r_{AB}	*P*-value	N	r_{AB}	*P*-value	N	$r_{AB.C}$	*P*-value
Summer 2004	91	0.236	**0.021**	171	0.197	**0.036**	234	0.178	**0.002**
Fall 2004	105	0.077	0.232	120	0.050	0.299	210	0.026	0.317
Spring 2005	55	0.069	0.302	136	0.148	0.089	160	0.069	0.188
Summer 2005	55	0.005	0.488	136	0.370	**0.006**	160	0.095	0.123
Fall 2005	36	0.073	0.333	91	0.274	**0.031**	104	0.179	**0.028**

Table 2.3. Number of dyads (N), standardized correlation coefficients of simple Mantel test (r_{AB}) or partial Mantel test ($r_{AB.C}$), and corresponding *P*-values comparing genetic relatedness and 95% home range overlap of adult raccoons in Busse Woods in northeastern Illinois from summer 2004 through fall 2005. Significant correlations (at Bonferroni correction $\alpha = 0.045$) are indicated by *P*-values in bold.

	MM			FF			MF		
	N	r_{AB}	*P*-value	N	r_{AB}	*P*-value	N	$r_{AB.C}$	*P*-value
Summer 2004	91	0.211	**0.039**	171	0.004	0.434	234	0.093	**0.044**
Fall 2004	105	0.186	0.048	120	-0.108	0.124	210	-0.003	0.505
Spring 2005	55	0.060	0.312	136	0.090	0.178	160	0.006	0.420
Summer 2005	55	0.038	0.379	136	0.140	0.128	160	-0.039	0.311
Fall 2005	36	-0.060	0.413	91	0.028	0.372	104	-0.022	0.409

Table 2.4. Number of dyads (N), standardized correlation coefficients of simple Mantel test (r_{AB}) or partial Mantel test ($r_{AB.C}$), and corresponding *P*-values comparing genetic relatedness and 50% home range overlap of adult raccoons in Busse Woods in northeastern Illinois from summer 2004 through fall 2005. Significant correlations (at Bonferroni correction α = 0.045) are indicated by *P*-values in bold.

	MM			FF			MF		
	N	r_{AB}	*P*-value	N	r_{AB}	*P*-value	N	$r_{AB.C}$	*P*-value
Summer 2004	91	0.181	0.065	171	0.195	0.072	234	0.122	0.074
Fall 2004	105	0.035	0.354	120	0.064	0.331	210	-0.005	0.467
Spring 2005	55	0.039	0.388	136	0.201	0.064	160	-0.052	0.242
Summer 2005	55	0.039	0.397	136	0.201	0.066	160	0.031	0.334
Fall 2005	36	0.002	0.474	91	0.189	0.106	104	0.117	0.113

Table 2.5. Number of dyads (N), standardized correlation coefficients of simple Mantel test (r_{AB}) or partial Mantel test ($r_{AB.C}$), and corresponding *P*-values comparing genetic relatedness and distance between centroids of adult raccoons in Busse Woods in northeastern Illinois from summer 2004 through fall 2005.

Season	Mean (m)	SD	Range (m)
Summer 04			
FF	761.30	568.1	18.5 - 2774.9
MF	674.42	488.2	34.6 - 2742.7
MM	597.28	310.7	54.6 - 1246.3
Fall 04			
FF	840.72	517.1	34.0 - 2412.6
MF	726.09	472.2	37.5 - 2592.3
MM	637.72	335.6	43.3 - 1259.9
Spring 05			
FF	391.32	219.2	18.6 - 752.3
MF	510.72	274.4	17.5 - 1064.1
MM	587.27	322.4	13.5 - 1095.4
Summer 05			
FF	477.67	225.7	42.2 - 971.9
MF	517.84	275.1	58.1 - 1249.8
MM	585.94	341.3	10.42 - 1231.2
Fall 05			
FF	451.99	240.7	55.5 - 1218.2
MF	432.65	250.3	19.4 - 1228.9
MM	458.98	270.2	39.5 - 912.0

Table 2.6. Mean range and standard deviation of distances between centroids (m) by season and dyad type of adult raccoons in Busse Woods in northeastern Illinois from summer 2004 through fall 2005.

	MM			FF			MF		
	N	r_{AB}	P-value	N	r_{AB}	P-value	N	$r_{AB.C}$	P-value
Summer 2004	10	-0.411	0.063	45	0.246	0.063	64	0.025	0.334
Fall 2004	15	-0.566	**0.007**	45	-0.060	0.358	63	-0.061	0.288
Winter 04/05	15	-0.257	0.197	45	0.185	0.111	64	0.019	0.375
Spring 2005	15	0.150	0.344	45	-0.102	0.246	64	-0.090	0.134

Table 2.7. Number of dyads (N), standardized correlation coefficients of simple Mantel test (r_{AB}) or partial Mantel test ($r_{AB.C}$), and corresponding P-values comparing genetic relatedness and contact rates of adult raccoons in Busse Woods in northeastern Illinois from summer 2004 through spring 2005. Significant correlations (at Bonferroni correction $\alpha = 0.046$) are indicated by P-values in bold.

		Individual		Age		
Group	Relatedness	A	B	A	B	No. of seasons
1	-0.16009	6308	6407	II	II	2/4
2	-0.00035	6328	6424	II	II	2/2
3	-0.00375	6453	6462	III	IV	3/3
3	-0.04246	6482	6453	I	III	2/3
3	-0.10421	6482	6462	I	IV	3/3
4	0.21724	6468	6485	I	III	2/3
4	0.15107	6488	6468	II	I	3/3
4	0.05504	6488	6485	II	III	3/3
4	-0.05101	6488	6490	II	III	1/1
4	-0.09622	6485	6490	III	III	1/1
4	-0.08776	6468	6490	I	III	1/1

Table 2.8. Group number, relatedness value, dyad members (A, B), age class, and number of seasons with significant contact rate out of total seasons data were available for male dyads in Busse Woods northeastern Illinois from summer 2004 through fall 2005.

	Individual		Age		
Relatedness	A	B	A	B	No. of seasons
0.35383	6456	3625	II	V	1/4
0.18345	6115	6473	III	I	1/3
0.10819	4014	6473	V	I	1/3
0.27777	6456	4047	II	IV	1/4
-0.05448	6425	6326	IV	III	2/4
0.00815	4005	6115	III	III	1/4
-0.04594	4005	4014	III	V	2/4
-0.10538	6456	6493	II	I	1/4
-0.04185	6416	3625	II	V	1/3

Table 2.9. Group number, relatedness value, dyad members (A, B), age class, and number of seasons with significant contact rate out of total seasons data were available for female dyads in Busse Woods, Il.

	Individual		Sex		Age		No. of seasons
Relatedness	A	B	A	B	A	B	
-0.02564	6407	3625	M	F	II	V	1/4
0.44848	6468	4047	M	F	I	IV	1/4
0.06462	6485	4005	M	F	III	III	3/4
0.28867	6485	4014	M	F	III	V	2/4
0.07418	6488	4005	M	F	II	III	2/3
0.12714	6488	4014	M	F	II	V	2/3
-0.12693	6482	6115	M	F	I	III	1/4
-0.14128	6453	6115	M	F	III	III	1/4
0.04844	6468	4005	M	F	I	III	3/4
-0.06686	6453	6456	M	F	I	II	1/4
-0.12209	6482	4047	M	F	I	IV	1/4
0.07959	6488	6115	M	F	II	III	1/3
0.04695	6462	4047	M	F	IV	IV	2/4
-0.13049	6308	4047	M	F	II	IV	1/4
0.08616	6407	4014	M	F	II	V	2/4
-0.06074	6308	6456	M	F	II	II	2/4
0.06588	6453	4047	M	F	I	IV	1/4
-0.19184	6407	4005	M	F	II	III	1/4
-0.01674	6308	3625	M	F	II	V	1/4

Table 2.10. Group number, relatedness value, dyad members (A, B), sex of dyad members, age class, and number of seasons with significant contact rate out of total seasons data were available for male-female dyads in Busse Woods, Il.

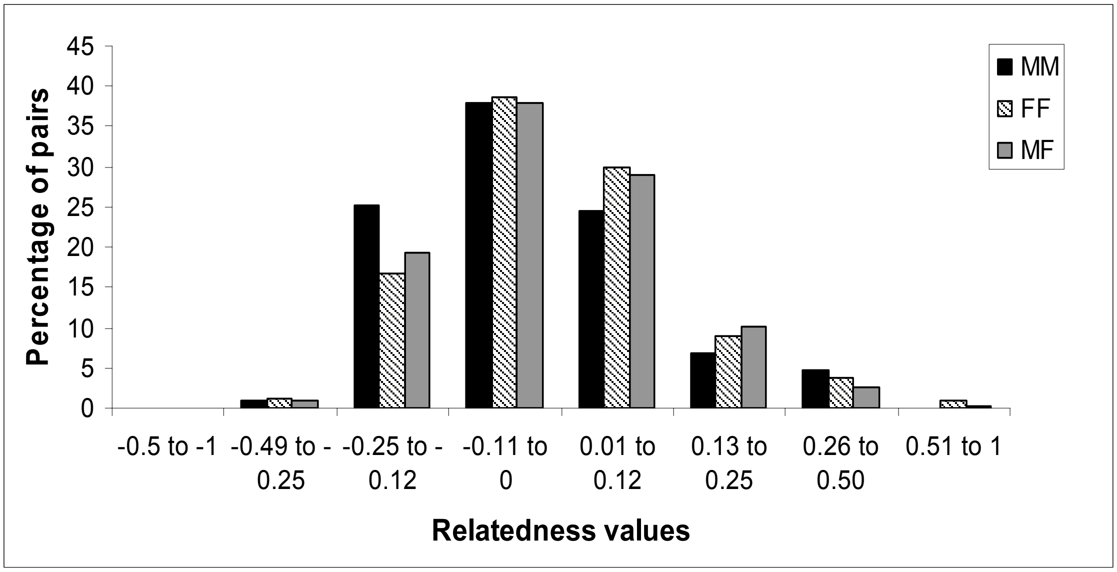

Figure 2.1. Distribution of relatedness by dyad type for adult raccoons captured in spring 2004 in Busse Woods in northeastern Illinois.

CHAPTER 3

THE RACCOON MATING SYSTEM: HOW CONTACT RATES AND DEN SHARING TRANSLATE INTO PROGENY

Recent advances in molecular technology have produced a greater understanding of the social behavior and structure of a wide variety of mammalian species. Purely observational data have led to false conclusions about social associations and mating behavior in many species due to their nocturnal, cryptic, or otherwise obfuscating nature (review in Hughes 1998). Observational data on who mates with whom is so routinely misleading that monogamy is now specified as either social, genetic, or both. Indeed, many studies on species previously described as monogamous or polygynous have often found high rates of extra pair paternity (Amos et al. 1995, Goossens et al. 1998, Bryja and Stopka 2005, Kitchen et al. 2006), leading to the discovery of more complex mating strategies.

Mating tactics differ between males and females due to their disparate investment in young (Feldhammer et al. 1999). Females are often required to provide a substantial investment in their young and therefore best increase their fitness by choosing a high quality mate. Circumstances exist, namely avoidance of male-driven infanticide (Bellemain et al. 2006, Ebensperger 1998, Wolff and Macdonald 2004), that favor multiple matings for females, which can result in a system of polyandry or promiscuity.

Except in systems where biparental care is obligatory, males are expected to seek polygynous or promiscuous mating opportunities (Feldhammer et al. 1999).

Males within Carnivora demonstrate a wide variety of mating tactics from exclusive territoriality and strict mate defense (Haley et al. 1994, Moehlman 1987), to the equitable sharing of mates among group members (Packer et al. 1991), to dyadic or group formation with resultant mating hierarchies (Creel and Waser 1993, Kays et al. 2000). Territoriality and/or mate defense are favored tactics when population densities are low (Fritzell 1978), resources are homogeneously distributed (Caro and Collins 1987) and male investment in offspring is high (Moehlman 1987). High density of reproductive females or low relatedness between male group members leads to the equitable sharing of females (Packer et al. 1991). Dominance hierarchies, often resulting from male coalitions, arise from mating access asymmetry attributed to a limited number of reproductive females (i.e. systems with 1 breeding alpha female) or high relatedness among male group members (Packer et al. 1991).

Male coalitions are thought to reduce competition (de Villiers et al. 2003) and galvanize the defense of mates (Grinnell et al. 1995). In lions (*Panthero leo*) and cheetahs (*Acinonyx jubatus*; Packer et al. 1991, Caro and Collins 1987), large male coalitions increase take-over success, tenure period, and access to better territories, which often result in access to more females. But large coalitions do not display equal mating opportunities for all coalition members. Therefore, relatedness between members needs to be high for non-breeding members to remain within the group. Small coalitions (2-3 members), are typically comprised of unrelated males, and breeding access is more equitable among members (Packer et al. 1991, Kays et al. 2000).

Male raccoons (*Procyon lotor*) have been documented to form coalitions of 2-4 members exhibiting large home range overlap between members, and little to no home range overlap with other males (Gehrt and Fritzell 1998a, Chamberlain and Leopold 2002, Prange and Gehrt unpublished data). However, it is currently unknown what benefits are derived from group membership, as much of raccoon social and mating behavior remains poorly understood due to their secretive, nocturnal, semi-arboreal lifestyle. At very low densities (Fritzell 1978), raccoons may exhibit little social interaction between conspecifics and polygyny is the presumed mating system. At more typical densities, where male coalitions have been reported, the mating system switches between polygyny and promiscuity based on the synchronicity of estrus periods (Gehrt and Fritzell 1999a). These descriptions of mating systems, however, are based solely on denning associations and spatial data from radio-telemetry studies. One recent study used genetic analysis and reported a promiscuous breeding system with a high rate (88%) of multiple paternity for a high-density population of raccoons (Roy Nielsen and Nielsen 2007). Unfortunately, only the distance between initial trap locations of parents was used to quantify social associations of successful parents, and parent behavioral data were lacking. No study to date has examined spatial distribution, social associations, male group membership, and instances of den sharing in relation to progeny produced from such behaviors. Therefore, more research is necessary to address raccoon mating strategies.

I used data from daytime resting locations, contact rates, denning behavior, and genetic analysis to examine social associations between assigned parents of captured juvenile raccoons. The adult population within my study site was monitored from 2004-

2006 to elucidate raccoon social associations (Prange and Gehrt unpublished data). Prange and Gehrt reported a surprisingly high number of interactions between many dyads; a total of 12,577 contacts involving 32 raccoons were recorded during the first 11 weeks of study alone. Of 473 dyads, 304 exhibited at least one contact, with the average contact rate being 0.4 contacts/day (range: 0-22.5) for an average of 1.5 minutes/day (range: 0-150.8). Prange and Gehrt (unpublished data) also identified four male coalitions based on within group high contact rates and spatial overlap.

Using these estimates of sociality and overlaying genetic analysis, I examined three main questions in regard to raccoon social behavior and mating success. First, I examined the prevalence of multiple paternity within a high raccoon density urban area. The rate of promiscuity is expected to be high a high-density environment (Roy Nielsen and Nielsen 2007). Secondly, I described the social associations (spatial proximity, contact rates and incidents of den sharing) between parents of assigned offspring. Finally, I examined group membership and fertilization success. If male coalitions among "solitary" species form for breeding access to females (Rood 1989, Waser et al. 1994, Gehrt and Fritzell 1999a), it is expected that instances of multiple paternity would be restricted to group males, and females should not breed with multiple groups.

METHODS

Study Area

I conducted fieldwork on a portion of the Ned Brown Forest Preserve in northeastern Illinois from March 2004 through July 2006. The 1,499 ha Preserve is surrounded by suburban development and is located approximately 30 km northwest of Chicago. Dwyer et al. (1985) estimated that over 1.5 million visitors attended the park annually (1985), and it is believed that at least as many visitors attended the park during the fieldwork period (Chris Anchor, pers. comm.). The preserve consisted of 51% woodlands, 19% wetlands (including open water), 18% tall grasses, and 12% mowed lawns, picnic shelters and roads. The preserve was primarily used for picnicking; garbage receptacles were uncovered which gave raccoons easy access to refuse for the 8 months of the year that the preserve was open to the public (April to November). Field work was concentrated in a smaller section of this preserve, Busse Woods, which was bounded to the north and east by 4-lane, high-volume highways and to the south and west by a large lake

Trapping and Capture

A 20-ha section of woods was designated as the core trapping area and efforts were made to capture all resident raccoons within this area. Thirty-two box traps (Tomahawk Live Trap Co., Tomahawk, Wisconsin) were set in places thought to maximize raccoon capture success (e.g., along creeks, near snags, etc.). Traps were baited with commercial brand cat food, checked daily between 0700 and 1200, and maintained during May 2004. During the third week of May, 12 additional traps were placed outside the periphery of the 20-ha core to ensure all resident animals had been captured.

All unmarked raccoons were sedated with an intramuscular injection of Telazol (Fort Dodge Laboratories, Fort Dodge, Iowa, USA; Gehrt et al. 2001). Immobilized raccoons were sexed, weighed, and marked with individually numbered ear tags (Monel #3, National Brand and Tag Company, Newport, Kentucky, USA). Adults were distinguished from juveniles by tooth wear (Grau et al. 1970) and reproductive condition

(Sanderson and Nalbandov 1973), whereas adults were assigned to multi-year age classes by tooth wear (Fritzell 1878b, Gehrt and Fritzell 1998b, Prange et al. 2003). Each age class encompasses approximately 14-28 months (Class I: 0-14, Class II: 15-38, Class III: 39-57, Class IV: 58-86, Class V: >86), which does not allow for discerning the precise year of birth (Grau et al. 1970). Previously marked individuals were released without handling. All individuals were processed in accordance with The Ohio State University's Animal Care and Use Protocols (ILACUC#2003R0062).

Genetics

Blood samples were collected from captured individuals and taken to the Brookfield Zoo (Brookfield, Illinois) for processing. DNA was extracted using standard phenol-chloroform techniques (Sambrook et al. 1989), and amplified with polymerase chain reaction (PCR) using an iCycler (Bio-Rad Laboratories, Hercules, California). Sixteen independent and highly variable microsatellite loci were employed from multiple published libraries. One locus, G10X, was obtained from black bears (*Ursus americanus*; Paetkau et al 1995); two loci, PFL9 and PFL11 (Kays et al. 2000), were cloned from kinkajous. All other primers were developed specifically for use in raccoons (P140, P161 (Van Den Bussche unpublished data), PLO-M2, PLO-M3, PLO2-14, PL0-M15, PLO-M17, PLO-M20, PLO3-71, PLO2-117, PLO3-117, PLO3-86, PLO2-123 (Cullingham et al. 2006)). PCR reactions equaled a total volume of 12.5 µL with 1.25 µL of 10% 10X buffer (ProMega Corp.), 0.5 units *Taq* (Flexi-go), 0.2 mM dNTP, 8pmol primer, and 30-50 ng DNA. $MgCl_2$ was adjusted to optimize reactions, with concentrations ranging between 1.6 and 2.4 mM (Table 2.1). After PCR products were visually checked by running samples through a 1.5% agarose gel, successful reactions were sized by a Beckman-Coulter CEQ 8000XL automated capillary genotyping system (Beckman-Coulter, Inc., Fullerton, California). Fragments were analyzed using Genetic Analysis System Software, version 8.0 (Beckman-Coulter, Inc., Fullerton, California). Automated allele calls were visually assessed by graphing the distribution of fragment size and locating natural breaks, or bins, in the distribution. Samples were re-run as positive controls to ensure consistent allele calling, and allele calls were used to construct individual genotypes.

Number of alleles per locus and allelic frequencies were calculated using the program Microsatellite toolkit (Park 2001). The program Microchecker screened the data for evidence of scoring errors, large allele drop out, and null alleles (Van Oosterhout et al. 2004). Results were screened for linkage disequilibrium and deviations from Hardy-Weinberg equilibrium (HWE) using Genepop (Raymond and Rouset 1995), and CERVUS (Marshall et al. 1998). Relatedness (*r*) was calculated using a log-likelihood ratio generated by the program Kinship 1.2 (Queller and Goodnight 1999). Relatedness ranges on a scale from -1 to 1, with a zero value indicating that the pair of individuals is approximately as related as expected by chance alone, given the allelic frequencies in the population. Positive relatedness values represent individuals that are more genetically similar; parents have a hypothetical relatedness value of 0.5 with their offspring and half-siblings have a hypothetical *r* of 0.25 with each other. I obtained raccoon blood samples of 2 known mother-offspring pairs from a separate study within the Chicago metropolitan area and examined those samples to determine if relatedness values varied widely from theoretical values.

Parentage Assignment Analysis

During the fall 2005 trapping session I obtained blood samples from juveniles captured in traps. Traps were set intentionally for radio collared adults and so were placed and maintained as described above. Blood samples from juveniles were processed and analyzed for basic genetic data (number of alleles per locus, deviations from HWE, etc.) in the same manner as samples from adults. Paternity analysis was conducted using the program CERVUS (Marshall et al. 1998). CERVUS has an advantage over other paternity packages in that it assigns paternity based on likelihood. The likelihood ratio is a computation of the probability the proposed parent is the true parent over the probability that the proposed parent is not the true parent. This method allows for mutations and genotyping errors which can be high when using a large number of loci, such as in this study. The analysis was run with the relaxed assumption that the proportion of candidate parents sampled was 72%. This estimate was based on the capture history, observation of few un-collared adults, and small size of the study area. When the main study began, it was believed that most, if not all, of the adult raccoons in the core area had been captured. However, this assumption became less valid over time as some juveniles at the beginning of the study matured to adults, resident individuals died, and new adults immigrated (*n*= 15). To ensure that paternity would be assigned for all juveniles, I genotyped these 15 adults that were captured after the initial trapping period. In CERVUS, I ran 10,000 simulations with strict and relaxed confidences at 95 and 80% respectively. I ran a paired parent analysis with known sexes, after simulation analysis, which yielded the final paternal results.

Spatial Distribution

All adults processed were fitted with proximity detectors (Sirtrack, Ltd., New Zealand) equipped with VHF radios to obtain estimates of animal locations and home ranges. Locations of animals were obtained by triangulation of ≥2 bearings from a truck-mounted 3-element antenna. Nocturnal locations were obtained minimally once per week for each individual, once per hour for 5 hours beginning after sunset. Visual observations of any radio collared raccoon were opportunistically recorded, but with no more than 1 location per hour included in seasonal home range estimates. Diurnal locations were often obtained daily by either triangulation from a vehicle, or homing in on signals with a hand held antenna and receiver. Error polygons for locations were always less than 5.0 ha, and usually considerably lower as telemetry error averaged 25.5 m (SD = 30.19 m) between estimated and known locations based on 300 bearings from 10 test collars.

For the broader study on social behavior, data were partitioned into seasonal home ranges; ranges were created using a minimum of 30 total locations, with no more than 15 locations being diurnal. Seasons were defined as summer (June - August), fall (September -November), winter (December - February), and spring (March - May), based on change in climate and biological factors associated with raccoon reproductive behavior (Prange et al. 2004). Winter home ranges were not calculated due to the reduction of raccoon movements during cold winter months (Prange et al. 2004). However, this study focused on the mating season that occurred from December 2004 through March 2005. Therefore, daytime resting locations were recorded at least weekly for much of the mating season. Most individuals had >10 locations available to analyze, and these locations were used to obtain an estimate of daytime resting areas, or rough approximations of population spatial structure during the primary mating period.

Fixed-kernel daytime resting areas (DRA) and core resting areas (CRA; 95% and 50% contours, respectively) were created using the Animal Movements extension in ArcView GIS 3.3 (Hooge and Eichenlaub 1997). Resting area overlap between a pair of raccoons (i.e. dyad) was calculated using the Neil's Utility extension in ArcView GIS 3.3 using the formula:

$$\text{Coefficient of overlap} = 2(\text{Overlap Area}_{1,2}) / (\text{Area}_1 + \text{Area}_2).$$

Contacts

Proximity detectors are also equipped with a UHF emitter and receiver which provided the capability to record when two or more individuals "contacted" each other. A contact was defined as when two or more individuals come within one meter of each other. The collars will also recorded the date and time contact was initiated, the duration of the contact (in seconds), and the identification number of the contacted collar. Data were stored in the collar's internal memory until subsequent downloading via interface and portable computer which was attempted every 3 months. For a more detailed description of the proximity detectors see Prange et al. (2006). Contact rates, persistence of contact rates throughout the year, and contacts indicative of den sharing were identified by Prange and Gehrt (unpublished data). Contact rates between assigned parents were descriptively, but not statistically, compared due to the small number of available comparisons. For each successfully identified mother and father, I documented the contact rate and instances of den sharing between parents. Additionally, I tallied the number of possible mates (those fitted with functioning radio collars) and examined how their contact rates compared to the contact rates of the observed successful mate with respect to the parent of interest.

Den sharing

Contacts that lasted for several hours during daytime were considered indicative of den sharing incidents. Because raccoons may mate with individuals that are related at up to the 3rd order relation (Roy Nielsen and Nielsen 2007), I separated den sharing incidents by high relatedness (<3rd order) and low relatedness (>3rd order) to determine if a pattern between relatedness and den sharing over the mating season would emerge. To determine the peak of the mating season, I counted back the average gestation time (63 days; Gehrt 2003) from the mean parturition date. Based on denning behavior recorded during a concurrent study on maternal behavior, I determined the mean parturition date (in 2005) to be April 17 (Hauver unpublished data). Because the peak of the mating season would occur between early to mid-February, I examined how incidence of denning behavior changed over the course of the mating season. Finally, I reported the relation between paternity and den sharing incidence.

RESULTS

Trapping and Capture

52 raccoons were captured during the initial trapping period; 42 (20 M, 22 F) of these were identified as adults and processed as described above. The majority of these captures were made within the first two weeks of trapping. Only three other individuals were captured during the third week, when traps were added outside the periphery of the core trapping area. No unmarked individuals were captured during the final week of trapping. This capture history coupled with observations from nightly telemetry rounds

suggested that most, if not all, adults within the core were radio collared by the end of May 2004.

Genetics

Blood samples were collected from all but one individual of the 42 adults processed in May 2004. I obtained relatedness estimates for 861 unique dyads (190 MM, 253 FF, 418 MF) from these samples. One individual was genotyped at 15 loci; all others were genotyped using 16 loci. The mean number of alleles per locus was 10.6 (range 4-24) and the mean observed heterozygosity was 0.74 (range 0.49-0.92, Table 2.1). No evidence of scoring errors, large allele drop out or null alleles were found. Exact tests showed that three of 16 loci deviated from Hardy-Weinberg equilibrium (Table 2.1); there was a deficiency in the number of observed heterozygotes in each case. One locus (PLO3-117) was noted to be sex-linked (Cullingham et al. 2006), but inclusion of this loci changed all relatedness values equitably among sampled individuals and was therefore kept in the analysis. The deviation from HWE may be due to violation of the assumptions of random mating and a large population. Deviations from HWE at multiple loci can be an indication of population substructure, where there may be an overrepresentation of closely related or inbred family groups (Marshall et al. 1998, Kitchen et al. 2005). No deviation from HWE or linkage disequilibrium was found for these 3 suspect loci in 2 previous studies (Cullingham et al. 2006, Roy Nielsen and Nielsen 2007) which employed the same loci. Both studies were conducted in areas >125 times the size of my trapping area, with nearly double the sample size. Additionally, the 2 sets of known mother-offspring processed for this study produced *r* values similar to

0.5 (0.47 and 0.54), lending credibility to my relatedness estimates. Therefore, I proceeded with all 16 loci in my analysis.

Parental analysis

Of 44 juveniles sampled, 17 (9M, 8F) were assigned at least 1 parent with ≥ 80% confidence (Table 31.). These 17 juveniles had 9 mothers (8 radio collared, 4 functioning during winter) and 7 identifiable fathers (4 radio collared, all functioning during winter). Relatedness between radio collared parents was low, with an average value of -0.021 (range: -0.074 – 0.042). In 6 instances, ≥2 offspring were assigned to the same mother, of which 5 of these "litters" had instances of multiple paternity (83.3%, Table 3.1). Female NC104 had 2 offspring (49 F and 82 M) from males NC102 and NC93. Neither the mother nor the 2 fathers in this case were radio collared. Female 6479 had 2 male offspring with males 6482 and 6453 and all 3 adults were radio collared. Female 6460 was assigned 2 offspring (68 F and 62 M), to 2 different non-sampled males based on incompatible assignments by CERVUS. Although the offspring from this female were captured in the study area, she had moved out and therefore was not included in the spatial and contact rates comparisons. Female 4344 had 2 female offspring, both were sired by male 6453, but the mother's radio collar was not functioning properly, inhibiting spatial or contact data collection. Female 6099 had offspring 53 F and 52 M from 2 different non-sampled males based on incompatible assignments by CERVUS. Female 217 and male 6491 were both assigned parentage to the male offspring 47, but the mother was not equipped with a functioning radio collar at that time. Female 6425 was the only female assigned maternity to more than 2 young. She had 3 offspring (51 F, 57 M, and

77 M) with 2 different males. Two of these 3 young (57 and 77) were assigned to 1 radio collared male (6424), while 1 offspring was assigned to a non-sampled male.

Males were also found to be the fathers of progeny from multiple mothers (Table 3.1), as 2 of 3 males who were assigned more than 1 offspring mated with more than 1 female. Most fathers (n=4) sired 1 offspring, but 2 males sired 2 offspring, and 1 male sired 4 offspring. Male 6482 had 2 offspring, 67 F and 79 M, with females NC89 and 6479 respectively. Male 6453 had 4 progeny by 3 different females; 1 (78 M) with female 6479, 1 (74 M) with female 4014, and 2 (70 F and 72 F) with female 4344. Male 6424 had 2 male offspring (57 and 77) with female 6425.

Spatial Distribution

Mean (+SD) male daytime resting areas (22.8 ha + 11.6) and core resting areas (4.1 ha + 2.5) were not significantly larger than those for females (17.6 ha + 13.1 and 3.1 ha + 2.6, respectively; DRA: $H = 2.79$, *d.f.* = 1, $P = 0.09$; CRA: $H = 0.69$, *d.f.* = 1, $P = 0.40$). DRA and CRA overlap were low within each dyad type. Average MM DRA was 0.169 (SD=0.215) and CRA was 0.085 (SD=0.172). Average FF DRA and CRA were 0.125 (SD=0.199) and 0.045 (SD=0.128) respectively. MF dyads averaged 0.168 (SD=0.213) and 0.081 (SD=0.163) percent overlap at their DRA and CRA levels, respectively.

Of the 17 juveniles assigned parents, 4 were assigned to mothers and fathers equipped with functioning radio collars, which allowed a description of resting area overlaps and parentage. For 3 of those 4 cases, the parents had very large coefficients of overlap at both 95 and 50% contours (Tables 3.2 and 3.3). In the remaining case parents shared only 11% of their daytime resting areas, with no core resting area overlap. Most often, the male with which the mother shared the most of her core resting area was the designated father of her offspring (Table 3.2). Additionally, most males sired offspring with the female with which they shared the greatest core resting overlap area (Table 3.3).

Paternity and Group Membership

Prange and Gehrt (unpublished data) identified two distinct male groups within my study site during winter, based on high rates of within group home range overlap and social tolerance. Males 6308, 6453, 6462, and 6482 formed one group, while males 6407, 6468, 6485, 6488, and 6490 formed the other group. Male 6424 had from a group with 6328 during summer and fall 2004, but 6328's signal was lost during winter and he was never recaptured again. Males 6491, 6483, and 6475 did not engage in group living throughout the year, and were classified as solitary. Of group males, only male 6424, 6453, and 6482 were assigned paternity to sampled offspring. Only 1 solitary male, 6491, was assigned paternity. However, 6491 (solitary) and 6482 (1st group)'s contact rate approached significance during winter and the pair den shared twice during winter.

Contacts and Parentage

Examination of contact rates between successful parents revealed different trends for monitored males and females (Table 3.4). Two of the 3 females whose contact rates were available, associated with the successful fathers more than most of the other males available for comparison at that time. The exceptional case, involved female 4014 and male 6453. The pair had a low contact rate of 0.111, but this is likely the result of two factors: the male's collar malfunctioned after mid-February, and he produced offspring with 2 additional females, likely cutting down the amount of time he could spend with any 1 female. Female 6425's second most frequently contacted male was assigned as the father to 2 of her 3 offspring, she contacted male 6424 at a rate of 0.32 contacts/day and spent an average of 68 seconds per day with him. Two of the 3 most frequently contacted males sired female 6479's 2 young; she had contact rates of 0.92 and 0.14 contacts/day and spent an average of 353 and 94 seconds/day with males 6453 and 6482, respectively.

This pattern did not hold true for monitored males, however, as the most frequently contacted females were never identified as mothers of young. Males 6453 and 6482 each contacted 5 females more frequently than the females with which they were known to have produced offspring. Additionally, male 6424 contacted 3 females more frequently than the female with which he was observed to have mated.

Den sharing

Inter-sexual den sharing, as indicated by extensive contacts during the diurnal period, was not reserved for unrelated individuals (Table 3.5). Of 31 unique MF dyads that den shared during the winter, just over half (n=17) were negatively related. Many dyads (n= 21) denned together more than once, yielding a total of 173 den sharing instances. Positively related MF dyads shared dens on more occasions (n=98) than negatively related individuals (n=75). The number of den sharing incidents between all available MF dyads ranged widely (0-19) and averaged 5.6 times (SD=5.7). While incidents of den sharing were recorded throughout the winter, a sharp increase in cohabitation was observed during the peak mating period (early to mid-February) for unrelated or distantly related individuals (Figure 3.1). Den sharing was common for males, as 73.3% of males (n=11) but only 55.6% of females (n=18) were recorded to den share with a member of the opposite sex.

Den sharing and Parentage

None of the assigned parents were recorded as sharing a den together during the mating season (Table 3.5). However, female 4014 den shared with 4 different males, all of whom were positively related to her, a total of 28 times; 3 of the 4 males were second order relatives ($r \geq 0.127$), while the remaining male was only slightly related ($r = 0.086$). Female 6099 co-denned with 1 male on 1 occasion and this male was also positively related to her around a second order relationship ($r = 0.114$). The other 2 radio collared mothers did not den with any male during the winter season. In contrast, all of the 4 radio collared males that were assigned paternity den shared with at least 1 female. Male 6482 denned with females 3625, 4047, and 6456, all of whom were unrelated to him. Male 6453 denned with the same 3 females as male 6482, plus an additional female 6416. All 4 females were unrelated to male 6453. Male 6491 denned with the same 3 females as male 6453. Females 3625 and 6456 were unrelated to him, and female 6416 was slightly positively related to him ($r = 0.042$). Male 6424 just denned with 1 female, 4047 (who also denned with males 6482 and 6453) who was unrelated to him.

DISCUSSION

As expected, I found a high rate (83.3%) of multiple paternity in this urban population of raccoons. The mating system for this population is best described as promiscuous, as both males (2 of 3) and females (5 of 6) produced offspring with more than 1 mate. Only 1 other study to date has examined multiple paternity in raccoons (Roy Nielsen and Nielsen 2007), and they reported results similar to this study. Roy Nielsen and Nielsen (2007) sampled 11 presumed whole litters from natal dens and found a promiscuous system, with multiple paternity existing at a rate of 88% in southern

Illinois raccoons. That study also exhibited a low rate of parentage assignment, but found sires were generally trapped within close proximity of females with which they produced offspring. Of the 2 males they found that were trapped farther than 1km from the litter mother's trap location, both fathered multi-sired litters. They concluded that high population densities led to the frequent inability of males to monopolize mating opportunities with females. Both of our studies were conducted in areas of high raccoon densities, therefore, the underlying mechanisms for such high instances of multiple paternity may be similar.

Red- winged Blackbirds, (*Agelaisu phoeniceus*; Gibbs et al. 1990), feral cats, (*Felis catus;* Say et al. 1999) and pygmy-field mice (*Apodemus microps*; Bryja and Stopka 2005) have each exhibited cases where multiple paternity increased with density. In sex-ratio neutral populations, high densities dictate a greater number of males, which can increase the risk of male-driven infanticide (Butynski 1982). Promiscuity has long been assumed to have evolved as a female counterstrategy to male-driven infanticide (Hrdy 1979, Ebensperger 1998, Wolff and Macdonald 2004), particularly for species in which destruction of a litter returns the female to estrus sooner. Raccoons are capable of second litters if the first litter is lost soon after parturition (Sanderson and Nalbandov 1973, Gehrt and Fritzell 1996, Gehrt 2003). This fact, coupled with high nestling mortality (Gehrt and Fritzell 1999b), a traditionally polygynous mating system (Fritzell 1978, Gehrt and Fritzell 1999a), and the bearing of altricial young (Johnson 1970), all suggest that infanticide is a reasonable reproductive strategy for male raccoons (Wolff and Macdonald 2004). However, no indisputable reports of male driven infanticide in raccoons have been made to date.

Another possible explanation for the high rate of multiple matings by females is inbreeding avoidance. Male raccoons are known to disperse from their natal areas (Urban 1970, Fritzell 1987, Gehrt and Fritzell 1998b), and stay in those new areas for the remainder of their lives, often producing multiple offspring within those areas (Roy Nielsen and Nielsen 2007, Hauver et al. unpublished data). Because females are philopatric (Gehrt and Frizell 1998b, Ratnayeke et al. 2002, Chapter 2) the chances of a daughter mating with her father may be high in such a system. Therefore, females may benefit by mating with all the resident males in an area to reduce the probability that her offspring would be highly inbred. Neither this study nor Roy Nielsen and Nielsen's (2007) observed highly related individuals producing offspring; females may rely on multiple mating among group members and cryptic choice to reduce the occurrence of highly inbred offspring.

As predicted, females most often bred with only 1 male group, even though a female did breed with multiple members of the same group. The only exceptions included 1 female that bred with a resident (sampled, but not radio collared) and a non-resident (non-sampled) male, and 1 female that mated with a group male and a solitary male. However, this solitary male was noted to associate with members of one group during winter (Prange and Gehrt unpublished data). I anticipated that juveniles would largely be sired by resident males who belonged to a coalition (Waser et al. 1994, Gehrt and Fritzell 1998a Gehrt and Fritzell 1999a). However, members from just 2 of the 3 male groups identified by Prange and Gehrt (unpublished data) were found to have produced offspring that emerged from the natal den. I found juveniles were twice as often assigned to resident females as they were to resident males. Roy Nielsen and

Nielsen (2007) also noted over half of their litters were sired by males not sampled. This could indicate that non-resident males temporarily move into new areas during the breeding season and successfully mate with resident females. Roaming behavior for breeding males has been recorded for raccoons (Gehrt and Fritzell 1998a) and may be a more common strategy among males than currently thought, but more information is needed on this possible tactic.

No other study has examined the contact rates and denning behavior of mated raccoons. I found that females often exhibited the highest rates of contact and overlap values with the fathers of their offspring, but males were highly social with many females besides the documented mothers of their offspring. Interestingly, there was no pattern in total time spent between successful males and the females they impregnated. While male 6453 and female 6479 contacted each other nearly every day throughout the season and spent over a total of 8.8 hours together, only one contact was recorded between the same female and male 6482 for a total of 6.75 minutes, yet each male fathered 1 of her 2 offspring. Goldman (1950) and Stains (1956) provided the only 2 reports of raccoon matings in the literature, and both describe a lengthier mating process between 30 and 54 minutes, respectively. However, my study showed long and consistent associations are not necessary between raccoons in order to mate successfully.

Den sharing between adult male and female raccoons during the mating season is often assumed to be a reliable surrogate for mating behavior (Gehrt and Fritzell 1999a). My results have complicated that view in several ways. While I observed a sharp increase in den sharing incidents between unrelated individuals that coincided with the peak of the mating season, none of the parents identified through genetic analysis den shared during the mating season. These results indicate that den sharing is not a requirement for mating success, and may prove to be quite rare for parents.

Many studies have noted the preference of certain den trees and that trees may be used by several raccoons at differing times throughout the year (Gehrt et al. 1990, Hadidian et al. 1991). There maybe attributes to den trees unknown to the human-observer which make a den more suitable, especially in winter months. In environments with harsh winters, such as the Midwest, perhaps den sharing is reserved for thermoregulation rather than mating opportunities. Den sharing as a form of communal nesting has been documented for raccoons (Mech and Turkowski 1966), as well as skunks, (*Mephitis mephitis*; Wade-Smith and Verts 1982), and many members of Sciuridae and Rodentia, (review in Feldhammer et al. 1999). Several studies have observed same-sex den sharing between raccoons (Rabinowitz and Pelton 1986, Gehrt and Fritzell 1998ab, Hadidian et al. 1991, Prange and Gehrt unpublished data), therefore, additional motivation separate from mating must exist for certain instances of den cohabitation.

Many of the raccoons within this study were not equipped with functioning radio collars at the time of this investigation. While the study surely missed associations between radio collared parents, the results represent a quasi-random sampling of mobile juveniles, and therefore provide useful data. Although the results reported here cannot be interpreted as a thorough assessment of mating associations, they do provide real insight into a previously little described phenomenon. New information has been gained by this study, and the rapid development and usage of data logging and molecular marker technologies promise to provide a more complete look at the mating strategies of many other secretive species.

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TABLES AND FIGURES

Juvenile	Mother	Father	*r*	Both parents equipped with functioning collars?
49 (F)	NC 104	NC 102	-0.132	No
82 (M)	NC 104	NC 93	-0.101	No
67 (F)	NC 89	6482	0.031	No
79 (M)	6479	6482	-0.074	Yes
78 (M)	6479	6453	-0.013	Yes
74 (M)	4014	6453	-0.106	Yes
70 (F)	4344	6453	-0.131	No
72 (F)	4344	6453	-0.131	No
68 (F)	6460	Not sampled	N/A	No
62 (M)	6460	Not sampled	N/A	No
52 (M)	6099	Not sampled	N/A	No
53 (F)	6099	Not sampled	N/A	No
54 (F)	Not sampled	NC 99	N/A	No
47 (M)	217	6491	0.0429	No
77 (M)	6425	6424	0.0421	Yes
57 (M)	6425	6424	0.0421	Yes
51 (F)	6425	Not sampled	N/A	No

Table 3.1. Identity of offspring (sex), mother, father, relatedness (*r*) between parents and ability to compare contact rates between parents of juveniles captured during fall 2005 in Busse Woods, Il.

Mother	Males	DRA	CRA
6479	6491	0.625	0.264
6479	**6482**	**0.524**	**0.554**
6479	6462	0.429	0.362
6479	**6453**	**0.352**	**0.264**
6479	6308	0.313	0.266
6479	6407	0.034	0.000
6425	**6424**	**0.484**	**0.583**
6425	6328	0.462	0.146
6425	6308	0.176	0.000
6425	6407	0.126	0.000
4014	6485	0.589	0.274
4014	6488	0.546	0.014
4014	6468	0.394	0.008
4014	6407	0.227	0.000
4014	6482	0.173	0.000
4014	6462	0.153	0.000
4014	6491	0.153	0.000
4014	6483	0.134	0.000
4014	6308	0.124	0.000
4014	**6453**	**0.111**	**0.000**

Table 3.2. Coefficient of daytime resting area (DRA) and core resting area (CRA) between assigned mothers 6479, 6425, and 4010 with whom their resting areas overlapped with between December 2004 and March 2005 in Busse Woods, Il. Observed successful matings indicated by bold type.

Father	Female	DRA	CRA
6424	6099	0.601	0.572
6424	**6425**	**0.484**	**0.583**
6424	6326	0.328	0.311
6424	3625	0.189	0.000
6453	6416	0.485	0.261
6453	3625	0.465	0.701
6453	6493	0.390	0.290
6453	6456	0.377	0.671
6453	4047	0.371	0.154
6453	**6479**	**0.352**	**0.264**
6453	6326	0.240	0.000
6453	6477	0.116	0.000
6453	**4014**	**0.111**	**0.000**
6453	6115	0.108	0.000
6453	4005	0.021	0.000
6482	3625	0.671	0.324
6482	4047	0.648	0.065
6482	6416	0.645	0.491
6482	6456	0.610	0.169
6482	6493	0.595	0.428
6482	**6479**	**0.524**	**0.554**
6482	6326	0.315	0.024
6482	4014	0.173	0.000
6482	6477	0.117	0.000
6482	6115	0.063	0.000
6482	4005	0.018	0.000

Table 3.3. Coefficient of daytime resting area (DRA) and core resting area (CRA) between assigned fathers 6424, 6453, and 6482 with all females for whom their resting area overlapped with between December 2004 and March 2005 in Busse Woods, Il. Observed successful matings indicated by bold type.

Female	Male	R	Female age	Male age	Contacts/day	Duration/day
6479	**6453**	**-0.013487**	**II**	**III**	**0.922**	**352.922**
6479	6491*	0.076741	II	I	0.478	101.800
6479	**6482**	**-0.074247**	**II**	**I**	**0.140**	**9.419**
6479	6462	-0.03318	II	IV	0.069	1.655
6479	6407	0.079116	II	II	0.011	0.156
6425	6328	0.025714	IV	II	0.458	66.271
6425	**6424**	**0.042069**	**IV**	**II**	**0.322**	**67.878**
6425	6407	0.205118	IV	II	0.167	75.156
6425	6308	-0.13791	IV	II	0.100	65.711
6425	6482*	-0.20877	IV	I	0.056	3.244
4014	6485	0.288666	V	III	19.861	8178.500
4014	6488	0.127136	V	II	10.835	3443.700
4014	6407	0.086157	V	II	6.244	2602.100
4014	6468	0.25882	V	I	1.620	303.700
4014	**6453**	**-0.105761**	**V**	**III**	**0.344**	**0.000**
4014	6308	-0.130412	V	II	0.013	2.291
4014	6482*	-0.203732	V	I	0.013	27.114
6456	6453	-0.066856	II	III	14.311	8588.878
4047	6453	0.065876	IV	III	3.978	2240.678
3625	6453	-0.058665	V	III	2.500	1636.989
6416	6453	-0.07937	II	III	2.267	644.033
6493	6453	0.137593	I	III	1.178	512.767
6479	**6453**	**-0.013487**	**II**	**III**	**0.922**	**352.922**
4014	**6453**	**-0.10576**	**V**	**III**	**0.344**	**0.000**
6326	6453	0.026852	III	III	0.089	18.422
6099*	6453	-0.10033	III	III	0.011	0.178

Table 3.4. Identification number, relatedness value (R), age, contact rates (contacts/day) and duration (sec/day) of contacts for all assigned parents and other radio collared individuals during the breeding season between December 2004 and February 2005 in Busse Woods, Il. Bolded entries indicate a parentage pair, while * indicates an individual who was assigned parentage of a juvenile with another mate. (CONTINUED)

Table 3.4. CONTINUED

4047	6482	-0.122092	IV	I	9.778	15009.867
3625	6482	-0.040783	V	I	1.711	708.867
6416	6482	-0.062901	II	I	1.578	536.767
6456	6482	-0.215576	II	I	1.456	420.167
6326	6482	-0.064882	III	I	0.267	491.500
6479	**6482**	**-0.074247**	**II**	**I**	**0.140**	**9.419**
6425*	6482	-0.020877	IV	I	0.056	3.244
4014*	6482	-0.20373	V	I	0.013	27.114
4047	6424	-0.151512	IV	II	0.922	304.667
6099*	6424	-0.110921	II	II	0.533	137.067
6326	6424	0.105128	III	II	0.378	96.133
6425	**6424**	**0.042069**	**IV**	**II**	**0.322**	**67.878**
3625	6424	-0.02564	V	II	0.056	4.922
6416	6424	-0.20384	II	II	0.022	0.278
6456	6424	-0.16054	II	II	0.022	0.356

Dyad F M	Total Days	Relatedness	Group status	Offspring?
3625-6308	4	-0.01674	Group 1	No
3625-6453	4	-0.058665	Group 3	No
3625-6462	3	-0.152245	Group 3	No
3625-6482	1	-0.040783	Group 3	No
3625-6491	2	-0.00635	Solitary	No
4005-6407	1	-0.191844	Group 1	No
4005-6468	16	0.048443	Group 4	No
4005-6485	16	0.064619	Group 4	No
4005-6488	12	0.074181	Group 4	No
4014-6407	5	0.086157	Group 1	No
4014-6468	1	0.25882	Group 4	No
4014-6485	15	0.288666	Group 4	No
4014-6488	7	0.127136	Group 4	No
4047-6308	7	-0.130491	Group 1	No
4047-6424	1	-0.151512	Group 2	No
4047-6453	3	0.065876	Group 3	No
4047-6462	14	0.046948	Group 3	No
4047-6482	19	-0.122092	Group 3	No
6099-6328	1	0.114032	Group 2	No
6326-6308	2	-0.147324	Group 1	No
6326-6407	1	0.105128	Group 1	No
6416-6308	1	-0.181102	Group 1	No
6416-6453	2	-0.07937	Group 3	No
6416-6491	3	0.041687	Solitary	No
6456-6308	8	-0.060737	Group 1	No
6456-6453	15	-0.066856	Group 3	No
6456-6462	1	-0.087876	Group 3	No
6456-6482	1	-0.215576	Group 3	No
6456-6491	3	-0.084842	Solitary	No
6115-6488	3	0.079596	Group 4	No
6493-6453	1	0.137593	Group 3	No

Table 3.5. Identification number, number of den sharing incidents as recorded by proximity detecting technology, relatedness value, male group membership status, and indication of resultant progeny of adult female and male raccoons between December 2004 and February 2005 in Busse Woods, Il.

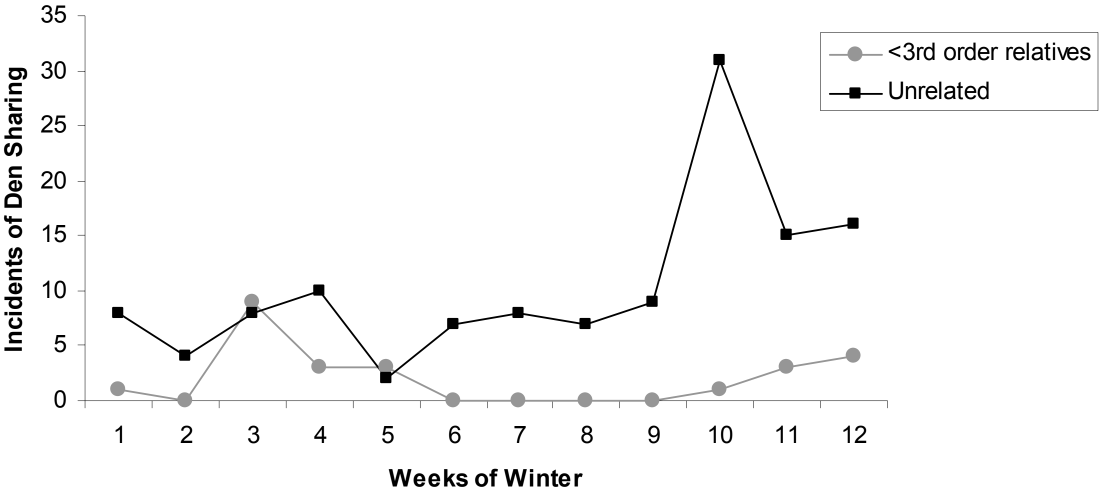

Figure 3.1. Incidents of den sharing of <3rd order relatives (n=6) and unrelated dyads (n=23) as determined by proximity detecting radio collars between adult male and female raccoons during the breeding season in Busse Woods, IL. Dates begin at December 1 2004 and continue until February 15 2005.

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