

MATING STRATEGIES AND PACK STRUCTURE OF COYOTES IN AN URBAN
LANDSCAPE: A GENETIC INVESTIGATION

A Thesis

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ABSTRACT

Coyotes (*Canis latrans*) have infiltrated many types of ecosystems, including urban and suburban systems, and yet certain aspects of coyote behavioral ecology remain unclear. There is a powerful motivation to fully understand the behavior of wildlife that finds suitable habitat in residential areas. As mating systems are the basis of social systems, the onus is on scientists to determine the basis of this carnivore's success in the suburban and urban areas of North America. Mating systems of coyotes have been extensively studied by observation, and the results have lead researchers to conclude that mated pairs are monogamous and that packs consist of close family members. However, recent genetic investigations into wildlife systems have revealed that conclusions based on observations can be misleading. As the coyote is a cryptic, nocturnal species, a genetic investigation may be the most straightforward way to determine the nature of relationships of parents and offspring, mates, and pack members.

Canids have been classified as "obligate monogamists", meaning that a dedicated mate is necessary for reproduction. This is due in part to the high demands that pups place on their parents, as for most species of Canidae they are born altricial in large litters and require an extended period of training to learn to hunt and survive on their own. Also, pups in many canid species require protection, as they face danger of intraspecific infanticide from neighboring territorial canids. The most common breeding strategy that canid species utilize to mitigate the high energy demands of raising young is monogamy, wherein one male and one female exhibit fidelity to each other. Some canids, such as

foxes (*Vulpes* spp. and *Urocyon* spp.), practice polygyny, wherein two females raise pups with one male in one den. Another breeding strategy, polyandry, is detected occasionally in wolf packs (*Canis lupus*), wherein one female is impregnated and tended by two males. These breeding strategies were revealed through genetic analysis of the offspring in the respective litters. Another interesting mating behavior is den sharing. According to the literature, there are instances of female coyotes sharing dens, with both females contributing pups to a “double-litter”. These observations are based on abnormally large litter sizes, den attendance by nursing females, and by size differences among pups. I have investigated 19 coyote litters and 103 offspring, and I found one double-litter and one instance of polygyny. The two mated pairs that contributed to the double-litter did not interbreed. The evidence strongly suggests that the majority of coyotes in this population are monogamous.

Coyotes share territories in pack-like groups, which have long been assumed to consist of family members. This assumption is based on the observed retention of offspring from one year into the next. The grown offspring will often serve as alloparent to its younger siblings. However, there are also accounts of seemingly unrelated coyotes joining established packs. I investigated the relatedness of coyote packs, and found that there are few instances of unrelated members in a pack. Out of 117 relationships between 62 pack members across 26 pack years, I detected 8 coyotes that were related at levels lower than expected for family members. Overwhelmingly, coyote packs consist of closely related family members. I also investigated home range overlap with relatedness, and found a weak correlation. Some animals that share high overlap are not related, and some animals that are highly related share small percentages of overlap.

The results of this study verify the findings of previous observation-based studies. However, as the coyote is a highly adaptable mammal with plastic behaviors, it is unknown whether these same results would be verified by studies of coyotes in more natural areas.

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Chapter 1: Coyotes in Urban Landscapes

Coyotes (*Canis latrans*) are native to North America, but historically, their range ended near the Eastern states, where the range of the grey wolf (*Canis lupus*) began (Bekoff 1977a). Coyotes have a historic range between 10° north latitude and 70° north latitude, from Costa Rica to northern Alaska (Bekoff 1977a). Competitive exclusion with the grey wolf kept the coyote out of the eastern states, but nearly a century after humans altered the landscape and extirpated the wolf from the region, the coyote is populating the former range of its competitor (Bekoff 1977a). More recently, coyotes have acclimated to urbanized areas across North America, which has created new management issues (Atkinson and Shackleton 1991; Atwood et al. 2004; Grinder and Krausman 2001; McClennen et al. 2001; Shargo 1998).

Coyotes exhibit sexual dimorphism: males are consistently larger than females, although a typical difference is only 1-3 kg (Parker 1995). Average weights of coyotes increase from west to east (Thurber and Peterson 1991): coyotes in California have reported average weights of 10 kg (female) and 11 kg (male), whereas coyotes in Iowa average 11 kg (female) and 13 kg (male), and coyotes in Maine average 14 kg (female) and 16 kg (male). Coyotes are typically just over 1 meter in length (from nose to rump), but this is also variable from west to east (Voigt and Berg 1999).

Studies to date show that coyotes establish territories and maintain bonds within a pack-like group (Bekoff 1977a). Within the pack, a social hierarchy is dominated by an alpha female and an alpha male (Bekoff 1977b). There are also beta females and beta males which help to ensure the feeding and survival of young (Bekoff 1977b). Members cooperatively defend the pack's territory, which helps to insure that the pack members have access to the resources on their territory (Patterson and Messier 2001). Whether the members of the group are necessarily a family unit is unclear. Grewal et al. (2004) determined, using genetic analysis, that members of eastern wolf (*Canis lycaon*) packs are not necessarily related, and found that unrelated adult eastern wolves have been adopted into established packs. As the eastern wolf is, on an evolutionary scale, closely related to the coyote, this information lends further doubt to the heretofore untested hypothesis that coyote packs consist only of an unrelated mating pair and their offspring.

Females are monoestrous and usually enter estrous in February (Kennelly 1978). Males enter breeding condition in January and remain in breeding condition until mid-March (Kennelly 1978). Breeding season can vary by altitude and latitude, but is always completed by April (Kennelly 1978). When females enter estrous, they are pursued by several males, but by the last few days of estrous she selects one male and mates several times with him (Parker 1995). The mated pair selects and excavates den sites, which are often abandoned dens of other animals (Bekoff 1977a). If there are no pre-established dens, coyotes dig out new dens, or create dens in hollow trees, brush piles, recessed stream banks, or even abandoned buildings (Bekoff 1977a; Parker 1995). Based on data collected to date, it appears that urban coyotes prefer city parks to residential or urban areas for denning, which may offer them refuge from human disturbance (Morey 2004).

Coyotes usually establish more than one den, and will switch dens after disturbance and periodically to escape fleas (Bekoff and Gese 2003; Parker 1995).

Gestation lasts 60-61 days (Bekoff 1978). Litter size is typically 4-9 pups, varying with factors such as resource availability and population density (Bekoff 1977a). Age of the mother can also be a factor, as younger females tend to have smaller litters (Bekoff and Gese 2003). Coyote females may share a den; however, literature to date assumes that the coyotes must be related in some fashion (mother-daughter, sister-sister) for this to occur (e.g., Bekoff 1977a).

Sex ratios at birth and in populations are typically equal, but some studies suggest that the male to female ratio at birth increases in saturated habitats, whereas in systems where coyotes are scarce and/or exploited, the female to male ratio increases (Berg and Chesness 1978; Parker 1995). The average weight for western coyote pups at birth is 200-300 grams, with females weighing slightly more than males (Parker 1995). In contrast, eastern coyote pup males weigh 280-400 grams at birth, and females weigh 320-440 grams (Parker 1995). Pups are born altricial; their eyes open after 12-16 days, and they can run 18-23 days after birth (Bekoff and Gese 2003). Pups reach adult size at about 9 months of age (Bekoff and Gese 2003).

Both parents devote energy to the survival of their offspring. During early neonatal development, the mother nurses the young while the father provides food for her (Bekoff 1977a; Camenzind 1978; Ryden 1974). Both parents assist in socializing the young in hunting behaviors, and the siblings aid in the socialization of each other through fighting and playing (Bekoff and Wells 1980). Coyotes typically disperse 4-10 months after birth, although the distance and timing of dispersal depend on available food sources

as well as coyote population densities (Bekoff 1977b; Harrison et al. 1991). About half of yearlings typically disperse by late autumn (October-November), another third disperse later in winter (January-February), and the remainder exhibit sporadic dispersal behavior, often staying longer with the family group (Harrison et al. 1991). The mated pair maintains the same territory year after year, usually until one of them dies (Andelt 1985; Patterson and Messier 2001; Sheldon 1992). Some research indicates that there is no sexual difference between dispersal distances, and other research suggests that males disperse farther (Bekoff 1977b; Berg and Chesness 1978). Maximum recorded dispersal distance of 544 km was traveled by an adult female (Carbyn and Paquet 1985), but average distances range between 80 and 160 km (Bekoff and Gese 2003). Dispersal is risky, and many dispersers die due to the combined effect of disperser naïveté and hostility dispersers encounter when venturing beyond known home ranges (Harrison 1992). Sacks et al. (2004) has used genetic methods to test whether coyotes are susceptible to perceived differences in bioregions, and found that coyotes may restrict their dispersal to bioregions similar to their natal ranges. While this does not explain why coyotes have successfully integrated into novel habitats, the evidence shows a definite genetic break between coyotes of two close yet geographically separate regions. Swihart et al. (2003) suggested that a combination of factors impact the dispersal ability of animals across fragmented landscapes. These factors include niche breadth, body size, vagility, and effects of social and territorial behavior.

Coyotes in undeveloped areas have home ranges that extend upwards of 50 square kilometers, whereas coyotes in urban areas tend to have home ranges that are bounded by human structures, and are, on average, substantially smaller (Shargo 1988, Atkinson and

Shackleton 1991). Atkinson and Shackleton (1991) reported an average home range size of $10.8 \pm 11.2 \text{ km}^2$ in a suburb of Vancouver, British Columbia, Canada. Shargo (1988) reported an average home range size of 1.1 km^2 for coyotes in the Los Angeles metropolis of California. Way et al. (2002) found that breeding adult coyotes in a suburban area of Cape Cod Massachusetts had an average home range size of $29.8 \pm 5.3 \text{ km}^2$. Andelt and Mahan (1980) tracked a yearling male in Lincoln, Nebraska that exhibited a home range of 7.4 km^2 . This home range was much smaller than those reported for nearby rural coyotes ($10.5\text{-}44.3 \text{ km}^2$), and the authors believed the difference could be attributed to the higher ecological diversity in the urban area that provided the urban coyote with greater food resources. Analysis of the coyote prey base revealed that the monocultures of modern agriculture did not sustain high populations of rodents or lagomorphs; thus, coyotes in rural areas needed larger home ranges to obtain enough prey to sustain themselves and their young. This argument was echoed in a study of Atwood and Weeks (2003), which found higher percentages of overlap among coyote home ranges in a suburban-urban matrix than in the neighboring rural area, and that the suburban-urban home ranges were significantly smaller than the rural home ranges. An excellent summary of home range sizes across a range of landscape types can be found in Bekoff and Gese (2003).

There is little evidence for size discrepancies of home ranges based on sex; however, breeding adults often constrict their home ranges during the nursing period (Andelt 1985; Harrison and Gilbert 1985). In general, transient coyotes, which do not defend a territory, have the largest home ranges (Andelt 1985; Bowen 1982; Gese et al. 1988). Among resident coyotes, non-breeding and breeding adults often have

comparable home range sizes, but the home ranges of pups and yearlings are significantly smaller (Andelt 1985).

Coyotes do not use the area within their home ranges equally, and will favor areas with high percent cover and/or high resource density (Atwood and Weeks 2003; Windberg 1995). Connectivity between patches of natural areas is not necessary for coyotes to successfully disperse and colonize new areas (Crooks 2002); however, coyotes often use roads, power lines, and railroad tracks to move quickly through human-dominated landscapes (Atwood et al. 2004; Way et al. 2004). Highways, rivers and short distances over lakes (i.e., between mainland and an island) have proven penetrable by coyotes (Sacks et al. 2004; Zoellick et al. 2004). One coyote can cause problems in several areas, especially if it is a transient and not committed to a territory (Andelt and Mahan 1980).

Researchers have noted that coyotes, which are active during diurnal periods in undeveloped regions, shift their activity budgets to crepuscular and nocturnal periods in urban areas to avoid human detection (Andelt 1985; McClennen et al. 2001). However, Way et al. (2004) found that breeding female coyotes in suburban areas may exhibit higher rates of diurnal activity during the period from April to June, which is likely due to the nursing mothers' increased need to forage.

Coyotes have highly plastic behaviors, which, in addition to their generalist, omnivorous diet, allows them to adapt to a wide variety of habitats (Andelt 1985; Bekoff and Wells 1980; Harrison 1992). In undeveloped areas, coyotes base their diet on lagomorphs, rodents, fruits, vegetation, and insects (notably grasshoppers), although the range of food sources for coyotes is so wide that it would be impractical to list all of the

items that have been found in the stomachs and scat of coyotes (Andelt 1985; Bekoff 1977a). Coyotes in northern Illinois feed mainly on eastern cottontail (*Sylvilagus floridanus*), small rodents (*Peromyscus* spp. and *Microtus* spp.), white-tailed deer fawns (*Odocoileus virginianus*), and vegetation such as berries and fruits (Morey 2004). It has been documented that domestic cats (*Felis catus domesticus*) and small dogs (*Canis familiaris*) comprise a small portion of the diets of coyotes in developed landscapes (Morey 2004; Quinn 1997). In areas where deer are present, one coyote depredates an average of one fawn per year (Voigt and Berg 1999). In areas where management solutions to deer overabundance are unaffordable, ineffective, or unpopular, the presence of coyotes could have a welcome impact on deer numbers. However, the majority of adult deer eaten by coyotes is found as carrion (i.e., killed by automobiles, hunters, or died of natural causes; Gese and Grothe 1995). Coyotes in colder regions are more dependent on white-tailed deer for winter survival, where snow cover makes predation on small rodents more difficult (Gese and Grothe 1995). Larger eastern coyotes have exhibited cooperative hunting behaviors to prey on deer (Parker 1995). This is in contrast to typical coyote hunting behavior, which is solitary (Bekoff 1977a).

Coyotes can have substantial impact on their prey species, and since some of their prey species include mesopredators, such as the domestic cat, this impact can create a trophic cascade effect (Crooks and Soulé 1999; but see also Gehrt and Prange 2006). In a landscape fragmented by development, domestic cats are often present in high numbers and are sustained at an inflated population density due to feedings by human sponsors. Cats are opportunistic hunters; a trait that can be a threat to wildlife, especially in areas where high human densities lead to high cat densities (Crooks and Soulé 1999). As

described by Crooks and Soulé (1999), the disappearance of a large predator has a mesopredator release effect on an ecosystem, meaning that once the apex predator is missing from the system, the population of mesopredators explodes, possibly leading to extinctions of prey species. Crooks and Soulé (1999) found that the presence of coyotes lead to depredation of mesopredators, and also lead to higher incidences of active, temporal avoidance of larger fragments by mesopredators. There were powerful secondary effects, most notably the fact that homeowners were informed about the presence of coyotes in the area, and, aware of the potential loss of their pet, chose to keep their cats indoors. As predicted, the bird diversity was higher in fragments where coyotes were present. These results were similar to those found by Henke and Bryant (1999), who determined that the removal of coyotes precipitated a drop in rodent species richness and diversity. However, coyotes are not restricted to eating mesopredators; coyotes are just as capable as cats or raccoons at eating ground birds, nestlings, and eggs (Zoellick et al. 2004). Also, there can be unexpected negative effects of predation on mesopredators, as Courchamp et al. described in 1999. According to Courchamp et al., as feral cat eradications were being carried out on islands, with the intention of protecting native bird species, the undesired effect was that the exotic rodent populations (notably *Rattus* spp.) increased rapidly. The rodents ate nestlings and eggs and competed with native species for resources.

Coyotes are susceptible to a wide range of parasites and diseases (Gier et al. 1978). The most common ectoparasites that affect coyotes are fleas (*Pulex simulans*, *Echidnophaga gallinacea*, and various others), ticks (*Dermacentor* spp., *Amblyomma* spp., and *Ixodes* spp.) and mites that cause sarcoptic mange (*Demodex canis* and

Sarcoptes scabiei). While fleas and ticks will occasionally transfer disease to coyotes, mange is a greater threat, presenting a fatal risk in colder regions (Gier et al. 1978). At least one coyote in our research area died of exposure due to mange (Stan Gehrt, pers. comm.), and another mange-affected coyote was euthanized in winter due to its critically poor health (Chris Anchor, pers. comm.). Internal parasites include flukes (*Alaria* spp.), tapeworms (*Taenia* spp.), hookworms (*Ancylostoma* spp.), and various others which can inhabit nearly every organ (Gier et al. 1978). These parasites impose higher nutritional demands on the infected animal, which generally works a greater effect on pups and elderly coyotes, but cause no fatal effects for most adults (Gier et al. 1978).

Diseases that affect coyotes can be viral, bacterial, fungal, rickettsial, or protozoan in nature (Gier et al. 1978). Diseases can be transmitted through prey (e.g. non-fatal Q fever and fatal listeriosis), through parasites (such as rocky mountain spotted fever, of which coyotes are carriers only and are not affected), or through contact with other coyotes or other animals (such as rabies, distemper, and fox encephalitis; Gier et al. 1978). As with parasites, coyotes at the ends of the age spectrum experience the greatest mortality from contacting disease, whereas healthy adults are likely to exhibit a range of resistance (Gier et al. 1978).

Coyotes in captivity can live up to 18 years, but life expectancy in the wild is understandably shorter (Bekoff and Gese 2003). The oldest known coyote in the wild, a 15.4 year-old male coyote, was documented by Gese (1990). Mortality rates are highest for juveniles, which are susceptible to disease and parasites, and face new dangers upon dispersal (Nellis and Keith 1976). Necropsies on harvested coyotes in Illinois showed

that yearlings had the lowest fat reserves of any age class, which could be due to dispersal activities (Nelson and Lloyd 2005).

Coyote populations in urban and suburban areas are growing and reports of attacks on humans and domestic pets are becoming more commonplace (Timm et al. 2004; Clayton 2004; Howell 1982). Conflict is bound to arise in areas where coyotes come in close contact with humans, whether coyotes actively seek human-related food sources (such as garbage or pet food) or attempt to avoid human interaction in a landscape permeated with human activity (Gompper 2002; Carbyn 1989). Although rare, attacks on humans by coyotes do occur, as several attacks have taken place in North America (Clayton 2004; Timm et al. 2004).

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Chapter 2: Mating Strategies of Suburban Coyotes

Introduction

The social systems of coyotes (*Canis latrans*) across developed landscape types have been studied in recent decades; research that has been fueled in part by the surprising efficiency with which coyotes have infiltrated urban and suburban areas (e.g., Atwood et al. 2004; Bekoff and Wells 1980, 1982; Gompper 2002; Grindler and Krausman 2001; McClennen et al. 2001; Riley et al. 2003; Shargo 1998). The basis of any mammalian social system is the mating system; which, in regards to coyotes, has been carefully investigated by many researchers in recent decades (Andelt 1985; Bromley and Gese 2001, Kennelly 1978, Parker 1995, Stockley 2003, Way et al. 2001), but has not yet been investigated on a molecular basis. For this study, I used a combination of genetic and radiotelemetry methods to analyze two aspects of the coyote mating system: the monogamous mated pair and the phenomenon of multiple litters in one den, also known as “double-litters”.

Monogamy is the rarest form of breeding system among mammals, estimated to occur in 3-5% of all mammalian taxa (Kleiman 1977; Mock and Fujioka 1990). However, it is the most common breeding system for canids (Sheldon 1992). Monogamy is defined by Wittenberger and Tilson (1980) as “a prolonged association and essentially exclusive mating relationship between one male and one female”. Recent scientific

advances, however, have made a new distinction necessary, as genetic investigations of offspring of supposedly monogamous parents have revealed that not all species that appear monogamous are actually so (Hughes 1998). Semantics help to clarify the situation: the term for a long-term mated pair is “social” monogamy, whereas “genetic” monogamy distinguishes whether the two members of the mated pair are sexually exclusive to all other possible mates (Hughes 1998; Morell 1998).

Social monogamy in mammals, as defined by Kleiman (1977), can be recognized in the field by three indicators: continual close proximity of the pair, displayed mating preferences, and breeding by only one pair in the social group. These three indicators have been repeatedly verified in observational studies of coyotes and other canid species (e.g., Allen et al. 1987; Asa and Valdespino 1998; Atwood and Weeks 2003; Bekoff 1977; Bekoff and Wells 1982). In addition, coyote mated pairs maintain long-term pair bonds, defend a territory jointly, exhibit an approximately 25-minute post-copulatory tie during mating, feed and raise pups together, and participate in the group-howl together (Andelt et al. 1979, Andelt 1985; Asa and Valdespino 1998; Bekoff 1977). In general, coyotes have large, altricial litters, and their offspring have long dependency periods (Kleiman and Eisenberg 1973). Mated pairs remain together until one mate dies, and they do not commonly “divorce” (Sheldon 1992). However, in two years of an observational study of 63 coyotes, Andelt (1985) witnessed two mated pairs divorce for undetermined reasons.

There are observed discrepancies that lend ambiguity to the accepted paradigm. Many transient coyotes apparently never form pairs, join packs, or establish territories (Camenzind 1978; Kamler and Gipson 2000). It should not be assumed, however, that

transients never mate (Gompper and Wayne 1996). Concerning monogamy, there are two observations in the literature of a single female mating with up to 3 males (Cadieux 1983; Gese et al. 1996). Double-litters are another departure from the typical mated pair-based mating strategy, yet are fairly common in the literature based on observational studies (Andrews and Boggess 1978; Camenzind 1978; Crabtree and Varley 1995; Kennelly 1978; Nellis and Keith 1976).

In the field of genetics, breakthroughs in the past two decades have led to cheaper, faster techniques, which have enabled researchers to uncover a wealth of new information on the secret behaviors of wildlife. Recent investigations of the mating behaviors of Canidae raise doubts as to whether any canid species is genetically monogamous. For instance, the red fox (*Vulpes vulpes*), the swift fox (*Vulpes velox*), and the island fox (*Urocyon littoralis*), all of which were thought to have exclusive mated pair systems, were shown through genetic analysis to be polygamous (Baker et al. 2004; Kitchen et al. 2006; Roemer et al. 2001). Observational and genetic investigations have shown that extra-pair mating occurs among two canid species that are phylogenetically closer to the coyote (Wayne et al. 1997), the Ethiopian wolf (*Canis simensis*) and the African wild dog (*Lycaon pictus*; Girman et al. 1997; Gottelli et al. 1994). As predicted by Moehlman and Hofer (1997), genetic investigations thus far of canid mating have revealed a flexible mating structure, similar to the findings of investigations into mating structure of socially monogamous birds (Hughes 1998).

The phenomenon of coyote double-litters has never been genetically investigated. If the mothers of both litters are closely related, then this phenomenon would be compatible with expectations derived from kin-selection theory (Hamilton 1964).

However, alpha female coyotes are known to discourage mating attempts of other coyotes in her pack with behavioral and physiological actions (Allen et al. 1987; Asa 1997; Moehlman and Hofer 1997; Ryden 1974), which suggests that double-litters, if they occur at all, would be rare occurrences. Double-litters that are noted in the literature were classified based on litter size (Gier 1975), breeding adult presence at the den (Andrews and Boggess 1978; Camenzind 1978), and perceived differences between sizes of the pups (Andrews and Boggess 1978; Nellis and Keith 1976). Due to the wide variations in coyote litter size and pup size, in addition to presence of alloparents at most dens (Bekoff and Gese 2003), it is possible that some, if not all, cases of double-litters were erroneously misclassified. In order to correctly define this unique breeding arrangement, genetic investigation is needed.

The main objective of this research is to combine radiotelemetry with genetic methods to determine the mating behavior of coyote mated pairs in a suburban landscape. The project utilizes DNA from blood, tissue and hair samples, as well as six years of radiotelemetry data and opportunistic sightings, to investigate extra-pair fertilizations and the phenomenon of double litters. The analysis will address two hypotheses; the first hypothesis (H_1) is that coyotes are monogamous. H_1 will be tested by comparing the genotypes of offspring with those of the putative parents. The second hypothesis (H_2) is that double-litters will not be present in the population. H_2 will be tested by comparing the genotypes of pups in litters to determine if they are full siblings.

Methods

Study Area and Study Animals. - Research was conducted in the following counties of northeastern Illinois: west Cook, east Kane, north Dupage and south McHenry (Figure 2.1). These counties are part of the greater Chicago metropolitan area, which is home to approximately 9.1 million people (U.S. Census Bureau 2000). The majority of the area has been sectioned by roads and developed, although examples of eastern tallgrass prairie, open oak stands, and a few scattered wetlands remain (Greenberg 2002; Sullivan 1999). The study area comprised of the following land use types: commercial/industrial (43%), residential (20%), agriculture (14%), undeveloped (13%) and other (10%; Stan Gehrt and Chris Anchor, pers. comm.). Native fauna included white-tailed deer (*Odocoileus virginianus*), red fox, grey fox (*Urocyon cinereoargenteus*), raccoons (*Procyon lotor*), voles (*Microtus spp.*), mice (*Peromyscus spp.*), beavers (*Castor canadensis*), squirrels (*Sciurus spp.*), opossums (*Didelphis virginianus*), eastern cottontail rabbits (*Sylvilagus floridanus*), groundhogs (*Marmota monax*) and muskrats (*Ondatra zibethicus*). Non-native fauna included house cats (*Felis catus domesticus*), domestic dogs (*Canis domesticus*), rats (*Rattus norvegicus*), and house mice (*Mus musculus*). Dominant food items in the diet included small rodents, white-tailed deer, lagomorphs, birds and fruit (Morey 2004). Human-associated items, such as garbage and pet food, were more prevalent in the diets of coyotes in residential areas, but were not the main source of food for coyotes (Morey 2004). Coyotes in this region have no natural predators. The top three causes of mortality were: collisions with vehicles, shooting, and mange (Stan Gehrt and Chris Anchor, pers. comm.). Average survival rates ranged from

0.58 to 0.70 across all age and sex classes, and individual coyotes often persisted in the area from year to year (Stan Gehrt and Chris Anchor, pers. comm.).

Coyotes were captured from 2000-2006 using padded foothold traps or with cable restraint devices. Snares were set in relatively natural areas, such as the private lands of the Max McGraw Wildlife Foundation and the Cook County forest preserves, to reduce human intrusion. During the course of the study, 1 coyote was euthanized after trapping, as a result of getting snared around the waist and suffering major physical trauma. No other animals were injured or died due to protocols implemented. Coyote pups were captured at den sites in the years 2000-2006 by technicians that excavated the dens with shovels and caught the pups by hand. Three larger pups were caught opportunistically by a technician who detected them in a field.

At capture, coyotes were transported in handling cages to a laboratory for processing. Adult coyotes were immobilized with Telazol (Fort Dodge Animal Health, Fort Dodge, Iowa). Pups that were excavated from dens did not require restraining techniques or Telazol, since they are relatively docile at this age. Reproductive condition was estimated by the size of testes (for males) and condition of teats (for females). Age was estimated based on size, weight, reproductive condition, and incisor wear (Parks 1979). All animals were assumed to have been born in early May (Bekoff 1977): each coyote year corresponds to the period from May 1 to April 30. The term “pup” refers to coyotes that are less than 6 months old, “yearling” refers to coyotes that are less than one year old, “subadult” refers to coyotes that are full-grown but not reproducing, and “adults” refers to full-grown, reproducing coyotes. Coyotes were bestowed unique alphanumeric identifications which include a reference to the trap location; for instance,

the 10th coyote trapped for this study was trapped in the Poplar Creek (PC) Forest Preserve, therefore the name for this coyote was PC10. Adult-sized animals were ear-tagged in both ears with colorful plastic tags (monel #3 or #4, National Band and Tag Company, Newport, Kentucky), and were fitted with radio-collars (Advanced Telemetry Systems, Isanti, Minnesota). Subcutaneous transponder chips (PIT tags, AVID Marketing Inc., Norco, California) were implanted into pups under the dermis of the scruff, to provide identification upon recapture.

Blood samples were typically drawn from an outer leg vein, using a sterile needle and syringe, whereas tissue samples were collected opportunistically from road-killed coyotes and nuisance coyotes that had been euthanized by Cook county wildlife officials. In some instances, hair samples with bulbs were obtained from pups when blood samples proved obtrusively difficult to obtain, due to small veins. After recovering from the Telazol, coyotes were released at the capture location. All coyotes were treated humanely following animal care and handling protocols approved by the Institutional Animal Care and Use Committee at The Ohio State University. All genetic samples were kept in frozen storage until DNA extraction procedures could be performed

Radiocollared coyotes were located via triangulation by a technician with a truck-mounted Yagi antenna and receiver. Daytime locations were detected at least twice a week, whereas nocturnal tracking shifts at 1-2 hour intervals were conducted 5-10 times per month. Daytime locations were helpful for locating den sites, whereas nocturnal locations provided movement and home range information. For more detailed radiotelemetry methods used in this project, see Morey (2004).

Home Range Analysis. - Radiotelemetry locations were entered into a Microsoft Access database, and then were transported into ArcGIS (ver. 3.2, ESRI; Environmental Systems Research Institute, Inc.). 95% minimum convex polygons (MCP) were constructed for each radiocollared member of a mated pair. Minimum convex polygons were preferred to fixed-kernal polygons because they tend to be more conservative, and for the purposes of this study, it was preferable to underestimate rather than overestimate percent overlap (Seaman and Powell 1996; Worton 1989). Percent overlap of MCP areas were determined using the Geoprocessing feature in ArcMaps (ver. 8.1, ESRI; Environmental Systems Research Institute, Inc.) using the formula (Atwood and Weeks 2003):

$$[(\text{area}_{AB}/\text{home-range}_A)(\text{area}_{AB}/\text{home-range}_B)]^{0.5}$$

When two coyotes exhibited a high proportion of overlap between their home ranges, they were considered to be interacting in some way, either as pack members or as members of a mated pair, depending on their age, sex, and behavior (Andelt 1985; Patterson and Messier 2001).

Genetic Methods. - Blood and tissue samples were extracted using a standard phenol-chloroform procedure (Sambrook et al. 1989). Hair samples were processed using Qiagen QIAamp Mini DNA Kit (Qiagen, Los Angeles, California). For polymerase chain reaction (PCR), genomic DNA was diluted to a working concentration of approximately 50 nanograms of DNA per microliter of solution.

I used 12 domestic dog microsatellites that amplified in coyotes (Sigma-Genesis; CXX109, CXX123, CXX172, CXX204, CXX213, CXX225, CXX250, FH2328, FH2161, FH2054, FH2380, FH2088) (Francisco et al. 1996; Ostrander et al. 1993; Roy et

al. 1994 ; Table 2.1). One locus that I attempted to use but had to exclude due to high failure rate was FH2001 (Francisco et al. 1996). Forward primers (Sigma Proligo, Sigma-Aldrich, The Woodlands, Texas) and reverse primers (Sigma Genosys, Sigma-Aldrich, The Woodlands, Texas), were diluted to 10% concentrations and combined before adding to the PCR reaction tube. All forward primers were labeled with WellRed dyes (Beckman-Coulter Inc., Fullerton, California). PCR reagents per 12.5- μ L reaction included 40 ng of DNA, 0.2 mM DNTP, 8 pmol primer, 0.5 U of *Taq* polymerase, and 10% 10X reaction buffer. The amount of $MgCl_2$ per locus was adjusted to facilitate better results with primers, with amounts ranging from 1.6-2.0 mM (Table 2.1). PCR reactions were facilitated by a thermocycler (Bio-Rad Laboratories, Hercules, California) and ran for 35 cycles, with varying annealing temperatures (Table 2.1).

Amplified microsatellite fragments were sized using a Beckman-Coulter CEQ 8000XL automated capillary genotyping system (Beckman-Coulter, Inc., Fullerton, California) with an internal size standard added to each sample. Fragments were analyzed using Genetic Analysis System Software, version 8.0 (Beckman-Coulter, Inc., Fullerton, California), and automated allele calls were checked visually with bins defined by frequency graphs of fragment sizes. Positive controls were periodically included to ensure that allele calls were reliable. Loci were scored individually, and the resulting allele calls were used to construct genotypes.

Genetic Analysis. – I used the program FSTAT (Goudet 2001) to check for redundant samples and to calculate gene diversity and F statistics at each locus (Weir and Cockerham 1984). I used the program GENEPOP (Raymond and Rousset 1995) to determine whether the population was in Hardy-Weinberg equilibrium, to check for

linkage disequilibrium, and to calculate gene frequencies for each locus. GENEPOP was also utilized to determine heterozygote excess or deficiency at each locus, as well as gene frequencies. Rates of heterozygote excess or deficiency can indicate whether a population is experiencing high rates of outbreeding or inbreeding, respectively. I used the program MICROCHECKER (van Oosterhout et al. 2003) to survey the loci for evidence of large allele dropout and for null alleles. Large allele dropout refers to the failure of detection of large alleles. This can happen when a large allele, which consists of a long sequence, and a small allele, which consists of a short sequence, are in the same replication procedure. The smaller allele will be replicated faster and therefore more copies of it will be made. This can lead to a failure of the large allele to replicate, which can lead to the erroneous designation of homozygous when the individual is actually heterozygous at that locus (Dewoody et al. 2006). Null alleles are caused by a mutation in the primer sequence of the microsatellite that disables the recognition of the template, which results in a failure of the microsatellite to replicate (Bruford and Wayne 1993).

Genotypes of pups were matched with parents using two programs: PASOS which is an acronym for 'Parental Allocation of Singles in Open Systems' (Duchesne et al. 2005) and KINSHIP (version 1.2, Goodnight and Queller 1999). A simple exclusion method was also included, which encompassed visual matching of genotypes of candidate parents with offspring.

PASOS uses an inclusive method to determine pedigrees, whereas KINSHIP calculates log-likelihood ratios of relatedness between dyads of individuals. PASOS allocates parents to offspring based on alleles and allele frequencies. The program was designed to identify parents in open systems, which is facilitated by a function that

calculates the proportion of missing parents from the sample. This was important for this study because sampling was incomplete due to the difficulty of trapping coyotes. PASOS accepts user-defined restricted error tolerance in order to include partially incorrect genotypes in the parental allocation procedure, which was especially useful for microsatellite loci that may have been mis-scored. As mis-scoring of microsatellites typically occurs in a step-wise fashion, PASOS incorporates a likelihood calculation that determines whether a mismatched locus between a candidate parent and offspring is likely due to scoring error. PASOS performs sequence simulations in order to identify the most reliable set of loci to be retained for allocation. These simulations allow an estimate of the overall allocation correctness rate, as well as error estimates for each allocation. PASOS allows the user to arrange the sequence of loci for the allocation procedure, which I used to decrease the possibility of false allocation due to a locus that was particularly difficult to score and thus prone to falsely scored alleles (FH2161).

KINSHIP estimates Grafen's relatedness coefficient (R ; Grafen 1985) between pairs of individuals, using the population allele frequencies and genotypes of the individuals to calculate the likelihood that the shared alleles of the 2 individuals are identical by descent. KINSHIP allows the user to set R_m and R_p ; two variables that define the probabilities that individuals share an allele by direct descent from their mother or father, respectively. I set the primary hypothetical R_m and R_p values at 0.5, as this is the relatedness coefficient expected between first-order relatives, such as parents and offspring or between full siblings. Unrelated individuals are expected to have an R -value of zero or less. KINSHIP calculated the significance of the hypothesis that each pair of individuals in the sample was related at a level of 0.5, by generating a ratio of the

log likelihood of relatedness. This result indicated whether the null hypothesis ($R=0$) or the primary hypothesis ($R=0.5$) was favored. The program ran a simulation based on allelic frequencies and hypothesized relationships, which was repeated 10,000 times to provide a distribution of log likelihoods and determine a significance level at 0.001. I ran successive tests with hypothetical R_m and R_p values set at 0.5 and 0.0, respectively, and also with R_m and R_p set at 0.25 and 0.25. These tests were performed to test the likelihood that two individuals would be related as half-siblings or as second-order relatives, respectively.

Genotypes of pups and candidate parents were sorted by year. I included all biologically possible parents in the analysis; i.e., a pup that was born in 2000 could have possibly been a parent in 2001 (Mengel 1971, but see also Bekoff 1977 and Moehlman 1987). Likewise, a yearling caught in 2001 was most likely a pup in 2000; hence was included in the cohort of pups for the previous year. Allocations for each year were first determined with PASOS, then parent-offspring pairs were checked against the results of KINSHIP. Visual checks of all loci for dyads was completed in order to verify that PASOS allocations and subsequent KINSHIP analyses were reliable. In cases where one parent was sampled and several offspring were also sampled, the unsampled parent was identified by exclusion. In these cases, the parent was given a unique name (UF or UM, for Unidentified Female or Unidentified Male) and a number, so that the genotype could be included as a potential parent in subsequent years.

Results

Mated Pair Analysis. - From January 2000 to December 2006, 266 coyotes were captured, 148 of which were radiocollared (Table 2.2). Radiotelemetry was fundamental to identifying potential mated pairs in the sample prior to genetic analysis, as well as to locate potential den sites. Of 8 potential mated pairs that were identified by radiotelemetry alone, genetic analysis of the offspring present in the attended dens revealed that 7 of them were breeding mated pairs (Table 2.3). The other potential mated pair, comprised of an adult male and adult female, was revealed through genetic analysis to be a likely father and daughter dyad.

As expected, the 2 members of each mated pair exhibited high home range overlap (Figure 2.2 and 2.3). Percent overlap ranged from 55.29 to 99.57, with one exception in 2004 of a low value of 19.81%, which is attributed to the abysmally low number of locations (9) that were collected on the male (PC21) due to a radiocollar battery that died. Excluding that erroneous value, the average home range overlap exhibited between two mated coyotes was $79.15\% \pm 12.94$.

Genetic Analysis. - Of the total sample of 266 coyotes, 241 viable genetic samples were obtained (Table 2.2). As revealed by FSTAT, 5 individuals were sampled twice, which decreased the total number of individuals to 236. Of these 5 twice-sampled individuals, three most likely occurred when a pup was sampled, released, and recaptured later as a new individual, most likely because the implanted microchip escaped detection. The other 2 redundant samples were apparently caused by labeling error. The majority of

animals were genotyped at all 12 loci, but some were not, due to the low concentrations of DNA in hair extractions. This was especially a problem with hair samples that were taken from pups in 2004-2005 which were often lacking roots and yielded very little genetic material. In all, 225 animals were genotyped at 12 loci, 7 were genotyped at 11 loci, and 4 were genotyped at 10 loci. In cases where there was insufficient DNA to genotype at least 10 loci, the animal was removed from the genetic study.

MICROCHECKER analysis found no evidence of large allele dropout or null alleles in the study population. GENEPOP revealed that the population was in Hardy-Weinberg equilibrium and linkage equilibrium. FSTAT calculated a F_{IS} score of 0.015, along with gene diversity for each locus (Table 2.1). GENEPOP determined expected and observed heterozygosity at each locus (Table 2.1). Locus 204 was the least polymorphic locus, but it was retained because it was reliable and enabled verification that a sample was working. In addition, it revealed a rare allele that was shared by only 2 coyotes, thereby increasing the likelihood of their relatedness.

Monogamy Analysis. - Monogamy was tested by identifying parents of juveniles and surveying the results for any instances of one parent mating with two different parents in the same year. By including young-of-the-year and yearlings of the subsequent year, I was able to investigate 201 offspring across the 6 years of the study. Potential parents were included in a year's analysis if they had been captured by that year and if they were adults at capture. Often, more than one combination of parents was offered by PASOS as a likely match, which resulted in a total of 327 possible parent combinations. These possible parent combinations were matched against the genotypes of the potential offspring, and alleles were checked for discrepancies. In the instances wherein a parent

combination matched the offspring, I verified whether those parents, separately or together, matched up with any other potential offspring in the same year.

Only one individual appeared to be an offspring of an extra-pair mating. Coyote WGN86 was caught as a yearling in 2003, so he was included in the pup cohort of 2002. His father appeared to be BW32, which had a litter of 11 pups in 2002 with an uncollected female (UF4), whom I was able to genotype by exclusion. After accounting for the alleles of BW32 in the genotype of WGN86, the remaining alleles did not match those of UF4. Thus, if WGN86 was indeed a pup in 2002, it is possible that he was the offspring of an extra-pair mating between BW32 and an unknown female.

Double-Litter Analysis. - I genotyped 19 litters, which ranged in size from 3 to 11 pups (average = 5.25 ± 2.20). These litter sizes may not reflect the total number of pups present in the den, since not all samples that were collected from pups yielded DNA. A total of 98 pups were included in 19 litters (Table 2.4). For the purposes of this study, a “litter” is defined as 3 or more pups in the same den. A minimum size of 3 pups enabled confirmation by matching genotypes that no more than two parents contributed to the litter. This is especially important in instances where only one parent is sampled, so that the missing parent’s genotype could be constructed by exclusion. 10 litters had both parents in the sample, 7 litters had one parent in the sample, and 2 litters had neither parent represented in the sample. In the 2 litters for which neither parent was sampled, I confirmed that there were no more than 4 alleles at each locus, as this is the maximum that 2 heterozygous parents could pass on to their offspring. In the 8 litters with one identified parent, I constructed a genotype of the missing parent by process of elimination. This constructed genotype could then be included as a potential parent in

other years. This technique cannot be applied to litters where no parents were genotyped, because at least one parent is needed to compare the alleles that the collected parent contributed to the litter so that the missing parent's genotype can be constructed.

One of the 19 litters was a double-litter, and my analysis revealed that 2 separate mated pairs contributed pups to the litter. The double-litter consisted of 5 pups, 2 of which (PC59 and PC63) were offspring from a sampled mated pair (PC4 and PC10), and the remaining 3 pups (PC60, PC61, PC62) were offspring from unidentified parents.

Discussion

Based on the results of this investigation, I fail to reject H_1 , as the overwhelming majority of offspring (200 out of 201) that I investigated did not result from extra-pair mating. I reject H_2 , based on the presence of one double-litter of 20 litters that were sampled.

Coyotes have long been described as monogamous based on observational studies, and the results of this study strongly support these conclusions. The results also support Moehlman's (1987) argument that mid-sized canids (such as jackals, *C. aureus* and *C. mesomelas*, and coyotes) exhibit a stricter form of monogamy than smaller canids (such as foxes, that tend to practice polygyny) and larger canids (such as wolves, that have been known to incorporate polyandry with monogamy). However, considering that canid social groups display a high degree of intraspecific flexibility (Andelt 1985; Moehlman and Hofer 1997), the results of this suburban study may not be wholly applicable to coyotes in other landscapes.

The evolution of monogamy in social species is a topic that has received a fair amount of attention in the scientific literature. Wittenberger and Tilson (1980) formed hypotheses to identify situations in which monogamy would be likely to evolve. The monogamy that is exhibited by coyotes falls under their guidelines of two of these hypotheses. The first hypothesis states that monogamy “should evolve when male parental care is both nonsharable and indispensable to female reproductive success”. The second hypothesis states that monogamy “should evolve even though the polygyny threshold is exceeded if aggression by mated females prevent males from acquiring additional mates”. There is observational evidence that supports these hypotheses. The first hypothesis is supported by evidence that coyote females cannot raise pups alone, and will abandon her litter if her mate does not support her (Kleiman 1977; Mengel 1971). The second hypothesis is supported by evidence that coyote females attack intruding females and suppress subordinate mating behavior, both hormonally and physically (Allen et al. 1987; Asa 1997; Camenzind 1978; Ryden 1974). In general, these hypotheses align with the breeding biology of the coyote and help to explain why coyotes are monogamous.

However, coyote mating behavior is not completely straightforward, as the unusual but not uncommon occurrences of double-litters illustrate. Nellis and Keith (1976) determined visually that 3 litters of 29 that they excavated from dens were double-litters, which resulted in a double-litter rate of 10.3% (with a 95% binomial probability confidence interval of 9.13%-11.47%). This study found that 1 litter of 20 was a double-litter, resulting in a rate of 5% (with a 95% binomial probability confidence interval from 4.98%-6.98%), which is the same rate that Crabtree and Varley (1995) estimated based

on an intensive 6-year study of 18 coyote packs in Yellowstone National Park. Based on radiotelemetry data for this study, the double-litter of 5 pups was tended by the pair of known parents (PC4 and PC10). Since neither member of the second mated pair was radiocollared, it is unknown whether they were present at the den. Based on observational studies of den-sharing coyotes, it seems likely that the unidentified mated pair were tending the pups jointly with PC4 and PC10 (Camenzind 1978; Crabtree and Varley 1995). It is also possible that the unidentified parents were killed or abandoned the litter, and the known mated pair adopted the orphaned pups. This is a speculative notion that has not been supported by observational evidence in the literature, but could be plausible if the adoptive parents were related to the adopted pups (Hamilton 1964). Unintended adoption is also a possibility, since coyotes appear to have no awareness of the identity of their pups until 5-6 weeks of age, as demonstrated by cross-fostering experiments by Kitchen and Knowlton (2006). Furthermore, pups have been observed moving between closely situated dens on their own, which could possibly lead to unintended adoption by adults (Ortega 1988). On the other hand, considering that adult coyotes have been observed invading dens and killing pups of neighboring breeding adults, it seems somewhat less likely that one mated pair would assume full responsibility for another mated pair's offspring (Camenzind 1978). To clarify the topic, the relationship between the two mated pairs that contribute to a double litter needs to be further investigated.

The high rate of monogamy, 99.5% (200 out of 201; with a 95% binomial probability 95% CI of 96.40-100.00%), in this population confirms the many studies that assert that coyotes are monogamous. The only instance of polygamy was especially

interesting because it was not an instance of a female seeking multiple mates (polyandry), as I had expected to find, but rather a male that mated with two separate females (polygyny). I expected, based on studies of similarly-sized canids (Moehlman 1987) and the two observations of multiple copulations of coyotes in the wild (Cadieux 1983; Gese et al. 1996), that if coyotes displayed any mating system besides monogamy, it would be polyandry, as it is possible for a female's ova to be fertilized by different males (Asa and Valdespino 1998). I assumed that a female would more likely "hedge her bets" by mating with multiple males, whereas males are restricted by their paternal duties, and may decline to seek extra-pair mating opportunities. Coyote social ecology necessitates that the female and pups are provisioned by the male while she is in the den; indeed, the pups would likely not survive without paternal help (Andelt et al. 1979). However, the literature provides several incidents of one male provisioning 2 females at 2 separate dens, sometimes separated by distances of 2.8 km (Crabtree and Varley 1995; Gese et al. 1996; Parker 1995; Way et al. 2001). It is likely that BW32, the father of the 2 litters, courted and provisioned 2 females at 2 different dens. This could increase male reproductive success, as BW32 produced 11 pups with UF4 in 2002, and an unknown number (but at least one: WGN86) with the second female. As Wittenberger and Tilson (1980) defined monogamy, 'cheating' does not negate monogamy. Indeed, as the pups would likely not survive without paternal care, the father of 2 litters must remain socially devoted to 2 females and their offspring. As long as he is able to sustain himself, his mates and his offspring, polygyny may be a lucrative strategy.

An important caveat of this research must be noted; that for some litters, it is probable that not all pups were collected. This may overestimate the number of

'complete' litters that were sampled. For instance, an observational study of coyotes in the National Elk Refuge in Wyoming, USA, noted that one mated pair moved their litter into 2 separate dens (Ryden 1974). As a result, 3 pups of this litter were cared for in one den, and 6 in the other. If coyotes were "den-splitting" in the Chicago area, one den may have been sampled while the other was not, with the result that incomplete litters would have been sampled with the false supposition that they were complete. Also, typical coyote dens often have several tunnels with chambers (Bekoff and Gese 2003; Camenzind 1978), which can shield pups from discovery and exclude them from the sample.

Developmental biology and early mortality rates could also decrease the likelihood of sampling entire litters. Stockley (2003) found an early reproductive failure rate in coyotes of 25.8%, meaning that of all available ova, only 74.2% become embryos. Green et al. (2002) noted that the ratio of placental scars to birthed pups range from 44% to 85% in wild-caught coyotes, meaning that not all embryos develop fully into pups. Crabtree and Varley (1995) determined that neonatal coyote pups in Yellowstone National Park experienced a mortality rate of 65% annually. Likewise, Gese et al. (1989) determined an annual survival rate for pups in Colorado to be 51%. In south Texas, Andelt (1985) discovered that 7 out of 11 pups, ranging from 1-6 months old, did not survive to adulthood, despite receiving inoculations against hookworm. Obviously, not all fertilized ova develop into viable pups, and not all pups survive to adulthood. These biological facts decrease the possibility that an extra-pair fertilization is detected before collection even begins. However, the survival rate of juvenile coyotes in this study was fairly high (61%; Stan Gehrt and Chris Anchor, pers. comm.) and the sample size was

large. Therefore, although it is possible that an instance of female extra-pair mating could have been overlooked, the results should not be strongly affected by these restrictions on data collection.

The conclusions reached by previous studies of coyote mating strategy appear to be accurate, at least concerning this population. As coyotes exhibit high rates of intraspecific plastic behaviors, the findings of this paper should be tested in different regions and landscape types. It is possible that the anthropogenic landscape affects the coyote mating system in ways that we do not yet understand (Fedriani et al. 2001; Rubenstein 2001). It appears, however, that monogamy is the most successful strategy for this canid. The single occurrence of polygyny may be related to factors such as prey abundance, landscape saturation, or scarcity of suitable mature males; future studies are needed to address this interesting behavior. Further investigation is also required to determine the relatedness of mated pairs that share dens, and to parse out the conditions that lead to den-sharing behavior.

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Tables and Figures

Locus	Annealing Temp (°C)	MgCl ₂ per rxn (mM)	Number of Alleles	Gene Diversity	H _e	H _o
CXX109	59	1.6	8	0.828	194	191
CXX123	56	1.6	6	0.709	164	165
CXX172	52	1.8	5	0.525	128	131
CXX204	59	1.8	3	0.256	51	54
CXX213	56	1.8	8	0.724	165	177
CXX225	56	1.6	10	0.714	151	143
CXX250	56	2.0	8	0.837	190	193
FH2328	52	2.0	17	0.908	209	205
FH2161	52	1.8	14	0.865	206	200
FH2380	52	1.8	4	0.595	138	149
FH2054	56	1.6	11	0.727	161	167
FH2088	56	1.6	10	0.845	190	196

Table 2.1 - Genetic diversity and heterozygosity of microsatellite markers for a population of urban coyotes in the Greater Chicago Metropolitan Area (2000-2006). H_e represents expected heterozygosity, and H_o represents observed heterozygosity.

	Male				Female				Total
	Caught	RC	G	RC & G	Caught	RC	G	RC & G	RC & G
Adults	30	29	29	28	17	17	16	16	44
Subadults	25	25	17	17	20	20	14	14	31
Yearlings	22	21	14	13	31	30	21	21	34
Pups	68	24	65	24	49	15	45	15	39
Total	145	99	125	82	117	82	96	66	148

Table 2.2 - Caught, radiocollared (RC) and genotyped (G) animals by sex and age cohort across 6 years of the study (2000-2006) in the Greater Chicago Metropolitan Area.

Male	Year	# locations	Female	# locations	% Overlap
10	2000	122	4	185	99.57
	2001	242		251	87.52
	2002	448		681	83.18
14	2000	65	13	66	88.62
	2001	44		121	59.91
	2002	575		650	76.95
21	2004	9	125	191	19.81
	2005	147		157	85.17
	2006				
88	2004	189	111	296	89.12
53	2004	125	113	137	55.29
115	2004	222	1	202	79.15
	2005	147		144	66.12
	2006				90.57

Table 2.3 - Home range overlap values for radiocollared mated pairs.

Year	Trap Site	Father Mother	Offspring
2000	MM	9 UF2	11, 20, 22, 23, 37
2001	MM	42 38	39, 40, 41, 92
2002	HW	UM3 49	56, 57, 58
	BW	32 UF4	64, 65, 66, 67, 68, 69, 70, 71, 72, 76, 80
	PC	4 10	59, 63
	PC	UM UF	60*, 61*, 62*
2004	PC	21 125	127, 128, 130, 131, 132
	HW	88 111	136, 138, 139, 140, 141, 142, 143
	WGN	115 1	145, 147, 148, 150, 151
	MM	53 113	154, 156, 157
	BW	182 UF12	178, 179, 183
2005	PC	UM 174	186, 187, 188
	PC	21 125	210, 211, 212, 213, 214
	WGN	115 1	222, 226, 227
	BW	182 UF12	215, 216, 217, 218, 219, 220, 221, 223, 224, 225

	HW	UM11 111	197, 198, 200, 202, 203
	PC	UM UF	204, 205, 206, 207, 208, 209
2006	PC	21 125	253, 254, 255, 256, 257, 258, 259
	WGN	115 1	263, 264, 265, 266
	MM	UM UF	249, 250, 251, 252

* - PC60, PC61 and PC62 were in the den of PC4 and PC10

Table 2.4 – Parents and offspring across all years of the study. Location codes are as follows: BW is Busse Woods Forest Preserve, HW is Highland Woods Forest Preserve, MM is Max McGraw Wildlife Foundation, PC is Poplar Creek Forest Preserve, and WGN is a natural area surrounding the WGN radio tower. In the Parents column, any parent marked UM is an uncollected male, and UF is an uncollected female. Any UM or UF with a number has a constructed genotype based on exclusion methods.

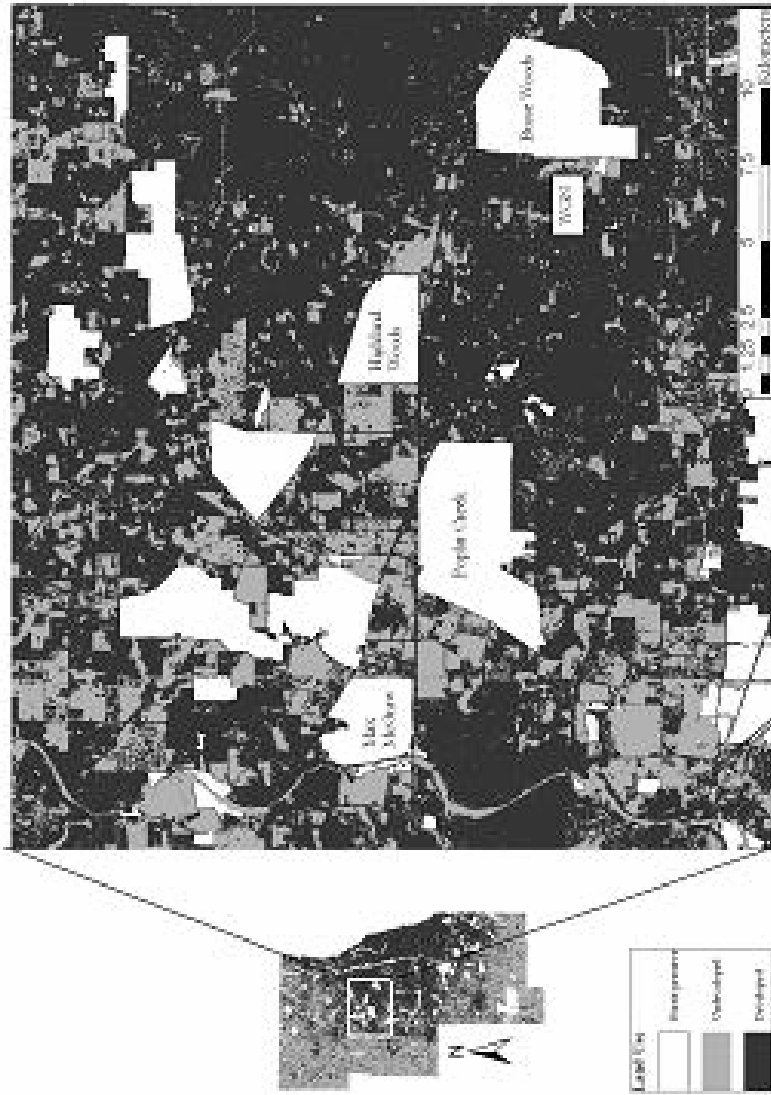


Figure 2.1 – Study area in the Greater Chicago Metropolitan Area, with labels on the major trap sites.

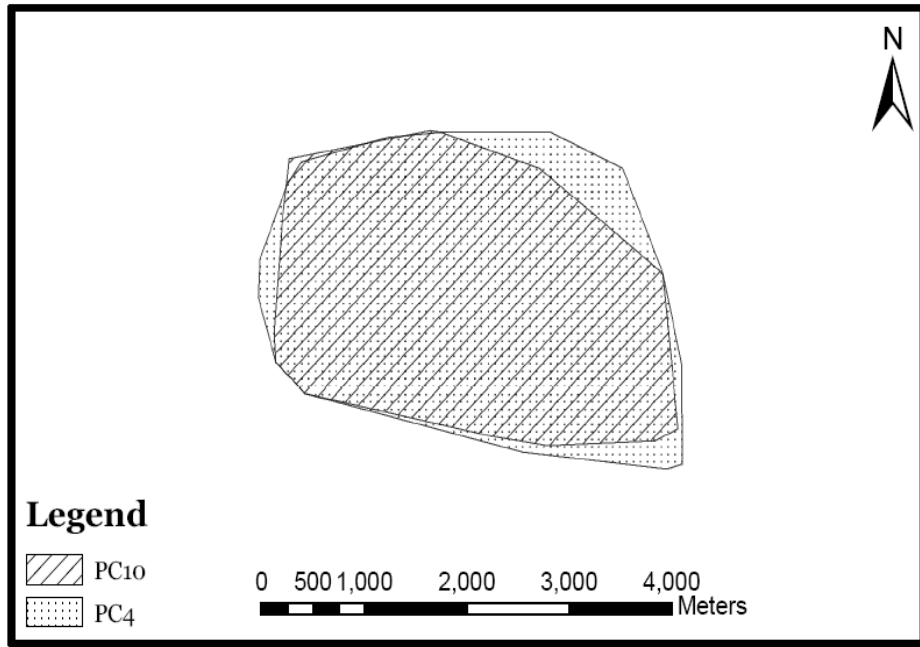


Figure 2.2 – Overlap of 95% MCP home ranges for mated pair, PC10 and PC4, in year 2000.

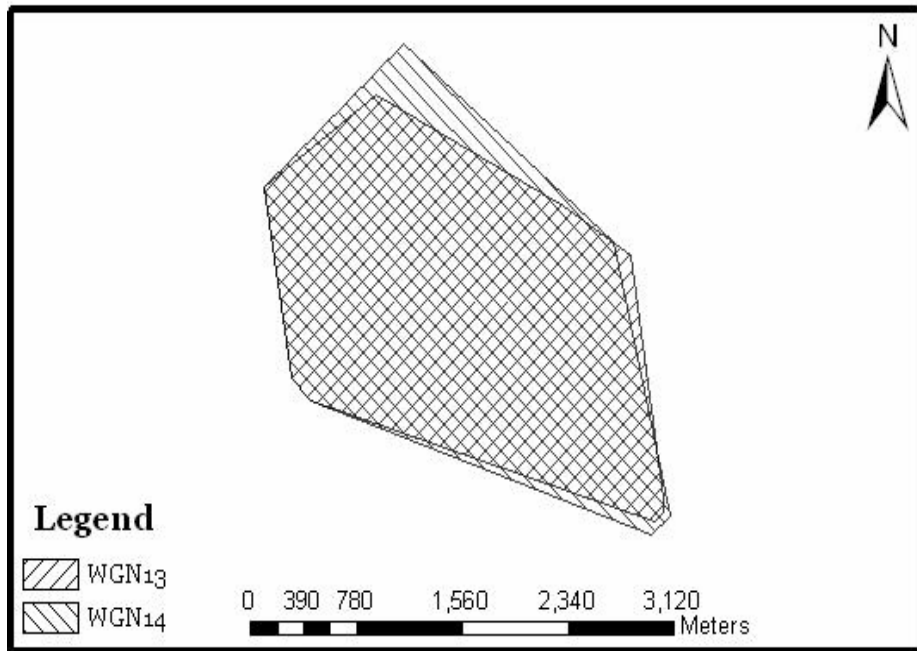


Figure 2.3 – Overlap of 95% MCP home ranges for mated pair, WGN13 and WGN14, in year 2000.

Chapter 3: Pack structure of suburban coyotes

Introduction

A wide range of cooperative living situations are exhibited in the Canidae, which include packs, communal dens, long-term and short-term mated pairs, as well as solitary adults that meet others only to mate (Macdonald and Moehlman 1982; Sheldon 1992). Although the term “pack” is used to describe differing situations across species, it is generally accepted to refer to a cohort of gregarious animals that share the same territory over a long period of time (e.g., Bekoff and Wells 1980; Girman et al. 1997; Lucchini et al. 2002). The relationships and interactions between the pack members can be pivotal to the reproductive success and the survival of its members (Mech 1995; Okoniewski 1982; Wrangham and Rubenstein 1986). There are advantages and disadvantages to pack membership; the advantages can include contributing to kin fitness, access to food and shelter, increased survivorship, and access to mates (Bowen 1981; Gese 2001; Gese et al. 1988; Hamilton 1964; Parker 1995; Vucetich et al. 2004; Windberg 1995; Wrangham and Rubenstein 1986). The disadvantages can include delayed breeding, resource sharing, increased risk of exposure to disease and parasites, and alloparenting responsibilities (Gier et al. 1978; Macdonald and Moehlman 1982; Parker 1995). Despite these disadvantages, the evidence in the literature strongly suggests that the advantages to

living in a pack, even for subordinate members, outweigh the disadvantages. These aspects of group living, as well as many others, are surveyed extensively in the literature.

Coyotes (*Canis latrans*) are moderately social canids (Bekoff 1977; Kleiman and Brady 1978). Coyotes exhibit a wide range of home range sharing, from solitary animals to members of large packs. For any period of time when a coyote is not a member of a mated pair or a pack, it is referred to in the literature as a “solitary animal” (Pruss 2002), a “transient” (Bekoff and Gese 2003), a “nomad” (Camenzind 1978), a “floater” (Crabtree and Varley 1995) or a “loner” (Andelt 1985; McClennen et al 2001). For the discussion of this project, these coyotes are referred to as transients. Some studies have argued that the percentage of transients in a population decreases as the size of the main prey item(s) increases, suggesting that pack membership is more important to coyote populations that prey upon larger species, such as elk (*Wapiti wapiti*) or deer (*Odocoileus* spp.; Bekoff and Wells 1980; Bowen 1981; Camenzind 1978). Across all populations, transients have home ranges that are much greater in size than those of resident coyotes (Andelt 1985; Bekoff and Gese 2003; Pruss 2002) and transients do not mark or defend a territory (Bekoff and Wells 1980; Gese and Ruff 1997; Gese et al. 1988; Gese 2001; Way 2002). In contrast, resident coyotes establish a territory and defend it (Allen et al. 1999). A resident coyote can be a member of a mated pair or a member of a pack or both (Allen et al. 1987; Bekoff and Gese 2003; Camenzind 1978; Pruss 2002).

Many studies of coyote social systems have described packs as family groups, which consist of an unrelated mated pair, often referred to as the “alpha” pair, their juvenile offspring, and often 1 or more offspring from previous years (Andelt 1985; Bekoff and Wells 1982; Macdonald and Moehlman 1982; Patterson and Messier 2001).

The grown offspring that remains with its parents is referred to in the literature as the “beta” (Allen et al. 1999), “associate” (Allen et al. 1987), “helper” (Bekoff and Wells 1982), “nursemaid” (Andelt et al. 1979), or “subordinate” coyote (Gese et al. 1996). Since the social relationships between pack members in this study were not observed at length, I will only be referring to an animal’s status as it relates to its breeding status (i.e., pup, subadult, adult). Although researchers have discerned intrapack relationships through great efforts of observation and familiarity with coyote packs, often these same researchers state that further research is necessary to determine the actual level of relatedness within packs (Asa and Valdespino 1998; Atwood and Weeks 2003), as well as to determine if coyotes are successfully avoiding inbreeding (Bekoff and Gese 2003; Way 2003).

The hypothesis that the coyote pack is a family group remains largely unchallenged in the literature; however, recent investigations in the field of animal behavior have revealed that assumptions about relationships based on observational research can be overturned by molecular investigations. For example, molecular studies of African wild dog (*Lycaon pictus*) packs found that a subadult male was the offspring of the alpha female but not of the alpha male, contrary to expectations that it was the offspring of both parents (Girman et al. 1997). A study of kit fox (*Vulpes macrotis mutica*) social groups found that an adult female in a trio of adults was related only to the alpha female and not to the alpha male (Ralls et al. 2001). Genetic investigations of gray wolf (*Canis lupus*) packs witnessed the adoptions of unrelated adults into established packs (Grewal et al. 2004; Lehman et al. 1992; Meier et al. 1995; von Holdt et al. 2007). In addition, 2 studies which incorporated prolonged observational data found evidence

that transient coyotes sometimes join established packs (Pruss 2002; Ryden 1974), a phenomenon that would not be expected under the hypothesis that a coyote pack consists only of a mated pair and their offspring. These investigations into pack structure have been conducted in the recent past and illuminate previously unknown aspects of the social and territorial nature of canids. Considering that “more is known about the ecology of coyotes than perhaps any other carnivore” (Bekoff and Gese 2003), a molecular study of their pack structure is possibly overdue.

As part of a large, comprehensive investigation of urban coyotes in the Greater Chicago Metropolitan area, I was provided access to radiotelemetry data and genetic samples, the combination of which enabled me to investigate coyote relationships across 26 pack-years. I tested the hypothesis (H_1) that a coyote pack is a family group. In addition, I tested a second hypothesis (H_2) that mated pairs are unrelated, and are therefore successfully avoiding inbreeding.

In addition to the hypotheses stated above, I investigated the overall relatedness of packs as well as the relationship between home range overlap and relatedness. The results may help researchers in this field elucidate the relatedness of a pack member based on behavior, which may in turn enable a deeper understanding of coyote social groups.

Methods

Study Area and Study Animals. - Research was conducted in the following counties of northeastern Illinois: west Cook, east Kane, north Dupage and south

McHenry (Figure 2.1). These counties are part of the Greater Chicago Metropolitan Area, which is home to approximately 9.1 million people (U.S. Census Bureau 2000). The majority of the area has been sectioned by roads and developed, although examples of eastern tallgrass prairie, open oak stands, and a few scattered wetlands remain (Greenberg 2002; Sullivan 1999). The study area comprised of the following land use types: commercial/industrial (43%), residential (20%), agriculture (14%), undeveloped (13%), and other (10%; Stan Gehrt and Chris Anchor, pers. comm.). Native fauna included white-tailed deer (*Odocoileus virginianus*), red fox (*Vulpes vulpes*), grey fox (*Urocyon cinereoargenteus*), raccoons (*Procyon lotor*), voles (*Microtus* spp.), mice (*Peromyscus* spp.), beavers (*Castor canadensis*), squirrels (*Sciurus* spp.), opossums (*Didelphis virginianus*), eastern cottontail rabbits (*Sylvilagus floridanus*), groundhogs (*Marmota monax*) and muskrats (*Ondatra zibethicus*). Non-native fauna included house cats (*Felis catus domesticus*), domestic dogs (*Canis domesticus*), rats (*Rattus norvegicus*), and house mice (*Mus musculus*). Dominant food items in the diet included small rodents, white-tailed deer, lagomorphs, birds and fruit (Morey 2004). Human-associated items, such as garbage and pet food, were more prevalent in the diets of coyotes in residential areas, but were not the main source of food for any coyotes (Morey 2004). Coyotes in this region have no natural predators. The top 3 causes of mortality included: collisions with vehicles, shooting, and mange. (Stan Gehrt and Chris Anchor, pers. comm.). Average survival rates ranged from 0.58 to 0.70 across all age and sex classes, and individual coyotes often persisted in the area from year to year (Stan Gehrt and Chris Anchor, pers. comm.).

Coyotes were captured from 2000-2006 using padded foothold traps or with cable restraint devices. Snares were set in relatively natural areas, such as the private lands of the Max McGraw Wildlife Foundation and the Cook County forest preserves, to reduce human intrusion. During the course of the study, one coyote was euthanized after trapping, as a result of getting snared around the waist and suffering major physical trauma. No other animals were injured or died due to protocols implemented. Coyote pups were captured at den sites in the years 2000-2006 by technicians that excavated the dens with shovels and caught the pups by hand. Three larger pups were caught opportunistically by a technician who detected them in a field.

At capture, coyotes were transported in handling cages to a laboratory for processing. Adult coyotes were immobilized with Telazol (Fort Dodge Animal Health, Fort Doge, Iowa). Pups that were excavated from dens did not require restraining techniques or Telazol, since they are relatively docile at this age. Reproductive condition of adults was estimated by the size of testes (for males) and condition of teats (for females). Age was estimated based on size, weight, reproductive condition, and incisor wear (Parks 1979). All animals were assumed to have been born in early May (Bekoff 1977): each coyote year corresponded to the period from May 1 to April 30. The term “pup” referred to coyotes that were less than 6 months old, “yearling” referred to coyotes that were between 6 and 12 months old, “subadult” referred to coyotes that were full-grown but not reproducing, and “adults” referred to full-grown, reproducing coyotes. Coyotes were bestowed unique alphanumeric identifications which include a reference to the trap location; for instance, the 10th coyote trapped for this study was trapped in the Poplar Creek (PC) Forest Preserve, therefore the name for this coyote was PC10. Adult-

sized animals were ear-tagged in both ears with colorful plastic tags (monel #3 or #4, National Band and Tag Company, Newport, Kentucky), and were fitted with radio-collars (Advanced Telemetry Systems, Isanti, Minnesota). Subcutaneous transponder chips (PIT tags, AVID Marketing Inc., Norco, California) were implanted into pups under the dermis of the scruff, to provide identification upon recapture.

Blood samples were typically drawn from an outer leg vein, using a sterile needle and syringe, whereas tissue samples were collected opportunistically from road-killed coyotes and nuisance coyotes that were euthanized by Cook County wildlife officials. In some instances, hair samples with bulbs were obtained from pups when blood samples proved obtrusively difficult to obtain, due to small veins. After recovering from the Telazol, coyotes were released at the capture location. All coyotes were treated humanely following animal care and handling protocols approved by the Institutional Animal Care and Use Committee at The Ohio State University. All genetic samples were kept in frozen storage until DNA extraction procedures could be performed.

Radiocollared coyotes were located via triangulation by a technician with a truck-mounted Yagi antenna and receiver. Daytime locations were detected at least twice a week, whereas nocturnal tracking shifts at 1-2 hour intervals were conducted 5-10 times per month. Daytime locations were helpful for locating den sites, whereas nocturnal locations provided movement and home range information. For more detailed radiotelemetry methods used in this project, see Morey (2004).

Genetic Methods. - Blood and tissue samples were extracted using a standard phenol-chloroform procedure (Sambrook et al. 1989). Hair samples were processed using Qiagen QIAamp Mini DNA Kit (Qiagen, Los Angeles, California). For

polymerase chain reaction (PCR), genomic DNA was diluted to a working concentration of approximately 50 ng of DNA per μL of solution.

I used 12 domestic dog microsatellites that amplified in coyotes: CXX109, CXX123, CXX172, CXX204, CXX213, CXX225, CXX250, FH2328, FH2161, FH2054, FH2380, FH2088 (Francisco et al. 1996; Ostrander et al. 1993; Roy et al. 1994). One locus that I attempted to use but excluded due to high failure rate was FH2001 (Francisco et al. 1996). Forward primers (Sigma Proligo, Sigma-Aldrich, The Woodlands, Texas) and reverse primers (Sigma Genosys, Sigma-Aldrich, The Woodlands, Texas), were diluted to 10% concentrations and combined. All forward primers were labeled with WellRed dyes (Beckman-Coulter Inc., Fullerton, California). PCR reagents per 12.5- μL reaction included 40 ng of DNA, 0.2 mM DNTP, 8 pmol primer, 0.5 units of *Taq* polymerase, and 1.25 μL 10X standard reaction buffer. The amount of MgCl_2 per locus was adjusted to facilitate results with different primers, with amounts ranging from 1.6-2.0 mM (Table 2.1). PCR reactions were facilitated by a thermocycler (Bio-Rad Laboratories, Hercules, California) and ran for 35 cycles, with varying annealing temperatures (Table 2.1).

Amplified microsatellite fragments were sized using a Beckman-Coulter CEQ 8000XL automated capillary genotyping system (Beckman-Coulter, Inc., Fullerton, California) with an internal size standard added to each sample. Fragments were analyzed using Genetic Analysis System Software (version 8.0; Beckman-Coulter, Inc., Fullerton, California) and automated allele calls were checked visually with bins defined

by frequency graphs of fragment sizes. Positive controls were periodically included to ensure that allele calls were reliable. Loci were scored individually, and the resulting allele calls were used to construct genotypes.

Genetic Analysis.- I used the program FSTAT (Goudet 2001) to check for redundant samples and to calculate gene diversity and F statistics at each locus (Weir and Cockerham 1984). I used the program GENEPOP (Raymond and Rousset 1995) to determine whether the population was in Hardy-Weinburg equilibrium, to check for linkage disequilibrium, and to calculate gene frequencies for each locus. GENEPOP was also utilized to determine heterozygote excess or deficiency at each locus. Rates of heterozygote excess or deficiency can indicate whether a population is experiencing high rates of outbreeding or inbreeding, respectively. I used the program MICROCHECKER (van Oosterhout et al. 2003) to survey the loci for evidence of large allele dropout and for null alleles. Large allele dropout refers to the failure of detection of large alleles. This can happen when a large allele, which consists of a long sequence, and a small allele, which consists of a short sequence, are in the same replication procedure. The smaller allele replicates faster and therefore more copies of it will be made. This can lead to a failure of the large allele to replicate, which can lead to the erroneous designation of homozygous when the individual is actually heterozygous at that locus (Dewoody et al. 2006). Null alleles are caused by a mutation in the primer sequence of the microsatellite that disables the recognition of the template, which results in a failure of the microsatellite to replicate (Bruford and Wayne 1993).

Genotypes of pack members were compared for relatedness using 2 programs: PASOS, which is an acronym for 'Parental Allocation of Singles in Open Systems' (Duchesne et al. 2005) and KINSHIP (version 1.2, Goodnight and Queller 1999). A simple exclusion method was also utilized, which encompassed visual matching of genotypes of potential relatives.

Parentage analysis was an important part of pack structure analysis, since I was addressing the assumption that a pack is fundamentally a family group. PASOS allocated parents to offspring based on alleles and allele frequencies. The program was designed to identify parents in open systems. PASOS accepts user-defined restricted error tolerance in order to include partially incorrect genotypes in the parental allocation procedure, which is especially useful for microsatellite loci that may have been mis-scored. As mis-scoring of microsatellites typically occurs in a step-wise fashion, PASOS incorporates a likelihood calculation that determines whether a mismatched locus between a candidate parent and offspring is likely due to scoring error. PASOS performed sequence simulations in order to identify the most reliable set of loci to be retained for allocation. These simulations also allowed an estimate of the overall allocation correctness rate, as well as error estimates for each allocation. PASOS allows the user to arrange the sequence of loci for the allocation procedure, which I used to decrease the possibility of false allocation due to locus FH2161 (Francisco et al. 1996). This locus was particularly difficult to score and was thus prone to falsely scored alleles. By setting up the allocation process so that FH2161 was the last locus to get matched between 2 genotypes, I was decreasing the opportunity for a mismatch.

KINSHIP estimated Grafen's relatedness coefficient (R ; Grafen 1985) between pairs of individuals using the population allele frequencies and the genotypes of the individuals to calculate the likelihood that the shared alleles of the 2 individuals are identical by descent (Queller and Goodnight 1989). KINSHIP created a matrix of relatedness values for each pair of genotypes in the population (Goodnight and Queller 1999). I used these coefficients of relatedness to determine how closely related 2 animals are; for example, an R of 0.5 indicates a first-order relationship (parent to offspring, full siblings) and an R of 0.25 indicates a second-order relationship (grandparent to grandchild, first cousins, aunt to nephew, etc.). However, these are standard values that could be expected in a generic population. I calibrated the values for first-order and second-order relationships in the study population with known relationships using bootstrapping methods in R (Ihaka and Gentleman 1996), with 10,000 simulations (Gompper et al. 1997). For calibrating first-order relationships, I constructed a sample based on the R values of 130 verified mother-offspring pairs. For calibrating second-order relationships, I based the sample on the R values shared between 42 verified grandparent-grandoffspring pairs.

Pack Member Analysis. - Radiotelemetry locations were entered into a Microsoft Access database, and then were transported into ArcMaps (v. 9.1, ESRI; Environmental Systems Research Institute, Inc.). ArcMaps was used to construct 95% minimum convex polygons (MCPs) for each genotyped and radiocollared coyote in the population with a minimum of 30 locations in a given year. MCPs were preferred to fixed-kernal polygons because they tend to be more conservative, and for the purposes of this study, it was preferable to underestimate rather than overestimate percent overlap (Gese et. al 1990;

Seaman and Powell 1996; Worton 1989). Percent overlap of MCP areas were determined using the “calculate area” geoprocessing function in ArcMAPS toolbox, which provided an area value for the 2 home ranges and the overlap area between them. These values were entered into Microsoft Excel and percent overlap was calculated using the following formula (Atwood and Weeks 2003):

$$[(\text{area}_{AB}/\text{home-range}_A)(\text{area}_{AB}/\text{home-range}_B)]^{0.5}$$

The value designated “area_{AB}” represents the overlap area of the home ranges of animal A and animal B. For each pair of animals that shared overlap in subsequent years, I averaged their home range overlap values.

Pack members share a core area that may be used as a rendezvous site and is the area that is most heavily marked and defended by pack members (Harrison et al. 1991; Patterson and Messier 2001; Way et al. 2001). Therefore, I was able to define pack members by first identifying the coyotes that shared substantial percentages of their 95% MCP home ranges (typically 30% or more), and I created an intersection area where all the coyotes sharing roughly the same area overlapped each other, using the intersect tool in the ArcMaps toolbox (Figures 3.1 and 3.2). This area will be referred to as the pack core for the rest of this chapter. Because transients will use the landscape with seemingly little regard for established territories (Allen et al. 1987; Camenzind 1978; Kamler and Gipson 2000), I established a cut-off point to exclude them from pack membership. Thus, a coyote was only considered a pack member if it exhibited at least 20% overlap with the pack core. It would be unlikely to include a transient in a pack inadvertently, since transient home ranges were substantially larger than resident home ranges, and would not be exhibiting overlap of a 5th or more of its home range with a defended pack

core. Also, transients tend to move across resident home ranges just along the periphery, and they avoid the interior space of residents' home ranges (Andelt 1985). This behavior further reduces the potential for a transient's home range to be included in the analysis.

For a general analysis of home range sharing, I addressed characteristics of shared overlap and investigated the relationships between home range overlap and relatedness. First, I constructed a histogram to demonstrate the frequency of classes of overlap percentages in increments of 10. Next, I investigated the differences between age classes on home range sharing with an ANOVA test, and I also displayed the frequencies in histograms. I ran a second ANOVA test to test for differences between age classes and overlap with the pack core, which is also demonstrated in frequency histograms. To test for correlation between home range overlap and relatedness, I performed a series of linear regression tests. The first linear regression included all coyotes that exhibited any amount of overlap. The second linear regression excluded all confirmed mated pairs; "confirmed" meaning that the mated pair had produced offspring that had been sampled and were thus confirmed breeders. The removal of the confirmed mated pairs could potentially strengthen the relationship between overlap and relatedness, since mated pairs are expected to share very low relatedness values (Sacks et al. 2005; Smith 1997). In a similar vein, I ran a linear regression that excluded all young-of-the-year to see if the relationship between overlap and relatedness would weaken. Next, I ran a series of linear regression tests that excluded confirmed mated pairs along with any values of percent overlap that fell below 25%, 50%, and 75%, respectively. This was to test whether relatedness increases as percent overlap increases, as would be expected if closely-situated pack members are close relatives.

I constructed ethograms that display the relatedness values between pack members across years, as well as tables that summarized the low and high relatedness values in packs. I compiled histories of each pack year by year in order to provide a written account of pack membership as well as the fate of pack members and territory inheritance. By following the same packs across consecutive years, I attempted to elucidate the social ecology of the packs.

Results

Population Genetics. - From January 2000 to December 2006, 266 coyotes were captured, 241 of which yielded potentially viable genetic samples. As revealed by FSTAT, 5 samples were redundant, which decreased the total genetic sample to 236. Three redundant samples most likely occurred when a pup was sampled, released, and recaptured later as a new individual, most likely because the implanted microchip escaped detection. The other 2 cases of redundant samples appear to be caused by labeling error. Hair samples taken from pups in 2004-2005 were often lacking roots and yielded very little genetic material. The majority of coyotes were genotyped at all 12 loci, but some were not, due to the low concentrations of DNA in hair extractions. In all, 225 coyotes were genotyped at all 12 loci, 7 were genotyped at 11 loci, and 4 were genotyped at 10 loci. In cases where the DNA was in too weak in concentration to genotype at least 10 loci, the coyote was removed from the genetic study.

The biostatistical program FSTAT calculated a F_{IS} score of 0.015, along with gene diversity for each locus (Table 2.1). GENEPOP revealed that the population is in Hardy-Weinberg equilibrium and in linkage equilibrium. MICROCHECKER analysis found no evidence of large allele dropout or null alleles in the study population. GENEPOP determined expected and observed heterozygosity at each locus (Table 2.1). Locus 204 was the least polymorphic locus, but it was retained because it was reliable and enabled verification that a sample was working. In addition, it revealed a rare allele that was shared by only 2 coyotes, thereby increasing the likelihood of their relatedness.

The 130 first-order R values, which ranged from 0.15 to 0.77, had an average of 0.46 ± 0.11 . The results of the first-order calibration, which was calculated by bootstrapping these first-order R values 10,000 times, indicated that coyotes in this population exhibited first-order relatedness values at 0.46 ± 0.01 (Figure 3.3). This is significantly different from the expected value of 0.50 ($\chi^2 = 0.004$, $p < 0.000$). The sample of 42 second-order R values ranged from -0.22 to 0.52, with an average of 0.11 ± 0.19 . Bootstrapping this sample gave an average of 0.11 ± 0.03 (Figure 3.4). In a similar manner to the first-order calibration, the second-order calibration also demonstrated a significant downward shift ($\chi^2 = 0.082$, $p < 0.000$) from the expected value of 0.25. This downward shift for the mean of first-order and second-order relationships could be caused by a paucity of microsatellite alleles or a low rate of polymorphism in the microsatellite loci that I used (Blouin 1996). It could also be caused by a higher-than-average rate of outbreeding (Gompper et al. 1997). In order to create a cut-off point between the first- and second-orders of relatedness, I used the median between 0.11 and 0.46, which is 0.29. Therefore, all pairs of coyotes that exhibit an R value greater than

0.29 were considered first-order relatives, whereas an R value less than 0.29 merited second-order relatedness status. Since the distance from 0.11 to 0.29 is 0.18, I created the cut-off point between second-order relatives and unrelated coyotes by subtracting 0.18 from 0.11. This created a cut-off point of -0.07.

Overlap Analysis. - Of the 236 coyotes genotyped, 148 were radiocollared (Table 3.1). For the general overlap analysis, wherein R values were tested against home range overlap values, all pairs of coyotes that exhibited any amount of overlap were initially included. Also, for the following analysis, the overlap values for all coyote pairs that recurred across multiple years were averaged.

I constructed a histogram to demonstrate the classes of overlap percentages in increments of 10 (Figure 3.5). The average overlap value was 0.44 ± 0.25 . As the graph demonstrates, the least common overlap percentage class was above 90%. Overlap percentages of such a high degree are typically only exhibited by mated pairs, and there were only 7 sampled mated pairs in the population. In order to deduce the effect of age classes on home range sharing, I constructed histograms that demonstrated the frequency of certain classes of overlap between 2 types of coyotes (adult with adult, adult with subadult, etc.), which are displayed in figures 3.6-3.11. An ANOVA test was performed to determine if there was any significant difference between average sharing values between the groups, which revealed that there was a difference between the groups ($F_{5, 266} = 2.82, p = 0.017$). A post-hoc Tukey's Honestly-Significant-Difference test was performed to determine which groups were different from the rest, and it showed that the overlap shared between pups and subadults was significantly different than the overlap shared between pups with pups ($T = -23.81, p = 0.039$) and the overlap shared between

subadults and subadults ($T = 18.46$, $p = 0.032$). In regards to the effect of age class on overlap with the pack core, a series of histograms illustrates the trends (Figure 3.12-3.14). On average, adults shared 0.50 ± 0.22 of their home range with the pack core, subadults shared 0.49 ± 0.26 , and pups shared 0.68 ± 0.22 . An ANOVA test revealed that there was significant difference between the age classes ($F_{2, 126} = 5.98$, $p = 0.003$). A post-hoc Tukey's Honestly-Significant-Difference test was performed to determine which age classes were significantly different, and it revealed that pup overlap with core was significantly different from adult overlap with core ($T = -17.65$, $p = 0.005$) and subadult overlap with core ($T = 18.81$, $p = 0.004$). Adult overlap with core and subadult overlap with core were not significantly different.

Before running the linear regression tests, I tested the data to see if it was normally distributed. I plotted the residuals against the predicted values with SYSTAT (version 10, SYSTAT Software Inc., San Jose, California) and deemed that a parametric test was appropriate (Sokal and Rohlf 1995). I also ran a Kolmogorov-Smirnov one sample test, which showed the data fit a normal curve (two-tail probability = 0.424). In order to determine if there was a relationship between home range sharing and relatedness, I ran tests of linear regression in Microsoft Excel. The first regression test was a comparison of relatedness values and overlap percentages across the entire population (Figure 3.15), and the results were significant but the relationship was not very strong (F value = 31.51, $R^2 = 0.14$, $SE = 0.27$, $p < 0.000$). The second linear regression excluded all confirmed mated pairs (Figure 3.16), and the results were again significant (F value = 50.60, $R^2 = 0.21$, $SE = 0.26$, $p < 0.000$). It appeared that the relationship between overlap and relatedness was strengthened by removing the mated

pairs. The next linear regression test included mated pairs but excluded all young-of-the-year (Figure 3.17), and the results were significant (F value = 19.76, $R^2 = 0.10$, SE = 0.27, $p < 0.000$). The decrease in the F value and the R^2 value indicates that the removal of the young-of-the-year demonstrated the effect that I predicted in the methods. Next, I ran a series of regression tests that excluded all mated pairs and sequentially removed the lowest 25%, 50%, and 75% percent overlap values (Figures 3.18-3.20). The results for the overlap values over 25% were significant (F value = 18.78, $R^2 = 0.12$, SE = 0.26, $p < 0.000$), as were the results for the overlap values over 50% (F value = 0.74, $R^2 = 0.01$, SE = 0.24, $p < 0.000$). However, the test for the overlap values over 75% was not significant (F value = 0.08, $R^2 = 0.004$, SE = 0.26, $p = 0.783$), which is likely due to the paucity of data.

Pack Structure Analysis. - Across all 6 years of data for this study, 26 pack cores were constructed, with a total of 62 coyotes included in the study (Figures 3.21-3.26). Counting each relationship between 2 pack members once, 117 relationships between pack members were investigated (Tables 3.2 and 3.3). Overall, there were 7 mated pair relationships, 8 unrelated relationships, 25 second-order relationships, and 77 first-order relationships. Two of the unrelated relationships were between suspected mated pairs (BW27 and BW50, MM51 and MM53), since the coyotes were unrelated adults of opposite sex that exhibited high overlap. Since no offspring of these potential mated pairs were sampled, their mated pair status could not be verified.

Pack Histories. - For many of the coyotes in this study, it was not possible to determine the nature of first-order or second-order relationships exhibited by pack members. Distinctions between relationships, such as those between parent-offspring and

full siblings, can be determined when pups are captured in dens, because the age and origin of the animal is known. Parentage analysis helped to determine pedigrees of some older animals. However, without information on the origin or birth-year of a coyote, genealogy may be impossible to discern. Therefore, for the following histories of packs, I reported pedigrees when possible and always provided relatedness values (Figures 3.21-3.26).

In the following pack histories, it is important to note that it is highly unlikely that any pack as described was the complete pack. Indeed, technicians who spotlighted the coyotes often saw uncollared coyotes acting socially towards collared animals. In addition, I have purposefully excluded animals that were sampled only genetically or that were radiocollared but not genetically sampled. I could not include coyotes for which either type of data was missing, with the exception of pups. I included young-of-the-year, which were often sampled genetically but not radiocollared, because pack membership and origin were known.

Max McGraw Wildlife Foundation West Pack - In 2000, coyotes MM6, MM11, MM22, and MM23 were present in this pack. The relatedness value for the pack members represented values expected for first- and second-order relationships. Coyotes MM11, MM22, and MM23 were full siblings, which were verified by exclusion tests. Coyote MM6 was a male subadult and related to MM11, MM22, and MM23 on a second-order level.

In 2001, the membership of this pack changed due to mortalities and dispersal events. Subadult MM23 dispersed early in 2001, and MM6 died in August. Male subadult MM37 was captured in May 2001 and exhibited a 95.19% overlap with the pack

core, but he dispersed 1 month later. Subadult MM37 was related to MM11, MM22, and MM23 at a first-order level, and his age indicated that he was most likely a full sibling with these 3 coyotes. In comparison to the relatedness values exhibited by his potential siblings, MM37 was related to MM6 at a second-order level (0.13).

In early 2002, subadult MM22 dispersed around the same time that the female subadult MM11 was found dead due to unknown causes. In April, 2 coyotes were captured that exhibited fidelity to this same territory. Adult female MM51 exhibited physical condition that she was breeding, and MM53 was a subadult male. Although MM51 and MM53 shared a high percentage of overlap (76.0%), they were unrelated ($R = -0.97$). This could be indicative of mated pair status, although there are no sampled offspring from this pair. Also, I checked the relatedness values of the previous 2 year's pack members with MM51 and MM53, and although every previous member shared relatedness with MM51 at values from 0.30-0.40, most other pack members were not related to MM53. The only exception was MM6, who shared a relatedness value of 0.18 with MM53. MM51 was hit by a car in July.

In 2003, MM53 remained in this area but did not overlap with any radiocollared animals. In early 2004, a female adult, MM113, was captured. MM113 and MM53 shared a negative relatedness value (-0.17) but a high overlap percentage of their home ranges (71.95%). In August, 3 pups were captured; MM154, MM156 and MM157. All 3 of these pups were full siblings and parentage analysis revealed them as the offspring of MM53 and MM113. A female yearling was found as roadkill in November 2004, which was revealed through parentage analysis to have been a pup from this litter. In mid-June of 2004, the collar of MM53 stopped working, and no further locations were obtained for

him until his body was found as a roadkill in January 2006 in an area northwest of the pack's territory. In July, MM113 was hit by a car. MM154 was also hit by a car in October, close to home. MM156, reportedly mangy, was shot by a home-owner in December. MM157 dispersed to a location approximately 1.6 km west of her origin, and continues to be tracked into the present.

Max McGraw Wildlife Foundation East – 2001 was the first year that coyotes exhibited fidelity and overlap to this area. Adults included female MM38 and male MM42, while 3 pups made up the rest of the known pack: female MM39, male MM40, and female MM41. The relatedness values for these pack members ranged from 0.26 to 0.77, indicating high levels of relatedness. Indeed, parentage analysis revealed that MM39, MM40 and MM41 were offspring of MM38 and MM42. What is most interesting about this pack is the second-order relatedness value shared between the mated pair ($R = 0.26$). The fact that the parents share so many similar alleles could explain why the full sibling offspring share relatively high relatedness values as well ($R = 0.59, 0.52, 0.53$). In 2001, MM41 dispersed.

In 2002, the structure of this pack changed dramatically. Alpha female MM42 was found dead in early December, possibly killed by exposure due to mange. Subadults MM39 and MM40 dispersed. MM40 was found as roadkill near Racine, Wisconsin, in October, indicating that he traveled at least 123.9 km from his origin. MM38, the alpha male, left the territory early December.

In late March of 2003, 2 female adults, MM92 and MM93, were trapped in the area and exhibited fidelity to approximately the same territory as the pack in 2002. Later that year, male subadult MM100 was captured. All 3 of these coyotes exhibited high

percentage overlap with the pack core (43.19-79.76%). Through parentage analysis, MM92 was revealed to be the offspring of MM38 and MM42, the alpha pair in the territory in 2002. MM92 and MM93 shared a high amount of overlap (82.82%); however, their relatedness value suggested that they were second-order relatives ($R = 0.18$), and therefore probably not a mated pair. Parentage analysis revealed that MM92 was likely the mother of MM100.

In January 2004, MM93 was euthanized by Cook County Animal Control at a residence in Chicago suburb Barrington Hills (approximately 8 km from the territory). Two pack members from the previous year, adult female MM92 and subadult male MM100, remained. Subadult female MM114 was captured in 2004 and exhibited pack membership. The relatedness values for these 3 pack members in 2004 ranged from 0.04 to 0.79. MM92 may have dispersed in May 2004; the last known location for her was 3.2 km east of the pack's territory. Near the end of 2004, MM114 was shot by a hunter in an area proximate to the pack core. No further locations were gathered on MM100. Since MM100 was one of the few animals that was fitted with a satellite collar, the most plausible cause for losing track of this animal was that the battery on the collar died.

Poplar Creek Forest Preserve Pack – In 2000, 2 adult coyotes of the opposite sex were captured. Adult female PC4 and adult male PC10 exhibited a home range overlap of 93.04%, and were related at the tail end of the second-order range ($R = -0.04$). In November of the same year, sub-adult PC21 was captured and exhibited strong overlap with the home ranges of PC4 and PC10. Parentage analysis revealed PC21 as the son of PC4 and PC10.

In 2001, PC4, PC10 and PC21 continued to exhibit fidelity to the pack core. Another male subadult, PC18, exhibited overlap with the pack core, and was revealed to be another son of PC4 and PC10. Male subadult PC43 was captured in November and exhibited overlap with the pack core, but was less related than any other member of the pack (excepting the low relatedness value shared between the mated pair; see Figure 3.23). He was possibly a nephew or grandson of PC4, and seemed to be related to PC10 and PC18 in a second-order manner. PC18 was hit by a car in May 2001 on a road that formed the perimeter of Poplar Creek Forest Preserve.

In 2002, PC4 and PC10 remained the alpha pair and PC21 remained a pack member. Five pups (MM59, MM60, MM61, MM62, MM63) were collected from a den, 2 of which (MM59 and MM63) were offspring of PC4 and PC10. The parentage of the other 3 was undetermined. PC43 began to exhibit wider movements, which are indicative of pre-dispersal exploratory movements (Harrison et al. 1991). Due to these wide-ranging movements, he did not share overlap with the pack core at a level that could have included him in the pack analysis. Another subadult male, PC44, was captured late in 2001 and overlapped the pack core by 30.81%, but was exhibiting similar pre-dispersal movements. Female subadult PC74 was captured in September 2002 and exhibited a 25.4% overlap with the pack core. However, she was also exhibiting wide-ranging movements and disappeared approximately 1 month after her capture. Alpha male PC10 died in Poplar Creek Forest Preserve in September 2002, cause of death unknown. Alpha female PC4 went missing in January of 2003. Subadult PC44 was found dead in November 2002, in Poplar Creek Forest Preserve, cause of death unknown.

No coyotes were exhibiting overlap in a pack-type manner in Poplar Creek Forest Preserve in 2003, but in 2004, movement data indicated that 4 animals may have formed a new pack. Adult male PC21, the offspring of PC4 and PC10, had remained in the area since birth. Seven coyotes were captured in May 2004, which included female adult PC125 and 6 pups (PC127, PC128, PC130, PC131, PC132, PC133). Only PC127 and PC131 were radiocollared with expandable foam-lined collars. Parentage analysis revealed that PC21 and PC125 were the parents of these pups. All 4 radiocollared pack members survived into the next year, and remained on the territory.

In 2005, the same 4 pack members continued to display high overlap values with the pack core (67.9% - 89.7%). A den was located and a litter of 5 pups (PC210, PC211, PC212, PC213, PC214) was genetically sampled and determined to be offspring of PC21 and PC125. In late 2005, female subadult PC234 was captured in the area. Movement data in 2006 showed that she shared 54.7% overlap with the pack core, and parentage analysis revealed that she was the daughter of PC21 and PC125. In May of 2006, 7 pups were found in a den (PC253, PC254, PC255, PC256, PC257, PC258, PC259) that proved to be offspring of PC21 and PC125. At the end of 2006, all 5 radiocollared pack members remained in the area and continued to exhibit high overlap with the pack core.

Highland Woods Golf Course Pack – In 2002, 3 coyotes exhibited movements that strongly indicated pack behavior. PC49 was an adult female, PC56 was a male pup and PC57 was a female pup. Parentage analysis revealed that PC49 was the mother of these 2 pups, as well as a third, PC58, that was captured but not radiocollared. The study of this pack was cut short, as PC49 was killed by an automobile in July, the same fate

suffered by her son, PC56, in December. PC57 was found dead in September of unknown causes.

In 2004, 3 coyotes began exhibiting pack-like behavior in the same area. Male adult PC88 was captured in March of 2003, female adult PC111 was captured in January of 2004, and male adult PC112 was caught the same day as PC111. Parentage analysis revealed that PC88 and PC111 were the parents of PC112. The parents shared only half of their respective home ranges with the pack core, whereas the home range of PC112 was essentially the core. In May 2004, a litter of 7 pups (HW136, HW138, HE139, HW140, HW141, HW142, HW143) was genetically sampled and determined to be offspring of HW88 and HW111. PC88 was killed by an automobile in July, and PC112 slipped his collar in late February. PC111 remained in Highland Woods and continued to be tracked through 2006. She shared her home range with 2 other coyotes in a pack-like manner in 2005; however, no genetic samples were obtained from these coyotes, so I was not able to analyze their relationships with her. In May 2005, a litter of 5 pups (HW197, HW198, HW200, HW202, HW203) was genetically sampled and determined to be the offspring of HW111 and an unknown male.

Busse Woods – There were no animals displaying pack-like overlap in this area until 2002. Male adult BW32 had been in the area at least since 2001. His mate was never caught, but 11 of his offspring were. In May 2002, a litter of 9 pups (BW64, BW65, BW66, BW67, BW68, BW69, BW70, BW71, BW72) were genetically sampled and determined to be the offspring of BW32 and an unknown female. In October 2002, female yearling BW67 and male yearling BW76 were recaptured and radiocollared. In November, male subadult BW80 was also caught. The relatedness values for these pack

members ranged from 0.18 to 0.63, even though parentage analysis confirmed that BW32 was the father for all, and exclusion methods confirmed that the pups were full siblings.

In February 2003, BW32 was killed by an automobile proximate to the territory. Male adult BW27 and female adult BW50 moved into the territory. Although BW67, BW76, and BW80 remained in the territory and continued to exhibit high overlap percentage with the core area, BW27 and BW50 exhibited the highest overlap with the core (76.29% and 73.50%, respectively). BW27 and BW50 had been roaming the area for at least 2 years previous to 2003; it is plausible that the death of the alpha male enabled them to establish the territory for their own. BW27 and BW50 exhibited very high overlap (88.30%) and a very low relatedness value ($R = -0.28$), which were strong indicators that they were a mated pair. BW27 was related to the remaining pack members, BW67, BW76, and BW80 ($R = 0.15, 0.34, \text{ and } 0.28$, respectively). BW27 was also related to BW32 at a second-order level ($R = 0.17$). BW27 was last located in the area in late October 2003. BW67 was killed by an automobile in August, 2003, close to home. BW80 was last located in his home range in June, which could either be due to a dead battery or a dispersal event.

In 2004, BW50 exhibited high home range overlap percentage (82.35%) with a different male adult, BW120, which was captured in April. These 2 coyotes were unrelated ($R = -0.09$), which means that they may have been a mated pair. Unfortunately, there weren't many locations gathered on these 2 possible mates, due to the fact that BW50 went off the air in late June, probably due to a dead battery. BW76 remained in the area until early May 2004, when she either made a dispersal event, which would be likely, considering her subadult status, or her radio-transmitter battery died.

In 2005, this area was subsumed by an entirely different group. Two adults, female BW178 and male BW182, and 2 female subadults, BW179 and BW183, were captured between February and March of 2005. The relatedness values of these pack members displayed high rates of relatedness ($R = 0.40 - 0.61$). All 4 displayed overlap percentages with the pack core that exceeded 50%. Parentage analysis revealed that BW182 was the father of BW178, BW179, and BW183. BW182 was also the father of a litter of 10 pups that was captured in the pack's territory (BW215, BW216, BW217, BW218, BW219, BW220, BW221, BW223, BW224, BW225) which were not collared at capture. In July, BW182 was found dead by technicians, cause of death unknown. In October, BW183 was killed by an automobile approximately 8 km from her home range.

In 2006, BW178 continued to exhibit high overlap percentage with the core area, which she shared with at least 3 subadults: BW220, BW223 and BW248. Two of these subadults, BW220 and BW223, were previously captured as pups in the den in 2005, and were identified by implanted microchips. The third subadult, BW248, was not closely related to BW178, BW220, or BW223 ($R = -0.04$ to $R = 0.02$), and parentage analysis revealed that BW182 was not the father of BW248. All 4 coyotes survived through the year.

WGN Station Pack - This pack established territory around the broadcasting tower for the radio station WGN, which bordered the western edge of the Ned Brown Forest Preserve (Busse Woods). In 2000, 2 adults were radiocollared in this area, female WGN13 and male WGN14. Male pup WGN12 was captured in August. Parentage analysis revealed that WGN12 was the offspring of WGN13 and WGN14. WGN12 died

due to unknown causes in September. In April 2001, WGN13 disappeared, and WGN14 relocated not long after.

In 2002, there were no animals exhibiting pack behavior in the WGN area that could be detected by movement data. In 2003, female adult WGN1 settled in this territory. Male adult WGN82 was exhibiting high overlap (74.51%) with WGN1. The shared relatedness value between WGN1 and WGN82 ($R = 0.62$) was high and parentage analysis revealed that WGN1 was the mother of WGN82. Early in 2003, another male adult, WGN85, and a male pup, WGN86, were also captured in the area, and together with WGN1 and WGN82 shared a pack core area. Both of these coyotes were also offspring of WGN1. Within the year, WGN82 dispersed to Franklin, Wisconsin, where his signal was detected by an airplane survey. Franklin is at least 104 km from WGN82's origin. Another pack member, WGN86, went missing in April. This was likely due to a dispersal event, since the battery in the collar was only 4 months old at that time, and would likely not have ran out of power.

In 2004, male adult WGN115 was captured. WGN115 shared 88.50% overlap with WGN1 and they shared a relatedness value of 0.06. Using parentage analysis, I found that WGN1 and WGN115 were the parents of WGN82, WGN85, and WGN86. This strongly suggests that WGN115 was sharing the territory before he was trapped and sampled. In May 2004, 5 pups were sampled (WGN145, WGN147, WGN148, WGN150, WGN151) that were the offspring of WGN1 and WGN115. Female pup WGN150 was recaptured a month later and radiocollared. WGN150 remained in the pack throughout the year, but dispersed in early 2005. Her body was found in June in a park approximately 24 km southeast of her origin, cause of death unknown.

In 2005, the pack core was maintained by WGN1 and WGN115, and 3 pups were genetically sampled (WGN222, WGN226, WGN227) which were revealed to be offspring of WGN1 and WGN115. In 2006, 4 pups were captured (WGN263, WGN264, WGN265, WGN266) that were offspring of WGN1 and WGN115 and 2 of these pups were radiocollared, WGN265 and WGN266. Throughout the rest of the study, all 4 animals displayed fidelity to the pack core area.

Discussion

Based on the results of this study, I fail to reject H_1 , as most coyote packs consisted of closely-related family members. Out of 117 relationships between pack members, I found 8 cases of seemingly unrelated pack members. Also, I fail to reject H_2 , as the relatedness values between 7 mated pairs were generally low enough as to be considered unrelated, with one exception (MM38 and MM42). The general investigation into the relationship between overlap and relatedness revealed a weak correlation, which was strengthened upon the removal of mated pairs from the sample. However, this correlation weakened as the values for overlap increased, which was an unexpected result.

The analysis of pack structure revealed relationships among many pack members that extend beyond the first-order relationships that were expected for family groups. There were 25 second-order relationships out of the total 117 relationships between pack members, which results in an average of $21.4\% \pm 2.36\%$. In some instances, the coyote was less related to some members but highly related to other members. It is possible that

the coyote was less related to the sampled coyotes but more related to another, unsampled coyote in the pack. It is also possible that the second-order relationships are a result of grandparents and grand-offspring present in the same pack, since double-litters, which have been recorded for this population (Chapter 2) are likely joint reproductive events between a mother and her daughter (Camenzind 1978).

I will elaborate here on one example of the differing types of relationships between pack members. In 2002, 2 adult coyotes that displayed the overlap and relatedness values that are within the range that is typically associated with mated pairs were captured. The female (MM51) and the male (MM53) were related in a starkly different manner to the all the pack members that had been sampled up to that year. The female was related closely to every other pack member with relatedness values from 0.30-0.40. In contrast, the male was negatively related to every other pack member except MM6, with which he shared relatedness at a second-order level ($R=0.18$). A plausible scenario is that MM51 may have been the mother to the pups in 2000 (MM6 and MM37), and accepted MM53 as a replacement mate for a mate that had died. The fact that MM6 was related to MM53 when no other animal in the pack exhibited relatedness to MM53 is a very curious one, but unfortunately this cannot be resolved without a concentrated observational study of pack member interactions or without complete knowledge of the origins of each pack member.

Another interesting finding of this study regards the relatedness of mated pairs, which is generally very low for this study population (-0.14 to 0.06). One exception is the mated pair from the eastern Max MacGraw pack of 2001, which shared a relatedness value of 0.26. There is no instance in the literature of a mated pair that is related at this

level. Wolves have been known to breed with close relatives, but only in captivity when no other mates are available (Laikre and Ryman 1991). In the wild, wolves breed with unrelated mates, thereby successfully avoiding inbreeding (Smith 1997). In this study, the trend revealed by F statistics and the average relatedness of mated pairs (0.00 ± 0.14) demonstrated that the mechanisms of dispersal and mate selection cooperate successfully to decrease the risk of inbreeding for this urban population.

Delayed dispersal of subadult canids is a subject that has received much attention in the literature (Andelt 1985; Gese et al. 1996; Girman et al. 1997; Harrison 1992; Way 2003). Subadults may remain in their parents' territory to increase their reproductive ability by delaying dispersal and by gaining parenting and defensive experience (Andelt 1985). Another explanation for why subadults delay dispersal is the possibility of inheriting the territory upon the death of one or both of its parents. This would provide the subadult with a space to breed, without the risks associated with dispersal and establishing territory in an unfamiliar place (Andelt 1985; Harrison 1992). There are 2 clear examples of this purported benefit in this study. Female MM92 was a subadult in the eastern Max MacGraw pack in 2002 when the alpha female died and her mate dispersed. MM92 remained in the territory and reproduced in 2003. Another example of territory inheritance was exhibited by the Poplar Creek pack. The mated pair, PC4 and PC10, raised male subadult PC21. In 2001 and 2002, PC4 and PC10 had other offspring that were sampled, and these offspring dispersed, while PC21 remained. Unknown causes killed PC10 in 2002 and PC4 dispersed in early 2003. However, PC21 remained in the territory, and in 2004 6 pups were captured that were the offspring of PC21. Territory inheritance was also witnessed 3 times among coyotes of Yellowstone by Gese

et al. (1996), and is considered to be a major factor in successful group living formations (Lindström 1986).

Adult coyotes that survive the death of a mate exhibit 2 interesting behaviors, 1 of which is similar to behavior in jackals (*Canis aureus* and *C. mesomelus*; Moehlman 1987). Moehlman (1987) found that jackals often lose their territory when they lose their mate, due to the inability of an unmated jackal to defend its territory from encroaching jackals that seek to inhabit the territory. In this study, 4 mates died and the responses differed among the 4 surviving mates. In 2 cases, the remaining mate stayed in the territory (MM53 and PC111). In the other 2 cases, the remaining mate dispersed from the territory (MM38 and PC4). In this sample, there appears to be no difference in the sex of the surviving mate across the 4 cases; indeed, 1 surviving mate that stayed was female and the other was male, and 1 surviving mate that dispersed was female and the other male. There may be circumstances that occurred beyond the auspices of this study, such as the presence and persistence of invading coyotes.

An important motivating factor that may play a role in deciding whether a surviving mate stays or leaves is the time of year in which the mortality occurs. In the 2 cases wherein the surviving mate stayed, the mortality occurred in July during the pup-raising season (Bekoff 1977). In contrast, in the 2 cases wherein the surviving coyote left, the mortality of the mate occurred in September and December. These 2 months are later in the year and the pups are developed to the point that they do not rely on the parents for survival (Bekoff 1978; Harrison 1992). In addition, the deaths of the mates occurred well in advance of the next breeding season, which starts in late January (Bekoff 1977). In the instances wherein the surviving parent is in the process of raising the pups,

there is a stronger incentive to protect the home territory. Subadults may be especially helpful in a situation like this, since they can help to raise the pups as well as to defend the territory (Camenzind 1978).

In regards to the overlap analysis, there is no clear explanation as to why the relationship between home range sharing and relatedness was weak. After removing confirmed mated pairs, there remained 2 suspected mated pairs in the sample, but that accounted for only 2 data points. The other possible explanation is that there are coyotes that share small percentages of overlap but are highly related, which could occur if 2 neighboring coyotes were first-order relatives that live close to each other due to short dispersal distances. However, observed dispersal distances in the literature are sufficiently large that the 2 coyotes would no longer be sharing overlap (Bowen 1982; Harrison 1992). Surveying the relatedness values across the pack members, I believe that unrelated coyotes are sharing space because they share relatedness with a common individual. If true, this would be similar to the findings of Ralls et al. (2001) and Girman et al. (1997), that found individuals that were offspring of one breeding adult but not of its mate.

In conclusion, this study generally supports the findings of previous research, using methods that were heretofore not employed simultaneously on coyote packs. The first-order relatedness of pack members correlates behavioral studies that have shown that grown offspring participate in the rearing, feeding, and protection of young as well as defense of the territory. Such cooperative behavior is congruent with the inclusive fitness theory (Hamilton 1964). Also, the unrelated status of most of the mated pairs confirms that coyotes in this population are successfully avoiding inbreeding. This is similar to the

findings of Smith et al. (1997), that found that wolf mated pairs were unrelated. Further studies on the population structure are recommended to determine if there are boundaries to gene flow within the urban matrix, which may explain the high relatedness that was discovered between one mated pair in this study.

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Tables and Figures

Year	Pups	Subadults	Adults	Mated pairs
2000	2	2	6	2
2001	6	13	12	2
2002	6	13	13	1
2003	0	7	10	0
2004	7	6	14	3
2005	5	6	13	2
2006	2	8	12	1

Table 3.1 – Radiocollared coyotes, classified by age cohort and mated pair status, that were included in the overlap study in the Greater Chicago Metropolitan Area.

Year	<u>Sites</u>											
	MM(west)		MM(east)		PC		HW		BW		WGN	
	low	high	low	high	low	high	low	high	low	high	low	high
2000	0.13	0.57	---	---	0.30	0.42	---	---	---	---	0.43	0.52
2001	0.13	0.68	0.52	0.59	-0.04	0.44	---	---	---	---	---	---
2002	-0.16	0.35	0.26	0.63	0.07	0.56	0.42	0.65	0.18	0.63	---	---
2003	---	---	0.13	0.79	---	---	---	---	-0.27	0.63	-0.05	0.62
2004	-0.40	0.38	0.04	0.79	0.46	0.57	0.42	0.58	-0.09	-0.09	0.38	0.70
2005	---	---	---	---	0.46	0.57	---	---	0.40	0.61	0.38	0.70
2006	---	---	---	---	0.21	0.59	---	---	-0.04	0.45	0.32	0.53

Table 3.2 – Summary of Grafen’s relatedness coefficient values shared between pack members, excluding values shared between confirmed mated pairs, sorted by year and site. Low and high qualifiers indicate the lowest and highest relatedness values, respectively, shared between pack members. Years with no data (indicated by ---) indicate years in which no radiocollared coyotes were displaying sufficient overlap to be considered pack members.

Site	Pack years	Total relationships	Mated pairs	First-order	Second-order	Unrelated
MM(W)	4	24	1	17	4	2
MM(E)	4	15	1	11	3	0
PC	6	27	2	14	11	0
HW	2	6	1	5	0	0
BW	5	28	0	16	6	6
WGN	5	17	2	14	1	0
TOTAL	26	117	7	77	25	8

Table 3.3 – All unique relationships between pack members, qualified by Grafen’s relatedness value into first- or second-order or unrelated status. Mated pairs were determined based on sampled offspring, and were not included in other categories.

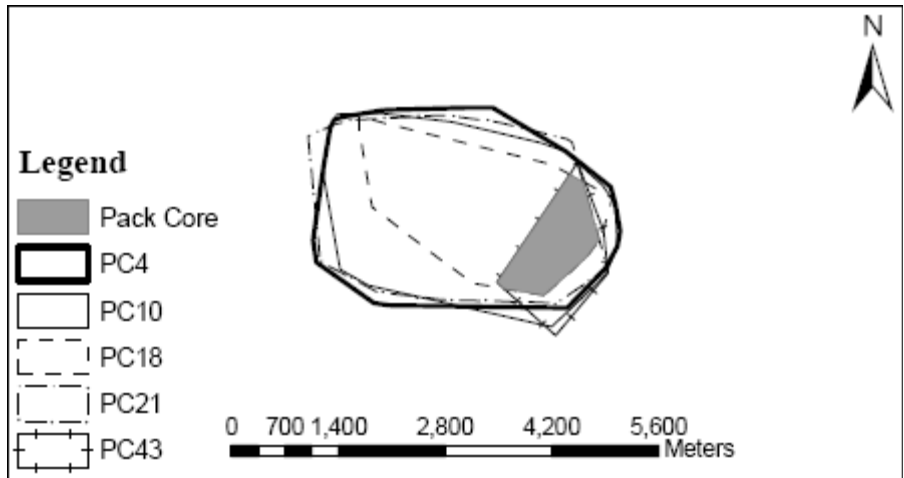


Figure 3.1 – Pack core (shaded in grey) formed by the overlapping 95% MCP home ranges of 5 resident coyotes in the Poplar Creek Forest Preserve in 2001. Home ranges of adults are represented by solid lines, subadults by dotted lines, and the pup is represented by a hatched line.

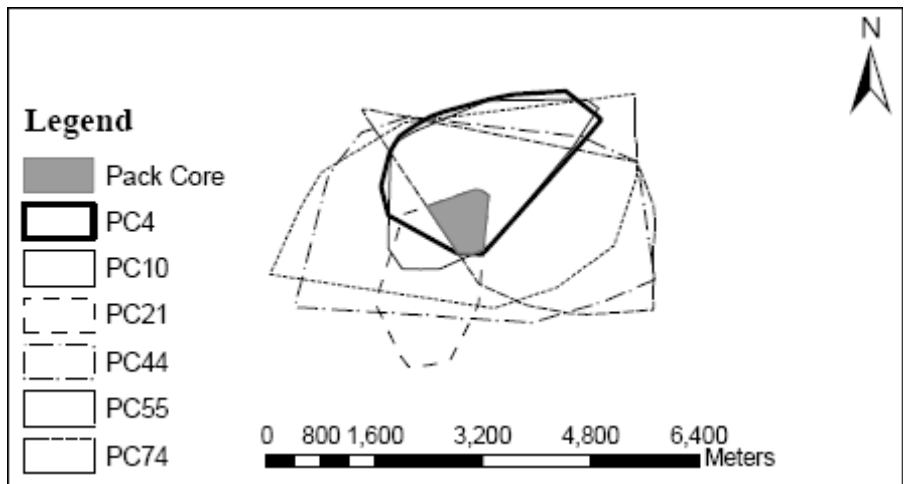


Figure 3.2 – Pack core (shaded in grey) formed by the overlapping 95% MCP home ranges of 6 resident coyotes in the Poplar Creek Forest Preserve in 2002. Home ranges of adults are represented by solid lines and the home ranges of subadults by dotted lines.

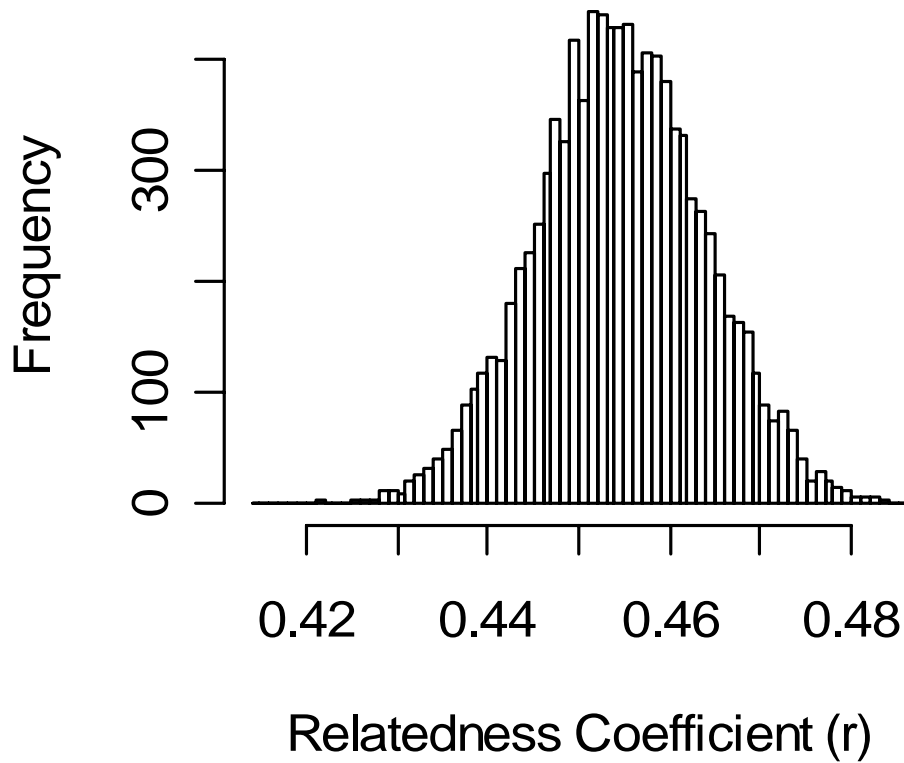


Figure 3.3 – Histogram of 10,000 bootstrap results using Grafen’s relatedness coefficient between known parents and offspring in order to calibrate first-order relatedness values for this study population (average = 0.46 ± 0.009).

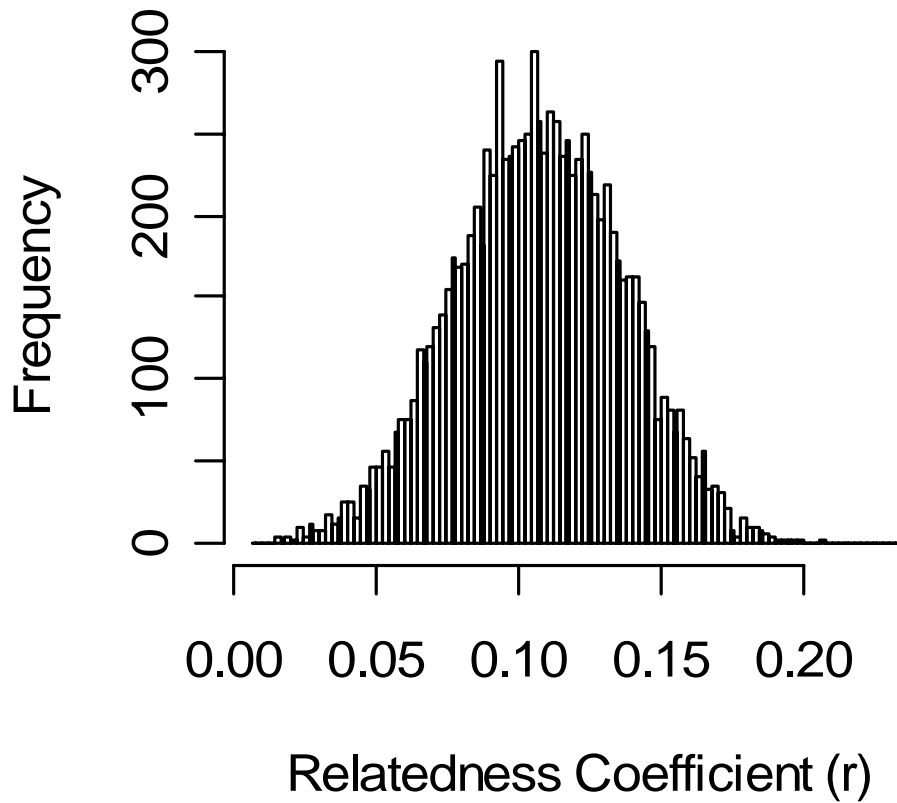


Figure 3.4 – Histogram of 10,000 bootstrap results using Grafen’s relatedness coefficient between known grandparents and grandoffspring in order to calibrate second-order relatedness values for this study population (average = 0.11 ± 0.03).

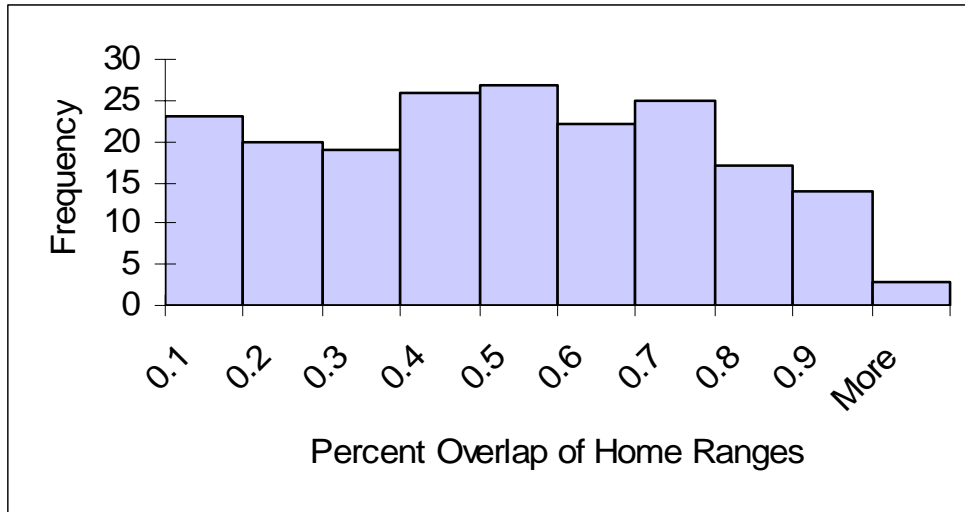


Figure 3.5 – Histogram illustrating classes of overlap percentages (average = 0.44 ± 0.25).

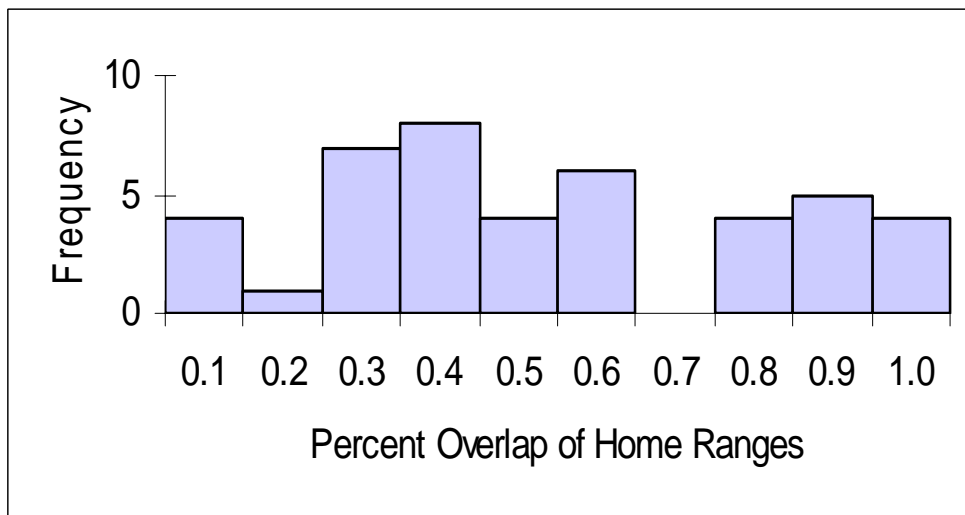


Figure 3.6 – Classes of home range sharing between adults, 2000-2006 (average = 0.51 ± 0.30).

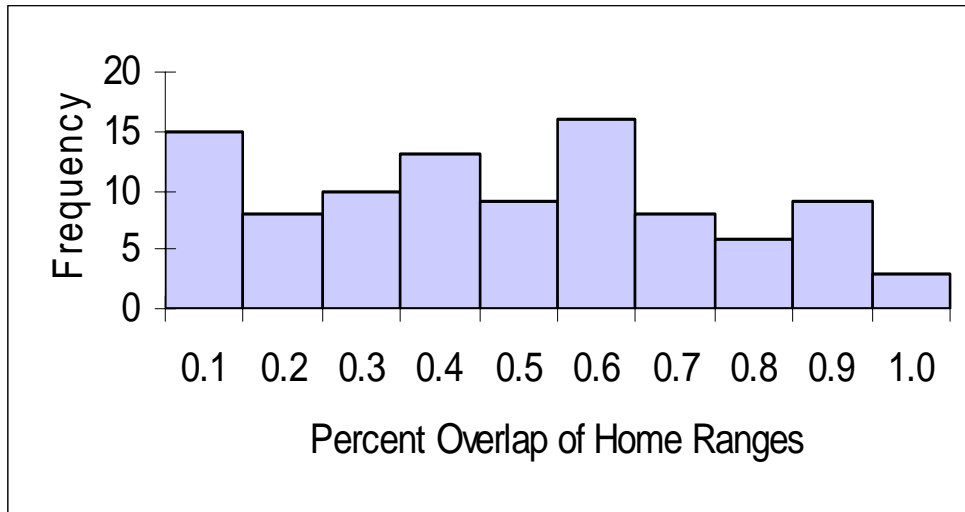


Figure 3.7 – Classes of home range sharing between adults and subadults, 2000-2006 (average = 0.43 ± 0.27).

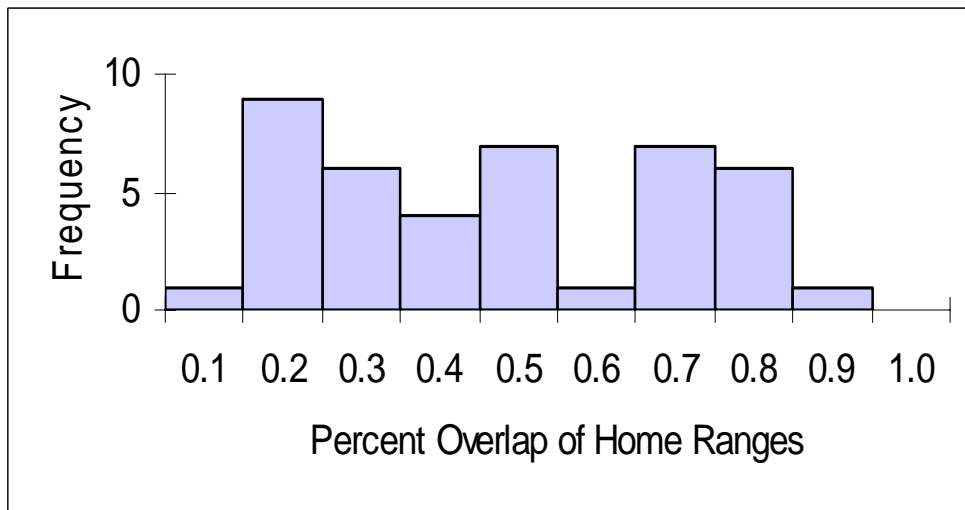


Figure 3.8 – Classes of home range sharing between adults and pups, 2000-2006 (average = 0.42 ± 0.24).

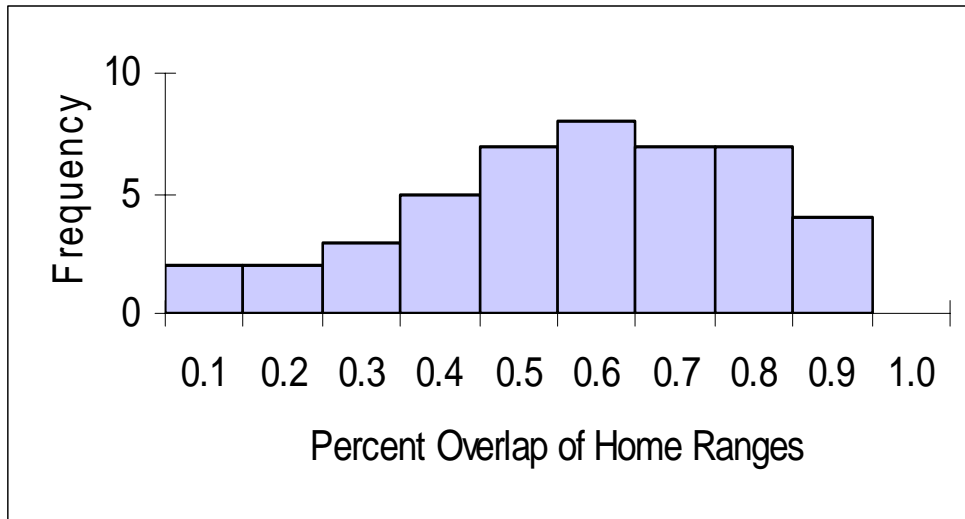


Figure 3.9 – Classes of home range sharing between subadults and subadults, 2000-2006
(average = 0.51 ± 0.23).

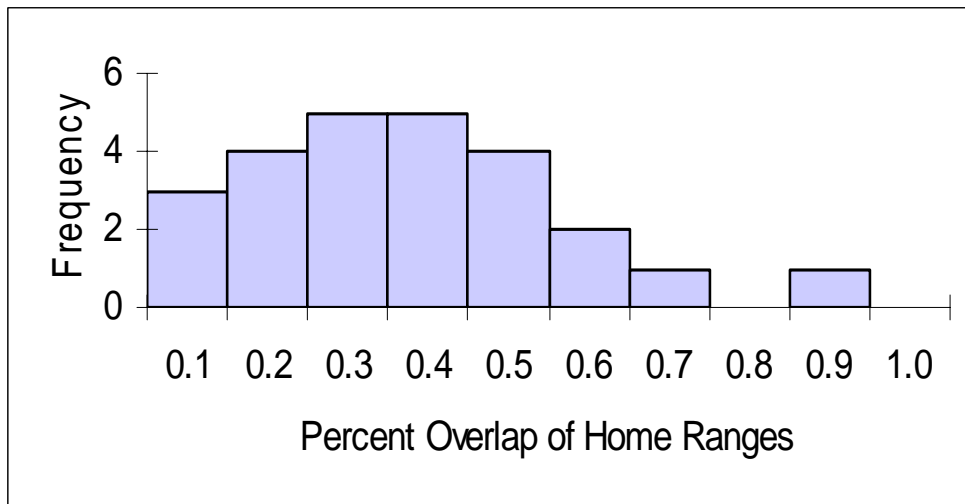


Figure 3.10 – Classes of home range sharing between subadults and pups, 2000-2006
(average = 0.33 ± 0.20).

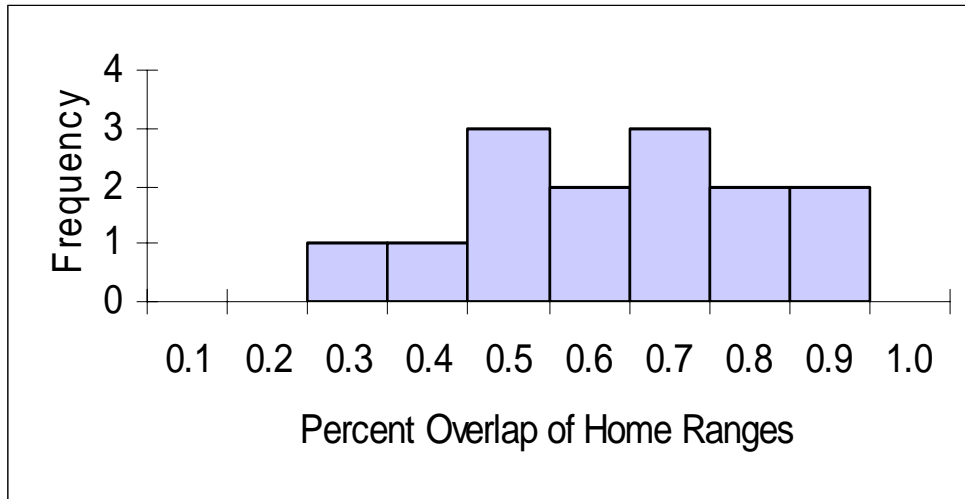


Figure 3.11 – Classes of home range sharing between pups and pups, 2000-2006 (average = 0.56 ± 0.20).

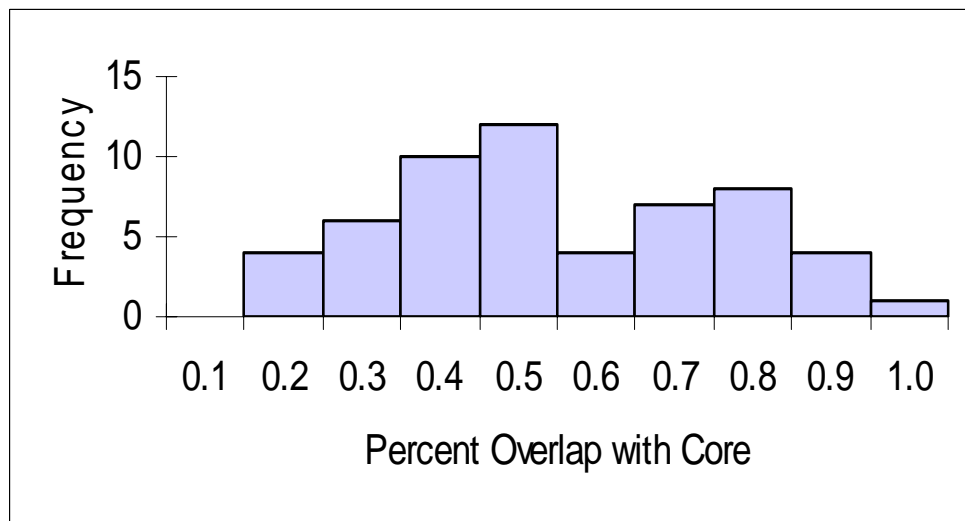


Figure 3.12 – Home range overlap with the packs' cores exhibited by adults, 2000-2006 (average = 0.50 ± 0.22).

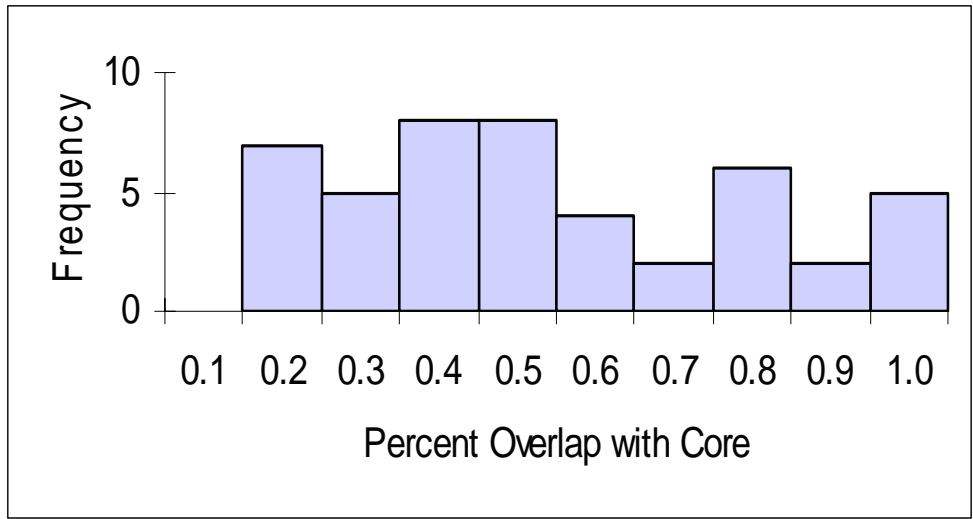


Figure 3.13 – Home range overlap with the packs’ cores exhibited by subadults, 2000-2006 (average = 0.49 ± 0.26).

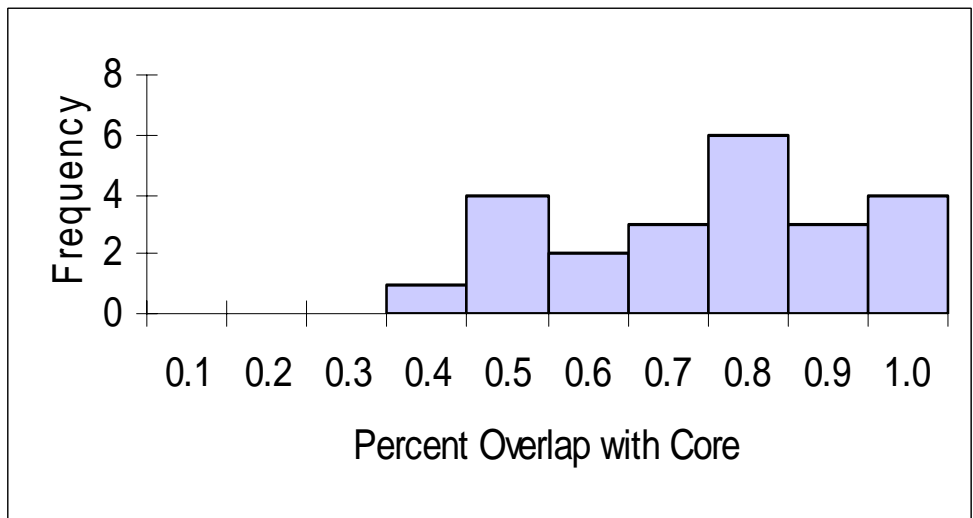


Figure 3.14 – Home range overlap with the packs’ cores exhibited by pups, 2000-2006 (average = 0.68 ± 0.22).

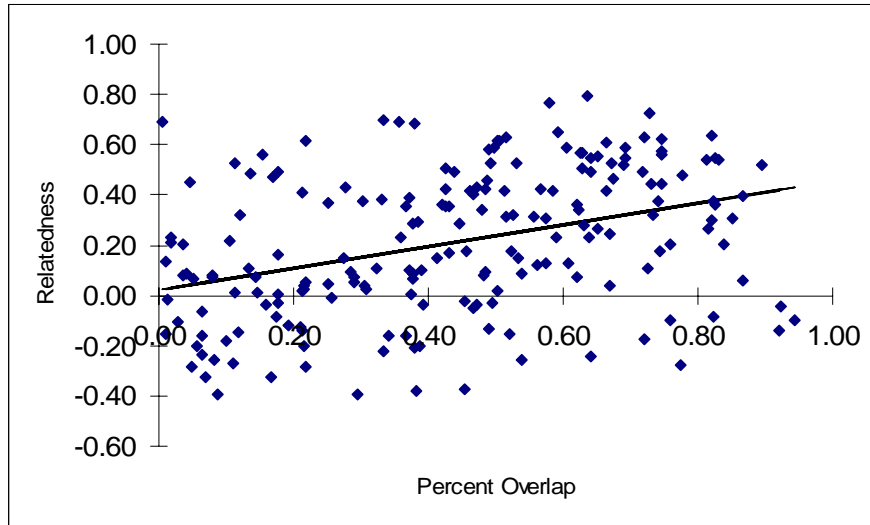


Figure 3.15 – Total population values of Grafen’s coefficient of relatedness and home range overlap percentages, 2000-2006 (F value = 31.51, $R^2 = 0.14$, SE = 0.27, $p < 0.000$).

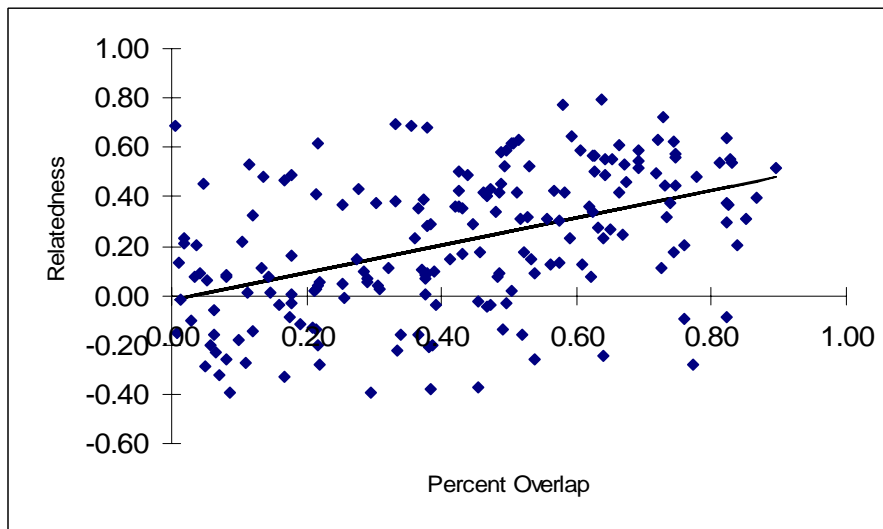


Figure 3.16 – Excluding mated pair values of Grafen’s coefficient of relatedness, the values for the remaining population, 2000-2006 (F value = 50.60, $R^2 = 0.21$, SE = 0.26, $p < 0.000$).

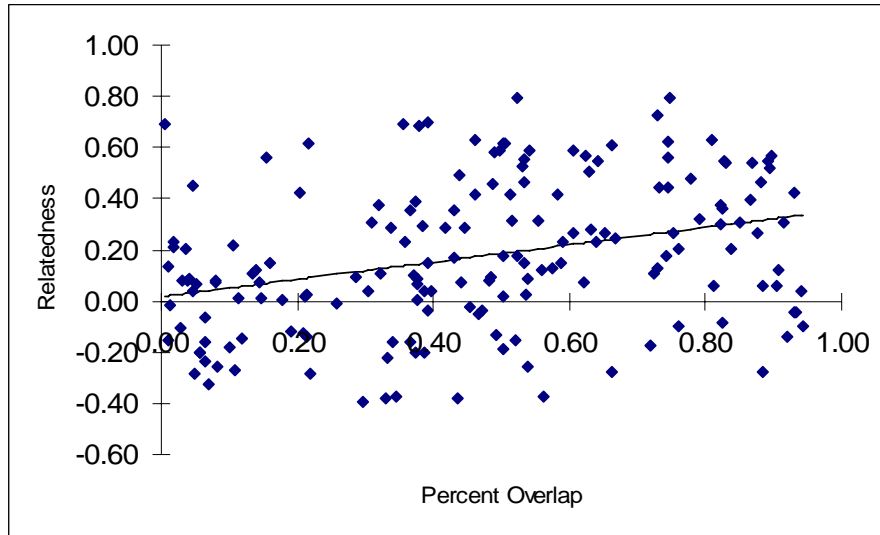


Figure 3.17 – Excluding relatedness values shared between young-of-the-year pups with all other coyotes, the values for the remaining population, 2000-2006 (F value = 19.76, $R^2 = 0.10$, SE = 0.27, $p < 0.000$).

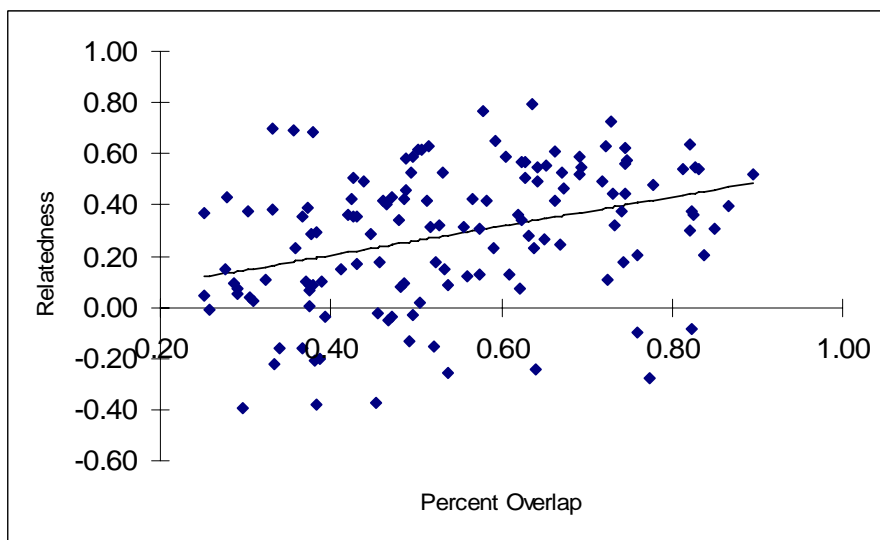


Figure 3.18 – Excluding mated pairs and all coyotes that share less than 25% overlap, the values for the remaining population, 2000-2006 (F value = 18.78, $R^2 = 0.12$, SE = 0.26, $p < 0.000$).

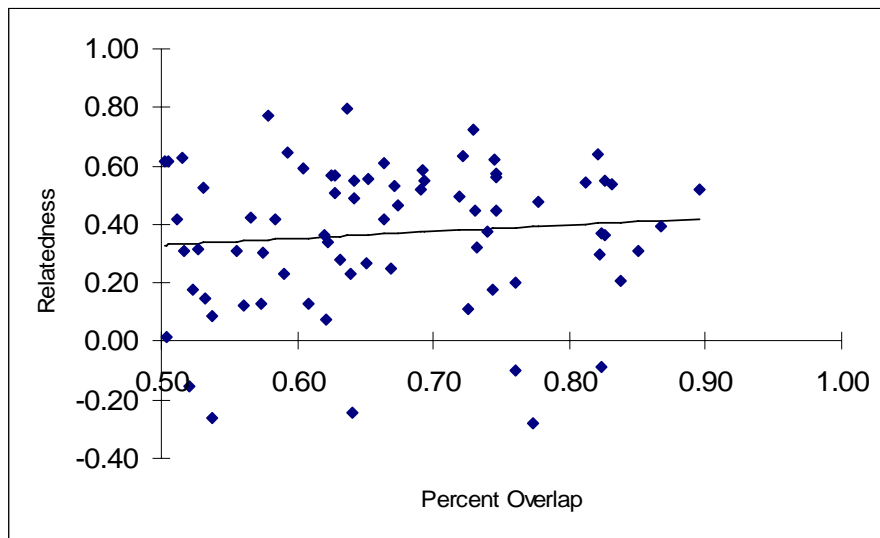


Figure 3.19 - Excluding mated pairs and all coyotes that share less than 50% overlap, the values for the remaining population, 2000-2006 (F value = 0.74, $R^2 = 0.01$, SE = 0.24, $p < 0.000$).

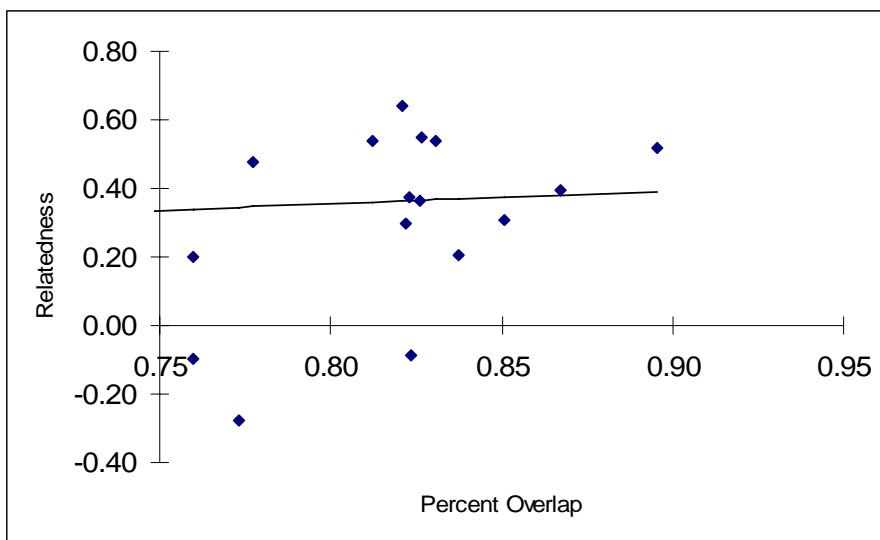


Figure 3.20 - Excluding mated pairs and all coyotes that share less than 75% overlap, the values for the remaining population, 2000-2006 (F value = 0.08, $R^2 = 0.004$, SE = 0.26, $p = 0.783$).

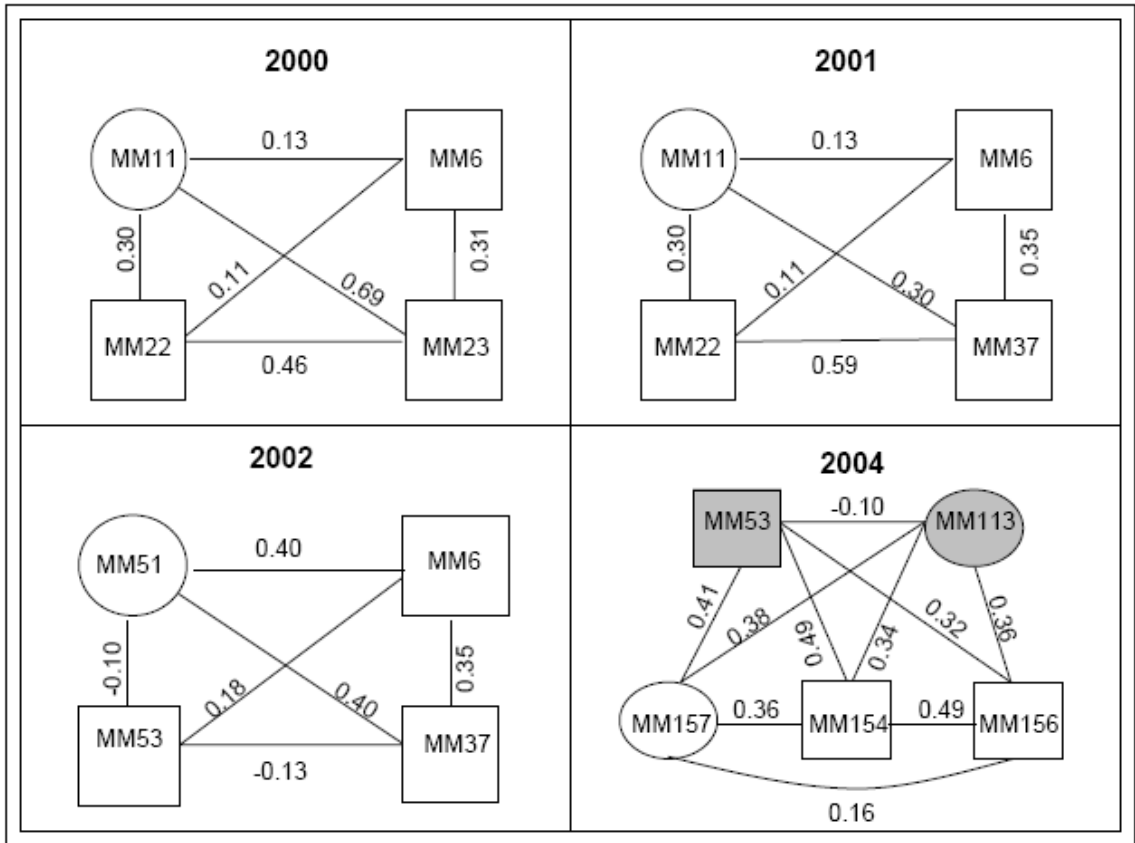


Figure 3.21 – Grafen’s relatedness coefficient between pack members in the western portion of the Max McGraw Wildlife Foundation property across 4 years. Circles represent females, squares represent males, and shaded shapes represent confirmed breeding adults.

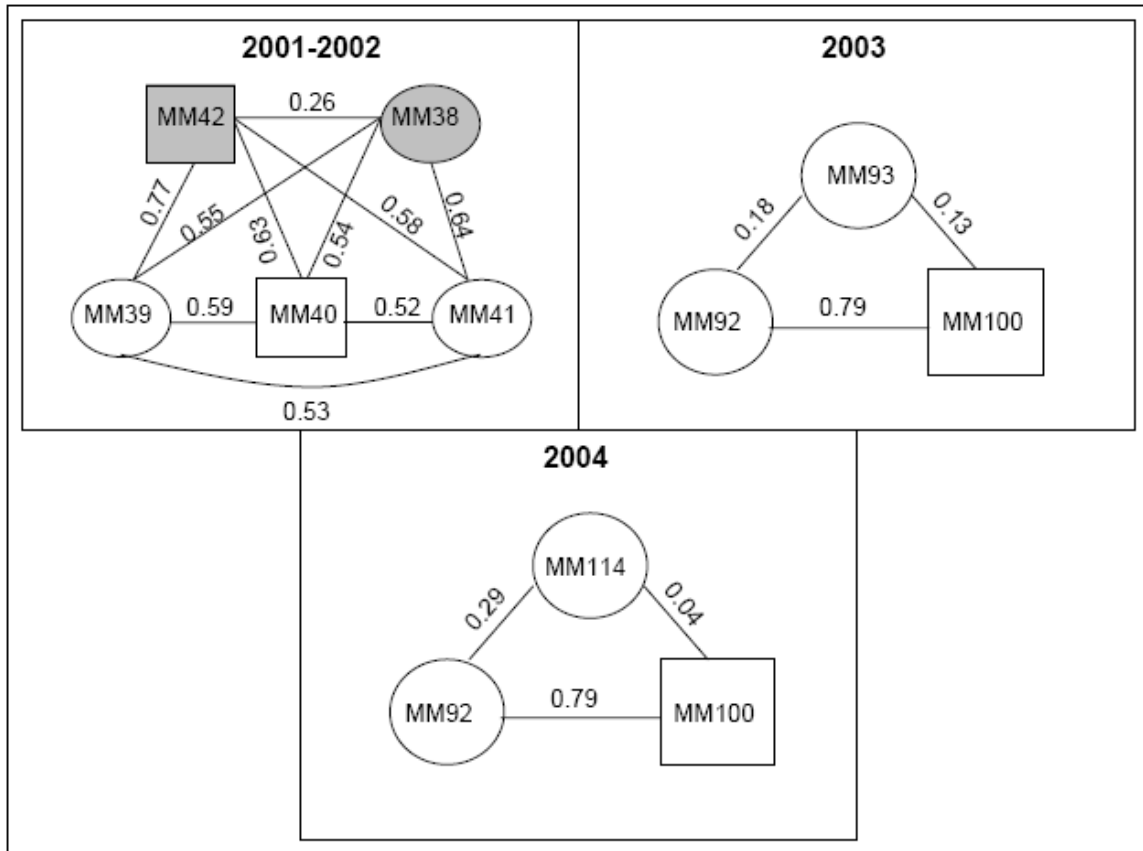


Figure 3.22 - Grafen's relatedness coefficient between pack members in the eastern portion of the Max McGraw Wildlife Foundation property across 4 years. Circles represent females, squares represent males, and shaded shapes represent confirmed breeding adults.

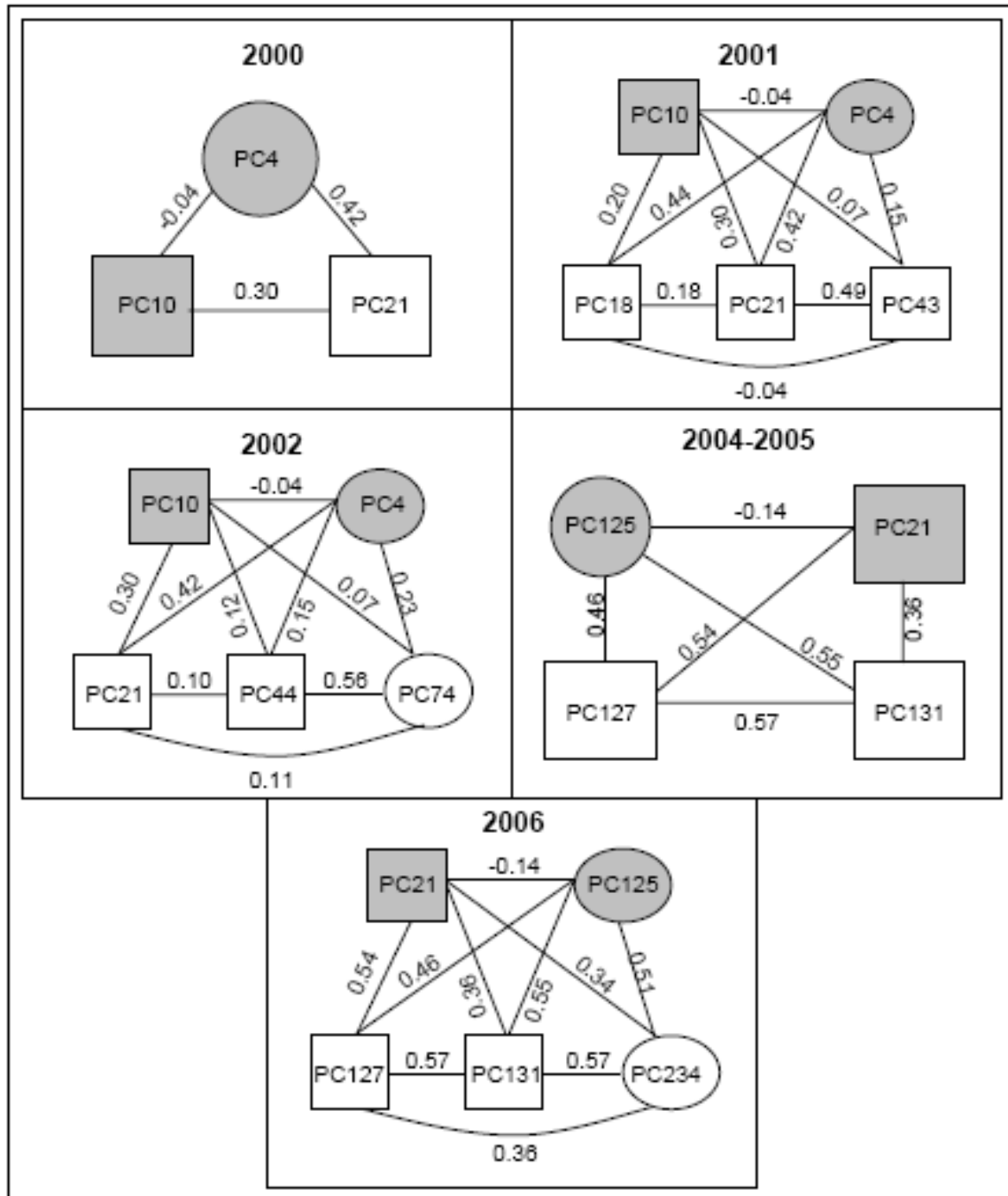


Figure 3.23 - Grafen's relatedness coefficient between pack members in the Poplar Creek Forest Preserve across 6 years. Circles represent females, squares represent males, and shaded shapes represent confirmed breeding adults.

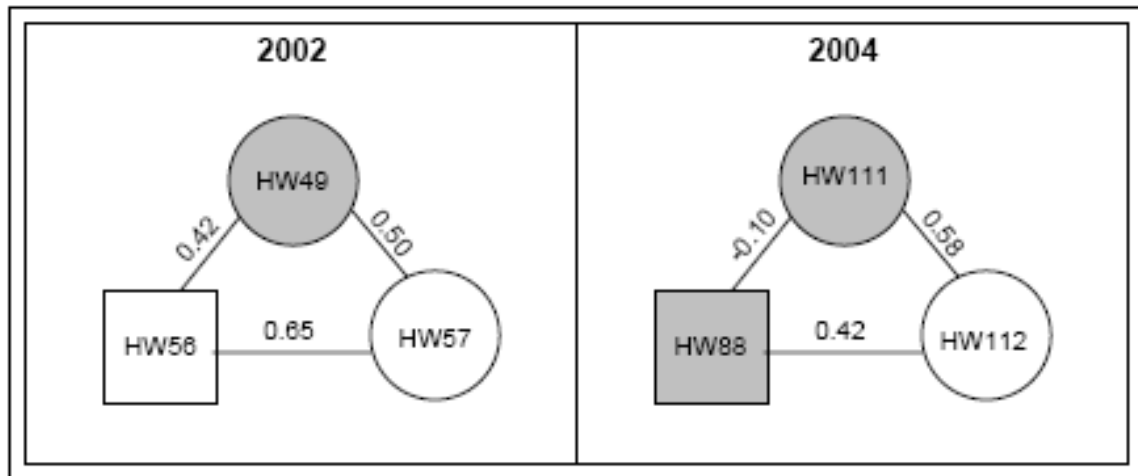


Figure 3.24 - Grafen's relatedness coefficient between pack members in the Highland Woods Forest Preserve across 2 years. Circles represent females, squares represent males, and shaded shapes represent confirmed breeding adults.

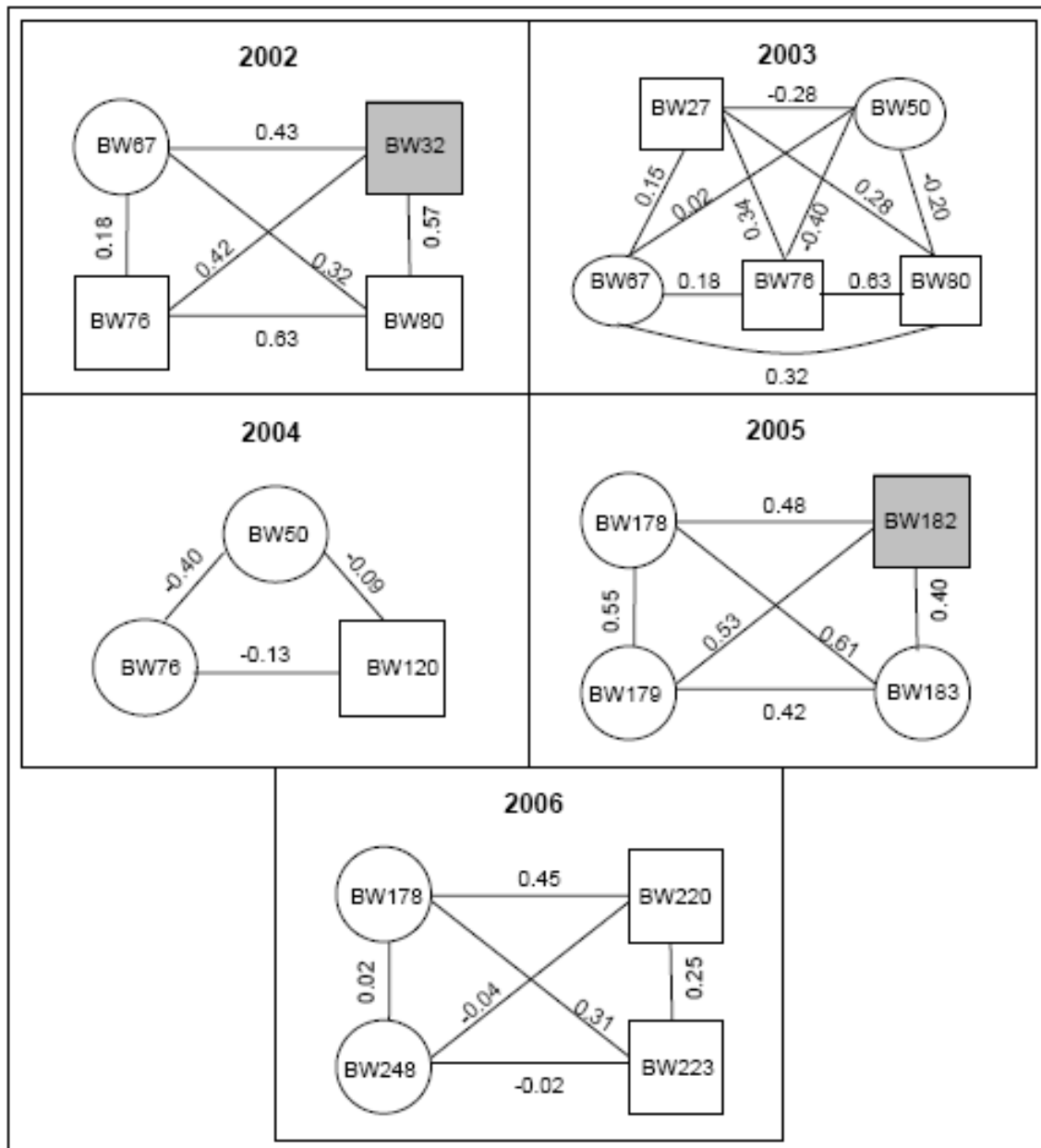


Figure 3.25 - Grafen's relatedness coefficient between pack members in the Ned Brown Forest Preserve (Busse Woods) across 5 years. Circles represent females, squares represent males, and shaded shapes represent confirmed breeding adults.

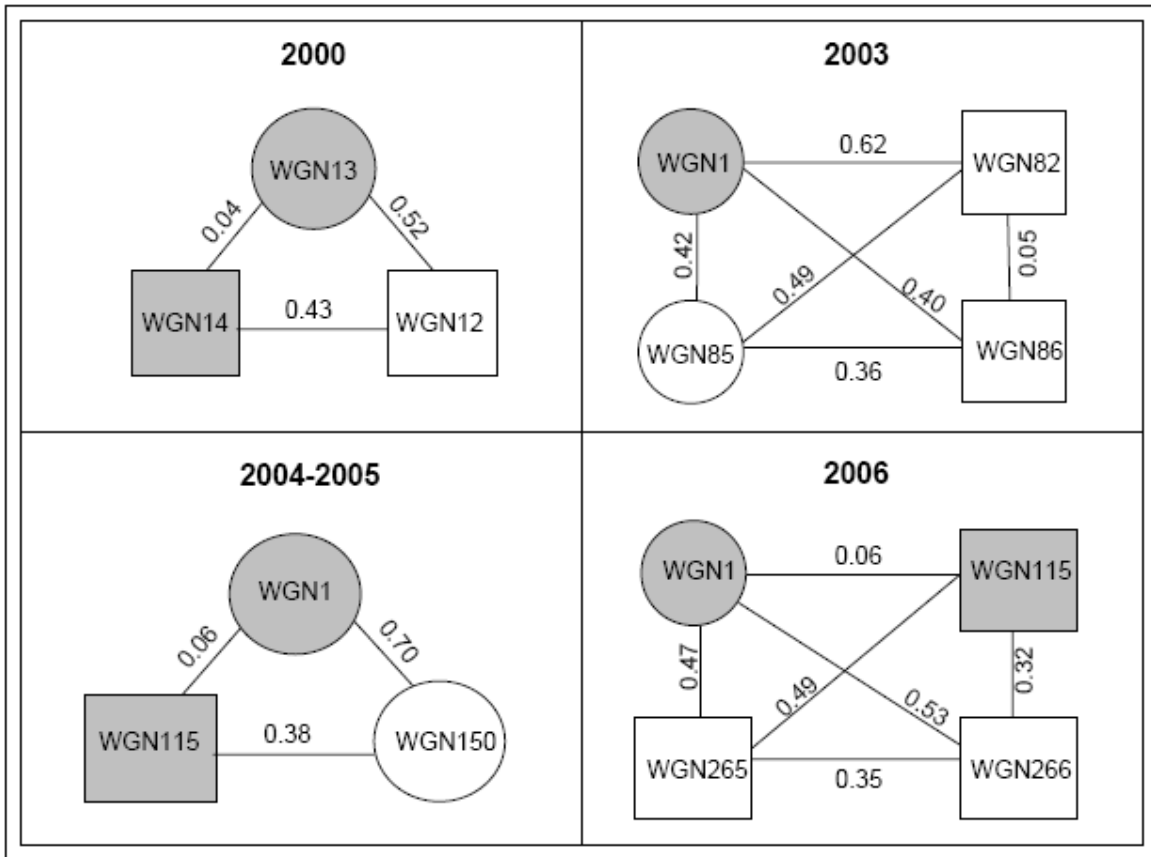


Figure 3.26 - Grafen's relatedness coefficient between pack members on the WGN property across 5 years. Circles represent females, squares represent males, and shaded shapes represent confirmed breeding adults.

