To the Graduate Council:

I am submitting herewith a dissertation written by Shyamala Ratnayeke entitled "Female Philopatry and Spatial Organization in the Raccoon (*Procyon lotor*)." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Life Sciences.

Michael R. Pelton, Major Professor

We have read this dissertation
and recommend its acceptance:

Accepted for the Council:

Associate Vice Chancellor and
Dean of The Graduate School

FEMALE PHILOPATRY AND SPATIAL ORGANIZATION IN THE RACCOON (*PROCYON LOTOR*)

A Dissertation

Presented for the

Doctor of Philosophy

Degree

The University of Tennessee, Knoxville

Shyamala Ratnayeke

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ABSTRACT

Among mammals, some of the most common types of cohesive social groupings originate from natal philopatry through the extended mother family. The recognition that females among some solitary mammals demonstrate natal philopatry suggests that an important part of understanding the evolution of social groupings in mammals is through establishing the conditions that lead to natal philopatry in solitary species. The North American raccoon, *Procyon lotor,* is a relatively solitary carnivore of the Procyonidae, a family that demonstrates both variability and flexibility in the nature and degree of sociality. This dissertation examines the conditions surrounding natal philopatry in a raccoon population in east Tennessee with the goals of identifying 1) the population correlates and individual consequences of female philopatry, and 2) the influence of philopatry and kinship on female spatial organization.

I gathered over three years of radio telemetry and mark-recapture data to obtain information on raccoon population ecology and female spatial relationships on the Oak Ridge Reservation. Most female offspring persisted on the natal area beyond dependence and beyond their mother's next breeding episode. Most dispersal was in the early Spring (Jan - Mar) when mortality was highest among philopatric females. Population density of raccoons on the study area was high relative to other raccoon populations in east Tennessee, as was the proportion of females in older age classes. Individual and population characteristics of young females at White Oak Lake indicated that philopatry under these demographic conditions was costly. Although female

raccoons are physiologically capable of reproduction at one year, lower body weight, delayed reproduction and higher mortality in younger females relative to older females suggested that competition from older females limited free access to food and breeding opportunities. The presence of a yearling daughter within the home range did not seem to incur reproductive costs to mothers. At least 50% of mothers who shared space with yearling daughters became pregnant the following year. No philopatric daughters became pregnant when their mothers were alive on the natal area.

DNA amplification employing primers of arbitrary sequence (RAPDs) indicated that female philopatry in raccoons led to a greater likelihood that neighbors were more related than expected by chance. Genetic distance based on RAPD band frequency was positively associated with spatial distance among females. Genetic similarity was positively associated with the extent of home range overlap. Philopatry seemed biased toward females; average female-female similarities at White Oak Lake were greater than average male-male similarities or average male-female similarities. High home range overlap among females with low and moderate levels of band sharing suggested that maternal inheritance of space was not a prerequisite for home range sharing. High home range overlap was less common among parous females. Spatial and temporal interaction among females was independent of the percentage of band sharing with most responses to shared areas being random. Individual spacing among most females was high relative to the distances between their activity centers, reflecting the predominantly solitary nature of female raccoons.

Hypotheses explaining the formation of cooperative social groups in carnivores invoke ecological, demographic and behavioral factors that influence an individual's reproductive opportunities and the probability of philopatry. Certain aspects of female philopatry in raccoons bear a close resemblance to circumstances hypothesized to promote natal philopatry in some social carnivores.

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CHAPTER 1

INTRODUCTION

The spatial distribution of individuals in a population is a consequence of complex and dynamic interaction among individuals, and between individuals and their environment (Brown and Orians 1970, Waser and Wiley 1979). The movement of individuals from their place of birth is one determinant of spatial distribution (Taylor and Taylor 1977), and has also been considered to have a major role in population regulation (Lidicker 1975), and the genetic structure of populations (Anderson 1970, Chepko-Sade et al. 1987). Dispersing individuals might benefit through more frequent encounters with mating partners, genetically more variable offspring, reduced levels of competition and access to more suitable breeding habitats (Greenwood 1980).

Nevertheless, many juvenile mammals, females in particular, exhibit natal philopatry. They show attachment to their natal site and may remain close to or within their natal home range past the age of independence from parents. This tendency has become increasingly recognized not only among social species, but, in many solitary mammals as well (Waser and Jones 1983). It has been suggested that an integral part of understanding the evolution of complex social groups is through establishing the conditions leading to natal philopatry in solitary species (Vehrencamp 1979, Waser and Jones 1983).

Among the Carnivora, reports of the seasonality, timing and distance of dispersal are quite frequently encountered (e.g., Storm et al. 1976, Cheeseman et al. 1988), but

few studies have been designed to establish the extent of natal philopatry by following identified juveniles from birth to adulthood and subsequent reproduction. In most polygynous mammals, it is important that young males reaching independence enhance their chances of acquiring mates, whereas, among females who invest heavily in offspring, acquiring a suitable breeding habitat is a priority. The sharing of home range space among mothers and daughters invokes strong benefits to daughters, and might be considered a form of kin-directed altruism and a likely precursor of gregariousness (Hamilton 1964). Information on the breeding destination of female young in relation to maternal home range, or whether mothers will share or modify space use to accommodate daughters, is less well documented for most mammals.

The terms 'solitary' and 'social' apply to a continuum of behavior patterns resulting in ambiguous definitions of each. I define solitary species as those whose individuals have infrequent encounters with conspecifics and are usually alone during peak periods of activity such as foraging. This does not imply that solitary individuals decrease the number of conspecifics recognized. Their social life may be quite complex involving the monitoring of neighbors' whereabouts and the coordination of movements in relation to other conspecifics (Leyhausen 1965). The North American raccoon, *Procyon lotor*, is a carnivore of the family Procyonidae whose members range from the comparatively solitary ringtail, *Bassariscus astutus*, (Trapp 1978) to the highly gregarious female-bonded groups of the coati, *Nasua narica* (Kaufmann 1962). Raccoons are usually solitary but sometimes show signs of gregariousness. Family groups may occur, with young remaining in the vicinity of the maternal home range

beyond independence and breeding maturity, and often beyond the mother's next breeding episode (Haugen 1954, Fritzell 1978a). Larger groups may use winter dens (Mech and Turkowski 1966) or congregate at feeding stations (Sharp and Sharp 1956). Raccoons seem to show flexibility in social organization and, though described as solitary (Kaufmann 1982), show signs of being on the edge of gregariousness. They are, thus, ideal for investigating the mechanisms of philopatry and spacing that might contribute towards a better understanding of the evolution of sociality.

The influence of ecological factors on the evolution of social structure can occur on at least three levels (Waser and Jones 1983); for example, the distribution of resources in space and time a) could determine whether individuals can benefit from association and cooperation, b) can reduce the costs of home range sharing and c) can increase the likelihood that individuals sharing home ranges are related. Natal philopatry among mammals has been frequently associated with home range sharing (Harris and Murie 1984, Woodruffe et al. 1993) and is probably the most common mechanism by which kin become neighbors. Some studies suggest that mothers assist their female offspring in acquiring adjacent territories (Yeaton 1972, Rogers 1987). Philopatry need not necessarily involve sharing or donating space to the offspring but, when it does, it can potentially reduce future parental reproductive success. From the aspect of social evolution, thus, philopatry becomes especially interesting when a mother may continue reproductive investment beyond weaning to increase the probability of producing reproductive offspring.

In a broad review of philopatry in mammals, Waser and Jones (1983) identify two broad types of philopatry that might occur (Table 1). Type A involves no parental investment and occurs when adult survivorship is so low that no parental competitors are present by the time offspring reach maturity. Young thus inherit the parental nest and home range. On the other hand, type B and its three variants require tolerance by the parent for grown offspring on the natal range. In relatively homogeneous habitats the first alternative might be favored if subdivisions of the maternal home range were to contain a complete set of critical resources. However, where resources are sparsely dispersed, spatially clumped or unpredictable, home range overlap might be more frequently encountered (alternative 2). This form of philopatry is regarded as being most compatible with gregariousness and the kind that is most commonly encountered among solitary mammals for whom data on philopatry are available. Alternative 3 is when parents abandon the home range to offspring and move away. This type of philopatry might be encountered when parents could easily acquire the resources for future reproduction because they have the advantage of time, experience, or size (e.g., Columbian ground squirrels, *Spermophilus columbianus*; Harris and Murie 1984).

Among mammalian carnivores, canids offer some of the best known examples of philopatry in a family with both gregarious and relatively solitary members. Although much of the evidence is inferred indirectly, communal denning among females of different species of foxes is suspected to originate through philopatry (Ables 1969, Egoscue 1975, MacDondald 1981). Thus, females that share home ranges and den together are likely to be close relatives. Variations on this theme occur among more

Table 1. Types of philopatry and predicted characteristics of each type among solitary mammals (Waser and Jones 1983).

Types of philopatry	Predictions
A. **Opportunistic philopatry**	
1. Parents die, relinquishing the original home range to offspring	Offspring may live adjacent to parent but home ranges are not shared. Parental home range does not contract to accommodate offspring. Proportion of philopatric young depends on adult mortality rates
B. **Philopatry by parental consent**	
1. Parents relinquish part of the home range range to offspring	Offspring have home ranges on the periphery of their parents. Parental home range contracts. Boundaries of areas used by parents and offspring are maintained by mutual avoidance. Spatial homogeneity in resource distribution
2. Parents tolerate offspring within home ranges into adulthood	Home ranges of parents and offspring may be congruent or overlap extensively. Offspring may eventually expand range beyond common area. Spatial heterogeneity in resource distribution.
3. Parents disperse leaving original home range to offspring	Lower rates of mortality among dispersing adults than among juveniles.

gregarious canids such as wolves, *Canis lupus*, jackals, *Canis aureus* and *Canis mesomelas*, and coyotes, *Canis latrans* (Mech 1970, Moehlman 1979, Bekoff and Wells 1982), and parallel examples occur in almost all gregarious carnivores which consist of matrilineal groups of variable size (reviewed in Waser and Jones 1983). Among solitary carnivores other than canids, female philopatry has probably been best studied in house cats. Although hunting is performed solitarily, female philopatry in house cats involves common home ranges, social tolerance and communal suckling of offspring born within matrilines (Laundré 1977, Dards 1978, Liberg 1980). Among larger cats, philopatry may take different forms. Cheetah, *Acinonyx jubatus*, and leopard, *Panthera pardus*, daughters have been reported to share and sometimes reproduce within the home ranges of mothers, but individuals avoid each other as adults (Bertram 1974, Frame and Frame 1981). Among tigers, *Panthera tigris*, in Chitwan, daughters remain on or adjacent to the mother's home range, but space use is modified so that each female's home range becomes gradually more exclusive as daughters reach the age of independence (Smith et al. 1987). Some of the most detailed data on philopatry in a family that is largely solitary come from Roger's (1987) study on black bears, *Ursus americanus*. Ninety percent of female offspring whose birth places and adult ranges were known, demonstrated philopatry, either remaining within the mother's home range, inheriting the range after her death, or expanding into adjacent areas that became vacant.

Philopatry is, therefore, definitely known to occur in some carnivores and is widely suspected to be present in most other members of the order. Less well known

are the comparative costs and benefits of philopatry relative to dispersal, the extent of philopatry, and the influence of ecological and demographic factors in shaping its patterns. For example, how long do offspring persist within natal areas, do mothers or offspring experience individual or mutual costs resulting from this behavior and do philopatric individuals fare better than those who disperse? The tendency for many philopatric individuals to share contiguous space has also led to the widespread, but largely untested, assumption that adults sharing home ranges are close kin and that the mutual tolerance that accompanies the sharing of space is a consequence of high genetic relatedness among females (e.g., Michener 1973). Philopatry may lead to a greater likelihood of kin being neighbors, but whether individuals make distinctions on the basis of relatedness is largely unknown for most solitary mammals.

I use Waser and Jones' (1983) broad classification of philopatry to frame and test hypotheses of female philopatry and female spatial organization in a population of raccoons on the Oak Ridge Reservation, Tennessee. In chapter 2, I identify population correlates that could potentially affect philopatry in female raccoons, present information on the movements and establishment of females born in the population, and discuss the results in the context of other studies of raccoons and current hypotheses of philopatry. In Chapter 3, I combine a genetic analysis of the population with spatial data to determine the influence of female philopatry on female spatial organization. Chapter 4 summarizes and integrates the preceding chapters.

CHAPTER 2

POPULATION CORRELATES OF FEMALE PHILOPATRY IN RACCOONS AT OAK RIDGE, TENNESSEE

Among the several ecological and population characteristics that might determine the extent and nature of philopatry, survivorship and habitat saturation have been cited as probable correlates. Murray (1967) proposed that an individual could maximize its chance of reproducing if it stayed near its birthplace until maturity or returned to its birthplace when it approached maturity, aggressively competed for breeding sites, or responded to dominant opponents by moving away. Based on Murray's (1967) argument, Waser and Jones (1983) proposed that in species with low adult survivorship, philopatry would arise opportunistically because young individuals would face little parental competition and would either inherit the parent's home range or find a vacant spot close by. A second hypothesis suggests that habitat saturation can also favor philopatry and ultimately the development of gregarious social systems. At such times, most suitable home ranges are occupied so parents tolerate their non-dispersing offspring (Brown 1974, Emlen 1982, Smith and Ivins 1983, Jones et al. 1988). Horn (1984) also states that if the local environment is deteriorating, dispersal is favored if better conditions exist elsewhere.

These ideas imply that remaining on the natal area entails both significant benefits and costs to offspring. For example, in all but deteriorating environments, familiarity with an area and the reduced risks and energetic costs associated with

philopatry would favor site tenacity, but younger individuals are likely to face competition from older established animals. Also, tolerance of offspring after they reach the age of independence is potentially costly to parents. These ideas further suggest that certain ecological and demographic characteristics of a species are important determinants of the occurrence and nature of philopatry. In a comprehensive review of philopatry across several mammalian species (Waser and Jones 1983), two salient features emerge. First, the factors driving philopatry can differ both among and within species and may be complex. Secondly, data that report the extent and nature of philopatry and identify factors relating to philopatry are remarkably few, particularly in solitary mammals.

Raccoons exhibit considerable population variation in both reproductive and behavioral traits (Kaufmann 1982). For example, although philopatry in raccoons seems female-biased (Fritzell 1978a) with most of the evidence anecdotal or inferred (Haugen 1954, Mech and Turkowski 1966), some studies report dispersal in both male and female raccoons within the year of birth at 6 - 7 months old (Stuewer 1943a, Urban 1970). Several researchers report sexual maturity in wild females at 10 months and that most will bear young by the time they reach one year of age (Kaufmann 1982), but this too is variable (Fritzell et al. 1985). The possible connection between density, female philopatry, reproduction and mortality has not been addressed in raccoons or most solitary carnivores.

The purpose of this chapter is two-fold. I attempt to identify specific characteristics of the natal social environment that are likely to relate to, or be a

consequence of, philopatry in raccoons. I also provide a description of the population ecology of raccoons in the study area within which the overall results may be interpreted. This is necessary for at least two reasons. First, unlike most raccoon populations that have been studied in the U.S., the population on the ORR is not hunted or trapped. Secondly, the ORR is surrounded by areas where raccoon hunting is a popular sport; thus the density of the study population is relatively high and surrounded by potential habitat openings for females dispersing out of the ORR. Both factors could influence patterns of natal philopatry. Likewise, the population ecology of raccoons at White Oak Lake may not be typical of other raccoon populations studied in the southeastern U.S.

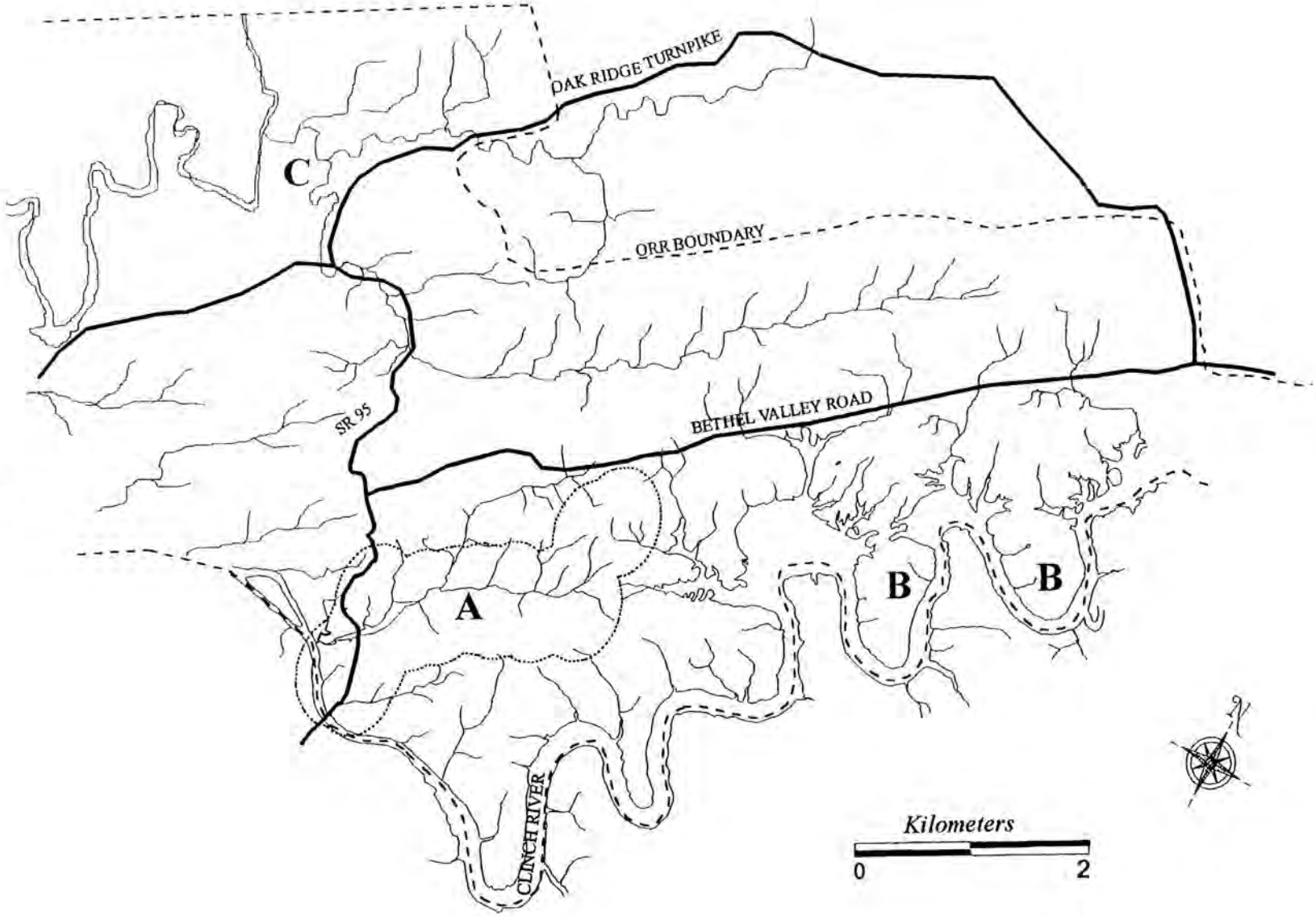
In this chapter, I present data on density, age structure, reproductive characteristics, mortality, and patterns of philopatry and home range establishment of female offspring in a raccoon population on the White Oak Lake area of the Oak Ridge Reservation (ORR). I used radiotelemetry to trace the fates of 22 female cubs to identify the extent and nature of female philopatry in raccoons. I also examined the conditions surrounding female philopatry by determining population characteristics of raccoons in the study area through mark-recapture techniques. If adult survivorship was low, philopatry would arise opportunistically since a daughter, on reaching sexual maturity, would be likely to inherit her mother's range or find a vacant space close by. If adult survivorship was high and daughters consequently remained on the natal area while mothers were alive, philopatry would be by 'parental consent' (Waser and Jones 1983). If female social organization is

competitive in raccoons, then females may maintain exclusive ranges. But, if space is not economically defendable, mothers and daughters may overlap in space but either or both may experience survival and reproductive costs. Alternatively, competition may be absent, or mothers and daughters may offset competition by maintaining cooperative associations with positive fitness consequences to both. Specifically, I asked: (1) whether young females were more likely to remain on the natal range than to disperse; (2) whether philopatry, when it occurred, was opportunistic or by 'parental consent' and (3) whether philopatry entailed a cost, either to mothers or offspring, in terms of decreased survival and reproduction.

Study area

The study area was located within the 150 km^2 area of the Department of Energy Oak Ridge Reservation (ORR) situated approximately 24 km west of Knoxville, Tennessee. The ORR is bordered on the north and east by the city of Oak Ridge and on the south and west by the Clinch River/Melton Hill impoundment. The ORR was protected from hunting and trapping from 1942 to 1985, after which managed hunts for white-tailed deer, *Odocoileous virginianus*, were permitted. Terrain in the ORR ranges in elevation from 226 m to 413 m above mean sea level. Annual precipitation between 1992 and 1995 averaged 118 cm. The main study area, referred to as White Oak Lake, was situated near the southwest boundary of the ORR and consisted of the White Oak Lake watershed and the areas directly surrounding it (Fig 1A). I also trapped raccoons in two subsidiary study areas, the Freels Bend site

Fig. 1. Map showing locations of study areas on the Oak Ridge Reservation. Approximate boundaries of the reservation are demarcated by dashed line. The three study areas were A) the main study site at White Oak Lake with dotted line indicating the composite male-female study area sampled by trapping, B) Freels Bend area, and C) East Fork area.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and the East Fork site. Raccoons in the Freels Bend area were monitored using telemetry through 1992.

The White Oak Lake study was initiated as part of a toxicity monitoring program which used raccoons as indicators of biologically available contamination, particularly of mercury and ^{137}Cs. Parts of the White Oak Lake flood plain contained underground waste sites which served as sources of contaminants to both ground and surface water. Clapp et al. (1995) give a detailed description of the flood plain and associated waste sites. Ashwood et al. (1994), report preliminary results of toxicity monitoring in raccoons at the White Oak Lake site.

At White Oak Lake, parallel northeast tending ridges constitute the northern and southern borders of the watershed. The habitat is predominantly oak-hickory forest mixed with pine, relatively small patches of bottomland hardwood, cedar-pine and cedar-hardwood forest. The East Fork area consists mainly of pine, with some pine-hardwood and oak-hickory forest, and the Freels Bend area is a mosaic of cedar, pine, oak-hickory forest, and grassland. Numerous water cachments, streams and springs throughout the three areas provide patches of wetland habitat for raccoons. Several dirt roads and some main roads dissect the study area providing good road access. Parr and Pounds (1987) and Mann et al. (1996) give detailed accounts of the geology, vegetational history and habitat composition of the ORR.

Methods

Trapping

Trap sites were distributed at intervals of roughly 0.2 km along stream banks in each of the three study areas. Trapping was conducted at White Oak Lake twice a year, from late March to May and from mid-September to November, to obtain data for population estimates. Trapping also was conducted for 10 - 14 days per month, between May and September, to capture as many family groups as possible and to examine the reproductive condition of females.

Raccoons were captured in live traps baited with sardines or catfood. After immobilization with 0.1 mg/kg ketamine hydrochloride, animals were weighed, measured, and ear-tagged with numbered rototags (NASCO Inc., Ft Atkinson, WI). Thirty one females and five male raccoons were radio-collared. Transmitters weighed 80 - 100 g and were equipped with activity switches (Telonics, Mesa AZ; Advanced Telemetry Systems Inc., Isanti MN). Twenty two female cubs were collared when they were three to six months old. Cubs between 1.2 - 1.5 kg body weight were radiocollared with transmitters weighing 73 g. Reproductive condition and general body condition were noted for almost all animals. A sample of muscle tissue was obtained from nearly all females and most the adult males for genetic analyses. To obtain samples of muscle, an incision of approximately 1 cm in length was made in the inner thigh after trimming the hair in the area and cleaning the skin with alcohol. Approximately 0.25 g of the underlying muscle was obtained with the aid of tissue forceps and scissors.

Raccoons were assigned to age classes based on tooth wear, following techniques developed by Grau et al. (1970): class I animals were approximately 0 - 14 months, class II were 15 - 38 months, class III were 39 - 57 months, class IV were 58 - 86 months and class V were >86 months. Female raccoons are physiologically capable of reproduction when they are 10 months old (Sanderson and Nalbandov 1973, Kaufmann 1982); therefore all raccoons in age classes II - V were referred to as adults. Cubs were individuals born within the current year (approximately 0 - 7 months). Yearlings were raccoons born the previous year. Yearlings were approximately 6 - 18 months old and overlapped with Age class II. Yearlings showed little tooth wear but could be distinguished from cubs because of larger body size. It was usually possible to distinguish yearlings that had entered age class II from older age class II raccoons based on a combination of less tooth wear and smaller body size.

A combination of body weight and schedule of tooth eruption (Montgomery 1964) was used to estimate the age of cubs. Sanderson (1961) regarded body weight as a reliable estimate of age for the first six months if reference curves are constructed with weights of local, known-aged animals. From captures of four solitary lactating mothers who were subsequently caught with young cubs, tooth eruption indicated that most cubs were between 3 - 3.5 month old and weighed between 900 - 1.2 kg when they began following their mother. This age corresponded with reports of cub development in wild raccoons (Stuewer 1943b, Schneider et al. 1971, Rabinowitz 1981). Recaptures of eight cubs indicated that the

mean rate of weight gain was between 350 - 450 g per month. Because the last new teeth to erupt were permanent canines at 3.5 months, the combination of body weight and tooth eruption was useful for estimating the age of cubs between 4 and 6 months.

Population size and density

I applied the Jolly Seber population estimator to mark-recapture data from the White Oak Lake area to obtain an index of population size. The Jolly Seber open population model provides information on capture probabilities, rates of survival, emigration and recruitment (Seber 1982, Jolly 1965). Assumptions of the classical model are equal probability of survival among individuals, equal probability of capture, individuals do not lose their marks, sampling time is instantaneous and animals are released immediately after the sample. Program JOLLY (Pollock et al. 1990), which includes chi-square tests to determine which of a variety of models was most appropriate for the data, was used for analysis. These models were of five types, the last four of which were restricted versions of the classical model A. Model A allowed survival and capture probabilities to vary over time, model A' allowed death but no immigration, model 2 allowed survival rates for animals captured for the first time to differ from those of unmarked or previously marked animals, model B assumed constant survival rates and model D assumed both constant survival rates and capture probabilities. To meet the assumption of equal probability of survival, offspring of the year were eliminated from the analysis and added after computing population estimates. I reported population estimates of the

models not rejected by the Chi-square tests but included a second test for equal catchability. This was because the tests in program JOLLY have low power and do not guarantee that all model assumptions have been met by the data (Pollock et al. 1990). The second test for equal catchability (Caughley 1977), compared frequencies of capture data to expected frequencies generated to fit a zero-truncated Poisson distribution.

Density was estimated by determining an effective study area and dividing the area by the estimated population size. To determine study area boundaries I circumscribed an arc half the mean home range diameter around each trap site and calculated the composite area contained within the periphery of the arcs. This was done separately for males and females. This method was recommended by Caughley (1977) who suggested that the area effectively sampled by a trap may be defined by a circle with a radius one-half the average home-range diameter of the target animal.

Natal dispersal and philopatry among females

I used radio telemetry to document movements and compare changes in mother-daughter distance with time among offspring born between 1992 and 1994. Methods for obtaining radio locations and sampling schedules are described in Chapter 3 which deals with home range overlap and spatial interaction among females in greater depth. I report changes in mother-daughter spacing as a function of cub age and month of the year. Distance from the mother for cubs $\geq$4 months

old was estimated from radio locations obtained within a space of 3 - 5 min, or sightings when the pair were resting during the day.

A study of natal philopatry and dispersal requires an operational definition of the period within which movement or non-movement is considered natal dispersal or natal philopatry. It also requires operational definitions of the terms 'resident', 'philopatry', and 'dispersal' (Gaines and McClenaghan 1980, Greenwood 1980). In all mother-daughter pairs, mothers were known residents, either from previous or subsequent monitoring. Cubs were residents if they were caught in the same trap with a lactating female, or if they were captured on the study area when they were <5 months old. This decision was based on the earliest detected dispersal in a female raccoon at White Oak Lake when she was an estimated to be 6.5 -7.5 months old.

Philopatry was defined as the continued use of the natal home range after the age of independence from parents. This definition is ambiguous because interactions among parents and philopatric offspring can continue throughout life. Waser and Jones (1983) define independence as beginning when offspring cease to forage in spatial association with the mother. In raccoons most offspring are weaned between seven and 16 weeks (Montgomery, 1969) and will travel periodically without their mother by the age of five months (Schneider et al. 1971). I classified females >5 months old as philopatric if they remained at their natal site until death or until they reached adulthood at one year. Females were defined as natal dispersers if they moved a straight line distance ≥ 1000 m, which was the average home range diameter of a female raccoon at White Oak

Lake, from the natal area within the year following their birth. Because they had moved temporarily out of the range of the mother's influence, females that dispersed but returned to settle in the natal area were also classified as dispersers (Jones et al. 1988).

Age-sex composition and reproductive activity

The age-sex composition of the White Oak population was calculated from capture data collected in 1993 and 1994, which were the only two years that included both spring and fall trapping seasons. I used data obtained from examining the reproductive status of females during capture to obtain an index of reproductive activity in different age classes (Fritzell 1978b, Stuewer 1943b). Although examining female reproductive condition does not give an estimate of fecundity it provides a useful index of relative reproductive activity across age classes. Female raccoons give birth to one litter per year (Kaufmann 1982) with most females becoming estrous between March and early April (Glass 1991, Rabinowitz 1981). Estrus is characterized by prominent red swelling of the vulva lasting five to six weeks. Gestation usually lasts 63 to 65 days and lactation for 3.5 - 4 months after cubs are born (Stuewer 1943b, Montgomery 1969). In East Tennessee, most females give birth between April and August (Rabinowitz 1981, Cantrell 1989).

During the reproductive season (March to October) of 1993 and 1994, I estimated the proportion of adult females in the population that were nulliparous, parous and non-parous. Nulliparous females were those that had not reproduced

before, parous females showed signs of current reproductive activity such as estrus, pregnancy or lactation, and non-parous females had reproduced at some period in their lifetime but did not reproduce that year. Reproductive status was based on signs of current or past reproductive activity (Sanderson 1950). These included appearance of the teats, signs of estrus, pregnancy or lactation. I was able to recapture most females during a reproductive season to confirm observations. All classifications of nulliparous females were confirmed in the fall but some non-parous females were caught only once. A female captured more than once in any year was reported only once for that year under the most advanced stage of reproduction. That is, if recorded as nulliparous in the spring but found in estrus, pregnant or lactating in the summer, she was listed once, as parous. Reproduction in 1993 and 1994 was regarded as separate events; therefore, some females were reported twice because they were captured in both years.

Body weight is a possible determinant of age at first reproduction (Fritzell et al. 1985), or the probability that a female raccoon will reproduce (Mech et al. 1968). I compared body weight and head-body length (tail excluded) across different age classes of adult females caught in the spring of 1993 to determine if variation in reproductive activity among different age classes was related to body size. Spring weights were used because pregnancy and lactation affect female body weight later in the year. I used a Kruskall-Wallis test (Sokal and Rohlf 1981) to determine if body weight and head-body length were independent of age class. Pair-wise contrasts

were then made to identify which age differed with $\alpha = 0.01$ to decrease type I error (Sokal and Rohlf 1981).

Survival

I estimated the mean annual survival rate and monthly mortality rate for females, excluding young of the year, with the Kaplan-Meier staggered entry design (Pollock et al. 1989), which calculates the number of deaths recorded during the number of days animals were radio-monitored. The approximate date and cause of death were determined by approaching animals that I suspected were dead. The model allows for censoring animals whose signals are lost because of radio failure or emigration from the area, with the assumption that censoring is random. The Kaplan-Meier model also allows for the staggered entry of new animals during the course of the study. Assumptions of the model are that newly tagged animals have the same survival function as previously tagged animals, animals have been randomly sampled, survival times are independent and that capture and radio-tagging of the animal does not influence its future survival.

I compared mortality among females of different age to determine if deaths occurred more or less frequently than expected between age categories. All radio collared animals that died were assigned age classes at the time of death. Expected frequencies of mortality per age class were based on the total radio days per age class. Frequencies of mortality by age class were reported, but age classes were

combined to determine if mortality in younger females (yearlings and age class II) was greater than in older females (age classes III - V).

Results

Population density

Unequal catchability was not detected in females ($df = 2$, $p = 0.31$), but was significant for males ($df = 1$, $p = 0.03$) (Table 2). Unequal catchability in males was probably because of temporary immigration of males into the study area during the spring mating season; of 33 adult males captured only once, 29 were caught during spring trapping sessions. However, the Jolly-Seber model is fairly robust to unequal probability of capture if capture probabilities are high and if coefficients of variation for population estimates (N) are under 20% (Pollock et al. 1990).

For population estimates of females, model A, which allows survival and capture probabilities to vary over time, and model D, which assumes constant survival rates and capture probabilities, were not rejected by the Chi-square tests for program JOLLY (Table 3 and 4). I used the Jolly-Seber estimates from model D, which had slightly smaller standard errors for the population estimates, for estimating female densities. Population estimates for males were made using model A, but had large variation around the estimates for spring and fall 1993 (Table 3 and 4).

Effective study areas for females and males were derived from mean home range radii of 499 m for females, and 670 m for males, circumscribed around each trap site. Study area for density estimation was 564.8 ha for females and 751.9 ha

Table 2. Observed frequency of capture of raccoons greater than age class 1 at the White Oak Lake study area and the zero-truncated Poisson frequencies expected if catchability is constant. Expected frequencies <5 were pooled.

Number of times captured	Observed Frequency		Expected frequency		$\frac{(f-E(f))^2}{Ef}$	Observed Frequency		Expected Frequency		$\frac{(f-E(f))^2}{Ef}$
	FEMALES					MALES				
1	34		31.75		0.16	36		29.69		1.34
2	21		22.86		0.15	12		20.10		3.26
3	8		10.97		0.80	8		9.12		
4	6		3.99			3		3.10		
5	2	8	1.14	5.40	1.25	4	15	0.84	13.25	0.23
6	0		0.27			0		0.19		
Total	71		Chi-square =2.36			63		Chi-square = 4.83		

Table 3. Mark-recapture data, 1992 - 1995, from the White Oak Lake study area used in Jolly-Seber analyses.

	Time of recapture					
	Spring-92	Spring-93	Fall-93	Spring-94	Fall-94	Spring-95
			FEMALES			
Marked	0	6	10	11	16	16
Unmarked	19	13	15	7	8	10
Caught	19	19	25	18	24	26
Released	19	19	25	18	24	26
			MALES			
Marked	0	4	6	16	13	13
Unmarked	21	20	6	6	2	8
Caught	21	24	12	22	15	21
Released	21	24	12	22	15	21

Table 4. Jolly-Seber population estimates of raccoons at the White Oak Lake study area (1993 - 1995). M = estimated number of marked animals in the population, N = estimated population size excluding cubs of the year, p = estimated probability that an animal alive is captured and SE = standard errors of the mean.

	M	SE	N	SE	95 % confidence interval	p	SE
Spring 93							
Females (A)[a]	6.0	0.0	19.0	...	... - ...	1.00	...
Females (D)[b]	6.8	0.9	25.3	3.6	18.3 - 32.3	0.70	0.07
Males (A)	7.3	1.7	36.7	12.4	12.4 - 60.9	0.55	0.22
Fall 93							
Females (A)	11.4	0.8	26.9	3.3	20.4 - 33.3	0.88	0.11
Females (D)	12.4	1.3	33.8	4.1	25.8 - 41.9	0.70	0.07
Males (A)	22.3	5.2	41.3	14.0	13.9 - 68.8	0.27	0.11
Spring 94							
Females (A)	23.7	3.7	37.5	8.1	21.6 - 53.3	0.46	0.12
Females (D)	21.6	1.8	31.6	3.2	25.4 - 37.8	0.70	0.07
Males (A)	17.4	0.7	23.5	3.9	15.8 - 31.1	0.92	0.07
Fall 94							
Females (A)	21.4	2.4	31.4	5.2	21.1 - 41.7	0.75	0.12
Females (D)	22.4	2.3	33.8	3.7	26.6 - 41.1	0.70	0.07
Males (A)	19.4	2.5	22.2	4.7	12.9 - 31.4	0.67	0.13
Spring 95							
Females (D)	22.9	3.5	37.2	5.0	27.3 - 47.0	0.70	0.07
MEAN (All years)							
Females (A)	15.4	1.1	28.7	...	... - ...	0.77	...
Females (D)	17.2	2.9	32.4	6.1	20.3 - 44.4	0.70	0.07
Males (A)	16.6	1.5	30.9	5.4	20.4 - 41.5	0.60	0.09

[a]Model A (Pollock et al. 1990): produces estimates from Spring '93 to Fall '94.
[b]Model D (Pollock et al. 1990); produces estimates from Spring '93 to Spring '95.

for males. The mean density of 1 raccoon/17.3 ha for adult females was fairly stable over the period of the study, showing a slight increase at the beginning of the study period. Densities of adult males declined from 1 raccoon/20.5 ha in spring 1993 to 1 raccoon/33.9 ha in the spring 1995 with a mean density of 1/24.3 ha. The mean density of adult males and females combined was 1 raccoon/10.1 ha. Mean cub density for the female study area was 1 raccoon/29.7 ha (1993-1994). Mean density of adults and cubs combined was 1 raccoon/7.6 ha or 13 raccoons/km^2.

Raccoon density at the White Oak Lake site may not be representative of the entire ORR; for instance, the East Fork and Freels Bend areas yielded capture frequencies too low for standard population estimates. Although methods used to derive density estimates vary somewhat among studies, density estimates for the White Oak Lake area (1 raccoon/ 7.6 ha) are comparable to other parts of East Tennessee with similar habitat, or higher. For example, the highest recorded density was 1 raccoon /7.2 ha in an unhunted area of Chuck Swan in 1988 (Glass 1991). Keeler (1978) and Rabinowitz (1981) reported 1 racccon/17.0 ha and 1 raccoon /17.8 ha respectively, for the Cades Cove area in the Great Smoky Mountains National Park. Most reported densities in East Tennessee have ranged from 1 raccoon/13.0 ha (Glass 1991), to 1 raccoon/23.1 ha (Woods 1978). Most private lands in East Tennessee are heavily hunted resulting in capture frequencies too low to calculate densities (Warr 1978, Minser and Pelton 1982).

Natal philopatry and dispersal among females

Of 14 male cubs and 24 female cubs captured in fall 1993 and 1994, five males and 11 females were recaptured as yearlings on the study area the next spring, and one male and four females were recaptured the following fall when they would have been >1 year old. None of the recaptured males showed signs of reproductive maturity evidenced by descended testes.

Daughters remained close to their mothers for up to four months but were frequently located by themselves after the fifth month. Mother-daughter spacing became consistently greater with the approach of the subsequent breeding season during which many females at White Oak Lake become pregnant (Fig. 2). Ten adult females identified as mothers (Table 5) were monitored for some duration during the year following birth of the cub. Of 20 female cubs followed at ≥ 5 months of age, 15 (75%) exhibited natal philopatry and five dispersed (Table 5). Seven philopatric females and two females that dispersed died in the year following their birth. Philopatry did not entail a higher probability of survival (Fisher's exact test, $p=1$), but the test is based on a fairly small proportion of dispersers.

Female offspring that did not disperse established home ranges that overlapped extensively with that of their mothers (Fig.3). Two dispersing yearlings, B18 and B09 returned to their natal area after dispersal. B18 moved 2.4 km from her natal range in March 1994 at an estimated 10 months of age. She was subsequently located moving and denning with B11, a female of similar age who was not a sibling. Between March 1994 and February 1995 the pair occupied the same

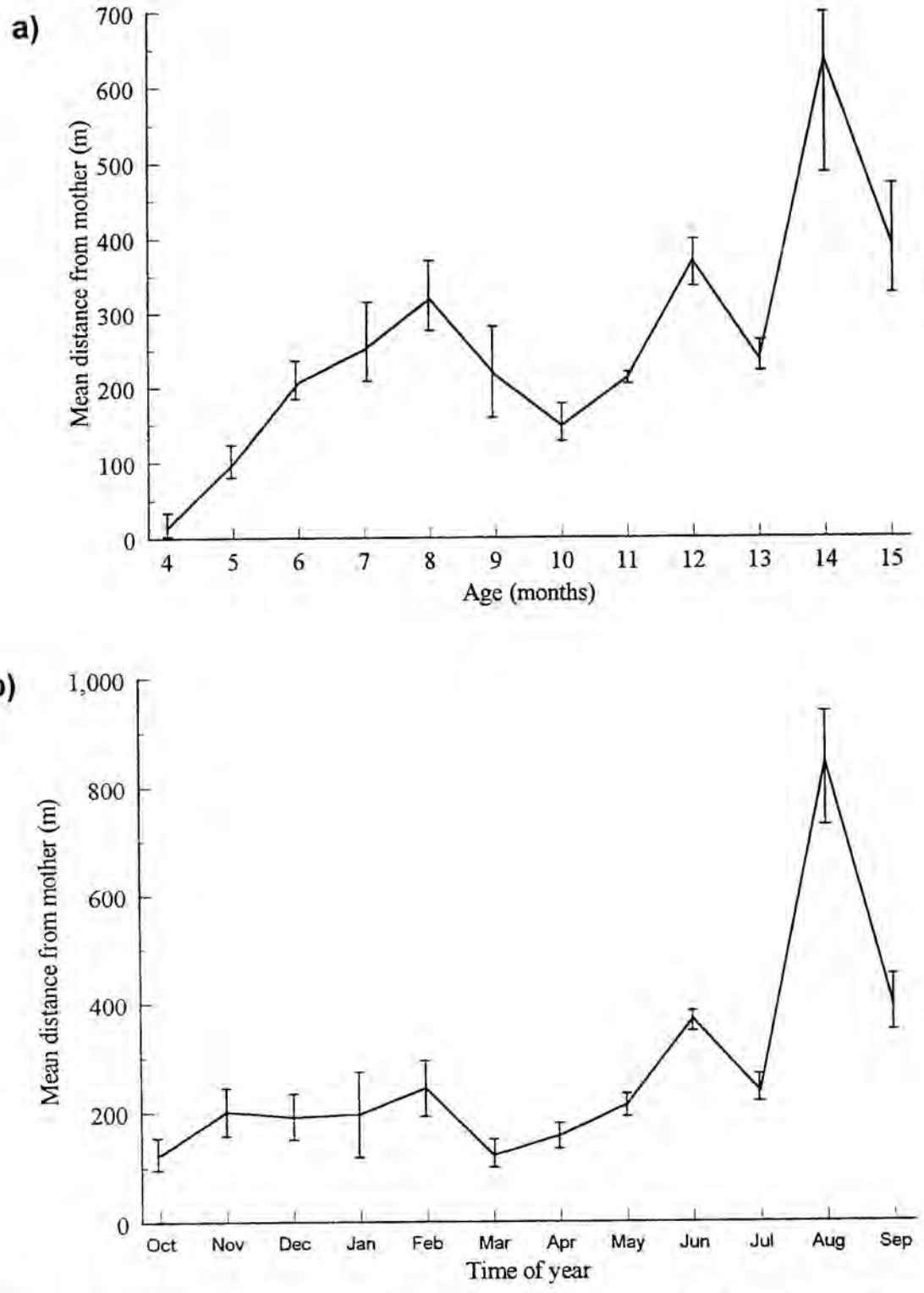


Fig.2. Mean inter-individual distance for 7 pairs of mothers and daughters from 165 total locations a) with increasing age of daughter, and b) time of year following exit from dens. Daughters that dispersed were not included.

Table 5. Capture and movement history of 22 radiocollared female cubs born on the White Oak Lake study area (1992 - 1995).

Cub	Initial capture			Mother	Duration in natal range[a] (mo)	Dispersal			Fate[b]
	Date	Weight (kg)	Age (mo)			Timing	Distance (km)	Duration (mo)	
G09	23 Oct, 92	1.5	4.0-5.0	Y34	4				Died in natal range
G13	11 Nov, 92	1.8	4.5-5.5	Unknown	3	Feb 93	4.1	6	Alive on disperal area, Aug-93
G23	10 Sep, 93	1.3	3.5-4.0	Y39	8				Died on natal range
B03	09 Oct, 93	2.2	4.5-5.5	Unknown	5				Died on natal range
B05	11 Sep, 93	1.6	4.5-5.5	Unknown	24				Alive on natal range, Sep-95
B07	11 Sep, 93	1.7	4.5-5.5	Unknown	2	Nov 93	3.7	4	Died on dispersal area
B09	12 Sep, 93	1.1	3.0-3.5	Y46	4	Jan 94	2.5	5	Returned to natal area, still alive in Aug-95
					14				
B11	13 Sep, 93	2.2	4.5-5.5	Unknown	23				Alive on natal range Aug-93
B15	20 Sep, 93	1.9	4.5-5.5	Unknown	6				Died on natal range
B18	25 Oct, 93	2.0	4.5-5.5	Y34	5	Mar 94	2.4	11[c]	Returned to natal area in Feb-95 and died there in March-95
					1				

[a] From date of initial capture and rounded off to the nearest month.

[b] Determined from last radio signal.

[c] During this period, returned briefly to natal range in Aug 94 for about 10- 12 days and again in October for about 3-6 days.

Table 5. continued.

Cub	Initial capture			Mother	Duration in natal range[a] (mo)	Dispersal			Fate[b]
	Date	Weight (kg)	Age (mo)			Timing	Distance (km)	Duration (mo)	
B20	02 Nov 93	2.0	4.5-5.5	Unknown	2	Mar 94	3.4	1	Died on dispersal area
G33	11 Sep 94	1.4	3.5-4.5	Y68	13				Alive on natal area in Sep-95
G34	15 Sep 94	1.4	3.5-4.5	Unknown	12				Alive on natal area in Aug-95
G35	16 Sep 94	1.4	3.5-4.5	Unknown	11				Alive on natal area in Aug-95
G37	23 Sep 94	1.5	3.5-4.5	Y40	9				Alive on natal area in Jun-95
G39	05 Oct 94	2.1	4.5-5.5	Y71	11				Alive on natal area in Aug-95
G40	06 Oct 94	2.9	5.5-6.5	Y69	2				Died on natal range
G41	15 Oct 94	0.9	3.0-3.5	Y70	7				Died on natal range
G44	15 Oct 94	0.9	3.0-3.5	Y70	<1				Died on natal range
G42	27 Oct 94	1.1	3.0-3.5	Y70	<1				Died on natal range
G47	20 Nov 94	1.2	3.0-3.5	Y75	7				Died on natal area in July-95
G48[d]	23 Nov 94	1.0	3.0-3.5	Y38	10				Alive on natal area in Sep-95

[d] Was radiocollared only in May 95

Fig.3. Positions of daughters' home ranges relative to mothers' home ranges in the White Oak Lake study area. Hatched polgons represent daughters' home ranges and open polygons represent mothers' home ranges. Table 5 gives identity of mother-daughter pairs, tenure of relationship and fate of daughters. B09 dispersed, but later returned to settle partly in her mother's home range.

G33
Y68
Y71
G39
Y39
G23
Y38
G48
Y69
G40
G41
B09
Y70
Y46
Y75
G47
G37
Y40
N
Kilometers
0
1

area and moved together, but B18 made occasional trips back to her natal area. The transmitter of her mother, Y34, ceased in July 1994, but it is likely that she still remained on the natal area. In March 1995, B18 was found dead in her natal range. Similar delayed fidelity to the natal site was displayed by B09 who dispersed from her natal area in January 1994, the year after she was born. She remained on a site 2.5 km away for five months, then returned to her natal area and was next located about 60 m from her mother Y46. She remained on an area which overlapped with her mother's home range until I stopped monitoring her in August 1995.

Age-sex composition and reproductive activity

The age-sex composition among females captured (1993-1994) was skewed towards females with a relatively small number of juveniles (Age Class I) compared to the number of adult females in the population (Table 6). Multiple captures of the same females during the reproductive period (March through October) provided an estimate of the proportion of adult females which were parous, non-parous and nulliparous. Between 1993 and 1994, 47% of all adult females examined were parous, 31% were nulliparous and the rest were non-parous (Table 7). Among parous females, at least two showed signs of estrus, nine became pregnant and at least 22 lactated. Two parous females in age class II exhibited signs of estrus but did not become pregnant. In the non-parous group, four females were caught only once, either towards the beginning, or towards the end of the breeding period (March - November), so it is uncertain whether they produced litters. At least 47% of the

Table 6. Frequencies, percentage composition (%) and sex ratios of raccoon age classes from live trapping data at White Oak Lake, TN (1993 - 1994).

Age Class		Males	Females	Sex Ratio
I	(0 - 14 months)	14 (20.0%)	24 (25.0%)	58:100
II	(15 - 38 months)	12 (17.1%)	16 (16.7%)	75:100
III	(39 - 57 months)	28 (40.0%)	19 (19.7%)	155:100
IV	(58 - 86 months)	15 (21.4%)	21 (21.9%)	71:100
V	(> 86 months)	1 (1.4%)	16 (16.7%)	6:100
Total		70	96	74:100

Table 7. Numbers and percentages of each age class of adult females showing different categories of reproductive activity (1993 -1994 pooled).

AGE CLASS	PAROUS[a]	NON-PAROUS[b]	NULLIPAROUS
Class II (15 - 38 mo)	3 (9.1%)	0 (0.0%)	13 (59.1%)
Class III (39 - 57 mo)	6 (18.2%)	5 (33.3%)	7 (31.8%)
Class IV (58 - 87 mo)	15 (45.5%)	5 (33.3%)	0 (0.0%)
Class V (> 86 mo)	9 (27.3%)	5 (33.3%)	2 (9.1%)
TOTAL	33	15	22

[a] Showed signs of estrus, pregnancy or lactation for at least one capture record per year.

[b] Had reproduced before but were not reproductively active that year.

adult females in the population did not reproduce in 1993 and 1994, and 31.4% had never reproduced. Eighty-one percent of the females in age class II and 39% of the adult females in age class III were nulliparous. The nulliparous age class V female who was captured in 1993 and 1994, was probably sterile.

Records of seven young adult females for which there were multiple recapture records for 2 - 3 years, confirmed that the age of first reproduction may be delayed for female raccoons at White Oak Lake. None showed signs of pregnancy as yearlings. Four females entered age class III nulliparous, but two subsequently became pregnant. Of three other females, one became pregnant but the other two were still nulliparous when examined in 1995 when all three were 28-30 months old.

Of 10 females who shared home ranges with yearling daughters (Table 5), five became pregnant the following year. Of the other five, one was not recaptured, but four showed no signs of pregnancy during the spring or summer when monitoring ceased. Except for B09, who evaded recapture and could not be examined, no daughters who remained on the natal area were seen pregnant or lactating while their mothers were alive.

Among females captured in spring 1993 and 1994, age classes did not differ by head-body length, but differed significantly by body weight, with body weight increasing through age class IV (Table 8). Increasing body weight showed a correspondence with the proportions of parous females in age classes II to V (Table 7). Pair-wise contrasts of body weight among age classes III to V were not significantly different ($p = 0.103$ to $p = 0.844$). Age class II raccoons had lower

Table 8. A comparison of mean weight and mean head-body length among four age classes of adult females captured in Spring (March - May) 1993 and 1994.

		Body weight (kg)		Head-body length (cm)	
Age Class	N	Mean	SE	Mean	SE
II	12	2.77	0.11	53.30	2.16
III	7	3.14	0.13	53.25	2.69
IV	8	3.65	0.22	51.50	1.29
V	7	3.17	0.13	55.57	1.21
		$X^2 = 12.2$ df = 3 p = 0.007		$X^2 = 4.05$ df = 3 p = 0.256	

body weight than age class IV (X^2 = 8.94, df = 1, p = 0.003), but were not significantly different from age class V (X^2 = 4.45, df = 1, p = 0.035) and age class III (X^2 = 3.90, df = 1, p= 0.048).

Survival rates

Annual survival rate of females (age classes II-V) estimated by the Kaplan-Meier method was 0.62 (N = 60, SE = 0.05, 95% CI of $\pm$ 0.1). This estimate was similar to the mean survival rate of 0.62 (Model A, SE = 0.05, 95% CI of $\pm$ 0.1) estimated from mark-recapture data by the Jolly-Seber method for adult females. Mortality was highest in the early spring, (March - April), especially among yearling females (N = 6 deaths) (Table 9). Frequency of mortality by age class (Table 10) indicated higher than expected mortality in yearlings and age class II females who were older than yearlings. Mortality was lower than expected among age classes IV and V. Mortality in young females (yearlings and age class II) was significantly higher than in females in age classes III - V combined (Table 10).

Of 23 total female mortalities, causes for 14 were unknown. Of these 14 deaths, eight raccoons were found dead inside a den. Four of the nine remaining deaths were possibly from distemper in spring 1993. Three individuals captured at this time showed symptoms of distemper. Three deaths were vehicular mortalities of a cub, a yearling and an age class III female. Two deaths of cubs were from predation and poaching.

Table 9. Monthly mortality rates, number of radio days monitored, and number of deaths among radiocollared female raccoons at Oak Ridge, 1992-1995.

Month	N	Radio days	No. of deaths	Mortality rate
January	55	1705	0	0.000
February	49	1372	0	0.000
March	48	1488	6	0.125
April	48	1440	4	0.083
May	56	1680	1	0.018
June	53	1590	1	0.019
July	50	1550	5	0.100
Aug	44	1364	0	0.000
Sept	40	1200	1	0.025
Oct	45	1395	1	0.022
Nov	57	1710	2	0.035
Dec	57	1769	2	0.035
Total	60	18263	23	0.383

Table 10. Observed and expected frequencies of mortality among different age classes of radio-collared females (1992 - 1995). Expected frequencies of mortality were based on the number of days each age class was monitored. Frequencies of mortality of age class II and age classes III to V were pooled to obtain expected frequencies ≥ 5.

Age Class	Radio-days	Observed no. of deaths		Expected no. of deaths	
Cubs[1]	1498	3			
Age Class II(Yearlings)[2]	3909	9	15	4.66	8.24
Age Class II[3]	3007	6		3.58	
Age Class III	2890	4		3.44	
Age Class IV	5134	1	5	6.13	11.76
Age Class V	1825	0		2.19	
Total	16765	20		20	

$X^2 = 9.44$ df = 1 p = 0.002

[1] Mortality and number of days cubs were followed are shown but not included in the totals and the Chi-square test.
[2] Offspring of the previous year (approximately 10 - 24 months).
[3] Excludes yearlings.

Discussion

When adult survivorship is low, young among some species that show natal philopatry often inherit the natal home range from parents. For example, in kangaroo rats, *Dipodomys spectabilis*, natal philopatry is opportunistic to some extent (Jones 1984) with young facing little parental competition for resources. Alternatively, in other species with high adult survivorship, philopatric offspring may remain in or adjoining the parental home range. Such situations increase the potential for cooperative behaviors to evolve, but may also reduce future parental reproductive success, especially if space is donated or shared.

Three primary findings emerge from this study. The first is that natal philopatry in raccoons conforms to the second pattern described above. Female young persist on natal areas beyond dependence and beyond their mothers next breeding episode. This is not surprising, considering that studies on raccoons report extensive range sharing among females (Fritzell 1978a, Rabinowitz 1981). Although sharing of space is not a necessary correlate of philopatry, it is a reasonable consequence because kinship might be expected to decrease the cost of mutual tolerance (Vehrencamp 1979). Most cubs at White Oak Lake were captured when they were between 3 - 4.5 months old indicating that cubs begin to exit the den and follow their mothers at the approximate age of three months. My radio telemetry data indicated mothers and daughters remained close until the daughters were 4 - 5 months old. Even though the association gradually became more distant, most female offspring occupied the mother's range and continued to do so as yearlings.

Second, despite potentially available habitat outside the ORR, most females remained on their natal area. Also, two cubs that dispersed showed attachment to the natal area by returning to it several months after dispersing. The position of the White Oak Lake area would require a relatively long foray to encounter habitat outside the ORR. It is significant therefore that the only disperser who was observed alive and established after one year, made the longest trip and moved out of the ORR. Also the two dispersing females that returned to the natal area made the shortest forays, neither one leaving the boundaries of the ORR. Hypotheses to explain female dispersal have usually been somatic or genetic. The somatic value of dispersal has usually been seen as an alternative to facing locally crowded conditions that result in competition for resources such as food, space, or mates (Moore and Ali 1984) whereas genetic explanations regard dispersal as a functional response to decrease inbreeding (Itani 1972, Packer 1979). The difficulty over which hypothesis best explains dispersal and whether they are mutually exclusive is appreciated here. Most female raccoons dispersed in the spring when mortality was highest among yearlings on the natal area, but this was also when yearling raccoons approach sexual maturity in most populations (Stuewer 1943b). Recaptures of cubs the following year were low for both males and females, showing no strong indication that males were more likely to disperse as yearlings. The low recapture rate may be because of high mortality in the spring. In a report of nine years of mark-recapture data on raccoons in Chuck Swan, East Tennessee, Glass (1991) indicated that philopatry was female-biased; recapture rates were 35% for females (N = 33) compared to 8% for

males (N = 34) who were marked as cubs and later killed in hunts or recaptured as adults. Although male raccoons often remain on the natal area for some months after weaning, there is little evidence that males remain on their natal area beyond reproductive maturity which can range between one to two years (Sanderson and Nalbandov 1973, Stuewer 1943a).

The third feature of the study provides new insights into female social organization in raccoons and the possible consequences of strong natal philopatry (Murray 1967). Although natal philopatry was more common than dispersal among females at White Oak Lake, the advantages of natal site fidelity such as enhanced survival or earlier opportunities to breed than dispersers (Storm et al. 1976, Rogers 1987), remain unclear. Natal dispersal at White Oak Lake was too infrequent to evaluate the relative benefits of being philopatric but, if young females represent a significant fraction of philopatric individuals, immediate prospects of enhanced fitness were low. Population characteristics of White Oak Lake revealed that mortality was frequent, body weight was relatively low and reproduction occurred later in young females at White Oak Lake than in similar aged females in other populations of raccoons (Stuewer 1943b, Kaufmann 1982). On the other hand, older females were more reproductively active, had lower mortality, and there was less evidence that sharing space with daughters reduced their reproductive success or survivorship.

Some features of the population ecology of raccoons might illuminate aspects of female social organization and the possible consequences of female philopatry in

some carnivores. I address two features in particular: population density and components of female fitness such as mortality and reproduction. At White Oak Lake, population densities were relatively high and the proportion (58%) of females in older age classes (III - V) was greater compared to other studies of raccoons in east Tennessee. For instance, Rabinowitz (1981) and Glass (1991) report percentages of 35 and 36, respectively, for females in age classes III - V in lower density populations. If space and resources are preconditions for successful reproduction (Greenwood 1980), young females entering the reproductive cohort of the population are likely to encounter more competition. No single study on raccoons has considered the connection between population density, high female philopatry, age at first reproduction and mortality in raccoon populations, but I use the available evidence to make inferences.

Raccoons can coexist at high densities in habitats such as bottomland hardwoods, marshes and flood plain forests (Kaufmann 1982), and occasionally aggregate where food resources are localized and plentiful (Tevis 1947, Sharp and Sharp, 1986) or when winters are harsh and suitable dens are limited (Whitney and Underwood 1952, Twitchell and Dill 1949). Kaufmann (1982) suggests that density in raccoons is related to food availability; that is, densities are comparatively low in pine forests or where pines are mixed with hardwoods. Thus, food availability is a possible limiting factor, even among species as opportunistic as raccoons.

Although several studies report that up to 60% of yearling females reproduce (Stuewer 1943b, Johnson 1970, Junge and Sanderson 1982), there is considerable

variation in this regard. Scheffer (1950) reported no reproduction among yearling females in Washington, and Fritzell (1978b) reported that only 14% of yearlings in North Dakota bred. Fritzell et al. (1985) later reported that proportions of parous females in age class II may differ dramatically among years and it was this particular age class that contributed to annual variation in overall female reproduction. Mean body weights of nulliparous yearlings were less than weights of parous yearlings in years when overall pregnancy rates were low (Fritzell et al. 1985). Nutrition and body weight has been considered responsible for low pregnancy rates and litter sizes in raccoons (Dunn and Chapman 1983), but Fritzell et al. (1985) suspected that nutrition, population density, weather and unidentified intrinsic or extrinsic factors contribute to high annual variation in pregnancy rates among yearling raccoons.

Nutrition has been considered a factor governing mortality in young raccoons, particularly yearlings during their first winter Kaufmann 1982). Evidence of high mortality in yearling raccoons also has been cited by Johnson (1970) and Mech (1968), who consider malnutrition and food scarcity to be the main causes. Johnson (1970) also considered the hazards of dispersal and moving apart from family groups to be partly responsible for the greater winter mortality in juveniles. The overall implications are that despite their opportunistic nature, nutrition is a limiting factor for raccoon populations and during periods of low food availability, younger animals suffer the consequences of higher mortality and decreased reproduction.

It is possible that younger animals still diverting most of their energy resources towards growth have less accumulated body fat which could, in turn, affect

reproduction and increase the risks of mortality. But the high variation in reproduction in age class II females suggests that, when resources are limited, social factors may increase the disadvantage of being a young female. Older, heavier and presumably more dominant females may have priority of access to the best feeding places and den sites and, despite reports of high conspecific tolerance among raccoons, the exclusion of younger animals from preferred areas is reported. For example, aggressive behavior of raccoons at localized feeding areas was suggestive of social dominance (Tevis 1947) and juveniles unaccompanied by adult females were usually driven away (Sharp and Sharp 1956). In such contexts, the benefits of remaining close to mothers are obvious even if it means that under certain conditions young may delay reproduction while they remain on the mother's home range.

What then are the individual consequences of high female philopatry in raccoons? Under certain ecological and demographic conditions that lead to habitat saturation, tolerance of philopatric daughters may incur reproductive costs to mothers, but for philopatric daughters, the costs of delayed reproduction and mortality seem more severe. Most reports of high fecundity in yearling raccoons come from studies on hunted populations in which turnover rates are probably high. In populations that are not exploited with low mortality in older females, does high female philopatry occur with delayed reproduction in younger females? Among raccoons, the only evidence that links high female philopatry with low reproduction in yearling females comes from Fritzell's (1978a, 1978b) studies, but also, most studies have not documented the extent of natal philopatry in female raccoons.

Comparisons of exploited and unexploited populations suggest that density-dependent population regulation may be most evident in populations close to carrying capacity (Fowler 1981). For example, in unexploited populations of beavers, *Castor canadensis*, Nordstrom (1972) observed lower reproductive rates, delayed sexual maturity and low dispersal relative to exploited beaver populations. Similar reproductive trends occur among fox squirrels from exploited and unexploited populations (Nixon et al.1986) and Minta (1990) attributed reproductive suppression in badgers, *Taxidea taxus*, to high densities in an insular population. Among a fairly high population of European badgers, *Meles meles*, Woodroffe et al. (1993) found higher rates of reproduction in immigrant females than philopatric females; breeding in female groups formed through natal philopatry was usually monopolized by one female suggesting that females dispersed to increase their chances of breeding. That reproduction is affected by demographic and ecological conditions which elevate resource competition among females is not always emphasized, but the population characteristics of several carnivores in saturated habitats support this explanation (e.g., Storm and Tzilkowski 1982, Minta 1990, Woodruffe and MacDonald 1995, this study). Although the precise mechanisms driving philopatry are uncertain, the circumstances surrounding philopatry in raccoons at White Oak Lake are consistent with the predictions of Murray (1967). Under conditions that limit resource availability such as high adult survivorship and high population density, philopatry entails immediate costs that can be high.

CHAPTER 3

THE RELATIONSHIP BETWEEN PHILOPATRY AND FEMALE SPATIAL ORGANIZATION IN RACCOONS

Resource inheritance is widespread in both solitary and social taxa and is considered to provide the basis for the origin and development of gregarious behavior (Brown 1974, Eisenberg 1977, Woolfenden and Fitzpatrick 1978). However, the role of kinship in determining patterns of spacing has begun to generate interest more recently (Waser and Wiley 1979, Waser and Jones 1983). In most polygynous species of mammals, juvenile males are the predominant dispersers (Dobson 1982) and the tendency for philopatry, is primarily among female offspring (Liberg and Von Schantz 1985). Social benefits accruing to philopatric females may be strong (Wrangham 1980) and it is, therefore, not surprising that in many gregarious mammals female kin are often organized into matrilineal social groups. Solitary species also are reported to show signs of "kin-clustering" in the dispersion patterns of females or both females and males. For instance, among thick-tailed bushbabies, *Galago crassicaudatus*, who are monogamous primates, female kin occupy home ranges close to or adjacent to those of close relatives (Clarke 1978); in banner-tailed kangaroo rats, *Dipodomys spectabilis*, up to 39% of male and female offspring remain on the natal range through reproductive maturity (Jones 1984).

Among solitary carnivores, female philopatry is widely suspected, but apart from a few studies such as female land tenure patterns in black bears, *Ursus americanus*, (Rogers 1987, Schenk 1994) and the Bengal tiger, *Panthera tigris* (Smith et al. 1987),

the relationship between kinship and spatial organization has been poorly documented. Part of the difficulty lies in following known individuals from birth to maturity. Most solitary carnivores are nocturnal, shy, and have life histories which involve extended periods of time between birth and sexual maturity (Gittleman 1986). Moreover, because the genetic relatedness of individuals cannot always be established from field observations, the influence of kinship on spatial and behavioral relationships is largely unknown. These features invoke practical difficulties in establishing the extent of philopatry and examining the mechanisms that lead to it.

Molecular techniques have contributed significantly to our understanding of social systems when individual relatedness has been speculative or unknown. The utility of different molecular techniques is dependent in part on the question, and the part of the genome examined (Hillis et al. 1996). For studies of parentage and kinship, allozyme electrophoresis has proved useful under certain conditions (McCracken and Bradbury 1981, McCracken 1984, Wilkinson 1985) but is frequently hampered by low variation (Simonsen 1982). It would seem that questions of maternity would best be investigated by employing genetic markers provided by rapidly evolving mitochondrial DNA, but applying mitochondrial markers to questions of single-generation maternity have been limited (Kessler and Avise 1985). The genotypic variability generated by recombination of nuclear genes far surpasses that of the rapidly mutating but non-recombining mitochondrial DNA (Avise 1994). Most conventional DNA fingerprinting techniques work by targeting more variable parts of the genome such as variable number of tandem repeat loci (Jeffreys et al. 1985a, 1985b), or by accessing large numbers of polymorphic

loci such as random amplified polymorphic DNA markers (RAPDs; Williams et al. 1990). One of the problems associated with such markers is that the allelic relationships of bands are often unknown and similarly sized bands from non-homologous loci may be confused, thus increasing the variance of similarity (Lynch 1988). Although this property limits the extent of information one can obtain, Lynch (1991) considers band-sharing informative about kinship if it is calibrated using individuals of known relatedness. Nevertheless, because of broad overlap in band-sharing distributions of relatives versus non-relatives in most species, attempting to interpret more remote relationships (e.g., grandmother, aunt, cousin) beyond that of parent-offspring, or full-siblings, is generally not possible with multilocus approaches.

Initially, most studies employing multilocus DNA fingerprinting focused on the determination of familial relationships (Wetton et al. 1987, Burke and Bruford 1987), particularly paternity (e.g., Burke et al. 1989, Westneat 1990) or were used to define groups of individuals as unrelated, moderately related or highly related at the level of siblings or parents and offspring (e.g., Packer et al. 1991, Gilbert et al. 1991, Wayne et al. 1991). Used in conjunction with field observations, these studies have confirmed or revealed inconsistencies in behavioral data emphasizing the need for an independent estimate of genetic relatedness. For example, among lions, *Panthera leo*, Packer et al. 1991) found that social groups, formerly considered to consist of highly related individuals within each sex, actually contained a significant proportion of unrelated individuals. Lehmann et al. (1992) found that genetic data indicated short-range dispersal to be more common among female wolves than males, although behavioral data revealed

no obvious bias in sex-dispersal. Used in these contexts, multilocus methods have proved invaluable in improving our understanding of relatedness and its behavioral correlates in animal populations.

Understanding the relationship between kinship and spatial organization requires an estimate of genetic relatedness among individuals and an understanding of their spatial distribution. I combine a multilocus fingerprinting approach with three years of observations of spatial relationships among female raccoons to determine whether kinship affects spatial organization among female raccoons.

The approach

I used a technique which employs gene amplification (RAPD assay; Williams et al. 1993) to assess genetic similarity among individuals in the White Oak Lake population. RAPD markers are generated by the amplification of random DNA segments with single six to10-oligonucleotide primers of arbitrary sequence. The technique is relatively cost effective, can be applied to a broad range of species, requires no knowledge of the target DNA sequence, is non-radioactive and requires only nanogram quantities of DNA (Hadrys et al. 1992). Despite these advantages of RAPD markers over those of more conventional RFLPs (restriction fragment length polymorphisms), the RAPD assay is sensitive to many factors in the PCR reaction which results in poor reproducibility (Pillay and Kenny 1995) unless reaction conditions are carefully standardized (Williams et al. 1993, Scott et al. 1992). Also, RAPDs behave as dominant markers which tends to make the estimation of allele frequencies less reliable than with codominant markers (Lynch and

Milligan 1994). This disadvantage of the dominant nature of RAPD markers can be partly compensated for by the ability to access larger numbers of polymorphic markers (Lu et al. 1995).

With data obtained from RAPDs I used an approach similar to Lehman et al. (1992), Wayne et al. (1991) and Gompper et al. (1997) to classify individuals as unrelated, moderately related or closely related at the level of siblings or parent-offspring. I first assessed the degree of RAPD band-sharing among individuals known to be closely related such as mothers and offspring from the field population. This provided an estimate of mean band-sharing and confidence intervals for individuals related at the level of siblings or parent-offspring. I then determined the average similarity among individuals drawn from two populations in East Tennessee who were likely to be unrelated. These two estimates provided the means for classifying individuals of unknown relationships within the Oak Ridge population and the basis for comparing measures of spatial distance or overlap with increasing or decreasing band similarity.

The Experimental system

The mating system in raccoons is either promiscuous or polygynous as inferred through telemetry data (Fritzell 1978a), with home ranges of an adult male encompassing those of one or more adult females. Extensive overlap among female home ranges (Kaufmann 1982) and persistence of young on the natal area (Chapter 2) suggests that philopatry is by 'parental consent' (Table 1) and, consequently, neighbors are likely to be close kin. Raccoons have been observed in groups consisting generally of a mother and

young of the year, groups of yearlings from the same litter and, occasionally, groups of adults and juveniles denning together in winter (Whitney and Underwood 1952). However, the general nature of adults is solitary (Kaufmann 1982). The foods consumed by raccoons range by season from nuts and berries to arthropods and vertebrates reflecting their generalist food habits. In comparison to other procyonids, the broad pattern of resource use in raccoons has been described as a fluctuating grain response (Forman 1985). Resources may be intermediate in distribution and predictability and female social and spatial organization in raccoons seems to reflect this pattern (Crook 1972, Emlen and Oring 1977). Most female raccoons have solitary lifestyles and overlapping ranges, but the temporal nature of resource use is unknown. Females produce one litter per year possibly fathered by more than one male. Dispersal seems predominantly male-biased with several reports of distances exceeding 20 km traveled by males (Forman 1985). Although female philopatry seems widespread, dispersal in female young also is documented (Stuewer 1943a, Cowan 1973, Chapter 2). Artificial relocation of animals from state to state by raccoon hunters, and relocation on a local level by people affected by nuisance raccoons, is common and likely to affect population structure at a local and regional level.

These social characteristics of raccoons have implications for the expected pattern of genetic relatedness and spatial organization among females in the population (Table 11). I related band-similarity among females to three spatial parameters which were home range overlap, distances between harmonic centers of activity, and measures of 'simultaneous' inter-individual distance. Each parameter differs qualitatively in the type

Table 11. Hypotheses of female philopatry and spatial organization that were tested.

Hypotheses	Predictions
1. Philopatry is predominantly demonstrated by female raccoons.	A positive association between genetic distance and physical distance among females. Average female-female similarity will be greater than average male-male similarity. Average male-female similarity will be less than average female-female similarity.
2. Female spatial and social organization is independent of relatedness.	No association between genetic similarity and home range overlap. No association between genetic distance and physical distance among females. Nature of spatial and temporal interaction is independent of relatedness.

of information it provides. Measures of home range overlap indicate how females in adjacent areas relate to each other on a spatial basis such as whether space is exclusive or shared. If females settle within or close to their natal area, home range overlap would be positively associated with band similarity. Comparing distances between harmonic centers of activity allow comparisons across a larger spatial scale. Non-adjacent females can be included and comparisons made across the entire 12 km^2 study area. If it were common for females to leave natal ranges and move several home ranges away, then genetic distance would show no association with spatial distance across an area smaller or proportional to dispersal distance. The first two spatial measures demonstrate patterns but tell us little about how space use might be modified by the presence of close relatives, or whether females partition common resources in a temporal manner. The third measure has both a spatial and temporal dimension to it and was used to examine how individuals might modify use of space relative to one another and to an area they share. If philopatry was more common among females, then average band-sharing similarity values within adult females in the White Oak Lake area should be greater than average male-male similarities or average male-female similarities.

Methods

Study area and general field methods.

Radio telemetry data were collected primarily in the White Oak Lake area of the ORR (Fig. 1). I defined the White Oak Lake study area as the 95% composite adaptive kernel home range of all females and males monitored. This area was 1197 ha, or 11.97

km^2 in size. Five females from the Freels Bend area, which was 7-10.5 km northeast of the White Oak Lake site, (Fig. 1) were also radio monitored during 1992. The study areas, capture techniques, radio-tagging, aging and descriptions of reproductive status of females are described in Chapter 2.

Genetic work

Collection of samples for genetic analyses

Tissue samples for genetic analyses were obtained from 146 raccoons at the White Oak Lake study area, with additional samples collected from two sites on the ORR situated 7-10 km from the White Oak Lake study area (Fig. 1). Samples from these two sites included 14 individuals from Freels Bend and 30 individuals from the East Fork area. Thirty four raccoons were obtained from the Chuck Swan Wildlife Management area, 50 km northeast of the ORR, during the hunting season in November 1992 and 1993, and two raccoons from coastal North Carolina. All females (N = 88), and 84% of the males (N = 58) captured on the White Oak Lake study area were sampled. Samples of seven females and 6 males used in trial VNTR analyses were not included in the results. Sites of capture, identification, sex and age classes of all raccoons used for genetic analyses are listed in Appendix B.1. Lactating females captured together with one or more cubs were considered mother and offspring. Cubs were either in the trap with the mother, or, when very young, would remain around the mother's trap. It was usually possible to catch young cubs by hand.

Raccoons were captured in live traps, anesthetized with 0.1 mg kg^{-1} ketamine hydrochloride, weighed, measured and ear-tagged for identification. To obtain muscle samples, an incision of approximately 1-cm in length was made in the inner thigh after trimming the hair in the area and cleaning the skin with alcohol. Small muscle biopsies (<0.25g) were obtained with the aid of tissue forceps and scissors. The samples were placed under ice until trapping was completed, after which they were stored at -20^0 C.

Laboratory work

Genetic analyses were performed in the Oak Ridge National Laboratory's, Plant Genetic lab. Genomic DNA was isolated from 242 muscle biopsies in batches of 25-36 samples at a time. Each sample of tissue was minced with a scalpel, suspended in 500 µL Lifton buffer (0.2*M* Sucrose, 50m*M* EDTA, 100m*M* Tris, 0.5% SDS) and digested with 30 µL of 20mg/ml proteinase-K for 12-16 hours at 60^0C. Twenty µL of 10 µg μL^{-1} ribonuclease A (Sigma Chemical Co., St. Louis) was added and digestion was continued for two hours at 37^0C. Samples were then extracted with an equal volume of buffered phenol for five minutes, vortexed briefly, spun at 5000 rpm and the aqueous layer containing the DNA was removed. The extraction was repeated with phenol:chloroform: isoamyl (24:24:1) and finally with chloroform:isoamyl (24:1). The presence of high molecular weight genomic DNA was verified at this stage by running 10 µL of the supernatant on 8 g L^{-1} agarose gel containing 0.1 µg mL^{-1} ethidium bromide in 45 m*M* tris-borate/ 1m*M* EDTA (TBE). Samples were treated with two-thirds volume 100% ice-cold ethanol and left overnight at -20^0C to precipitate. DNA pellets were recovered by

microcentrifugation, washed with 75% ethanol, vacuum-dried, suspended in 500 μL 10m*M* Tris-HCL/1mM EDTA (pH7.5) and quantified with a TKO 100 fluorometer (Hoefer Scientific Instruments, San Francisco, CA).

Approximately 300 primers were screened to select those that produced clearly identifiable polymorphic bands. Five individual DNA samples (two from Chuck Swan and three from Oak Ridge) were diluted to 5ng μL^{-1} and used to screen 294 decamer primers (picked from series AA 1-20 through AN 1-20, Operon Technologies, Inc., series 100-200 University of British Columbia). One hundred and forty eight primers were also screened in paired combinations. Based on the presence of well amplified polymorphic bands, twenty six primers were chosen for analyzing the DNA profiles of 226 raccoons. RAPD-PCR was performed according to the protocol of Gunter et al. (1996) with minor modifications. Each RAPD reaction contained 50 m*M* KCl, 10 m*M* Tris-HCl, pH 8.0, 1 mL L^{-1} Triton X-100, 2.5 m*M* $MgCl_2$, 200 μ*M* each dNTP, 0.5 units of Taq polymerase (Promega), 100 μg mL^{-1} bovine serum albumin, 10 ng primer and 10 ng of template DNA in a total volume of 10 μL.

Amplification reactions of all genotypes by a single primer were set up in a single aliquot of master mix containing all components except template DNA. Three reaction sets were necessary to run RAPD-PCR on 242 samples in a 96-well thermocycler. Therefore, in addition to internal negative controls used in sets A, B and C, two types of positive controls were included: 1) templates from set A and B were used in sets B and C, 2) individuals sampled more than once in the field and for whom separate DNA extractions were conducted, were included in different reaction sets. Out of 76 total

fragments from 18 primers that were scored, 71 fragments were repeatable among 13 individuals who were sampled more than once (Table 12) and all 76 fragments were repeatable among templates from sets A and B that were used in sets B and C.

Amplifications were performed in a Perkin Elmer-Cetus thermocycler for 35 cycles of the following steps: denaturation at 94^{0}C for 5 sec, annealing at 36^{0}C for 30 sec, and polymerization at 72^{0}C for one min. Amplification products were analyzed by electrophoresis on 10 cm 15 g L^{-1} agarose gels containing 0.1 μg mL^{-1} ethidium bromide in TBE and photographed under UV light with Polaroid type 55 positive/negative film (e.g., Fig. 4). A 100-base pair (bp) marker (BRL) was used as a molecular size standard for RAPD markers.

Genetic Data Analysis

Bands (fragments) for each individual were scored for presence or absence. Monomorphic markers were excluded from the analysis. Lynch and Milligan (1994) recommend that bands whose observed frequency is less than 1-(3/N) be used for an unbiased estimation of population genetic parameters. I included a band if it was present in at least five individuals and absent in at least seven. The degree of band-sharing between two individuals was used as a measure of relatedness. A computer package RAPDPLOT 2.3 (Kambhampati et al. 1991) was used to generate matrices based on pair-wise similarity (Nei and Li 1979) and matching (Apostol et al. 1993) coefficients with the following formulae:

$$\text{Similarity } (S) = 2N_{AB}/(N_A + N_B) \text{ and}$$

Table. 12. Incidence of non-repeatability among two or more replicate DNA samples. Replicates consisted of the same individuals sampled at different times with some DNA extracted at different times. Primers are identified by number in Appendix B.3.

Duplicate samples	PRIMER NUMBER																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
1. 41 120*	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
2. 48 186*	0(1)	1	1	1	1	1	1	0(1)	1	1	1	1	1	1	1	1	1	1	1
3. 65 94*	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
4. 76 115*	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
5. 77 86	1	1	1	1	1	1	1	1	1	1	1	0(1)	1	1	1	1	1	1	1
6. 78 216*	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
7. 123 188*	0(1)	1	1	1	1	1	1	1	0(1)	1	1	1	1	1	1	1	1	1	1
8. 138 175*	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
9. 151 165*	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
10. 163 184	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
11. 184 228*	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
11. 167 236*	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
12. 166 173	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
13. 143 176*	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

1 = both templates matched for all loci scored for that primer.
0 = questionable matches and number of loci ( ) where a mismatch occurred.
*DNA obtained from different extractions.

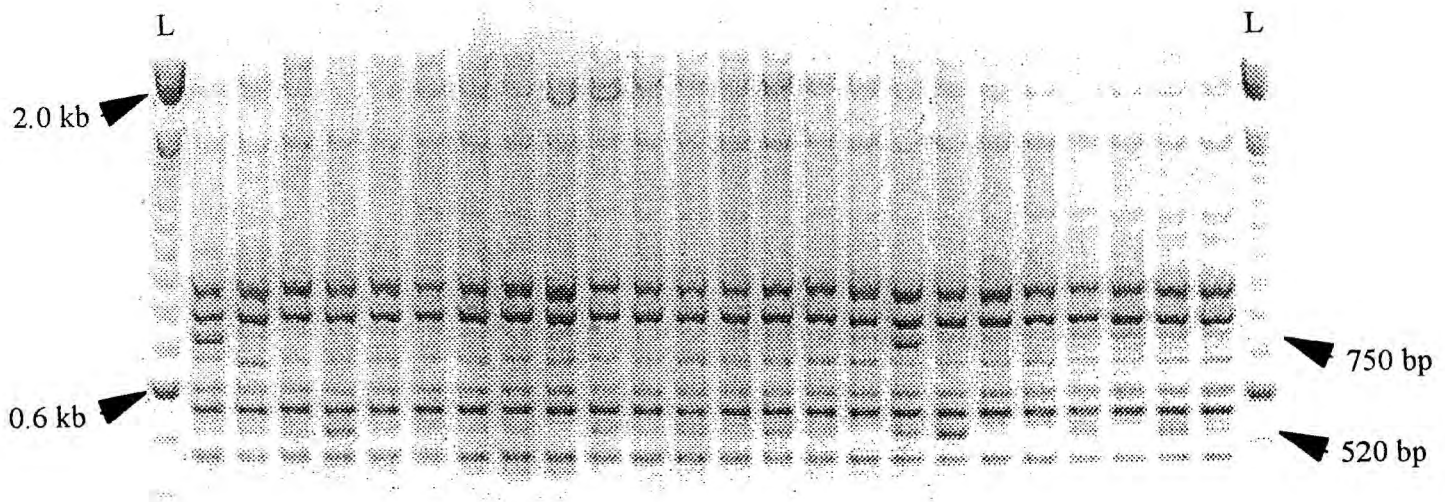


Fig. 4. Ethidium bromide stained DNA fragments amplified from 24 raccoon genotypes. Primer AL04 amplified two products, (750 bp and 520 bp) which were polymorphic. L = 100 bp ladder used to determine the approximate molecular weight of each fragment.

Matching $(M) = N'_{AB}/N_T$

where N_{AB} is the number of shared bands in both individuals A and B, N_A is the number of bands in individual A, N_B is the number of bands in individual B, N'_{AB} is the total number of matches (i.e., bands absent or present) in individuals A and B, and N_T is the number of fragments scored in the overall study. Because pair-wise S values were not independent an unbiased estimation of the standard error was calculated as $[2S\ (1\text{-}S)\ (2\text{-}S)/n\ (4\text{-}S)]^{0.5}$ in which n was the number of fragments per individual and S the mean of all pair-wise S values (Lynch 1991). To express the percentage of similarity or matching between A and B, I used the term band similarity or band matches. The percentage genetic distance between A and B ($Ds = 1 - S$ or $Dm = 1 - M$) was expressed as band-sharing distance and band-matching distance. The inclusion of slightly more fragments in the low frequency range tended to increase the variance of the similarity index slightly and, at the same time, inflate the matches among the rest of the individuals. For the sake of comparison, results of both similarity and matching indices were reported in some initial analyses. These metrics showed a strong correspondence; thus, the similarity index was used in subsequent analyses.

I performed bootstrap analysis of Nei's genetic distance, D_N (Nei 1972) to determine if there was genetic differentiation between raccoon populations from Oak Ridge and Chuck Swan. I identified three sub-populations on the Oak Ridge reservation as White Oak Lake, East Fork and Freels Bend, and included two genotypes from North Carolina to serve as an outgroup. Using RAPDDIST (Black IV 1995) with Lynch and Milligan's (1994) correction for allele frequencies, the combined data set was randomly

subsampled a 100 times to produce 100 distance matrices. Bootstrapping leads to an estimate of the sampling distribution of the estimate D_N and the bootstrap scores are interpreted as a measure of accuracy of the specified branching pattern (Weir 1996). If band frequencies are consistently different for a large number of fragments, bootstrap support for derived branches will be high. High bootstrap scores (>90%) imply strong support for a particular cluster. Cluster analysis was performed with the NEIGHBOR program of the phylogeny inference package PHYLIP 3.5c (Felsenstein 1993). CONSENSE was then used to generate a single unrooted tree with the amount of bootstrap support indicated on the individual branches.

Standard parametric or non-parametric tests are inappropriate for comparisons among pair-wise similarity values which are interdependent (Dietz 1983). To assess the significance of differences between two similarity distributions, a permutation test appropriate for similarity data was used (Wayne et al. 1991, Lehman et al. 1992). With a SAS program written by Dr. A. Saxton (University of Tennessee), the observed difference between the means of the two groups was first computed, data from the two groups were pooled and the pooled data randomly sub-sampled 1000 times. Each sub-sampling calculated the difference between the observed and theoretical mean calculated from the pooled data and the one-tailed probability of the two means being different was tested.

Female spatial organization

Collection of telemetry data.

Wild raccoons are mostly nocturnally active and secretive. Although I attempted to used direct observation as much as possible, radiotelemetry was the principal technique used to locate raccoons. Radio-collared animals were located from the ground with a portable receiver (TR-2, Telonics Inc., Mesa, AZ), a 5-element vehicle-mounted antenna (Wildlife Materials, Carbondale, IL) and a 2-element hand-held H-antenna. Two to five locations were obtained on each raccoon per week. Radio collared individuals were located only once a night during a five hour tracking period. Night time tracking periods were from 1700 h-2200 h, 2200 h-0300 h and 0300 h-0800 h. Raccoons were located only once during a day time tracking period from 0800-1700 h. During daylight, animals were frequently located by approaching den sites. Most night time locations, when raccoons were active, were obtained by triangulation.

Estimation of home ranges and activity centers

Home range estimation assumes that observations of an animal are spatially independent. Independence of locations was tested with Schoener's ratio t^2/r^2 in which t^2 is the mean squared distance between successive locations and r^2 the mean squared distance from the center of activity (Swihart and Slade 1985). Radio locations were autocorrelated ($p \leq 0.05$) for approximately 50% of raccoons ($N = 43$). Independence of locations is influenced by the lag time between sequential observations which should ideally be the minimum time interval over which an animal could occur, in a probabilistic

sense, anywhere in its home range. Swihart and Slade's (1985) assumptions of spatial and temporal randomness is violated when an animals use of its home range is influenced by physical heterogeneity, when home range centers shift seasonally, if animals travel along well-defined paths in a predictable manner, or an animal's mobility varies seasonally (Lair 1987, Minta 1990). Thus, characteristics of animals that violate the assumptions of spatial independence are often biologically meaningful. Lair (1987) concluded that home ranges can provide unbiased estimates of space use patterns even when successive points are not independent statistically, provided they are biologically independent. A sampling interval long enough to allow an animal to move from any point in its home range to any other point is therefore sufficient. I chose to use biological independence in which serial locations were separated by a major activity shift. Therefore, a raccoon was located only once for a particular night and once during daytime shifts.

I used the adaptive kernel method to estimate home ranges. The adaptive kernel method is a non-parametric technique recommended for its flexibility and robustness (reviewed in Worton 1987, 1989). In principal, it is similar to the harmonic mean estimator where the contours of area that it produces are directly related to the frequency of occurrence of an individual within its home range. A sample size of 30-100 locations is recommended for the estimation of home range with non-parametric methods (Worton 1987), although sample size may also depend on the type of species being studied. For example, home ranges of smaller species which show high site-fidelity can be adequately represented with smaller sample sizes (Bekoff and Mech 1984). Because sample sizes of locations differed among raccoons, I determined the minimum number of locations

required to estimate home ranges by regressing home range size against number of locations for 22 female raccoons with N >50 locations. When home range size is regressed against number of locations, the asymptote of the curve (Bekoff and Mech 1984), or the percentage increase in area estimates (Messier and Barrette 1982), indicate adequate sample sizes for home range estimation. Both 95% and 50% adaptive kernel home ranges were calculated at increments of 10 locations for each raccoon. Ninety five percent contours showed the most change at <40 locations; the change in home range size for every 10 additional locations thereafter was <10 % (Appendix A.1), but increased again at over 90 locations because of variance introduced by fewer individuals. Fifty-percent contours of home range showed the most increase at <20 locations; the change in home range size for every 10 additional locations thereafter was <10% for up to 110 locations. I used a minimum of 40 locations for estimating all 95% home range contours.

I used the distance between harmonic centers of activity for dyads of females as a measure of dispersion. This was preferable to comparing distance among sites of capture, the latter sometimes being peripheral to an individual's home range. The harmonic center of activity is considered the best measure of an animal's point of greatest activity and its position is minimally affected by occasional forays outside the home range (Dixon and Chapman 1980, Lair 1987). I considered the 50% adaptive kernel home range to represent the core area of a raccoon. Because most adaptive kernel 50% home ranges remained stable at >20 locations, a minimum of 20 locations were used to determine harmonic centers of activity.

Several species show marked shifts in centers of activity over time. If such shifts are extreme, centers of activity may be less useful as an index of dispersion unless data for each dyad is adjusted for a similar sampling duration. To determine if differences in sample size or duration changed the position of the harmonic center of activity, I compared shifts in centers of activity with increments of 20 locations for all raccoons with 50 or more locations. I first determined the harmonic center of activity for each raccoon with all its locations and compared it with harmonic centers of activity calculated in increments of 20 locations (Appendix B.2). The mean shift in the center of activity was 92 meters (10% of the mean 95% home range diameter). Also, 70 of 71 shifts in activity centers remained within the contours of the 50% home range. The one exception was female Y03; the center of activity with the first 20 locations was <50 m outside the boundary of her 50% home range contour.

Apart from some yearling females who occasionally made unpredictable movements, adult females demonstrated high site fidelity. This seems to be characteristic of female raccoons; Fritzell (1978a), for example, found little seasonal or annual change in home range size among female raccoons. Home range estimates of female raccoons at Oak Ridge obtained with 5-6 months data did not show marked changes in size when data which extended beyond this period were included in the estimates, nor did they show marked changes in central tendency with ≥20 locations. Thus, comparisons of overlap and spatial distance among data sets that differed slightly in sample size and sample duration were made. The programs CALHOME (Kie et al. 1994) and HOMERANGE

(Ackerman et al. 1990) were used to estimate home ranges and harmonic centers of activity.

The association between RAPD band sharing, spatial distance and home range overlap

Females included in the analysis of spatial distance were adults and yearlings followed in the White Oak Lake area only. Analyses of home range overlap included females in the Freels Bend area. For each pair of females compared in the White Oak Lake sub-population, the pair-wise band-sharing distance and the distance between each animal's harmonic center of activity was calculated. Thirty-eight different females (Appendix B.5) for whom harmonic centers of activity were calculated and for whom genetic data were available were analyzed. Comparisons among females were limited to those who were monitored at similar times. A female who died was not compared with another female who was sampled subsequent to her death. However, if a female's radiocollar was removed or her radio signal ceased, I compared her with another female if sampling of the latter began in the same month. Thus, I assumed that the censored animal was alive and continued the same pattern of space use as she did while radio monitored. Except for a few yearling females whose movements were occasionally unpredictable, female raccoons who were recaptured after being censored were never captured outside their home ranges.

The association between band-sharing similarity and home range overlap was examined among 28 females (Appendix B.6) for whom 95% adaptive kernel home ranges

were calculated and band-sharing data were available (Appendix B.4). Home range overlap for two raccoons, 'A' and 'B', was expressed as a percentage of:

2 x (area of overlap of A and B)/(home range area of A + home range area of B).

Only females with overlapping ranges were analyzed. If a female was censored, I compared her with another female if at least six months data for both were gathered during the same period. If a female died, locations of other females she was compared with were considered only to the time of her death to ensure that areas of overlap did not include expansion into the deceased female's area. Two yearling females that dispersed and returned to the natal area had disjunct home ranges. I omitted the temporary dispersal range of B09 from the home range estimates and used only the area she returned to and occupied from June 1994 until monitoring ceased in August 1995. B18, however, periodically returned to her natal range and consequently had two distinct home ranges; thus, both areas were included in estimates of home range overlap.

The comparison of two matrices in which one represents band-sharing values for pairs of females and the other, corresponding pair-wise overlap estimates (or measures of spatial distance) for the same group of individuals, must consider the dependencies among similarity values (Dietz 1983). Also, many distance or similarity measures violate the assumption of normality which can be overcome with a distribution-free test for independence. A permutation test appropriate for such similarity or distance data was used to test associations between band-sharing distance and spatial distance, and between band similarity and percentage home range overlap (Dietz 1983). The test used Hubert's (1978) application of the Kendall's tau statistic which accounted for the "linked"

character of the matrix entries; thus internal comparisons within each of the corresponding matrices contributed to the final correlation index. This property of the Kendall's tau application made it preferable to the Mantel's-*Z* or Spearman's rho approach that make only between-matrix comparisons (Hubert 1978). The correspondence between the two matrices was measured by two variants of the cross-product statistic Kendall's (1975)tau, which were K_c and K_u. K_c and K_u referred to the products of the "connected" (pairs of distances with a point in common), and "unconnected" pairs of distances, in which Kendall's tau (K) = $K_c + K_u$. Large values of K suggested a positive association between the two matrices. With a SAS program written by Dr. A. Saxton (University of Tennessee), K, K_c, and K_u were calculated and their relative size evaluated against 5,000-10,000 permutations generated by shuffling the elements of one matrix at random. The observed value of K and its components (K_c and K_u) were compared to the permutation distribution of the corresponding theoretical values to test the two-tailed probability that the matrices were independent.

Inter-individual distance and the simultaneous use of space.

A subset of the data used to calculate home ranges was used to analyze spatial and temporal interaction. These consisted of locations obtained for two individuals within a narrow window of time, thus considered statistically "simultaneous". Minta (1992, 1993), who defined the window of "simultaneity" to be dictated by the animal's primary sensory mode and mobility, considered locations on two badgers simultaneous if they were within 48 h of each other, whereas Mace and Waller (1997) chose an interval

of one hour for grizzly bears. I estimated average travel rates for females at Oak Ridge by comparing distances moved between consecutive locations during periods of activity. The mean movement rate per hour was 40.1 m (range = 4 m-345 m) for 160 sets of consecutive locations. I considered locations from two raccoons statistically simultaneous if they were within 2.5 h of each other although the average time difference between locations for two raccoons was much less (26 min). Except for one pair of females whose data were obtained within a 4-month period, data for all other female pairs were obtained over a period of at least six months. For mother-daughter pairs, I used locations collected after the daughter was approximately five months old based on the tendency for most cubs to begin moving alone at this age (Chapter 2).

I analyzed data on simultaneous locations in females using two approaches. The first was an analysis of covariance of simultaneous inter-individual distances between dyads that differed in relatedness (Sokal and Rohlf 1981). I used linear regression to display the relationship between median inter-individual distance which was the dependent variable Y, and physical distance which was the independent variable X, for dyads with high, moderate and low relatedness. I chose the distance between harmonic centers of activity as the best average measure of physical distance (X) between two individuals and used the median inter-individual distance to reduce the effect of large outliers (Sokal and Rohlf 1981). This method compared inter-individual spacing across several pairs of raccoons, but simulated the results that could be obtained if a constant value of the independent variable X was used. Sixty eight pairs (37 individuals) with $\geq$20 simultaneous locations were used in the analysis. The mean number of locations per pair

was 42. Mean home range diameter was roughly 1000 m, so I included pairs that had harmonic activity centers $\leq$1089 m, because at this distance, raccoons could potentially encounter neighbors at home range boundaries. Assumptions of the covariance model are that slopes of Y on X for all groups are parallel and linear, and the regression for each group is significant. I used the SAS General Linear Models Procedure to determine if these assumptions were met by the data, to test if intercepts were significantly different from zero and to make pair-wise contrasts for equality of intercepts among the three groups of females.

The preceding analysis gives an impression of inter-individual spacing across pairs of female raccoons with overlapping or adjacent ranges, but behavior with regard to the simultaneous use of shared areas is unknown. Thus a second approach that tested spatial and temporal interaction among pairs of females with overlapping ranges was used (Minta 1992). The pair's (α and β's) association is portrayed as binomial events forming a 2 x 2 classification of each being either present or not in a shared area at the same time. Observed frequencies of presence and absence for each animal are compared to expected frequencies adjusted according to the size of the home range of each and the area of overlap. Home range overlap could take two forms; the entire home range of β could be enclosed within the range of α (termed an enclosed pair) or the overlap zone (OZ) could be only a portion of each animal's home range (termed an overlapping pair). For each pair, three areas of the combined 95% adaptive kernel home ranges were mapped: the home range area unique to α ($area_A$), that unique to β ($area_B$) and the OZ ($area_{AB}$). For enclosed pairs, when β is contained within α's home range, $area_{AB} = area_B$. Simultaneous

locations were overlaid on the combined home range map to determine where they lay relative to each of the three areas. For overlapping ranges the four possibilities were 1) both α and β were in the OZ, 2) neither raccoon was in the OZ, 3) α was in the OZ alone, and 4) β was in the OZ alone. Probabilities of expected spatial use were calculated as in Minta (1992). For enclosed ranges, only the probability of α being within β's range or outside it was calculated. Points intersecting the boundary of the OZ were counted as being in the OZ.

Two hypotheses of spatially independent home range use by each animal relative to the other, and one null hypothesis of temporally independent home range use by the animals were tested by partitioning an overall Chi-square test with df = 3 to make three independent comparisons (Minta 1992). This approach was analogous to partitioning an analysis of variance into spatial "main effects" (each animal's purely spatial attraction to, or avoidance of the shared area) and "temporal interaction" (the sum of the of simultaneous use and non-use of the shared area by α and β). The "main effects" suggested by the first twin hypotheses asked whether α and β used their respective areas as expected relative to the size of the OZ. These were denoted by Minta's (1992) coefficients of spatial interaction, $L_{A:\bar{A}}$, and $L_{B:\bar{B}}$, for α's and β's presence:absence in the OZ. The third hypothesis of independent temporal interaction, denoted by L_{ixn}, examined the pair's solitary vs. simultaneous use of the shared area; did solitariness = simultaneity relative to overall home range use? As coefficients approached zero, use of the OZ became random. Coefficients <0 suggested avoidance, and coefficients > 0 suggested attraction. The terms "attraction" and "avoidance" were used as in Minta (1992) to

describe greater or less use than expected of the OZ. Although the terms imply a behavioral response, it would require more rigorous testing such as data from direct observation to establish their true nature.

Despite the obvious advantages of Minta's (1992) method to address spatial and temporal interaction, it's dependence on home range estimates which lack associated precision estimates, and which differ widely in their properties, cannot be disregarded. Thus, Minta (1992) advocates that locations meet the assumptions of biological independence, simultaneity and temporal randomness as best as possible, and that sample sizes are similar per animal. The choice and consistent application of a home range estimator that best represents the home ranges of the animal under study is also desirable. Thus, 95% adaptive kernel home range boundaries were calculated from a minimum of 40 locations after data sets were adjusted for similar sampling periods. I also used at least 30 simultaneous locations per pair excepting one mother daughter pair with 27 simultaneous locations.

Departures from random expectation, coefficients of interaction and their associated probabilities, were calculated as in Minta (1992) with α set at 0.05. I followed Minta's (1992) recommendations of the use of the χ^2 statistic which remains relatively stable when expected frequencies are <5 (Larntz 1978). Also, cell frequencies of zero, which may arise when home range overlap is <10% or >90%, were replaced with pseudo Bayes estimates. I finally tested the hypothesis that response to the OZ was independent of relatedness using a permutation test for association between band similarities and coefficients of spatial and temporal interaction. Because each pair did not constitute two

unique females, I assumed that A's interaction with B was independent of A's interaction with C. Such cross-correlation with other conspecifics was possible and though the description of the dyad was not impaired, the interpretation of the interaction was uncertain (Minta 1992). Thus females were represented more than once, in the analysis of covariance (Appendix A.2) and spatial and temporal analysis, but were fairly well distributed across the different categories of relatedness.

For the analysis of covariance I classified females into groups based on band-sharing data. Because highly related females were not necessarily mother-daughter pairs, I included additional analyses with known mothers and daughters, and three highly related pairs of females I believed were mother and daughter. I based the putative relationship on field observations which were facilitated by the relatively small number of cubs born in the study area. In addition, many adult females were not lactating. Individuals of each pair were captured at the same trap sites repeatedly or observed resting together during the day. The mother was either the only adult female who showed signs of lactating in the area, or was one of two lactating females in which the offspring of one female was already known. I lumped the two groups of low and moderate relatedness in some analyses because females who had moderate relatedness had only a 2.5% chance of being mother and daughter.

Triangulation error analysis

Directional accuracy was tested every six to eight months as in White and Garrot (1990). Test collars were placed on the study area in areas typically used by raccoons

and were located from positions typically used for obtaining radio locations for raccoons. I also located dens by triangulation and then approached them. If the den's position could be readily determined on a map, the distance from the actual location to the triangulated location was then calculated to determine error. The distribution of 70 error distances ranged from 0 m to 180 m with a mean of 55 m (SD = 47.6, 95% CI = $\pm$ 11). Under most field conditions when animals were active, error was probably greater. I minimized error as much as possible by attempting to get as close to the animal as possible. Good road access facilitated triangulation data collection from distances of less than 500 m from the focal animal most of the time. I also minimized the time between successive fixes to $\leq$5 min, and obtained a third azimuth when angles between two azimuths were $<40^0$ and $>145^0$.

Radio tracking by triangulation provides only an estimate of an animal's location. The desired accuracy of this estimate was reasonable in comparison to the size of raccoons' home ranges at White Oak Lake (Appendix B.4) indicating that a mean error of 55 m would not adversely affect analyses of dispersion and home range overlap. However, tests of spatial and temporal interaction are relatively more dependent on the sample size of locations and the position of locations on two overlapping home ranges. The effect of error might tend to decrease the power of the test to detect an interaction (White and Garrot, 1986). Using a SAS program written by Michael Janis (University of Tennessee), I generated simulated locations based on the distribution of error distances. Tests of spatial and temporal interaction were repeated for five pairs of females with the simulated locations. The percentage difference between the new and original X^2 values

were then calculated. I report these values to show the relative effects that telemetry error or sample size may have on this analysis.

Results

The results are divided into two sections. The first titled "Genetic relationships" describes the correlation between RAPD marker similarity and individuals of known relatedness. I then use this relationship to classify raccoons of unknown relatedness as having high, low or moderate relatedness. In this section, I also examine sex-dependent trends in genetic similarity among the White Oak Lake population and genetic distance between raccoons at Chuck Swan and the three sub-populations at Oak Ridge. The second section titled "The relationship between band-sharing and spatial organization" describes (1) the association between genetic similarity, spatial distance and home range overlap, and (2) variation in inter-individual distance and spatial and temporal interaction.

Genetic relationships

Twenty-six primers, used to obtain RAPD profiles for 226 raccoons, produced approximately 260 bands. Three primers which showed inconsistent clarity, along with five primers which revealed minimal polymorphism, were not used. Only 18 primers had bands (N = 76) that occurred in the range of 0.02-0.97 (Appendix B.3).

To determine the level of relatedness among unknown individuals, I first analyzed raccoons of presumptively known relationships. These were females trapped together with cubs that were considered mother and offspring. Females suspected of being mother

and daughter based on other types of field observations were not included. Mean similarity (S) among mother-offspring dyads was 87.6 (N = 30, SE = 2.6, CI = $\pm$ 5.1) (Fig. 5). Chuck Swan animals were expected to have low relatedness to Oak Ridge animals from White Oak Lake, Freels Bend and East Fork. Only adult females and cubs were used to determine the range of similarity for raccoons with low relatedness because male raccoons have high vagility. Mean similarity among dyads of presumably unrelated animals was 62.5 (N = 3770, SE = 4.0, 95% CI = $\pm$ 7.9) (Fig. 5). Individuals with low relatedness therefore, were defined as pairs that fell below S = 70.4, the upper bound of the 95% confidence interval of the mean (S = 62.5). Individuals with high relatedness were defined as pairs with S >82.5, the lower bound of the 95% confidence interval of the mean (S = 87.6).

Although a continuum of pair-wise band-sharing values was used in some analyses, it was desirable to establish discrete categories of relatedness for some questions. The objective of creating categories was to identify the class most likely to have mother-daughter, or sister-sister dyads and those that would not. Individuals that were between the S = 82.5 and S = 70.4 had less than a 2.5% chance of being mother and daughter. Therefore, I defined three categories of relatedness to describe relationships among specific individuals; high relatedness (S $\geq$82.5), low relatedness (S $\leq$70.4), and moderate relatedness (70.4< S <82.5).

Mean band similarities among siblings (N = 16, S = 88.4, SE = 2.5) were not different from those of mother-offspring pairs (N = 30, S = 87.6, SE = 2.6, p = 0.4). Mean band similarities between adults of the same sex in the White Oak Lake study area

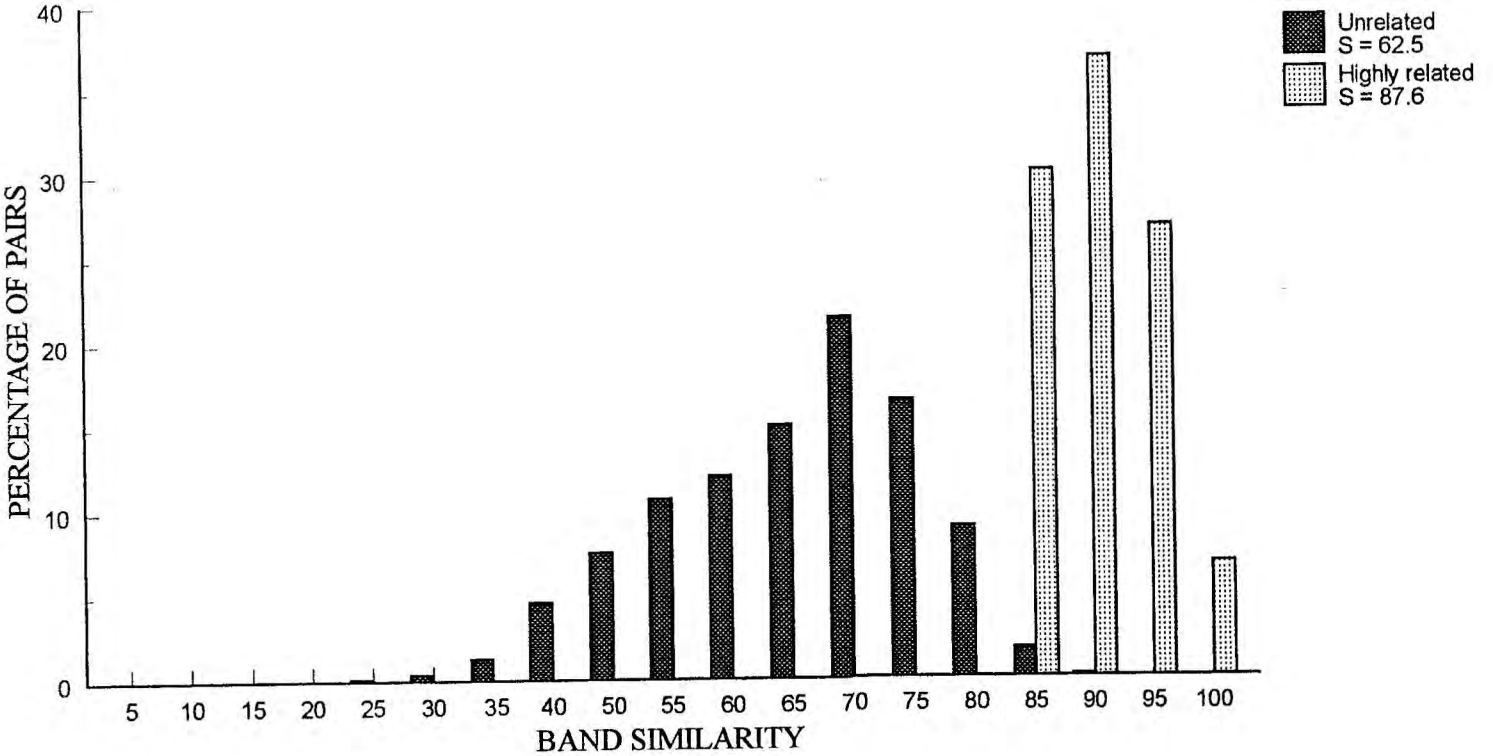


Fig. 5. Frequency distributions of band similarity (S) values among pairs of raccoons expected to have low relatedness (N = 3770, Chuck Swa vs. Oak Ridge) and pairs (N = 30) expected to have high relatedness such as mothers and offspring.

differed. Including all sexually mature males in age classes III-V and any males in age class II who had descended testes, mean band similarities among males were 63.0 (N = 630, SE = 4.0). Adult females, including all females in Age Class II-V, had mean band similarities of 70.3 (N = 2016, SE = 3.7) which were significantly higher (p = 0, Fig. 6a). Adult males were also genetically less similar to adult females than were adult females to each other. Mean male-female band similarities (S = 65.9, N = 2304, SE = 3.9) were significantly higher than average female-female band similarities (Fig. 6b, p = 0). Average band similarities among adult males at White Oak Lake were similar to those of individuals expected to be unrelated, such as Chuck Swan females plus young versus White Oak Lake females plus young. Mean male-male band similarities were not significantly different from those of unrelated individuals (p = 0.8).

Bootstrap analysis of Nei's (1972) genetic distance among all raccoons from Chuck Swan and Oak Ridge supported a separate cluster for the three Oak Ridge sub-populations only 83% of the time (Fig. 7a). When adult males were removed from both populations, 98% of bootstrap scores supported the three Oak Ridge sub-populations as a cluster distinct from Chuck Swan and North Carolina samples (Fig. 7b).

The relationship between band-sharing and spatial organization

The association between genetic similarity, spatial distance and home range overlap

The association between band sharing and band matching distance and the distance between harmonic centers of activity was positive and significant for female raccoons followed in the 12 km^2 White Oak Lake study area (Table 13, Fig.8). There

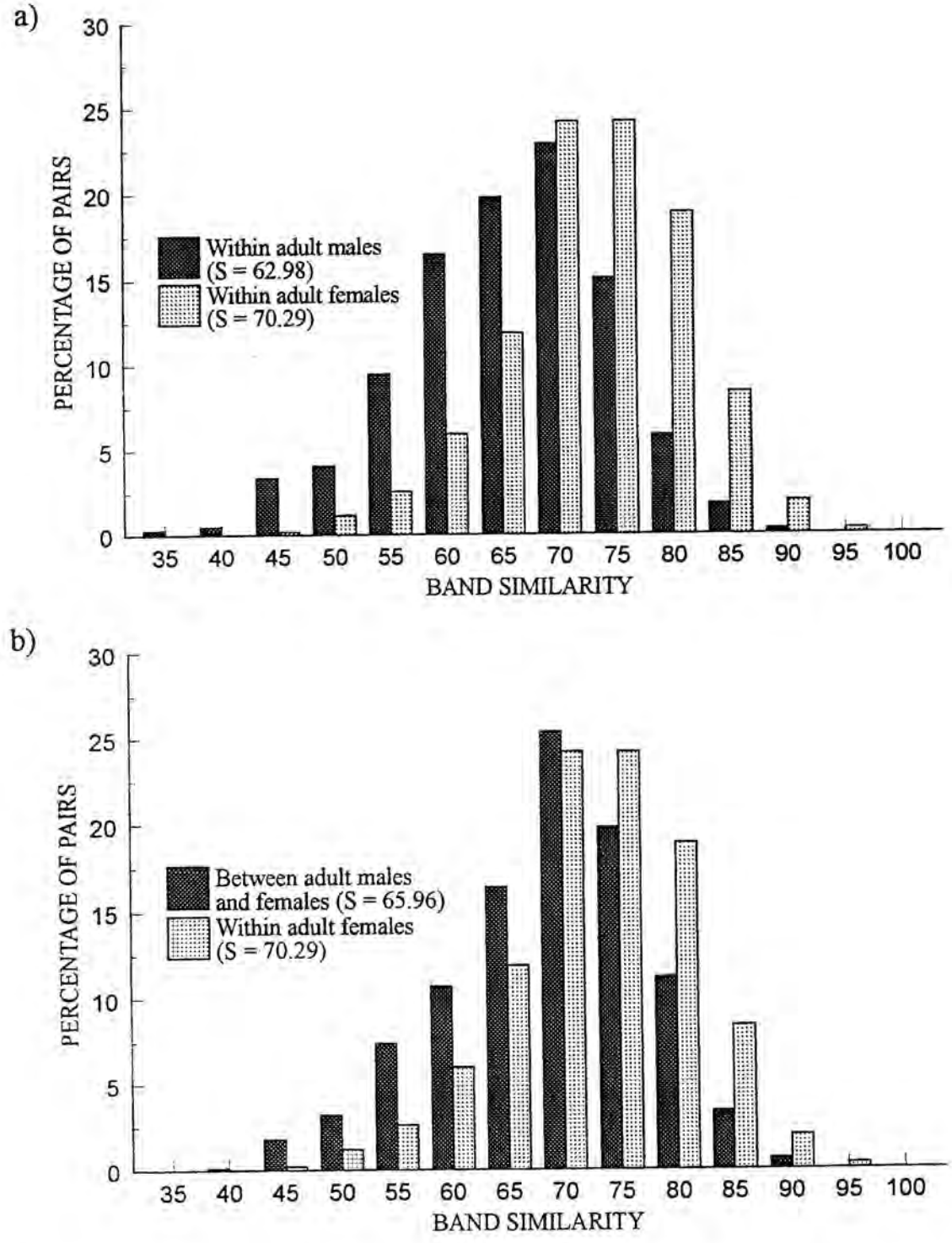
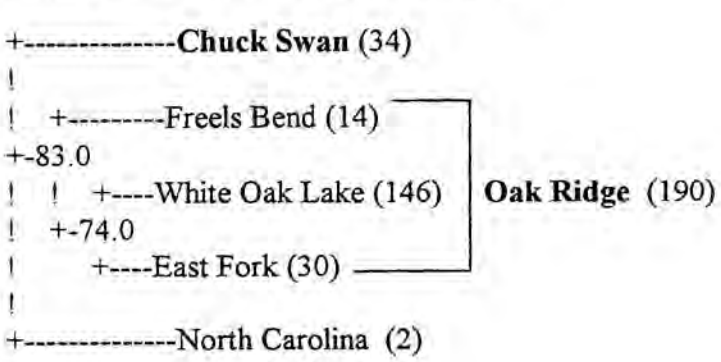


Fig.6. Frequency distributions of band similarity (S) values a) adult male-adult male vs. adult female-adult female, and b) adult male-adult female vs. adult female -adult female.

a) MALES, FEMALES AND YOUNG



b) FEMALES AND YOUNG ONLY

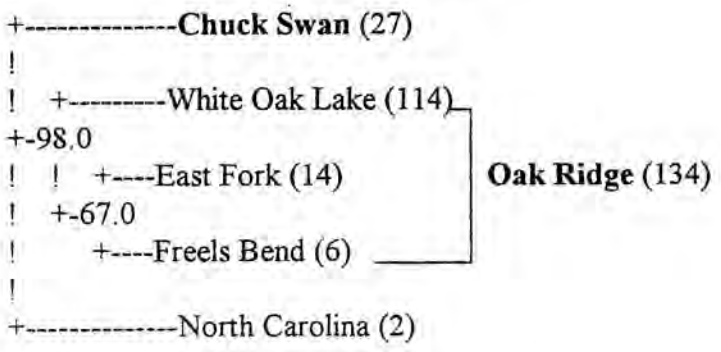


Fig. 7. Unrooted consensus tree displaying populations grouped by Nei's (1972) genetic distance. 1) Oak Ridge (Freels Bend, East Fork, White Oak Lake), 2) Chuck Swan and 3) North Carolina populations. Numbers at the forks indicate the number of times the population to the right of that fork occurred among the dendrogram, out of a 100 dendrograms. Numbers in parentheses indicate number of raccoons in each population.

Table 13. Observed values of Kendall's tau statistics, means, standard deviations (SD), and probabilities for tests of association between genetic distance and distance between harmonic centers of activity (HCA), and between genetic similarity and % home range overlap (HRO), for females with overlapping home ranges. *D*s = band-sharing distance, *D*m = band-matching distance, *S* = band similarity, *M* = band matches.

Comparison	Spearman's rho	Number of Permutations		Observed	Theoretical	SD	p
*D*s vs.HCA	0.288	5000	K	9727.00	25.26	1862.95	0.0000
N = 315 pairs			K_c	268.00	1.47	87.04	0.0020
			K_u	9459.00	23.79	1804.27	0.0000
*D*m vs. HCA	0.279	5000	K	9410.00	55.74	1875.18	0.0000
N = 315 pairs			K_c	355.00	0.86	86.28	0.0000
			K_u	8436.00	54.87	1815.91	0.0000
S vs. HRO	0.349	10000	K	516.00	2.31	174.65	0.0028
N = 65 pairs			K_c	52.00	0.20	13.68	0.0011
			K_u	464.00	2.11	165.30	0.0001
M vs. HRO	0.327	10000	K	539.00	-2.63	173.40	0.0012
N = 65 pairs			K_c	50.00	-0.19	13.48	0.0001
			K_u	489.00	-2.44	164.05	0.0020

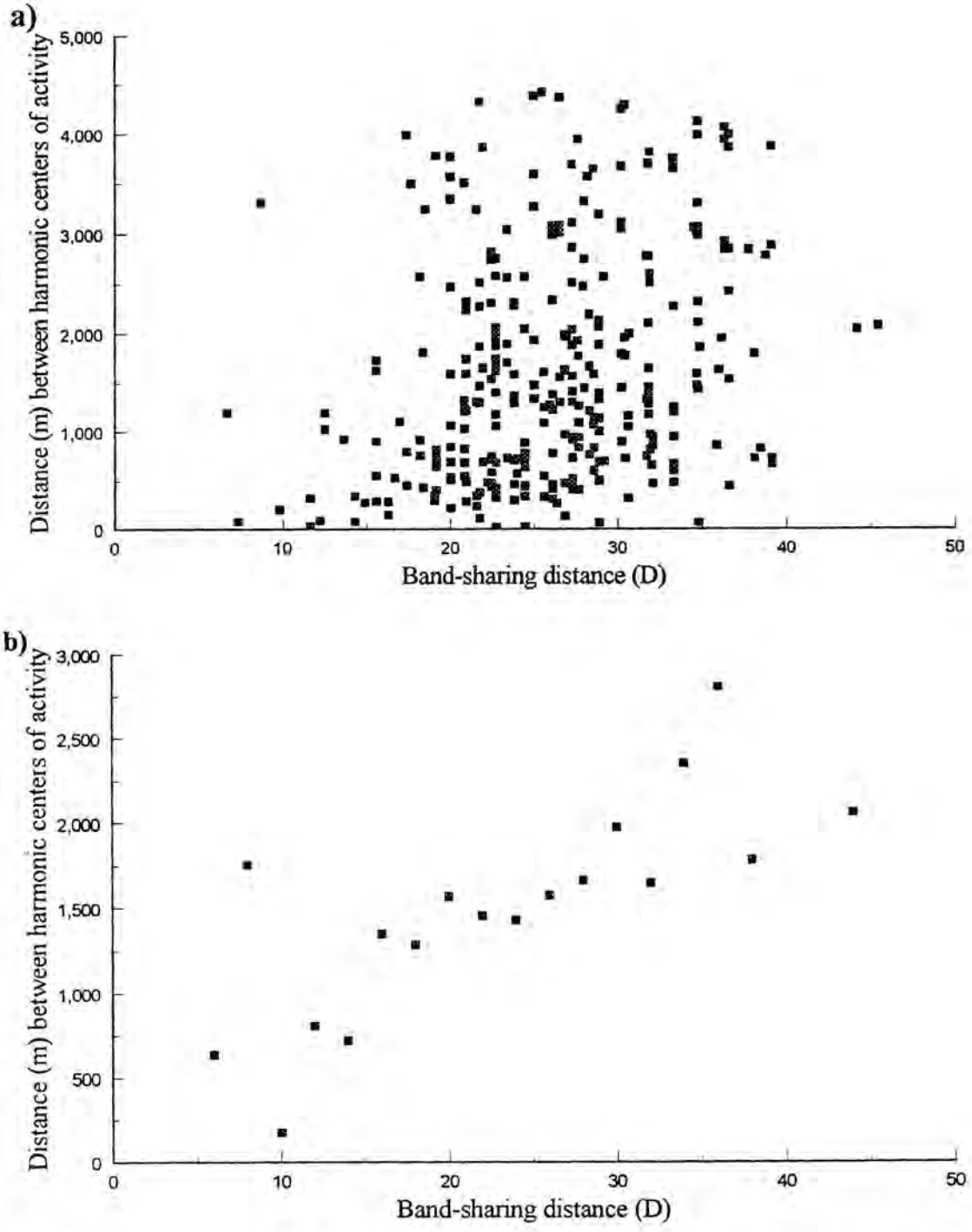


Fig. 8. a) Significant positive association between band-sharing distance *(D)* and spatial distance among pairs of females. Each data point represents a pair.
b) Mean increase in distance between harmonic centers of activity for every 2 % increase in D. Data from Fig.8a was pooled to display trend, not test, positive association.

was also a positive association between band similarity and band matching and the percentage of home range overlap (Fig. 9, Table 13). These results indicate that females that lived in greater proximity and shared space were more likely to be closely related. When females followed only as yearlings were removed from the analyses, the association between band-sharing distance and spatial distance among older females was still significant ($N = 203$, $K = 3346$, $p = 0.0002$), as was the association between band similarity and percentage home range overlap ($N = 60$, $K = 450$, $p = 0.0027$). This indicated that many females may live on or close to their natal range well beyond the average age of sexual maturity of 10 months for female raccoons.

Average 95% adaptive kernel home range size among adult female raccoons was 78.2 ha ($N = 30$, $SE = 7.3$) (Appendix B.4). Average male home range size was 229.2 ha ($N = 2$) with one male's range completely enclosed by the other male's. Thirteen pairs of females displayed high (≥50%) home range overlap in which at least two females had low relatedness and five females had moderate relatedness (Table 14). Thus maternal inheritance of space was not a necessary condition for sharing home ranges.

Of 65 instances of home range overlap, 13 overlapping ranges were among females who were pregnant or lactating when followed. High home range overlap (≥ 50%) between two females was less common when both were reproductively active (Table 14). Of 13 pairs who showed high overlap, nine pairs consisted of at least one young female who was nulliparous for the duration of radio monitoring. Of the remaining four pairs, two comprised females Y35 and Y07 who had reproduced before but showed no signs of reproduction and died during sampling. Y38 had high overlap with two

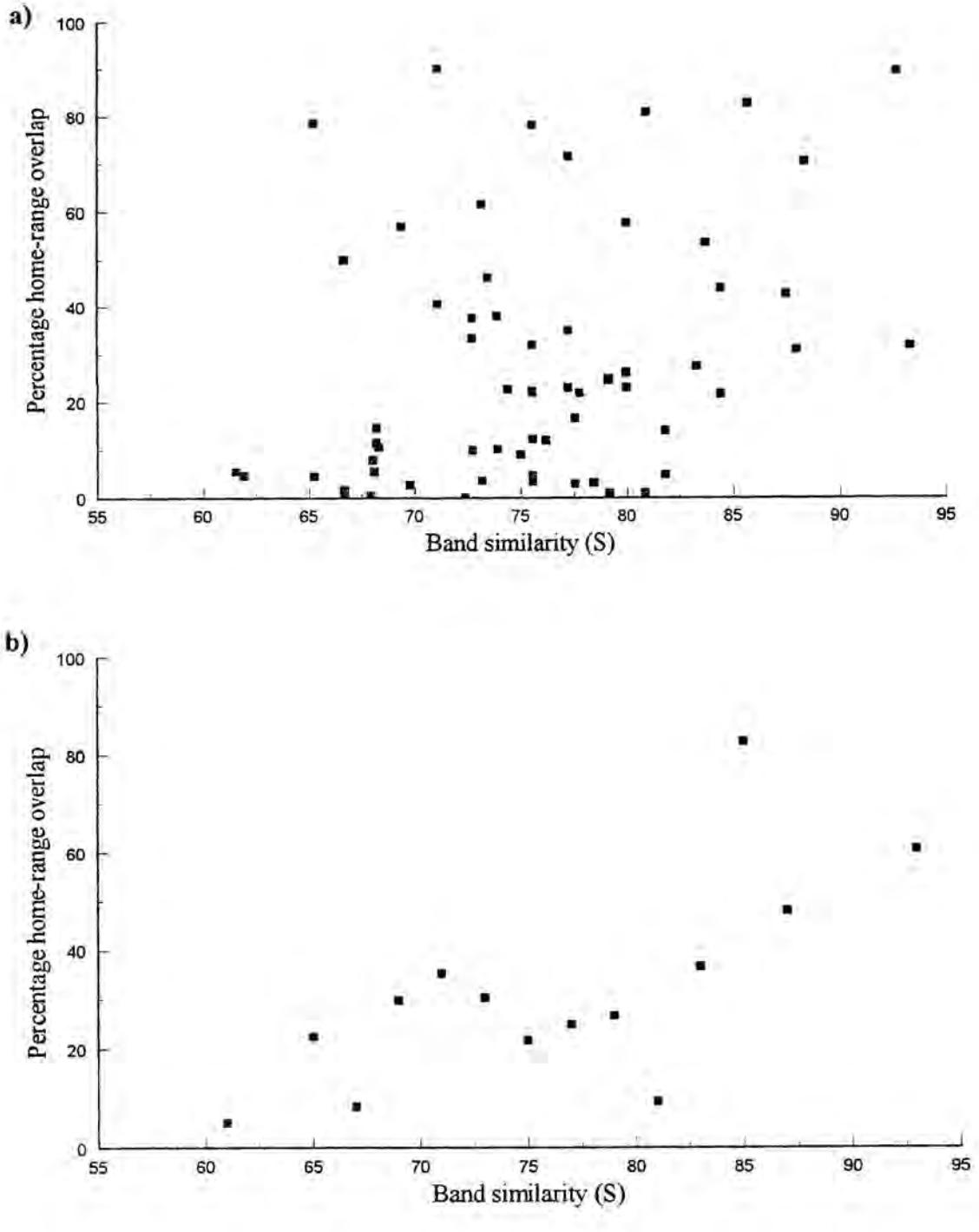


Fig.9. a) Relationship between band similarity (S) and percentage home range overlap among pairs of females.

b) Mean percentage overlap for every 2% increase in band-sharing similarity.

Table 14. Identity, age class of female when monitoring began, reproductive status for duration pair was monitored, % home range overlap and band similarity among 13 pairs of female raccoons that demonstrated ≥ 50% home range overlap.

Female Pair	Age Class	Reproductive status	Percentage overlap	Band similarity
1. G03	2	Nulliparous[1]	70	88.37
Y07	3	Non-parous[2]		
2. Y36	2	Nulliparous	78	75.56
Y35	4	Non-parous		
3. Y38	3	Parous[3]	58	80.00
Y34	3	Parous		
4. Y39	5	Suspected parous	78	65.22
Y35	4	Non-parous		
5. Y39	5	Suspected parous	90	71.11
Y36	2	Nulliparous		
6. Y40	4	Parous	62	73.17
Y07	3	Non-parous		
7. Y40	4	Parous	50	66.67
G03	2	Nulliparous		
8. Y41	5	Parous	72	77.27
Y38	3	Parous		
9. G19	2	Nulliparous	83	85.71
Y33	5	Parous		

[1] Had not reproduced before.
[2] Had reproduced before, but was currently non-reproductive.
[3] Was seen pregnant or lactating.

Table 14. continued.

Female Pair	Age Class	Reproductive status	Percentage overlap	Band similarity
10. B18	1	Nulliparous	57	69.39
B11	1	Nulliparous		
11. G33	1	Nulliparous	53	83.72
Y47	3	Suspected parous		
12. G33	1	Nulliparous	89	92.68
Y68	3	Parous		
13. G37	1	Nulliparous	81	80.95
Y40	4	Parous		

parous females, but became pregnant much later in the year. Controlling for the ratio of nulliparous (N = 9) to parous females (N = 19) for whom home ranges were calculated, high overlap was less likely among reproductively mature females (observed = 4, expected = 7.7) than among nulliparous pairs and parous-nulliparous pairs combined (observed = 9, expected = 5.3, $X^2 = 4.4$, df = 1, $p < 0.05$).

Variation in inter-individual distance and spatial and temporal interaction

If, for example, two females frequently moved together, used overlap zones simultaneously, or approached common range boundaries through mutual attraction, their average inter-individual distance would be smaller than if they had demonstrated mutual avoidance in similar contexts. Was there a tendency for highly related individuals to associate more closely than females who were less related?

Slopes for the three categories of relatedness met the assumptions of linearity ($R^2 = 0.87$, $p = 0.0001$) and parallelism ($F = 0.38$, $p = 0.69$) with a significant regression displayed by each group ($p = 0.0001$). An overall test for $Y = 0$ among the three groups was significant (Fig. 10a, $F = 10.79$, $p = 0.0001$) indicating that there was heterogeneity among groups. Intercepts for the high and moderately high groups, were significantly different from zero (Table 15). Intercepts larger than zero are to be expected among individuals who are mostly solitary; as home ranges begin overlapping and centers of activity approach zero, unless two individuals remain together most of the time, median inter-individual distance is likely to show a corresponding increase depending on the home range area available to each raccoon. Therefore, the contrasts among groups are of

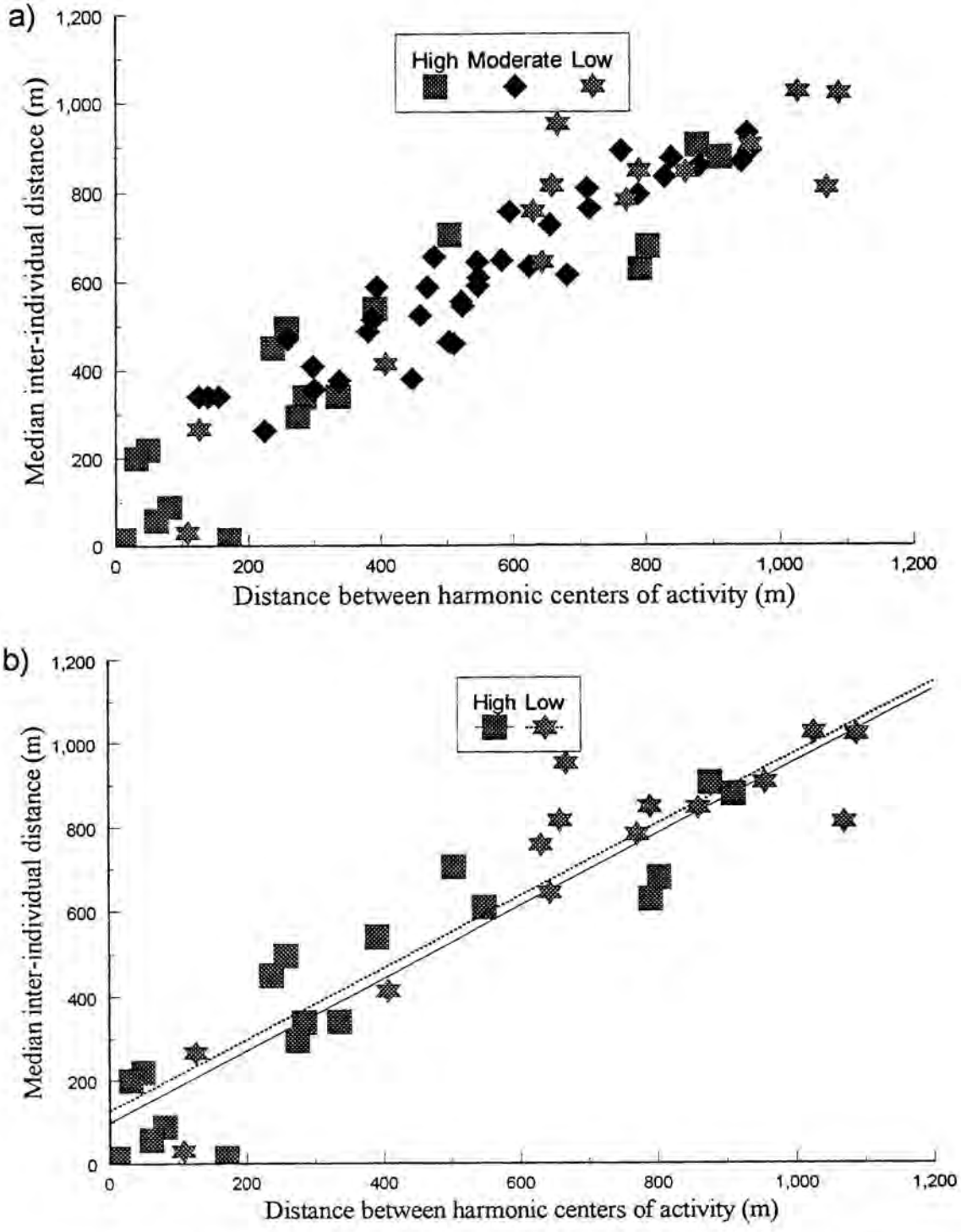


Fig.10. a) Inter-individual distance as a function of spatial distance among female dyads with high, moderate and low relatedness.
b) Contrast of inter-individual distance as a function of spatial distance among dyads with high and low relatedness.

Table 15. Slopes, R^2, intercepts (I) and probabilities that I = 0 from analysis of covariance of inter-individual distance among three groups of females. Groups represent female dyads classified by degree of band similarity.

Groups compared	N	Slope	R^2	Intercept	Standard Error (I)	T	p
High	17	0.85	0.82	99.03[a]	45.96	2.16	0.0500
Moderate	37	0.77	0.87	186.38[a]	28.56	6.53	0.0001
Low	14	0.85	0.81	128.15[a]	84.69	1.51	0.1561

[a] Intercepts with the same letter do not differ.

primary interest. Pair-wise comparisons of intercept difference among groups with high vs. low relatedness (Fig. 10b) and moderate vs. low relatedness (Fig. 11a) were insignificant at $\alpha = 0.05$ (Table 15).

Because highly related females were not necessarily mother-cub pairs, I modified the highly related group to include six known mother-offspring pairs, and three pairs of females with high similarity who were likely to be mother and daughter based on field observations. I lumped the two groups of low and moderate relatedness and displayed their median inter-individual distance relative to the mother-daughter group (Fig. 11b). A contrast of the intercepts of the two groups was not significant ($F = 2.40$, $p = 0.12$). Although sample sizes for the mother-daughter group are small with some tendency for mother-daughter dyads to be clustered toward the lower end of the regression, there is much variation displayed by both groups. The intercept for mother-daughter dyads was slightly smaller, but there were several females with moderate and low relatedness whose average spacing was comparable to those of mothers and daughters. Also, two mother-daughter pairs had spacing that was similar to females with low-moderate relatedness. Four pairs with small inter-individual distances comprised mothers with young daughters. Included in this cluster was a pair of yearling females, B18 and B11, who were not siblings, had low relatedness, and who remained together most of the time. Spacing between mothers and older daughters who were >9 to10 months, was comparable to spacing between females who had low to moderate relatedness. Thus, temporal spacing between two females was less likely to depend on their genetic relationship than on relative age.

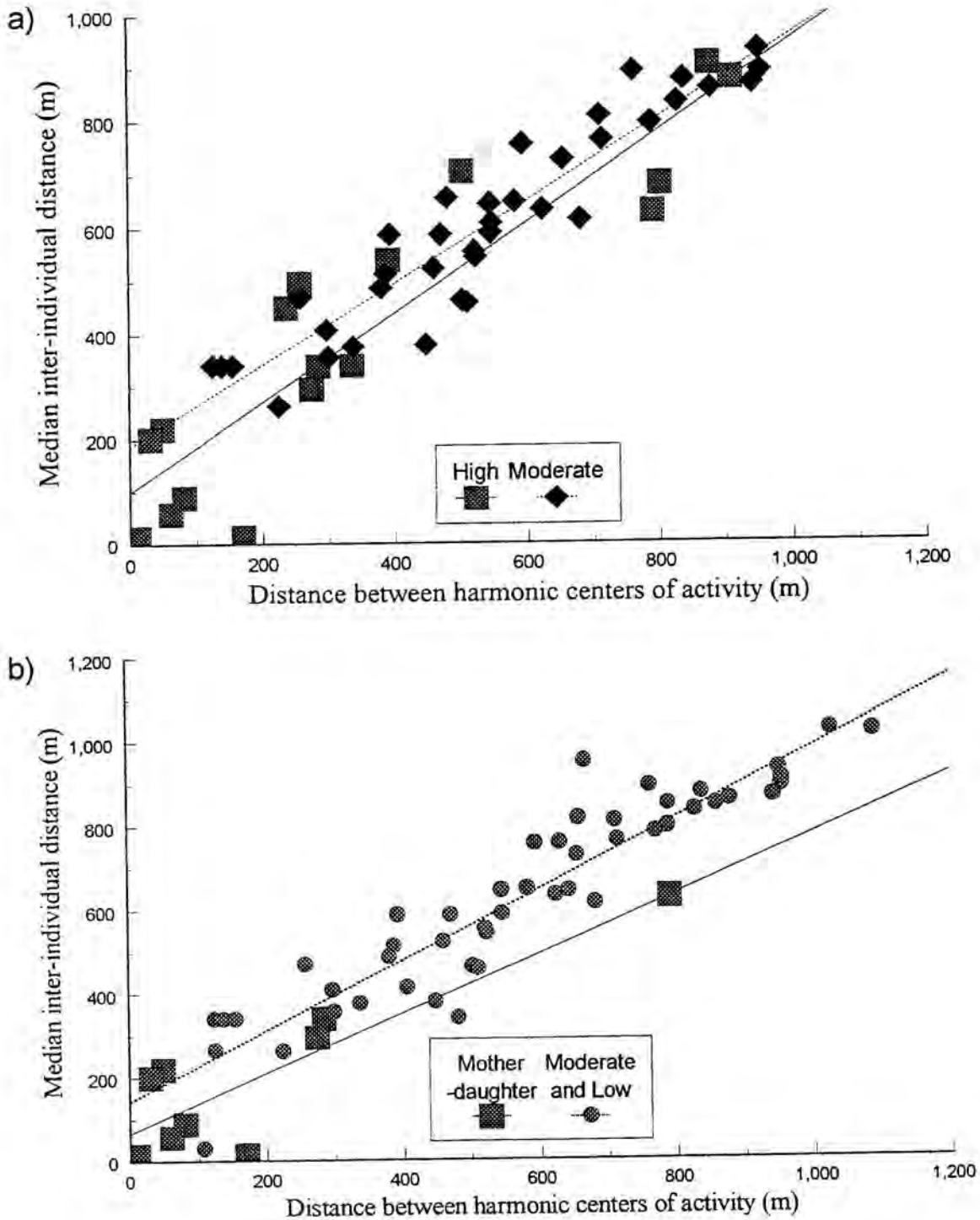


Fig.11. a). Contrast of inter-individual distance as a function of spatial distance among female dyads with high and moderate relatedness.
b) Contrast of inter-individual distance as a function of spatial distance; mother -daughter dyads vs. dyads with moderate and low relatedness combined.

Female raccoons responded differently to shared areas but the nature of the response seemed independent of relatedness. Based on the significance of Chi-square tests, coefficients of pure spatial responses to overlap zones (OZ) were more random (61.7 %) than non-random across all 25 pairs of females (Table 16, Appendix B.7). Of non-random spatial responses, attraction to the OZ was more common (66.7 %) than avoidance. Temporal responses were detected only twice in females with moderately high relatedness and were not mixed with spatial responses. Both pairs used their home ranges as expected, but the coordination of each female's movements to and from the OZ were nonrandom relative to one another. In one pair, Y41 and Y38, simultaneity exceeded solitariness in the OZ (Table 17). Solitariness in the OZ exceeded simultaneity for Y38 and Y34; both were more likely use the OZ alone, although examination of the role of each female (Appendix B.7) showed that this was more pronounced in Y34 than in Y38.

Results of tests of spatial and temporal interaction using simulated locations based on triangulation error showed that the mean percentage of locations that were classified differently from the original locations was 9.6% (Appendix B.8). The conclusions based on the new Chi-square values did not differ, nor did the trends for attraction or avoidance to shared areas. The mean difference between original and error-based Chi-square values was ± 1.14 (range = 0.12- 3.23, SD = 1). The critical Chi-square value above which an interaction may be determined as avoidance or attraction is 3.84. Triangulation error could therefore result in misclassifying a few interactions with Chi-square values close to this critical value; for example, pairs that might actually show attraction or avoidance may

Table 16. Spatial interactions among 25 pairs of females with enclosed or overlapping home ranges. Coefficients refer to spatial association ($L_{A:\bar{A}}$, $L_{B:\bar{B}}$) and temporal interaction (L_{ixn}) of individuals α and β. L = 0 represents random use of the OZ, L > 0 represents greater than expected use of the OZ and L < 0, spatial avoidance of the OZ, ns = not significant.

Pair α β	Band similarity	$L_{A:\bar{A}}$	χ^2	p	$L_{B:\bar{B}}$	χ^2	p	L_{ixn}	χ^2	p
[2]Y40-G37[1]	80.95	2.314	7.91	<.005						
[2]G33-Y68[1]	92.68	1.516	10.65	<.005						
[3]Y07-G03	88.37	1.190	7.57	<.010	0.754	2.84	ns	0.190	0.12	ns
[3]G19-Y33	85.71	-1.363	10.77	<.005	0.972	6.67	<.010	-1.133	3.83	ns
[2]Y46-B09	87.50	0.118	0.12	ns	0.166	0.23	ns	0.407	1.33	ns
[4]Y26-Y25	88.00	0.277	1.31	ns	-0.671	3.98	<.050	-0.035	0.01	ns
[4]Y41-Y34	84.44	0.261	1.05	ns	0.872	11.72	<.001	0.136	0.33	ns
[4]Y34-Y33	83.33	-0.235	0.67	ns	-0.470	2.21	ns	-0.151	0.17	ns
Y36-Y35	75.56	0.906	3.97	<.050	0.690	3.01	ns	0.891	2.41	ns
[4]Y41-Y38	77.27	0.544	2.12	ns	0.471	2.69	ns	1.217	8.50	<.005
[4]Y38-Y34	80.00	-0.188	0.65	ns	0.416	2.55	ns	-0.750	7.77	<.010

[1] Enclosed home ranges: coefficients and probabilities refer to the raccoon (α) with the larger home range.
[2] Known mother-daughter pairs.
[3] Pairs suspected of being mother and daughter.
[4] Both females known or suspected to be parous for some period during monitoring.

Table 16. continued.

Pair α β	Band similarity	$L_{A:\bar{A}}$	χ^2	p	$L_{B:\bar{B}}$	χ^2	p	L_{ixn}	χ^2	p
^{4}Y41-Y39	80.00	-0.644	2.94	ns	-0.494	2.20	ns	-0.025	0.00	ns
0.0[illegible]8-Y36	72.73	0.973	14.67	<.001		0.00	ns	0.426	3.20	ns
G19-Y34	77.78	-0.098	0.10	ns	-1.377	5.27	<.025	-0.161	0.07	ns
Y41-Y35	75.56	-0.454	1.25	ns	0.102	0.10	ns	-0.384	0.66	ns
Y39-Y36	71.11	-0.129	0.05	ns	0.700	2.12	ns	-0.072	0.01	ns
Y40-Y07	73.17	-0.097	0.09	ns	0.506	1.80	ns	-0.567	2.16	ns
^{4}Y28-Y25	71.11	0.602	4.71	<.050	1.008	18.09	<.001	0.311	1.65	ns
^{4}Y39-Y38	75.56	0.196	0.58	ns	0.432	2.59	ns	-0.085	0.10	ns
Y41-Y36	72.37	-0.266	0.84	ns	-0.856	6.99	<.010	0.318	0.87	ns
^{4}Y33-Y07	73.91	-1.597	7.63	<.010	-1.698	5.38	<.025	1.273	0.84	ns
Y38-Y35	75.56	-0.731	2.51	ns	-0.118	0.13	ns	0.355	0.51	ns
B18-B11[1]	69.39	2.400	32.15	<.001						
Y39-Y35	65.22	0.247	0.35	ns	1.092	6.46	<.010	-0.111	0.03	ns
Y40-G03	66.67	0.344	1.50	ns	0.778	4.70	<.050	0.194	0.33	ns

be classified as showing random use of shared areas. The coefficients of interaction ($L_{A:\bar{A}}$, $L_{B:\bar{B}}$, and L_{ixn}) were therefore used to determine if the simultaneous use or non-use of shared areas was likely to differ by degree of band similarity. A permutation test for association between band similarities and coefficients of spatial interaction were not significant ($p = 0.29$, $N = 1000$ permutations) as was a test between band similarities and coefficients of temporal interaction ($p = 0.36$, $N = 1000$ permutations). These results indicated that responses to shared areas were independent of band similarity.

There was no consistent tendency for avoidance or attraction to the OZ among parous females. Nine pairs of females who demonstrated overlap were known to be reproductively active during monitoring (Table 16). Spatial avoidance was demonstrated by three pairs, spatial attraction by three, and the remaining twelve responses were random. Reproductive status, therefore, did not seem to affect the simultaneous use of shared areas.

Spatial interaction among some mother-daughter pairs (Fig. 12, 13) and females of low and moderate relatedness (Figs. 14, 15.) display a range in degrees of overlap with examples of random spatial use, spatial attraction, or avoidance. Resource patchiness, abundance and predictability, is likely to determine responses to shared areas (e.g., Fig. 16) but were not accounted for in this study. The relative positions of activity centers for each female and their relative inter-individual distance, are displayed to demonstrate that despite high simultaneous use of shared areas, inter-individual spacing among adult females is comparatively high, also among putative mother-adult daughter pairs Y07-G03 (Fig. 13) and Y33-G19 (Fig. 12) who had almost identical centers of activity.

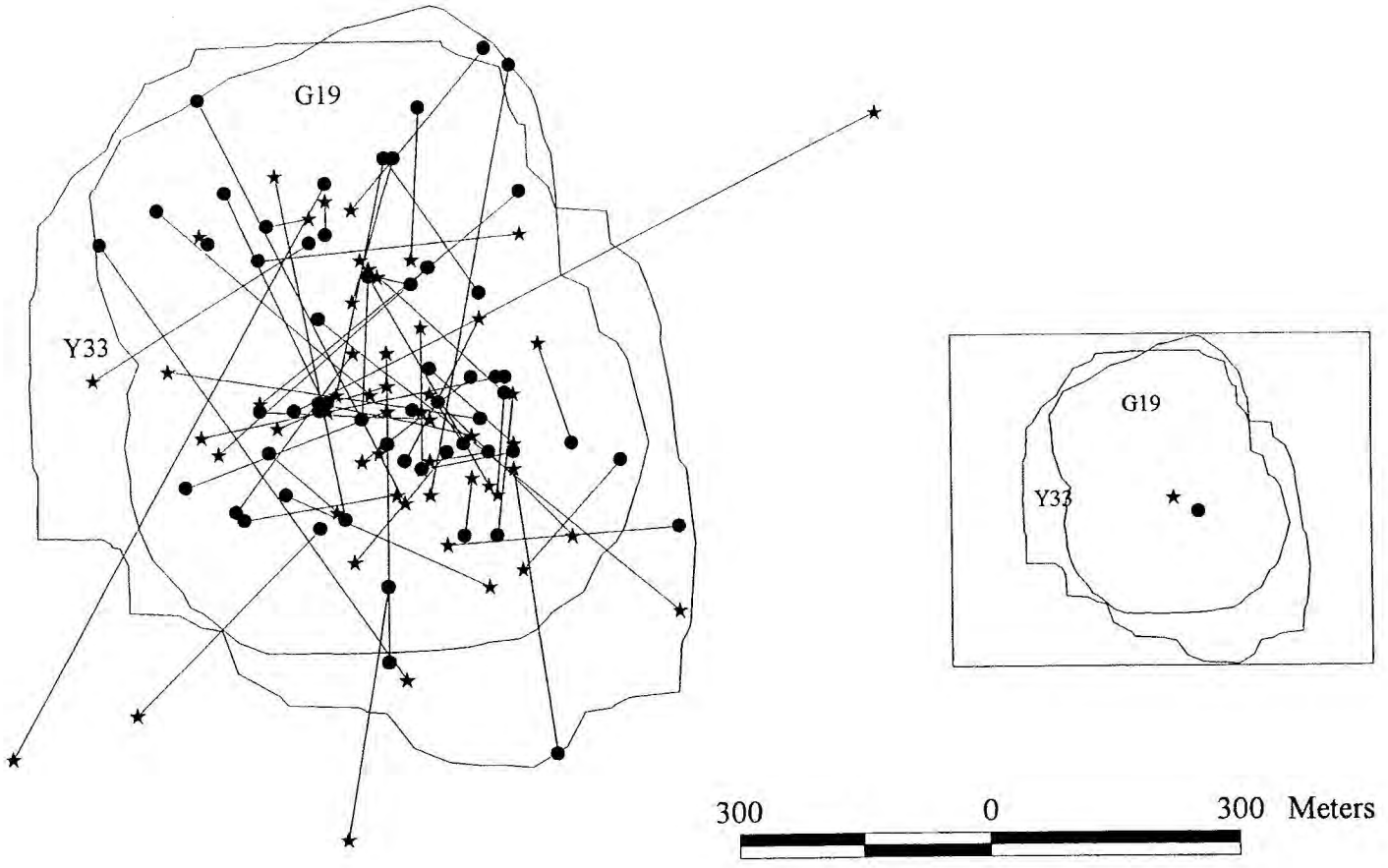


Fig. 12. Spatial interaction between Y33 (star) and putative daughter G19 (dot), May 1993-May 1994. Locations are a subset of those used to calculate 95 % home ranges. Y33 exhibited spatial attraction and G19 spatial avoidance of the overlap zone (OZ). Inset shows position of each female's harmonic center of activity (HCA). Distance between HCAs was 31 m, median inter-individual distance was 200 m.

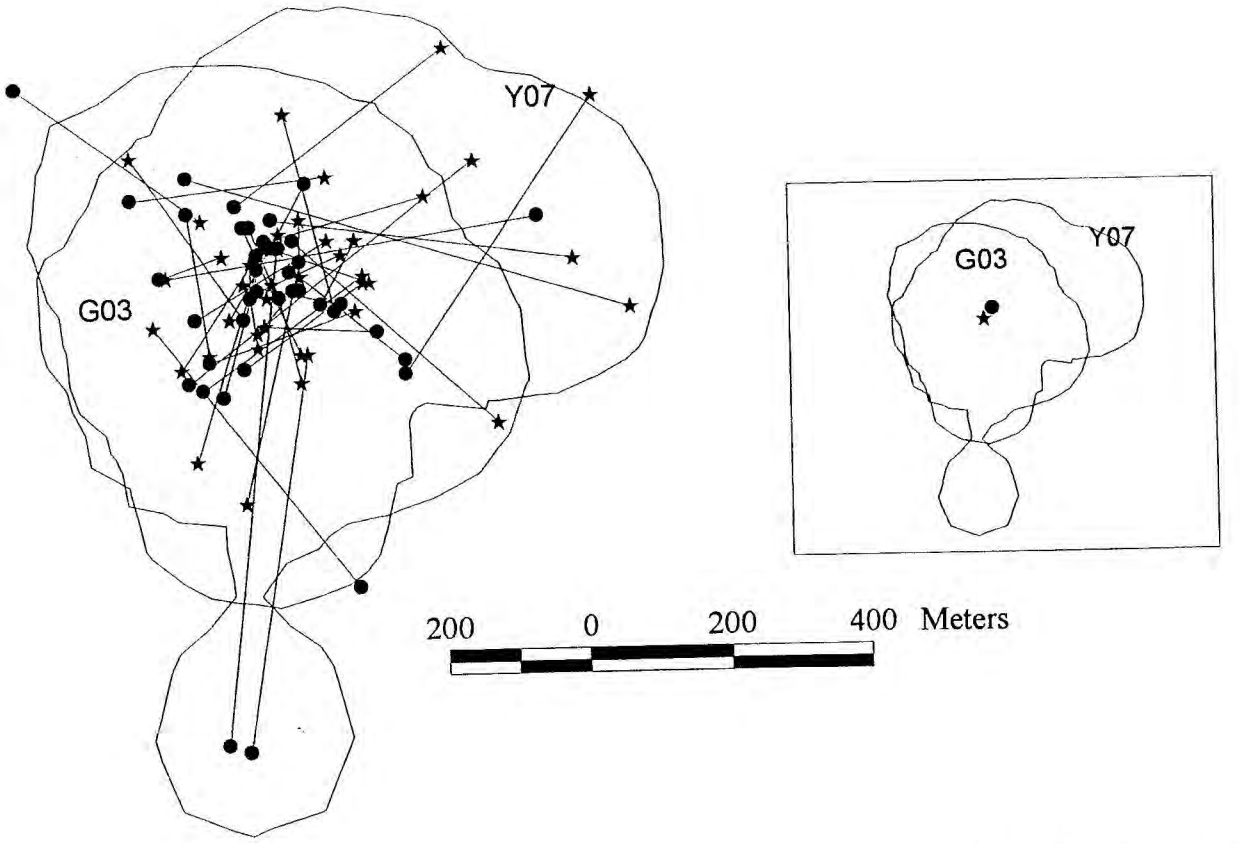


Fig.13. Spatial interaction of female Y07 (star) and putative daughter G03 (dot), April 1993-Sep 1993. Y07 used the OZ more than expected. G03 used the OZ as expected. Distance between HCAs was 49 m, median inter-individual distance was 219 m.

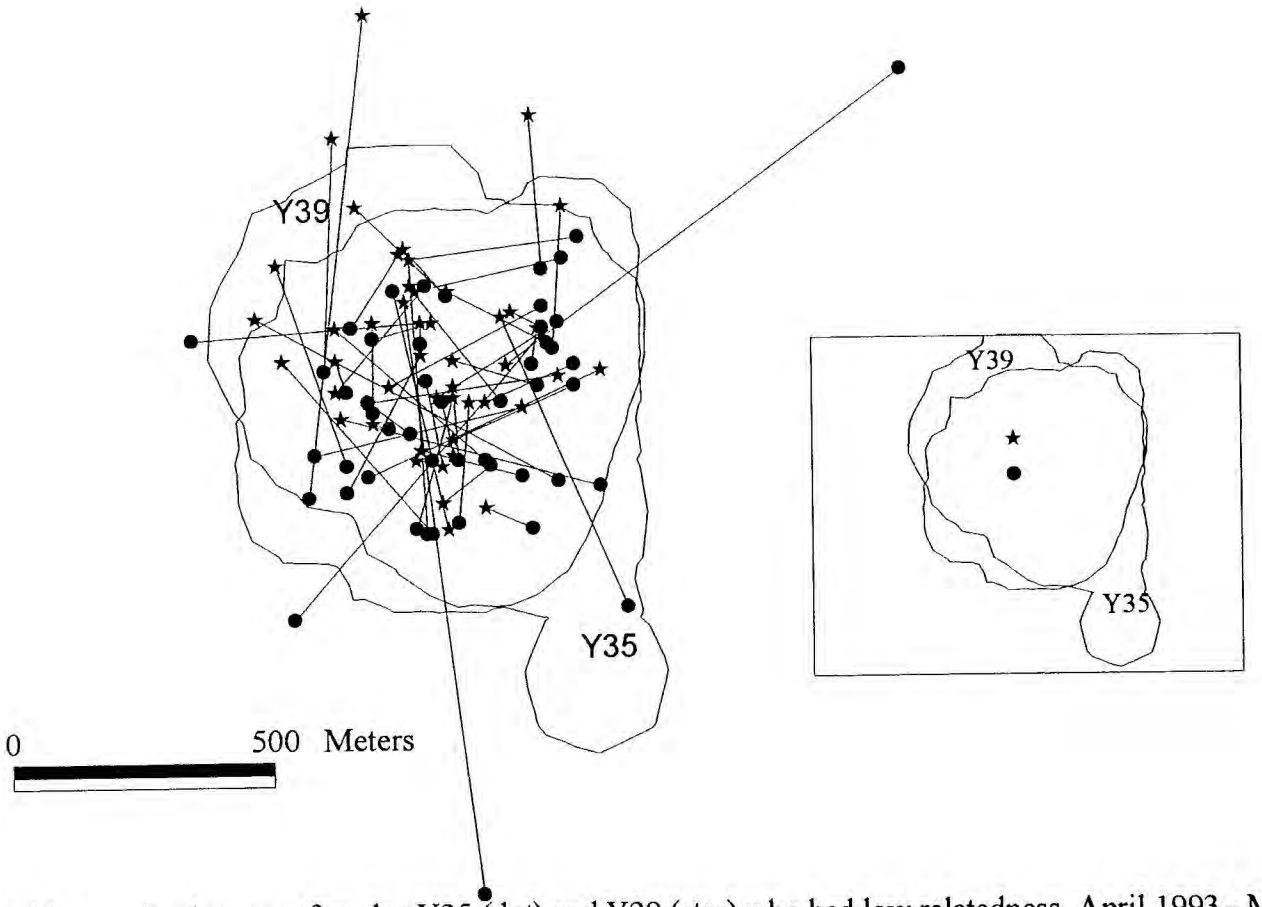


Fig.14. Spatial interaction between females Y35 (dot) and Y39 (star) who had low relatedness, April 1993 - Mar 1994. Y35 used the OZ more than expected, Y39 used the OZ as expected. Distance between HCAs was 125 m. Median inter-individual distance was 265.9 m.

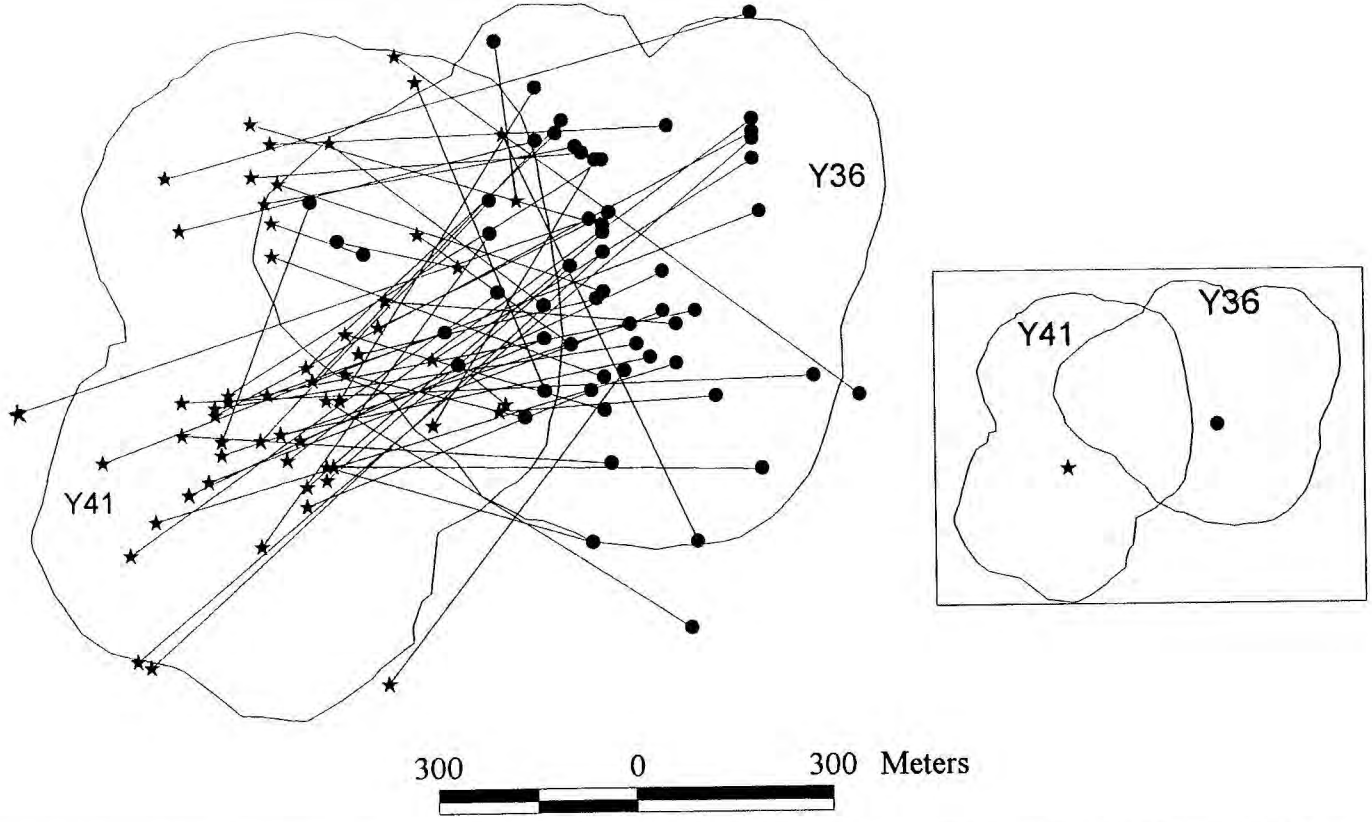


Fig. 15. Spatial interaction between moderately related females Y36 (dot) and Y41 (star), April 1993-April 1994. Y36 used the OZ less than expected. Y41 used the OZ as expected. Distance between HCAs was 522 m, median inter-individual distance was 555 m.

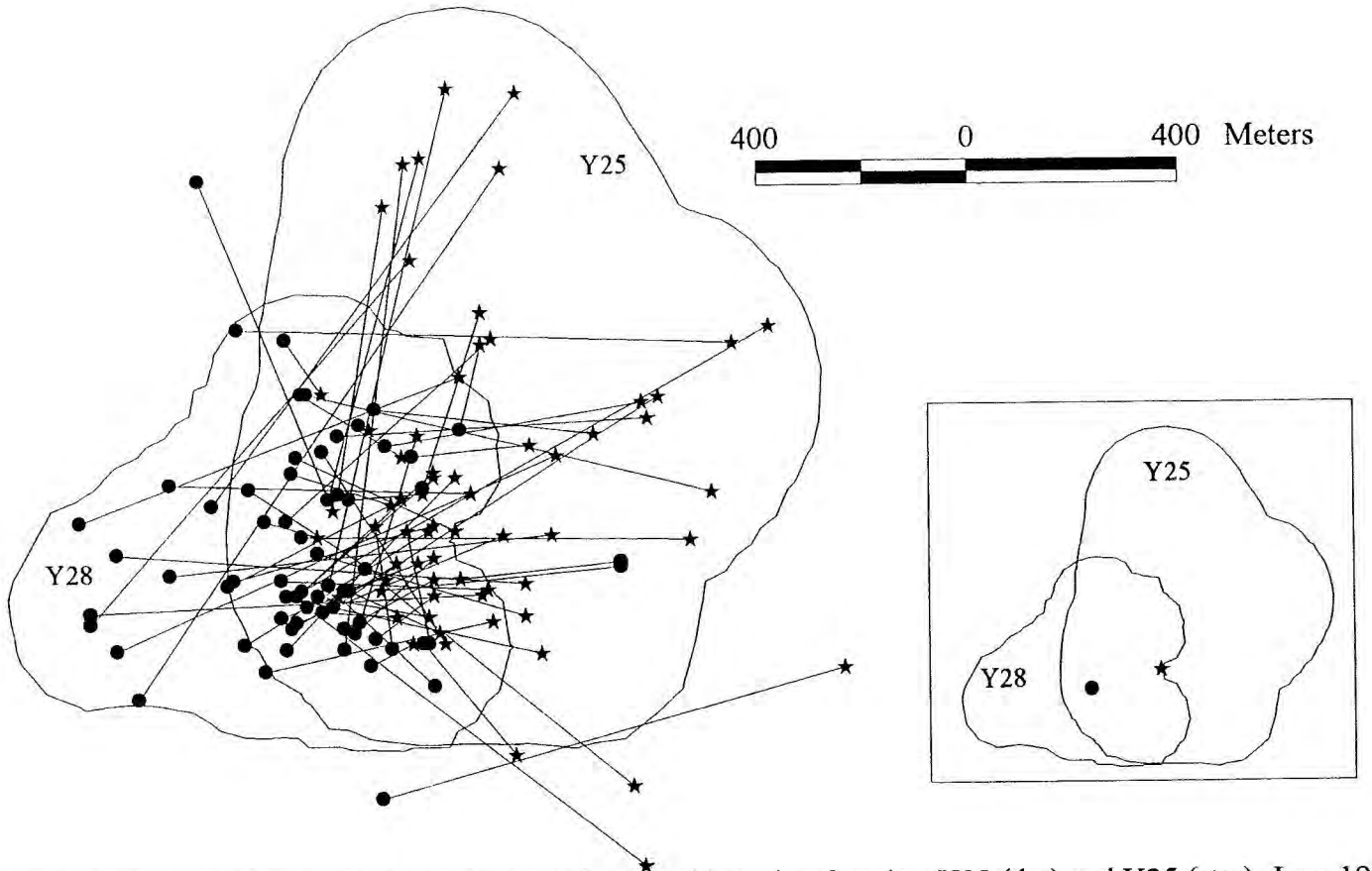


Fig. 16. Symmetrical spatial attraction between moderately related lactating females, Y28 (dot) and Y25 (star), June 1992 - Dec 1992. Distance between HCAs was 298 m, median inter-individual distance was 408 m. OZ included a small patch of oak-hickory forest, a pond and a barn with haystacks which were used by both raccoons. Non-overlapping areas were mostly pasture.

Discussion

What are the spatial and social consequences of philopatry in a solitary carnivore like the raccoon? My results in general support the hypotheses that 1) female spatial distribution is not randomly associated with genetic relatedness, 2) interactions among neighboring females is independent of relatedness, and 3) philopatry seems to be female-biased in raccoons.

The relationship between female philopatry and spatial organization. In many species, the degree of faithfulness to natal sites or social groups is usually sex-biased (Greenwood 1980). Among birds like the Florida scrub jay, *Aphelocoma coerulescens*, (Woolfenden and Fitzpatrick 1984) and a few mammals like chimpanzees, *Pan troglotydes* (Wrangham 1979), family groups and territory acquisition tend to be patrilineal and most dispersal is by females. In most mammals, site fidelity is female biased with social groups consisting of female matrilines (Eisenberg 1977). Do parallel examples exist among more solitary mammals via home range sharing or home range inheritance?

Genetic data and behavioral observations from my study indicate that raccoons seem to demonstrate the predicted pattern of mammalian philopatry and home range accession. Significant positive correlations between genetic distance and spatial distance indicates that neighboring females tend to be more related than expected by chance. Similarly, significant positive associations between home range overlap and genetic similarity indicate that females who share more space tend to be more related than expected by chance.

How do such patterns arise? Inferences of population spatial structure with genetic data can be misleading unless the nature of the molecular data is addressed and placed in the context of past and current observations (O' Brien 1987, Avise et al. 1992). The molecular approach used here allowed assessments of genetic relatedness among particular pairs of individuals, after calibrating the extent of RAPD band sharing against known kinship among raccoons for which field observations were available. Besides such calibrations often being non-linear, the large variances in levels of band-sharing allow only the most general inferences of kinship (Lynch and Milligan 1994, Avise 1994). Individuals with large degrees of band sharing may be mother and daughter, but may also share high similarity through other means (e.g., have the same father, be sibs, or half sibs). A positive association between genetic distance and spatial distance in females requires that a sizable fraction of females demonstrate philopatry (Chapter 2), but other factors can enhance or weaken this relationship. Many raccoon males will reside in the same areas for years (Fritzell 1978a, Forman 1985) and possibly father daughters in contiguous areas. Thus the association between genetic similarity and geographic distance can be enhanced by nonrandom mating because females living in adjacent areas may be fathered by one male. Multiple mating is suspected in raccoons and greater ranging behavior in males is frequently reported. Both factors can weaken the association between genetic similarity and geographic distance because offspring from the same litter will share lower similarity, or, males could father females in widely separate areas who would consequently be highly related. Thus the high variance around the correlation between relatedness and geographic distance in raccoons is not surprising and may be

conservative evidence of female philopatry. The slightly stronger association between band similarity and home range overlap, together with weak or insignificant associations between relatedness and geographic distance, has been echoed in other studies of mammals that display female philopatry. For example, with allozymes, van Staaden et al. (1994) did not detect an association between genetic distance and geographic distance among pairs of Richardson's ground squirrels, *Spermophilus richardsonii*, in an 18.5 ha study area, but demonstrated a weak although significant correlation between coancestry and geographic distance. Neighboring females tended to be more related than expected by chance, not only in the population, but also within single matrilines. Low levels of female dispersal can also introduce high variation in the relationship between relatedness and geographic distance. Using both mitochondrial and microsatellite markers, Ishibashi et al. (1997) found that neighboring grey-sided vole, *Clethrionomys rufocanus*, females were frequently from the same maternal lineage and that relatedness between females correlated negatively with geographic distance. However, there was enormous variation in these relationships. Some matrilines showed a dispersed distribution indicating that some females dispersed and settled among unrelated females. The use of both mitochondrial and highly variable nuclear markers in Ishibashi et al.'s study permitted stronger inferences.

Greater within-sex similarity in females than in males is evidence of stronger site fidelity in females and the greater dispersal tendencies of males. Also, the stronger differentiation in genetic distance between Oak Ridge and Chuck Swan populations when adult males were excluded from the data set suggests stronger site fidelity in females and

greater movements among males. However, distributions of adult male-adult female similarity values show several males on the high end of the distribution suggesting that dispersal among males may not always be the rule; some males may remain on or close to the natal area as adults. The possibility that natal philopatry may extend into adulthood may be more common in males than previously thought. For example, in white-nosed coatis, *Nasua narica*, Gompper and Wayne (1996) found higher band-similarity between adult males and adult females occupying the male's home range than among adult males and females from non-overlapping areas. Although male coatis tend to move widely during the breeding season, familiarity with the natal range was thought to be important for males too.

Allozyme surveys of raccoon populations have indicated high similarity among raccoons from different geographic areas in the southeastern U.S. (Dew and Kennedy 1980, Beck and Kennedy 1980) and within geographic regions (Hamilton and Kennedy 1987) leading to the suggestion that "*Procyon lotor* may be genetically equivalent throughout its range" (Dew and Kennedy 1980). Considering the natural vagility of raccoons and that artificial dispersal is high, this is not a startling suggestion. Reports of movements exceeding 20-100 km have been reported for male raccoons (Priewert 1961, Lynch 1967, Forman 1985), with movement rates reaching 0.3-10 km per night (Fritzell 1978a). Thus the differentiation between Oak Ridge and Chuck Swan females resulting from genetic distance analysis is surprising and suggestive that some RAPD markers target mitochondrial sites or regions of the genome not surveyed by allozymes. For example, Lorenz et al. (1994) demonstrated a number of fragments in RAPD profiles of

sugar beet were of organellar origin, particularly mtDNA. Several studies comparing genetic distance estimates based on allozymes vs. RAPD markers have found that RAPD markers reveal population structure not detected using allozymes (Tuskan et al. 1996).

Is spatial organization a consequence of kinship or philopatry in female raccoons? Among gregarious animals, matrilineal kinship is a common correlate of social behaviors involving increased tolerance, affiliative behaviors such as social grooming, and coalition formation during aggressive encounters (Gouzoules and Gouzoules 1987). Do solitary animals make similar distinctions on the basis of relatedness? High home range overlap among some female raccoons with low relatedness indicates that female raccoons are unlikely to discriminate between kin and non kin with regard to the amount of space they share; that is, the relationship between home range sharing and relatedness seems to be a consequence of common female philopatry and not necessarily one based on kinship. But is the use of shared areas temporally partitioned? For example, Leyhausen (1965) observed that house cats, use the same area but not at the same time. Minta (1993) detected similar behavior among adult female badgers, *Taxidea taxus*. Among raccoons at White Oak Lake, temporal use of shared areas was random for most females, but, when spatial interaction was observed, attraction to shared areas was more common than avoidance. Although there was closer association among females with young yearling daughters (<8-10 months) and between two non-sibling yearlings, mean distances older females maintained from each other were relatively high, regardless of relatedness. Most females were not found together with other female raccoons indicating that, although females may share common areas, they usually remain solitary.

If kinship is not a strong predictor of female spatial and temporal interaction, is it possible that reproductive status might be? Among other procyonids, female coatis, *Nasua narica*, who are gregarious will separate from their groups and live solitarily during pregnancy and parturition (Kaufmann 1962). Groups of kinkajous, *Potos flavus*, usually consist of only one breeding female (Kays pers. comm.). Female raccoons at Oak Ridge who shared large proportions of space were usually nulliparous or only one individual was parous. When both individuals were parous, areas of overlap were less extensive but were used simultaneously by some pairs of females. Spatial avoidance was infrequent, although symmetrical spatial avoidance which comes closest to the classic concept of territoriality (Minta 1992), was demonstrated once between two reproductive females of moderate relatedness who had about 10% home range overlap. Overall, there was indication that parous females shared less space, but analyses of spatial interaction did not detect consistent signs of intrasexual avoidance. Fritzell (1978a) reported extensive home range overlap among female raccoons, but only in one instance did two parous females, one of which was a yearling, have almost congruent home ranges. Although the pair remained solitary, they gave birth to litters 30 m apart in an abandoned farm site in North Dakota, a habitat where food and denning resources for raccoons are likely to be localized and patchy. Solitary female coatis have been observed to den less than 100 m apart in southeast Arizona, a habitat where water and large den trees are localized in canyons (Ratnayeke et al. 1994). Only a fraction of raccoons at White Oak Lake were followed and habitat features indicating the distribution and availability of resources were not accounted for. Reproductive status may be a likely predictor of

female spatial and temporal interaction if resource availability and distribution can be adequately measured and incorporated in such analyses. In raccoons, individual recognition and dominance hierarchies also will complicate interpretations of spatial and temporal interaction. For example, Barash (1974) found that neighboring raccoons, when placed in captivity, demonstrate dominance-subordinate relations more quickly and have fewer fights than 'strangers' trapped more than 8 km apart. Thus, individuals that share a common space or even feed in close proximity do not necessarily fare equally well.

Waser and Jones (1983) suggest that when close kin forage alone, but in a common area, it may be mutually beneficial to time foraging patterns to avoid areas recently depleted by one another. On the other hand, Minta (1992) interprets an analogous pattern of space use as despotic. Clearly, interpretations of spatial and temporal interaction that depend heavily on remote techniques will be limited and tentative, especially if the sole nature of the interaction data depends on one individual's location relative to another. Social interaction can be complex and, even among readily observed or well-habituated individuals, it frequently requires long and careful study for correct interpretation (von Frisch 1965, Altmann 1965). Among carnivores who rely on several, probably subtle, modes of communication, both the recognition and reliable interpretation of interaction is a challenge.

CHAPTER 4

CONCLUSIONS

Population structure is a consequence of complex social, historical and physical relationships between the individuals and groups that compose it. Among mammals, the common phenomenon of male dispersal and female philopatry has generated interest in how behavior and relationships among individuals affect the spatial and genetic structure of populations (Chepko Sade et al. 1987, Shields 1987) and eventually the nature of mammalian sociality (Eisenberg 1977). The influence of philopatry in shaping mammalian sociality has led to increased interest in philopatry and spatial organization in solitary mammals, "...yet the extent and nature of philopatry has been rarely documented,...the probabilities that particular neighbors will have particular degrees of relatedness are as yet uncalculated for any solitary mammal,...no studies of solitary mammals have explicitly investigated the relative movements of same-sex individuals whose ranges overlap..." (Waser and Jones 1983).

In the past 14 years, much information regarding philopatry and social organization has been collected, particularly on smaller mammals, such as rodents and lagomorphs, who show various levels of social complexity. High density and habitat saturation seem to favor philopatry in some studies (McGuire et al. 1993, Jones et al. 1988). Spatial clustering of kin because of female philopatry seems widespread (e.g., Boonstra et al. 1987, Lambin et al. 1992, Salvioni and Lidicker 1995). But the relative costs and benefits of philopatry are not clearly resolved. Some studies report that

philopatry causes no detectable costs to mothers and is often beneficial to offspring (Jones 1984, Jones et al. 1988, Solomon 1991, Moses and Millar 1994), whereas some report that such relationships are competitive and can suppress reproductive success in younger individuals (Armitage 1986, Rieger 1991) or decrease reproductive output among parents (Cockburn et al. 1985, Johnson 1986). Clearly, much variation exists with regard to costs and benefits of philopatry for different species.

The nature and circumstances surrounding female philopatry in most solitary carnivores is less well known. What is the nature of female philopatry and what are the implications of strong natal philopatry in raccoons? The nature of philopatry in raccoons conforms most closely with Waser and Jones' (1983) definition of philopatry by parental consent (type B.2, Table1). In a relatively dense, unhunted population of raccoons at White Oak Lake, most female raccoons remained on the natal area and shared space with mothers. Although female raccoons in most regions of the U.S. are physiologically capable of reproduction at one year, lower body weight, delayed reproduction, and higher mortality in younger females relative to older females at White Oak Lake suggests that under certain ecological and demographic conditions, female competition can limit the availability of breeding resources to younger females. Although, dispersal was too infrequent to evaluate the relative costs and benefits of philopatry, fitness consequences of strong philopatry in raccoons at Oak Ridge invoke the predictions of Murray (1967) and Hamilton and May (1977), that is, reduced survivorship and fecundity of philopatric young, possible subordination of young in the social system, and reduced access to critical resources when population densities are high.

What is the effect of kinship on social organization among female raccoons? Natal philopatry contributes significantly to female spatial organization in raccoons; female raccoons exhibit site fidelity which results in a non-random distribution of genotypes in which closely related individuals have a greater likelihood of being neighbors. This relationship is possibly enhanced by a polygynous mating system. However, the role of kinship in determining who will share space seems unimportant. High overlap among some unrelated females indicates that maternal inheritance of space is not a necessary condition for home range sharing in female raccoons. Furthermore, the nature of spatial and temporal interaction among females of different relatedness suggests that raccoons do not make distinctions on the basis of kinship. Similar conclusions resulted from studies on the grey-sided vole, *Clethrionomys rufocanus*, (Ims 1989) and Richardson's ground squirrel, *Spermophilus richardsonii*, (van Staaden et al. 1994). In these species, philopatry was a more likely determinant of spatial overlap or proximity than selective sociability among kin. On the other hand, in black bears, *Ursus americanus*, Rogers (1987) detected differential behavior between kin and non kin. Mothers assisted their daughters in acquiring home ranges and were on occasion observed to behave aggressively to non kin. It is surprising therefore, that Schenk (1994) did not find a relationship between band-sharing and home range overlap in a fairly dense population of black bears in northern Ontario. Schenk (1994) suggested that high survivorship in adult female black bears forced young to eventually disperse to find vacant breeding space.

A common element underlies much of the variation described in the preceding studies on philopatry in mammals. Conditions that favor mutually beneficial relationships between mothers and daughters seem related to the nature of resources, especially their distribution, abundance and renewability (Ostfeld et al. 1985, Lambin et al. 1992). If resource competition has little potential to reduce reproductive output, mothers would be more likely to promote post-weaning survival and philopatry in their daughters (Moses and Millar 1994). Food distribution and availability has been considered a strong determinant of spacing and reproductive success among several carnivores (e.g., Moehlman 1989, Angerbjörn et al. 1991). It can increase or decrease the potential for encounters and competition between females which in turn can affect reproduction. That high home range overlap among raccoons is less common when two females are parous is, therefore, expected. Resource competition is expected to be most evident among parous females and may take the shape of temporary territoriality in some species (Jannett 1978, Ostfeld et al. 1985). Although temporal use of overlapping areas is usually not partitioned for most parous raccoons at White Oak Lake, inter-individual spacing indicates solitary lifestyles which suggests that female raccoons forage and raise young more efficiently alone, despite the presence of older offspring and some nonkin within their home range. The tolerance of philopatric offspring is therefore potentially costly unless mothers can offset costs by being more solitary during pregnancy and lactation. The actual mechanisms by which they achieve this could not be determined, except that inter-individual spacing between mothers and philopatric daughters increased considerably as the birth season approached.

What are the circumstances of philopatry in a solitary carnivore that might contribute to understanding the evolution of more complex sociality in carnivores? The many pressures that lead to cooperative behavior cannot be explained by the narrow set of variables that any one study might examine. For example, environmental factors are vital variables driving the nature of social interaction which requires that they are studied on a finer scale. But what corollaries might be derived from this study when viewed in the context of social mammals that have been fairly well studied?

Hypotheses explaining the retention of young on the natal range in social carnivores, social primates and birds that display cooperative breeding have regarded high population densities and limited breeding resources to promote philopatry (Goldizen and Terborgh 1989). A common correlate in several of these studies is delayed breeding in younger individuals (Frame et al. 1979, Moehlman 1982, Rood 1982, Woodruffe and MacDonald 1995). Although demographic data are fewer for the carnivores, Goldizen and Terborgh (1989) connected delayed breeding in tamarins, *Saguinus fuscicollis*, with high population densities and high survival among breeding individuals. Similar circumstances surround cooperative breeding in birds (reviewed in Goldizen and Terborgh 1989). Delayed breeding or reproductive suppression has been attributed to intrinsic causes such as behavioral dominance of older females, usually when resource competition is intense (Rubenstein and Wrangham 1986). Wolff (1997) points out that such suppression is common in social carnivores (Mech 1970, Creel and Waser 1991, Woodruffe and MacDonald 1995) and can be adaptive in two contexts; first, the threat of infanticide which is most likely when space is limited should promote younger females to

conserve reproductive effort until such time when they can successfully reproduce; second, the observation that delayed sexual maturation occurs when younger individuals remain in contact with opposite-sex parents is widespread in social mammals including carnivores (e.g., Moehlman 1982, Creel and Waser 1991) and may serve to decrease inbreeding. The circumstances surrounding philopatry in raccoons thus bears a certain resemblance to many species that have cooperative systems. Although kinship does not seem to be a necessary condition for sharing space in raccoons, the tolerance of neighbors can evolve if the probability of their being close kin is high enough (Waser and Jones 1983), or, if associations between individuals are mutually beneficial regardless of kinship (Trivers 1971, Wrangham 1982). In raccoons, the high probability of sharing space with kin through retention of young on the natal range as well as the delayed sexual maturation of philopatric young, are all common or necessary correlates of sociality among many cooperatively breeding carnivores. That these conditions have not promoted a system of alloparenting or shared responsibility of rearing offspring in raccoons may depend on the nature of their resource base and different pressures that affect the successful rearing of young.

In conclusion I made the following findings:

1. Natal philopatry was a common occurrence among female raccoons at the White Oak Lake study area. Most female young persisted on the natal area beyond dependence and beyond their mother's next breeding episode. Thus, philopatry involved sharing the maternal home range. Population density of raccoons at White Oak Lake (1/7.6 ha) was high relative to other raccoon populations in east Tennessee. Also, the proportion of

females in older age classes was high. Despite high densities, philopatry was more common than dispersal. Most dispersal was during the early Spring when mortality was highest among philopatric females. There was no indication philopatry entailed greater fitness benefits in terms of survival and reproductive success, but dispersal occurred too infrequently to test this prediction. Although female raccoons are physiologically capable of reproduction at one year, lower body weight, delayed reproduction and higher mortality in younger females suggested that competition from older females limited the availability of breeding resources and food to younger females. The presence of a yearling daughter on the home range did not seem to incur a reproductive cost to mothers. At least 50% of mothers with yearling daughters became pregnant the following year. No philopatric daughters became pregnant when their mothers were alive on the natal area.

2. Female philopatry in raccoons resulted in a non-random distribution of genotypes in which closely related individuals were more likely to be neighbors. Genetic distance, based on RAPD band frequency, was positively associated with spatial distance among females. Genetic similarity was positively associated with the extent of home range overlap. This relationship was possibly enhanced by polygynous mating. The high variance in the association was most likely caused by high male movement and possibly some female dispersal. Site fidelity was more common in female than male raccoons: average female-female similarities at White Oak Lake were greater than average male-male similarities or average male-female similarities. High overlap among females with low and moderate relatedness indicated that maternal inheritance of space was not a

necessary condition for home range sharing. High home range overlap (> 50 %) between females was less common when both were parous. Spatial and temporal interaction among females was independent of relatedness. Most responses to areas of home range overlap were random. Inter-individual distances among most females were high relative to the distances between their activity centers, reflecting the solitary nature of female raccoons.

LIST OF REFERENCES

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Ables, E. D. 1969. Home-range studies of red foxes (*Vulpes vulpes*). J. Mammal. 50:108-120.

Ackerman, B. B., F. A. Leban, M. D. Samuel, and E. O. Garton. 1990. User's manual for Program Home Range. Second Edition. Tech. Rep. 15, Forestry, Wildlife and Range Experiment station, University of Idaho, Moscow, Idaho, USA.

Altmann, S. A. 1965. Sociobiology of rhesus monkeys: II, stochastics of social communication. J. Theor. Biol. 8:490-522.

Anderson, P. K. 1970. Ecological structure and gene flow in small mammals. Symp. Zool. Soc. Lond. 26:299-325.

Angerbjörn, A., B. Arvidson, E. Norén, and L. Strömgren. 1991. The effect of winter food on reproduction in the Arctic fox, *Alopex lagopus*: a field experiment. J. Anim. Ecol. 60:705-714.

Apostol, B. L., W. C. Black IV, B. R. Miller, P. Reiter, and B. J. Beaty. 1993. Estimation of family numbers at oviposition sites using RAPD-PCR markers: Applications to the mosquito *Aedes aegyptii*. Theor. Appl. Gen. 86:991-1000.

Armitage, K. B. 1986. Marmot polygyny revisited: determinants of male and female reproductive strategies. Pp. 303-331 in: (D. I. Rubenstein and R. W. Wrangham eds.) Ecological aspects of social evolution. Princeton University Press, Princeton.

Ashwood, T. L., M. S. Ratnayeke, L. A. Baron, and R. T. Stevens. 1994. Assessment of contaminants in the terrestrial environment. In: (T.L. Ashwood ed.) Eighth annual report on the ORNL biological, monitoring and abatement program. Draft ORNL/TM-12767. Oak Ridge National Laboratory, Oak Ridge, Tenn.

Avise, J. C. 1994. Molecular markers, natural history and evolution. Chapman Hall, New York, London.

Avise, J. C., R. T. Alisauskas, W. S. Nelson, and C. D. Ankney. 1992. Matriarchal population genetic structure in an avian species with female natal philopatry. Evolution 46:1084-1096.

Barash, D. P. 1974. Neighbor recognition in two "solitary" carnivores: the raccoon (*Procyon lotor*) and the red fox (*Vulpes vulpes*). Science 185:794-796.

Beck, M. L., and M. L. Kennedy. 1980. Biochemical genetics of the raccoon, *Procyon lotor*. Genetica 54:127-132.

Bekoff, M., and L. D. Mech. 1984. Simulation analyses of space use: home range estimates, variability, and sample size. Beh. Res. Meth. Instr. and Comp. 6:32-37.

Bekoff, M., and M. C. Wells. 1982. Behavioral ecology of coyotes: social organization, rearing patterns, space use, and resource defense. Z. Tierspsychol. 60:281-305.

Bertram, B. R. 1974. Radiotracking leopards in the Serengeti. African Wildlife Leadership Foundation News 2:7-10.

Brown, J. L., and G. H. Orians. 1970. Spacing patterns in mobile animals. Ann. Rev. Ecol. System. 1:239-262.

Brown, J. L. 1974. Alternate routes to sociality in jays - with a theory for the evolution of altruism and communal breeding. Am. Zool. 14:63-80.

Black IV, W. C. 1995. FORTRAN programs for the analysis of RAPD-PCR markers in population. Colorado State University, FT Collins, CO 80523.

Boonstra, R., C. J. Krebs, M. S. Gaines, M. L. Johnson, and I. T. M. Craine. 1987. Natal philopatry and breeding systems in voles (*Microtus* spp.). J. Anim. Ecol. 56:655-673.

Burke, T., and M. W. Bruford. 1987. DNA fingerprinting in birds. Nature 327:149-152.

Burke, T., N. B. Davies, M. W. Bruford, and B. J. Hatchwell. 1989. Parental care and mating behavior of polyandrous dunnocks *Prunella modularis* related to paternity by DNA fingerprinting. Nature 338:249-251.

Cantrell, M. A. 1989. Characteristics of a managed raccoon population in east Tennessee with an emphasis on summer dog training and fall harvest. M. S. Thesis, University of Tennessee, Knoxville. 140pp.

Caughley, G. 1977. The Analysis of Vertebrate Populations. John Wiley and Sons. N. Y. 234 pp.

Cheeseman, C. L., W. J. Cresswell, S. Harris, and P. J. Mallinson P. J. 1988. Comparison of dispersal and other movements in two Badger (*Meles meles*) populations. Mammal Rev. 18:51-59.

Chepko-Sade, D. B., W. M. Shields, J. Berger, Z. Tang Halpin, W. T. Jones, L. L. Rogers, J. P. Rood, and A. T. Smith A.T. 1987. The effects of dispersal and social structure on effective population size. Pp.287-323 in: (D. B. Chepko-Sade and Z. Tang Halpin, eds.) Mammalian dispersal patterns. University of Chicago Press.

Clapp, R. B., J. A. Watts, and M. A. S. Guth, eds. 1995. Third annual environmental restoration monitoring and assessment report for FY 1994, Oak Ridge National Laboratory, Oak Ridge, Tennessee.

Clarke, A. B. 1978. Sex ratio and local resource competition in a prosimian primate. Science 201:163-165.

Cockburn, A., M. P. Scott, and C. R. Dickman. 1985. Sex-ratio and intra-sexual kin competition in mammals. Oecologia 66:427-429.

Cowan, W. F. 1973. Ecology and life history of the raccoon (*Procyon lotor hirtus* Nelson and Goldman) in the northern part of its range. Ph. D. thesis. Univ. North Dakota. 176pp.

Creel, S. R., and P. M. Waser. 1991. Failure of reproductive suppression in dwarf mongooses (*Helogale parvula*): accidental or adaptation? Behav. Ecol. 2:7-15.

Crook, J. H. 1972. Sexual selection, dimorphism, and social organization in the primates. Pp. 231-281 in: (B. G. Campbell, ed.) Sexual selection and the descent of man. Aldine, Chicago.

Dards, J. L. 1978. Home ranges of feral cats in Portsmouth Dockyard. Carnivore Genet. Newsl. 3:242-253.

Dew, R. D., and M. L. Kennedy. 1980. Genic variation in the raccoon, *Procyon lotor*. J. Mammal. 61:697-702.

Dietz, E. J. 1983. Permutation tests for association between two distance matrices. Syst. Zool. 32:21-26.

Dixon, K. R., and J. A. Chapman. 1980. Harmonic mean measure of animal activity areas. Ecology 61:1040-1044.

Dobson, F.S. 1982. Competition for mates and predominant juvenile male dispersal in mammals. Anim. Behav. 30:1183-1192

Dunn, J. P., and J. A. Chapman. 1983. Reproduction, physiological responses, age structure and food habits of raccoon *Procyon lotor* in Maryland, USA. Zeitschrift fuer Saugetierkunde 48:161-175.

Egoscue H. J. 1975. Population dynamics of the kit fox in western Utah. Bull. South Calif. Acad. Sci. 74:122-127.

Eisenberg, J. F. 1977. The evolution of the reproductive unit in the Class Mammalia. Pp. 39-71 in: (J. S. Rosenblatt and B. R. Komisaruk, eds.) Reproductive behavior and evolution. Plenum Press, New York.

Emlen, S. T. 1982. The evolution of helping. I. An ecological constraints model. Am. Nat. 119:29-39.

Emlen, S. T., and L. W. Oring. 1977. Ecology, sexual selection and the evolution of mating systems. Science 197:215-223.

Felsenstein, J. 1993. PHYLIP (Phylogeny Inference Package) version 3.5c. Department of Genetics, University of Washington, Seattle, WA.

Forman, L. 1985. Genetic variation in two procyonids: phylogenetic, ecological and social correlates. Ph.D. Dissertation, New York University, New York. 238pp.

Fowler, C. W. 1981. A review of density dependence in populations of large mammals Current Mamm. 1:401-441.

Frame, G. W., and L. H. Frame. 1981. Swift and enduring: cheetahs and wild dogs of the Serengeti. E. P. Dutton, NY.

Frame, L. H., J. R. Malcolm, G. W. Frame, and H. van Lawick. 1979. Social organization of African wild dogs (*Lycaon pictus*) on the Serengeti Plains, Tanzania, 1967-1978. Z. Tierpsychol. 50:225-249.

Frisch, K. von. 1967. The dance language and orientation of bees. Trans. by L. E. Chadwick. Belknap Press of Harvard University, Cambridge.

Fritzell, E. K. 1978a. Aspects of raccoon *(Procyon lotor)* social organization. Can. J. Zool. 56: 260- 271.

Fritzell, E. K. 1978b. Reproduction of raccoons (*Procyon lotor*) in North Dakota. Am. Midl. Nat. 100:253-256.

Fritzell, E. K., G. F. Hubert, B. E. Meyen, and G. C. Sanderson. 1985. Age-specific reproduction in Illinois and Missouri raccoons. J. Wildl. Manage. 49:901-905.

Gaines, M. S., and L. R. McClenagahan, Jr. 1980. Dispersal in small mammals. Annu. Rev. Ecol. Syst. 11:163-169.

Gilbert, D. A., C. Packer, A. E. Pusey, J. C. Stevens, and S. J. O'Brien. 1991. Analytical DNA fingerprinting in lions: parentage, genetic diversity and kinship. J. Heredit. 82:378-386.

Gittleman, J. L. 1986. Carnivore life history patterns: allometric, phylogenetic, and ecological associations. Am. Nat. 127:744-771.

Glass, S. L. 1991. Ecology and Population Dynamics of Raccoons in East Tennessee. M.S. Thesis, University of Tennessee, Knoxville. 201 pp.

Goldizen, A. W., and J. Terborgh. 1989. Demography and dispersal patterns of a tamarin population: possible causes of delayed breeding. Am. Nat. 134:208-224.

Gompper, M. E., J. L. Gittleman, and R. K. Wayne. 1997. Genetic relatedness, coalitions and social behaviour of white-nosed coatis, *Nasua narica*. Anim. Behav. 53:781-797.

Gompper, M. E., and R. K. Wayne. 1996. Genetic relationships among individuals within carnivore societies. Pp.429-452 in: (J. L. Gittleman, ed.) Carnivore behavior ecology and evolution. Vol. 2. Cornell University Press, Ithaca, NY.

Gouzoules, S., and H. Gouzoules. 1987. Kinship. Pp. 299-305 in: (B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, and T. T. Struhsaker, eds.) Primate Societies. University of Chicago Press, Chicago.

Grau, G. A., G. C. Sanderson, and J. P. Rogers. 1970. Age determination of raccoons. J.Wildl. Manage. 34:364-372.

Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Anim. Behav. 28:1140-1162.

Gunter, L. E., G. A. Tuskan, and S. D. Wullschleger. 1996. Diversity among populations of switchgrass based on RAPD markers. Crop Sci. 36:1017-1022.

Hadrys H., M. Balick, and B. Schierwater. 1992. Applications of random amplified polymorphic DNA (RAPD) in molecular ecology. Mol. Ecol. 1:55-63.

Hamilton, M. J., and M. L. Kennedy. 1987. Genic variability in the raccoon *Procyon lotor*. Am. Midl. Nat. 118:266-274.

Hamilton, W. D. 1964. The genetical theory of social behavior, I, II. J. Theoret. Biol. 7:1-52.

Hamilton, W. D., and R. M. May. 1977. Dispersal in stable habitats. Nature 269:578-581.

Harris, M. A., and J. O. Murie. 1984. Inheritance of nest sites in female Columbian ground squirrels. Behav. Ecol. Sociobiol. 15:97-102.

Haugen, O. L. 1954. Longevity of the raccoon in the wild. J. Mammal. 35: 439.

Hillis, D. M., B. K. Mable, and C. Moritz. 1996. Applications of molecular systematics. Pp. 515-543 in: (D. M. Hillis, C. Moritz and B. K. Mable, eds.) Molecular Systematics. Sinauer Ass. Inc. Massachussetts, USA.

Horn, H. S. 1984. Some theories about dispersal. Pp.54-62 in: (I. R. Swingland and P. J. Greenwood, eds.) The ecology of animal movement. Clarendon Press, Oxford.

Hubert, L. J. 1978. Generalized proximity function comparisons. Br. J. Math. Statist. Psychol. 31:179-192.

Ims, R. A. 1989. Kinship and origin effects on dispersal and space sharing *in Clethrionomys rufocanus*. Ecology 70:607-616.

Ishibashi, Y., T. Saitoh, S. Abe, and M. C. Yoshida. 1997. Sex-related spatial kin structure in a spring population of grey-sided voles Clethrionomys rufocanus as revealed by mitochondrial and microsatellite DNA analyses. Mol. Ecol. 6:63-71.

Itani, J. 1972. A preliminary essay on the relationship between social organization and incest avoidance in non-human primates. Pp. 165-171 in: (F. Poirier, ed.) Primate socialization. Random House, New York.

Jannett, F. G. Jr. 1978. The density-dependent formation of extended families of the montane vole, *Microtus montanus nanus*. Behav. Ecol. Sociobiol. 3:245-263.

Jeffries, A. J., V. Wilson, and S. L. Thein. 1985a. Hypervariable "minisatellite" regions in human DNA. Nature 314: 67-73.

Jeffries, A. J., V. Wilson, and S. L. Thein. 1985b. Individual-specific "fingerprints" of human DNA. Nature 316:76-79.

Johnson, A. S. 1970. Biology of the raccoon (*Procyon lotor varius* Nelson and Goldman) in Alabama. Auburn Univ. Agric. Exp. Stn. Bull. 402. 148pp.

Johnson, C. N. 1986. Philopatry, reproductive success of females, and maternal investment in the red-necked wallaby. Behav. Ecol. Sociobiol. 19:143-150.

Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. Biometrika 52:225-247.

Jones, T. W. 1984. Natal philopatry in bannertailed kangaroo rats. Behav. Ecol. Sociobiol. 15:151-155.

Jones, W. T., P. M. Waser, L. F. Elliot, N. E. Link, and B. B. Bush. 1988. Philopatry, dispersal and habitat saturation in the banner-tailed kangaroo rat, *Dipodomys spectabilis*. Ecology 69:1466-1473.

Junge, R. E., and G. C. Sanderson. 1982. Age related reproductive success of female raccoons. J. Wildl. Manage. 46:527-529.

Kambhampati, S., W. C. Black IV, and K. S. Rai. 1991. RAPD-PCR for identification and differentiation of mosquito species and populations: techniques and statistical analysis. J. Med. Ent. 29:939-945.

Kaufmann, J. H. 1962. Ecology and social behavior of the coati, *Nasua narica*, on Barro Colorado Island, Panama. Univ. Calif. Publ. Zool. 60:95-222.

Kaufmann, J. H. 1982. Raccoons and allies. Pp.567-585 in: (J. A. Chapman and G. A. Feldhammer, eds.) Wild mammals of North America: Biology, Management, and Economics. John Hopkins Univ. Press, Baltimore.

Keeler, W. E. 1978. Some aspects of the natural history of the raccoon *(Procyon lotor)* in Cades Cove, the Great Smoky Mountains National Park. M. S. Thesis, University of Tennessee, Knoxville.

Kessler, L. G., and J. C. Avise. 1985. Microgeographic lineage analysis by mitochondrial genotype: variation in the cotton rat (*Sigmodon hispidus*). Evolution 39:831-837.

Kie, J.G., J. A. Baldwin, and C. J. Evans. 1994. Calhome home range analysis program. U. S. Forest Service.

Lair, H. 1987. Estimating the location of the focal center in red squirrel home ranges. Ecology 68:1092-1101.

Lambin, X., C. J. Krebs, and B. Scott. 1992. Spacing system of the tundra vole (*Microtus oeconomus*) during the breeding season in Canada's western Arctic. Can. J. Zool. 70:2068-2072.

Larntz, K. 1978. Small sample comparisons of exact levels for chi-squared goodness of-fit statistics. J. Amer. Statist. Assoc. 73:253-263.

Laundré, J. 1977. The daytime behavior of domestic cats in a free-ranging population. Anim. Behav. 25:990-998.

Lehmann, N., P. Clarkson, L. D. Mech, T. J. Meier, and R. K. Wayne. 1992. A study of the genetic relationships within and among wolf packs using DNA fingerprinting and mitochondrial DNA. Behav. Ecol. Sociobiol. 3:83-94.

Leyhausen, P. 1965. The communal organization of solitary mammals. Symposia of the Zoological Society of London. 14: 249-263.

Liberg, O. 1980. Spacing patterns in a population of rural free roaming domestic cats. Oikos 35:336-349.

Liberg, O., and T. von Schantz. 1985. Sex-biased philopatry and dispersal in birds and mammals: the Oedipus hypothesis. Am. Nat. 126:129-135.

Lidicker, W. Z. 1975. The role of dispersal in the demography of small mammals. Pp. 103 -128, in: (F.B. Golley, K. Petrusewicz, and L. Ryzcowski, eds.) Small mammals: their productivity and population dynamics. Cambridge University Press, New York.

Lorenz, M., A. Weihe, and T. Börner. 1994. DNA fragments of organellar origin in random amplified polymorphic DNA (RAPD) patterns of sugar beet (*Beta vulgaris L.*)

Lu, M., A. E. Szmidt, and X. Wang. 1995. Inheritance of RAPD fragments in haploid and diploid tissues of *Pinus sylvestris* (L.). Heredity 74:582-589.

Lynch, G. M. 1967. Long-range movement of a raccoon in Manitoba. J. Mammal. 48:659-660.

Lynch, M. 1988. Estimation of relatedness by DNA fingerprinting. Mol. Biol. Evol. 5:584-599.

Lynch, M. 1991. Analysis of population genetic structure by DNA fingerprinting. Pp. 113-126 in: (T. Burke, G. Dolf, A. J. Jeffreys and R. Wolff, eds.) DNA fingerprinting: approaches and applications. Birkhäuser Verlag Basel.

Lynch, M., and B. G. Milligan. 1994. Analysis of population genetic structure with RAPD markers. Molecular Ecology 3:91-99.

MacDonald, D. W. 1981. Resource dispersion and the social organization of the red fox, *Vulpes vulpes*. Pp. 918-949 in: (J. Chapman and D. Pursely, eds) Worldwide Furbearer Conf. Proc. II, Worldwide Furbearer Conference, Inc. Frostburg.

Mace, R. D., and Waller, J. S. 1997. Spatial and temporal interaction of male and female grizzly bears in northwestern Montana. J. Wildl. Manage. 61:39-52.

Mann, L. K., P. Parr, L. R. Pounds, and R. L. Graham. 1996. Protection of biota on nonpark lands: examples from the US Department of Energy Oak Ridge. Reservation. Env. Manage. 20:207-218.

McCracken, G. F. 1984. Communal nursing in Mexican free-tailed bat maternal colonies. Science 223:1090-1091.

McCracken, G. F., and J. W. Bradbury. 1981. Social organization and kinship in the polygynous bat *Phyllostomus hastatus*. Behav. Ecol. Sociobiol. 8:11-34.

McGuire, B., L. L. Getz, J. E. Hofmann, T. Pizzuto, and B. Fraser. 1993. Natal dispersal and philopatry in prairie voles (*Microtus ochrogaster*) in relation to population density, season, and natal social environment. Behav. Ecol. Sociobiol. 32:293-302.

Mech, L. D. 1970. The Wolf. University of Chicago Press, Chicago.

Mech, L. D., D. M. Barnes, and J. R. Tester. 1968. Seasonal weight changes, mortality, and population structure of raccoons in Minnesota. J. Mammal. 49:63-3.

Mech, L. D., and F. J. Turkowski. 1966. Twenty three raccoons in one winter den. J. Mammal. 47:529-530.

Messier, F., and C. Barrette. 1982. The social system of the coyote (*Canis latrans*) in a forested habitat. Can. J. Zool. 60:1743-1753.

Michener, G. R. 1973. Field observations on the social relationships between adult female and juvenile Richardson's ground squirrels. Can. J. Zool. 51:33-38.

Minser, W. G., and M. R. Pelton. 1982. Impact of hunting on raccoon populations and the management implications. Agric. Exp. Sta. Univ. of Tennessee Bull. No. 612. 32pp.

Minta, S. C. 1990. The badger, *Taxidea taxus* (Carnivora: Mustelidae): Spatial-temporal analysis, dimorphic territorial polygyny, population characteristics, and human influences on ecology. Ph. D. Dissertation, University of California, Davis. 310 pp.

Minta, S. C. 1992. Tests of spatial and temporal interaction among animals. Ecological Applications 2:178-188.

Minta, S. C. 1993. Sexual differences in spatio-temporal interaction among badgers. Oecologia 96:402-409.

Moehlman, P. D. 1979. Jackal helpers and pup survival. Nature 277:382-383.

Moehlman, P. D. 1982. Socioecology of silver-backed and golden-backed jackals (*Canis mesomelas* and *Canis aureus*). Spec. Publ. Am. Soc. Mammal. 7:423-453.

Moehlman, P. D. 1989. Intraspecific variation in canid social systems. Pp. 143-163 in: (J. L. Gittleman, eds.) Carnivore behavior, ecology, and evolution. Cornell University Press.

Montgomery, G. G. 1964. Tooth eruption in pre-weaned raccoons. J. Wildl. Manage. 28:582-584.

Montgomery, G. G. 1969. Weaning of captive raccoons. J. Wildl. Manage. 33:154-159.

Moore, J., and R. Ali. 1984. Are dispersal and inbreeding avoidance related? Anim. Behav. 32:94-112.

Moses, R. A., and J. S. Millar. 1994. Philopatry and mother-daughter associations in bushy-tailed woodrats: space use and reproductive success. Behav. Ecol. Sociobiol. 35:131-140.

Murray, B. G., Jr. 1967. Dispersal in vertebrates. Ecology 48:975-978.

Nei, M. 1972. Genetic distance between populations. Am. Nat. 106:283-292.

Nei, M., and W. H. Li. 1979. Mathematical model for studying genetic variation in terms of restriction endonucleases. Proc. Natl. Acad. Sci. USA 76:5269-5273.

Nixon, C. M., L. P. Hansen, and S. P. Havera. 1986. Demographic characteristics of an unexploited population of fox squirrels (*Sciurus niger*). Can. J. Zool. 64:512-521.

Nordstrom, W. R. 1972. Comparison of trapped and untrapped beaver populations in New Brunswick. M. S. Thesis. Univ. New Brunswick. Fredericton. 104 pp.

O'Brien E. 1987. Correlation between population structure and genetic structure in the Hutterite population. Pp. 193-210 in: (D. B. Chepko-Sade and Z. Tang Halpin, eds.) Mammalian Dispersal Patterns. University of Chicago Press.

Ostfeld, R. S., W. Z. Lidicker, Jr., and E. J. Heske. 1985. The relationship between habitat heterogeneity, space use, and demography in a population of California voles. Oikos 45:433-442.

Packer, C. 1979. Inter-troop transfer and inbreeding avoidance in *Papio anubis*. Anim. Behav. 27:1-36.

Packer, C., D. A. Gilbert, A. E. Pusey, and S. J. O'Brien. 1991. A molecular genetic analysis of kinship and cooperation in African lions. Nature 351:562-564.

Parr, P. D., and L. R. Pounds. 1987. Resource management plan for the Oak Ridge reservation. Vol. 23, Oak Ridge National Environmental Research Park, Research Sites, and State Natural Areas, 60 pp.

Pillay, M., and S. T. Kenny. 1995. Anomalies in direct pair-wise comparisons of RAPD fragments for genetic analysis. Bio Techniques 19:694-698.

Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. J. Wild. Manage. 53(1): 7-15.

Pollock, K. H., J. D. Nichols, C. Brown, and J. E. Hines. 1990. Statistical inference for capture -recapture experiments. Wildl. Monogr. 107:1-97.

Priewert, F. W. 1961. Record of an extensive movement by a raccoon. J. Mammal. 42:113.

Rabinowitz, A. R. 1981. The ecology of the raccoon (Procyon lotor) in Cades Cove, Great Smoky Mountains National Park. Ph.D. Diss., University of Tennesee, Knoxville. 133pp.

Ratnayeke, M. S., A. Bixler, and J. L. Gittleman. 1994. Home range movements of solitary reproductive female coatis, *Nasua narica,* in southeastern Arizona. Journ. Zool. 233:322-326.

Rieger, J. F. 1991. Female investment strategies and reproductive success in the Uinta ground squirrel, *Spermophilus armatus*. Ph. D. Thesis, University of Michigan, Michigan.

Rogers, L. L. 1987. Effects of food supply and kinship on social behavior, movements, and population growth of black bears in northeastern Minnesota. Wildl. Monogr. 97:1-72.

Rood, J. P. 1982. The social system of the dwarf mongoose. Spec. Publ. Am. Soc. Mammal. 7:454-488.

Rubenstein, D. I., and R. W. Wrangham. 1986. Socioecology: origins and trends. Pp. 3-17 in: (D. I. Rubenstein and R. W. Wrangham, eds.) Ecological aspects of social evolution. Princeton University Press, Princeton.

Salvioni, M., and W. Z. Lidicker. 1995. Social organization and space use in California voles: seasonal, sexual, and age-specific strategies. Oecologia 101:426-438.

Sanderson, G. C. 1950. Methods of measuring productivity in raccoons. J. Wildl. Manage. 14:389-402.

Sanderson, G. C. 1961. Techniques for determining age of raccoons. Illinois Nat. Hist. Surv. Bio. Notes 45. 16pp.

Sanderson, G. C., and A. V. Nalbandov. 1973. The reproductive cycle of the raccoon in Illinois. Illinois Nat. Hist. Surv. Bull. 31:29-85.

Sanderson, G. C. 1950. Methods of measuring productivity in raccoons. J. Wildl. Manage. 14:389-402.

Schenk, A. 1994. Genetic relatedness, home range characteristics and mating patterns of black bears (*Ursus americanus*) in northern Ontario, Canada. Ph.D. thesis, University of Waterloo, Waterloo, Ontario.

Schneider, D. G., L. D. Mech, and J. R. Tester. 1971. Movements of female raccoons and their young as determined by radio-tracking. Anim. Behav. Monogr. 4:1-43.

Scott, M. P., K. M. Haymes, and S. M. Williams. 1992. Parentage analysis using RAPD PCR. Nucleic Acids Res. 5493.

Seber, G. A. F. 1982. The Estimation of Animal Abundance and Related Parameters. Macmillan Publ. Co. Inc., New York. 654 pp.

Sharp, W. M., and L. H. Sharp. 1956. Nocturnal movements and behavior of wild raccoons at a winter feeding station. J. Mammal. 37:170-177.

Shields, W. M. 1987. Dispersal and mating systems: investigating their causal connections. Pp. 3-24 in: (D. B. Chepko-Sade, and Z. Tang Halpin, eds.), Mammalian dispersal patterns. University of Chicago Press.

Simonsen, V. 1982. Electrophoretic variation in large mammals. II. The red fox, *Vulpes vulpes*, the stoat, *Mustela erminea*, the weasel, *Mustela nivalis*, the pole cat, *Mustela putorius*, the pine marten, *Martes martes*, the beech marten, *Martes foina*, and the badger, *Meles meles*. Hereditas 96:299-305.

Smith, A. T. and B. L. Ivins. 1983. Colonization in a pika population: dispersal vs. philopatry. Behav. Ecol. Sociobiol. 13:37-47.

Smith, J. D. L, C. W. McDougal, and M. E. Sunquist. 1987. Female land tenure system in tigers. Pp.97-109 in: (R. L. Tilson and U. S. Seal, eds.) Tigers of the World. Noyes Publications

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. W. H. Freeman and Company, New York.

Solomon, N. G. 1991. Current indirect fitness benefits associated with philopatry in juvenile prairie voles. Behav. Ecol. Sociobiol. 29:277-282.

Staaden, M. J. van, R. K. Chesser, and G. R. Michener. 1994. Genetic correlation and matrilineal structure in a population of *Spermophilus richardsonii*. J. Mammal. 75:573-582.

Storm, G. L., R. D. Andrews, R. L. Phillips, R. A. Bishop, D. B. Siniff, and J. R.Tester. 1976. Morphology, reproduction, dispersal and mortality of midwestern red fox populations. Wildl. Monogr. 49:1-82.

Storm, G. L., and W. M. Tzilkowski. 1982. Furbearer population dynamics: a local and regional management perspective. Pp. 69-90 in (G. C. Sanderson, ed.) Midwest furbearer management. Kansas Chapter Wildlife Society. Bloomington, IN.

Stuewer, F.W. 1943a. Raccoons, their habits and management in Michigan. Ecolog. Monogr. 13:203-257.

Stuewer, F. W. 1943b. Reproduction of raccoons in Michigan. J. Wildl. Manage. 7:60-73.

Swihart, R. K., and N. A. Slade. 1985. Testing for independence of observations in animal movements. Ecology 66:1176-1184.

Taylor, L. R., and R. A. J. Taylor. 1977. Aggregation, migration and population mechanics. Nature, Lond. 265: 415-421.

Tevis, L. Jr. 1947. Summer activities of California raccoons. J. Mammal. 28:323-332.

Trapp, G. R. 1978. Comparative behavioral ecology of the ringtail and grayfox in southwestern Utah. Carnivore 1:3-32.

Trivers, R. L. 1971. The evolution of reciprocal altruism. Quart. Rev. Biol. 46:35-57.

Tuskan, G. A., K. E. Francis, S. L. Russ, W. H. Romme, and M. G. Turner. 1996. RAPD markers reveal diversity within and among clonal and seedling stands of aspen in Yellowstone National Park, U.S.A. Can. J. For. Res. 26:2088-2098

Twitchell, A. R., and H. H. Dill. 1949. One hundred raccoons from one hundred and two acres. J. Mammal. 30:130-133.

Urban, D. 1970. Raccoon populations, movement patterns, and predation on a managed waterfowl marsh. J. Wildl. Manage. 34:372-382.

Vehrencamp, S. L. 1979. The roles of individual, kin and group selection in the evolution of sociality. Pp.351-394 in: (P. Marler and J. Vandenberg, eds.), Social Behavior and Communication, Plenum Press, New York.

Warr, E. L. 1978. Evaluation of the habitat, density, and distribution of a raccoon population in east Tennessee. M. S. Thesis, University of Tennessee, Knoxville. 121pp.

Waser, P. M., and W. T. Jones. 1983. Natal philopatry in solitary mammals. Quart. Rev. Biol. 58:355- 390.

Waser, P. M., and R. H. Wiley. 1979. Mechanisms and the evolution of spacing in animals. Pp. 159-224 in (P. Marler and J. Vandenbergh, eds.) Social Behavior and Communication. Plenum Press, New York.

Wayne, R. K., D. A. Gilbert, N. Lehman, K. Hansen, A. Eisenhawer, D. Girman, R. O. Peterson, L. D. Mech, P. J. P. Gogan, U. S. Seal, and R. J. Krumenaker. 1991. Conservation genetics of the endangered Isle Royale gray wolf. Conserv. Biol. 5:41-51.

Weir, B. S. 1996. Intraspecific differentiation. Pp. 385-405 in: (D. M. Hillis, C. Moritz and B. K. Mable, eds.) Molecular Systematics. Sinauer Ass. Inc. Massachussetts, USA.

Westneat, D. F. 1990. Genetic parentage in the indigo bunting: a study using DNA fingerprinting. Behav. Ecol. Sociobiol. 27:67-76.

Wetton, J. H., R. E. Carter, D. T. Parkin, and D. Walters. 1987. Demographic study of a wild house sparrow population by DNA fingerprinting. Nature 327:147-149.

White, G. C. and R. A. Garrot. 1986. Effects of biotelemetry triangulation error on detecting habitat selection. J. Wildl. Manage. 50:509-513.

White, G. C. and R. A. Garrot. 1990. Analysis of wildlife radio-tracking data. Academic Press, Inc.

Whitney, L. F. and A. B. Underwood. 1952. The raccoon. Practical Science Publ., Co., Orange, Conn. 177 pp.

Wilkinson, G. S. 1985. The social organization of the common vampire bat: II Mating system, genetic structure, and relatedness. Behav. Ecol. Sociobiol. 17:111-121.

Williams, J. G. K., A. R. Kubelik, K. J. Livak, J. A. Rafalski, and S. V. Tingey. 1990. DNA polymorphisms amplified by arbitrary primers are useful as genetic markers. Nucleic Acids Res. 18:6531-6535.

Williams, J. G. K., M. K. Hanafey, J. A. Rafalski, and S. V. Tingey. 1993. Genetic analysis using random amplified polymorphic DNA markers. Met. Enzymol. 218:705-740.

Wolff, J. O. 1977. Population regulation in mammals: an evolutionary perspective. J. Anim. Ecol. 66:1-13.

Woodruffe, R., D. W. Macdonald, and J. da Silva. 1993. Dispersal and philopatry in the European badger, *Meles meles*. J. Zool., Lond. 237:227-239.

Woodruffe, R., and Macdonald, D. W. 1995. Female/female competition in European badgers *Meles meles*: effects on breeding success. J. Anim. Ecol. 64:12-20.

Woods, J. W. 1978. Population characteristics of raccoons (*Procyon lotor*) on the Chuck Swan Wildlife Management Area, Tennessee. M. S. Thesis, University of Tennessee, Knoxville. 93 pp.

Woolfenden, G. E., and J. W. Fitzpatrick. 1984. The Florida Scrub Jay. Princeton University Press, Princeton, NJ.

Worton, B. J. 1987. A review of models of home range for animal movement. Ecological Modelling 38:277-298.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70(1): 164-168.

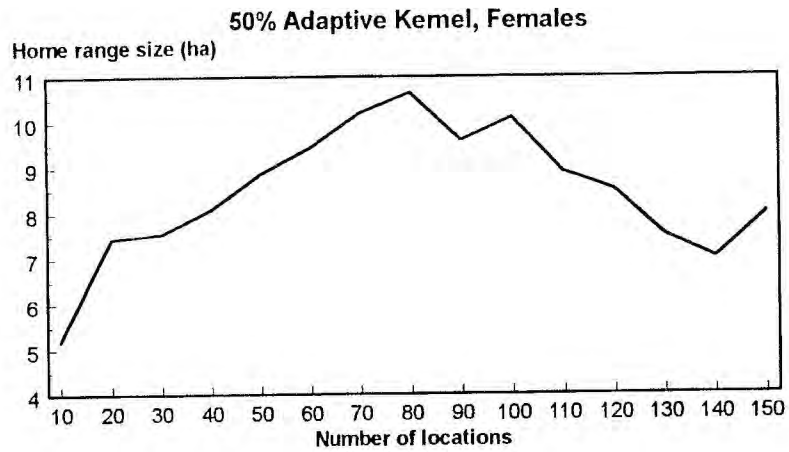
Wrangham, R. W. 1979. On the evolution of ape social systems. Soc. Sci. Information 18:334-68.

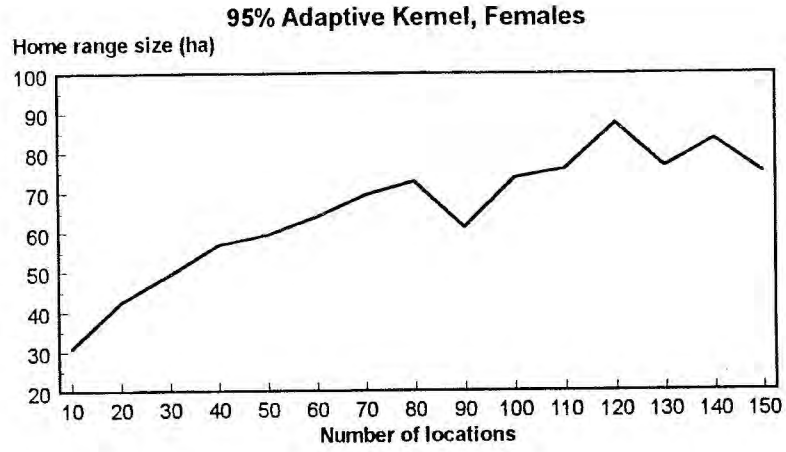
Wrangham, R. W. 1980. An ecological model of female-bonded primate groups. Behav. 75:262-300.

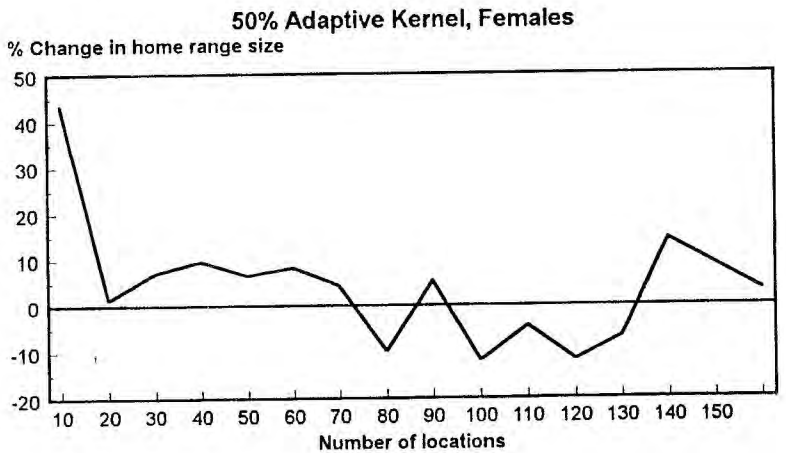
Wrangham, R. W. 1982. Mutualism, kinship and social evolution. Pp. 269-289 in: (King's College Sociobiology Group, ed.) Current problems in sociobiology. Cambridge University Press, Cambridge.

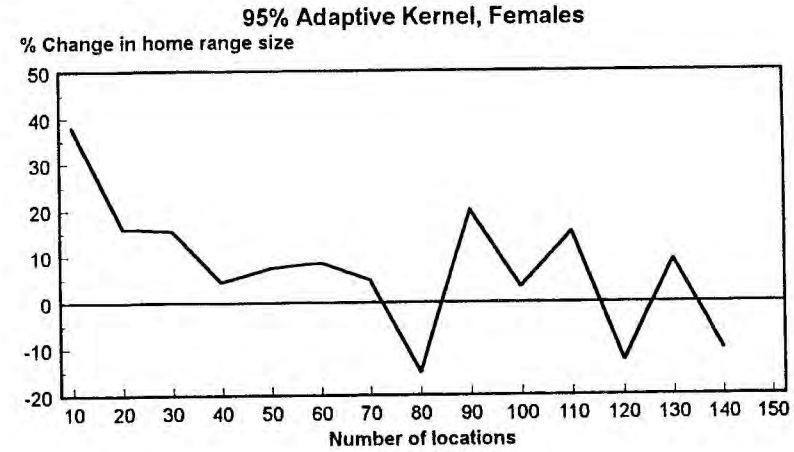
Yeaton, R. I. 1972. Social behavior and social organization in Richardson's ground squirrel *(Spermophilus richardsonii)* in Saskatchewan. J. Mammal. 53:139-147.

APPENDICES

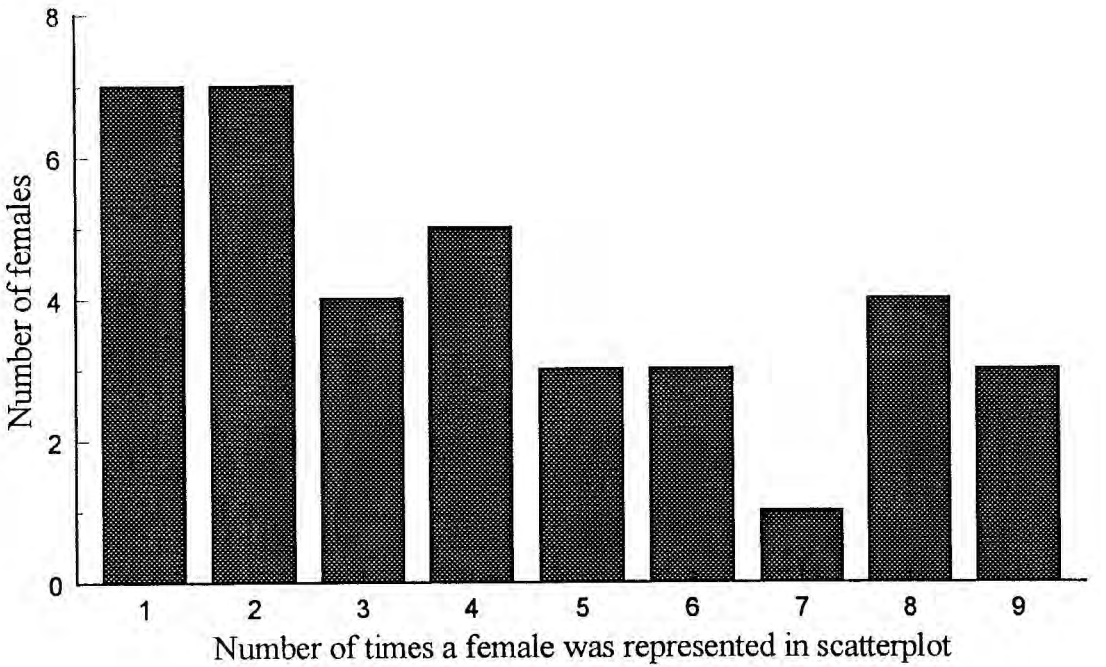








Appendix A.1. Relationships between adaptive kernel home range size and percentage change in home range size with number of raccoon locations, Oak Ridge, Tennessee.



Appendix A.2. Frequency distribution of the number of times a female was represented in the analysis of covariance of inter-individual distance among groups that differed by relatedness.

Appendix B.1. Sites, identification (ID), sex (M = male, F = female), date of first capture, mean x and y UTM of trap site (if captured), and age category (or class) of all raccoons used in genetic analyses.

Site	ID	Sex	Date	X UTM	Y UTM	Age class
North Carolina	NC1	F	Nov, 92	[1]		Adult[2]
North Carolina	NC2	F	Nov, 92			1
Chuck Swan	CS1	F	Nov, 92	[3]		Adult
Chuck Swan	CS2	M	Nov, 92			1
Chuck Swan	CS3	F	Nov, 92			Adult
Chuck Swan	CS4	M	Nov, 92			Adult
Chuck Swan	CS5	F	Nov, 92			Adult
Chuck Swan	CS6	F	Nov, 92			Adult
Chuck Swan	CS7	F	Nov, 92			Adult
Chuck Swan	CS8	F	Nov, 92			Adult
Chuck Swan	CS9	F	Nov, 92			Adult
Chuck Swan	CS10	M	Nov, 92			Adult
Chuck Swan	CS11	M	Nov, 92			Adult
Chuck Swan	CS12	M	Nov, 92			1
Chuck Swan	CS13	M	Nov, 92			1
Chuck Swan	CS14	F	Nov, 92			1
Chuck Swan	CS15	F	Nov, 92			1
Chuck Swan	CS16	F	Nov, 92			Adult
Chuck Swan	CS19	M	Nov, 92			Adult
Chuck Swan	CS20	F	Nov, 92			Adult
Chuck Swan	CS21	F	Nov, 92			Adult
Chuck Swan	CS22	F	Nov, 92			Adult
Chuck Swan	CS23	M	Nov, 92			Adult
Chuck Swan	CS24	F	Nov, 92			Adult
Chuck Swan	CS25	F	Nov, 92			Adult
Chuck Swan	CS26	F	Nov, 92			1
Chuck Swan	CS27	F	Nov, 92			1
Chuck Swan	CS28	F	Nov, 92			Adult
Chuck Swan	CS29	F	Nov, 92			1
Chuck Swan	CS30	M	Nov, 92			Adult
Chuck Swan	CS31	F	Nov, 92			Adult
Chuck Swan	CS32	M	Nov, 92			Adult
Chuck Swan	CS33	F	Nov, 92			Adult
Chuck Swan	CS34	F	Nov, 92			Adult
Chuck Swan	CS35	F	Nov, 92			Adult
Chuck Swan	CS36	F	Nov, 92			Adult
Freels Bend	Y19	F	04 27 92	747840	3981520	2
Freels Bend	Y23	F	04 30 92	747780	3981770	2
Freels Bend	Y21	F	04 28 92	748150	3980850	3
Freels Bend	Y26	F	05 05 92	750340	3982930	3

[1] North Carolina animals were from road kills in Dare county, North Carolina.

[2] North Carolina and Chuck Swan adults were not assigned to age classes.

[3] All genetic samples were obtained from the check station on the Chuck Swan Wildlife Management Area during the Fall '92 and '93 raccoon hunts.

Appendix B.1. continued

Site	Ear tag	Sex	Date	X UTM	Y UTM	Age class
Freels Bend	Y28	F	06 21 92	750340	3982930	3
Freels Bend	Y25	F	06 17 92	751000	3982430	2
Freels Bend	R34	M	05 05 92	747700	3982100	1
Freels Bend	R27	M	04 28 92	748030	3981185	2
Freels Bend	R29	M	04 29 92	747780	3981770	1
Freels Bend	R33	M	04 30 92	747840	3981520	1
Freels Bend	R35	M	05 05 92	750880	3982600	4
Freels Bend	R36	M	06 17 92	750340	3982930	2
Freels Bend	R26	M	04 27 92	750640	3981770	2
Freels Bend	R31	M	04 30 92	750880	3982600	2
East Fork	EF2	F	11 22 92	739220	3980870	4
East Fork	EF3	F	11 22 92	739220	3980870	1
East Fork	G29	F	11 12 93	738160	3982770	1
East Fork	G27	F	10 11 93	739220	3983680	1
East Fork	Y60	F	10 26 93	740300	3984400	2
East Fork	Y31	F	06 25 92	738550	3983195	2
East Fork	G28	F	11 12 93	738160	3982770	1
East Fork	G26	F	10 11 93	739220	3983680	1
East Fork	Y29	F	06 24 92	738870	3983200	2
East Fork	Y55	F	10 02 93	734000	3878400	4
East Fork	Y30	F	06 24 92	738230	3983190	2
East Fork	Y76	F	12 30 94	737920	3981040	5
East Fork	EF1	M	11 28 92	740060	3984600	2
East Fork	EF4	M	11 22 92	739220	3980870	1
East Fork	R39	M	26 06 92	739220	3983680	2
East Fork	R80	M	10 12 93	735100	3978300	3
East Fork	R79	M	10 05 93	734500	3977690	3
East Fork	R81	M	10 26 93	741080	3982050	1
East Fork	R41	M	10 07 92	736730	3981265	1
East Fork	R76	M	10 03 93	738900	3983750	1
East Fork	R60	M	05 06 93	738160	3982770	3
East Fork	R61	M	05 07 93	738160	3982770	2
East Fork	R38	M	05 03 93	737920	3981040	2
East Fork	R62	M	05 07 93	735070	3981320	2
East Fork	R40	M	08 07 92	738160	3982770	2
East Fork	R64	M	05 08 93	738790	3983820	2
East Fork	R63	M	05 08 93	738790	3983820	2
East Fork	R110	M	12 30 94	737920	3981040	1
East Fork	R107	M	12 03 94	735070	3981320	1
East Fork	R108	M	12 03 94	735070	3981320	1
East Fork	R106	M	11 20 94	738160	3982770	3
White Oak	G01	F	04 09 92	741653	3976152	1
White Oak	G07	F	04 17 92	742570	3977350	1
White Oak	Y64	F	03 31 94	741470	3976880	5
White Oak	Y37	F	04 04 93	744070	3978050	5

Appendix B.1. continued.

Site	Ear tag	Sex	Date	X UTM	Y UTM	Age class
White Oak	Y48	F	09 14 93	743850	3977860	4
White Oak	B20	F	11 02 93	742130	3976960	1
White Oak	Y62	F	11 08 93	742745	3977450	5
White Oak	Y11	F	04 17 92	743300	3977650	4
White Oak	Y39	F	04 09 93	743485	3977770	5
White Oak	Y52	F	09 19 93	743850	3977860	3
White Oak	Y41	F	04 12 93	743075	3977600	5
White Oak	G17	F	04 26 93	744490	3978160	2
White Oak	Y38	F	04 09 93	742920	3977550	3
White Oak	B11	F	09 13 93	744400	3978180	1
White Oak	G15	F	04 09 93	744400	3978180	2
White Oak	Y43	F	05 28 93	743485	3977770	3
White Oak	Y34	F	11 05 92	742570	3977350	3
White Oak	Y44	F	06 04 93	743420	3977800	4
White Oak	Y46	F	09 12 93	743075	3977600	4
White Oak	Y53	F	09 19 93	742165	3977500	5
White Oak	B18	F	10 25 93	742920	3977550	1
White Oak	B05	F	09 11 93	742185	3977130	1
White Oak	G03	F	04 10 92	741730	3976268	1
White Oak	Y40	F	04 11 93	741850	3976850	4
White Oak	Y51	F	09 18 93	744070	3978050	4
White Oak	Y63	F	11 10 93	741515	3976755	5
White Oak	Y47	F	09 12 93	744490	3978160	3
White Oak	Y57	F	10 24 93	742920	3977550	3
White Oak	Y36	F	04 04 93	743485	3977770	2
White Oak	B09	F	09 12 93	742855	3977500	1
White Oak	T02	F	04 01 92	743075	3977600	3
White Oak	Y05	F	04 09 92	743075	3977600	3
White Oak	B07	F	09 11 93	743850	3977860	1
White Oak	G30	F	04 08 94	742165	3977500	1
White Oak	G05	F	04 10 92	741660	3976805	1
White Oak	G23	F	09 10 93	743393	3977710	1
White Oak	Y54	F	09 20 93	744230	3979000	3
White Oak	G38	F	04 15 94	742350	3977155	3
White Oak	G11	F	10 24 92	742165	3977500	2
White Oak	Y49	F	09 14 93	743300	3977650	3
White Oak	Y61	F	11 07 93	744400	3978180	5
White Oak	Y50	F	09 18 93	743668	3977815	2
White Oak	B03	F	09 10 93	743960	3977955	1
White Oak	Y33	F	07 23 92	742158	3977045	4
White Oak	G19	F	05 27 93	742130	3976960	2
White Oak	Y07	F	04 17 92	741705	3976740	3
White Oak	B15	F	09 20 93	743850	3977860	1
White Oak	Y45	F	09 10 93	741575	3976035	3
White Oak	Y15	F	04 18 92	743850	3977860	3

Appendix B.1. continued.

Site	Ear tag	Sex	Date	X UTM	Y UTM	Age class
White Oak	G21	F	06 04 93	743300	3977650	2
White Oak	Y32	F	07 23 92	741538	3975890	3
White Oak	Y65	F	04 22 94	743485	3977770	2
White Oak	B13	F	09 14 93	744490	3978160	1
White Oak	B22	F	12 18 93	742800	3976800	1
White Oak	Y35	F	04 03 93	743485	3977770	4
White Oak	G42	F	10 27 94	741770	3976450	1
White Oak	Y66	F	07 26 94	741705	3976680	5
White Oak	G39	F	10 05 94	744490	3978160	1
White Oak	Y71	F	07 05 94	744400	3978180	4
White Oak	G34	F	09 15 94	741730	3976268	1
White Oak	Y75	F	11 15 94	741640	3976150	4
White Oak	G47	F	11 20 94	741640	3976150	1
White Oak	G46	F	11 20 94	741640	3976150	1
White Oak	Y70	F	10 27 94	741770	3976450	4
White Oak	G44	F	10 15 94	741770	3976450	1
White Oak	G41	F	10 15 94	741770	3976450	1
White Oak	Y67	F	07 26 94	744400	3978180	3
White Oak	G37	F	09 23 94	741730	3976268	1
White Oak	G40	F	10 06 94	741560	3976630	1
White Oak	Y69	F	10 06 94	741560	3976630	4
White Oak	G33	F	09 11 94	744493	3978725	1
White Oak	Y68	F	09 11 94	744360	3978580	3
White Oak	G48	F	04 30 95	742570	3977350	2
White Oak	G35	F	09 16 94	741730	3976268	1
White Oak	G32	F	05 19 94	741470	3976880	2
White Oak	G45	F	11 19 94	741810	3976650	1
White Oak	G43	F	10 28 94	742165	3977500	2
White Oak	G36	F	09 16 94	744070	3978050	1
White Oak	G31	F	05 17 94	742165	3977500	2
White Oak	Y78	F	05 03 95	744230	3979000	3
White Oak	G49	F	05 26 95	744230	3979000	2
White Oak	Y80	F	05 07 95	744490	3978160	5
White Oak	Y81	F	06 16 95	741850	3976850	3
White Oak	Y98	F	07 30 95	745120	3979450	4
White Oak	G51	F	07 30 95	745120	3979450	1
White Oak	G50	F	07 30 95	745120	3979450	1
White Oak	Y88	F	07 30 95	744230	3979000	3
White Oak	Al1298	F	07 30 95	744230	3979000	1
White Oak	R43	M	07 23 92	741730	3976268	1
White Oak	R03	M	04 09 92	741575	3976035	3
White Oak	R11	M	04 09 92	743300	3977650	2
White Oak	R1	M	04 01 92	741560	3976630	2
White Oak	B01	M	09 10 93	741850	3976850	1
White Oak	T19	M	04 01 92	741375	3975880	3

Appendix B.1. continued.

Site	Ear tag	Sex	Date	X UTM	Y UTM	Age class
White Oak	R07	M	04 09 92	742165	3977500	1
White Oak	R1330	M	04 12 92	743850	3977860	2
White Oak	R66	M	05 28 93	743118	3977610	3
White Oak	R72	M	09 13 93	743960	3977955	3
White Oak	R75	M	09 19 93	743075	3977600	1
White Oak	R70	M	09 11 93	741470	3976880	3
White Oak	R87	M	10 25 93	743485	3977770	2
White Oak	R1308	M	04 18 92	741993	3977058	2
White Oak	R1306	M	04 17 92	743850	3977860	2
White Oak	R42	M	07 16 92	742185	3977130	3
White Oak	R1328	M	04 12 92	743485	3977770	2
White Oak	R21	M	04 10 92	743485	3977770	2
White Oak	R67	M	05 29 93	744400	3978180	3
White Oak	R1332	M	04 12 93	742980	3977520	3
White Oak	R82	M	11 06 93	742130	3976960	1
White Oak	R73	M	09 14 93	743485	3977770	3
White Oak	R57	M	04 25 93	741515	3976755	3
White Oak	R59	M	04 27 93	741515	3976755	3
White Oak	R84	M	11 08 93	741575	3976035	1
White Oak	R86	M	11 12 93	741575	3976035	3
White Oak	R71	M	09 13 93	742570	3977350	1
White Oak	R74	M	09 19 93	743188	3977600	1
White Oak	R23	M	04 10 92	741560	3976630	3
White Oak	R2	M	04 09 92	741375	3975880	2
White Oak	R49	M	04 11 93	741475	3975958	2
White Oak	R45	M	04 02 93	744070	3978050	2
White Oak	R48	M	04 09 93	744070	3978050	2
White Oak	R56	M	04 25 93	744400	3978180	3
White Oak	R47	M	04 04 93	742150	3976809	2
White Oak	R19	M	04 10 92	742743	3977390	2
White Oak	R58	M	04 26 93	741653	3976152	2
White Oak	R46	M	04 02 93	741858	3976953	2
White Oak	R05	M	04 09 92	741850	3976850	2
White Oak	R88	M	10 26 93	744280	3978105	3
White Oak	R51	M	04 17 93	744445	3978170	3
White Oak	R68	M	05 30 93	741730	3976268	2
White Oak	R50	M	04 11 93	741850	3976730	2
White Oak	R15	M	04 10 92	743850	3977860	1
White Oak	R97	M	09 30 94	741850	3976730	3
White Oak	R94	M	09 16 94	744490	3978160	1
White Oak	R93	M	09 15 94	741730	3976268	1
White Oak	R100	M	10 05 94	744490	3978160	1
White Oak	R113	M	04 29 95	741560	3976630	3
White Oak	R104	M	11 20 94	741640	3976150	1
White Oak	R105	M	11 20 94	741770	3976450	1

Appendix B.1. continued.

Site	Ear tag	Sex	Date	X UTM	Y UTM	Age class
White Oak	R99	M	10 04 94	741730	3976268	1
White Oak	R112	M	04 28 95	742745	3977450	2
White Oak	R101	M	10 25 94	744070	3978050	1
White Oak	R95	M	09 30 94	743310	3977750	1
White Oak	R114	M	05 03 95	744950	3979290	3
White Oak	R111	M	04 28 95	742920	3977550	3
White Oak	R91	M	05 14 94	741470	3976880	3

Appendix B.2. Shifts in harmonic center of activity (HCA) over time for female raccoons. N = total number of radio locations per animal.

Raccoon		Shift (m) in HCA with 20 additional locations[1]						Mean shift	95% HR	% shift in
ID	N	20	40	60	80	100	120	in HCA	diameter (m)	HCA
B05	68	81.25	20.77					51.01	791.56	6.44
B11	50	124.05	30.52					77.29	947.18	8.16
G03	52	88.31	56.79					72.55	744.58	9.74
G19	59	97.05	62.05					79.55	697.81	11.40
Y03	112	49.19	167.61	211.06	211.06	19.39		131.66	728.25	18.08
Y07	137	358.93	248.09	77.74	37.37	120.86	35.38	146.40	1099.30	13.32
Y13	62	96.94	70.57					83.76	965.15	8.68
Y17	107	33.72	46.67	12.75	32.63	69.45		39.04	1201.36	3.25
Y21	83	161.81	70.44	81.44				104.56	1135.46	9.21
Y23	90	190.83	201.22	58.43	19.59			117.52	882.41	13.32
Y25	82	84.60	28.18	58.91				57.23	1207.70	4.74
Y26	85	128.60	105.28	42.68	0.00			69.14	955.87	7.23
Y28	71	19.57	109.04	84.78				71.13	832.54	8.54
Y32	73	38.04	40.39	17.06				31.83	987.44	3.22
Y33	149	38.31	96.46	34.00	63.80	89.65	0.00	53.70	980.13	5.48
Y34	84	84.90	74.20	35.75				64.95	934.94	6.95
Y35	56	218.86	267.55					243.21	865.74	28.09
Y36	63	73.14	94.36					83.75	850.39	9.85
Y38	102	48.70	56.50	61.47	118.98			71.41	979.68	7.29
Y39	62	239.70	230.91					235.31	808.50	29.10
Y40	99	165.36	136.98	132.18	70.51			126.26	974.40	12.96
Y41	67	75.89	8.20					42.05	881.33	4.77
Total								92.01	924.20	9.96

[1]Distance (in meters) between center of activity estimated with total number of locations and center of activity estimated with increments of 20 locations.

Appendix B.3. Codes, sequences and band frequencies of the random primers use to examine band-similarity in *Procyon lotor*.

Primer Codes	Sequence	Fragment[1]	Frequency (N=226)
1. OPAL 09	CAGCGAGTAG	1400	.080
		1100	.075
		580	.146
		1050	.049
		1000	.965
2. UBC 145	TGTCGGTTGC	580	.204
3. OPAB 09	GGGCGACTAC	1310	.035
OPAJ 13	CAGCCGTTCC	1200	.066
		590	.035
		505	.088
		460	.027
		400	.044
		300	.111
		510	.022
4. OPAA 17	GAGCCCGACT	550	.261
		560	.332
		540	.146
		450	.310
5. UBC 114	TGACCGAGAC	650	.456
6. OPAM 15	GATGCGATGG	1200	.040
		710	.951
7. OPAL 04	ACAACGGTCC	750	.128
		520	.761
8. OPAN 07	TCGCTGCGGA	1050	.053
		1000	.933
		900	.301
		850	.469
		750	.252
		710	.106
		625	.159
9. OPAJ 15	GAATCCGGCA	800	.164
		655	.088
		650	.133
		710	.031
10. OPAM 16	TGGCGGTTTG	1325	.951
		1290	.965
		900	.960
		840	.942

[1]Approximate molecular weight of bands expressed as base pairs.

Appendix B.3. continued

Primer Codes	Sequence	Locus no.	Frequency (N=226)
10. OPAM 16 cont.		800	.027
		600	.111
		500	.022
11. UBC 159	GAGCCCGTAG	1900	.142
		900	.593
		910	.850
		890	.150
		800	.792
		700	.088
		710	.111
		650	.093
		500	.150
12. OPA 02	TGCCGAGCTG	1060	.142
		850	.142
		800	.549
		625	.044
		500	.403
		800	.022
13. OPAA 19	TGAGGCGTGT	1200	.841
		1000	.102
		950	.412
		800	.062
		700	.858
		650	.973
		750	.035
		1400	.059
14. OPAC 01	TCCCAGCAGA	1150	.602
		910	.031
15. OPAN 06	GGGAACCCGT	975	.823
		750	.058
		320	.044
16. OPAD 04	GTAGGCCTCA	450	.389
17. OPAM 07	AACCGCGGCA	1100	.195
		1000	.058
		850	.150
		600	.027
18. OPAL 05	GACTGCGCCA	500	.465
		560	.739

Appendix B.4. Identification, sex (F = female; M = male), age class when tracking commenced, radio-tracking period and number of locations (N) for raccoons for which 95% adaptive kernel home ranges (ADK) and harmonic centers of activity (HCA) were calculated. Home ranges for raccoons with ≥ 40 locations were calculated.

ID	Sex	Age Class	Period followed (mo/yr)	N	95% ADK (ha)	HCA	
						x utm	y utm
1. Y17*	F	2.0	05/92 - 05/93	107	113.40	742843	3977124
2. Y03*	F	2.0	05/92 - 04/93	112	41.67	742103	3977352
3. G03	F	2.0	04/93 - 03/94	52	43.56	741603	3976566
4. Y07	F	3.0	05/92 - 09/93	137	94.95	741626	3976589
5. Y13*	F	2.0	07/92 - 10/92	62	73.19	743459	3977790
6. Y32	F	3.0	07/92 - 04/93	73	76.61	741683	3875753
7. Y33	F	4.0	07/92 - 05/94	149	75.48	742333	3976924
8. Y34	F	3.0	11/92 - 07/94	84	68.86	742830	3977102
9. Y21	F	3.0	05/92 - 12/92	83	101.30	748279	3980828
10. Y23	F	3.0	05/92 - 12/92	90	61.18	747786	3981497
11. Y25	F	2.0	06/92 - 12/92	82	114.60	750379	3982059
12. Y26	F	3.0	05/92 - 12/92	85	71.79	750207	3982909
13. Y28	F	3.0	06/92 - 12/92	71	54.46	750150	3982060
14. Y35	F	4.0	04/93 - 03/94	58	58.89	743492	3977403
15. Y36	F	2.0	04/93 - 04/94	65	56.82	743511	3977381
16. Y38	F	3.0	04/93 - 08/95	103	75.41	743074	3977555
17. Y39	F	4.0	04/93 - 07/94	62	51.36	743555	3977429
18. Y40	F	4.0	04/93 - 06/95	99	74.60	742037	3976353
19. Y41	F	5.0	04/93 - 05/94	67	61.03	743087	3977228
20. G19	F	1.0	05/93 - 05/94	59	38.26	742402	3976882
21. Y44	F	4.0	06/93 - 03/94	43	90.19	743455	3978131
22. B05	F	1.0	11/ 93 - 09/95	68	49.23	742165	3977294
23. Y46	F	5.0	05/94 - 01/95	40	72.55	743172	3976502
24. B09	F	1.0	11/93 - 08/95	67	97.48	742174	3976745
25. B11	F	1.0	04/94 - 08/95	50	70.49	744099	3977799
26. Y47	F	3.0	11/93 - 04/95	41	260.69	744619	3978996
27. B18[1]	F	1.0	11/93 - 03/95	53	174.20	743780	3977825
28. Y68	F	3.0	11/94 - 09/95	46	78.36	744512	3979034

[1] Home range estimate for this female was disjunct (comprised a dispersal range and a natal range which she returned to sporadically). She was not included in mean home range estimates for females.

* No genetic data available.

Appendix B.4. continued

ID	Sex	Age Class	Period followed (mo/yr)	N	95% ADK (ha)	HCA x utm	HCA y utm
29. G33	F	1.0	09/94 - 09/95	46	95.02	744488	3979005
30. G37	F	1.0	10/94 - 06/95	40	53.41	741809	3976169
31. Y69	F	4.0	10/94 - 08/95	42	70.22	741590	3976675
32. Y01	F	3.0	05/92 - 07/92	24		742785	3978055
33. T02	F	3.0	05/92 - 07/92	37		743150	3977795
34. Y05	F	3.0	05/92 - 07/92	32		742863	3977652
35. Y71	F	4.0	10/94 - 08/95	27		744442	3977743
36. G41	F	1.0	10/94 - 04/95	23		742025	3976410
37. Y70	F	4.0	10/94 - 04/95	24		741879	3976509
38. Y75	F	4.0	12/94 - 08/95	32		741465	3975900
39. G47	F	1.0	12/94 - 07/95	30		741341	3976052
40. G34	F	1.0	10/94 - 08/95	35		741435	3976375
41. G35	F	1.0	10/94 - 08/95	38		741792	3976178
42. G39	F	1.0	10/94 - 08/95	27		744663	3977905
43. R42	M	3.0	04/93 - 12/93	45	103.60	742118	3977220
44. R47	M	3.0	04/93 - 03/94	66	354.80	741683	3976454
45. R51	M	3.0	04/93 - 08/93	22		744835	3978272

Appendix B.5. Identification of female pairs, distance between harmonic centers of activity (HCA distance) for each pair, percentage band-similarity and percentage band-matches between the pair.

No.	Female pair	HCA distance	Percentage		No.	Female pair	HCA distance	Percentage	
			Similarity	Matches				Similarity	Matches
1	Y32 - Y07	839	72.37	84.21	30	Y38 - Y36	470	72.73	84.21
2	T02 - Y07	1943	77.27	86.84	31	Y39 - Y07	2104	68.18	81.58
3	T02 - Y32	2514	78.26	86.84	32	Y39 - Y33	1322	79.17	85.53
4	Y05 - Y07	1630	73.17	85.53	33	Y39 - G03	2134	71.11	82.89
5	Y05 - Y32	2236	79.07	88.16	34	Y39 - Y34	795	82.61	89.47
6	Y05 - T02	321	88.37	93.42	35	Y39 - Y35	68	65.22	78.95
7	Y33 - Y07	782	73.91	82.89	36	Y39 - Y36	65	71.11	82.89
8	Y33 - Y32	1339	75.00	82.89	37	Y39 - Y38	497	71.11	85.53
9	Y33 - T02	1194	87.50	90.79	38	Y40 - Y07	474	73.17	85.53
10	Y33 - Y05	900	84.44	89.47	39	Y40 - Y33	642	75.56	84.21
11	G03 - Y07	33	88.37	93.42	40	Y40 - G03	483	66.67	81.58
12	G03 - Y33	813	68.09	78.95	41	Y40 - Y34	1090	74.42	85.53
13	Y34 - Y07	1308	72.73	84.21	42	Y40 - Y35	1794	69.77	82.89
14	Y34 - Y33	528	83.33	88.16	43	Y40 - Y36	1796	61.90	78.95
15	Y34 - G03	1339	71.11	82.89	44	Y40 - Y38	1587	71.43	84.21
16	Y35 - Y07	2036	72.73	84.21	45	Y40 - Y39	1860	65.12	80.26
17	Y35 - Y33	1254	66.67	77.63	46	Y41 - Y07	1594	79.07	88.16
18	Y35 - G03	2067	71.11	82.89	47	Y41 - Y33	813	80.85	86.84
19	Y35 - Y34	728	69.57	81.58	48	Y41 - G03	1625	77.27	86.84
20	Y36 - Y07	2044	55.81	75.00	49	Y41 - Y34	286	84.44	90.79
21	Y36 - Y33	1264	72.34	81.58	50	Y41 - Y35	442	75.56	85.53
22	Y36 - G03	2075	54.55	73.68	51	Y41 - Y36	451	72.73	84.21
23	Y36 - Y34	736	75.56	85.53	52	Y41 - Y38	327	77.27	86.84
24	Y36 - Y35	30	75.56	85.53	53	Y41 - Y39	509	80.00	88.16
25	Y38 - Y07	1740	79.07	88.16	54	Y41 - Y40	1366	76.19	86.84
26	Y38 - Y33	973	68.09	78.95	55	G19 - Y07	829	61.54	72.37
27	Y38 - G03	1773	72.37	84.21	56	G19 - Y33	80	85.71	88.16
28	Y38 - Y34	515	80.00	88.16	57	G19 - G03	860	64.15	73.68
29	Y38 - Y35	444	75.56	85.53	58	G19 - Y34	481	77.78	82.89

Appendix B.5. cont.

No.	Female pair	HCA distance	Percentage Similarity	Percentage Matches	No.	Female pair	HCA distance	Percentage Similarity	Percentage Matches
59	G19 - Y35	1208	66.67	75.00	88	B09 - Y34	746	77.55	84.21
60	G19 - Y36	1216	71.70	78.95	89	B09 - Y35	1473	65.31	77.63
61	G19 - Y38	950	67.92	76.32	90	B09 - Y36	1480	75.00	82.89
62	G19 - Y39	1276	74.07	81.58	91	B09 - Y38	1210	79.17	85.53
63	G19 - Y40	643	66.67	76.32	92	B09 - Y39	1541	77.55	84.21
64	G19 - Y41	767	71.70	78.95	93	B09 - Y40	415	73.91	82.89
65	Y44 - Y33	1648	68.18	80.26	94	B09 - Y41	1032	79.17	85.53
66	Y44 - G03	2425	63.41	80.26	95	B09 - G19	266	73.68	78.95
67	Y44 - Y34	1204	66.67	81.58	96	B09 - Y44	1887	71.11	81.58
68	Y44 - Y35	728	61.90	78.95	97	B09 - B05	548	79.17	85.53
69	Y44 - Y36	752	68.29	82.89	98	B11 - Y33	1971	73.08	78.95
70	Y44 - Y38	691	78.05	88.16	99	B11 - G03	2784	61.22	73.68
71	Y44 - Y39	709	76.19	86.84	100	B11 - Y34	1448	72.00	80.26
72	Y44 - Y40	2273	66.67	82.89	101	B11 - Y35	724	76.00	82.89
73	Y44 - Y41	975	73.17	85.53	102	B11 - Y36	721	77.55	84.21
74	Y44 - G19	1633	64.00	75.00	103	B11 - Y38	1054	69.39	78.95
75	B05 - Y33	406	72.34	81.58	104	B11 - Y39	658	68.00	77.63
76	B05 - G03	920	72.73	84.21	105	B11 - Y40	2518	68.09	78.95
77	B05 - Y34	692	80.00	88.16	106	B11 - Y41	1162	69.39	78.95
78	B05 - Y35	1332	71.11	82.89	107	B11 - G19	1928	72.41	76.32
79	B05 - Y36	1349	68.18	81.58	108	B11 - Y44	725	60.87	75.00
80	B05 - Y38	946	72.73	84.21	109	B11 - B05	1999	69.31	78.95
81	B05 - Y39	1397	71.11	82.89	110	B11 - B09	2194	71.70	78.95
82	B05 - Y40	949	66.67	81.58	111	Y47 - Y33	3085	73.47	80.26
83	B05 - Y41	924	86.36	92.11	112	Y47 - G03	3873	60.87	75.00
84	B05 - G19	474	67.92	76.32	113	Y47 - Y34	2605	68.09	78.95
85	B05 - Y44	1538	63.41	80.26	114	Y47 - Y35	1951	63.83	76.32
86	B09 - Y33	239	78.43	84.21	115	Y47 - Y36	1959	69.57	80.26
87	B09 - G03	599	66.67	78.95	116	Y47 - Y38	2113	65.22	77.63

Appendix B.5. cont.

No.	Female pair	HCA distance	Percentage Similarity	Percentage Matches	No.	Female pair	HCA distance	Percentage Similarity	Percentage Matches
117	Y47 - Y39	1894	76.60	84.21	146	Y46 - Y41	731	72.73	84.21
118	Y47 - Y40	3694	72.73	82.89	147	Y46 - G19	859	67.92	76.32
119	Y47 - Y41	2339	73.91	82.89	148	Y46 - Y44	1653	78.05	88.16
120	Y47 - G19	3063	65.45	72.37	149	Y46 - B05	1281	68.18	81.58
121	Y47 - Y44	1450	69.77	81.58	150	Y46 - B09	1027	87.50	92.11
122	Y47 - B05	2986	65.22	77.63	151	Y46 - B11	1594	65.31	76.32
123	Y47 - B09	3323	72.00	78.95	152	Y46 - Y47	2883	60.87	75.00
124	Y47 - B11	1305	78.43	85.53	153	Y46 - B18	1456	68.18	81.58
125	B18 - Y33	1705	76.60	84.21	154	Y68 - Y38	2063	77.27	86.84
126	B18 - G03	2515	72.73	84.21	155	Y68 - Y40	3648	66.67	81.58
127	B18 - Y34	1194	93.33	96.05	156	Y68 - B05	2922	63.64	78.95
128	B18 - Y35	510	71.11	82.89	157	Y68 - B09	3271	75.00	82.89
129	B18 - Y36	519	72.73	84.21	158	Y68 - B11	1302	73.47	81.58
130	B18 - Y38	756	81.82	89.47	159	Y68 - Y47	114	78.26	85.53
131	B18 - Y39	455	75.56	85.53	160	Y68 - B18	1413	72.73	84.21
132	B18 - Y40	2281	76.19	86.84	161	Y68 - Y46	2865	72.73	84.21
133	B18 - Y41	915	81.82	89.47	162	G33 - Y38	1986	73.17	82.89
134	B18 - G19	1669	71.70	78.95	163	G33 - Y40	3570	71.79	85.53
135	B18 - Y44	446	63.41	80.26	164	G33 - B05	2849	63.41	80.26
136	B18 - B05	1700	77.27	86.84	165	G33 - B09	3195	71.11	81.58
137	B18 - B09	1935	75.00	82.89	166	G33 - B11	1223	73.91	82.89
138	B18 - B11	320	69.39	78.95	167	G33 - Y47	149	83.72	89.47
139	B18 - Y47	1441	65.22	77.63	168	G33 - B18	1333	68.29	82.89
140	Y46 - Y33	939	72.34	81.58	169	G33 - Y46	2784	68.29	82.89
141	Y46 - G03	1570	72.73	84.21	170	G33 - Y68	81	92.68	96.05
142	Y46 - Y34	691	71.11	82.89	171	G37 - Y38	1876	77.27	86.84
143	Y46 - Y38	1058	77.27	86.84	172	G37 - Y40	294	80.95	89.47
144	Y46 - Y39	1003	71.11	82.89	173	G37 - B05	1180	68.18	81.58
145	Y46 - Y40	1145	71.43	84.21	174	G37 - B09	683	79.17	86.84

Appendix B.5. cont.

No.	Female pair	HCA distance	Percentage Similarity	Percentage Matches	No.	Female pair	HCA distance	Percentage Similarity	Percentage Matches
175	G37 - B11	2811	77.55	84.21	204	Y70 - Y38	1588	76.19	86.84
176	G37 - Y47	3986	65.22	77.63	205	Y70 - Y40	221	80.00	89.47
177	G37 - B18	2574	81.82	89.47	206	Y70 - B05	835	71.43	84.21
178	G37 - Y46	1403	77.27	86.84	207	Y70 - B09	378	78.26	85.53
179	G37 - Y68	3939	63.64	78.95	208	Y70 - B11	2568	76.60	84.21
180	G37 - G33	3861	63.41	80.26	209	Y70 - Y47	3700	68.18	80.26
181	G34 - Y38	2020	77.27	85.53	210	Y70 - B18	2312	76.19	86.84
182	G34 - Y40	602	71.43	82.89	211	Y70 - Y46	1293	76.19	86.84
183	G34 - B05	1174	68.18	81.58	212	Y70 - Y68	3648	71.43	84.21
184	G34 - B09	827	79.17	85.53	213	Y70 - G33	3572	71.79	85.53
185	G34 - B11	3021	65.31	75.00	214	Y70 - G37	347	80.95	89.47
186	G34 - Y47	4124	65.22	76.32	215	Y70 - G34	464	76.19	85.53
187	G34 - B18	2757	77.27	85.53	216	Y70 - Y69	333	74.42	84.21
188	G34 - Y46	1742	77.27	86.84	217	Y71 - Y38	1380	73.91	81.58
189	G34 - Y68	4067	63.64	77.63	218	Y71 - Y40	2776	68.18	78.95
190	G34 - G33	3992	63.41	78.95	219	Y71 - B05	2320	65.22	81.58
191	G34 - G37	427	77.27	85.53	220	Y71 - B09	2477	72.00	84.21
192	Y69 - Y38	1725	84.44	90.79	221	Y71 - B11	347	78.43	85.53
193	Y69 - Y40	550	74.42	85.53	222	Y71 - Y47	1266	79.17	76.32
194	Y69 - B05	845	80.00	88.16	223	Y71 - B18	666	60.87	81.58
195	Y69 - B09	588	77.55	85.53	224	Y71 - Y46	1775	69.57	86.84
196	Y69 - B11	2749	72.00	80.26	225	Y71 - Y68	1293	78.26	88.16
197	Y69 - Y47	3816	68.09	78.95	226	Y71 - G33	1220	79.07	78.95
198	Y69 - B18	2474	80.00	88.16	227	Y71 - G37	3067	65.22	77.63
199	Y69 - Y46	1591	80.00	88.16	228	Y71 - G34	3303	65.22	85.53
200	Y69 - Y68	3755	66.67	80.26	229	Y71 - Y69	3044	76.60	78.95
201	Y69 - G33	3681	66.67	81.58	230	Y71 - Y70	2844	63.64	85.53
202	Y69 - G37	551	84.44	90.79	231	Y75 - Y38	2308	77.55	85.53
203	Y69 - G34	338	75.56	85.53	232	Y75 - Y40	730	76.60	85.53

Appendix B.5. cont.

No.	Female pair	HCA distance	Percentage Similarity	Percentage Matches	No.	Female pair	HCA distance	Percentage Similarity	Percentage Matches
233	Y75 - B05	1560	73.47	82.89	262	G35 - Y38	1881	72.73	84.21
234	Y75 - B09	1104	83.02	88.16	263	G35 - Y40	302	76.19	86.84
235	Y75 - B11	3247	81.48	85.53	264	G35 - B05	1177	77.27	86.84
236	Y75 - Y47	4420	74.51	81.58	265	G35 - B09	685	79.17	85.53
237	Y75 - B18	3011	73.47	82.89	266	G35 - B11	2820	77.55	84.21
238	Y75 - Y46	1810	81.63	88.16	267	G35 - Y47	3992	82.61	88.16
239	Y75 - Y68	4371	73.47	82.89	268	G35 - B18	2582	77.27	86.84
240	Y75 - G33	4294	69.57	81.58	269	G35 - Y46	1418	68.18	81.58
241	Y75 - G37	437	77.55	85.53	270	G35 - Y68	3944	72.37	84.21
242	Y75 - G34	476	77.55	84.21	271	G35 - G33	3866	78.05	88.16
243	Y75 - Y69	785	75.56	86.84	272	G35 - G37	19	77.27	86.84
244	Y75 - Y70	736	80.85	88.16	273	G35 - G34	408	77.27	85.53
245	Y75 - Y71	3500	82.35	88.16	274	G35 - Y69	536	80.00	88.16
246	G39 - Y38	1627	84.44	90.79	275	G35 - Y70	342	85.71	92.11
247	G39 - Y40	3050	69.77	82.89	276	G35 - Y71	3077	73.91	84.21
248	G39 - B05	2572	75.56	85.53	277	G35 - Y75	429	81.63	88.16
249	G39 - B09	2746	77.55	85.53	278	G35 - G39	3350	80.00	88.16
250	G39 - B11	574	76.00	82.89	279	G41 - Y38	1610	74.42	84.21
251	G39 - Y47	1092	72.34	81.58	280	G41 - Y40	139	73.17	84.21
252	G39 - B18	887	75.56	85.53	281	G41 - B05	897	69.77	82.89
253	G39 - Y46	2047	75.56	85.53	282	G41 - B09	404	80.85	86.84
254	G39 - Y68	1139	71.11	82.89	283	G41 - B11	2572	70.83	78.95
255	G39 - G33	1075	71.45	84.21	284	G41 - Y47	3723	66.67	77.63
256	G39 - G37	3341	80.00	88.16	285	G41 - B18	2324	79.07	86.84
257	G39 - G34	3572	80.00	86.84	286	G41 - Y46	1253	74.42	84.21
258	G39 - Y69	3310	91.30	94.74	287	G41 - Y68	3673	69.77	78.95
259	G39 - Y70	3114	69.77	82.89	288	G41 - G33	3596	75.00	80.26
260	G39 - Y71	275	85.11	90.79	289	G41 - G37	285	79.07	86.84
261	G39 - Y75	3775	80.00	86.84	290	G41 - G34	489	79.07	85.53

Appendix B.5. cont.

No.	Female pair	HCA distance	Percentage Similarity	Percentage Matches
291	G41 - Y69	411	72.73	90.79
292	G41 - Y70	89	87.80	92.11
293	G41 - Y71	2841	62.22	76.32
294	G41 - Y75	700	70.83	80.26
295	G41 - G39	3113	72.73	82.89
296	G41 - G35	284	83.72	89.47
297	G47 - Y38	2272	78.26	86.84
298	G47 - Y40	739	72.73	84.21
299	G47 - B05	1467	78.26	86.84
300	G47 - B09	1062	80.00	86.84
301	G47 - B11	3244	78.43	84.21
302	G47 - Y47	4384	75.00	82.89
303	G47 - B18	2994	73.91	84.21
304	G47 - Y46	1868	78.26	86.84
305	G47 - Y68	4330	78.26	86.84
306	G47 - G33	4254	69.77	82.83
307	G47 - G37	465	73.91	84.21
308	G47 - G34	315	73.91	82.89
309	G47 - Y69	648	80.85	88.16
310	G47 - Y70	684	77.27	86.84
311	G47 - Y71	3511	79.17	86.84
312	G47 - Y75	204	90.20	93.42
313	G47 - G39	3783	80.85	88.16
314	G47 - G35	451	82.61	89.47
315	G47 - G41	672	66.67	78.95

Appendix B.6. Percentage overlap , distance between activity centers (HCA), and band similarity and band matches for all pairs of females with adjacent and overlapping home ranges

	Females	Percentage overlap	HCA	Band	
				Similarity	Matches
1	Y23 - Y21	0.38	831	66.67	82.89
2	Y26 - Y25	30.96	868	88.00	90.79
3	Y28 - Y25	40.62	229	71.11	82.89
4	Y28 - Y26	2.70	852	69.77	82.89
5	Y32 - Y07	9.93	839	72.73	84.21
6	Y33 - Y07	10.16	782	73.91	82.89
7	G03 - Y07	70.49	33	88.37	93.42
8	G03 - Y33	0.00	813	68.09	78.95
9	Y34 - Y07	0.00	1308	72.73	84.21
10	Y34 - Y33	27.47	528	83.33	88.16
11	Y35 - Y33	0.00	1254	66.67	77.63
12	Y35 - Y34	0.00	728	69.57	81.58
13	Y36 - Y33	0.00	1264	72.34	81.58
14	Y36 - Y34	3.39	736	75.56	85.53
15	Y36 - Y35	78.09	30	75.56	85.53
16	Y38 - Y33	5.49	973	68.09	78.95
17	Y38 - Y34	57.68	515	80.00	88.16
18	Y38 - Y35	22.29	444	75.56	85.53
19	Y38 - Y36	37.64	470	72.73	84.21
20	Y39 - Y34	0.00	795	82.61	89.47
21	Y39 - Y35	78.48	68	65.22	78.95
22	Y39 - Y36	90.11	65	71.11	82.89
23	Y39 - Y38	31.97	497	75.56	85.53
24	Y40 - Y07	61.58	474	73.17	85.53
25	Y40 - Y33	12.27	642	75.56	84.21
26	Y40 - G03	49.93	483	66.67	81.58
27	Y40 - Y34	0.00	1090	74.42	85.53
28	Y41 - Y33	1.04	813	80.85	86.84
29	Y41 - Y34	43.91	286	84.44	90.79
30	Y41 - Y35	21.98	442	75.56	85.53
31	Y41 - Y36	33.33	451	72.73	84.21
32	Y41 - Y38	71.58	327	77.27	86.84
33	Y41 - Y39	26.14	509	80.00	88.16
34	G19 - Y07	5.57	829	61.54	72.73
35	G19 - Y33	82.59	80	85.71	88.28
36	G19 - G03	0.00	860	64.15	73.68
37	G19 - Y34	21.83	481	77.78	82.89
38	G19 - Y35	0.00	1208	66.67	75.00
39	G19 - Y36	0.00	1216	71.70	78.95
40	G19 - Y38	0.58	950	67.92	76.32
41	G19 - Y39	0.00	1276	74.07	81.58
42	G19 - Y40	1.66	643	66.67	76.32
43	G19 - Y41	0.00	767	71.70	78.95
44	Y44 - Y34	0.00	1204	66.67	81.58
45	Y44 - Y35	4.66	728	61.90	78.95
46	Y44 - Y36	10.54	752	68.29	82.89
47	Y44 - Y38	0.00	691	78.05	88.16
48	Y44 - Y39	11.98	709	76.19	86.84
49	Y44 - Y41	3.56	975	73.17	90.79
50	B05 - Y34	23.05	692	80.00	88.16

Appendix B.6. cont.

	Females	Percentage overlap	HCA	Band	
				Similarity	Matches
51	B05 - Y38	0.04	946	72.37	84.21
52	B05 - Y40	0.17	949	66.67	81.58
53	B05 - Y41	0.00	924	86.36	92.11
54	B09 - Y34	16.59	746	77.55	84.21
55	B09 - Y38	1.06	1210	79.17	85.53
56	B09 - Y40	38.01	415	73.91	82.89
57	B09 - Y41	0.68	1032	79.17	85.53
58	B09 - B05	24.95	548	79.17	85.53
59	B11 - Y38	0.00	1054	69.39	78.95
60	B11 - Y39	7.94	658	68.00	77.63
61	B11 - Y41	0.00	1162	69.40	78.95
62	Y47 - B11	3.21	1305	78.43	85.53
63	B18 - Y34	31.74	1194	93.33	96.05
64	B18 - Y38	13.97	756	81.82	89.40
65	B18 - Y39	4.74	455	75.56	85.53
66	B18 - Y41	4.84	915	81.82	89.47
67	B18 - B05	34.96	1700	77.27	86.84
68	B18 - B09	9.00	1935	75.00	82.89
69	B18 - B11	56.89	320	69.39	78.95
70	B18 - Y47	4.53	1441	65.22	77.63
71	Y46 - Y38	22.91	1058	77.27	86.84
72	Y46 - Y40	0.00	1145	71.43	84.21
73	Y46 - B05	11.51	1281	68.18	81.58
74	Y46 - B09	42.65	1027	87.50	92.11
75	Y46 - B18	14.61	1456	68.18	81.58
76	Y68 - B11	0.00	1302	78.26	85.53
77	Y68 - Y47	46.22	114	73.47	81.58
78	G33 - B11	0.00	1223	73.91	82.89
79	G33 - Y47	53.42	149	83.72	89.47
80	G33 - Y68	89.41	81	92.68	96.05
81	G37 - Y40	80.79	294	80.95	89.47
82	G37 - B05	0.00	1180	68.18	81.58
83	G37 - B09	24.53	683	79.17	86.84
84	Y69 - Y40	22.63	550	74.42	85.53
85	Y69 - B05	0.00	845	80.00	88.16
86	Y69 - B09	2.89	588	77.55	85.53
87	Y69 - G37	21.65	551	84.44	90.79

Appendix B.7. Observed (o) and expected (p) frequencies based on spatial expectation of α and β's use of the overlap zone (OZ): o_{11}, p_{11} = α and β present; o_{12}, p_{12} = β alone; o_{21}, p_{21} = α alone; o_{22}, p_{22} = α and β absent; N = total observations.

α and β	o_{11}	p_{11}	o_{12}	p_{12}	o_{21}	p_{21}	o_{22}	p_{22}	N
Y40-G37*	26	19.33	1	7.67					27
G33-Y68*	41	34.68	2	7.83					43
Y07-G03	30.25	20.44	5.25	10.41	5.25	6.73	0.25**	3.43	41
G19-Y33	45.25	40.56	5.25	1.09	7.25	15.92	0.25	0.43	58
Y46-B09	9	6.33	5	6.33	9	10.67	11	10.67	34
Y26-Y25	5	6.90	5	10.25	27	20.47	31	30.38	68
Y41-Y34	21	12.02	18	13.70	12	16.95	11	19.33	62
Y34-Y33	2	4.99.	10	12.32	14	14.03	40	34.66	66
Y36-Y35	43	32.33	3	8.33	5	9.81	2	2.53	53
Y41-Y38	45	32.60	2	8.17	10	17.77	6	4.45	63
Y38-Y34	20	24.45	33	21.99	15	13.99	5	12.58	73
Y41-Y39	1	3.86	10	12.16	7	9.63	38	30.35	56

* Home range of β was enclosed by home range of α.

**Cell frequencies of 0 were replaced with pseudo Bayes estimates as in Minta (1992).

Appendix B.7. cont.

α and β	o_{11}	p_{11}	o_{12}	p_{12}	o_{21}	p_{21}	o_{22}	p_{22}	N
Y38-Y36	18	8.50	9	18.26	14	9.92	17	21.32	58
G19-Y34	0.25	2.64	2.25	6.01	14.25	12.90	34.25	0.58	51
Y41-Y35	1	2.60	12	9.46	6	7.55	28	27.39	47
B18-B11*	30	13.76	4	20.24					34
Y39-Y36	51.25	47.93	3.25	2.66	4.25	7.97	0.25	0.44	59
Y40-Y07	14	14.46	15	10.63	7	7.44	2	5.47	38
Y28-Y25	27	12.31	9	7.79	22	28.10	8	17.80	66
Y39-Y38	9	6.50	12	9.04	19	18.60	20	25.86	60
Y41-Y36	4	6.67	7	14.07	12	12.63	37	26.63	60
Y33-Y07	0.25	0.95	1.25	6.67	2.25	10.16	85.25	71.22	89
Y38-Y35	2	2.25	10	10.60	3	6.86	34	29.04	49
Y39-Y35	39.25	31.58	6.25	5.91	5.25	11.38	2.13	0.04	51
Y40-G03	20	13.38	21	20.45	4	6.39	5	9.78	50

Appendix B.8. Original coefficients ($L_{A:\bar{A}}$, $L_{B:\bar{B}}$, L_{ixn}) and chi-square values of spatial and temporal interaction, and new error-based coefficients, chi-squares, number of misclassified locations, and misclassification rates (%) obtained from analysis with simulated locations incorporating triangulation error for five pairs of females. N = total number of simultaneous locations.

Female pair	$L_{A:\bar{A}}$	χ^2	$L_{B:\bar{B}}$	χ^2	L_{ixn}	χ^2	N	No. in error	%
α β			ORIGINAL						
Y07-G03	1.19	7.57	0.75	2.84	0.19	0.12	41		
G19-Y33	-1.36	10.77	0.97	6.67	-1.13	3.83	58		
Y26-Y25	0.28	1.31	-0.67	3.98	-0.04	0.01	68		
Y36-Y35	0.91	3.97	0.69	3.02	0.89	2.42	53		
Y39-Y35	0.25	0.35	1.09	6.46	-0.11	0.03	51		
			ERROR						
Y07-G03	0.92	5.00	0.72	2.57	0.04	0.01	41	2	4.9
G19-Y33	-1.16	7.54	1.16	7.47	-0.92	2.12	58	4	6.9
Y26-Y25	0.14	0.33	-0.86	6.65	-0.21	0.41	68	12	17.7
Y36-Y35	1.22	4.78	0.73	3.38	0.73	1.14	53	4	7.6
Y39-Y35	-0.54	1.70	1.32	6.59	-0.49	0.51	51	4	7.8

VITA

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