SPATIAL ECOLOGY OF GRAY FOXES ON A LONGLEAF PINE FOREST AND THE SURROUNDING LANDSCAPE IN SOUTHWESTERN GEORGIA

A Thesis

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ABSTRACT

In the southeastern United States, industrial agriculture dominates the landscape, and much of the native land cover is in decline. Longleaf pine forests were once a dominant ecosystem in this region, but have largely disappeared. However, little research has been conducted on how this loss affects wildlife, especially mammalian predators. With increasing restoration efforts for longleaf pine it is important to assess the impact on species that inhabit those landscapes. Gray foxes *(Urocyon cinereoargenteus)* are native to the Southeast, but are adaptable to a wide range of habitats. Therefore, during 2002-2006 I studied a population of gray foxes on land managed for longleaf pine (Ichauway plantation) and the surrounding agriculture and residential landscape.

Gray fox habitat selection did not differ across seasons ($P > 0.050$) at any of the 3 spatial scales examined, but was non random at all scales ($P = 0.050$). Gray foxes preferred habitat types that were rare or not available on Ichauway including residential areas, hardwood forests, and industrial agriculture. Gray foxes were largely found partially or completely off Ichauway. In fact, gray foxes that overlapped Ichauway were found closer (L=12.06, P <0.001) to the borders of Ichauway than expected. Annual survival was 0.610 ± 0.100. Sixteen deaths were documented, and human causes (i.e., vehicle collisions) accounted for most (n = 10) of these. Gray fox mortality from human caused sources may have been higher than in most other populations because of the selection of anthropogenic habitat and lack of trapping. Home range sizes differed between seasons ($F_{2,34} = 3.97$, P=0.030), with home ranges in winter (152.43 ± 32.02 ha) being larger than either breeding (91.42±12.93 ha) or kit-rearing (99.68±18.27 ha) seasons. Grafen’s kinship coefficient was used to examine relatedness through genetic analysis. No correlation was detected between distance of trapped gray foxes with one another and their

genetic distance for either 2004-2005 or 2005-2006 ($P > 0.1$). Preliminary evidence suggested that closer relatives may be more apt to overlap one another's spatial use area.

CHAPTER 1: INTRODUCTION, STUDY AREA, AND GERNERAL METHODS

The gray fox *(Urocyon cinereoargenteus)* is a mid-sized predator that ranges from southern Canada throughout the contiguous United States, and into northern Central America (Fritzell and Haroldson 1982). The ability of the gray fox to inhabit an area is largely influenced by its strong dependence on forests (Hall 1981). This dependence is likely due to the ability of gray foxes to climb trees as a predator avoidance tactic (Alderton 1994, Feeney 1999). Gray foxes are commonly preyed upon by larger carnivores, such as coyotes and bobcats (Fedriani et al. 2000, Farias et al. 2005). Because of their strong dependence on forested lands, deforestation has resulted in declining gray fox populations in parts of their range (Alderton 1994, Harrison 1997). In fact, Fritzell (1987) found that tree planting and fire suppression in parts of the Great Plains allowed gray foxes to live in this previously uninhabitable area, due to the increase of trees and a shrubby understory.

Historically, the longleaf pine/wiregrass *(Aristida spp.)* ecosystem was a prominent forest type across the southeastern United States, originally comprising as much as 37 million hectares (Landers et al. 1995). Extensive logging, development, and anthropogenic changes in the timing and frequency of prescribed fire have caused the decline of this ecosystem to 1.19 million ha of the historic range (Outcalt and Sheffield 1996). Because of this decline, the longleaf pine/wiregrass system has been described as one of the most endangered ecosystems in the world (Outcalt and Sheffield 1996, Brockaway and Lewis 1997).

In addition to direct habitat loss, fragmentation has impacted longleaf ecosystems. Seventy-five percent of the remaining contiguous blocks of longleaf are =100 acres each, and in Georgia the larger blocks are predominantly privately owned (Outcalt and Sheffield 1996). The lack of public ownership of remaining longleaf forest tracts may inhibit research opportunities and place this ecosystem at greater risk due to monetary incentives for timber harvest and development.

There has been a recent increase in conservation and restoration of the longleaf pine ecosystem (Means 1996), but little research has been conducted on predators in this system. The study area for this research has ongoing mesopredator research projects (i.e., raccoons and bobcats; Storey 2001, Godbois 2003, Lynch 2005); thus, this study added an additional component to the investigation of predator spatial ecology within this threatened forest ecosystem.

OBJECTIVES

The main objective of this study was to improve knowledge of gray fox spatial ecology in a longleaf pine forest in southwest Georgia. More specifically, my goals were to:

1. Radio track gray foxes and estimate home range size.
2. Examine habitat selection.
3. Estimate annual and seasonal survival.
4. Determine cause-specific mortality rates.
5. Use molecular genetic techniques to evaluate the effect of relatedness on the spatial distribution across the study area.

THESIS FORMAT

This thesis is the result of a radio telemetry study conducted on gray foxes over a 5 year period from 2002-2006. The 1st chapter introduces the topic, states objectives, describes the study area, explains general project methods, and states general results. The 2nd chapter discusses gray fox spatial ecology, which includes home range size and habitat use between seasons. Annual, seasonal, and sex-specific survival estimates are reported. The 3rd chapter reports preliminary findings of an ongoing study of the effects of relatedness on gray fox spatial distribution.

STUDY AREA

This study was conducted on the Joseph W. Jones Ecological Research Center at Ichauway, (hereafter known as Ichauway) and surrounding public and private land. Ichauway was a former hunting preserve for northern bobwhite *(Colinus virginianus)*, but is now an ecological research center managed for longleaf pine that encompassed 12,000 ha. I defined the study area as Ichauway in its entirety, and all the land on which gray foxes were monitored (Figure 1.1), which totaled 21,224 ha. Trapping only occurred on Ichauway. The study site was located within the Southeastern Coastal Plain, in Baker County, Georgia, 16 km south of Newton ($31^0$19'N, $80^0$20'W). Average annual precipitation was 132 cm, and average temperature ranged from 11.1^0 C in winter to 27.2^0 C in summer (Boring 2001). Ichauway was managed on a 2-year prescribed fire rotation; burning primarily occurred during winter and early spring. Ichauway was dominated by a multi-story longleaf pine canopy and mixed-species hardwoods in the mid-and under-stories. Mixed pine and hardwood dominated forests, food plots and agricultural fields, and riparian hardwood zones constituted the remaining land (Goebel et al. 1997). Surrounding lands were comprised of industrial agricultural fields, plantations managed for northern bobwhite, soft wood timber plantations, and state land managed primarily for deer, dove (*Zenaida macroura*), and turkey (*Meleagris gallopavo)* hunting. I delineated a total of 9 habitat types: mixed pine/hardwood, mature pine, hardwood, wetland, wildlife food plots and non-industrial agriculture, industrial agriculture, residential, and shrub/scrub (Figure 1.2). The mature pine category mostly consisted of longleaf, although other pine species that were managed similarly to longleaf were included.

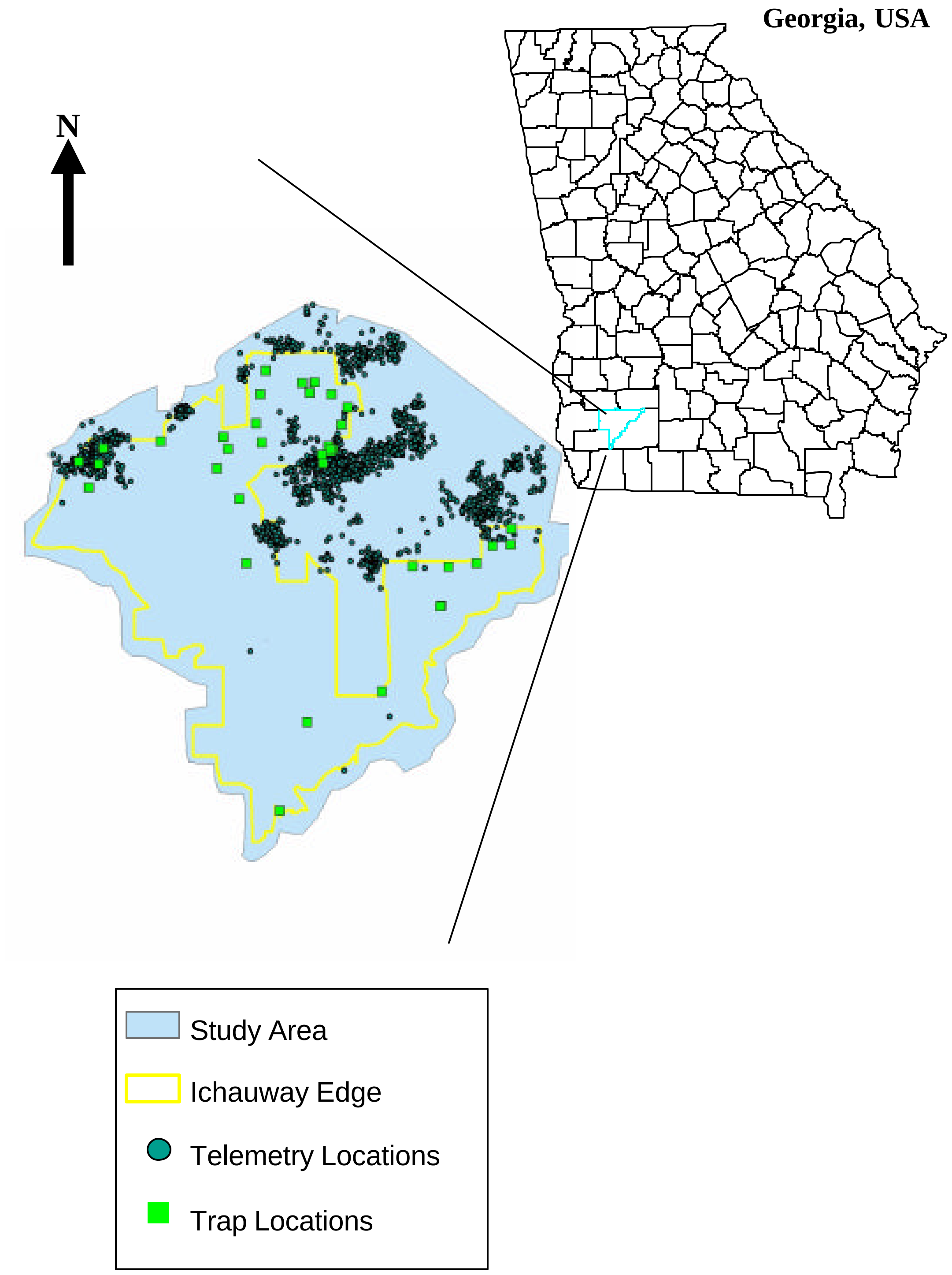

Figure 1.1. The study area encompassed 24,000 ha in Baker County, Georgia. This study occurred between 2002-2006. The outlined area shows the boundary of Ichauway, which encompasses 12,000 ha. All gray fox telemetry locations and locations of trapped gray foxes are also displayed.

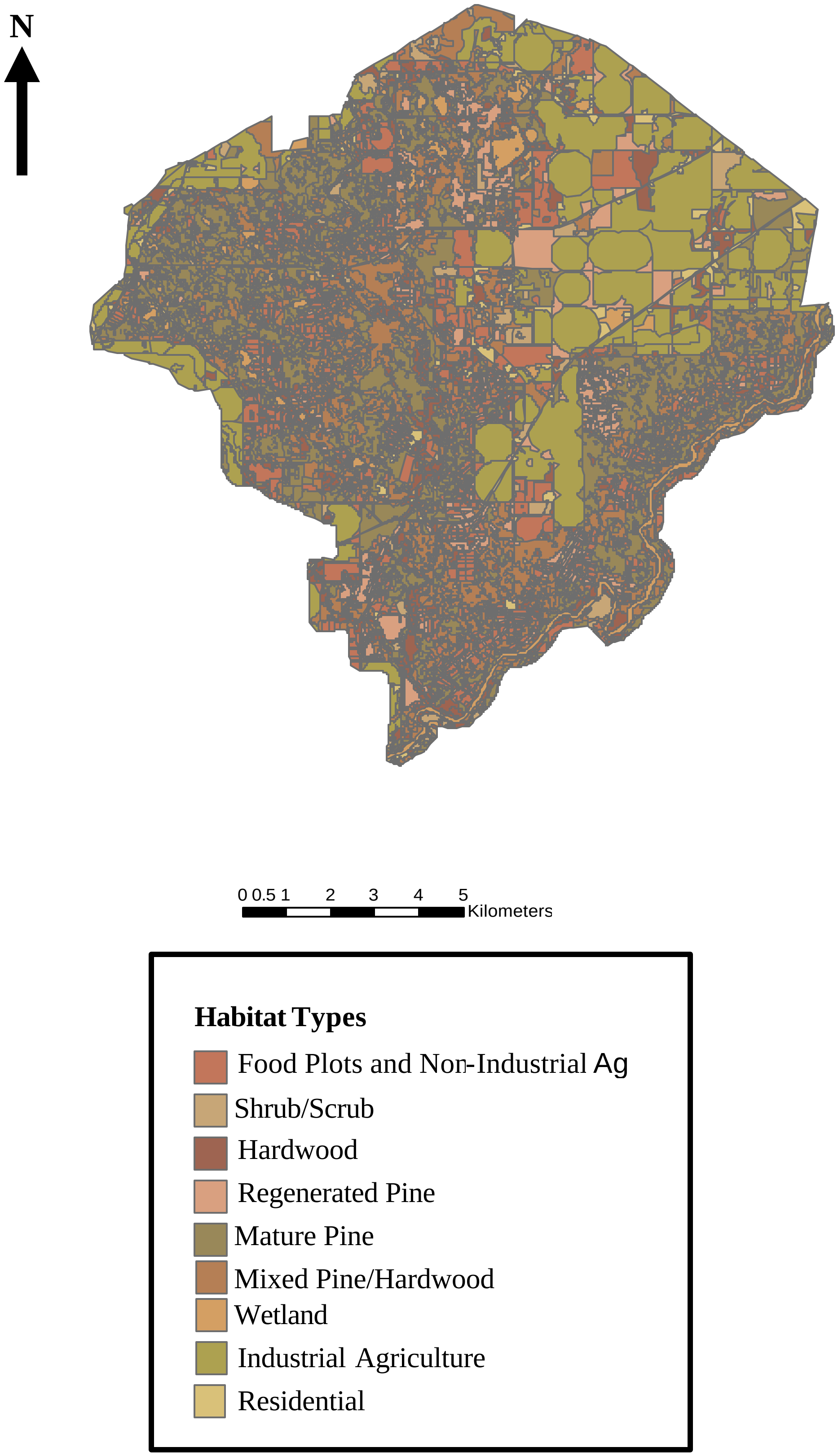

Figure 1.2. The 9 delineated habitat types are overlaid onto the study area in Baker County, Georgia. Gray foxes were studied on this site from 2002-2006.

Ichauway was split into multiple-use and conservation zones. Multiple-use zones, which comprised approximately 60% of Ichauway, were managed for northern bobwhite. This management included food plots and supplemental feeding, as well as low intensity predator removal to promote bobwhite populations. Predators were primarily harvested from November-February and included opossums *(Didelphis virginianus)*, raccoons *(Procyon lotor)*,coyotes (*Canis latrans*), armadillos (*Dasypus novemcinctus),* and prior to this study gray foxes. The conservation zones, which encompassed the remaining 40%, did not practice organized predator removal, although opossums, raccoons, and armadillos were occasionally harvested. Gray foxes were not removed from Ichauway, although they continued to be harvested on surrounding plantations.

GENERAL METHODS

Gray foxes were captured and handled under the Louisiana State University Agricultural Center Institutional Animal Care and Use Protocol Number A03-04 and the Joseph W. Jones Ecological Research Center's site wide trapping permit. I targeted both age classes (juvenile/adult) and sexes during trapping. Trapping was conducted from October 2002-March 2006. Intensive trapping (trapping =5 days/week and =20 traps/week) occurred October through March each year, but some trapping occurred throughout the year. Traps were located throughout the 1,700 kilometers of primary, secondary, and tertiary roads and firebreaks on Ichauway. Trapping was restricted to Ichauway.

I used number 3 and 1.5 Victor padded foot-hold traps, 1.75 laminated offset foot-hold traps (Minnesota Trapline Products, Pennock, MN), and Tomahawk cage traps (Tomahawk Live Trap Co., Tomahawk, WI) to capture gray foxes. All foothold traps were modified by placing 3 swivels along the trap chain. One swivel was placed at the base of the trap, 1 in the middle of the chain, and 1 at the end of the chain. This allowed the animal to move a full 360^0 radius around the trap.

When a gray fox was captured, I used a net and wooden pole to restrict movement and then immobilized it by placing electrical tape around the rostrum and legs (Chamberlain and Leopold 2000). Weight, sex, age (juvenile or adult), reproductive condition, and standard measurements (e.g., total body length and tail length) were recorded (See Appendix 1). Age was determined by tooth wear and weight (Wood 1958), as well as facial markings and tail wear (Lord 1961).

Injuries resulting from capture and physical condition of the gray fox were also noted. Each individual was given a unique ear tattoo, and was fitted with a homemade refurbished (Kenward 2000) TS-38 collar (Telemetry Solutions, Concord, CA USA) or M2110 mortality sensitive radio transmitter (Advanced Telemetry Systems, Inc., Isanti, MN). Transmitters had to be <5% of the animal's body weight for gray foxes to be collared (White and Garrott 1990). Gray foxes were then released at the capture site. Processing took about 20 minutes from the time the gray fox was found in the trap to release.

Telemetry

I used triangulation to estimate gray fox locations. After an adjustment period of =7 days, gray foxes were monitored using a 3 element Yagi antenna (Sirtrak, New Zealand) and TRX 2000S receiver (Wildlife Materials, Inc., Carbondale, Illinois, USA). Seasons were delineated as winter (dispersal) (Oct. 1-Jan. 31), breeding (Feb.1-May 31), and kit-rearing (Jun. 1-Sep. 30; Chamberlain and Leopold 2000).

Gray foxes were radio tracked from November 2002-May 2006. From 2002-2004, = 2 telemetry locations were recorded for each gray fox from fixed locations, with = 15 minutes allowed between bearings. Beginning in 2005 and lasting for the remainder of the study, = 3 telemetry bearings were taken for each gray fox from fixed stations. No more than 20 minutes elapsed between first and last bearings. To minimize error, each azimuth was =30^0 of the previous reading, with a total angle between 45^0 and 135^0 (Kitchings and Story 1979). From 2002-2004, =3 locations were recorded for each gray fox every week. To sample throughout the diel period, weeks were rotated (i.e., 2 day points and 1 night point were taken in 1 week, and the following week 2 night points and 1 day point were recorded). Beginning in 2005 and lasting the remainder of the study, =4 locations were recorded on each gray fox/week, and =40 locations were obtained for each individual/season. To ensure that the entire diel period was sampled for each individual, I took = 2 telemetry points for every hour throughout the season. Throughout the duration of this study, points on individual animals were separated by =8 hours to maintain independence (White and Garrot 1990).

General Results

From 2002-2006, 51 gray foxes (19 females and 32 males) were captured and 42 (15 females and 27 males) were radio collared. Five gray foxes were released without collars and 3 were euthanized due to injury from capture. From 2002-2004, the average time to record a telemetry location was 7 minutes. The average time it took to record a telemetry point for the remainder of the study was 9.5 minutes. Gray foxes were monitored for 3 kit-rearing seasons (n = 13), 4 breeding seasons (n = 23), and 4 winter (dispersal) seasons (n = 9). Six gray foxes were identified as young of the year.

CHAPTER 2: SPATIAL ECOLOGY OF GRAY FOXES (*UROCYON CINEREOARGENTEUS)* ON A LONGLEAG PINE FOREST AND SURROUNDING LANDSCAPE IN SOUTHWEST GEORGIA

Forest fragmentation and loss of habitat is a major threat to carnivores worldwide (Sunquist and Sunquist 2001). In the southeastern United States, the historical longleaf pine (*Pinus palustris*) forests have largely been replaced by industrial agriculture and other anthropogenic habitats (Outcalt and Sheffield 2006). In fact, longleaf pine forests have been reduced to only 3% of their former range (Ware et al. 1993). A diversity of species such as the flatwoods salamander (*Ambystoma cingulatum*), red-cockaded woodpecker (*Picoides borealis*), and gopher tortoise (*Gopherus polyphemus*) have been affected by the decline and fragmentation of longleaf pine forests (James et al. 2001). For example, with increased fragmentation and patchiness of longleaf forests, red-cockaded woodpeckers living in small social groups have been shown to be negatively affected, and at times extirpated, from areas with high levels of forest patchiness due to loss of foraging and dispersal opportunities (Conner and Rudolph 1991). Additionally, the gopher tortoise, a species that is believed to be a keystone in the longleaf pine forest, has declined by approximately 80% within the last 100 years (Auffenberg and Franz 1982). The impact of the conversion of this historic forest type on carnivores is not well understood, perhaps largely due to the lack of opportunities to conduct studies in the few remaining fragments of longleaf pine forests.

Gray foxes are a medium sized carnivore that is believed to be common throughout its range (Fritzell and Haroldson 1982), despite low annual survival (Wood 1958, Lord 1961, Wood and Odum 1964, Wigal and Chapman 1983, Nicholson and Hill 1984, Alderton 1994). Of all canids, gray foxes may be the most closely related to hardwood forests (Hall 1981, Alderton 1994, Harrison 1997). Despite their abundance, little is known about some factors of gray fox ecology and life history. Survival estimates are an important factor in understanding a species life history and longevity. However, few estimates are available for gray foxes, and what is available suggests low annual survival rates. Trapping has traditionally been cited as the major source of gray fox mortality (Weston and Brisbin 2003), but with decreases in fur prices and trapping effort (Armstrong and Rossi 2000), current survival rates and causes of mortality are unknown. Additionally, most studies examining gray fox survival have been conducted on carcasses that were collected by trapping or collecting road killed gray foxes to develop an age structure (Wood 1958, Sullivan 1956, Weston and Brisbin 2002), which limits inferences that can be made concerning cause-specific mortality.

Obtaining a sufficient sample size to study these aforementioned aspects of life history, especially when studying a species with low annual survival, can be difficult. Numerous studies have found that with increased sample size the precision and accuracy of home range and habitat use estimates increases (Garton et al. 2001, Erickson et al. 2001). Many studies of gray foxes suffer from low sample sizes, and as a result report estimates of space use and vital rates with low precision. For example, Progulske and Labisky (1997) pointed out that many studies in gray fox literature (Nicholson 1982, Tucker et al. 1993, Haroldson and Frtizell 1984, Foote 1984, Follman 1973, Yearsley and Samuel 1980), including their own, only reported information on = 10 gray foxes. The study with the largest sample size and longest duration was Chamberlain and Leopold (2000), who radio-tracked 37 gray foxes over 6 years. Chamberlain and Leopold (2000) also noted that while there are numerous studies on gray fox home range and habitat use, few of these studies have explored habitat use at multiple spatial scales. Examining habitat use at multiple scales is important to better understand the cumulative habitat needs of a species (Johnson 1980).

Therefore from 2002-2006, I studied a population of gray foxes on a longleaf pine forest (Ichauway) and surrounding lands consisting of industrial agriculture, pine plantations, and residential areas in southwest Georgia (see chapter 1 for a detailed description of the study area; Figure 2.1.). My objectives were to: (1) determine seasonal differences in habitat use, (2) estimate annual and seasonal survival rates, and (3) determine cause specific mortality.

METHODS

Habitat Selection

I used the Euclidean distance approach (Conner and Plowman 2001, Conner et al. 2003) to evaluate (1) if habitat use was non-random, (2) which habitats were preferred and which were avoided, and (3) if habitat selection differed among seasons. This approach is similar to compositional analysis (Aebischer et al. 1993), in that it uses a multivariate analysis of variance (MANOVA), to test for differences in seasonal habitat selection using the gray fox as the experimental unit. To compensate for yearly differences I blocked by year. However, distances between animal locations or random locations and habitats are used for the dependent variable, not the log-ratio differences (Conner and Plowman 2001, Conner et al. 2003). If the MANOVA was significant (a = 0.05), I used *t*-tests on each habitat type to create a ranking matrix, which ranked habitats in order of preference based on the value and direction of the *t*-statistic. Additionally, when habitat use was non-random (significant MANOVA) I used the use/random ratio to determine preference or avoidance of habitats. If the use/random ratio was < 1 the animal preferred that habitat, but if the use/random ratio was > 1 the animal avoided that habitat (Conner and Plowman 2001).

To assess habitat selection, I used an annually updated landcover created in ArcGIS in which 9 habitat types (see chapter 1) were delineated (Table 2.1). I generated 25,000 random points across the study area and 100 points within both the core area (see below) and total

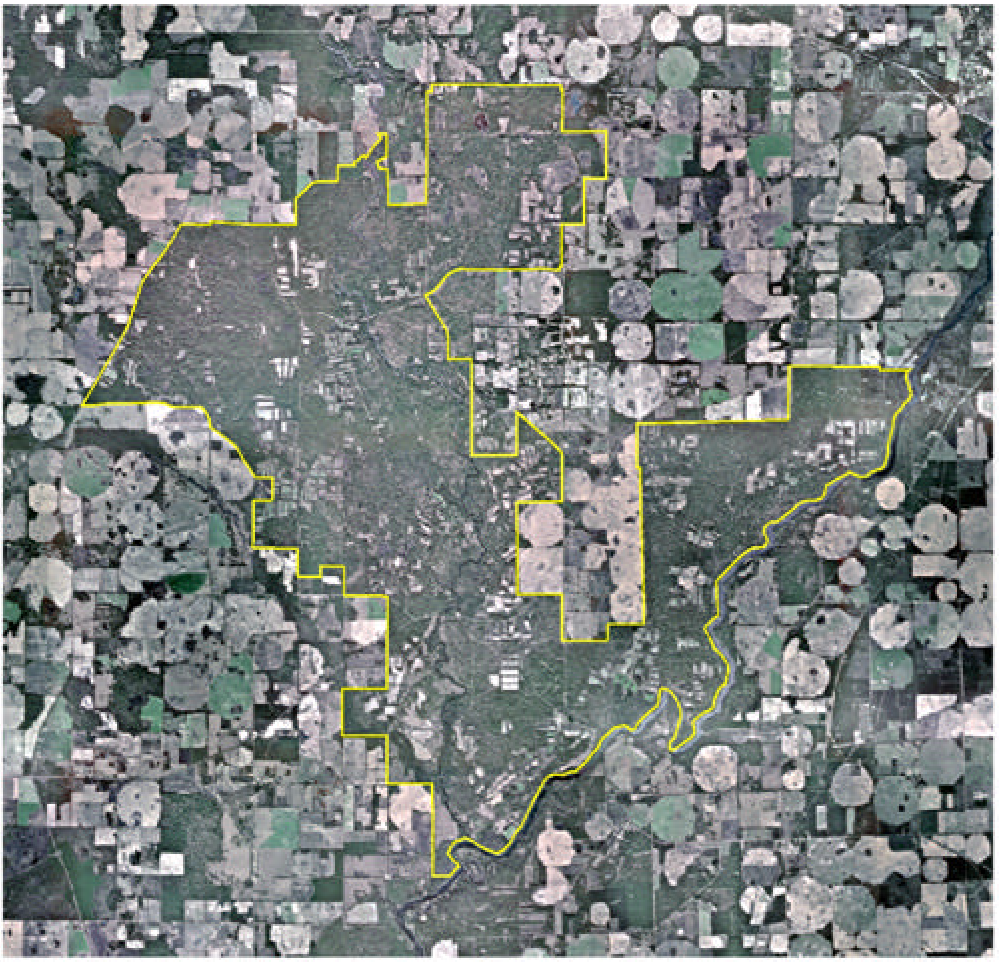

Figure 2.1. An aerial photograph of the study site taken in 2005 in Baker County, Georgia. Ichauway proper is outlined in yellow to depict the difference in land cover between Ichauway proper and the surrounding industrial agricultural landscape.

home ranges for each gray fox using Hawth's Analysis Tools (Beyer 2004). I then intersected the habitat coverage with both point coverage files (gray fox locations and random locations). I examined habitat selection at 3 spatial scales based somewhat on Johnson's (1980) criteria: 1st order (selection of a home range), 2nd order (selection within a home range), and 3rd order (selection of a core area). I used program Locate III (Nams 2005) to calculate locations from bearings obtained with telemetry (for telemetry methods, see Chapter 1). When 3 or more bearings were recorded, the location of the animal was estimated using the maximum-likelihood method (Lenth 1981). I created a coverage in ArcGIS (ESRI 2005) containing all gray fox locations and used program Home Range Tools (HRT; Rodgers et al. 2005) to develop fixed kernel polygons for 95% total and 50% core seasonal (see chapter 1) home ranges. I used the least squares cross validation method to calculate a smoothing parameter for the fixed kernels (Seaman et al. 1999). As recommended by Seaman et al. (1999), I only created home ranges for gray foxes with =30 locations per season (see general methods in chapter 1).

For 1st order selection, I compared distances of random points within the home range to distances of random points throughout the study area to the nearest edge of each habitat type. For 2nd order selection, I compared the distance of gray fox locations within the home range to the distance of random points within the home range to the nearest edge of each habitat type. For 3rd order selection, I compared distances from gray fox locations within the core area with distances from gray fox locations within the home range to the nearest edge of each habitat type. A distance of 0 was used when a gray fox location or random location was within a specific habitat type.

When the points were spatially displayed in ArcGIS, I noticed a positive association between gray fox locations and the Ichauway property boundary. In fact, only 35%

Table 2.1. Properties, sums (in hectares), and proportions (proportion of the landscape) of the 9 habitat types delineated within the gray fox study area in Baker County Georgia from 2002-2006. Values are shown for both the entire study area and Ichauway alone.

		Ichauway		Total Study Area	
Habitat type	Description	Sum	Proportion	Sum	Proportion
Residential	Residential areas and roads.	217.697	0.018	577.877	0.027
Industrial Agriculture	Land that is used for farming cash crops (i.e. cotton, peanuts) usually managed as center pivot agriculture.	0	0	4557.322	0.215
Regenerated Pine	Young pines (< 10 cm dbh) pine forests, usually managed as pine plantations.	1131.427	0.076	1355.075	0.064
Hardwood	Overstory dominated by hardwoods.	1131.427	0.092	1799.593	0.085
Shrub/Scrub	Overstory dominated by shrubs.	212.342	0.017	588.164	0.028
Food Plot	Area planted with crops meant for wildlife consumption, such as sorghum, corn, millet, etc	1592.226	0.130	2413.158	0.114
Wetland	Depressional wetlands, swamps, creeks that seasonally or annually holds water.	638.470	0.052	765.882	0.036
Pine	Mature pines (> 10 cm dbh) pine forests. This encompasses longleaf, loblolly, and slash pine	4253.325	0.347	5080.075	0.239
Mixed Pine/Hardwood	30% < Hardwood < 70%.	3278.924	0.268	4087.087	0.193

(1038/2948) of the telemetry points fell on Ichauway and almost all of these points appeared to be quite close to the property boundary (< 1/2 km from the edge; Figure 2.2). Therefore, I compared distances to the Ichauway border between actual gray fox locations and 25,000 points randomly spaced throughout Ichauway to determine if gray foxes were located closer to the property boundary than expected by chance.

Survival

I monitored gray fox survival through the use of systematic point locations (see universal methods: systematic point locations) from 21 September 2002- 1 August 2006. Gray foxes that died or were censored (due to loss of radio signal) = 7 days after being trapped were not used in the analysis in case their fate was influenced by trapping. For example, trap-related injuries may have directly or indirectly caused a death, or the trauma experienced by being trapped may have caused the animal to leave the study area.

When a carcass was located, I established the cause of death based on an evaluation of the mortality site and field observation of the carcass. For example, gray foxes that were defined as road kills were found on or near (i.e. in a roadside ditch) roads and had obvious signs of trauma that most likely resulted from vehicle collisions. If the cause of death could not be determined on scene, the carcass was frozen and shipped to the Southeastern Cooperative Wildlife Disease Service, Athens, Georgia for necropsy.

I estimated annual survival rates using the Kaplan-Meier method (Pollock et al. 1989). I tested for differences in survival rates among years using a chi-squared test. Because there was no difference in survival over years, I pooled years and stratified by season (breeding, kit-rearing, and winter). Because years were pooled, I assumed that all animals entered on day 1 the season and animals that had not been censored or experienced mortality by the end of the season were censored on the last day of the season and reentered the 1st day of the following season.

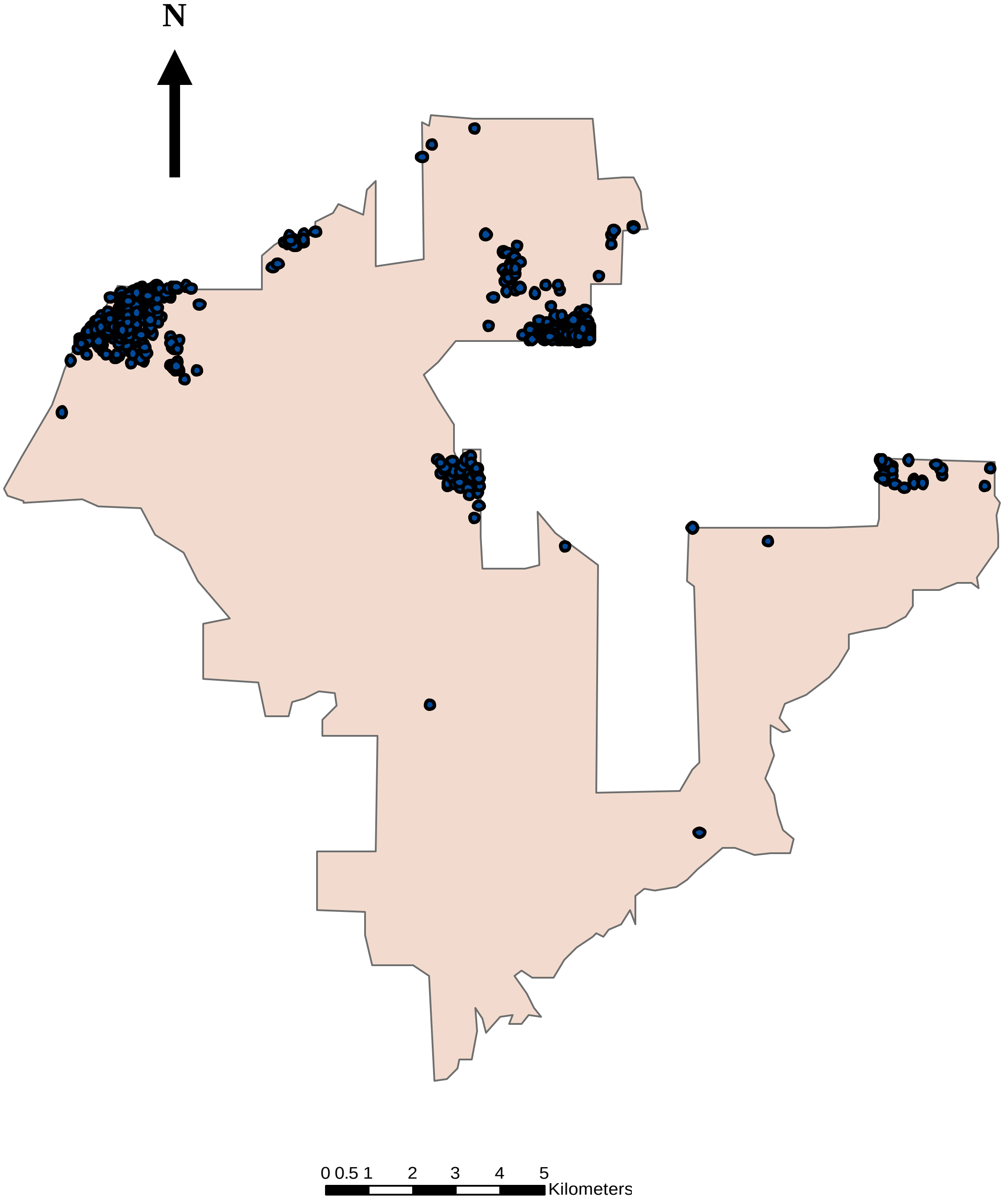

Figure 2.2. Display of all gray fox locations on Ichauway in Baker County, Georgia, from 2002-2006. This exhibits the lack of interior use of Ichauway by collared gray foxes.

I then tested for differences in survival rates between sex and among seasons using a log-rank test. I used PROC LIFETEST (Allison 2005) in SAS for all the aforementioned analyses. PROC LIFETEST requires all seasons to be of equal length, so all seasons were comprised of the same interval length.

I classified deaths under 3 mortality agents: unknown, natural (disease, predation), and human (vehicle collision, trapping). I calculated cause-specific mortality rates for each of the 3 agents each season and year using program MICROMORT (Heisey and Fuller 1985). MICROMORT uses the Mayfield Method (Mayfield 1961) to estimate cause-specific mortality rates for specific competing agents, but does not test for differences between them. Therefore, I tested for yearly differences in probabilities of mortality by specific agents using program Contrast (Sauer and Williams 1989). Because there was no significant difference among years in probability of mortality from any specific agents, I pooled data across years and tested for differences in mortality agents by sex and season and total likelihood of each mortality agent occurring per animal per season.

RESULTS

Habitat Selection

A total of 2,948 gray fox locations from 23 individuals were used in the habitat analysis. Estimates of space use and comparisons of space use across seasons are reported in chapter 3.

1st Order

At the 1st order scale, non random selection was detected ($L = 110.63$, $P < 0.001$), but there were no seasonal effects ($L = 1.07$, $P = 0.400$). The ranking matrix suggested that industrial agriculture and residential habitats were the most preferred, and both were used more than expected ($P < 0.001$). All other habitats did not differ from each other, but mature pine and mixed pine/hardwood were ranked least preferred, and mixed pine/hardwood was an avoided habitat bordering on significance ($P = 0.069$) (mean use/availability ratio > 1; Table 2.2).

2nd Order

No difference was detected among seasons ($L = 0.98$, $P = 0.490$), but again habitat selection was non-random ($L = 26.91$, $P = 0.001$). Gray foxes were found closer to hardwood, mature pine, pine regeneration, shrub/scrub, and residential than expected, with hardwood forests ranked highest ($P < 0.05$; Table 2.2).

3rd Order

At the 3rd order scale, non random selection was detected ($L = 5.16$, $P = 0.001$), but there were no seasonal effects ($L = 1.01$, $P = 0.470$) on habitat selection. Hardwood was ranked 1st and gray foxes were found closer to this habitat then would be expected when compared to random points ($P < 0.001$). Gray foxes were found closer then expected to both shrub/scrub and residential habitats, although residential habitats were ranked 8th. Industrial agriculture ranked 2nd, but gray foxes were not found closer then expected to this habitat type ($P = 0.107$; Table 2.2).

Thirty-five percent (1,038) of gray foxes locations were on Ichauway, and were closer to the edge of the site than expected ($L = 12.06$, $P = 0.001$; Figure 2.1).

Survival

From December 2002-July 2006, 33 gray foxes were monitored for survival. Sixteen gray foxes died (4 females, 12 males) and 17 were censored (7 females and 10 males) due to loss of the radio signal, radio failure, or completion of the project. I sent 5 gray foxes to the Southeastern Cooperative Wildlife Disease Study in Athens, Georgia for clinical evaluation of cause of death. Ten deaths were due to human-induced mortality (2 were trapped and harvested; 8 were struck by motor vehicles), 4 were from unknown causes, and 2 were due to natural causes

Table 2.2. Matrix of available habitat types ranked in order of preference (1 most preferred-9 least preferred) by gray foxes based on the value and direction of the *t*-statistic from 2002-2006 in Baker County, Georgia. The 3 spatial scales examined, 1st order (selection of a home range), 2nd order (selection within a home range), and 3rd order (selection of a core area) are listed. Significant differences ($P < 0.05$) are indicated by different letters.

	1st order				2nd Order				3rd order			
Habitat Type	Mean	*t*	*P*	Rank	Mean	*t*	*P*	Rank	Mean	*t*	*P*	Rank
Human	-0.6154	-21.78	<0.0001	1A	-0.1252	-4.37	0.0002	4B,C	-0.1096	-3.82	0.0009	8D
Industrial Agriculture	-0.6469	-11.80	<0.0001	2A	-0.0309	-0.70	0.4920	3B,C,D	0.0675	1.68	0.1065	2B
Regenerated Pine	-0.2199	-1.89	0.0718	3B	-0.1156	-2.75	0.0118	7C,D	0.0017	0.03	0.9742	6C,D
Hardwood	-0.0595	-0.45	0.6586	4B,C	-0.2188	-5.72	<0.0001	1A	-0.1891	-4.76	<0.0001	1A
Shrub/Scrub	-0.1448	1.27	0.2165	5C,	0.0645	-2.43	0.0239	5B,C,D	-0.0822	-2.52	0.0196	3B,C
Food Plot	-0.1974	0.97	0.3426	6C,D	-0.0384	-1.21	0.2384	6D	-0.0469	-1.82	0.0828	4B,C,D
Wetland	-0.4102	1.59	0.1253	7C,D	-0.0079	-0.39	0.6978	8D	-0.0249	-1.30	0.2080	5C,D
Pine	-0.7304	1.71	0.1014	8D	-0.1627	-4.00	0.0006	2A,B	-0.4161	1.92	0.0681	9D
Mixed	1.0124	1.91	0.0699	9D	0.0284	0.73	0.4740	9D	0.0272	1.34	0.1955	7D

(2 predation, 1 due to canine hepatitis infection; Table 2.3). An individual gray fox had a 34% probability of experiencing a human-induced mortality, an 11% probability of dying from unknown causes, and an 8% probability of experiencing a death due to natural causes annually (Table 2.3).

Mean annual survival was 0.610 (CI = 0.414-0.806). There was no difference in survival among years ($?_3^2 = 5.88$, $P = 0.210$) or between sexes ($?_1^2 = 01.89$, $P = 0.170$), so I pooled years and sexes for seasonal comparisons. Survival did not differ across seasons ($?_2^2 = 0.68$, $P = 0.710$). Probability of suffering a human-induced mortality was greater than both unknown ($?_2^2 = 4.21$, $P = 0.040$) and natural causes ($?_2^2 = 6.62$, $P = 0.010$), and was the primary cause of death every season. Probabilities of suffering mortalities from unknown and natural causes were similar ($P > 0.050$; Table 2.3).

DISCUSSION

Pine forests were ranked 2nd in 2nd order habitat selection, and were used significantly more than expected across the study area. However, gray foxes in this study were consistently found either off, or on the periphery, of Ichuaway (Figure 2.1). Forest structure of longleaf pine forests managed with fire differs greatly from industrial pine forest dominated by loblolly and slash pine (Hedman et al. 2000). Chamberlain and Leopold (2000) and Casselman (1989) both found that pine plantations managed for saw timber were preferred by gray foxes. Wood and Davis (1959), however, believed that the increase in timber plantations and the decrease of cultivated areas may result in smaller gray fox populations in Georgia. More recent research has shown that industrial pine plantations may be preferred, or at least not avoided by gray foxes (Casselman 1989, Progulske and Labisky 1997, Chamberlain and Leopold 2000, this study). In fact, pine regeneration was used more than expected at 2nd order selection in this study. Mixed pine/hardwood forests were ranked low across spatial scales, but gray foxes were not found

Table 2.3. Rates of survival (and 95% confidence interval) and probability (and 95% confidence interval) that a gray fox will meet each of 3 mortality agents (human, natural, and unknown) both annually and seasonally in Baker County, Georgia between 2002-2006.
n^a = Number of gray foxes at risk during each season.
n^b = Number of gray foxes that died each season.
n^c = Number of gray foxes that died due to that mortality agent each season.

				Seasonal Cause-Specific Mortality					
Season	n^a	Survival	n^b	Human 95%CI	n^c	Natural 95%CI	n^c	Unknown 95%CI	n^c
Breeding (1 Feb-31 May)	40	0.814 (0.679-0.949)	6	0.086 (0.000-0.179)	3	0.029 (0.000-0.084)	1	0.029 (0.000-0.084)	2
Kit-Rearing (1 Jun-30 Sep)	22	0.748 (0.554-0.941)	6	0.200 (0.025-0.373)	4	0.000 (0.000-0.000)	0	0.099 (0.000-0.230)	2
Winter (1 Oct-31 Jan)	36	0.816 (0.637-0.994)	4	0.132 (0.000-0.271)	3	0.088 (0.000-0.204)	1	0.000 (0.000-0.000)	0
Composite		0.610 (0.414-0.806)	16	0.336 (0.164-0.508)	10	0.082 (0.000-0.171)	2	0.114 (0.000-0.237)	4

farther away from this habitat type more than expected when compared to availability on the study area. The low ranking of mixed pine/hardwood forests was surprising based on the preference of these habitats in other studies (Wood et al. 1958, Progulske and Labisky 1997, Chamberlain and Leopold 2000). However, mixed forests with dense understory vegetation also were found to be avoided by Wood et al. (1958) in southern Georgia. They attributed avoidance to a lack of food in these areas. In southern Georgia and northern Florida, woodland, agricultural edge and early successional old fields were the habitat types selected most often (Wood et al.1958). Areas with escape cover usually contain minimal prey (Labisky and Hovis 1987), so these areas need to be close to open habitats that provide plant and animal prey (Progulske and Labisky 1997). Industrial agricultural field boundaries and property lines in my study area were often comprised of hardwood forests and/or young industrial pine stands, which may have provided both abundant food sources (edible crops) and escape cover. Similarly, Best et al. (1995) synthesized bird research conducted in Iowa and found that the most species diversity and abundance was found in agricultural areas that had some sort of shelter belt or fence row land cover within the agricultural matrix.

Industrial agriculture and hardwood forests were ranked as highly used at all spatial scales, whereas mixed pine/hardwood was consistently ranked as avoided across spatial scales. Residential areas and industrial agriculture were important determinants of home range selection by gray foxes (1st order selection). However, residential areas ranked low for the smallest spatial scale (3rd order). This may reflect the placement of residential areas being inherently close to industrial agriculture, which was an important habitat type at all spatial scales. More likely, it is due to a paucity of residential areas (2% of total land area) on the study area when compared to industrial agriculture and pine forests (Table 2.1). Either distance or classification-based habitat analysis can be influenced by presence/absence and placement of a habitat type in the study area being examined (Dussault et al. 2005). For example, hardwood forests were found in this study and others (Yearsley and Samuel 1980, Haroldson and Fritzell 1984) to be important to gray foxes, but I ranked it as 4th in 1st order habitat selection, likely due to the absence of hardwood in the study area compared to the more prevalent mature pine and industrial agriculture. In fact, hardwood was ranked first, and was used more than expected compared to availability, for both 2nd and 3rd order habitat selection, which are both smaller spatial scales (Johnson 1980).

Shrub/scrub habitat was used more than expected at both 1st and 3rd orders, presumably because of quality escape cover and foraging opportunities (Trapp and Hallberg 1975, Trapp 1978, Fritzell and Haroldson 1982). Habitat selection by gray foxes is strongly influenced by small mammal abundance (Chamberlain and Leopold 2000) and typically parallels forage availability (Wood et al. 1958). Availability of quality foraging opportunities may partially explain the lack of use of Ichauway by gray foxes. Fire affects forests by minimizing hardwood understory (escape cover for gray foxes), and reducing various species of soft mast, an important forage item for gray foxes (Johnson and Landers 1978, Cypher 1993). Johnson and Landers (1978) found that fire stunted soft mast growth for at least 1 year after burning. Ichauway is burned on a 2 year rotation, so soft mast availability is compromised, and plant communities in the understory are primarily herbaceous. Fritzell (1987) suggested that fire suppression assisted gray foxes in inhabiting areas that had previously been inhospitable to them. Other omnivorous mesomammals, such as raccoons (Jones et al. 2004) and opossums (Jones et al. 2002) were found to predate fewer bird nests on recently burned areas of Ichauway than on areas that had not been burned, suggesting reduced use of that habitat by these species when consistent fire regimes were in place. Chamberlain et al. (2003) also found that frequent fire negatively affected raccoon habitation of recently burned areas. Lastly, although many studies have noted that seasonal differences in habitat use mirror food availability (Follman 1973, Yearsley and Samuel

1980), gray foxes in this study did not select habitats differentially by season. Gray foxes are omnivorous and opportunistic in their diet (Fritzell and Haroldson 1982), which contributes to risk spreading within food webs and allows species greater flexibility in patterns of habitat selection (den Boer 1968).

Significant use of anthropogenic habitats was not surprising, but the extreme lack of use on Ichauway was not expected. Gray foxes appear to tolerate, and may even thrive, in areas of anthropogenic activity, but the degree to which they are affected (either positively or negatively) is largely unknown. Core areas of space use have particularly been understudied, and because this is the area that is presumably most important to the animal (Ewer 1998), it is important to study habitat selection in these areas. It has been suggested that anthropogenic habitats (ex. garbage dumps, agricultural fields, and residences) are used when preferred natural habitats are unavailable (Fuller 1978, Haroldson and Fritzell 1984, Tucker et al. 1993, Harrison 1997). In core areas of home ranges (3rd order selection) gray foxes preferred hardwood forests and avoided residential areas. This may be due to the increased concealment opportunities in hardwood habitats that may be lacking in residential areas. Hardwood forest also would provide gray foxes with food opportunities both in small mammal abundance (Chamberlain and Leopold 2000, Haroldson and Fritzell 1984) and soft mast (Hockman and Chapman 1983). Riley (2006) studied gray foxes in a national park that abutted highly anthropogenic areas. He found that most gray foxes intensively used anthropogenic habitats, but all core use areas (urban and rural) were inside the park boundary. Harrison (1997) also found that gray foxes in both urban and rural zones heavily utilized anthropogenic habitats. Habitat selection in the Harrison (1997) study was not reported at the core area level, but gray foxes used forested habitats removed from residential areas more during the day, when gray foxes should be minimally active, than at night when they preferred anthropogenic habitat.

Living in anthropogenic areas may increase the likelihood of gray foxes being affected by communicative diseases due to increased contact with domestic dogs and cats (Little et al. 1998). Riley et al. (2004) found both bobcats (*Lynx rufus*) and gray foxes infected with diseases that can be linked back to domestic animals in anthropogenic areas significantly more than those animals that did not use anthropogenic areas. Past studies of gray foxes have found high levels of mortality due to diseases, particularly rabies and distemper (Trapp and Hallberg 1975, Amundson and Yuill 1981, Carey 1982, Davidson et al. 1992). This study documented a death due to canine hepatitis, a rare disease in canids (Amundson and Yuill 1981, Nicholson and Hill 1984). Until this study no case of a gray fox death due to canine hepatitis had been documented in Georgia (Gerhold et al. in press), and in fact only 1 other case had ever been reported in gray foxes (Nicholson and Hill 1984). The gray fox that was infected was in a residential area and may have been in frequent contact with domestic dogs and cats, which are transmitters of the disease (Kimber et al. 2000). Similar findings of disease transmission have been documented for species such as raccoons (i.e. rabies; Kappus et al. 1970) and African wild dogs (*Lycaon pictus*, canine distemper, Alexander and Appel 1994).

It has been suggested that in areas that have high densities of upper tiered predators, gray foxes may be displaced into anthropogenic areas (Gosselink et al. 2003, Riley 2006). Additionally, gray fox populations may increase with removal of higher order predators (Crooks & Soule 1999, Henke & Bryant 1999). The threat of predation due to high bobcat and coyote density has been suggested to influence space use (Tannerfeldt at al 2002, Chamberlain et al. 2004) and resource partitioning of gray fox populations (Fedriani et al. 2000, Chamberlain and Leopold 2005, Weston and Brisbin 2003). Coexistence of predators, especially those that compete, is widely considered to be dependent on the level of heterogeneity of habitats available within a landscape (Chesson 1985, Hanski 1994, Durant 1998). A combination of spatial and temporal heterogeneity in habitat is important factor in determining coexistence of competitors (Chesson 1985, Durant 1998). My study area may exhibit both spatial and temporal heterogeneity due to the temporal rotation of seasonal and annual crops and the variety of habitat types interspersed throughout the study area. Gray fox populations may increase with removal of higher order predators (Crooks and Soule 1999; Henke and Bryant 1999). Previous research has mostly focused on gray fox and coyote interactions, but very little research has been conducted on gray fox and bobcat competition. Gray foxes, however, may have more niche overlap with bobcats than coyotes (Riley 2006). For example, gray foxes are relatively unique among canids in their ability to climb trees (Feeney 1999), and when in danger they may climb trees to escape (Fritzell and Haroldson 1982). Bobcats, unlike coyotes, are able to climb which abolishes the gray fox's primary avoidance tactic. Core area habitat use also may be influenced by predation threats to gray foxes. Chamberlain et al. (2004) found that gray foxes tended to maintain core areas that did not overlap those of bobcats and coyotes. Additionally, bobcat space use is more negatively affected by urban areas than gray foxes (Riley 2006), which may allow gray foxes to seek refuge in residential areas. Long term research of bobcats on my study area has shown bobcat home ranges distributed throughout the Ichauway portion of the study area (Godbois 2002, Cochran 2003, Doughty 2004, Lynch 2005). Likewise, predation is a major threat to gray fox populations (Weston and Brisbin 2003, Farias 2005) and may influence gray fox spatial use (Fedriani et al. 2000). However, I only observed 1 predation events in this study. Of the 4 deaths attributed to unknown causes that I observed, only 1 of them was potentially caused by predators based on a lack of either internal or external trauma on the majority. Fedriani et al. (2000) found that gray fox densities were lower in areas heavily trafficked by coyotes and bobcats, and gray foxes seem to require some brushy habitat (i.e. hardwood or regenerated pine) for escape cover (Wood et al. 1958, Chamberlain and Leopold 2000, Fedriani et al. 2000), which is negatively affected by the burning regime on Ichauway. Because gray fox density has an inverse relationship with larger predators, this may suggest that Ichauway, due to its land management practices, has a high predation risk for gray foxes, potentially causing them to avoid the longleaf pine forest. This may in turn increase the risk of vehicle mortality due to the use of anthropogenic habitats. Farias et al. (2005) reported that all but 1 gray fox death was caused by predation, and most known deaths (29%) reported by Weston and Brisbin (2003) were caused by predation.

Vehicle collisions accounted for the primary cause of mortality on my study site. There were 2 major roadways bisecting my study area. Both were 2 lane roads with a speed limit of 55 miles per hour, and heavily trafficked by commercial shipping vehicles and tourists going to and from Florida. Bobcats (Lovallo and Anderson 1996), gray wolves (*Canis lupin*; Theil 1985), and grizzly bears (*Ursus arctos*, McLellan and Shackleton 1988) have been shown to actively avoid heavily trafficked roads. However, more generalist species, such as opossums (Kanda et al. 2006), cane toads (*Bufo marinus*, Brown et al. 2006), and red foxes (*Vulpes vulpes*, MacDonald 1979) are more tolerant of heavily trafficked roads, and may even use roads for foraging and ease of travel. Weston and Brisbin (2003) noted that vehicle collisions were probably biased towards younger animals. I do not believe that my study was biased in that manner because most gray foxes (71%) that died from vehicle collisions had been tracked for at least a year and were found dead on roads that I had observed them crossing numerous times.

Vehicle collisions may impact the gray fox population on my study site in a manner similar to trapping. Gray foxes experience a high level of annual mortality, and the age structure of gray foxes shows that most animals in a population are < 2 years old (Wood 1958, Lord 1961, Wood and Odum 1964, Wigal and Chapman 1982). In fact, gray foxes have been referred to as an annual crop and juvenile gray foxes may constitute up to 60% of the population

(Davis and Wood 1959). Trapping has traditionally been cited as the major source of gray fox mortality, but with decreases in fur prices (Cypher 2003), it is unclear whether gray fox populations in many areas are currently affected by trapping. Annual mortality rates in harvested populations are 50%-64% annually (Wood 1958, Lord 1961), suggesting that harvest has a large impact on yearly survival of gray foxes. For example, it was estimated that in Wisconsin half of the gray fox population was harvested every year (Alderton 1994). Weston and Brisbin (2003) studied a population of animals that did not experience harvesting pressures and found that older gray foxes (> 2 years) made up most of the population, and mortality was estimated to be only 31% annually. I found similar annual mortality rates in my sample as other gray fox populations that experienced high trapping pressure (61%). Trapping on properties neighboring Ichauway accounted for only 12% of mortalities, so trapping pressure may not have been as severe on this population as it is on other populations. While other studies have found vehicle collisions to result in some mortality, it has been relatively insignificant compared to other mortality agents. For example, Nicholson and Hill (1984) had a 14% mortality rate due to vehicle collisions in their study in Alabama, and Farias et al. (2005) did not report any deaths of collared gray foxes due to vehicle collision. Farias et al. (2005) did not report habitat use, so it is not possible to examine if gray foxes used anthropogenic areas where they would be more likely to meet a vehicle collision fate. However, their study was conducted in a national recreation area and surrounding areas where motorists may be more aware and sympathetic to animal crossings than I experienced on my study area. Vehicle mortality being the most prevalent cause of death was probably the reason that morality rates and cause specific mortality did not differ between years and seasons due to vehicle traffic on the study area being consistent throughout the seasons and over the years.

In conclusion, intensively managed longleaf pine forests did not appear to be conducive to gray fox use in this study. Within longleaf ecosystems gray foxes appear to require a more diverse landscape, specifically containing hardwood forests. It is likely that foraging habitats, which in this study consisted of industrial agriculture and residential areas, are reduced as a consequence of intensive management for longleaf savannahs. The requirements of escape cover for predator avoidance and prey availability in this study may have been met with the mosaic of anthropogenic habitats (i.e. residential and industrial agriculture) interspersed with hardwood forests surrounding the managed longleaf forest.

CHAPTER 3: POTENTIAL EFFECTS OF KINSHIP ON SPACE USE AND HOME RANGE OVERLAP OF GRAY FOXES

Space use can offer insight into species behavior and life history, as well as environmental and seasonal constraints, such as food availability. Space use of gray foxes varies across their geographic range, by season, and habitat type (Follman 1973, Nicholson and Hill 1981, Foote 1984, Sawyer and Fendley 1990, Chamberlain and Leopold 2000). Several studies have shown overlap in space use between foxes of the same sex (Nicholson and Hill 1981, Progulske 1982, Haroldson and Fritzell 1984, Chamberlain and Leopold 2000), but the extent of overlap has been variable. For example, Chamberlain and Leopold (2000) found minimal space use overlap between non-mated pairs, whereas Haroldson and Fritzell (1984) found frequent overlap of both home range and core use areas. It has been suggested that gray foxes may be more inclined to have overlapping spatial areas with close relatives than with non-relatives (Tucker et al. 1993, Chamberlain and Leopold 2000) but no evidence to support this theory is available. With recent increases in knowledge and availability of DNA analysis, genetic studies are becoming more prevalent in wildlife research and management studies (Mills et al. 2000). Numerous studies on many different species have recently used radio telemetry to examine how relatedness influences spatial use overlap and spatial distribution (*see* Roemer et al. 2001, Stoen et al. 2005, Ralls and White 2003, Janecka et al. 2006). Several fox species also have been examined. For example, Ralls et al. (2001) found extensive space use overlap and den sharing by closely related kit foxes (*Vulpes macrotis*). No research has been conducted on kinship factors in gray fox spatial ecology. Therefore, I set out to establish differences in space use of gray foxes among seasons, and examine if genetic relatedness influences home range overlap and spatial location of trapped gray foxes.

METHODS

Home Range Size

See chapter two for the methods used to delineate 95% home ranges and 50% core use area kernel polygons. I used an analysis of variance (ANOVA) blocked by year to assess differences in space use among seasons. I blocked by year to compensate for year effects on seasonal comparisons of space use and unequal sample sizes among years. Based on past research males and females do not significantly differ in either home range size or habitat selection (Follman 1973, Nicholson and Hill 1981, Foote 1984, Casselman 1989, Sawyer and Fendley 1990, Chamberlain and Leopold 2000) therefore I combined home ranges of males and females. All statistical tests were performed in SAS (SAS Institute 2006).

Genetics

A 3mm tissue sample was taken from each ear of every fox trapped. The samples were immediately frozen (n=27) or placed in a 99% ethanol solution until they were sent to the USDA Rocky Mountain Research Station's genetics laboratory for processing. Six microsatellite loci were used for the analysis based on Weston et al. (2004). Departure from the Hardy-Weinburg equilibrium was tested for using F_{IS}, which measures departures from H-W equilibrium within a subpopulation. Pairwise relatedness between all pairs of gray foxes was established using Grafen's relatedness coefficient (*r*) (Queller and Goodnight 1989). The kinship coefficient ranged from -1 - +1. A positive coefficient indicates some level of relatedness, and a coefficient of -1-0 indicated little or no relatedness. Full siblings or parent-offspring coefficients should fall close to 0.5. Genetic analysis was conducted by the USDA Rocky Mountain Research Stations Wildlife Genetics Laboratory.

I identified home ranges as either overlapping or non-overlapping based on whether or not the home range for each individual gray fox had any overlap with a home range of another gray fox of the same sex. I also included male gray foxes with > 15 telemetry locations into this analysis by creating kernel estimates as explained earlier. I tested male gray foxes with both composite (all seasonal home ranges over years that overlapped) and sequential (only home ranges that simultaneously overlapped) home ranges. I averaged (and calculated the standard error) all kinship coefficients (*r*) of foxes with overlapping home ranges and also averaged (and calculated a standard error) kinship coefficients for all foxes without home range overlap.

I used a GIS layer that displayed all of the roads on the study area and marked where each fox was trapped or found as a road kill. I used the Point Distance feature in ArcMap 9.1 to establish distances from each location where a fox was trapped or found as a road kill to all other locations of trapped foxes. I entered these distances into a distance matrix along with their respective kinship coefficients for all trapped foxes. The genetic and trap distance matrices were compared for spatial correlation using a Mantel test based on the methods described in Moyer et al. (2006). The Mantel test is a nonparametric test that examines potential correlation between the 2 distance matrices (trap and genetic distance; Mantel 1967). I used the Mantel for Windows program for calculations with 10,000 permutations. I pooled all data to test for correlation in composite captures and mortalities (all captures and mortalities throughout years). I then partitioned these data into seasons. Genetic samples were only taken during the 2004-2006 trapping seasons, so I delineated seasons used for the Mantel Test as October-June because all samples were taken between those months and only during the 2004-2006 trapping seasons.

RESULTS

Home Range

From 2002-2006, 23 (8 females and 15 males) foxes were radio-tracked over 4 breeding seasons (n = 23), 3 kit-rearing seasons (n = 13), and 4 winter seasons (n = 9). Home range size differed among seasons ($F_{2,34}$ = 3.97, P = 0.03). Winter home ranges (152.43 ± 32.01 ha) were significantly larger than home ranges during both breeding and kit rearing seasons (Table 3.1). The breeding (91.42 ± 12.93 ha) and kit rearing (99.68 ± 18.27 ha) seasons did not differ. Core areas also differed among seasons ($F_{2,34} = 5.20$, $P = 0.0188$). Winter core areas (33.19 ± 7.39 ha) were significantly larger than core areas during both breeding (17.86 ± 2.42) and kit rearing (21.05 ± 4.12) seasons. Neither breeding nor kit rearing core areas differed from each other (Table 3.1).

Genetics

From 2004-2006 32 genetic samples were taken. Three were from foxes killed by vehicles, and 29 were from trapped animals. Observed heterozygosity (H_O) was 0.80 and expected heterozygosity (H_E) was 0.77. Based on an F_{IS} value of -0.047 the population was within Hardy-Weinberg proportions. A negative F_{IS} value indicates an excess of heterozygotes, but this proportion did not significantly vary from 0. Home ranges were established for 26 of these foxes (5 females, 21 males). I selected to use foxes with > 20 locations to create a home range.

Ten simultaneously tracked gray foxes and 16 composite (all overlapping home ranges throughout years) gray foxes had intra-sexual (male) overlapping home ranges. There was no intra-sexual female home range overlap, which was likely due to a small sample size (n = 5). The average kinship coefficient for males with overlapping home ranges was 0.057 (± 0.105) and non-overlapping home ranges was -0.007 (± 0.039). Only 4 intersexual dyads had both DNA samples and established home ranges. The kinship coefficients between male-female dyads were -0.237, -0.186, -0.068, and 0.048.

A total of 32 gray foxes were trapped or found dead over 2 trapping seasons (15 from the 2004-2005 trapping season and 17 from the 2005-2006 season) and were entered into a Mantel

Table 3.1. Gray fox average seasonal (kit-rearing, breeding, and winter) 95% home range and 50% core use area (and standard errors) in hectares. The number of gray foxes monitored (n) is also denoted.

	Kit-Rearing		Breeding		Winter	
Contour	n	HR	n	HR	n	HR
50%	13	17.9 (2.4)	23	21.1 (4.1)	9	33.2 (7.4)
95%	13	99.4 (12.9)	23	99.7 (18.3)	9	152.4 (32.0)

test to test for spatial distance and genetic distance correlation. No spatial distance and genetic distance correlation was detected for either 2004-2005 or 2005-2006 ($P > 0.1$).

DISCUSSION

Home Range

Comparisons of home range size among studies are tenuous for 2 primary reasons. First, there is no protocol for the classification of seasons for fox studies. Not all studies even classify seasons; some only report average, annual, and/or total home range size of foxes (Trapp 1978, Foote 1979, Yearsley and Samuel 1980, Haroldson and Fritzell 1984, Riley 2006). Methods of delineating home ranges (i.e. kernel estimates versus minimum convex polygons) also differ among studies, and different methods of home range estimation can result in different estimates of space use, even when the data used are the same (Woodruff and Keller 1982). Additionally, very few studies defined a core area within the home range (*but see* Progulske and Labisky 1997, Riley 2006, Chamberlain and Leopold 2000).

Home range size is dependent on the quality and type of surrounding habitat, rather than latitude and climate (Trapp and Hallberg 1975, Fritzell and Haroldson 1982). For example, homogeneous habitats appear to demand larger home ranges than areas with heterogeneity of habitats (Trapp and Hallberg 1975, Progulske and Labisky 1997). Foxes are thought to be monogamous (Fritzell and Haroldson 1982) and, unlike some other canids, a fox family group usually does not extend beyond a male, female, and their dependent young (Lord 1961).

I classified seasons based on the biological phases of the fox life cycle (*sensu* Sawyer and Fendly 1997, Chamberlain and Leopold 2000). The studies of Sawyer and Fendly (1997) and Chamberlain and Leopold (2000) were conducted in South Carolina and Mississippi, respectively. My study was conducted in a similar habitat and climate as the aforementioned studies, so gray foxes in my study probably experienced a similar life cycle (i.e. time of breeding, whelping, etc.).

Winter home range was significantly larger than the other 2 seasons. This was similar to most other gray fox studies that reported a winter home range (Follman 1973, Trapp 1973, Progulske and Labisky 1997). Larger home ranges may occur in winter due to lack of dependent offspring, dispersal of young from natal ranges to find their own home range and to mate, defense of territories for established foxes, and a decline in prey abundance (Follman 1973, Nicholson and Hill 1981, Sawyer and Fendley 1990). Wood et al. (1958) found that gray foxes in southwestern Georgia largely preyed insects, peanuts, and berries. During the winter, all of these resources would be limited, potentially forcing gray foxes to expand their home range. Smaller home ranges during breeding and kit-rearing seasons were also similar to other studies (Follman 1973, Trapp 1973, Progulske and Labisky 1997, Sawyer and Fendley 1990), likely due to increased food availability and biparental care demands (Follman 1973, Trapp 1973, Progulske and Labisky 1997 Chamberlain and Leopold 2000).

Genetics

The reported findings provide an initial look at how relatedness may influence gray fox spatial arrangement. However, I am reporting and discussing these results with extreme caution due to the low sample size and short time period. It was not surprising that I failed to detect correlation between spatial distance and genetic distance. The method of using trap and mortality locations as the geographic distance for the Mantel test may be influenced by factors such as dispersal or exploratory efforts by gray foxes. For example, Farias et al. (2005) reported that most gray foxes that experienced mortality were found on the periphery or outside of their home range. Similar findings have been reported for other animals including white-nosed coatis (Gompper 1998) and swift foxes (Sovada et al. 1998, Kitchen et al. 1999). Trapping also can be biased in a similar fashion by catching animals on the periphery of home ranges or during dispersal (Slough and Mowat 1996). Based on personal observations and reports of collared gray foxes that were killed away from the study area, gray foxes in this study have dispersed up to 24 kilometers. Other studies also have reported long dispersal distances of up to 135 kilometers (Banfield 1974). However, the short temporal duration and small sample size of this study may be impacting this result.

Kinship has been shown to affect home range overlap in numerous other species. Stoen et al. (2005) and Moyer et al. (2006) found that brown bears (*Ursus arctos*) and black bears (*Ursus americanus*), were more likely to have overlapping or neighboring home ranges with closely related individuals than with non relatives. White-nosed coatis (*Nasua narica*; Gompper 1998), raccoons (Ratnayeke et al. 2002), and bobcats (Janecka et al. 2006) also are more prone to overlap or share neighboring home ranges with close relatives. Studies on swift foxes (Kitchen et al. 2005), kit foxes (Ralls et al. 2001), and African wild dogs (Girman et al. 1997) also have found spatial kin clustering. The average kinship coefficient for the 2 groups of gray foxes I examined may be misleading due to 1 or 2 kinship coefficients influencing the overall mean. The average kinship coefficient for gray foxes with overlapping home ranges is higher (0.05) than for gray foxes without overlapping home ranges (= -0.007). In fact, the median kinship coefficient for non-overlapping home ranges, which in this case may be a more accurate measure, was -0.05. Additionally, there were instances of overlapping home ranges between male gray foxes that have a kinship coefficient that suggests close relatedness. For example, 2 males who were trapped within 1 week of and 5.3 kilometers apart from each other had the most extensive spatial area intra-sexual overlap (Figure 3.1). These individuals shared a kinship coefficient of 0.48. The capture sites of these gray foxes may also be indicative of the lack of significance in the Mantel test. Also, trapping only occurred on Ichauway, not the entire study area, so there were likely unmonitored gray foxes that had spatial overlap with monitored individuals. In fact, while the 2 gray foxes described above were caught on Ichauway, both of their home ranges were completely off of Ichauway. Island gray foxes (*Urocyon littoralis*) were no more likely to hold home ranges closer to or overlapping with related individuals than they were to non-relatives (Roemer et al. 2001). Additionally, in a study of a population of coyotes that experienced high mortality due to anthropogenic removal efforts, Williams et al. (2003) suggested that the lack of spatial and genetic distance correlation exhibited in their population was due to a high turn over in individuals. This may also be the case in my population which experiences high annual mortality (see chapter 2). Ralls et al. (2001) found an excess of homozygotes, which they suggested was indicative of low dispersal rates. While insignificant, an excess of heterozygotes and lower relatedness was found in this study, which may be suggestive of dispersal away from the natal range.

CONCLUSIONS

These findings are preliminary due to a small sample size, limited spatial scale, and a short temporal scale. Also, field observations could not be incorporated which would make the genetic findings more robust. However, this analysis does suggest that home range overlap may be influenced by kinship. Due to the high mortality rate in this population (see chapter 2) and other gray fox populations (*see* Wood 1958, Lord 1961, Wood and Odum 1964, Wigal and Chapman 1982, Nicholson and Hill 1984, Alderton 1994) it may be difficult to use a combination of radio telemetry and genetic comparison to establish kinship effects on spatial distribution. A less invasive and labor intensive approach, such as hair snares, may be optimal. Studies have used hair snares to estimate population numbers and densities (Taberlet et al. 1997), sex ratios (Taberlet et al. 1993), and spatial structure of relatives (Girman et al. 1997). Trapping often becomes less effective in warmer months because of increased food availability and

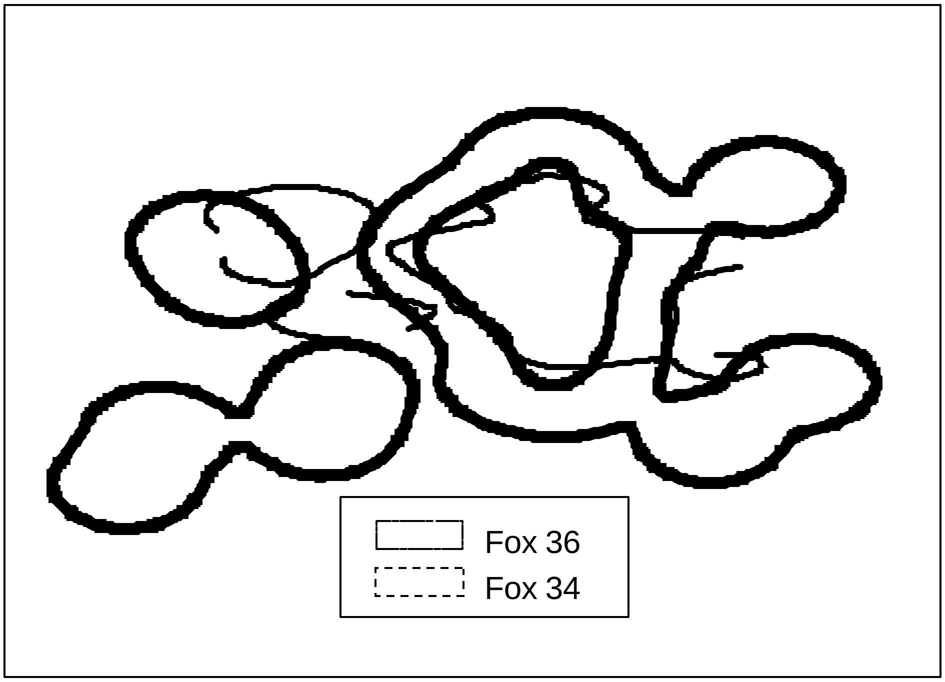

Figure 3.1. Home range overlap of 2 highly related male gray foxes during winter and breeding seasons during 2005. Both the 95% total home range and the 50% core area are denoted.

restricted home range due to demands of kits (Chamberlain and Leopold 2002). Hair snares may be more effective to answer questions concerning gray fox population ecology at both a seasonal and annual scale, which could offer a comprehensive description of population structure.

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APPENDIX: MEASUREMENTS AND TRAPPING NOTES

Trapping

All 3 foxes that were euthanized due to trap injuries (see chapter 1) suffered from broken legs. This was probably due to 2 factors: the trap being too heavy and the swivel at the bottom of the chain being jammed. All of mortally injured gray foxes, were trapped using the 1.75 laminated offset foot-hold traps (Minnesota Trapline Products, Pennock, MN).

Measurements

Gray foxes are sexually monomorphic (Fritzell and Haroldson 1982). However, males tend to be slightly larger in size, though not significantly (Fritzell and Haroldson 1982). Morphological measurements were taken on 51 foxes (19 females and 32 males). Length measurements were taken in centimeters and weight was taken in kilograms. There were no differences between sexes for weight (t = 2.03, P = 0.14) or total length (t = 2.01, P = 0.11), which were 2 of the indices I used to establish age (juvenile/adult).

Table Appendix. Average (and standard errors) of female, male, and pooled measurements of trapped gray foxes in southwest Georgia from 2002-2006.

	N	Length	Foot	Ear	Tail	Weight
Female	19	92.15(5.07)	12.77(0.85)	6.44(0.96)	31.26(1.66)	4.02(0.53)
Male	32	94.87(5.96)	13.35(1.97)	6.32(0.59)	32.44(2.15)	4.24(0.43)
Pooled	51	93.84(5.74)	13.13(1.65)	6.37(0.74)	31.99(2.04)	4.15(0.48)

VITA

Danielle Lolene Temple was born on June 4, 1979 in Norwalk, Connecticut, to Sandy and Dan Temple. She and her younger brother, Bobby, grew up in Weston, Connecticut, until 1995 when she moved with her family to Alpharetta, Georgia. Danielle attended Roswell High School and graduated in 1997. Danielle then headed to Olympia, Washington, to attend The Evergreen State College, where she majored in environmental studies. After graduating with a Bachelor of Science in May 2001, Danielle worked for 4 years on seasonal wildlife and natural research positions throughout the western and southeastern United States and Panama. These projects examined a variety of critters and related conservation issues ranging from the effects of timber management on bats to the issues that arise when a major road way bisects wolverine and fisher home ranges.

Danielle entered the School of Renewable Natural Resources at Louisiana State University in the fall of 2004 as a master's student in wildlife. Her thesis research examined gray fox spatial ecology in a longleaf pine forest and surrounding industrial landscapes. Danielle should complete her master's degree in May 2007 and graduate with a Master of Science in wildlife from Louisiana State University in August 2007.