SPACE USE, INTERACTIONS, EXTRA-TERRITORIAL FORAYS AND HABITAT SELECTION OF GRAY FOXES (*UROCYON CINEREOARGENTEUS*) IN SOUTHWESTERN GEORGIA

by

NICHOLAS ROBINSON DEUEL

(Under the Direction of Karl V. Miller and Michael J. Chamberlain)

ABSTRACT

From February 2014 through December 2015, I used GPS telemetry to investigate space use, spatial overlap, mated pair interactions, extra-territorial forays, habitat selection, and diurnal refugia of gray foxes (*Urocyon cinereoargenteus*) in Southwestern Georgia. Core area size varied seasonally, with smaller core areas maintained during spring than winter and summer. Spatial overlap was greatest for putative mated pairs and did not differ between spring and summer. Mated pair members appeared to frequently interact with each other, with greater interaction rates in spring and during diurnal periods. I recorded 25 extra-territorial forays from 10 of 26 gray foxes seasonally monitored. Twelve forays from 3 of 8 males monitored in winter corresponded with the gray fox breeding season. Habitat selection did not vary by season or time of day (diurnal vs. nocturnal). Hardwoods, human structures and roads were selected at all spatial scales.

INDEX WORDS: anthropogenic, core area, diurnal refugia, Euclidean distance approach, extra-territorial forays, GPS telemetry, gray fox, habitat selection, hardwoods, home range, human structures, kernel density estimation, mated pair interactions, space use, spatial overlap, *Urocyon cinereoargenteus*

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DEDICATION

I would like dedicate my thesis to my parents, Gary and Shelley Deuel, and my late grandparents, Roger and Helen Robinson, and Paul and Thelma Deuel.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

INTRODUCTION

Gray foxes (*Urocyon cinereoargenteus*) are a common, medium-sized, omnivorous canid found from southern Canada to northern Central America, including most of the contiguous United States (Fritzell and Haroldson 1982). Gray fox range has expanded since the early 20th century to include previously unoccupied areas in southern Canada and the Midwestern United States, possibly due to encroachment of hardwoods, absence of fire, habitat alteration, and climate change (Fritzell and Haroldson 1982, McAlpine et al. 2008). Conversely, where clearing of forests has occurred, and distribution and abundance of coyotes (*Canis latrans*) has increased, gray fox populations may be declining (Harrison 1993, Willingham 2008). The ability of gray foxes to climb is unique among North American canids and may explain why the species is strongly associated with forests (Feeney 1999). Climbing helps gray foxes avoid predators, like coyotes, and consume arboreal food resources (Grinnell et al. 1937, Feeney 1999).

Gray foxes are an important furbearer (Elsken-Lacy et al. 1999), agricultural pest (Hockman and Chapman 1983), vector of diseases (Davidson et al. 1992), predator of game bird nests (Hernandez et al. 1997) and small mammals (Kuenzi et al. 1998), and likely play a role in seed dispersal of mast producing plant species (Wilson and Thomas 1999). However, due to a perception of low economic value and ecological importance for the species, gray foxes have received relatively little research attention and our understanding of gray fox ecology is limited (Elbroch and Allen 2013). As a result, there are many ecological questions about gray foxes that have not been thoroughly investigated. All previous studies evaluating gray fox movements and habitat use have used location data infrequently collected with Very High Frequency (VHF) technology via triangulation. The use of Global Positioning System (GPS) technology to obtain frequent locations with high precision and accuracy is likely to yield new information about gray fox ecology, as it has done with other species (Hulbert 2001). I employed GPS technology in an attempt to provide new valuable insights into gray fox ecology which may assist managers working in landscapes inhabited by gray foxes.

LITERATURE REVIEW

Space Use

Home range sizes of gray foxes are highly variable across their geographical range, varying from 75 ha (Yearsley and Samuel 1980) to 676 ha (Haroldson and Fritzell 1984), with most studies reporting estimates ranging from 100 ha to 350 ha (Sawyer and Fendley 1990, Chamberlain and Leopold 2000, Temple et al. 2010). Likewise, previous studies have noted substantial variation in home range sizes among individuals on the same study area (Haroldson and Fritzell 1984, Sawyer and Fendley 1990, Tucker et al. 1993).

Gray fox home ranges vary seasonally, and tend to be largest during breeding and dispersal, intermediate during pup-rearing, and smallest during denning (Nicholson 1982, Chamberlain and Leopold 2000, Temple et al. 2010). Larger home range estimates during breeding and dispersal seasons are likely due to increased movements resulting from absence of pup-rearing responsibilities and decreasing abundance of prey (Sawyer and Fendley 1990). Conversely, smaller home ranges during denning are due to reduced movements associated with denning activities. However, as pups age home range sizes increase as a result of increased pup mobility (Follman 1973). Although gray foxes lack significant sexual dimorphism (Samuel and

Nelson 1982), home range sizes of males are generally slightly larger than females (Follman 1973, Yearsley and Samuel 1980, Sawyer and Fendley 1990). However, male and female home ranges are both smaller and movement rates are less during denning, suggesting some degree of male investment in rearing young (Follman 1973, Nicholson 1982, Sawyer and Fendley 1990).

Accurate and reliable estimates of home range size are foundational to assess space use requirements of a species. Variation in gray fox home range estimates is affected by a number of environmental influences (Trapp and Hallberg 1975, Fuller 1978). However, variations in estimates of space use also may be influenced by sampling intensity (Haroldson and Fritzell 1984) and the home range model used to obtain estimates (Seaman and Powell 1996). Although some studies have used adaptive (Chamberlain and Leopold 2000, Riley 2006) or fixed kernels (Temple et al. 2010) to estimate gray fox home ranges, most studies have used the minimum convex polygon method (Haroldson and Fritzell 1984, Sunquist 1989, Sawyer and Fendley 1990), which tends to overestimate size and include areas not used by study animals (Harris et al. 1990). All previous home range studies conducted on gray foxes have obtained relatively infrequent location data (i.e., ≤ 4 locations/week) using VHF technology techniques. Greater number of animal locations should provide more reliable home range estimates (Girard 2002), and early concerns regarding autocorrelation of animal locations associated with frequently collected GPS data (Seaman and Powell 1996, Hansteen et al. 1997, Kernohan et al. 2001) have been largely unfounded (Fieberg 2007).

Spatial Overlap and Mated Pair Interactions

Understanding the spatial organization of a species is important when considering management practices because population density can be influenced by territoriality and pair bonding (Krebs 1971). Gray foxes were once believed to show a low degree of territoriality (Hovis et al. 1984), but more recent studies have provided evidence that supports a greater degree of territoriality and pair bonding (Tucker et al. 1993, Chamberlain and Leopold 2000). Because gray foxes are socially monogamous, spatial overlap occurs when an adult male and female form a pair-bond to rear young and maintain exclusive territories (Nicholson et al. 1985, Tucker et al. 1993, Chamberlain and Leopold 2000). Relatedness may explain extensive spatial overlap of same sex fox combinations and opposite sex fox combinations that are not pair-bonded (Tucker et al. 1993, Chamberlain and Leopold 2000). For example, adult foxes are known to tolerate the presence of their young prior to juvenile dispersal beginning in fall (Nicholson 1982, Tucker et al. 1993). Information on effects of seasonality on spatial overlap of gray foxes is limited, but Chamberlain and Leopold (2000) suggested that overlap in space use of mated pairs is similar throughout the year, and overlap of neighboring foxes may increase during breeding. Likewise, pair-bonded gray foxes were closer than expected to each other within their shared home ranges, whereas neighboring foxes avoided each other within shared spaces.

Extra-Territorial Forays

Extra-territorial forays have been documented in many canid species, such as red foxes (*Vulpes vulpes*; Soulsbury et al. 2011), swift foxes (*Vulpes macrotis*; Nicholson et al. 2007) and gray wolves (*Canis lupus*; Messier 1985). These forays can be motivated by breeding opportunities (Soulsbury et al. 2011), dispersal (Dique et al. 2003), seeking information about neighboring areas (Fedy and Stutchbury 2004) and food resources (Tsukada 1997). Although dispersal movements have been reported in gray foxes (Nicholson et al. 1985, Chamberlain and Leopold 2002), the existence of extra-territorial forays has not been documented, perhaps due to infrequent locations provided by traditional VHF telemetry. Gray foxes that engage in dispersal movements are typically young males or adults that disperse to look for vacant territories and/or a female to pair and mate with for the breeding season (Nicholson et al. 1985). Young males generally disperse away from their natal area in the fall, whereas adult males and females may sometimes disperse from their territory following mate loss (Chamberlain and Leopold 2002).

Habitat Selection

Prior studies reported that gray foxes selected hardwood forests (Fuller 1978, Chamberlain and Leopold 2000, Temple et al. 2010), mixed pine-hardwood forests (Progulske and Labisky 1997, Chamberlain and Leopold 2000), mature pine forests (Chamberlain and Leopold 2000), 9-14 year old pine forests (Sawyer and Fendley 1994), and anthropogenic habitats (Harrison 1997, Riley 2006, Temple et al. 2010). Differences in habitat selection across studies likely reflect site-specific differences in habitat availability, prey abundance (Chamberlain and Leopold 2000), forage availability (Wood et al. 1958), and predator communities (Fedriani 2000, Chamberlain and Leopold 2005). Habitat availability not only affects gray fox habitat selection, but it may also influence cause-specific mortality. Fedriani (2000) found predation rates of gray foxes by coyotes and bobcats (*Lynx rufus*) to be higher (91% of mortalities) in a predominantly treeless landscape than studies conducted in forest dominated landscapes (10-25% of mortalities) (Chamberlain 1999, Weston and Brisbin 2003, Temple et al. 2010).

As with geographical differences in habitat selection, seasonal habitat use of gray foxes also varies based on availability of resources. For example, gray foxes consume soft mast, small mammals, birds, and insects (Hockman and Chapman 1983), all of which vary seasonally with regards to availability (Hockman and Chapman 1983, Fritzell 1987). However, whether habitat selection varies seasonally is not well understood, as some studies have found differences in seasonal habitat selection (Folmann 1973, Sawyer and Fendley 1994), whereas others did not (Chamberlain and Leopold 2000, Temple et al. 2010).

Finer-scale temporal (e.g., nocturnal versus diurnal) assessment of habitat selection may provide greater insight into ecology of wild animals. Studies conducted on gray foxes have generally found them to select habitat types with dense brushy understories during diurnal periods (Nicholson 1982, Haroldson and Fritzell 1984, Sawyer and Fendley 1994, Yearsley and Samuel 1980), whereas selection during nocturnal periods tends to be more random (Haroldson and Fritzell 1984, Sawyer and Fendley 1994) or within open habitat types (Follman 1973, Yearsley and Samuel 1980, Harrison 1997). Differences between nocturnal and diurnal habitat selection likely reflect balancing predation risk and foraging opportunities (Sunquist 1989).

Understanding habitat selection is essential to effectively manage any wildlife species. Although gray fox habitat selection has been studied in many portions of their geographic range, recent technological advancements in tracking technology have resulted in an ability to address gray fox habitat selection in a more robust manner. All habitat selection studies conducted on gray foxes have used relatively infrequently obtained location data (i.e., ≤ 4 locations/week on average; Sawyer and Fendley 1994, Chamberlain and Leopold 2000, Temple et al. 2010) based on VHF technology. Location error associated with VHF technology is greater (95 m; Pellerin et al. 2008) relative to data collected with GPS technology (10-30 m; D’Eon et al. 2002), and because GPS data collection occurs as programmed, data collection frequency is only limited by battery life of the tracking unit. GPS technology also allows researchers to more easily identify refugia and obtain a sufficient number of locations to effectively evaluate diurnal and nocturnal habitat selection.

OBJECTIVES

To better understand gray fox ecology, I established the following objectives:

1. Determine if home range size and core area size varies seasonally
2. Determine degree of spatial overlap of mated pairs and neighboring foxes
3. Evaluate mated pair interactions temporally (i.e., diurnal vs. nocturnal, and seasonal)
4. Describe extra-territorial forays by season
5. Examine temporal (i.e., diurnal vs. nocturnal and seasonal) habitat selection at 3 spatial scales
6. Examine seasonal diurnal refugia selection

THESIS FORMAT

This thesis was written in manuscript format in which chapters 2 and 3 represent manuscripts to be submitted for publication. Chapter 1 is an introduction to the thesis. Chapter 2 describes space use, overlap, mated pair interactions and extra-territorial forays on a study area in Baker County, Georgia. Chapter 3 describes habitat selection and diurnal refugia selection. Chapter 4 is a summary of results and management implications for this research.

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CHAPTER 2

GRAY FOX SPACE USE, SPATIAL OVERLAP, MATED PAIR INTERACTIONS AND EXTRA-TERRITORIAL FORAYS IN SOUTHWESTERN GEORGIA

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ABSTRACT

Despite previous studies that have evaluated space use patterns, little is known about gray fox spatial and movement ecology. Therefore, we obtained GPS location data from 34 gray foxes (20 males and 14 females) from February 2014 until December 2015 in southwestern Georgia, USA to investigate spatial and movement ecology. Home range sizes were similar across seasons, whereas core area sizes varied seasonally. Smaller core areas were maintained during spring than winter and summer. Home range (spring – 92.3%; summer – 94.8%) and core area overlap (spring – 86.8%; summer – 84.5%) was greatest for mated pairs and did not differ between spring and summer. For neighboring foxes, home range overlap (20.3%) was less. Mated pair members frequently interacted with each other (29.4% of all simultaneous locations ≤ 40 m). Mated pairs interacted with each other more diurnally during spring (49.9%) than summer (31.5%), while nocturnal interactions were similar for spring (18.0%) and summer (19.3%). We recorded 25 extra-territorial forays from 10 of 26 gray foxes seasonally monitored. Twelve forays from 3 of 8 males monitored in winter corresponded with the gray fox breeding season. Our results suggest mated pairs form strong pair bonds, but that some males make extra-territorial forays during the breeding season, presumably to seek extra-pair copulations.

INTRODUCTION

Gray fox (*Urocyon cinereoargenteus*) social ecology is poorly understood. All prior studies conducted on gray fox movements and space use have obtained relatively infrequent location data (i.e., ≤ 4 locations/week) using Very High Frequency (VHF) telemetry techniques. However, accurate and reliable estimates of home range size are foundational to assess space use requirements of a species. The advancement of Global Positioning System (GPS) technology suitable for small canids now allows the investigation of interactions between individuals, documentation of rare movements, and the ability to obtain precise estimates of space use and overlap (Fieberg and Kochanny 2005).

Home range sizes of gray foxes are variable across their geographical range, ranging from 75 ha (Yearsley and Samuel 1980) to 676 ha (Haroldson and Fritzell 1984), with most studies reporting estimates ranging from 100 ha to 350 ha (Sawyer and Fendley 1990; Chamberlain and Leopold 2000; Temple et al. 2010). Likewise, previous studies have noted substantial variation in home range sizes among individuals on the same study area (Haroldson and Fritzell 1984; Sawyer and Fendley 1990; Tucker et al. 1993). Gray fox home ranges vary seasonally (Sawyer and Fendley 1990; Chamberlain and Leopold 2000; Temple et al. 2010), and tend to be largest during breeding (Follman 1973; Sawyer and Fendley 1990; Chamberlain and Leopold 2000) and dispersal (Nicholson 1982; Temple et al. 2010), intermediate during pup-rearing (Jeselnik 1981; Sawyer and Fendley 1990), and smallest during denning (Jeselnik 1981; Nicholson 1982; Sawyer and Fendley 1990). Larger home range estimates during breeding and dispersal seasons are likely due to increased movements resulting from absence of pup-rearing responsibilities and decreasing abundance of prey (Sawyer and Fendley 1990). Conversely, smaller home ranges during denning are likely a function of reduced movements associated with denning activities, but as pups age home range sizes increase as a result of increased pup mobility (Follman 1973). Although gray foxes lack significant sexual dimorphism (Samuel and Nelson 1982), home range sizes of males are generally slightly larger than females (Follman 1973; Yearsley and Samuel 1980; Sawyer and Fendley 1990). However, male and female home ranges are both smaller and movement rates are less during denning, suggesting some degree of male investment in rearing young (Follman 1973; Nicholson 1982; Sawyer and Fendley 1990).

Understanding the spatial organization of a species is important when considering management practices because population density can be influenced by territoriality and pair bonding (Krebs 1971). Gray foxes were once believed to show a low degree of territoriality (Hovis et al. 1984), but more recent studies have provided evidence that supports a greater degree of territoriality and pair bonding (Tucker et al. 1993; Chamberlain and Leopold 2000). Because gray foxes are socially monogamous, spatial overlap occurs when an adult male and female form a pair-bond to rear young and maintain exclusive territories (Nicholson et al. 1985; Tucker et al. 1993; Chamberlain and Leopold 2000). Relatedness may explain extensive spatial overlap of same sex fox combinations and opposite sex fox combinations that are not pair-bonded (Tucker et al. 1993; Chamberlain and Leopold 2000). Information on effects of seasonality on spatial overlap of gray foxes is limited, but Chamberlain and Leopold (2000) suggested that overlap in space use of mated pairs is similar throughout the year, and overlap of neighboring foxes may increase during breeding season. There is a lack of information on the interactions of gray fox mated pairs (Haroldson and Fritzell 1984; Chamberlain and Leopold 2000). Haroldson and Fritzell (1984) studied a single mated pair that was found together 13.5% of the time, while Chamberlain and Leopold (2000) found mated gray foxes closer than expected to each other within their home ranges. Neither study provides a detailed account of mated pair interactions. Interactions may differ temporally during a 24-hour period because gray foxes typically rest diurnally and forage during crepuscular and nocturnal periods (Haroldson and Fritzell 1984; Farias et al. 2012). Understanding mated pair interactions will provide insight into the strength of gray fox pair-bonds and the extent that males participate in rearing young.

Although dispersal movements have been reported in gray foxes (Nicholson et al. 1985; Chamberlain and Leopold 2002), the existence of extra-territorial forays has not been documented, perhaps due to infrequent locations provided by traditional VHF telemetry. Extra-territorial forays have been documented in many canid species, such as red foxes (*Vulpes vulpes*; Soulsbury et al. 2011), swift foxes (*Vulpes velox*; Nicholson et al. 2007) and gray wolves (*Canis lupus*; Messier 1985). These forays can be motivated by breeding opportunities (Soulsbury et al. 2011), dispersal (Dique et al. 2003), seeking information about neighboring areas (Fedy and Stutchbury 2004), and food resources (Tsukada 1997). Extra-territorial forays are likely important to gene flow, population regulation, and disease transmission (Soulsbury et al. 2011).

There have been many movement and home range studies of gray fox, but our knowledge of their spatial ecology remains limited due to VHF sampling constraints. Therefore, we used GPS technology to evaluate gray fox space use, spatial overlap, mated pair interactions and extra-territorial forays in southwestern Georgia.

MATERIALS AND METHODS

Study Area

We conducted our study at the Joseph W. Jones Ecological Research Center at Ichauway, and surrounding lands in Baker County, Georgia, USA. Topography was mostly flat, with elevation ranging from 27 – 200 m above sea level. Climate was subtropical with hot, humid summers and mild, wet short winters. Temperatures generally ranged from 11 °C – 27.5 °C throughout the year and the average annual precipitation was 131 cm (Goebel et al. 1997).

Ichauway consisted of approximately 12,000 ha of land in the Southeastern Coastal Plain primarily managed to maintain and restore the longleaf pine (*Pinus palustris*)-wiregrass (*Aristida beyrichiana*) ecosystem. Land use on Ichauway included 7,250 ha of longleaf pine forest, with the remaining 1,920 ha consisting of slash (*P. elliottii*) and loblolly pine (*P. taeda*) forests, mixed pine-hardwood forests and lowland hardwood hammocks (Boring 2001). Pine forests were characterized by an open canopy, a sparse midstory, and a dense herbaceous understory. Management practices included prescribed fires on an approximate 2-year rotation; these fires limited hardwood encroachment and resulted in a diverse herbaceous understory of wiregrass and other native ground cover species. Hardwood removal through mechanical means such as roller chopping and logging was also performed to maintain open canopies and promote herbaceous ground cover. Predator trapping occurred on Ichauway, with removal mainly consisting of opossums (*Didelphis virginiana*), raccoons (*Procyon lotor*), coyotes (*Canis latrans*), bobcats (*Lynx rufus*) and prior to this study, gray foxes.

In contrast to Ichauway, surrounding lands were dominated by large center pivot agricultural fields with hardwood forests, pine forests, mixed pine-hardwood forests, pasture and residential areas interspersed throughout. Agricultural fields were primarily planted with corn (*Zea mays*) or cotton (*Gossypium* spp.) in the spring and harvested in the fall. Some agricultural fields were bisected by hedgerows typically made up of hardwoods. Hardwood dominated stands in the surrounding areas were generally not actively managed; whereas, some pine stands were managed for timber production or quail hunting.

Trapping

We used MB-450-FOX/OS foot-hold traps (Minnesota Brand, Pennock, MN) and Victor 1.75 laminated offset foothold traps (Oneida Victor, Euclid, OH) baited with lure/bait to capture gray foxes. Trapping was conducted from February 2014-August 2015.

We restrained captured gray foxes using a catch-pole and secured the animal by placing electrical tape around the rostrum and legs. We used a blindfold to reduce animal stress. Weight, age (juvenile or adult), sex, reproductive condition and basic measurements (total body length, tail length, hind-foot length and ear length) were recorded. We used tooth wear, weight (Wood 1958) and facial markings (Lord 1961) to determine whether captured animals were adults or juveniles.

Each gray fox was given a unique ear tattoo and/or ear tags in both ears, and adult animals ≥ 3.6 kg were fit with a 180 g GPS Collar (GPS Logger W500, Advanced Telemetry Systems, Isanti, MN). We released collared gray foxes at the capture site. All trapping and handling procedures were approved by the University of Georgia Institutional Animal Care and Use Committee (IACUC #A2013 07-017-Y1-A0).

GPS Data Collection

Initially, we programmed GPS collars to record a location every 3.25 hours (7-8 locations/day) until they dropped off 1 year after deployment. Beginning in January 2015, we programmed GPS collars to record a location every 2 hours (12 locations/day) or every 1 hour and 30 minutes (16 locations/day) until cessation of data collection (31 December 2015). We monitored foxes once every week with a 3-element Yagi antenna and hand-held radio telemetry receiver (Wildlife Materials, Carbondale, IL) to determine status (alive/dead) and general location. We downloaded location data when collars were retrieved following collar drop off or when the animal died. For some collars (n = 16), location data were remotely downloaded in the field using a laptop computer and handheld antenna (LairdTech, London, United Kingdom).

Space Use

For analyses, we considered winter (i.e., breeding season) as 1 Jan. – 31 Mar., spring (i.e., denning-early pup-rearing season) as 1 Apr. – 30 Jun., summer (i.e., late pup-rearing season) as 1 Jul. – 30 Sep., and fall (i.e., dispersal season) as 1 Oct. – 31 Dec (Wood 1958, Nicholson et al. 1985). Individuals with ≥ 1.5 months of location data within a season were included in analyses (see below).

We generated seasonal 95% (home range) and 50% (core area) fixed kernel polygons using adehabitatHR (Calenge 2006) package with R software (R Core Team 2013). We used a rule-based ad hoc method to select bandwidth by finding the smallest 0.10 increment of h_{ref} that resulted in a contiguous rather than disjointed 95% and 50% polygon, and contained no lacuna within the home range (Kie 2013). We sequentially reduced the reference bandwidth (h_{ref}) in increments of 0.10 (0.9 h_{ref}, 0.8 h_{ref}, 0.7 h_{ref}…0.1 h_{ref}) until an estimated home range fractured into 2 or more polygons and, selected the smallest increment of h_{ref} that resulted in a continuous polygon as the bandwidth.

We used RCommander (Fox 2005) to conduct an analysis of variance (ANOVA) to evaluate effects of sex, season, and their interaction on home range and core area sizes. When significant differences were found, we used Tukey multiple comparison tests to determine differences among seasons or between sexes.

Spatial Overlap

We estimated overlap of seasonal home ranges and core areas by intersecting home ranges and core areas of neighboring gray foxes and determining the area of the overlap region in

ArcGIS (ESRI, Redlands, CA). We counted number of locations for each individual within the overlap region to obtain a proportion of each individual's locations within the overlap region (Chamberlain and Leopold 2005). For each season, we calculated overlap indices for male-female and male-male combinations by modifying the ratio of Ginsberg and Young (1992) to quantify association:

$$\text{Overlap} = [(n1 + n2) / (N1 + N2)] \times 100$$

Where n1 and n2 were numbers of locations for individuals 1 and 2 within the same overlap region and N1 and N2 were total number of locations for each individual (Gehrt and Fritzell 1998). Male-female combinations that had > 50% home range and core area overlap were assumed to be mated, whereas pairing combinations that had ≤ 50% home range and core area overlap were considered to be neighboring. We conducted ANOVA to determine if home range and core area overlap of mated pairs differed seasonally.

Mated Pair Interactions

To assess mated pair interactions, we determined how often mated pair members that shared home ranges were simultaneously recorded ≤ 40 m from each other. Based on location error for GPS collars (10-30 m; D'Eon et al. 2002), we assumed that simultaneous locations ≤ 40 m from each other likely represented pairs either moving or resting together. We obtained proportions for each gray fox pairing for each season by dividing the number of times that simultaneous gray fox locations were separated by ≤ 40 m by the total number of simultaneous locations. To assess whether mated pair interaction frequency differed based on time of day (TOD), we compared how often gray foxes were simultaneously recorded a certain distance from each other for diurnal and nocturnal periods. Night and crepuscular (≤ 1 hour before and after dawn and dusk, respectively) locations were considered as nocturnal locations, whereas all other locations were used as diurnal locations. We used chi-square contingency tests to determine if mated pair interaction frequency differed across seasons, TOD, TOD within seasons and TOD across seasons.

Extra-Territorial Forays

We defined extra-territorial forays as any occasion where a gray fox traveled ≥ 0.5 km outside of its home range boundaries for ≥ 8 h. To avoid using erroneous locations, only movements with at least 2 consecutive locations outside the home range boundary were considered forays. We obtained the distance from 95% KUD boundary and total path distance for each foray using ArcMap. We recorded the date and time when each foray started and ended, and duration of each foray.

RESULTS

During 2014-2015, we collected 56,920 GPS locations from 34 (20M, 14F) individual gray foxes. Overall GPS fix success rate was 86.14%.

Space Use

We calculated seasonal home ranges and core areas for 26 (15M, 11F) individual gray foxes. There was no significant interaction between sex and season for home range size ($F_{3,44}$ = 0.302, P = 0.824) or core area size ($F_{3,44}$ = 1.486, P = 0.232). Home range size did not vary seasonally ($F_{3,44}$ = 0.930, P = 0.434), whereas core area size varied seasonally ($F_{3,44}$ = 4.793, P = 0.006). Tukey multiple comparison tests revealed that spring core areas were smaller than winter (P = 0.023) and summer (P = 0.014; Table 2.1).

Spatial Overlap

We identified 4 putative mated pairs during spring and summer. Home range ($F_{1,6}$ = 1.648, P = 0.247) and core area ($F_{1,6}$ = 0.149, P = 0.713) overlap for mated pair members did not vary between spring and summer seasons (Table 2.2; Table 2.3). For neighboring foxes that had bordering home ranges, we had 3 male-male and 2 male-female sets. Home range overlap for neighboring foxes was 20.3 ± 6.7% (range: 2 – 47%, n = 6) overall, 47% (n = 1) for winter, 16.5 ± 6.1% (range: 2 – 28%, n = 4) for spring and 9% (n = 1) for summer. Home range overlap for female-female sets did not occur. Neighboring foxes did not have overlapping core areas.

Mated Pair Interactions

We monitored 3 mated pairs that had simultaneous locations during spring and summer. Simultaneous locations of pair members were on average 339.6 ± 5.2 m apart, with 29.4 ± 0.1% of locations ≤ 40 m. Mated pairs were more frequently together in spring than summer (χ^2 = 67.773, df = 1, n = 6705, $P < 0.001$) and diurnally than nocturnally (χ^2 = 400.127, df = 1, n = 6705, $P < 0.001$). In spring (χ^2 = 373.784, df = 1, n = 3303, $P < 0.001$) and summer (χ^2 = 66.988, df = 1, n = 3402, $P < 0.001$), mated pairs were more frequently together during diurnal than nocturnal periods. During the day, mated pairs were more frequently together in spring than summer (χ^2 = 113.007, df = 1, n = 3217, $P < 0.001$). During the night, mated pairs were found together similarly in spring and summer (χ^2 = 0.909, df = 1, n = 3488, $P = 0.340$) (Table 2.3).

Extra-Territorial Forays

We identified 25 (17M, 8F) extra-territorial forays from 10 (6M, 4F) of 26 (15M, 11F) individual gray foxes that were seasonally monitored (Table 2.4). Mean maximum distance from the home range boundary was 4.4 ± 1.9 km (range = 0.6 – 23.2 km). Mean duration of forays was 19.1 ± 3.1 h (range = 8 – 65 h) and total distance traveled averaged 15.4 ± 4.2 km (range = 2.1 – 91.1 km).

Thirteen (12M, 1F) forays from 4 (3M, 1F) of 12 (8M, 4F) gray foxes monitored during winter occurred from 19 Jan. to 7 Feb. 2015, with one male taking 6 forays and a second taking 5 forays. Mean maximum distance from the home range boundary in winter was 7.4 ± 2.2 km (range = 1.3 – 23.2 km) for males and 1.0 km for females. Mean duration of forays in winter for males was 13.1 ± 2.1 h (range = 8 – 29.3 h) and 65 h for females, whereas total distance traveled on a foray in winter averaged 25.5 ± 7.9 km (range = 7.3 – 91.1 km) and 3.9 km for males and females, respectively.

Three forays from 1 (1F) of 23 (13M, 10F) gray foxes monitored during spring occurred from 21 to 29 June 2015. Six forays (2M, 4F) from 4 (2M, 2F) of 17 (8M, 9F) gray foxes monitored during summer occurred from 3 to 24 Sept 2015. Mean maximum distance from the home range boundary in summer was 0.9 ± 0.3 km (range = 0.6 – 1.2 km) for males and 1.7 ± 0.7 km (range = 0.6 – 3.5 km) for females. Mean duration of forays in summer for males was 9 h and 27.4 ± 11.6 h (range = 9 – 58.5 h) for females, while total distance traveled in summer for males averaged 3.4 ± 0.4 km (range = 3 – 3.8 km) and 7.3 ± 2.9 km (range = 3 – 15.5 km) for females. One mated pair forayed together from 13 to 14 Sept 2015. Three forays from 1 (1M) of 7 (2M, 5F) gray foxes being monitored occurred in fall from 1 to 11 Oct 2014 (Fig. 2.1).

DISCUSSION

Our home range size estimates were larger than estimates from a previous study conducted on our study site that used VHF data [winter – 152.4 ha, breeding – 91.4 ha, kit rearing – 99.7 ha as reported in Temple et al. (2010)]. GPS permitted greater sampling intensity and an even sampling schedule throughout the diel period during our study, which may have resulted in larger home range estimates (Girard 2002; Mills et al. 2006). Home range size is known to increase with sampling effort until reaching an asymptote (Seaman et al. 1999; Powell 2000). Because fewer locations are used to derive estimates in VHF studies, the failure to reach an asymptote may be more likely and could potentially lead to smaller home range estimates in some cases. The method used to select bandwidth can also influence kernel-based home range estimates (Kie 2013). We used an ad hoc method, which has been shown to outperform the least-squares cross-validation method used by Temple et al. (2010). Another contributing factor that may have influenced home range estimates was the occurrence of a confirmed canine distemper outbreak in the area in 2014 (Brent Howze, GADNR, pers. comm.) that reduced population density of gray foxes. Studies conducted on other species have recorded larger home range sizes when population density is low due to less intraspecific competition for resources (Macdonald and Bacon 1982; Ostfeld 1985).

Although we failed to detect seasonal differences in home range sizes, core areas were smaller during spring (denning and early pup-rearing). Other studies have reported constriction of space use by gray foxes during denning and pup-rearing seasons (Follman 1973; Nicholson 1982; Sawyer and Fendley 1990). Based on visual observations during periodic walk-in checks, most monitored gray foxes in our study were suspected to have been mated during the denning and early pup-rearing season. Females make repeated visits to dens during pup-rearing, and have a strong affinity to den sites; however, both sexes actively rear pups and show affinity to dens or areas around them (Nicholson et al. 1985), which likely contributes to smaller core areas for both sexes during this time. Larger core areas during the remainder of the year are likely due to increased activity brought on by reduced pup-rearing responsibilities (Jeselnik 1981; Nicholson 1982).

We observed a greater degree of spatial overlap for members of mated pairs than reported in previous studies (Tucker et al. 1993; Chamberlain and Leopold 2000), likely because VHF data may underestimate overlap in space use due to less accurate home range estimates (Fieberg and Kochanny 2005). Home ranges and core areas of mated pairs showed extensive overlap in spring and summer, providing further evidence that gray foxes form strong pair-bonds (Tucker et al. 1993; Chamberlain and Leopold 2000). Although social monogamy as a social system is rare in most mammals, it is common in canids (Geffen et al. 1996) and birds (Black 1996). Chamberlain and Leopold (2000) found spatial overlap of gray fox mated pairs to be similar across seasons, which suggests pair-bonds may be maintained throughout the year. However, the pair-bond is likely strongest during winter, when mating occurs, and pup-rearing season, when pair members share parental responsibilities in rearing offspring (Nicholson et al. 1985; Chamberlain and Leopold 2000). Similar to other studies (Tucker et al. 1993; Chamberlain and Leopold 2000), we found minimal spatial overlap among neighboring foxes that were not pair-bonded. This lack of overlap suggests gray foxes are territorial and mated pairs exclude other foxes from their shared home ranges and core areas.

We found members of mated pairs together over twice as often as previously reported [29.4% versus 13.5% as reported in Haroldson and Fritzell (1984)]. Our results suggest gray fox mated pairs frequently travel, forage and rest together within their shared territories. Mated pairs interacted more in spring than summer, but this difference was mainly driven by a higher frequency of diurnal interactions in spring (49.9% during spring and 31.5% during summer), whereas frequency of nocturnal interactions (18.1% during spring and 19.3% during summer) were similar across both seasons. These results suggest mated pairs frequently rest together in spring near den sites when pups are young and provides further evidence of direct paternal care in gray foxes (Nicholson et al. 1985). Paternal care is common in canids, although the degree as to how much care males provide varies across species (Malcolm 1985). Our findings of mutually exclusive core areas, along with mated pair members diurnally being together approximately half the time during denning and pup-rearing, suggest male gray foxes heavily invest in pup-rearing. Even with fewer pup-rearing responsibilities in summer, mated pairs still diurnally rested together more than they nocturnally traveled and/or foraged together. Gray foxes prefer dense vegetative cover (Nicholson 1982; Haroldson and Fritzell 1984; Sawyer and Fendley 1994) and occasionally trees (Yeager 1938) as diurnal refugia. Resting together during diurnal periods may help strengthen pair-bonds and be effective as an antipredator strategy (Mysterud and Østbye 1995). Nocturnally foraging independently would be advantageous for pair members when hunting small mammals (Ralls and White 2003). Although we found a large decrease in diurnal interactions from summer to spring, nocturnal interactions remained constant across both seasons, perhaps because mated pairs may alternate foraging at night where one member stays with the young, while the other forages, as reported in red foxes (Maas and Macdonald 2004).

Our results are the first documentation of extra-territorial forays by gray foxes. For many species, movements outside of established home ranges through unfamiliar areas are risky, energetically costly, and can threaten the survival of an individual (Metzgar 1967; Larsen and Boutin 1994; Fraser et al. 2001). Extra-territorial forays can be motivated by breeding opportunities (Soulsbury et al. 2011), dispersal (Dique et al. 2003), seeking information about neighboring areas (Fedy and Stutchbury 2004) and procuring food resources (Tsukada 1997). During winter, all extra-territorial forays occurred from late January to early February in our study, which corresponds with the gray fox breeding season in southern Georgia (Wood 1958). The majority of winter forays were by 3 adult males who may have been seeking extra-pair copulations with neighboring estrous females, as reported for other canid species (Roemer et al. 2001; Baker et al. 2004; Soulsbury et al. 2011). Although gray foxes are socially monogamous (Nicholson et al. 1985; Chamberlain and Leopold 2000), Weston Glenn et al. (2009) found multiple paternity in some litters, which suggests they may not always be genetically monogamous. In socially monogamous species, males can maximize their reproductive success by breeding females in neighboring territories (Soulsbury et al. 2011). The largest male (5.0 kg) monitored in our study and an above average sized male (4.4 kg) were responsible for 11 of the 13 total forays during breeding. Seeking extra-pair copulations with neighboring females may be a more successful mating strategy for larger males (Cavallini 1998; Iossa et al. 2008) that have higher genetic fitness (Zahavi 1975). Based on prior interactions, the establishment of a dominance hierarchy between neighboring individuals may develop (Barash 1974). Dominant males may choose to intrude into territories with weak male territory holders and attempt to breed with females (Soulsbury et al. 2011). Additionally, 1 female fox made a foray just outside of her home territory during breeding. Instead of passively playing a role in extra-pair copulations, females of other socially monogamous species may seek them out with neighboring males that possess higher genetic fitness than their pair-bonded mate (Smith 1988; Kempenaers et al. 1992).

Despite a large number of foxes monitored during spring, no gray foxes left their territories in April and May, presumably because of pup-rearing responsibilities at this time. From March to August, the only forays we observed were by a single female fox in June. Because these were movements likely not motivated by breeding or dispersal, she may have been seeking access to food resources (Tsukada 1997). From early September to early October, we observed 9 forays that corresponded with the dispersal of offspring and cessation of pup rearing responsibilities (Nicholson et al. 1985). Adult gray foxes have relatively low annual survival rates [61%; Temple et al. (2010)] and both sexes continue to independently rear pups following mate loss, with a lone male’s ability to rear pups being dependent on whether pups have been weaned (Chamberlain and Leopold 2002). When the pups disperse from their natal range, lone adults may be motivated to seek out a new mate to pair with for the upcoming breeding season if their mate died between the time of whelping and pup dispersal.

Our results demonstrate that home ranges and core areas of gray fox mated pairs overlap extensively during spring and summer. Within these shared spaces, mated pairs frequently interact with each other, particularly during diurnal periods in spring when resting together near den sites. Our results also suggest mates form strong pair-bonds through spring and summer, and that males invest in rearing pups. We observed extra-territorial forays that coincided with the gray fox breeding season, which suggests that male gray foxes may seek extra-pair copulations.

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Table 2.1. Seasonal home range (95% kernel utilization distribution contour) and core area (50% kernel utilization distribution contour) averages (ha) for male and female gray foxes (and standard errors) from 2014-2015 in Baker County, Georgia. Significant differences ($P < 0.05$) among seasons for core area size are indicated by different letters. Number of individual gray foxes in each season is denoted by n.

Season	n	Home range	Core area
Winter	12	217.0 ± 53.8	17.8 ± 3.7 (a)
Spring	23	160.8 ± 31.7	10.2 ± 0.9 (b)
Summer	17	215.2 ± 31.8	17.4 ± 1.8 (a)
Fall	7	200.9 ± 43.7	18.0 ± 4.8 (ab)

Table 2.2. Average percent home range (95% kernel utilization distribution) and core area (50% kernel utilization distribution) spatial overlap for gray fox mated pairs (n = 4), along with percentage of simultaneous locations ≤ 40 m for gray fox mated pairs (n = 3) for spring and summer (and standard errors) from 2014-2015 in Baker County, Georgia. One mated pair (F25/M38) did not have simultaneous locations due to different GPS location schedules.

Season	Home range overlap	Core area overlap	All locations	Diurnal locations	Nocturnal locations
Spring	92.3 ± 1.7%	86.8 ± 3.7%	34.1 ± 0.1%	49.9 ± 0.1%	18.1 ± 0.1%
Summer	94.8 ± 1.0%	84.5 ± 4.5%	24.9 ± 0.1%	31.5 ± 0.1%	19.3 ± 0.1%

Table 2.3. Average percent home range (95% kernel utilization distribution) and core area (50% kernel utilization distribution) spatial overlap for gray fox mated pairs (n = 4), along with percentage of simultaneous locations ≤ 40 m for gray fox mated pairs (n = 3) shown individually for spring and summer from 2014-2015 in Baker County, Georgia. F25/M38 did not have simultaneous locations due to different GPS location schedules.

Mated pair	Season	Home range overlap	Core area overlap	All locations	Diurnal locations	Nocturnal locations
F36/M34	Spring	91%	88%	36%	48%	25%
	Summer	96%	93%	36%	43%	29%
F39/M37	Spring	95%	96%	44%	70%	20%
	Summer	96%	85%	28%	42%	21%
F42/M40	Spring	88%	85%	19%	30%	16%
	Summer	92%	72%	13%	9%	10%
F25/M38	Spring	95%	78%	-	-	-
	Summer	95%	88%	-	-	-

Table 2.4. Extra-territorial forays of gray foxes from 2014-2015 in Baker County, Georgia.

Animal ID	Sex	Season[1]	Start date / time	End date / time	Total time (h)	Distance from home range boundary (km)	Total path distance (km)
7	M	1	2/6/2015 / 0:30	2/7/2015 / 5:45	29.3	1.6	8.2
9	F	2	6/21/2015 / 4:00	6/21/2015 / 12:00	8	0.8	2.5
9	F	2	6/23/2015 / 22:00	6/24/2015 / 18:00	20	0.8	3
9	F	2	6/29/2015 / 2:00	6/29/2015 / 14:00	12	0.7	2.1
14	F	1	1/23/2015 / 21:15	1/26/2016 / 14:15	65	1	3.9
15	M	4	10/1/2014 / 16:15	10/3/2014 / 00:45	31.5	4.8	14.1
15	M	4	10/9/2014 / 19:15	10/11/2014 / 00:30	29.3	3.6	11.9
15	M	4	10/4/2014 / 22:15	10/6/2014 / 00:15	26	0.9	5.1
20	M	1	1/19/2015 / 18:00	1/20/2015 / 20:00	26	3.4	19.2
20	M	1	1/21/2015 / 6:00	1/22/2015 / 20:00	14	3.1	10.5
20	M	1	1/31/2015 / 4:00	1/31/2015 / 12:00	8	3.1	8.6
20	M	1	1/26/2015 / 22:00	1/27/2015 / 12:00	14	1.6	7.3
20	M	1	1/14/2015 / 18:00	1/15/2015 / 2:00	8	1.3	10.6
21	M	1	1/24/2015 / 16:00	1/25/2015 / 8:00	16	23.1	91.1
21	M	1	1/21/2015 / 22:00	1/22/2015 / 6:00	8	15.4	30.9
21	M	1	1/25/2015 / 12:00	1/25/2015 / 20:00	8	18.8	71.7
21	M	1	1/20/2015 / 18:00	1/21/2015 / 2:00	8	6.6	15
21	M	1	1/20/2015 / 0:00	1/20/2015 / 10:00	10	4.9	17.6
21	M	1	1/19/2015 / 0:00	1/19/2015 / 8:00	8	5.9	15.5
32	F	3	9/12/2015 / 19:30	9/15/2015 / 6:00	58.5	3.5	15.5
32	F	3	9/4/2015 / 19:30	9/6/2015 / 3:00	31.5	1.6	7.4
33	M	3	9/3/2015 / 19:30	9/4/2015 / 4:30	9	1.2	3.8
34	M	3	9/13/2015 / 18:00	9/14/2015 / 3:00	9	0.6	3
36	F	3	9/13/2015 / 18:00	9/14/2015 / 3:00	9	0.9	3
36	F	3	9/24/2015 / 1:30	9/24/2015 / 12:00	10.5	0.6	3.1

[1] Four 3 month seasons (1 = Winter, 2 = Spring, 3 = Summer, 4 = Fall)

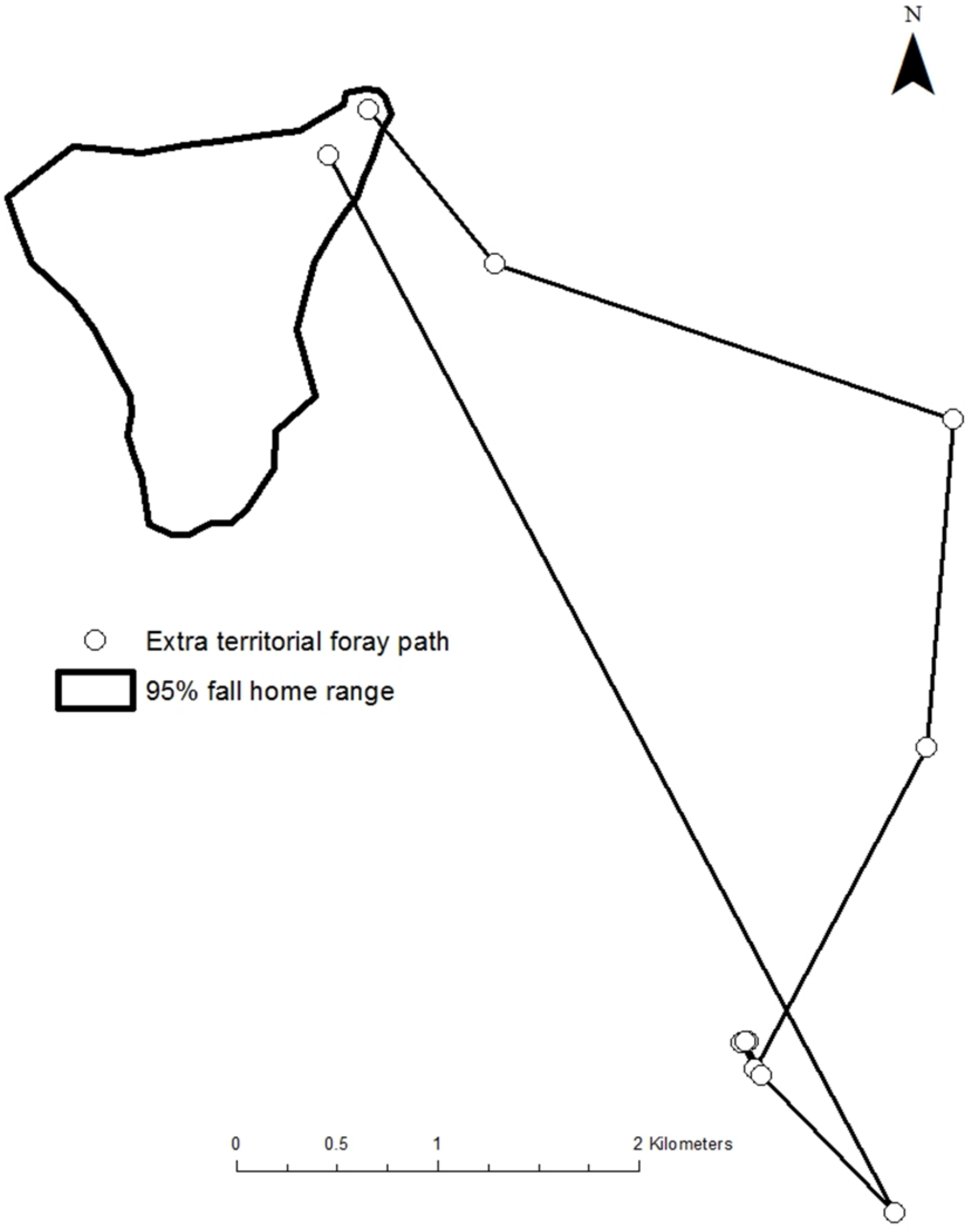

Figure 2.1. Example of an extra-territorial foray. This represents movement of a male gray fox during Sept 2014 in Baker County, Georgia.

CHAPTER 3

HABITAT SELECTION AND DIURNAL REFUGIA OF GRAY FOXES IN SOUTHWESTERN GEORGIA

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ABSTRACT

Understanding habitat selection of gray foxes (*Urocyon cinereoargenteus*) is essential to evaluate their distribution and potential response to land use change. Few studies have evaluated their temporal habitat selection or have explicitly identified habitats used for diurnal refugia. Therefore, we used GPS collars to obtain location data for 34 individual gray foxes (20 males and 14 females) from February 2014 to December 2015 to evaluate temporal (seasonal, diurnal versus nocturnal) habitat selection and selection of diurnal refugia in southwestern Georgia, USA. We analyzed habitat selection at 3 spatial scales, including selection of the home range, selection within the home range, and selection of the core area. Habitat selection was non-random ($P < 0.001$) and consistent among seasons, between day and night, and between sexes ($P > 0.05$) for all scales of analyses. Hardwoods, human structures and roads were selected ($P < 0.05$) at all spatial scales, whereas pines were selected ($P > 0.05$) at random at all levels of selection. Selection of habitats for diurnal refugia did not vary seasonally or by sex ($P > 0.05$), with foxes selecting ($P < 0.05$) mixed pine-hardwood, roads, human structures and hardwood habitats. Gray foxes were observed on the ground while resting, and we found no evidence of gray foxes diurnally resting in trees. Our results suggest that on our study area, gray foxes are an edge species that prefer forests with a hardwood component in areas near human structures and major roads.

INTRODUCTION

Understanding habitat selection of gray foxes (*Urocyon cinereoargenteus*) is essential to understanding their distribution and potential response to land use change. Individuals should select available habitats that maximize fitness [1], which means they must balance predation risk and foraging opportunities [2]. For gray foxes, habitats with abundant and available prey [3], and ample escape cover that reduces probability of encounter with predators [4], [5] should be preferred. An individual land use type may not possess both food and cover in proximity [6]. Additionally, needs for food and cover likely vary temporally, and few studies of habitat selection have evaluated habitat use relative to time of day or activity status (i.e. active or inactive) [7].

Although gray fox habitat selection has been studied in many portions of their geographic range [3], [4], [8], recent technological advancements (i.e., smaller batteries and Global Positioning System (GPS) receivers) in tracking technology have resulted in an ability to address gray fox habitat selection in a more robust manner. GPS technology provides locations with greater precision and accuracy [9], and because automated sampling occurs at programmed intervals, it is now possible to collect sufficient data to robustly compare habitat selection between day and night, and more easily identify and evaluate refugia.

Prior studies reported that gray foxes selected hardwood forests [3], [4], [10], mixed pine-hardwood forests [3], [11], mature pine forests [3], 9-14 year old pine plantations [8], and areas in close proximity to humans [4], [5], [12]. Differences in habitat selection across studies likely reflect site-specific differences in habitat availability, prey abundance [3], forage availability [13], and predator communities [14], [15].

Gray fox habitat use also varies seasonally based on availability of resources. For example, gray foxes consume soft mast, small mammals, birds, and insects [16], all of which vary seasonally in availability [16], [17]. However, seasonal habitat selection by gray foxes is poorly understood, with some studies suggesting seasonal differences in selection [8], [18], whereas others did not [3], [4].

Finer-scale temporal (e.g., nocturnal versus diurnal) assessment of habitat selection may provide greater insight into ecology of wild animals. Studies conducted on gray foxes have generally found them to select habitat types with dense brushy understories during diurnal periods [8], [19], [20], [21], whereas selection during nocturnal periods tends to be more random [8], [19] or within open habitat types [12], [18], [21]. Coyotes (*Canis latrans*) and bobcats (*Lynx rufus*) are known to prey on gray foxes [4], [22]. Therefore, differences between nocturnal and diurnal habitat selection likely reflect balancing predation risk with foraging opportunities [23]. Understanding finer-scale temporal habitat preferences will provide more detailed insight into resource requirements of gray foxes.

Therefore, we used GPS technology to evaluate temporal influences (i.e., diurnal vs. nocturnal, and seasonal) on gray fox habitat selection in southwestern Georgia. We also quantified habitat associated with sites used as diurnal refugia by gray foxes.

MATERIALS AND METHODS

Study Area

We conducted our study at the Joseph W. Jones Ecological Research Center at Ichauway, and surrounding lands in Baker County, Georgia, USA. Topography was mostly flat, with elevation ranging from 27 – 200 m above sea level. Climate was subtropical with hot, humid summers and mild, wet short winters. Temperatures generally ranged from 11 °C – 27.5 °C throughout the year and the average annual precipitation was 131 cm [24].

Ichauway consisted of approximately 12,000 hectares of land in the Southeastern Coastal Plain primarily managed to maintain and restore the longleaf pine (*Pinus palustris*)-wiregrass (*Aristida beyrichiana*) ecosystem. Land use on Ichauway included 7,250 ha of longleaf pine forest, with the remaining 1,920 ha consisting of slash (*P. elliottii*) and loblolly pine (*P. taeda*) forests, mixed pine-hardwood forests and lowland hardwood hammocks [25]. Pine forests were characterized by an open canopy, a sparse midstory, and a dense herbaceous understory. Management practices included prescribed fire on an approximate 2-year rotation; fires limited hardwood encroachment and resulted in a diverse herbaceous understory of wiregrass and other native ground cover species. Hardwood removal through mechanical means, such as roller chopping and logging, was also performed to maintain open canopies and promote herbaceous ground cover. Predator trapping occurred on Ichauway, with removal mainly consisting of opossums (*Didelphis virginiana*), raccoons (*Procyon lotor*), coyotes, bobcats and prior to this study, gray foxes.

In contrast to Ichauway, surrounding lands were dominated by large center pivot agricultural fields with hardwood forests, pine forests, mixed pine-hardwood forests, pasture, and residential areas interspersed throughout. Agricultural fields were primarily planted with corn (*Zea mays*) or cotton (*Gossypium* spp.) in the spring and harvested in the fall. Some agricultural fields were bisected by hedgerows typically made up of hardwoods. Hardwood dominated stands in the surrounding areas were generally not actively managed, whereas some pine stands were managed for timber production or quail hunting.

Trapping

We used MB-450-FOX/OS foot-hold traps (Minnesota Brand, Pennock, MN) and Victor 1.75 laminated offset foothold traps (Oneida Victor, Euclid, OH) baited with lure/bait to capture gray foxes. Trapping was conducted from February 2014-August 2015 throughout Ichauway.

We restrained captured gray foxes using a catch-pole and secured the animal by placing electrical tape around the rostrum and legs. We used a blindfold to reduce animal stress. Weight, age (juvenile or adult), sex, reproductive condition and basic measurements (total body length, tail length, hind-foot length and ear length) were recorded. We used tooth wear, weight [26] and facial markings [27] to determine whether captured animals were adults or juveniles.

Each gray fox was given a unique ear tattoo and/or ear tags in both ears, and adult animals ≥ 3.6 kg were fit with a 180 g GPS Collar (GPS Logger W500, Advanced Telemetry Systems, Isanti, MN). We released collared individuals at the capture site. All trapping and handling procedures were approved by the University of Georgia Institutional Animal Care and Use Committee (IACUC #A2013 07-017-Y1-A0).

GPS Data Collection

Initially, we programmed GPS collars to record a location every 3.25 hours (7-8 locations/day) until they dropped off 1 year after deployment. Beginning in January of 2015, we programmed GPS collars to record a location every 2 hours (12 locations/day) or every 1 hour and 30 minutes (16 locations/day), until cessation of data collection (31 December 2015). We monitored foxes once every week with a 3-element Yagi antenna and hand-held radio telemetry receiver (Wildlife Materials, Carbondale, IL) to determine status (alive/dead) and general location. We downloaded location data when collars were retrieved following collar drop off or when the animal died. For some collars (n = 16), location data were remotely downloaded in the field using a laptop computer and handheld antenna (LairdTech, London, United Kingdom).

Data Analysis and Statistical Methods

For analyses, we considered winter (i.e., breeding season) as 1 Jan – 31 Mar, spring (i.e., denning-early pup-rearing season) as 1 Apr – 30 Jun, summer (i.e., late pup-rearing season) as 1 Jul – 30 Sep, and fall (i.e., dispersal season) as 1 Oct – 31 Dec [20], [26]. Individuals with ≥ 1.5 months of location data within a season were included in that season's sample. For fine-scale temporal data (time of day; hereafter TOD) analysis, night and crepuscular (≤ 1 hour before and after dawn and dusk, respectively) locations were classified as nocturnal locations, while remaining locations were considered diurnal locations. We combined nocturnal and crepuscular time periods because gray foxes are most active during crepuscular and nocturnal time periods [19], [28].

We delineated 9 habitat types (wetland, human structures, grassland/pasture, hardwood, pine, mixed pine-hardwood, shrub/scrub, cultivated crop, and road; Table 3.1) and digitized a landcover database in ArcGIS (ESRI, Redlands, CA) using 2015 NAIP imagery. We used 2011 National Land Cover Data [29] and annually updated landcover data (Jones Center 1997, 2015) to aid in delineation of habitat types.

We analyzed habitat selection and diurnal refugia of gray foxes using the Euclidean distance approach of comparing average distances to each habitat type for gray fox locations relative to expected values [30], [31], [32]. We created distance raster layers (30 × 30 m) for each of the 9 habitat types using the Euclidean Distance Tool in ArcGIS. We calculated the distance to the nearest representative of each habitat type for each cell within the raster layers and from each gray fox location using the Rgui, 3.1.0 (http://cran.r-project.org/) package with R software [33]. For each gray fox, we calculated distance ratios (mean observed/mean expected) for each of the 9 habitat types. If the ratio for a given habitat type was < 1 foxes were found nearer to the habitat than expected, but if > 1 they were found at distances greater than expected [31].

Johnson [34] defined 1st order to be the selection of a geographical range, 2nd order to be the selection of a home range, 3rd order to be the selection within a home range. We examined habitat selection at 3 spatial scales based on a modification of Johnson's [34] criteria: 1st level (selection of a home range), 2nd level (selection within a home range), and 3rd level (selection of a core area).

We used adehabitatHR [35] package with R software [33] to generate 100% minimum convex polygon (MCP) around all gray fox locations, and seasonal 95% and 50% fixed kernel polygons for each individual. We used a rule-based ad hoc method for selecting bandwidth by finding the smallest 0.10 increment of h_{ref} that resulted in a contiguous rather than disjointed fixed kernel polygon, and contained no lacuna within the home range [36]. We sequentially reduced the reference bandwidth (h_{ref}) in increments of 0.10 (0.9 h_{ref}, 0.8 h_{ref}, 0.7 h_{ref}…0.1 h_{ref}) until an estimate fractured into 2 or more polygons, and selected the smallest increment of h_{ref} that resulted in a continuous polygon as the bandwidth.

For 1st level analyses, we used 100% MCP around all locations to determine habitat availability, and used seasonal 95% fixed kernel polygons to determine habitat used. For 2nd level analyses, we used seasonal 95% fixed kernel polygons to determine habitat availability, and used gray fox locations to determine habitat used. For 3rd level analyses, we used seasonal 95% fixed kernel polygons to determine habitat availability, and used seasonal 50% fixed kernel polygons to determine habitat used.

For 1st level analyses, we compared distances of raster cells within the home range to distances of raster cells within the study area to the nearest edge of each habitat type. For 2nd level analyses, we compared distances of gray fox locations within the home range to the distances of raster cells within the home range to the nearest edge of each habitat type. For 3rd level analyses, we compared distances of raster cells within the core area to distances of raster cells within the home range to the nearest edge of each habitat type.

For 1st and 3rd levels of habitat selection, we conducted a MANOVA to assess whether selection varied as a function of sex, season, and an interaction of sex and season. For 2nd level of habitat selection, we conducted a MANOVA to assess whether selection varied as a function of season, sex, TOD, an interaction of sex and season, an interaction of TOD and season, and an interaction of TOD and sex. We evaluated TOD for 2nd level of habitat selection because fox locations could be characterized by TOD. In all analyses, we used univariate t-tests to determine which habitat types were selected, not selected/avoided, or avoided. We ranked habitat types in order of preference based on the value and direction of the t-statistic and used univariate paired t-tests to investigate differences in selection between habitat types for each ranking matrix [31].

To evaluate selection of diurnal refugia, we identified coordinates of consecutive diurnal locations that were ≤ 40 m from each other, and used the mean of these locations to generate diurnal refuge sites. For example, if 2 or more consecutive locations were ≤ 40 m, the UTM coordinates were averaged and treated as a single diurnal refuge site. We used MANOVA to evaluate effects of sex, season and their interaction on gray fox selection of diurnal refugia within their 95% seasonal home ranges. We ranked habitat types in order of preference based on the value and direction of the t-statistic and used univariate paired t-tests to investigate differences in selection between habitat types for each ranking matrix [31]. During diurnal VHF tracking efforts, we periodically homed in on gray foxes and flushed them from their resting site. We recorded whether collared gray foxes were diurnally resting on the ground or in a tree. Homing was conducted no more than once a month on an individual gray fox to limit disturbance.

RESULTS

We collected 56,920 GPS locations from 34 (20M, 14F) individual gray foxes. Overall GPS fix success rate was 86.14%. Although 33 of 34 collared gray foxes from which we collected data were captured on Ichauway, only 14% of locations were recorded on Ichauway.

Habitat Selection

At all levels of selection, season and sex did not interact ($F_{3,51} \leq 1.089$, $P \geq 0.362$) to influence habitat selection, and selection was similar ($F_{3,55} \leq 1.184$, $P \geq 0.259$) across seasons and between sexes ($F_{1,57} \leq 0.878$, $P \geq 0.551$). Habitat selection was non-random ($P < 0.001$) at all levels of selection (Table 3.2).

At the 1st level of selection, gray foxes were found nearer ($P < 0.05$) to hardwood, human structures, road, grassland/pasture and cultivated crop than expected based on availability; distances to other habitats were as expected based on availability ($P > 0.05$). At the 2nd level of selection, season and TOD ($F_{3,110} = 0.831$, $P = 0.710$), and sex and TOD ($F_{1,110} = 0.805$, $P = 0.847$) did not interact to influence selection. Habitat selection did not vary ($F_{1,116} = 1.293$, $P = 0.249$) by TOD. Gray foxes were found nearer ($P < 0.05$) to hardwood, human structures, roads and mixed pine-hardwood than expected based on availability; distances to other habitats were as expected based on availability ($P > 0.05$). At the 3rd level of selection, gray foxes were found nearer ($P < 0.05$) to human structures, road, hardwood, and mixed pine-hardwood than expected based on availability; distances to other habitats were as expected based on availability ($P >$ 0.05).

Diurnal Refugia

Season and sex did not interact ($F_{3,57} = 1.079$, $P = 0.374$) to influence selection of diurnal refugia, and selection was similar across seasons ($F_{3,55} = 1.272$, $P = 0.186$) and sexes ($F_{1,57} = 1.537$, $P = 0.166$). Diurnal refugia selection was non-random ($P < 0.001$) and gray foxes were found nearer ($P < 0.05$) to mixed pine-hardwood, road, human structures, hardwood, and shrub/scrub than expected; distances to other habitats were as expected ($P > 0.05$) (Table 3.3). During diurnal homing, we recorded 108 observations from 28 collared gray foxes. All direct observations were of gray foxes resting on the ground.

DISCUSSION

Similar to other studies [3], [4], we found little variation in season and sex-specific habitat selection in gray foxes. Gray foxes also selected habitats similarly during diurnal and nocturnal periods, suggesting they rested in the same habitat types used for foraging. Further, rankings and selection of habitats associated with diurnal refugia were similar to habitat selection analyses at other spatial scales. Thus, suitable diurnal refugia apparently occurs within habitat types that are also preferred for other resources, but may rely on microhabitat features at a smaller scale than delineated in our study.

Hardwood forests, human structures and roads ranked highly at all 3 spatial scales. Furthermore, although sometimes not significant, observed distances were always less (i.e., all had negative t-statistics except cultivated crop at 2nd level of selection) than expected, providing evidence that edges are important to gray foxes [32]. Edges provide both abundant prey and facilitate foraging [37]. Edges also may provide travel corridors [38] and escape cover from coyotes and bobcats that also use edge habitat [39], [40].

Similar to a prior study on our study site [4], hardwoods were important to gray foxes at all spatial scales. Other studies have suggested gray foxes are closely associated with forests [41] and where available, hardwood forests were consistently preferred [3], [4]. Chamberlain and Leopold [3] found small mammal abundance strongly affected gray fox habitat selection. Therefore, hardwood forests on our study site may have provided sufficient prey for gray foxes. Additionally, many hardwood tree species such as live oak (*Quercus virginiana*), water oak (*Quercus nigra*), and laurel oak (*Quercus laurifolia*) have large sprawling branches that may provide better arboreal escape cover from coyotes than pines. Gray foxes also forage arboreally [42], [43] and hardwood trees may provide opportunities to predate birds, bird nests, insects and squirrels.

Although not selected at the 1st level of selection, gray foxes in our study selected mixed pine-hardwood for 2nd and 3rd levels of selection, suggesting that presence of hardwoods may result in mixed forests being used at fine spatial scales. Additionally, mixed pine-hardwood was selected and ranked 1st for diurnal refugia, suggesting that it may possess the most favorable combination of available refugia and foraging opportunities.

Pine forests were selected at random and were generally poorly ranked (7th-9th) at all levels of selection. Gray foxes may be less common in longleaf pine forests because of high densities of coyotes (1.44 coyotes/km^2; [44]) and bobcats (1.2 bobcats /km^2; [LM Conner, unpublished data]), and a lack of escape cover available in this forest type. Pine forests available to gray foxes on our study site were burned approximately every 2-3 years. Frequent fire limits production of soft mast [45], which is an important food for gray foxes [16]. Thus, lack of soft mast, reduced hardwood cover, and use by potential predators may explain why mature pine was of relatively low importance to gray foxes [19].

Although most gray foxes (97%) were captured on Ichauway, only 14% of locations were recorded on Ichauway. In comparison, Temple et al. [4] reported 35% of total gray fox locations recorded on Ichauway from foxes captured on Ichauway. Removal of mature hardwoods from within the longleaf pine matrix occurred since this previous study [4] was conducted on our study site [46] and may be the reason for this discrepancy. Similarly, in a comparison of habitat selection by raccoons before and after hardwood removal on our study site, hardwood removal resulted in reduced use by raccoons. Chamberlain and Leopold [3] found hardwood stands to be important to gray foxes in pine dominated forests and suggested that the removal of hardwoods in these forests may be detrimental to gray fox populations. Hardwood removal from within pine dominated forests may be an alternative to traditional lethal control in limiting nest predation of ground nesting species by gray foxes.

Areas near human structures were important to gray foxes, similar to previous studies that found foxes selected residential areas [4], [5], [12]. These structures are associated with human activity; as a result, larger predators such as coyotes and bobcats avoid these areas [5], [47], [48], [49], [50]. Additionally, human presence contributes to availability of anthropogenic food sources (e.g., garbage and pet food [12]), which may benefit gray foxes. Therefore, areas near human structures may provide gray foxes with habitat that both reduces the probability of an encounter with predators while providing abundant food. Public roads were also selected at all levels of selection. Public roads differ from private roads on the study area in that they are more developed and have more traffic. Some roads may be less used by bobcats and coyotes because both species use paved roads as territorial boundaries ([5], MJ Cherry, per. comm.) and avoid areas with high levels of human activity [50]. Further, coyote transients frequently use areas along the boundaries of territorial coyote residents [51], [52], [53], and coyote residents avoid roads [40]. Thus, like transient coyotes, gray foxes may use areas near roads to avoid competition and potential predation from resident coyotes. Unfortunately, we were unable to study whether gray foxes selected roads in the absence of human structures because home ranges generally included public roads that had human structures along them. Because individuals will sacrifice feeding effort to reduce predation risk [54], gray fox selection of areas near human structures may be an attempt to avoid predation.

Raccoons regularly seek refuge in mature hardwood trees, and it has been suggested that protection from predators, shade and presence of cavities in these trees contribute to their selection [47], [55]. Some [56] have suggested that gray foxes also rest in trees, but limited evidence exists for such behavior [57]. We found no evidence of gray foxes diurnally resting in trees, yet they were often found in areas with low, sprawling branches that may facilitate climbing. It is possible that foxes abandoned their arboreal refuge when they detected an approaching researcher. Regardless of whether gray foxes routinely seek refuge in tree canopies, we suggest their association with hardwoods provided both foraging opportunities and escape cover.

Red foxes (*Vulpes vulpes*) avoid aggressive encounters with coyotes by maintaining home ranges along the boundaries or outside of coyote territories [58]; thus minimizing spatial overlap with coyotes. In contrast, kit foxes (*Vulpes macrotis*) use underground dens to facilitate escape from aggressive encounters [59]. Our data suggest that gray foxes may employ strategies of both red and kit foxes. Similar to kit foxes, gray foxes may use habitat elements (i.e. dense cover and trees with branch structure that facilitates climbing) to share space with coyotes [5],

[15]. They may also use developed roads and areas near human dwellings to minimize spatial overlap with coyotes. Interestingly, gray foxes can persist in treeless landscapes with few human dwellings, but they may suffer higher mortality rates from coyotes in these environments [22], [60].

Our habitat selection results differed little from those of an earlier study [4]. However, rankings of individual habitats differed slightly. Overall, cultivated cropland was less important and mixed pine-hardwood was more important than during the earlier study. At the 2nd level of selection, pine was less important, and at the 3rd level of selection, human dwellings were more important than reported in the earlier study. These minor differences between our study and Temple et al. [4] may be due to the GPS technology employed in our study [9] or it may be due to changes in predator abundance or resource availability that may have occurred between the two studies. Investigating gray fox habitat selection in the absence of their predators would provide valuable information regarding influences of top-down versus bottom-up influences on habitats selected by gray foxes.

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Table 3.1. Descriptions, area (hectares), and proportion of the total landscape of the 9 habitat types delineated within the gray fox study area in Baker County, Georgia from 2014-2015.

Habitat Type	Description	Area	Proportion
Wetland	Depressional wetlands, swamps, creeks	1109	0.04
Human Structure	Residential areas, farm buildings, sheds	510	0.02
Grassland\Pasture	Pasture, fields, non-industrial agriculture	2488	0.09
Hardwood	Overstory dominated by hardwoods	3031	0.11
Pine	Overstory dominated by pines	7443	0.28
Mixed Pine\Hardwood	30% < Hardwood < 70%	3638	0.14
Shrub\Scrub	Overstory dominated by shrubs	1347	0.05
Cultivated Crop	Center pivot industrial agriculture	6909	0.26
Road	Public roads	419	0.02

Table 3.2. Habitat types ranked in order of preference (1 most preferred-9 least preferred) at 3 spatial scales by gray foxes from 2014-2015 in Baker County, Georgia. Significant differences (P < 0.05) among ranks are indicated by different letters. S = Selected, NS = Not Selected (used as expected).

	1st level[a]				2nd level[b]				3rd level[c]			
Habitat Type	t	P	Conclusion	Rank	t	P	Conclusion	Rank	t	P	Conclusion	Rank
Hardwood	-26.49	<0.001	S	1A	-3.61	<0.001	S	1A	-3.36	0.001	S	3A
Human Structures	-19.76	<0.001	S	2A	-3.27	0.002	S	2A,B	-3.61	<0.001	S	1A
Road	-12.66	<0.001	S	3A	-3.18	0.002	S	3A,B	-3.43	<0.001	S	2A
Mixed	-0.61	0.55	NS	8D	-2.23	0.030	S	4A,B,C	-3.34	0.001	S	4A
Grassland / Pasture	-9.23	<0.001	S	4B	-1.22	0.230	NS	6B,C	-0.79	0.430	NS	8B
Cultivated Crop	-6.79	<0.001	S	5C	0.23	0.822	NS	9B,C	-0.32	0.756	NS	9B
Pine	-1.65	0.10	NS	7D	-0.83	0.410	NS	7B,C	-1.32	0.190	NS	7A,B
Shrub / Scrub	-2.24	0.03	S	6C,D	-1.63	0.110	NS	5A,B,C	-1.86	0.069	NS	5A,B
Wetland	-0.24	0.812	NS	9D	-0.79	0.433	NS	8C	-1.44	0.155	NS	6A,B

[a] Selection of a home range

[b] Selection within a home range

[c] Selection of a core area

Table 3.3. Habitat types ranked in order of preference (1 most preferred-9 least preferred) for selection of diurnal refugia by gray foxes from 2014–2015 in Baker County, Georgia. Significant differences (*P* < 0.05) among ranks are indicated by different letters. S = Selected, NS = Not Selected (used as expected).

Habitat Type	t	P	Conclusion	Rank
Mixed	-2.81	0.006	S	1A
Road	-2.69	0.009	S	2A
Human Structures	-2.47	0.016	S	3A
Hardwood	-2.40	0.020	S	4A
Shrub / Scrub	-2.12	0.038	S	5A
Wetland	-1.50	0.140	NS	6A
Grassland / Pasture	-0.87	0.385	NS	7A
Pine	-0.74	0.460	NS	8A
Cultivated Crop	0.06	0.950	NS	9A

CHAPTER 4

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

We found that home ranges and core areas of gray fox mated pair members overlapped extensively, and that pair members frequently interacted with each other. These findings provide further evidence that gray foxes form strong pair bonds and that social behavior is important to gray fox ecology. Because pups rely on rearing from both sexes, harvesting adult gray foxes during the denning season may negatively influence recruitment into the population by causing decreased pup survival (Chamberlain and Leopold 2000). Future studies should investigate how the removal of adult male or female gray foxes in spring affects the survival of pups.

Ours was the first study to investigate extra-territorial forays of gray foxes. Although gray foxes are socially monogamous, Weston Glenn et al. (2009) found DNA evidence of multiple paternity in some gray fox litters. All extra-territorial forays in the winter season, which accounted for 13 of 25 total forays for the entire the study, occurred within a 2-week period during the peak breeding season for gray foxes in southern Georgia (Wood 1958). Males accounted for all except 1 of these winter forays, which suggests some males seek to mate with estrous females in neighboring territories. Our findings suggest that extra-territorial forays by males during the breeding season may be to provide opportunities for males to breed with neighboring females, resulting in the possibility of multiple paternity in litters (Weston Glenn et al. 2009).

Wildlife managers interested in managing gray fox populations should understand the importance of forests, particularly hardwoods. Hardwood patches in an agriculturally dominated landscape (Temple et al. 2010), hardwood hammocks in a pine dominated forest (Chamberlain and Leopold 2000) and riparian hardwoods (Fuller 1978) are all important to gray foxes. Our research and other studies (Harrison 1997, Chamberlain and Leopold 2000, Temple et al. 2010) suggest that the removal and/or conversion of hardwood forests to pine forests or agricultural fields may negatively affect gray foxes. Because we found gray foxes to diurnally and nocturnally prefer hardwoods, these forests may fulfill both food and cover requirements. Hardwood removal from within pine dominated forests may be an alternative to traditional lethal control in limiting nest predation of ground nesting species by raccoons (Kirby 2015) and gray foxes. Removal of mature hardwood trees within the pine-matrix alters space use patterns of raccoons possibly by limiting diurnal refuge sites (Kirby 2015). Because our findings suggest gray foxes don’t readily use trees as diurnal refuge sites, there are likely other reasons why hardwood forests are important them.

Our research suggests that gray foxes may benefit from the lack of predators and/or abundance of food resources around anthropogenic structures in a rural setting. Harrison (1997) found a threshold for gray fox avoidance of residential areas between 50 and 125 residences/km^2. Gray foxes should benefit from anthropogenic structures as long as residential density is low (< 50 residences/km^2) and there is sufficient forest cover adjacent to these structures.

Gray foxes prefer dense brushy understories (Nicholson 1982, Haroldson and Fritzell 1984, Sawyer and Fendley 1994) for diurnal refugia. We found diurnal refugia selection to be similar to our habitat selection results, except mixed pine-hardwood was ranked higher for diurnal refugia. Mixed pine-hardwood forests may contain an abundance of areas with dense brushy understories.

Our results demonstrate that home ranges of gray fox mated pairs overlap extensively, whereas overlap of non-mated neighboring foxes is minimal. For species like gray foxes that form pair-bonds, maintain exclusive territories, and share similar space with their mates, mean home range sizes could be used to estimate maximum adult population density (Tucker et al. 1993, Burch et al. 2005). Results using this method are more accurate if the species is continuously distributed across the landscape. On our study site, cultivated cropland and pine forests were the dominant habitat types accounting for 54% of the total area, but were of low relative importance to gray foxes. Conversely, hardwood forests, human structures, roads, and mixed pine-hardwood forests accounted for just 29% of the total area, and were of high relative importance to gray foxes. Selection of habitat types that were relatively rare on the landscape suggests gray foxes were likely not continuously distributed on our study site.

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