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Despite numerous studies estimating gray fox *Urocyon cinereoargenteus* home range sizes, there have been few studies to evaluate more nuanced space use patterns; thus little is known about gray fox spatial ecology beyond estimates of home range size. We used GPS-technology to track 34 gray foxes (20 males and 14 females) from February 2014 until December 2015 in southwestern Georgia, USA. Home range sizes were similar among seasons ($p > 0.05$), but core area sizes were smaller during spring than during winter and summer ($p < 0.05$). As would be expected, home range overlap was much greater between mated pairs than among neighboring animals and core area overlap among neighbors did not occur. Members of a mated pair apparently interacted frequently, with 29.4% of all simultaneous locations occurring within 40 m of each other. Members of mated pairs interacted more diurnally during spring (49.9%) which is concurrent with denning, than during summer (31.5%), while nocturnal interactions were similar during spring (18.0%) and summer (19.3%). We recorded 25 extra-territorial forays from 10 of 26 gray foxes. Three male foxes were responsible for nearly half (12) of these forays. Because these forays took place during the breeding season, we suggest males may have been seeking extra-pair copulations.

Recent advances in tracking technology, such as Global Positioning Systems (GPS), have revolutionized our understanding of animal ecology, challenged longstanding paradigms, and provided the opportunity to pursue new and exciting questions that were not possible with conventional tracking systems (Kays et al. 2015). These technological advancements facilitated the emergence of the discipline of movement ecology which has broadened our understanding of numerous spatial phenomena and processes (Nathan et al. 2008), such as intraspecific interactions. Automated high frequency tracking schedules have revealed often surprising behaviors that may provide a mechanistic explanation for fundamental concepts in ecology such as territoriality, mating systems, and dispersal. The gray fox *Urocyon cinereoargenteus* is an example of a species that to our knowledge has previously only been studied using conventional tracking techniques and consequently, information regarding the nuanced nature of intraspecific interactions is sparse and convoluted. For example, there is conflicting information in the literature on the basic biology of the species, such as whether or not breeding pairs exhibit territorial behavior (Hovis et al. 1984, Nicholson et al. 1985, Tucker et al. 1993, Chamberlain and Leopold 2000).

Annual 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, there is much individual variation in home range size within a given study area (Haroldson and Fritzell 1984, Sawyer and Fendley 1990, Tucker et al. 1993). Not surprisingly, gray fox home ranges also vary seasonally (Sawyer and Fendley 1990, Chamberlain and Leopold 2000, Temple et al. 2010). Home ranges tend to be largest during breeding season (Follman 1973, Sawyer and Fendley 1990, Chamberlain and Leopold 2000) when pup rearing responsibilities have diminished and resource abundance may be low (Nicholson 1982, Temple et al. 2010), intermediate during pup-rearing season (Jeselnik 1981, Sawyer and Fendley 1990), and smallest while denning when adult movements are restricted as a result for caring for young (Jeselnik 1981, Nicholson 1982, Sawyer and Fendley 1990).

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).

Adult gray foxes are socially monogamous and form pair-bonds (Nicholson et al. 1985, Tucker et al. 1993, Chamberlain and Leopold 2000) which contribute to the spatial behavior of each pair member. Haroldson and Fritzell (1984) reported on a single mated pair that was found together 13.5% of the time, and Chamberlain and Leopold (2000) found mated gray foxes closer than expected to each other within their home ranges. Interactions among members of a mated pair may differ at fine temporal scales (Haroldson and Fritzell 1984, Farias et al. 2012). Understanding how mated pair interactions vary over time may allow inference regarding foraging and pup-rearing roles of pair-bonded gray foxes.

Hovis et al. (1984) suggested that gray foxes were not territorial, but more recent studies suggest otherwise. Because gray foxes are socially monogamous, spatial overlap is common between adults in a pair-bond and these pairs maintain exclusive territories (Nicholson et al. 1985, Tucker et al. 1993, Chamberlain and Leopold 2000). Researchers suggest that incidence of overlap among non-paired individuals is likely the result of relatedness among overlapping individuals (Tucker et al. 1993, Chamberlain and Leopold 2000).

Extra-territorial forays (i.e. temporary movements outside of an established home range) 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). In these species, extra-territorial forays may be motivated by breeding opportunities (Soulsbury et al. 2011), exploration prior to 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). 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 insufficient sampling intensity resulting from traditional monitoring methods (Kays et al. 2015).

Clearly, prior research has provided evidence that gray foxes form pair-bonds; however, there is less evidence regarding the degree of territoriality exhibited by bonded pairs. There are even fewer data available to quantify interactions among members of a mated-pair and to infer why specific interactions occur. Finally, extra-territorial forays may contribute substantively to population processes, but occurrence of these forays has not been documented or quantified in gray foxes. Therefore, we used GPS tracking technology to provide additional estimates of gray fox home ranges and to more importantly, examine territoriality and spatial interactions of pair-bonded animals, and to assess occurrence of extra-territorial forays in gray foxes. This study represents the first use of GPS technology to study the spatial ecology of gray foxes.

Material 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 a.s.l. Climate was subtropical with hot, humid summers and mild, wet short winters. Temperatures generally ranged from 11–27.5°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 cover on Ichauway included 7250 ha of longleaf pine forest, with the remaining 1920 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 two-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. In an attempt to reduce northern bobwhite *Colinus virginianus* nest predation, 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. We considered impacts of prior gray fox removals and removal of conspecifics to be negligible due to rapid immigration and recolonization (Conner and Morris 2015). Although gray foxes were not removed during our study, a canine distemper outbreak substantially reduced gray fox populations during the first year of our study. By the second year of the study, we considered the gray fox population to have recovered from the outbreak.

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 peanuts *Arachis hypogaea*, 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 dense, immature, and 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) 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.

Data collection and analyses

Initially, we programmed GPS collars to record a location every 3.25 h (7–8 locations day^{-1}) until a remote drop-off mechanism released the collar after a year deployment. Beginning in January 2015, we programmed GPS collars to record a location every two h (12 locations day^{-1}) or every one h and 30 min (16 locations day^{-1}) until cessation of data collection (31 December 2015). 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).

For analyses, we considered winter (i.e. breeding season) as 1 January – 31 March, spring (i.e. denning-early pup-rearing season) as 1 April – 30 June, summer (i.e. late pup-rearing season) as 1 July – 30 September, and fall (i.e. dispersal season) as 1 October – 31 December (Wood 1958, Nicholson et al. 1985). Individuals with ≥ 1.5 months of location data within a season were included in analyses for that season.

We generated seasonal 95% (home range) and 50% (core area) fixed kernel utilization distributions (KUD) polygons using adehabitatHR (Calenge 2006) package with R software (<www.r-project.org>). We used a rule-based ad hoc method to select bandwidth by finding the smallest 0.10 increment of h_{ref} (i.e. the smoothing parameter controlling bandwidth) 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 two 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.

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 then 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 percent overlap 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 $>50\%$ core area overlap indices were assumed to be mated, whereas lesser indices were considered representative of neighboring animals. We conducted ANOVA to determine if home range and core area overlap of mated pairs differed seasonally.

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 interacting pairs. We estimated the proportion of time paired foxes were together seasonally 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 frequency of mated pair interactions differed temporally, we used χ^2 contingency tests to determine if mated pair interaction frequency differed across seasons, time-of-day (TOD), TOD within seasons and TOD across seasons. For these analyses, night and crepuscular (≤ 1 h before and after dawn and dusk, respectively) locations were considered as nocturnal locations, whereas all other locations were used as diurnal locations.

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

Results

During 2014–2015, we collected 56 920 GPS locations from 34 (2 0M, 14 F) individual gray foxes. Overall GPS fix success rate was 86.14%. However, data were inadequate to for eight animals. Thus, we calculated seasonal home ranges and core areas for 26 (15 M, 11 F) individual gray foxes (Supplementary material Appendix 1 Table A1). There was no significant interaction between sex and season for home range size ($F_{3,44} = 0.30$, $p = 0.82$) or core area size ($F_{3,44} = 1.49$,

Table 1. Seasonal home range (95% kernel utilization distribution contour) and core area (50% kernel utilization distribution contour) averages (ha) and standard errors for male and female gray foxes 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)

[a]Winter = 1 January – 31 March, spring = 1 April – 30 June, summer = 1 July – 30 September, fall = 1 October – 31 December.

$p = 0.23$). Core area size varied ($F_{3,44} = 4.79$, $p = 0.01$) seasonally, but home range size did not ($F_{3,44} = 0.93$, $p = 0.43$). Tukey's multiple comparison tests revealed that core areas were smaller during spring than during winter ($p = 0.02$) and summer ($p = 0.01$; Table 1).

We monitored four putative mated pairs during spring and summer and none during fall or winter (Fig. 2). Home range ($F_{1,6} = 1.65$, $p = 0.25$) and core area ($F_{1,6} = 0.15$, $p = 0.71$) overlap for members of mated pairs did not vary between spring and summer seasons (Table 2). We monitored three mated pairs that had simultaneous locations during spring and summer (Table 3). Overall, simultaneous locations of paired foxes averaged 340 ± 5.2 m (mean ± SE) between animals, with 29.4 ± 0.1% of locations occurring together (i.e. ≤ 40 m between locations). Mated pairs were more frequently together during spring (34.8 ± 0.1%) than summer (25.7 ± 0.1%; $\chi^2 = 67.77$, df = 1, $p < 0.01$) and diurnally (40.3 ± 0.1%) than nocturnally (20.18 ± 0.03%; $\chi^2 = 400.13$, df = 1, $p < 0.01$).

We monitored three male–male and two male–female sets of neighboring foxes (i.e. foxes with adjacent or overlapping home ranges but core area overlap < 50%). Summer (47%) and winter (9%) home range overlap only occurred for one male–male pair. Spring home range overlap occurred for two male–female pairs (2 and 11%) and for two male–male pairs (25 and 28%). We monitored no neighboring females; thus we do not know if female–female home range overlap occurred. No neighboring foxes had overlapping core areas.

We identified 25 (17 M, 8 F) extra-territorial forays (Fig. 1) from 10 (6 M, 4 F) of 26 (15 M, 11 F) individual gray foxes (Table 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).

Table 3. Number of locations together (i.e. < 40 m between simultaneous locations) and total number of locations obtained on gray fox mated pairs tracked during spring (1 April – 30 June) and summer (1 July – 30 September) of 2015. Data are further divided based on time-of-day (diurnal = > 1 h after sunrise and < 1 h before sunset) and nocturnal locations.

Pair	Season	Time	Together	Total
M34 and F36	spring	diurnal	285 (48%)	594
M34 and F36	spring	nocturnal	138 (24%)	575
M34 and F36	summer	iurnal	256 (43%)	591
M34 and F36	summer	octurnal	173 (29%)	591
M37 and F39	spring	diurnal	396 (70%)	569
M37 and F39	spring	nocturnal	114 (20%)	578
M37 and F39	summer	diurnal	126 (42%)	297
M37 and F39	summer	nocturnal	118 (21%)	572
M40 and F42	spring	diurnal	147 (30%)	495
M40 and F42	spring	nocturnal	45 (9%)	492
M40 and F42	summer	diurnal	109 (16%)	671
M40 and F42	summer	nocturnal	65 (10%)	680

[a]spring = 1 April – 30 June; summer = 1 July – 30 September.

Most forays occurred during winter when three of eight monitored male foxes went on 12 forays (one for six forays, one for five forays and one for one foray). A female also took a foray during winter. All winter forays occurred between 19 January and 7 February 2015. 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 was 65 h for the lone female, whereas total distance traveled on a foray in winter averaged 25.5 ± 7.9 km (range = 7.3–91.1 km) for males and was 3.9 km for the female foray.

Gray foxes went on six forays during summer; four of these were the results of movements of two of nine monitored females. The remaining two summer forays resulted from the movements of two of eight males. All summer forays occurred between 3 and 24 Sept 2015. Two forays were the result of a mated pair that forayed together from 13 to 14 September 2015. Mean maximum distance from the home range boundary during 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. Both male summer forays were 9 h, and female forays averaged 27.4 ± 11.6 h (range = 9–58.5 h). Total distance traveled while on foray in summer averaged 3.4 ± 0.4 km (range = 3–3.8 km) for males and 7.3 ± 2.9 km (range = 3–15.5 km) for females. During spring we monitored 23 (13 M, 10 F) gray foxes, one female took three separate forays between 21 June and 29 June 2015. We monitored seven (2 M, 5 F) foxes during fall, and one male took three forays between 1 and 11 October 2014 (Fig. 1).

Table 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 (F 25/M 38) did not have simultaneous locations due to different GPS location schedules.

Season[a]	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%

[a] Spring = 1 April – 30 June, summer = 1 July – 30 September.

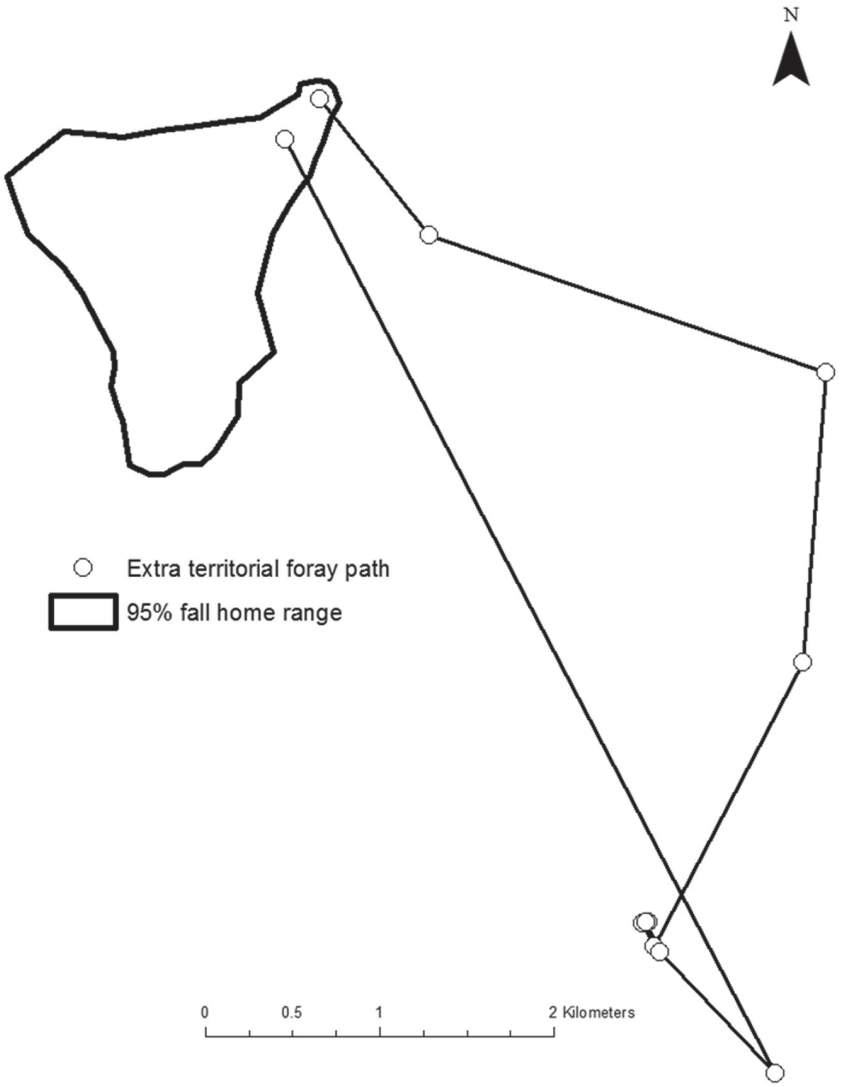

Figure 1. Example of an extra-territorial foray. This represents movement of a male gray fox from 1 to 3 October 2014 in Baker County, Georgia.

Discussion

Our novel use of GPS technology revealed aspects of the spatial ecology of foxes that were previously unknown. We provide new data regarding the spatial ecology of mated pairs and the arrangement of home ranges that are likely important to the social interactions of foxes. In addition, this study is the first to document extra territorial forays in gray foxes. Extra territorial forays are known to occur in multiple canid species (Messier 1985, Nicholson et al. 2007, Soulsbury et al. 2011), but the drivers of this phenomenon remain largely unknown. It is often assumed that extra territorial forays are associated with increasing breeding opportunities or mate selection. On one hand, our results support that premise in that the majority of extra territorial forays occurred during the breeding season. However, we documented forays during all seasons and even document a mated pair that embarked on a foray together, suggesting that there are motivations for forays that transcend breeding.

Our home range size estimates were larger than estimates from a previous study conducted on our study site (Temple et al. 2010); differences in home range size estimates may have been due to methodological differences between studies. Although both studies used fixed kernel densities to estimate home range area, we used an ad hoc method to determine band width because it outperforms the least-squares cross-validation method (Kie 2013) used by Temple et al. (2010). We also used GPS tracking technology, as opposed to VHF as used in the earlier study, which permitted greater sampling intensity and may have resulted in larger home range estimates (Seaman et al. 1999, Powell 2000, Girard et al. 2002, Mills et al. 2006, Towerton et al. 2016). In an extreme example, Towerton et al. (2016) observed red fox home range sizes generated using GPS to be an order of magnitude larger than those generated using VHF technology. In addition to methodological explanations for differences in home range size estimates between the studies, differences may have been influenced by differences in gray fox population size. Studies conducted on

Table 4. Extra-territorial forays of gray foxes from 2014–2015 in Baker County, Georgia.

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

[a]W = 1 January – 31 March, S = 1 April – 30 June, SU = 1 July – 30 September, F = 1 October – 31 December.

other species have recorded larger home range sizes when population density is lower due to less intraspecific competition for resources (Macdonald and Bacon 1982, Ostfeld 1985). A canine distemper outbreak during 2014 (Brent Howze, Georgia Dept. of Natural Resources, pers. comm.) substantially reduced the gray fox population on our study area. If presence of neighboring territory holders affects gray fox home range size, this disease outbreak may have resulted in larger home range estimates.

Although we failed to detect seasonal differences in home range sizes, core areas were smaller during spring (i.e. denning and early pup-rearing seasons). 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). 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 associated with 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. 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 and share in pup-rearing activities (Tucker et al. 1993. Chamberlain and Leopold 2000). Although social monogamy as a mating system is rare in most mammals, it is common in canids (Geffen et al. 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 pairs 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, suggesting gray foxes are territorial and exclude other foxes from at least a portion of pair's home range.

We found members of mated pairs together over twice as often as previously reported, 29.4% versus 13.5% in Haroldson and Fritzell (1984), suggesting gray fox mated pairs may travel, forage, and rest together more than we previously realized. This observation was likely made possible by increased sampling frequency and accuracy provided by GPS technology; older VHF technology lacks spatial accuracy and obtaining simultaneous locations on two or more animals using VHF technology is logistically very difficult. Lack of accuracy and inability to obtain simultaneous locations would lead to a biased estimate, suggesting animals were separated more than they were. Mated pairs interacted more during spring than summer, but this difference was mainly driven by a higher frequency of diurnal interactions during spring (49.9% during spring and 31.5% during summer), while the frequency of nocturnal interactions (18.1% during spring and 19.3% during summer) was similar across both seasons. Paternal care is common in canids (Malcolm 1985), and because mated pairs frequently rested together during the period when pups would be restricted to areas near den sites, we suggest our data provides further

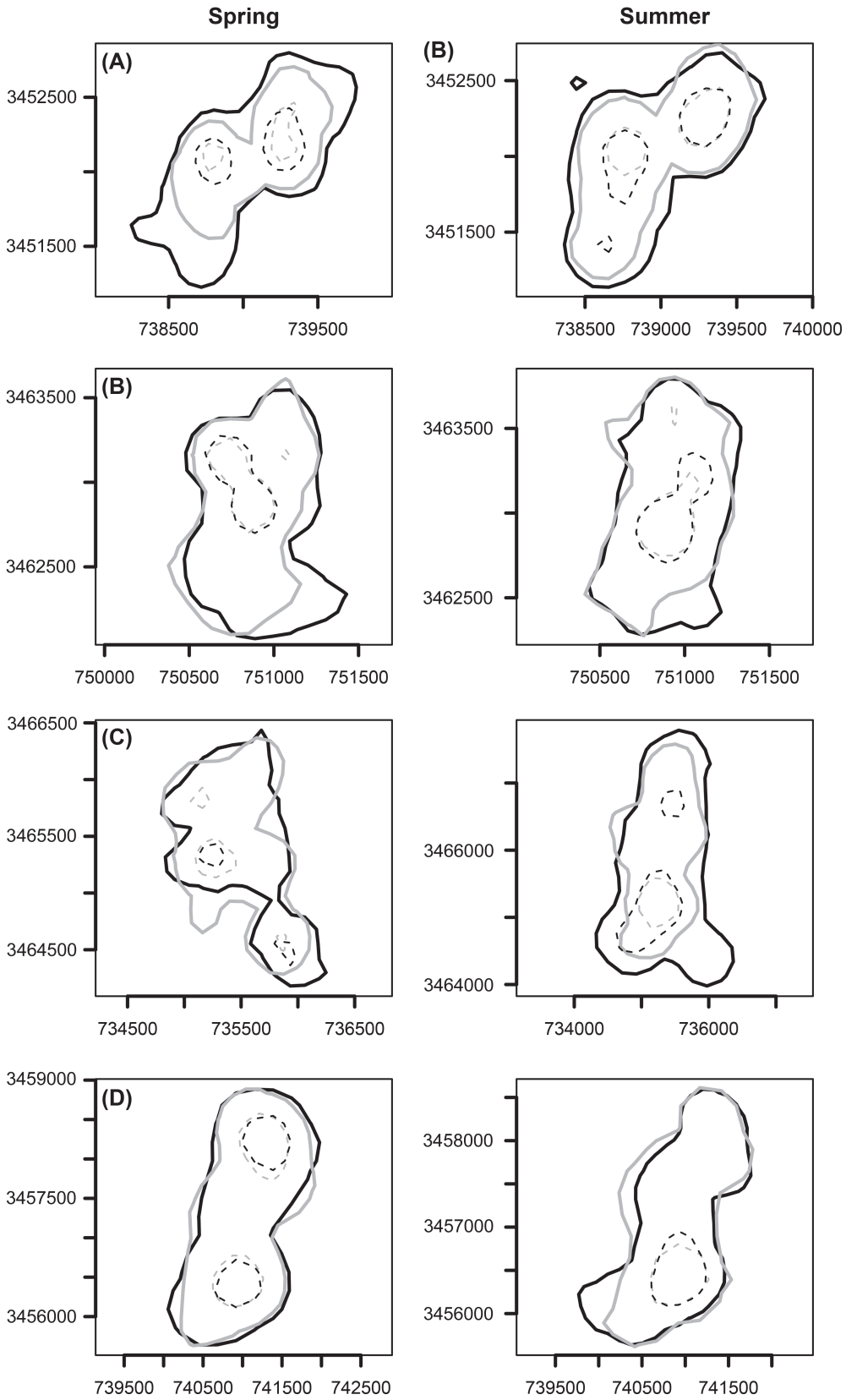

Figure 2. Home ranges and core areas for socially monogamous pairs of gray foxes on the Joseph W. Jones Ecological Research Center during 2014–2015. Each row represents a unique pair of foxes (A = M 34, F 36; B = M 37, F 39; C = M 40, F 42; D = M 38, F 25). Solid lines and dashed lines represent 95% and 50% isopleths estimated using an adaptive kernel density model respectively. Black lines represent males and gray lines represent females. Axis units are in meters.

evidence of paternal care in gray foxes (Nicholson et al. 1985). Even with fewer pup-rearing responsibilities in summer, mated pairs often rested together during daylight hours more than they traveled together at night. Resting together during diurnal periods may help strengthen pair-bonds and be effective as an antipredator strategy (Mysterud and Østbye 1995); whereas foraging independently at night would be advantageous for pair members when hunting small mammals (Ralls and White 2003). Foraging independently may also permit one parent to remain with young while the other forages (Maas and Macdonald 2004).

Traveling outside of an established home range through unfamiliar areas is both risky and energetically costly (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). Extra-territorial forays occurred during all seasons and at least one mated pair forayed together; thus, we found ample evidence that forays occur for reasons other than increasing breeding opportunity. However, more extra-territorial forays occurred during winter than any other season, and all winter forays corresponded 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, suggesting some degree of infidelity.

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 another large male (4.4 kg) were responsible for 11 of the 13 total forays during breeding season. Seeking extra-pair copulations with neighboring females may be a more successful mating strategy for larger males (Cavallini 1998, Iossa et al. 2008) and lead to increased 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, one female fox made a foray just outside of her home range during breeding. Instead of passively playing a role in extra-pair copulations, females of other socially monogamous species may seek out copulations with neighboring males that possess higher genetic fitness than their pair-bonded mate (Smith 1988, Kempenaers et al. 1992). Genetic studies of paternity would provide useful insight into the breeding system in this species.

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 movements were 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 nine 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 pups would be restricted to areas near den sites. Our results also suggest mates form strong pair-bonds through spring and summer, and that males invest in rearing pups.

Sympatric coyotes and gray foxes use similar resources, overlapping in diet and space use (Neale and Sacks 2001, Chamberlain and Leopold 2005). However, Temple et al. (2010) noted that gray foxes were located in areas that provided decreased threat of predation from coyotes. Similarly, spatial distribution of gray foxes during our study area appears to be relegated to 'fringe habitats' typically avoided by coyotes. Further research should explore how prey abundance, competition with other predators, and predation risk influence gray fox ecology. Coyote–gray fox interactions may be particularly interesting to investigate because anecdotal evidence from our study area suggests that gray fox populations are much lower now than they were in the 1960s prior to coyote establishment.

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Supplementary material (available online as Appendix wlb-00326 at <www.wildlifebiology.org/appendix/wlb-00326>). Appendix 1. Excel file containing gray fox ID number, sex, ID number of fox's mate, year monitored, winter (1 January – 31 March) tracking period, number of days tracked during winter, number of GPS locations obtained during winter, 95% fixed kernel home range size (ha) during the winter, 50% fixed kernel home range size during winter, winter ETFs (extra-territorial forays), spring (1 April – 30 June) tracking period, number of days tracked during spring, number of GPS locations obtained during spring, 95% fixed kernel home range size during spring, 50% fixed kernel home range size during spring, spring ETFs, summer l (1 July – 30 September) tracking period, number of days tracked during summer, number of GPS locations during summer, 95% fixed kernel home range size during summer, 50% fixed kernel home range size during summer, summer ETFs, fall (1 October – 31 December) tracking period, number of days tracked during fall, number of GPS locations obtained during fall, 95% fixed kernel home range size during fall, 50% fixed home range size during fall, and fall ETFs.