JULIE LYNN MURRAY WESTON
Demographics of a Protected Population of Gray Foxes (*Urocyon cinereoargenteus*) in
    South Carolina
(Under the Direction of I. LEHR BRISBIN, JR.)

Nearly all data published on gray fox demographics, such as density, age structure, sex ratio, and reproduction, come from populations subject to harvest pressure, while virtually nothing is known of these demographic parameters in unharvested populations. This study was initiated to explore the demographics of a protected population of gray foxes located on the U.S. Department of Energy's Savannah River Site, near Aiken, South Carolina. Foxes ($n = 75$) were trapped January through March from 1998-2000. Results indicated a high-density population of 0.97 foxes/km^2. Age structure of the current SRS gray fox population differed significantly from the age structure at the same site from 1954-56 ($\chi^2 = 30.38$, *d.f.* $= 2$, $P < 0.001$). The greatest numbers of foxes were in the 10-month-old (37.2%) and $\geq$34-month-old (52.6%) age classes while the least number of foxes were in the 22-month-old age class (10.3%). The sex ratio was biased toward females (58.7%). Although litter size (3.6 young/litter) was smaller than in some other populations, the percentage of barren females was 11.1%, which is higher than most other populations. Although immigration and emigration could not be quantified, the results suggest this population could serve as a source for surrounding gray fox populations.

INDEX WORDS: Age structure, Demographics, Gray Fox, Home Range,
                      Reproduction, Survival, *Urocyon cinereoargenteus*

DEMOGRAPHICS OF A PROTECTED POPULATION OF

GRAY FOXES (*UROCYON CINEREOARGENTEUS*)

IN SOUTH CAROLINA

by

JULIE LYNN MURRAY WESTON

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Approved:

Major Professor: I. Lehr Brisbin, Jr.

Committee: John Carroll
              Steven Castleberry
              Robert Cooper
              Michael Smith

Electronic Version Approved:

Gordhan L. Patel
Dean of the Graduate School
The University of Georgia
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DEDICATION

I would like to dedicate this dissertation to my husband, Michael D. Weston, for immeasurable love and support during this work. I have been truly blessed.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Nearly all data published on gray fox demographics come from populations subject to harvest pressure, while virtually nothing is known of those same parameters under the absence of harvest. Without this baseline for comparison, population biologists are unable to fully understand how gray fox populations respond to harvest pressure. Because absence of harvest is one aspect of habitat quality, and because habitat quality is known to influence survival and reproduction (Van Horne 1983), populations living without harvest pressure are likely to exhibit demographic parameters different from their harvested counterparts. The study was undertaken to quantify the demographics of just such a protected population of gray foxes, and to compare those demographics to other populations in the literature which were exposed to harvest.

Gray foxes occur in a wide variety of habitats across the United States, being present everywhere except the northwestern U.S. and the Great Plains (Fritzell 1987). They experience harvest pressure for their fur, and sport hunting with hounds is popular, particularly in the southeast. Most of the published data on gray fox demographics has come from an examination of those foxes caught and killed by trappers. To obtain the best baseline for comparison with harvested populations, gray foxes also should be studied under conditions believed to be the most favorable to their survival and reproduction. Van Horne (1983) defines habitat quality as a combination of 1) density, 2) mean individual survival probability, and 3) mean expectation of future offspring, such that habitat quality is high when these factors are high.

To meet these conditions, gray foxes first require appropriate habitat. In the eastern portion of their range, Fritzell (1982) reported that gray foxes selectively utilized deciduous forest, especially when interspersed with old fields. Trapp (1973) and Fuller (1978) reported that western gray foxes avoided agricultural areas. Fuller (1978) also

reported that gray foxes selected riparian habitats. In South Carolina studies, gray foxes preferred 5-14 year old pine habitats (Sawyer 1988) as well as mixed pine hardwood (Jeselnik 1981).

This type of mixed pine habitat is unsuitable for red foxes (*Vulpes vulpes*), which prefer open agricultural land and old fields (Follmann 1973; Trapp and Hallberg 1975). Because gray foxes and red foxes are similar-sized canids, they are potential competitors for the same food and shelter resources (Follmann 1973) in areas where they coexist. Another favorable condition for the gray fox, then, is an absence of competition from red foxes.

Presence of coyotes is another consideration. Their effect on gray foxes is largely unknown, but most researchers do not believe coyotes are a significant threat to gray fox populations (Sargeant 1982; Small 1971; Wooding 1984) unless the coyote population is dense (Davis 1974). In part this may be due to coyotes selecting larger prey than gray foxes select (Fritzell 1987; Voigt and Berg 1987), as well as the observation that coyotes prefer more open habitats (Voigt and Berg 1987) to the wooded habitats occupied by gray foxes. Dense woodland habitat coupled with the ability of the gray fox to climb trees implies that coyotes would have a difficult time catching gray foxes (Wooding 1984).

Protection from harassment is also favorable. This includes the absence of hunting or trapping pressure, as well as limited exposure to domestic dogs. Domestic dogs recently vaccinated for distemper are thought to shed a small amount of infective virus in their feces for a short period of time after vaccination (W. R. Davidson, pers. comm.), and thus may be a potential source of distemper infection in gray foxes. Because distemper is nearly 100% fatal to gray foxes (Davidson et al. 1992b), populations isolated from domestic dogs may have a reduced likelihood of infection. The best conditions for gray foxes, then, include woodland habitat, as well as the absence of red foxes, domestic dogs, and harvest pressure.

Although nothing is known of gray fox demographics under highly favorable conditions, many studies carried out under conditions of harvest are available for

comparison. Ignoring home range overlap and using home range size to calculate a rough estimate of density (Chamberlain and Leopold 2000; Jeselnik 1981), a great deal of variation may be noted, from 0.15 gray foxes/km^2 in the Missouri Ozarks (Haroldson and Fritzell 1984) to 0.83 gray foxes/km^2 (Follmann 1973) in Illinois. The highest densities, however, and possibly the best habitat, have been documented from a protected population living on the Savannah River Site (SRS) in South Carolina. On the SRS, home range sizes are smaller than in other populations and density may range from 0.41-0.84 foxes/km^2 (Jeselnik 1981; Sawyer 1988), although Jeselnik (1981) noted home range overlap suggesting density was as high as 1.24 foxes/km^2.

Most other demographic data from harvested populations show remarkable similarity as well. Age structure, for example, is nearly always the same, with ca. 60% of the population consisting of 10-month-olds, 22% of the population 22-month-olds, and 18% of the population $\geq$34-month-olds. This trend is noticeable not only for gray foxes in the southeastern United States, but also in other parts of the country. Average age for these populations is 1.8 years (Lord 1961; Wigal and Chapman 1983; Wood 1958; Wood and Odum 1964).

This short life span also is reflected in low average survival rates, which have been reported to range from 0.37 per year in Florida (Lord 1961) to 0.52 per year in Maryland (Wigal and Chapman 1983). The factors contributing to high mortality rates in Alabama have been reported to be due to automobile collisions (14%), trappers (29%), and diseases such as distemper and canine hepatitis (43-57%—Nicholson and Hill 1984).

Another striking similarity among studies of gray fox demographics is the sex ratio, which is rarely reported to differ from 1:1 (Layne 1958; Lord 1961; Nicholson 1982; Sawyer 1988; Sullivan 1956; Wigal and Chapman 1983; Wood 1958; Wood and Odum 1964). In New York, however, the sex ratio differed from 1:1 (1.4M:1F) with a significant preponderance of males (Layne and McKeon 1956). In almost all of these studies there was a slight preponderance of males, which is usually attributed to the

male's greater mobility and vulnerability during the breeding season when trapping occurs (Layne 1958; Layne and McKeon 1956; Sheldon 1949).

Most studies also report consistent reproductive parameters. Gray foxes from various populations have been reported to give birth to 3.7-4.6 young/litter. Not all foxes in a population will reproduce in a given year. Barren rates typically range from 2.0% in Illinois (Layne 1958) to 6.5% in Alabama (Sullivan 1956), though they may occasionally be as high as 45% (Wigal and Chapman 1983).

These similarities across a wide variety of habitats suggest that gray fox populations are capable of adapting to a great diversity of conditions with very little change in their demographics. Yet nearly all these studies were conducted under conditions of harvest and no two are comparable with respect to either location or habitat types. The environmental factors influencing gray fox demography can only be understood by controlling one or two of these factors while varying the others. The Savannah River Site offers the opportunity to design a study to control for location effects across time. Wood and Odum (1964) evaluated the age structure and sex ratio of the gray fox population from 1954-56 shortly after this site was closed to the public and the area was primarily abandoned agricultural land. Agricultural areas typically are avoided by gray foxes (Fuller 1978; Trapp 1973), although this habitat may be used in the southeast (Wood et al. 1958) in areas where competition with red foxes is reduced or absent (Trapp and Hallberg 1975). Red foxes were present on the SRS until 1969, after which only one was trapped in 1976 (Jenkins et al. 1979). Coyotes have lived on the SRS since ca. 1989 (Cothran et al. 1991), but the abundance of woody vegetation on the SRS coupled with the gray fox's ability to climb trees (Wooding 1984) likely allows gray foxes to avoid extensive coyote depredation.

Currently the SRS is primarily woodland habitat and presumably more favorable to gray fox populations than agricultural areas (Fritzell and Haroldson 1982; Fuller 1978; Jeselnik 1981; Sawyer 1988; Trapp 1973). Since the 1950s, harvest pressure has changed as well. Although harvest data for foxes are sparse prior to the 1970s, 943 foxes (both

red and gray) were harvested in the state of South Carolina during the winter of 1950-51 just before the SRS was closed to public access (Novak et al. 1987). Presumably some of that harvest occurred in areas now protected by SRS borders (O. E. Baker, pers. comm.).

The objectives for this study, then, were to compare demographic parameters such as density, age structure, survival, sex ratio, and reproductive output in the unharvested SRS population to those same parameters in harvested populations published in the literature. In particular, this study was conducted 1) to determine if the age structure and sex ratio of the current SRS population differ from the same population in 1952-54 when habitat was less favorable and harvest was allowed, 2) to use age structure data to compare the median age and maximum life expectancy of the current SRS population to harvested populations reported in the literature, 3) to determine if survival of the current SRS population differs from harvested populations, 4) to determine if and how reproduction is influenced by highly favorable conditions, and 5) to examine the relationship between harvest and age structure.

CHAPTER 2

MATERIALS AND METHODS

Study Site: The U.S. Department of Energy's Savannah River Site (SRS) is a nuclear production facility encompassing ca. 78,000 ha in South Carolina along the north shore of the Savannah River (Fig. 1). The SRS spans two physiographic provinces of South Carolina, the Sandhills and the Upper Coastal Plain. The upland areas of the site (>82 m elevation) are located in the Sandhill province on the Aiken Plateau subregion (ca. 12,000 ha), while the Upper Coastal Plain lies on the Pleistocene Coastal Terraces. The upland areas of the site in the Aiken Plateau are characterized by poor, deeply eroded sandy soils. In contrast, the Pleistocene Coastal Terraces have well-drained soils which historically were used for agriculture (White and Gaines 2000; Wood and Odum 1964; Workman and McLeod 1990).

Currently, 74% (ca. 57,720 ha) of the land is actively managed for wood and pulp production by the Savannah River Natural Resource Management and Research Institute (NRMRI). These managed areas are planted primarily with loblolly (*Pinus taeda*) and longleaf (*P. palustris*) pine, and those areas covered with slash pine (*P. elliottii*) are gradually being replanted with longleaf (U. S. Forest Service 1999; White and Gaines 2000). The remaining 1/3 of the site consists of old fields, upland and bottomland hardwoods, ponds, marshes, and Carolina bays. Pine management on the SRS consists primarily of clearcutting, leaving the debris on the ground, and allowing a 1-year period of inactivity followed by a prescribed burn. Then new trees are planted, and herbicide applied several months later to release the seedlings from competition (U. S. Forest Service 1999; White and Gaines 2000).

These management practices have resulted in a mosaic of pine species and ages across the SRS. Currently, 11.9% (8,686 ha) of the SRS is planted pine 0-10 years old, while mature longleaf, loblolly, and slash pine $\geq$30 years old covers an additional 44.5%
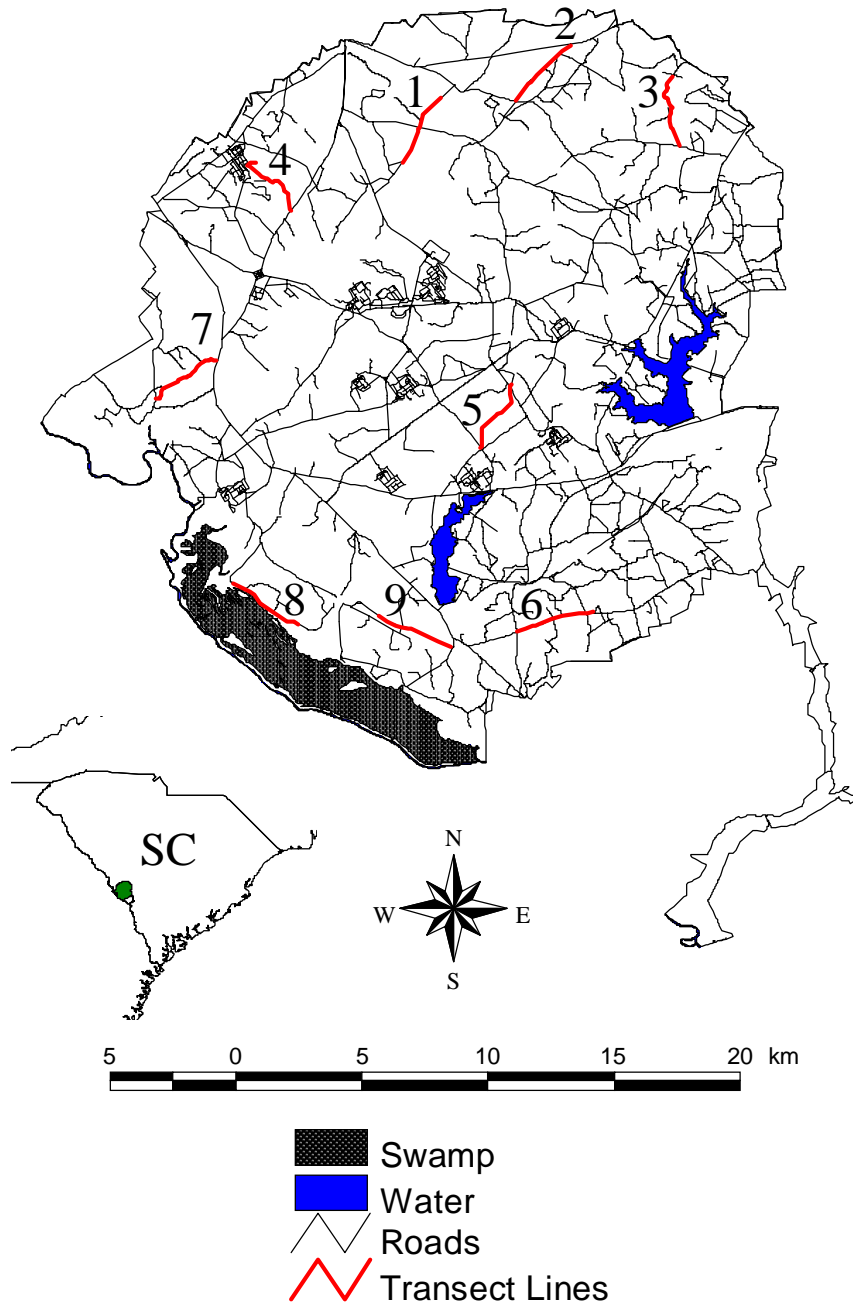
FIGURE 1—Location of scent-station transect lines on the U.S. Department of Energy's Savannah River Site. Lines 1-3 are in xeric habitat, 4-6 are in mesic habitat, and 7-9 are in hydric habitat.

(32,576 ha—White and Gaines 2000). Because gray foxes prefer woodlands and ecotonal areas to agriculture (Follmann 1973; Fritzell and Haroldson 1982; Fuller 1978; Jeselnik 1981; Sawyer 1988; Trapp 1973), current habitat conditions on the SRS are likely better suited to this species than were the agricultural fields present when the site was closed in 1951. Although past studies have documented radionuclides and other contaminants in furbearers at this site (Cumbie and Jenkins 1975; Gaines et al. 2000; Jenkins and Fendley 1968; Lord 2000), all concluded that contaminant levels were too low to affect population parameters. The large size of the SRS, then, along with the interspersion of pine species of different ages, the absence of red foxes, domestic dogs, and harvest, probably provide the most favorable habitat conditions for gray foxes in the southeastern United States.

Scent-Station Surveys: A population index of gray foxes on the SRS was obtained using standard scent-station methodology (Linhart and Knowlton 1975). Nine transect lines were placed $\geq$1 km apart along little-used roads around the SRS (Fig. 1) with 12 stations/transect and successive stations placed on opposite sides of the road 0.32 km (0.2 mi) apart. Three transect lines each were placed in each of 3 regions, xeric, mesic, or hydric, to assess both the abundance and distribution of SRS gray foxes. Scent-stations were constructed in 1997 by clearing an area of vegetation and sifting powdered agricultural lime ca. 1 cm deep in a 1-m circle. However, the lime was found to harden in the presence of moisture and failed to show clear tracks of light-weight carnivores such as skunks and opossums. So although gray fox footprints could still be readily identified, the tracking medium was changed to fine-grained sand during 1998 and 1999 to more thoroughly index all furbearer species.

In 1997, 4 scents were used to test their attractiveness to gray foxes. The 4 scents tested were bobcat urine (On Target A.D.C., Cortland, IL), gray fox urine (On Target A.D.C., Cortland, IL), fatty acid scent (FAS—Pocatello Supply Depot, Pocatello, ID), and Magna-Glan animal lure (MGL; Russ Carman, New Milford, PA). Scents were

assigned to stations in a series of 3- 4 x 4 latin squares resulting in a 4 x 12 array. In this design, the rows were associated with the 4 weeks of the study and the columns were associated with the stations along the transect line. The arrangement of scents within the latin squares was such that each scent at a station was followed temporally by each other scent an equal number of times, but was never followed by itself. Spatially, each scent at a station neighbored each other scent 6 times but neighbored the same scent only 2 times in an effort to control for any residual effects of neighboring scents. The order of the first 4 scent-stations was determined randomly in the first period. To reduce the chance of contaminating a station with the residual odor of a previous attractant, attractants were placed in a 1.5 ml centrifuge capsule secured to a 7mm diameter wooden dowel and planted firmly in the soil so that the capsule was ca. 8 cm above the ground (Andelt and Woolley 1996). Occasionally, an animal would knock over the stick and capsule, contaminating the ground with that particular scent. When this occurred, the stick and capsule were removed, the lime where the attractant likely fell was removed and disposed of away from the station, and the rest of the area was left exposed to the environment for ca. 1 week to allow the attractant to volatilize. When the station was activated the following week, fresh lime was put over the entire area to further mask any residual scent. The numbers of visited and unvisited stations were compared with Fisher's exact test on a 4x2 table for scent differences (SAS proc FREQ) with a significance level of $P < 0.05$. If a difference was indicated then all possible 2-group comparisons were made using a Fisher exact test with permutation-style adjusted P-values (proc MULTTEST, SAS v. 6.12—SAS Institute 1998). Otherwise, all procedures were the same.

In 1998 and 1999 the only attractant used was FAS. A plaster disc (25 x 5 mm) saturated with FAS was placed in the center of the station to attract furbearers. Scent stations were set in the morning and checked for tracks the following morning. A station was counted as visited if at least one identifiable track was present at the station. Tracks were identified according to Murie (1954). A visitation index (Linhart and Knowlton 1975) was computed by

$$\text{Index} = (\text{\# stations visited} / \text{total \# of stations}) \times 1000.$$

Because juvenile gray foxes begin dispersing by October, population levels were expected to be highest during September (Nicholson et al. 1985). Therefore, scent-stations were run once per week for four weeks during the month of September in each year from 1997-1999.

Trapping and Handling: Gray foxes were trapped using size 1 1/2 Victor® soft catch® leg-hold traps. Occasionally, gray foxes were obtained in the autumn when box traps ($\geq$ 152.4 x 40.6 x 48.3 cm) were set with dog food to catch lost hunting hounds. Otherwise, trapping occurred January-March each year. Leg-hold traps were placed along little-used roads, primarily at intersections to increase the likelihood of capture. Leg-hold traps were set using a dirt hole set (Hawbaker 1974) baited with one of five commercially available lures as attractants (Liquid Fox and Coyote Lure and Fox Gland Lure, On Target, A.D.C., Cortland, IL; Fox #1, Fox #2, and Caven Canine Force, Chagnon Enterprises, Manistique, Mi). These lures were chosen based on recommendations from the companies as being the most attractive and specific to gray foxes. Traps were checked each day at dawn. A total of 107 trap locations was used all three years resulting in 771, 827, and 931 trap-nights in 1998, 1999, and 2000, respectively (total = 2529 trap-nights). In an attempt to capture more females to radio-collar and to recapture females that had moved out of the areas trapped all three years, other locations were trapped for an additional 297, 143 and 962 trap-nights in 1998, 1999, and 2000, respectively.

After capture, foxes were restrained using a catch pole. The fox was then anesthetized using a combination of Ketamine (13.0 mg/kg body weight) and Xylazine (2.6 mg/kg body weight) given in the hip muscle. Foxes were weighed using a bathroom scale ($\pm$0.1 kg) and body measurements were taken of total length, tail length, hind foot length, and ear length using a metric tape ($\pm$0.1 cm). Both ears were tagged using size 4

monel ear tags (National Band and Tag Co.). Sex of the fox was then determined and female reproductive condition was assessed based on development of the teats (Layne 1958). The amount of wear on the molars was examined to obtain a field estimate of the fox's age (Wood 1958), as discussed below. Samples taken for future studies not part of this work included ca. 1 g of hair from between the shoulder blades and a small piece of tissue (ca. 2 mm^2) removed from the tip of the ear with a new scalpel blade.

Every female caught in 1998 and 1999 ($n = 25$; Appendix 1) was equipped with a radio-collar (ca. 60 g for collars from AVM Instrument Co., Livermore, CA and ca. 140 g for collars from Telonics, Inc., Mesa, AZ) transmitting in the 163-164 MHz range (Appendix 1). Total handling time was ≤ 20 minutes. Each radio-collar was equipped with a mortality sensor which operated by increasing signal frequency when the collar remained motionless for ≥ 8 hours. When a mortality signal was received, either the collar alone was retrieved if off the animal, or the collar and body were recovered if the female had died. Recovery of radio-collars after the last known date alive ranged from 9.5 hours to 94 days.

In the final year of the study, all 30 gray foxes trapped ($n = 12M$ and $18F$) from January-March 2000 were sedated with twice the usual dosage of Ketamine and Xylazine, and ca. 30 cc of blood was collected via a heart stick for a disease study carried out through the Southeastern Cooperative Wildlife Disease Study unit. Finally, the fox was euthanized with an injection of Beuthanasia-D (1ml/10 lbs. body weight) into the heart. Animals were then frozen from 1-3 months until they were necropsied during April, 2000.

Radiotelemetry: Gray fox locations were determined by triangulation using a Model TR-2 radio receiver and an H-antenna (Telonics, Inc. Mesa, AR). A 7-day post-release readjustment period was allowed before any locational data were collected (Jeselnik 1981) to avoid recording behavioral changes due to handling. The animal's true location was considered to be the center of the triangle created by the intersection of the three

compass bearings from each of three triangulation points and was determined using a SAS program described by White and Garrott (1990). If the area of the error polygon was >44,200 m^2 (i.e., >2% of the average home range size, chosen based on natural breaks in the data) the location was considered unreliable and removed from the data set. Triangle sizes within the data set ranged from 43.1-28,472.3 m^2 with a mean of 2,721.4 m^2 ($SD = 3199.4$). Because gray foxes are most active during the evening hours, especially around sunrise and sunset (Haroldson and Fritzell 1984), most tracking occurred during these times. Frequent opportunistic radio-locations were supplemented with 2-5 evening tracking sessions lasting 6 hours each, primarily during the months of April, June, July, and November. During these tracking sessions, the fox was located every 30 minutes for the entire 6-hour period ($n = 13$ locations/6-hr. period).

Home Range Analysis: For data from a given fox to be considered in the home range and habitat preference analyses two criteria had to be met; 1) a minimum of 30 locations (Seaman et al. 1999), and 2) a minimum of 40% of the locations from each of two seasons: food abundance (May-Oct.) and food scarcity (Nov.-Apr.). For the six foxes that met these two criteria, locational fixes were imported into the program CALHOME, and home ranges were estimated using the 95% use contour of the adaptive kernel method (Seaman and Powell 1996; Worton 1987; Worton 1989). Because the adaptive kernel method does not require locations to be independent of each other (Swihart and Slade 1997), all locations from the 6-hour tracking sessions were included along with the locations collected opportunistically. For each season, at least 2 6-hour tracking sessions ($n = 26$ locations) were attempted for each fox plus enough opportunistic locations to increase the sample size to $\geq$30 locations/fox. One female (GF-126), however, removed her collar twice (collared in both 1998 and 1999), so only 1 6-hr tracking session/season was possible, though her combined locations did allow for an across-seasons home range estimate. Differences in seasonal home range size were tested using 5 of the 6 foxes (omitting GF-126 due to insufficient data) by first checking for normality with a Shapiro-

Wilks test (Shapiro et al. 1968), then checking equality of variance with an F-ratio test, then testing seasonal home range sizes with a paired *t*-test (Sokal and Rohlf 1995).

Habitat Preference: Habitat types were obtained using a digitized 1999 SRS habitat map (Wiggins-Brown et al. 2000) containing 33 habitat types and reclassifying those habitats into the following four categories: open area, hardwood, open canopy pine, dense canopy pine (Appendix 2). Compositional analysis was performed using minimum convex polygon home ranges (as recommended by Aebischer et al. 1993) generated by CALHOME, which were then imported into ArcView to calculate the area and percent of those four habitat types both within the SRS boundary and within each fox's home range. To determine if gray foxes preferred one habitat type over another, compositional analysis was carried out on two levels. At the first level, the proportion of habitat types within all gray fox home ranges was compared to the proportion of those habitats available within the boundary of the SRS in order to determine if gray foxes showed a preference for habitats when establishing a home range. At the second level, the proportion of a fox's radio-locations within each habitat type was compared to the proportion of that habitat type available within the boundary of the fox's home range in order to determine if gray foxes showed a preference for habitats when utilizing their territory (Aebischer et al. 1993). These analyses were performed using a SAS program (SAS Institute 1998) written by Ott and Hovey (1997).

Density Estimates: Several methods of density estimation were employed. First, density estimates were based on mark-recapture data obtained from trapping results. Because some areas were trapped for only 1 or 2 years of the study, only those foxes caught in locations trapped during all 3 years were considered in the mark-recapture analysis. Population size was estimated using the Chapman estimator (Krebs 1999a; Pollock et al. 1990) for each pair of years, then all 3 years of trapping data were combined and analyzed using the Schnabel estimator (Krebs 1999a) and Chao's time-variation model

(Chao 1989). Chao's time-variation method was calculated using the program, "Ecological Methodology" (Caughley Closed Population Estimators routine—Krebs 1999b). Based on home range data from this study and two other studies on female SRS gray fox home range size (1.06 km^2, and 1.39 km^2—Jeselnik 1981; Sawyer 1988, respectively), every trap was assumed to have potentially captured a fox within a 1-km radius of the trap location. To calculate this effective trapping area, the locations of foot-hold traps used every year were imported into the program ArcView and a 1-km buffer was constructed around these traps (Appendix 3). The cumulative area of the buffer was considered to be the effective trapping area when calculating density and equaled 134.3 km^2.

Because recaptures were expected to be rare and could bias the results of the above methods, an additional estimate of population density was calculated using home range size and assuming no home range overlap. Because gray foxes are known, however, to share home ranges (Jeselnik 1981) a second estimate of density was calculated using the percentage home range overlap between two mated pairs reported by Jeselnik (1981). Because this is the most common method of estimating carnivore density it is also the most easily comparable to values in other canid studies.

Rate of Increase (r): Using the two Chapman estimates of population size within the effective trapping area, the observed rate of increase (*r*) from year to year was calculated by

$$r_t = \ln (N_{t+1} / N_t), \quad \text{where t = time in years.}$$

Because *r* also may be calculated by regressing index values against time (Caughley and Birch 1971), a second estimate of *r* was obtained by regressing scent-station indices against time using the statistical program, SAS (SAS Institute 1998). Because *r* = slope, the probability of the slope differing from zero is equivalent to the probability of the

growth rate differing from zero. Significance for this and all other tests was assigned at $P \leq 0.05$.

Age Structure: Ages of 39 foxes were estimated by assessing tooth wear (Wood 1958). Because this method has been criticized as being inaccurate for gray foxes in Wisconsin (Root and Payne 1984), foxes with levels of tooth wear intermediate between two age classes were considered to belong to the younger of those age classes, to most closely approximate age structure data from comparable studies. Because foxes ≥ 34 months old often had similar amounts of tooth wear, foxes were assigned to only three categories (rounded to the average age during the trapping season): 10 months (7-12 months), 22 months (19-24 months), and ≥ 34 months (>31 months). Although Wood (1958) noted variability in this method as well, all his inaccuracies occurred from June-December, whereas foxes aged from January-May were aged with 100% accuracy when using cementum analysis as a standard. Because trapping and aging in this study was done from January-March, this method was likely to be suitable.

However, age based on tooth wear is a subjective assessment prone to errors, while cementum analysis is a quantitative method subject to fewer errors (Fiero and Verts 1986; Grau et al. 1970). In mammals, cementum is deposited on the roots of teeth each year alternating between opaque bands (laid down in summer) and dark annuli (laid down in winter—Larson and Taber 1980). The first dark band of cementum is not laid down until ca. 18 months of age, thus an animal trapped in the autumn would be 0.5 years older than the count of cementum annuli, while an animal caught in late winter would be 1 year older than the count (Allen 1974; Goodwin and Ballard 1985; Linhart and Knowlton 1967). Although Johnson (1970) found many cementum annuli were indistinct in raccoons from Alabama, he examined the area of the premolar between the roots (i.e., at the base of the crown) instead of examining the more distinct annuli in the root tip. In raccoon studies which examined the root tip, Fiero and Verts (1986) found cementum annuli provided reasonably accurate age estimates, though they had some difficulty

distinguishing between the 1- and 2-year-old age classes. Using known-age raccoons in Illinois, however, Grau, et al. (1970) reported cementum analysis was the most accurate aging technique up to 4 years old, after which cementum tended to underestimate the true age. Therefore, age classes in this study were limited to 10 months, 22 months, and ≥34 months old.

Because premolars could not be removed from a live animal without damaging the jaw, cementum analysis was impossible for 39 gray foxes for which only tooth-wear age was available. To correct for the error inherent in aging by tooth wear, age based on tooth wear was compared to age based on cementum analysis for 31 road-killed ($n = 9$ on SRS, $n = 22$ off SRS), 31 euthanised (all on SRS) and 5 dead (all on SRS) gray foxes collected from the SRS and surrounding areas. From these 67 dead foxes, age was estimated by both the tooth-wear method and by the cementum method, and the frequency of correct and incorrect tooth-wear age classifications calculated (assuming cementum age to be correct). Cementum ages were obtained by removing a pre-molar (usually the lower left) and sending the tooth to Matson's Laboratory (Milltown, Montana) for analysis.

To determine if either the sex of the fox or the year in which the fox was aged caused variation in the ability to correctly age foxes by tooth wear, age based on tooth wear was compared to age based on cementum analysis using a weighted kappa statistic as outlined by Fleiss (1981). This test was conducted using SAS (proc FREQ, test wtkap) and resulted in estimates of agreement between the two aging methods (weighted kappa) for each combination of sex and year. Data from foxes collected in 1998 and 1999 were combined to increase sample size; thus four combinations of sex and year (1998/99 and 2000) were possible. To determine if data from male foxes could be combined across years, an overall (across-years) kappa value was first calculated from the two male by year kappa values. This overall kappa value was then compared to the two male by year kappa values with a χ^2 test as described by Fleiss (1981). A similar

calculation was done for females. If the χ^2 test was non-significant ($P > 0.05$), the data from both years were grouped for that sex.

Within these groups, the 67 foxes with both a tooth-wear age and a cementum age were separated based on tooth-wear age. Assuming the cementum age of the fox was the correct age, the frequencies of correct and incorrect age classifications were calculated within each tooth-wear age group. These proportions represented the error in tooth-wear aging and were ultimately used as the correction factors needed to adjust the ages of the 39 foxes aged by tooth wear alone.

Chi-square tests were used to compare age structures among years and between sexes, as well as age structures based on cementum analysis vs. adjusted tooth-wear, and age structure from this study vs. that of the SRS 1952-54 (Wood and Odum 1964).

Finally, age structure of the current SRS population was compared to the age structures of 5 other populations published in the literature using ecological longevity curves, as outlined by Dapson (1971). In this method, individuals in the population are arranged chronologically from oldest to youngest and their relative frequency in the population is considered to be 1/N (n = total number of individuals in the population). Relative cumulative frequencies (RCF) are calculated by summing the individual frequencies from oldest to youngest, then RCF is plotted against age. In this case the Y variable, RCF, is non-random, hence the regression of X (Age) on Y (RCF) must be used instead of the typical Y on X. Dapson (1971) notes this regression is rarely rectilinear, and suggests that one or both axes must be transformed, usually with the square, cubic or quadratic roots of one variable. In this study, both RCF and age could be either untransformed or transformed up to the sixth root, thus, 36 ($n = 6^2 = 36$) regressions were run for each gray fox population. The regression producing the highest correlation coefficient, r, was determined to provide the best fit of the data to the line. Because RCF is equal to the probability of occurrence, when RCF = 0.5 is used in the equation the result is an estimate of the median ecological longevity (MEL), or the age at which half the population is younger and half older. MEL, therefore, is an index of relative

population age. Similarly, RCF = 0 represents the maximum ecological longevity (MAX), or the age beyond which no animals are expected to occur. As such, MAX is a measure of environmental favorability or habitat quality.

Survival and Mortality: Due to small sample sizes, several survival estimates were calculated to check for agreement. Because the age structure of the SRS population of gray foxes did not show fewer individuals in each successively older age class, a life table analysis was impossible.   Krebs (1999a) provides an alternative survival estimate based on the number of animals in each age group. This method is most likely to provide a survival estimate comparable to other studies using life table methodology.

Next, yearly survival of radio-collared females was calculated using Mayfield's maximum likelihood method, computed using the program, "Ecological Methodology" (Mayfield routine—Krebs 1999b). Although foxes were radio-collared January-March, the Mayfield method assumes all animals were marked at one time. Therefore, all foxes were considered to begin their monitoring in January. Because batteries had a maximum life span of 12-13 months, December was considered the end of the year for which a fox could have survived. Because radio signals were likely to be lost either to battery failure, emigration from the SRS, or a fox pulling the collar off, survival was first calculated using only those females whose fates were known ($n = 12$). Females of known fate were those known to have died during the year they were collared ($n = 5$) or known to have survived through December ($n = 7$). Then, the same calculations were performed using survival of radio-collared females of both known and unknown fates. A fox of unknown fate ($n = 6$) was one for which the radio-signal was lost due to one of the above-stated reasons, at which point the fox was assumed to have died. Although this likely was not the case in most instances, this assumption provided the most conservative estimate of survival. The Kaplan-Meier estimate of survival, however, allows for newly tagged animals to be entered into the sample at any time and for animals to be lost from the sample at any time without making assumptions about the fates of radio-collared

individuals. This staggered entry design coupled with the ability to censor data provides the most robust estimate of survival.

When a fox was recovered dead, the body was examined to determine the cause of death. If cause could not be easily determined with a gross examination in the field, the remains were sent to the Southeastern Cooperative Wildlife Disease Study in Athens, Georgia for analysis.

Reproduction: Reproductive tracts from 23 SRS female gray foxes were removed and examined for evidence of reproductive activity (Appendices 4, 5). First, both uterine horns were split open and placental scars counted. Ovaries were then removed and placed in 10% formalin. The ovaries were sent to Matson's Laboratory (Milltown, Montana) to be sectioned and the number of corpora lutea counted. Based on examinations of the reproductive tracts, the incidence of resorption was calculated (i.e., the percent of females resorbing at least one embryo) along with the extent of resorption (i.e., the average percent of a resorbing female's litter actually being resorbed). Barren rate was calculated as the number of females old enough to have reproduced at least once but which showed no sign of having done so. Females in this category were typically 11- to 23-month-old females (based on cementum analysis) showing no signs of being or having been pregnant. Total pre-natal mortality was then calculated based on the number of corpora lutea, placental scar counts, the incidence and extent of resorption, and the barren rate. Corpora lutea and placental scar counts were compared to similar values in other studies using a Shapiro-Wilks for normality (Shapiro et al. 1968) followed by an F-test for homogeneity of variances and a *t*-test (Sokal and Rohlf 1995).

CHAPTER 3
RESULTS

Trapping: The 107 trap locations which were leg-hold trapped every year for three years resulted in 2.7 foxes/100 trap-nights (21 foxes/771 trap-nights), 1.6 foxes/100trap-nights (13 foxes/827 trap-nights; includes 2 recaptures), and 1.0 foxes/100 trap-nights (9 foxes/931 trap-nights; includes 1 recapture) in 1998, 1999, and 2000, respectively. Additional leg-hold traps caught 0 foxes/100 trap-nights (0 foxes/297 trap-nights), 4.2 foxes/100 trap-nights (6 foxes/143 trap-nights), and 2.1 foxes/100 trap-nights (20 foxes/962 trap-nights) in 1998, 1999, and 2000, respectively. Four additional foxes were caught in box traps set for hunting hounds, and 5 foxes causing a nuisance in industrialized areas were trapped by P. Johns in box traps and moved (except one pregnant female that was returned). Thus, a total of 75 different foxes were handled in this study.

Only 4 foxes died due to leg-hold trapping. In one case a stick became wedged in the trap chain preventing the chain from swiveling and causing the fox to break both the radius and ulna of the front right leg. This fox was euthanised. The other three deaths were attributed to coyote kills.

Scent-Station Surveys: During 1997, visitation indices (#visits/#stations x 1000) for MGL, FAS, gray fox urine, and bobcat urine were 166.67 (18/108), 66.67 (7/105), 84.11 (9/107), and 74.77 (8/107), respectively. Despite gray foxes showing a statistically significant ($P = 0.05$) preference among attractants visited, none of the 6 multiple comparisons tests were significant. Therefore, data from all four scents were combined to arrive at the total visitation index for 1997. Scent-station indices for 1997, 1998, and 1999 were 98.36, 94.91, and 97.22, respectively. Although MGL showed the highest

visitation index, FAS was used exclusively for the remaining 2 years for its standardization and comparability to other studies.

Home Range, Density, and Rate of Increase (r): According to the 95% use contour of the adaptive kernel method, average seasonal home range size (excluding GF-126 due to small within season sample sizes) during food scarcity was 2.14 km^2 ($n = 5$), which was significantly larger (*paired t* = 2.90, *d.f.* = 4, *one-tailed P* = 0.022) than during food abundance when home range size was 1.18 km^2 ($n = 5$—Table 1). Average across-season home range size (including GF-126) was calculated to be 2.21 $\pm$ 0.96 km^2 ($n = 6$), ranging from 1.00 km^2 to 3.54 km^2 (Table 1; Appendices 6-11).

The most conservative density estimate, assuming no home range overlap, was 0.45 foxes/km^2, or 61 foxes in the effective trapping area of 134.3 km^2. Jeselnik (1981), however, provided strong evidence that gray foxes on the SRS overlap home ranges. According to Jeselnik's (1981) data, 87% of a fox's home range was shared with its mate. Because average home range size in this study was 2.21 km^2, a mated pair will share 87% or 1.92 km^2 of their home ranges while using 0.29 km^2 exclusively. A mated pair, then, should require 2.50 km^2 for a density of 0.80 foxes/km^2. Jeselnik (1981) also reported that 35% of a fox's home range was shared with a neighboring fox other than its mate. Applying this percentage to the 2.50 km^2 required for a mated pair yields an estimate of 4.12 km^2 shared by 4 foxes for a density of 0.97 foxes/km^2. Because the total land available to gray foxes on the SRS is 788.2 km^2 (excluding area covered by water) the total number of gray foxes on the SRS ranges from 355 (assuming no home range overlap) to 765 foxes (assuming mated pairs and neighbors sharing home ranges).

Estimates of population size using mark-recapture methodology rely on having several recaptures. In this study, 3 gray foxes were recaptured: 2 females (GF-107 and GF-126) first caught in 1998 were recaptured in 1999, and 1 male (GF-163) caught in 1999 was recaptured in 2000. The two females were recaptured 1.8 km and 0.63 km

TABLE 1—Foxes used in home range analysis, showing the number of telemetry locations within the seasons of food abundance (May-Oct.) and food scarcity (Nov.-Apr.) and 95% adaptive kernel home range estimates.

	Food Abundance		Food Scarcity		# Locations Used For Home Range[a]	Home Range (km^2)
Fox	# 6-hr Tracking Sessions	# Opportunistic Locations	# 6-hr Tracking Sessions	# Opportunistic Locations		
GF-107	2	16	-	-	38	1.025
GF-107	-	-	3	9	46	1.193
GF-107 Total	2	16	3	9	84	1.378
GF-120	2	16	-	-	36	0.494
GF-120	-	-	2	0	24	0.802
GF-120 Total	2	16	2	0	60	0.996
GF-126	1	4	-	-	17	1.224
GF-126	-	-	1	8	21	2.929
GF-126 Total	1	4	1	8	38	3.011

TABLE 1 continued—Foxes used in home range analysis, showing the number of telemetry locations within the seasons of food abundance (May-Oct.) and food scarcity (Nov.-Apr.) and 95% adaptive kernel home range estimates.

| Fox | Food Abundance | | Food Scarcity | | # Locations Used For HR | Home Range (km^2) |
	# 6-hr Tracking Sessions	# Opportunistic Locations	# 6-hr Tracking Sessions	# Opportunistic Locations		
GF-131	2	12	-	-	35	1.102
GF-131	-	-	2	1	27	3.012
GF-131 Total	2	12	2	1	62	2.268
GF-151	2	10	-	-	36	2.620
GF-151	-	-	3	7	46	4.079
GF-151 Total	2	10	3	7	82	3.544
GF-180	2	8	-	-	32	0.651
GF-180	-	-	2	0	26	1.616
GF-180 Total	2	8	2	0	58	2.068

[a]Unreliable locations not used.

from the site of first capture within the home range they had occupied the previous year, while the male was recaptured 5.0 km from the site of first capture. According to the Chapman estimator (95% confidence limits in parentheses), the total number of gray foxes living in the effective trapping area between 1998 and 1999 was 102 (34, 169), which was not statistically higher than the estimate of 69 (15, 77) foxes for 1999-2000 (t = 0.865, $d.f.$ = 2, $one\text{-}tail\ P$ > 0.20). These estimates yielded mean densities of 0.76 gray foxes/km^2 and 0.51 gray foxes/km^2, respectively.

The Schnabel estimator extends the Chapman method to >2 trapping occasions (95% confidence limits in parentheses). Using all three trapping seasons (1998-2000), the Schnabel method estimated 184 (68, 675) foxes for a mean density of 1.37 gray foxes/km^2. Chao's time-variation method also considers all three trapping seasons and estimated 181 (89, 444) gray foxes for a mean density of 1.35 gray foxes/km^2. Schnabel's estimate was not higher than Chao's estimate (t = 0.055, $d.f.$ = 4, $one\text{-}tail\ P$ > 0.45).

Using the population sizes estimated from the Chapman method, rate of increase was –0.39, indicating a population which slowly declined from 1998 through 1999. When regressing scent-station indices against time, the resulting slope estimated the rate of increase as –0.57, which did not differ from zero (P = 0.790) and was very similar to the estimate using population sizes. Therefore, the gray fox population size was considered essentially stable across all 3 years of the study.

Habitat Preference: An examination of the four habitat types within each fox's home range indicated a high degree of variation in habitat patch size (Table 2). Based on the methodology outlined by Aebischer et al. (1993), female gray foxes on the SRS (n = 6) showed no habitat preferences when selecting a home range within the SRS boundary (Λ = 0.459, P = 0.45). Despite the inability to distinguish a preference for one habitat over another, habitat preference was ranked as follows: open area > open canopy pine > dense canopy pine > hardwoods (Table 3). Similarly, female gray foxes showed no habitat

TABLE 2—Habitat patchiness[a] within home ranges of 6 female gray foxes (home range size, HR, in ha, given in parenthesis), showing the number of patches (*n*) of each habitat type, the mean patch size (in ha), and the range of patch sizes (in ha).

	Open Area			Hardwood			Open Canopy Pine			Dense Canopy Pine			Sum		
Fox (HR)	*n*	Mean (*SD*)	Range	*n*	Mean (*SD*)	Range	*n*	Mean (*SD*)	Range	*n*	Mean (*SD*)	Range	*n*	Mean (*SD*)	Range
GF-107 (137.8)	22	0.55 (1.27)	0.09-6.16	65	0.99 (2.30)	0.06-11.70	49	0.91 (2.03)	0.06-11.35	7	2.34 (3.03)	0.09-7.74	143	0.96 (2.13)	0.06-11.7
GF-120 (99.6)	26	1.75 (3.86)	0.06-17.54	32	0.29 (0.54)	0.06-2.42	26	1.35 (3.82)	0.06-19.65	14	0.68 (2.02)	0.06-7.67	98	1.01 (2.93)	0.06-19.65
GF-126 (301.1)	52	0.45 (1.22)	0.06-7.79	93	1.09 (4.87)	0.06-41.20	78	1.50 (5.22)	0.06-42.57	25	2.31 (4.19)	0.06-15.86	248	1.21 (4.43)	0.06-42.57
GF-131 (226.8)	25	0.60 (1.72)	0.06-8.72	130	0.32 (0.70)	0.06-5.82	34	4.33 (22.89)	0.06-133.76	14	1.53 (2.98)	0.06-10.82	203	1.11 (9.44)	0.06-133.76

TABLE 2 continued—Habitat patchiness[a] within home ranges of 6 female gray foxes, showing the number of patches in each habitat (*n*), the mean patch size (in ha), and the range of patch sizes (in ha).

Fox		Open Area			Hardwood			Open Canopy Pine			Dense Canopy Pine			Sum	
	n	Mean (*SD*)	Range	*n*	Mean (*SD*)	Range	*n*	Mean (*SD*)	Range	*n*	Mean (*SD*)	Range	*n*	Mean (*SD*)	Range
GF-151 (354.4)	31	1.27 (3.25)	0.06- 16.41	116	0.53 (1.57)	0.06- 13.67	71	2.22 (6.67)	0.06- 44.21	39	2.45 (6.49)	0.06- 34.73	257	1.38 (4.63)	0.06- 44.21
GF-180 (206.8)	45	2.47 (11.93)	0.06- 77.19	72	0.32 (0.83)	0.06- 5.58	45	1.07 (2.15)	0.06- 13.42	21	1.12 (1.45)	0.06- 4.79	183	1.13 (6.06)	0.06- 77.19
Sum (1326.5)	201	1.23 (6.03)	0.06- 77.19	508	0.59 (2.42)	0.06- 41.20	303	1.82 (8.84)	0.06- 133.76	120	1.87 (4.44)	0.06- 34.73	1132	1.17 (5.68)	0.06- 133.76

[a]A patch is defined as a set of contiguous 30-m x 30-m pixels of the same habitat type. A pixel was counted as part of the home range if at least 2/3 of the pixel occurred within the home range boundary. Therefore, the smallest detectable patch size was 0.06 ha.

TABLE 3—*P*-values associated with *t*-statistics comparing the proportions of habitat types within female gray fox home ranges with proportions of total available habitat types within the SRS boundary.

	Open Area[a]	Hardwood	Open Canopy Pine	Dense Canopy Pine
Open Area	·	0.401	0.691	0.529
Hardwood	0.401	·	0.105	0.213
Open Canopy Pine	0.691	0.105	·	0.756
Dense Canopy Pine	0.529	0.213	0.756	·

[a]the smallest *P*-value that can be obtained is 0.001.

preferences when utilizing habitat available within their home range ($\Lambda = 0.679$, $P = 0.72$). Based on the observed t-statistics, however, habitat preference was ranked as: open area > hardwoods > open canopy pine > dense canopy pine (Table 4).

Age Structure: Weighted kappa values for females in 1998/99 and 2000 were 0.516 (*d.f.* = 3, $P = 0.01$) and 0.5249 (*d.f.* = 3, $P = 0.004$), respectively, while values for males in 1998/99 and 2000 were 0.1698 (*d.f.* = 3, $P = 0.230$) and 0.7938 (*d.f.* = 3, $P < 0.001$), respectively. Because values of kappa between 0.40 and 0.75 represent fair to good agreement between aging methods (Fleiss 1981), only males from 1998/99 failed to show a correlation between aging methods.

Next, an overall (across-years) kappa value was calculated for each sex to determine if yearly kappa values were similar enough to combine. For females, overall κ = 0.5212 was not statistically different from either of the female by year kappas ($\chi^2 = 0.001$, *d.f.* = 1, $P > 0.900$), but for males overall $\kappa = 0.702$ was significantly different from the male by year kappas ($\chi^2 = 6.57$, *d.f.* = 1, $P < 0.025$). Therefore, data from females were combined across all years to obtain one set of adjustment factors to apply to the group of SRS females aged by tooth wear alone. Ages of male foxes aged by tooth wear alone, however, were adjusted separately by year (Table 5).

Unadjusted age structure of the 39 SRS gray foxes aged by tooth wear alone consisted of 15 10-month-olds (38.5%), 12 22-month-olds (30.8%), and 12 $\geq$34-month-olds (30.8%). Readjusting the number of foxes in each age class using the tooth-wear error frequencies (Table 6) resulted in 16 foxes in the 10-month-old age group (40.0%), 5 foxes in the 22-month-old age group (13.0%), and 19 foxes in the $\geq$34-month-old age group (48.0%). Age structure of the 38 SRS gray foxes aged using cementum analysis resulted in 13 foxes in the 10-month-old age group (34.2%), 3 foxes in the 22-month-old age group (7.9%), and 22 foxes in the $\geq$34-month-old age group (57.9%). The age structure based on adjusted tooth-wear did not differ from the age structure based on cementum analysis ($\chi^2 = 0.99$, $P = 0.611$—Table 7). When both aging methodologies

TABLE 4—*P*-values associated with *t*-statistics comparing the proportions of radio locations for each female gray fox in each habitat type with the proportion of each habitat type within their home range.

	Open Area[a]	Hardwood	Open Canopy Pine	Dense Canopy Pine
Open Area	·	0.670	0.606	0.219
Hardwood	0.670	·	0.833	0.309
Open Canopy Pine	0.606	0.833	·	0.331
Dense Canopy Pine	0.219	0.309	0.331	·

[a]The smallest *P*-value that can be obtained is 0.001.

TABLE 5—Frequency of correct and incorrect age classifications for each tooth-wear age group. Because the weighted kappa statistics indicated that the correlation between tooth-wear age and cementum age differed between males aged in 1998/99 and 2000, these groups were considered separately. The frequencies shown are the proportion of foxes in a given tooth-wear age category whose cementum age either confirmed the age class or reassigned them to another age class.

A.

Males, 1998/99

	Cementum		
Tooth Wear (*n*)	10-months (*n*)	22-months (*n*)	≥34-months (*n*)
10-months (2)	0.5 (1)	0.5 (1)	0 (0)
22-months (1)	0 (0)	0 (0)	1.0 (1)
≥34-months (8)	0.25 (2)	0.25 (2)	0.5 (4)

B.

Males, 2000

	Cementum		
Tooth Wear (*n*)	10-months (*n*)	22-months (*n*)	≥34-months (*n*)
10-months (7)	1 (7)	0 (0)	0 (0)
22-months (6)	0.5 (3)	0.33 (2)	0.17 (1)
≥34-months (7)	0 (0)	0 (0)	1 (7)

C.

Females, 1998/99-2000

	Cementum		
Tooth Wear (*n*)	10-months (*n*)	22-months (*n*)	≥34-months (*n*)
10-months (19)	0.79 (15)	0.11 (2)	0.11 (2)
22-months (6)	0.33 (2)	0 (0)	0.67 (4)
≥34-months (11)	0.18 (2)	0 (0)	0.82 (9)

TABLE 6—Number of foxes aged by tooth wear that were correctly assigned or reassigned to a cementum age category. The numbers shown are derived by multiplying the number of foxes in a tooth-wear age class (given in parentheses in the first column) by the frequencies shown in Table 6.

A. Males, 1998/99

	Corrected Age		
Tooth Wear (n)	10-months	22-months	$\geq$34-months
10-months (4)	2	2	0
22-months (7)	0	0	7
$\geq$34-months (6)[a]	2	2	3
Total (17)	4	4	10

[a]Due to rounding error, the corrected number is greater than the uncorrected number.

B. Males, 2000

	Corrected Age		
Tooth Wear (n)	10-months	22-months	$\geq$34-months
10-months (0)	0	0	0
22-months (1)	1	0	0
$\geq$34-months (0)	0	0	0
Total (1)	1	0	0

C. Females, 1998/99-2000

	Corrected Age		
Tooth Wear (n)	10-months	22-months	$\geq$34-months
10-months (11)	9	1	1
22-months (4)	1	0	3
$\geq$34-months (6)	1	0	5
Total (21)	11	1	9

TABLE 7—Age structure, in percent (N), based on adjusted tooth-wear and cementum analysis.

Method	n	10-months	22-months	$\geq$34-months
Adjusted Tooth-Wear[a]	40	40.0 (16)	13.0 (5)	48.0 (19)
Cementum[a]	38	34.2 (13)	7.9 (3)	57.9 (22)
Total	78	37.2 (29)	10.3 (8)	52.6 (41)

[a]There was no difference between the values estimated by the two methods (see text for statistics).

were combined, age structure was not found to differ among the years ($\chi^2 = 1.13$, $P = 0.890$—Table 8) or between males and females ($\chi^2 = 1.56$, $P = 0.459$—Table 9). The final age structure, then, included ages of both male and female gray foxes from all three years of the study, yielding 29 foxes in the 10-month-old age group (37.2%), 8 foxes in the 22-month-old age group (10.3%), and 41 foxes in the $\geq$34-month-old age group (52.6%—Table 9). The age structure of the current SRS gray fox population differed significantly from the 1954-56 SRS age structure ($\chi^2 = 30.38$, $P < 0.0001$—Table 10; Fig. 2).

A comparison of ecological longevity curves for 6 gray fox populations, including those in this study (Fig. 3), further supported the conclusion that the current SRS gray fox population was older than all other populations previously studied. Median ecological longevity (95% confidence limits in parentheses) for the current SRS population was 2.97 (2.70, 3.24) years, which was older ($t = 5.35$, $d.f. = 162$, *one-tailed P < 0.001*) than the next oldest population in Maryland (Wigal and Chapman 1983) which had a MEL = 1.78 (1.44, 2.13). Gray foxes in the Maryland population (Wigal and Chapman 1983), however, were expected to live significantly longer ($t = 5.23$, $d.f. = 162$, *one-tailed P < 0.001*) than the current SRS population as indicated by MAX = 16.15 (15.34, 16.94) and MAX = 13.95 (13.79, 14.11), respectively.

Long life span in this population was further confirmed by an examination of SRS gray fox cementum age (Fig. 4; Appendix 12). Based on cementum data, only 36.1% ($n = 13$) of the population were ca. 1 year old, and only 5.6% ($n = 2$) were ca. 2 years old. The remaining 58.3% ($n = 21$) consisted of individuals 3-10 years of age. For males (Fig. 4; Appendix 13), 46.2% ($n = 6$), 0%, and 53.8% ($n = 7$) were 1-, 2-, and 3-5-year-olds, respectively. For females (Fig. 4; Appendix 14), 1-, 2-, and 3-10-year-olds were 30.4% ($n = 7$), 8.7% ($n = 2$), and 60.9% ($n = 14$), respectively. Road-killed foxes from the areas surrounding the SRS (Fig. 4; Appendices 15, 16, 17) consisted of 62.5% ($n = 15$), 16.7% ($n = 4$), and 20.8% ($n = 5$) 1-, 2-, and 3-13-year-olds, respectively, which differed significantly ($\chi^2 = 8.99$, $P = 0.011$) from the age structure of the 36 cementum-aged foxes

TABLE 8—Age structure, in percent, of SRS gray foxes by sex and year (adjusted tooth-wear and cementum analyses combined).

Year	Sex	n	10-months	22-months	$\geq$34-months
1998[a]	Male	9	22.2 (2)	22.2 (2)	55.6 (5)
	Female	14	50.0 (7)	7.1 (1)	42.9 (6)
	Total	23	39.1 (9)	13.0 (3)	47.8 (11)
1999[a]	Male	11	36.4 (4)	18.2 (2)	45.5 (5)
	Female	13	38.5 (5)	7.7 (1)	53.8 (7)
	Total	24	37.5 (9)	12.5 (3)	50.0 (12)
2000[a]	Male	13	38.5 (5)	7.7 (1)	53.8 (7)
	Female	18	33.3 (6)	5.6 (1)	61.1 (11)
	Total	31	35.5 (11)	6.5 (2)	58.1 (18)

[a]There was no difference between the values estimated by the two methods (see text for statistics).

TABLE 9—Age structure, in percent (N), of SRS gray foxes by sex (combined across years and aging methods).

Sex	n	10-months	22-months	>34-months	Ave. Age[b]
Male[a]	33	33.3 (11)	15.2 (5)	51.5 (17)	2.8 yrs. (13)
Female[a]	45	40.0 (18)	6.7 (3)	53.3 (24)	3.9 yrs. (23)
Total	78	37.2 (29)	10.3 (8)	52.6 (41)	3.5 yrs. (36)

[a]There was no difference between the values estimated by the two methods (see text for statistics).

[b]Based on cementum ages from Tables 13-15.

TABLE 10—Age structure, in percent, of gray fox populations living under conditions of harvest vs. recently abandoned agriculture (males and females combined across years) and no harvest.

Location	Harvest/Agriculture	n	10-months	22-months	$\geq$34-months	Ave. Age[a]	Reference
Maryland	Harvest	129	61.2	8.5	30.2	2.3 yrs.	Wigal and Chapmann, 1983
Georgia	Harvest	435	61.1	28.3	10.5	1.5 yrs.	Wood, 1958
Florida	Harvest	55	52.7	27.3	19.9	1.8 yrs.	Wood, 1958
Florida	Harvest	263	61.6	24.7	13.7	1.6 yrs.	Lord, 1961
SRS, 1954-56	Agriculture	120	62.5	21.7	15.8	1.6 yrs.	Wood and Odum, 1964
SRS, 1998-2000	No Harvest	78	37.2	10.3	52.6	3.5 yrs.	This Study

[a]Calculated as the average of cementum ages.
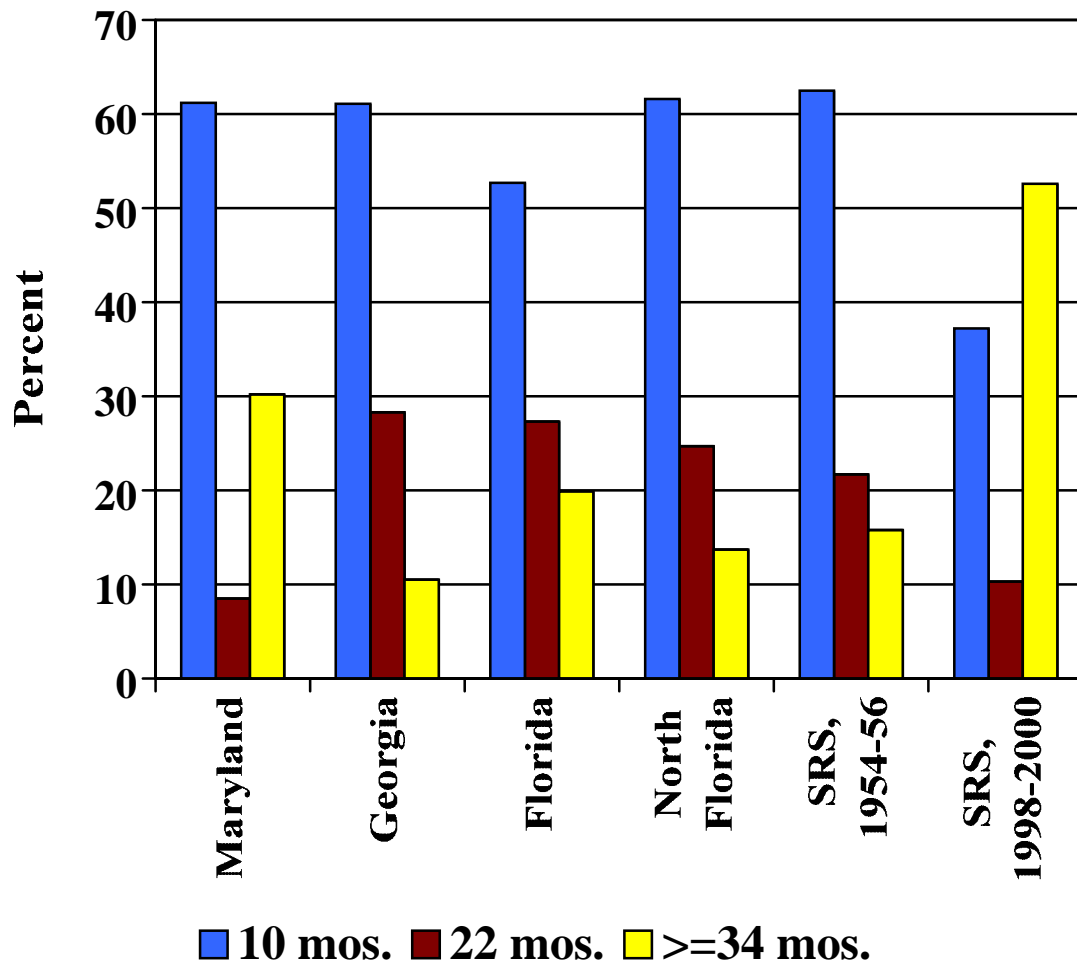
FIGURE 2—Percent of southeastern populations that are made up of gray foxes of various ages, including results from this and other studies (Lord 1961; Wigal and Chapman 1983; Wood 1958; Wood and Odum 1964).
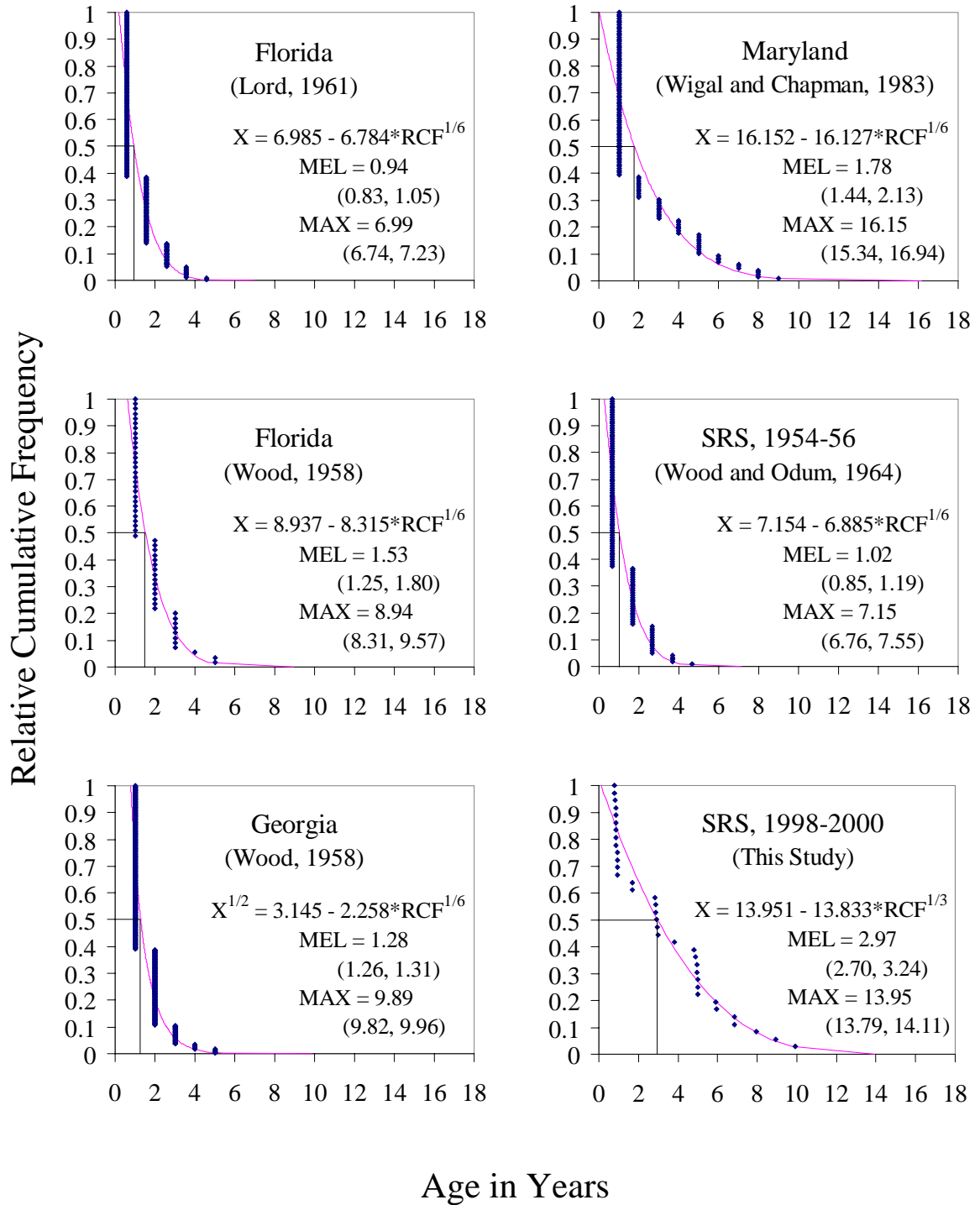
FIGURE 3—Ecological longevity curves for six populations of gray foxes, showing median (MEL) and maximum (MAX) ecological longevity values, 95% confidence limits, and equations for the lines.
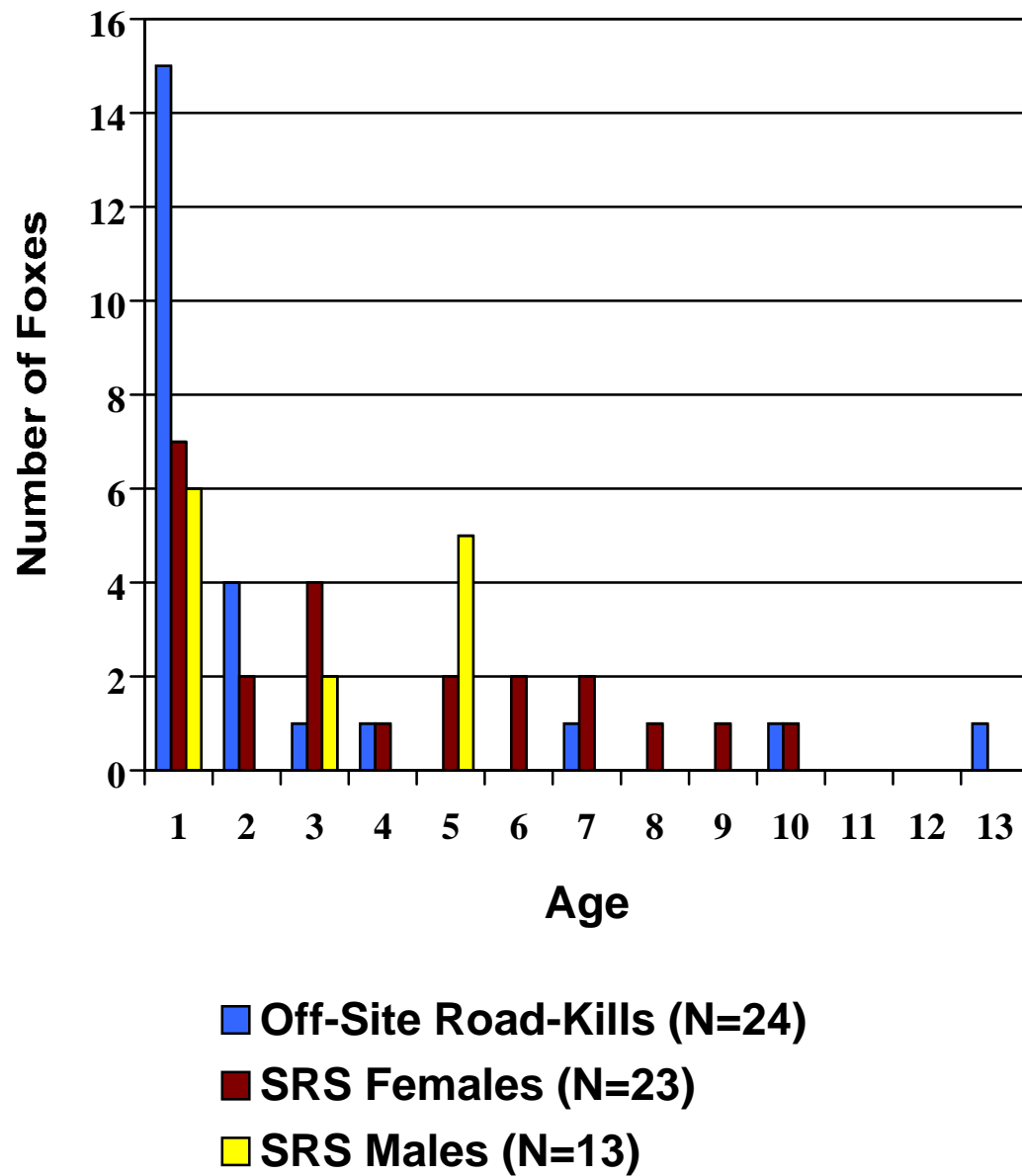
FIGURE 4—Number of cementum-aged gray foxes per age class, rounded to the nearest year, for foxes collected as road-kills from areas surrounding the SRS, and for SRS females and males. Ages of three recaptured foxes are given as the age at first capture only.

from the SRS. For comparison, 2 gray foxes living at the St. Louis Zoological Park lived

at least 11 years, 3 months, thus several wild gray foxes on the SRS and surrounding

areas have approached the oldest known aged foxes living in captivity.

Survival: The first estimate of survival (Table 11) came from Krebs' method (1999a)

using the number of animals in each age group.   Using data from 1998-2000, this method

yielded a survival rate of 0.69 per year (0.63, 0.74). Using only females whose fates

were known ($n = 6$ and $n = 8$ for 1998 and 1999, respectively), Mayfield's maximum

likelihood method estimated survival for 1998 and 1999 as 0.97 per year (0.89, 1.00) and

0.78 per year (0.60, 0.92), respectively (Table 11). Using foxes of both known and

unknown fate and assuming foxes of unknown fate died at the time their signal was lost,

annual survival rates for 1998 ($n = 8$) and 1999 ($n = 12$) were 0.81 (0.68, 0.91) and 0.62

(0.44, 0.78), respectively. To increase sample size, data from both years were combined

and survival calculated again. Using foxes of known fate ($n = 12$), annual female

survival was 0.95 (0.90, 0.98), while using foxes of both known and unknown fate ($n = $

18), survival was 0.87 (0.81, 0.92).

   The Kaplan-Meier method differs from Mayfield's maximum likelihood method

by integrating data from animals of both known and unknown fate without making any

assumptions about those animals whose signal was lost. According to this method,

annual survival rates for 1998 ($n = 8$) and 1999 ($n = 10$) were 0.88 (0.65, 1.00) and 0.43

(0.06, 0.80), respectively, while average survival for both years was 0.61 (0.20, 0.84).

Causes of Mortality: Due to difficulties associated with battery failures, inability to

recapture many females to replace batteries, foxes removing radio-collars, and occasional

inability to locate transmitter signals from females suspected of emigrating from the SRS,

mortality data were limited. Of 25 female gray foxes collared during the course of this

study (Appendix 1), 16 were of unknown fate due to the above-mentioned factors, 7 died,

and 2 were still alive at the end of this project when their batteries expired. Of the 7

females that died (Appendices 18, 19), 2 (28.6%) died of unknown causes, 2 (28.6%)

TABLE 11—Survival estimates for SRS gray foxes, 1998-1999.

Method	Year	n	Annual Survival (95% CL)
# of foxes in each age group	1998-1999	77	0.69 (0.63, 0.74)
Mayfield's Maximum Likelihood	1998		
Known Fate		6	0.97 (0.89, 1.00)
Known + Unknown Fate		8	0.81 (0.68, 0.91)
Mayfield's Maximum Likelihood	1999[a]		
Known Fate		8	0.78 (0.60, 0.92)
Known + Unknown Fate		12	0.62 (0.44, 0.78)
Mayfield's Maximum Likelihood	1998-1999		
Known Fate		12	0.95 (0.90, 0.98)
Known + Unknown Fate		18	0.87 (0.81, 0.92)
Kaplan-Meier	1998	8	0.88 (0.65, 1.00)
	1999	10	0.43 (0.06, 0.80)
	1998-1999	18	0.61 (0.20, 0.84)

[a]Includes 2 foxes originally caught in 1998 that were recaptured in 1999.

were killed by coyotes, 1 (14.3%) died from an automobile collision, 1 died of rabies and another was strongly suspected to have died of rabies (28.6%). Therefore, 40% of the deaths from known causes were attributed to coyotes, making these instances the first documented occurrence of coyote predation on gray fox. Although this latter fox died one year before the confirmed rabies case, rabies was believed to be the cause of death because both deaths occurred within ca. 4.3 km of each other, the unconfirmed case was underweight despite advanced pregnancy, and a raccoon trapped at the same site a few days prior to the unconfirmed case was extremely disoriented and severely underweight. Most mortality occurred during the month of April that had 5 deaths (2 coyote, 2 rabies, and 1 automobile), followed by 1 death in January (unknown), and 1 one in June (unknown).

Sex Ratio: The male:female sex ratios for 1998, 1999, and 2000 were 0.62:1 (8M:13F), 0.85:1 (11M:13F), and 0.67:1 (12M:18F), respectively. Sex ratios did not differ among years ($\chi^2 = 0.31$, $P = 0.856$), nor were any of them statistically different from 1:1 ($P = 0.192$, $P = 0.419$, $P = 0.181$ for 1998, 1999, and 2000, respectively). Combining all foxes across years, the cumulative sex ratio was 0.70:1 (31M:44F), which approached a significant difference from a 1:1 sex ratio ($P = 0.08$).

Reproduction: Because most necropsied females were euthanised from January-March but pregnancy often could not be verified until early March, sample sizes were small. The results, however, were comparable to other studies (Table 12). Average number of corpora lutea/female was 3.8 ($SD = 0.60$; $n = 11$), which was not less than the 4.6 reported from Maryland ($t = 2.05$, $P = 2.92$—Wigal and Chapman 1983), but was less than reported from Illinois ($t = 2.72$, $P < 0.05$—Layne 1958). The average number of implantations (counted as placental scars or embryos) in this study was 3.6 ($SD = 0.70$; $n = 10$), which was similar to the 3.77 from Illinois ($t = 0.663$, $P > 0.05$—Layne 1958) and the 4.48 from Florida ($t = 1.494$, $P = 0.074$—Lord 1961), but less than the 4.42 from

TABLE 12—Reproductive characteristics of gray fox populations[a].

Location	Ave. # Corpora Lutea	Ave. # Placental Scars	% Implanting	% Barren	Incidence of Resorption (%)[b]	Extent of Resorption (%)[c]	Total Pre-Natal Mortality	Reference
Florida		4.48 (16)						Lord, 1961
Alabama		3.84 (26)		6.5 (31)				Sullivan, 1956
Georgia		4.56 (141)						Wood, 1958
Maryland	4.6 (12)	4.42 (12)	88.0 (12)	45.0 (31)			39.0%	Wigal & Chapman, 1983
New York		3.66 (35)		3.3 (90)				Sheldon, 1949
New York	5.2 (47)	4.40 (42)	78.1 (27)	3.8 (53)	13.6 (44)	52.4 (21)	30.0%	Layne & McKeon, 1956
Illinois	4.4 (32)	3.77 (56)	85.8 (50)	2.0 (49)	37.0 (19)	52.0 (27)	32.0%	Layne, 1958
SRS, 1998-2000	3.8 (11)	3.6 (10)	94.7 (10)	11.1 (18)	40.0 (10)	46.2 (13)	31.3%	This study

[a] Sample sizes are given in parentheses.

[b] Defined as the percent of pregnant females that resorbed at least one embryo.

[c] Defined as the average percent of a litter that is resorbed in females that resorb at least one embryo.

Maryland ($t = 2.79$, $P = 0.006$—Wigal and Chapman 1983) and the 4.56 from Georgia ($t = 3.894$, $P < 0.001$—Wood 1958).

Assuming one corpora lutea was equivalent to one released egg, total percent implanting was calculated as

$$(\# \text{ implantations} / \# \text{ corpora lutea}) \times 100$$

resulting in an implantation rate of 94.7%. Four of the 10 pregnant females examined had at least one resorbing embryo, therefore, the incidence of resorption was 40%. Of those females experiencing resorption, a total of 6 embryos were resorbed out of 13 implanting, making the extent of resorption 46.2%. Of all females on the SRS old enough to have reproduced at least once, 2 females out of 18 failed to breed, making the barren rate 11.1%.

Based on these numbers, the total pre-natal mortality was estimated: of 100 females, a total of 380 corpora lutea would potentially be released. Of these 100 females, however, 11.1% would fail to breed, leaving only 89 breeding females. These 89 females would release 338 corpora lutea, of which 18 would fail to implant, leaving an average of 3.60 implantations/breeding female. Because 40% of the breeding females will experience resorption, 36 would not give birth to all the implanted embryos. These 36 resorbing females would resorb 46.2% of their litters, or 1.66 embryos/litter. Therefore, resorbing females would give birth to 1.94 pups/litter for a total of 69 pups. Those 53 females not resorbing would give birth to 3.6 pups/litter for a total of 192 pups. A total number of 261 pups would therefore be born to the 100 females. Because 261 pups would be born out of a potential maximum of 380 corpora lutea, the total pre-natal mortality would be 31.3%.

Combining pre-natal mortality with the sex ratio yields 153.6 pups born/100 foxes of both sexes, which is the highest birth rate of any population reported in the literature (Table 13). Furthermore, as the number of females/100 SRS foxes increased the number of corpora lutea/female decreased ($r^2 = 0.915$, Fig. 5).

TABLE 13—The number of pups produced per 100 foxes (male and female) for 4 gray fox populations.

Location	Sex Ratio (M:F)	# Females/100 Foxes	# Corpora Lutea/Female	Total # Corpora Lutea	Total Pre-Natal Mortality	# Pups/100 Foxes	Reference
Maryland	1.2:1	45.5	4.6	209.1	39.0%	127.5	Wigal & Chapman, 1983
Illinois	1.1:1	47.6	4.4	209.5	32.0%	142.5	Layne, 1958
New York	1.4:1	41.7	5.2	216.7	30.0%	151.7	Layne & McKeon, 1956
SRS 1998-2000	0.7:1	58.8	3.8	223.5	31.3%	153.6	This Study
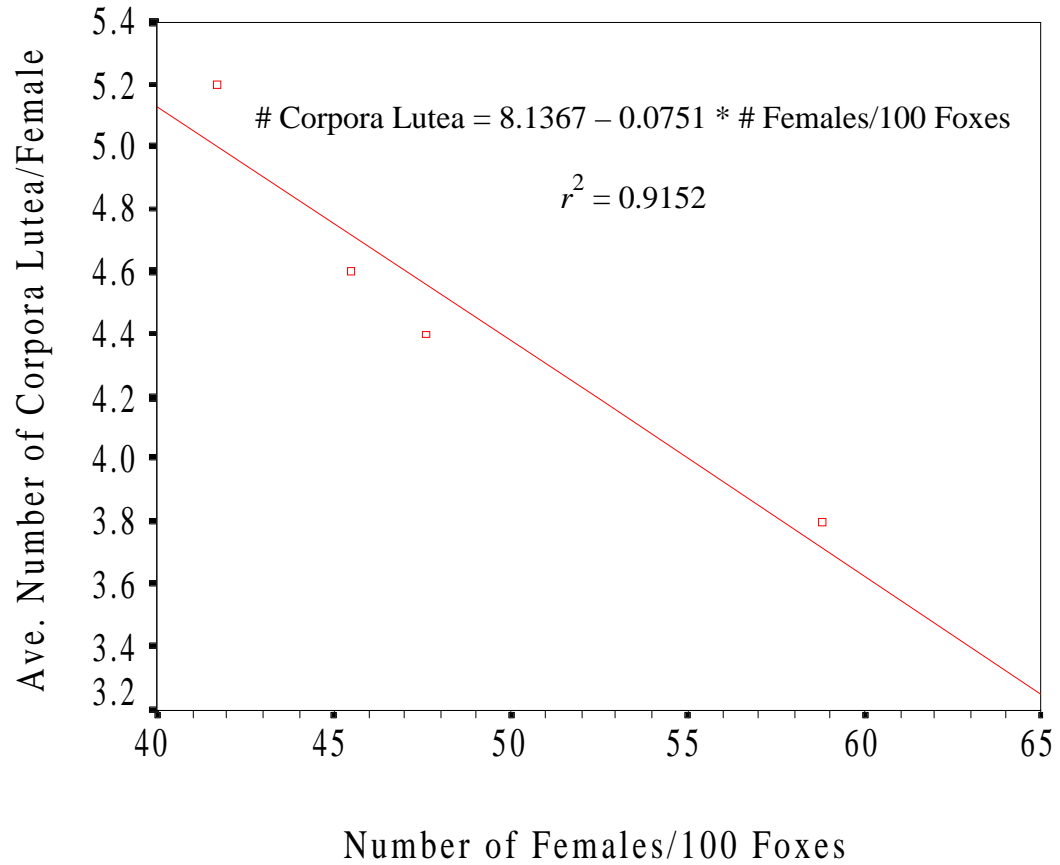
FIGURE 5—Regression of the average number of corpora lutea/female on the number of female gray foxes/100 foxes.

CHAPTER 4

DISCUSSION

Home Range, Density, and Rate of Increase (r): Average catch per unit effort (CPUE) in this study was 1.92 gray foxes/100 trap-nights. Calculating the same effort using Wood and Odum's (1964) data for the SRS 1954-62 yields an average of 4.5 gray foxes/100 trap-nights. The first year they trapped, however, yielded an unusually high number of captures. When data from 1954 were removed, then CPUE was only 3.7 gray foxes/100 trap-nights. Although the greater CPUE on the SRS 1954-62 seems to suggest a larger population than this study documented, the two studies are in fact not directly comparable. Wood and Odum (1964) conducted their survey during November when they believed density and movement were greatest, while trapping in this study occurred January-March after many young foxes had dispersed.

Although density is often calculated using a mark-recapture estimate of population size, this method was deemed unreliable in this study for two reasons. First, the characteristics of the SRS gray fox population violate one of the primary assumptions of mark-recapture methodology, population closure (Krebs 1999a; Pollock et al. 1990). Closed populations are assumed to have no losses due to death or emigration, and no additions due to birth or immigration. But estimates in this study were based on data separated by a time interval of 1 year, during which births and deaths were documented in this study, thereby violating population closure. Emigration off-site also was strongly suspected in this study, and was mentioned as a possibility when Sawyer (1988) failed to locate 3 of 23 radio-collared gray foxes on the SRS in 1985. Violation of closure is even more likely with the Schnabel and Chao's time-variation estimates, which cover intervals of 2 years. The second problem is that, with the exception of Chao's estimate, mark-recapture methods rely heavily on the number of recaptures. In three years of trapping, only 3 gray foxes were recaptured out of 75 different individuals trapped. Most of these

methods are considered unreliable with less than 7 recaptures, and this was reflected in the large confidence limits around each estimate. Chao's estimate, however, is specific for low numbers of recaptures, thus this estimate of 1.30 gray foxes/km^2 is potentially accurate. Because of such common inadequacies, however, most carnivore researchers have found these methods unsatisfactory. A common solution has been to estimate density using home range size and overlap.

Mean home range size ($\pm SD$) across all seasons for female SRS gray foxes ($n = 6$) was 2.21 km^2 (± 0.96). Assuming no home range overlap yields a conservative density estimate of 0.45 foxes/km^2 (Table 14).   Minimum female density on the SRS based on across-season home range size and no overlap has been reported as 0.94 foxes/km^2 (home range = 1.06 km2—Jeselnik 1981) and 0.44 foxes/km^2 (home range = 2.29km2—Sawyer 1988). Because gray fox females are known to share home ranges with their mates and possibly their adult 'helper' female offspring (Chamberlain and Leopold 2000; Jeselnik 1981; Sawyer 1988; Wooding 1984), these estimates likely underestimate true density. Jeselnik (1981), for example, reported a high degree of home range overlap and suggested that true gray fox density on the SRS was 1.24 foxes/km^2. Because females in this study were too widely separated to share home ranges, percent overlap could not be calculated. Using instead the average percent home range overlap Jeselnik (1981) found between mated pairs (87%) and among neighboring foxes (35%), 2 mated pairs in this study would be expected to share 4.12 km^2 for a density estimate of 0.97 foxes/km^2. This estimate, however, assumes that home range sizes of males are equal to those of females. On the SRS, both Jeselnik (1981) and Sawyer (1988) reported male across-season home ranges were larger than female ranges (22% and 10% larger, respectively), though these results were not statistically significant ($P > 0.05$). Because Chao's density estimate is the most accurate of the mark-recapture methods and because Chao's estimate is higher than the estimate based on home range overlap, the density estimate of 0.97 gray foxes/km^2 is reasonable.

TABLE 14—Average across-season home range sizes for female gray foxes and the corresponding density estimate (number of foxes/km^2) assuming no home range overlap and the researcher's estimate of true density (both sexes) given their observed home range overlap.

Location	Home Range in km^2 (n)	Density	Citation
Florida	3.7 (3)	0.27-unknown	Labisky and Progulske, 1982
Alabama	9.33 (10)	0.11-0.63	Nicholson, 1982; Nicholson and Hill, 1984
Alabama	4.1 (5)	0.24-unknown	Wooding, 1984
SRS, 1979	1.06 (7)	0.94-1.24	Jeselnik, 1981
SRS, 1985	2.29 (6)	0.44-unknown	Sawyer, 1988
SRS, 1998-2000	2.21 (6)	0.45-0.97	This study

Lower density estimates have been reported for other southeastern states. In Florida, Labisky and Progulske (1982) reported female density as 0.27 foxes/km^2 (minimum area home range = 3.7 km^2; n = 3), but believed that density for both sexes could be as high as 1.0 fox/km^2. This estimate was similar to Wooding's (1984) findings in Alabama where 5 females had average home ranges (minimum convex polygon) of 4.1 km^2, or 0.24 foxes/km^2, yet home range overlap was noted between several animals implying that true density was higher. In another Alabama study, Nicholson (1982) reported average adult female home range size (minimum convex polygon) was 9.33 km^2, for a density of 0.11 foxes/km^2, although Nicholson and Hill (1984) reported 5 foxes (both sexes) lived in 8.0 km^2 yielding a density of 0.63 foxes/km^2. This result further emphasizes the potential for home range data to underestimate gray fox density. The estimate of 0.97 foxes/km^2 reported for female gray foxes in this study, then, appears to be higher than that of most other southeastern populations.

Although the rate of increase calculated using the Chapman method indicated a slowly declining population (r = -0.39), this method is likely to be unreliable due to few recaptures and lack of population closure. Regressing scent-station indices against time resulted in a rate of growth equal to -0.57, which did not differ from zero (P = 0.790), thus indicating stable numbers. Scent-station methodology, however, also has been criticized as inaccurate, and several researchers have pointed out its inability to detect anything but the grossest of population changes (Diefenbach et al. 1994; Minser 1984).

If these estimates are correct, however, the likelihood is that the slow decline indicated merely represents a transitory situation in which the population fluctuates around a mean growth rate of zero. The total number of gray foxes living on the SRS, then, ranges from a conservative estimate of 385 to a more liberal 765 foxes.

Habitat Preference: Although sample size was small (n = 6) and the results were not significant, the compositional analysis did reveal informative trends. The lack of any

detectable habitat preference, for example, is not surprising because gray foxes have been reported as being habitat generalists (Haroldson and Fritzell 1984) that prefer ecotonal areas (Jeselnik 1981) and areas with a diversity of fields and woods rather than large areas of one habitat type (Wood et al. 1958). Gray foxes on the SRS live in just such a diversity of habitat patches (Table 2).

When selecting a home range within the SRS boundaries, however, gray foxes seem to select open areas and avoid hardwoods. The tendency for gray foxes in this study to prefer open areas is similar to the findings of several other researchers (Haroldson and Fritzell 1984; Labisky and Progulske 1982; Trapp 1973; Yearsley and Samuel 1980) who reported preferences for open brushy areas. This tendency, however, is contrary to Sawyer and Fendley (Sawyer and Fendley 1994) who actually found that gray foxes on the SRS used the 0-4 year-old pine/oldfield habitat less than expected. Several researchers have also noted an aversion to hardwoods (Chamberlain and Leopold 2000; Labisky and Progulske 1982).

When selecting areas within their home range, open areas again ranked highest and hardwoods ranked second. This apparent increase in hardwood use, however, is probably an anomaly based on habitat use by only one fox (GF-107). Hardwoods accounted for 46.29% of this fox's home range which she used 57.14% of the time (based on the number of radio-locations). The other 5 foxes averaged only 18.37% ($\pm$7.35) hardwood in their home ranges and used this habitat an average of 18.64% ($\pm$10.44) of the time. When this fox was removed from the analysis of habitat preference within home ranges, hardwoods fell in rank to third after open area and open canopy pine, though again, no overall habitat preference was detected ($\Lambda = 0.261$, $P = 0.365$). In general, then, hardwoods are unlikely to be preferred at either level of analysis.

At both levels, however, female gray foxes seem to prefer open canopy pine and avoid dense canopy pine. Because nearly all telemetry locations were taken during the evening when foxes were expected to be foraging, this suggests the possibility that open canopy pine offers more food resources. Because open canopies allow more light to the

forest floor, such areas are more likely to support an understory component than would dense canopies. Labisky and Progulske (1982) reported gray foxes preferred areas with dense understories. Such habitats are abundant on the SRS, with open canopy pine (40.3% of the SRS) associated with all stand ages, but dense canopy pine (14.2% of the SRS) almost exclusively found in stands >30 years old (U. S. Forest Service 2000; Wiggins-Brown et al. 2000).

The relationship between stand age and understory gains support from other studies. In Mississippi, gray foxes selected for areas with abundant small mammals, which were usually found in mature pine ($\geq$30 years), 0-8 year-old pine, and hardwood (Chamberlain and Leopold 2000). Sawyer (1988) also found that SRS gray foxes preferred 5-14-year-old pine and mixed pine-hardwood. Other studies (Atkeson and Johnson 1979; Kirkland 1990; Loeb 1997; O'Connell and Miller 1994; Umber and Harris 1974) show similar findings, reporting that oldfields and young pine stands (<10 yrs.) have an abundance of small mammals and plant species producing soft mast, all of which are important foods for gray fox (Greenberg and Pelton 1991; Novaro et al. 1995; Wood et al. 1958). Beyond stand ages of 10 years, however, small mammal abundance typically decreases (Atkeson and Johnson 1979; Kirkland 1990; Loeb 1997; O'Connell and Miller 1994; Umber and Harris 1974).

Although few data are available for mature pine stands, Loeb (1997) reported an increase in abundance in the most mature stands (>60 years) on the SRS. Harris, et al. (1974) reported bird and small mammal abundance and diversity in Florida was much greater in mature longleaf pine than any other habitat type. Hedman (2000) went further, reporting longleaf pine stands to have significantly more herbaceous species and greater herbaceous cover than those of loblolly or slash pine. The interspersion of old and young pine on the SRS, along with mixed pine-hardwood creates a mosaic of habitats and ecotonal areas, which may be favorable to gray foxes (Jeselnik 1981).

Age Structure: The current age structure of SRS gray foxes differs greatly from those of all other populations of this species, including this same population from 1954-56 (Table 10; Figs. 2, 3). This dramatic difference is most likely due to a combination of habitat changes on the SRS and the absence of harvest. Although the pine plantations currently prevalent on the SRS may not be ideal habitat, it is likely to be better suited to gray foxes than the agricultural habitat that predominated in the early 1950s (Follmann 1973; Fuller 1978; Haroldson and Fritzell 1984; Trapp 1973; Yearsley and Samuel 1980). As habitat on the SRS was allowed to undergo succession and harvest was eliminated, conditions became more favorable to gray foxes and more individuals survived to older ages.

Comparing populations with ecological longevity curves (Fig. 3) confirms the unusual demographics of the SRS population. These equations predict median ecological longevity (MEL) for the SRS foxes as 2.97 years, which is significantly higher ($P > 0.05$) than any other population studied. Maximum ecological longevity (MAX) is also higher than any other population except Maryland (13.95 vs. 16.15 years, respectively). Because MAX is a measure of environmental favorability (Dapson 1971), the conditions in Maryland at the time of the study may have been even more favorable to gray foxes than the current SRS conditions, although the greater proportion of SRS foxes $\geq$34 months old suggests otherwise.

The age structure of the current SRS population thus appears to be unusual, with 10-, 22-, and $\geq$34-month-olds comprising 37.2%, 10.3%, and 52.6% of the population, respectively. Merging the 22- and $\geq$34-month-old age groups as adults, this age structure yields a combined juvenile:adult ratio of 0.59:1, the lowest ratio yet noted for a wild gray fox population. Previous studies have reported juvenile:adult ratios as 1.6:1 (Lord 1961; Wigal and Chapman 1983; Wood 1958), and 1.7:1 (Wood and Odum 1964). The low juvenile to adult ratio in the current SRS population is apparently stable because low ratios were observed in each of the three years of this study. In 1998, 1999, and 2000 the juvenile:adult ratios were 0.64:1, 0.60:1, and 0.55:1, respectively. Because these ratios for 1998 and 1999 were based primarily on adjusted tooth-wear while the ratio for 2000

was based primarily on cementum analysis, the true ratio is likely to be similar to the 0.55:1 estimate found using the more accurate cementum method. The average ratio of 0.60:1, therefore, is probably a reasonable estimate.

The lower proportion of juveniles (ca. 10 months) in the SRS population may be due to either low adult reproductive rates, low juvenile survival, or high juvenile emigration from the SRS prior to the sampling period. The large percentage of reproductive females ≥ 2 years old suggests that low reproduction is an unlikely explanation. This is further supported by a reproductive rate of 3.60 young/litter, a total pre-natal mortality rate of 31.3%, and a production of 153.6 pups/100 foxes, all of which are comparable to other studies (Tables 12, 13).

Low juvenile survival also is unlikely for several reasons. First, juveniles are subject to the same mortality factors as adults. Distemper and rabies are the two diseases most likely to cause high levels of mortality in gray fox populations, and both are considered 100% fatal to adults and juveniles alike (Davidson et al. 1992b). Thus, diseases likely to kill juveniles would also be likely to kill adults as well, and because the age structure is biased toward adults and adult survival is high, juveniles are not likely to be exposed to unusual mortality from either distemper or rabies. Juveniles, however, are more susceptible than adults to canine parvovirus and starvation (W. R. Davidson, pers. comm.). Although a study of gray foxes imported illegally from Indiana to South Carolina (February 1990) revealed antibodies to canine parvovirus in all 18 foxes examined (Davidson et al. 1992a), not a single case was diagnosed by the Southeastern Cooperative Wildlife Disease Study out of 157 gray foxes examined from 1972-1989 (Davidson et al. 1992b). The fact that gray foxes are known to survive parvovirus infections (W. R. Davidson, pers. comm.), coupled with the lack of reported cases in the state of South Carolina, suggests that parvovirus infection is also unlikely to be an important cause of the low proportion of juvenile foxes in the current SRS population.

Starvation is also improbable. Because this population meets Van Horne's (1983) requirements for good habitat quality, parents are likely to be able to find ample food

resources while raising their young. This is further supported by studies examining the relationship of managed pine stands to small mammal populations and fruit-bearing shrubs and vines (Harrington and Edwards 1999; Harris et al. 1974; Hedman et al. 2000; Loeb 1997; Mengak et al. 1989; O'Connell and Miller 1994), all of which are frequently used by gray foxes as food sources (Greenberg and Pelton 1991; Nelson 1933; Wood et al. 1958). Even though these foods are also eaten by coyotes, Small (1971) reported no evidence of food competition between coyotes and gray foxes because they appeared to forage in different areas. Thus, starvation of juvenile foxes is unlikely.

Road deaths are also unlikely to explain the low proportion of juveniles, as vehicular traffic density is relatively low on the SRS, and only 15 foxes were collected dead on SRS roads from July 1997-December 1999. Of these, 5 were juveniles <10-months-old, making the juvenile:adult ratio for road-killed foxes 0.50:1, which does not differ from the 0.59:1 obtained from age structure data ($\chi^2 = 0.08$, $P = 0.776$).

The most probable explanation, then, is high juvenile emigration. High juvenile emigration often occurs when densities are high and the chances of obtaining an adult home range in the area are low (Murray 1967). Based on home range estimates, gray fox density on the SRS is among the highest ever reported, thereby supporting the hypothesis of high juvenile emigration. Anecdotal evidence further supports this supposition. Of 25 females radio-collared during this study, signals from 11 females were lost shortly after release, and only 2 of those 11 were known to have found vacant territories. Subsequent helicopter flights over the SRS revealed that those 2 foxes had emigrated 4.1 (GF-151) and 9.4 (GF-120) km from their capture location where they found home ranges and lived for several months (Appendix 20). Because the longest axis length for the 6 home ranges averaged 2.3 km, a fox was considered to have emigrated if it moved >2 km away from the site of initial capture. Another fox (GF-117) was relocated 5.3 km from her capture location, but was never found again (Appendix 21). Two other females were nuisance animals removed from a secured area, fitted with radio-collars and released 13.3 km away from the site of their capture on 11/5/98. One moved 12.8 km (GF-145) before

finding a home range on the SRS where she was known to live until her collar failed shortly after 4/6/99 (Appendix 20). The other (GF-146) was last known 4.7 km away from her release location on 11/10/98, though she was never found afterwards (Appendix 21). GF-117 and the remaining six foxes, which were never found after release, were assumed to be emigrating. A more extensive airplane search covering the SRS and surrounding areas (encompassing a ca. 16 km border around the SRS east of the Savannah River) failed to relocate those foxes. If these foxes did emigrate off the SRS and out of the area covered by aerial surveys, the minimum distances they traveled just to reach the edge of the site ranged from 1.4-8.5 km. If these foxes emigrated further than the area covered by aerial surveys, then the minimum emigration distances (from release site to the edge of airplane surveys) ranged from 17.4-24.5 km. Studies in Alabama have reported juvenile gray foxes emigrating 7.3 km (Sullivan 1956) and 3-24 km (Nicholson et al. 1985), while one juvenile gray fox vixen in New York was reported to have dispersed 83.9 km (Sheldon 1953).

High juvenile emigration, however, explains more than just the low juvenile:adult ratio. High emigration also explains the unusually low proportion of 22-month-olds and the unusually high proportion of $\geq$34-month-olds—an age structure similar to that reported by Wigal and Chapman (1983) in Maryland (Table 10). Although these authors did not comment on their unusual age distribution, a likely explanation can be found by examining trends in canid social structure. When examining sociality among canids, Moehlman (1989) found that small canids (<6.0 kg) are usually monogamous, but on occasion are polygynous. This leads to a tendency toward a female-biased sex ratio, female helpers, and male dispersal. Although she had no data on gray fox social structure, average weight of gray foxes in this study was 3.9 kg ($n = 68$) which indicates their potential to follow this social pattern. If they do, then in high-density situations where vacant home ranges are few, a recently mature 10-month-old fox may not be able to secure its own territory. In such cases, a 10-month-old female may forego reproduction during her first year to live on her parents' territory and help raise their new

litter. By age 2, however, this helper female may disperse to raise her own young. A 10-month-old male fox, however, would almost never be allowed to stay and would be forced to emigrate. This social structure is known to occur in red foxes (Macdonald 1979; Schantz 1982) which weigh ca. 4.5 kg (Ables 1975), thus, the smaller gray fox likely follows this pattern as well. Under this scenario, then, the proportion of 10-month-olds in this study would consist of those trapped foxes that were still in the process of emigrating, plus those helper females remaining on their parents' range, plus a few 10-month-olds that managed to establish adult territories of their own on the SRS. Those few 10-month-olds that managed to establish home ranges on the SRS would be the only foxes available to become members of the 22-month-old age class the following year, thus explaining the low proportion of 22-month-olds. For those foxes that do manage to establish a territory, the chances of entering the oldest age group and living a long life are good, hence, the large proportion of individuals in the $\geq$34-month-old age group. In fact, average life span (calculated from cementum ages—Table 10, Appendix 12) for the SRS gray fox population is 3.5 years—a sharp contrast to the 1.8 years reported for other populations (Table 10). Thus, good habitat and lack of harvest lead to high density, and high density interacts with social structure to produce an unusually low proportion of 10- and 22-month-olds and an unusually high proportion of $\geq$34-month-olds.

The above scenario suggests differential dispersal between the sexes, which in turn could lead to age structure differences. Without quantifying immigration and emigration for the SRS population and surrounding areas, however, this possibility can neither be supported nor refuted. In this study, male and female age structures do not differ ($\chi^2 = 1.56$, $P = 0.459$—Table 9). The percentages of males in the 10-month-old, 22-month-old, and $\geq$34-month-old age classes are 33.3% ($n = 11$), 15.2% ($n = 5$), and 51.5% ($n = 17$), respectively. The same percentages for females are 40.0% ($n = 18$), 6.7% ($n = 3$), and 53.3% ($n = 24$).

Assuming emigrating foxes are more likely to be hit by cars, data from road-killed foxes collected from areas surrounding the SRS also fail to support differential dispersal

between the sexes. Average age ($\pm SD$) of road-killed males was 2.8 (± 3.8) years while average age for road-killed females was 1.5 (± 2.0) years (Appendix 16). Although males were not statistically older than females ($P = 0.145$), this at first suggests that road-killed males were adults likely to have established home ranges already, while road-killed females may have been emigrating, which seems contrary to Moehlman's (1989) prediction that small canid males should disperse earlier than females. However, many of these road-killed foxes were collected in the vicinity of a protected urban forest (Hitchcock Woods). The two oldest foxes (GFRK-07 and GFRK-38, ca. 10 and 13 years old, respectively) were both males that were killed on the edge of this forest. If those two are removed from the calculations, then average age of off-site road-killed males was only 1.4 (± 0.9) years, which is almost exactly the same as the average age of 1.5 (± 2.0) years for road-killed females.

Continuing to exclude the two oldest males, average age ($\pm SD$) of road-killed gray foxes (males and females combined) collected from areas surrounding the SRS was 1.4 (± 1.4) years (Appendix 16), which is significantly lower ($P < 0.001$) than the 3.5 (± 2.6) years (Table 9) of the SRS population. Although the road-killed foxes were from areas subject to harvest pressure (5,989 gray foxes harvested in South Carolina from 1997-2000), the lower average age of this sample cannot be attributed solely to harvest, as this sample seems to have been biased toward emigrating individuals more likely to be hit by cars. This is supported not only by the average age of road-killed foxes, but also by the observation that 16 of the 24 (66.6%) road-killed foxes were hit from August-January when foxes were potentially emigrating.

Although the average age of the SRS population cannot be directly compared to a nearby harvested population, the lack of harvest pressure on the SRS may allow more individuals to reach the ≥ 3-year-old age class and further explain the low proportion of juveniles (ca. 10 months) in this study. What little data exist, however, can neither support nor refute this possibility (Table 15—Carmichael and Baker 1996). Using linear regression analysis on the data provided in Carmichael and Baker (1996), trapping

TABLE 15—Average annual harvest and number of trapping licenses sold versus age

structure for southeastern gray fox populations[a].

State	# Trapping Licenses per 100 sq. mi.	Annual Harvest per 100 sq. mi.	% Juveniles	% $\geq$3.5 yrs.
Arkansas	15.8	16.9	64.2	10.6
Kentucky	15.3	-	54.7	12.8
Georgia	4.5	37.4	61.0	13.8
North Carolina	11.2	0.8	59.0	8.4
South Carolina	1.7	23.5	51.9	13.3
Texas	-	13.3	59.2	-
West Virginia	-	60.8	61.2	-

[a]From Carmichael (1996).

license sales/100 mi^2 is not related to the percentage of either juveniles (Proc REG, $P = 0.465$, $r^2 = 0.189$) or adults ($P = 0.380$, $r^2 = 0.261$). Annual harvest/100 mi^2 also fails to explain the percentage of juveniles ($P = 0.766$, $r^2 = 0.025$), though a positive relationship appears to exist between annual harvest and the percentage of adult gray foxes ($P = 0.052$, $r^2 = 0.900$). These numbers, however, are based on only a few states so their significance is unclear. Slough and Mowat (1996), however, found harvested lynx (*Lynx lynx*) populations had 40% more yearlings than that in an untrapped refugium. It appears, then, that the absence of harvest combined with an abundance of appropriate habitat has resulted in a high-density population of relatively old-aged gray foxes on the SRS.

Survival and Mortality: In this study, mortality was caused by automobile collisions (14.3%), coyotes (28.6%), rabies (28.6%), and unknown factors (28.6%). In comparison, Nicholson and Hill (1984) noted motor vehicle collisions accounted for 14% of all confirmed deaths, trappers were responsible for 29%, and disease accounted for 43%, though death due to disease may have been as high as 50%. In addition to the 2 radio-collared females killed by coyotes, another 8 month-old female gray fox was found by chance on a dirt road on the SRS on November 5, 1998, whose death was determined by SCWDS to be caused by a coyote. Although coyotes have long been known to kill red foxes and cause their populations to decline (Sargeant 1982; Small 1971), this study provides the first documentation of coyotes killing gray foxes. Whether or not coyotes cause population-level effects on gray foxes is unknown at this time; however, both radio-collared females killed by coyotes were killed while they were potentially pregnant or raising pups.

In Nicholson and Hill's (1984) study, 4 deaths occurred in July, 3 in January, 2 in October and December, and 1 each in February, June, and September. In this study, April was the month of greatest mortality with 4 deaths, followed by 2 deaths in January, and 1 one in June (Appendix 18). No particular time of year, then, poses a greater risk to gray foxes than any other time of year. One aspect that should be noted here, however, is

that 5 of the 7 deaths in this study occurred while females were probably raising young. Of those 5, 2 were known to be pregnant, 1 was known to be barren, and the other 2 were recovered in a decayed state, which precluded an assessment of their reproductive condition.

Averaging the three estimates for 1998-1999 (1-number of foxes in each age group, 2-Mayfield known + unknown, and 3-Kaplan-Meier) yields an average annual survival of 0.72. Although the most conservative 1998-1999 Mayfield estimate yielded annual survival of 0.87, this method has the disadvantage of assuming all animals are marked at one time. In this study, foxes were marked each year over a period of three months but were entered into the estimator as if they were all caught in January, thus inflating the Mayfield estimates. Additionally, foxes that died or whose signal was lost were either not considered at all or assumed to have died. The effects of this assumption are unknown. The Kaplan-Meier estimate, however, is a staggered entry design that allows animals to be entered or removed at any time while making no assumptions about fates of unknown individuals. The Kaplan-Meier estimate is also comparable to the estimate based on the number of foxes in each age group; therefore, the 1998-1999 Kaplan-Meier annual survival estimate of 0.61 is likely the most accurate.

Despite the conservative nature of these estimates, however, survival of gray foxes on the SRS appears to be greater than has been reported elsewhere. Combining all age groups, Wigal and Chapman (1983) estimated mean survival rate of gray foxes in Maryland as 0.52. In Florida, Lord (1961) reported annual survival rate of adults (>7 months) to be only 0.37—a value much lower than any of the survival rates estimated for SRS gray foxes. In Georgia, Wood (Wood 1958) reported adult survival as 0.50. These survival estimates are all lower than the yearly survival estimate of 0.61 for this population. This difference is understandable because these other studies were carried out under conditions of exposure to harvest. The high survival rate on the SRS, then, allows this population to have the highest proportion of adult foxes ever reported.

Sex Ratio: The sex ratio of the gray fox population on the SRS differs from others reported in the literature, nearly all of which report fewer females than the SRS population. In Georgia and Florida, Wood (1958) noted the ratio of males to females was 1.2:1, which did not differ from the expected 1:1 ratio. Similarly, in the years after the closing of the SRS to pubic access, the ratio was 1.08:1 (Wood and Odum 1964); in Illinois it was 1.1:1 (Layne 1958), and in Alabama the male:female ratio was 0.98:1 (Sullivan 1956). Working with the SRS gray fox population in 1987, Sawyer (1988) reported the ratio was 1.27:1. In 1998-2000, however, the SRS has relatively fewer males, with a male:female ratio of only 0.7:1. The sex ratio was skewed toward females in all three years of the study (0.62:1, 0.85:1, and 0.67:1 for 1998, 1999, and 2000, respectively). Any trapping bias should actually have favored males because males exhibit greater mobility than females during the trapping season (Layne and McKeon 1956).

This skewed sex ratio is supported by Moehlman's (1989) prediction that small canids (<6 kg) tend to exhibit a bias toward females, though the results of this study and those in the literature indicate that gray foxes may only show this bias under extremely favorable conditions. Furthermore, high quality habitat, which can include a lack of harvest pressure, has occasionally been found to favor female-biased sex ratios in pocket gophers (*Thomomys bottae*—Patton and Feder 1981), voles (*Microtus californicus*—Ostfeld et al. 1985), and house mice (*Mus musculus*—DeLong 1967). In these species, low-density populations favor a 1:1 sex ratio while high-density populations in the best habitats are biased toward females.

The low proportion of males in this population also supports Moehlman's (1989) prediction that small canids have a bias toward male emigration. Furthermore, no 2-year-old males were found in the sample of 13 cementum-aged male foxes from the SRS (Appendix 13), also indicating a tendency for young males to disperse.

Reproduction: In many cases a high-density population might be expected to be reproductively inhibited and have a reproductive output lower than that of a low-density population on a per-female basis. In fact, SRS gray foxes have an average of 3.6 young/litter (*SD* = 0.70)—a number lower than most other populations (Table 12). However, the female bias in the SRS population compensates for this slightly lower litter size resulting in the highest number of pups born/100 foxes (Table 13). Furthermore, according to the age structure, this reproductive rate is accomplished primarily by old-aged foxes. Although the sample sizes in this study were too small to test the relationship between age and reproductive output, the end result is the same; an old age structure in these gray foxes did not necessarily hinder the population's reproductive output as it does in many other species.

Reproductive output is also influenced by the percentage of barren females. In the SRS population, the barren rate was 11.1%, which was slightly higher than reported for Alabama and several times higher than reported for Illinois and New York (Table 12). In England, a high-density population of red foxes had a higher barren rate than a low-density population even though the mean litter size was almost identical (Harris and Smith 1987). The relatively high barren rate of the SRS foxes, then, may be due to the high density.

Combining barren rate with other reproductive parameters yields a total pre-natal mortality of 31.3%, which is comparable to other studies (Table 12). So despite a relatively high barren rate for SRS gray foxes, the total pre-natal mortality remained about the same. For that to occur, either the percentage of ova implanting must be higher or the incidence and extent of resorption must be lower in SRS gray foxes than in most other populations. The percentage of ova implanting appeared higher in SRS gray foxes, while resorption remained approximately the same as other populations (Table 12). Furthermore, combining pre-natal mortality with the sex ratio yielded the highest number of pups born/100 total foxes of any population studied (Table 13). In SRS gray foxes, then, the association between high density, high stress, and lowered reproductive output

(Christian 1950; Christian and Davis 1956) may not apply. This suggests that the high quality habitat and lack of harvest on the SRS may alleviate some of the stress that would otherwise be expected to reduce reproduction. Even under the high density conditions reported here, stress is likely to be low because the social system of the gray fox may allow for tolerance of neighboring non-reproductive individuals when conditions are favorable (Moehlman 1989). This high rate of reproduction meets the third and final requirement for high quality gray fox habitat. The end result then, is a large, high-density population filled with old foxes that continue to reproduce at the same level as lower-density harvested populations.

Management Implications: Understanding population parameters under ideal circumstances enables researchers to better understand the effects of harvest on gray foxes. For example, this study demonstrated that populations can reach densities at least as high as ca. 1 gray fox/km^2, which can be helpful in assessing habitat quality elsewhere. Based on the results of this study, favorable habitat for the southeastern gray fox appears to be a mixture of pine species and ages interspersed with patches of open area. This is also helpful in assessing habitat quality in managed areas.

We also know that reproductive output for both managed and protected populations remains roughly the same. There is no evidence, then, that the harvest levels associated with previous studies have altered gray fox reproductive capabilities at the population level. Furthermore, the average pre-natal mortality coupled with high density, high survival rates, and an old age structure strongly suggested that this population functions as a source population for the surrounding areas. To qualify as a source, a population's birth rate must exceed the death rate and emigration must exceed immigration (Pulliam 1988). The number of pups born/100 foxes along with the high survival rate in this population suggest that the first requirement has been met (Tables 11, 13). Because immigration and emigration were not quantified, it is unknown at this time if the second requirement is met. However, the high density and old age of resident foxes

implies that very few vacant home ranges are available to 10-month-old individuals. If we make the reasonable assumption that the likelihood of a fox finding a given vacant territory is inversely proportional to the distance that such a territory is from its natal range, then vacant territories on the SRS are most likely to be claimed by foxes born on the site. This suggests that immigration is probably lower than emigration. This supposition, however, needs to be tested with further studies of non-harvested populations, which can quantify these important movements. Populations living in suburban areas surrounded with patches of woodland are particularly good candidates that may even have higher densities than reported for the SRS.

Another unanswered question is the relationship between age structure and harvest pressure. In South Carolina, a harvest pressure of 23.5 gray foxes/100 mi^2 vs. no harvest pressure on the SRS resulted in 51.9% vs. 37.2% juveniles, respectively (Carmichael and Baker 1996, and this study, respectively). While the additional factor of density was uncontrolled, these findings point to a potentially important relationship.

In summary, gray fox populations appear to be capable of more complex demographics than was previously predicted—data from harvested populations simply have not told the complete story. Only by understanding populations in the absence of harvest can we begin to understand the impacts of harvest itself.

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APPENDICES

APPENDIX 1—Fates of 25 radio-collared female gray foxes (for descriptions of deaths see Appendix 18).

Fox	Date Captured	Date of Last Transmitter Contact	Reason For Loss	Number of Locations Before Loss
GF-100	1/13/98	4/24/98	Unknown, presumed emigrating	2
GF-107[a]	1/18/98	12/17/98	Collar replaced after 11 mos. before battery failure	64 (84 total)
GF-107[a]	12/17/98	6/22/99	Died of unknown causes	20 (84 total)
GF-113	1/25/98	1/25/98	Body & collar found 4/17/98 buried 9 cm below ground by coyote	0
GF-117	1/28/98	5/13/98	Last known 5.3 km away from her capture location, so presumed to be emigrating	2
GF-120[a]	1/31/98	12/2/98	Presumed battery failure after 10 mos.	60
GF-124	2/18/98	2/18/98	Unknown, presumed emigrating	0
GF-126[a]	2/26/98	7/22/98	Pulled collar off	19 (38 total)
GF-126[a]	2/18/99	4/17/99	Presumed battery failure after 2 mos. because home range had been established for $\geq$14 mos.	19 (38 total)
GF-128	2/27/98	2/27/98	Unknown, presumed emigrating	0
GF-131[a]	3/4/98	11/19/98	Presumed battery failure after 8 mos.	62
GF-134	3/6/98	4/8/98	Presumed collar failure based on abnormal signal	1

APPENDIX 1 continued—Fates of 25 radio-collared female gray foxes.

Fox	Date Captured	Date of Last Transmitter Contact	Reason For Loss	Number of Locations Before Loss
GF-137	3/11/98	11/18/98	Presumed battery failure after 8 mos.	29
GF-138	3/13/98	3/13/98	Unknown, presumed emigrating	0
GF-141	3/27/98	4/9/98	Presumed collar failure based on abnormal signal	1
GF-143[b]	10/16/98	10/19/98	Relocated fox moved ca. 2.3 km from release location and therefore presumed emigrating	0
GF-145[b]	11/5/98	4/6/99	Moved 12.8 km from release location, signal found on 11/23/98, presumed battery failure after 5 mos.	7
GF-146[b]	11/5/98	11/10/98	Mortality signal heard from air but never found from ground, so either died or pulled collar off	0
GF-148	12/3/98	12/18/98	Presumed emigrating because only 8 months old	1
GF-150	12/10/98	1/4/99	Moved ≥ 1.1 km from capture location, signal found and recovered dead 4/8/99 from unknown causes	3
GF-151[a]	12/22/98	1/12/00	Presumed battery failure after 13 mos.	82
GF-167	2/12/99	3/31/99	Pulled collar off	1
GF-173	2/20/99	3/11/99	Pulled collar off	1

APPENDIX 1 continued—Fates of 25 radio-collared female gray foxes.

Fox	Date Captured	Date of Last Transmitter Contact	Reason For Loss	Number of Locations Before Loss
GF-175	2/23/99	4/6/99	Killed by coyote	4
GF-178	3/1/99	4/17/99	Killed by car 4/17/99	15
GF-179	3/12/99	4/17/99	Moved 1.8 km from capture location, signal found 4/5/99, recovered dead from rabies 4/19/99	2
GF-180[a]	5/6/99	12/8/99	Presumed battery failure after 7 mos.	58

[a]Foxes for which a home range was calculated (Appendices 6-11).

[b]Foxes causing a nuisance to site operations which were trapped and moved >13 km from capture location.

APPENDIX 2—Reclassification of 33 SRS habitat types[a] into 4 generalized habitat types used in the analysis of gray fox habitat preference.

Original Classification	Reclassification
1. Industrial	3. Open Area
2. Water	Eliminated as unusable
3. Bare Soil/Bare Surfaces	3. Open Area
4. Sparse Herbaceous Vegetation	3. Open Area
5. Grasses and Forbs	3. Open Area
6. Shrubs, Grasses, and Forbs	3. Open Area
7. Disturbed and Revegetated in 1997	3. Open Area
8. Marsh/Macrophytes[b]	4. Hardwoods
9. Young Open-Canopy Loblolly	5. Open-Canopy Pines
10. Open-Canopy Loblolly	5. Open-Canopy Pines
11. Young Dense-Canopy Loblolly	6. Dense-Canopy Pines
12. Dense-Canopy Loblolly	6. Dense-Canopy Pines
13. Young Open-Canopy Longleaf	5. Open-Canopy Pines
14. Open-Canopy Longleaf	5. Open-Canopy Pines
15. Young Dense Canopy Longleaf	6. Dense-Canopy Pines
16. Dense-Canopy Longleaf	6. Dense-Canopy Pines
17. Young Open-Canopy Slash	5. Open-Canopy Pines
18. Open-Canopy Slash	5. Open-Canopy Pines
19. Young Dense-Canopy Slash	6. Dense-Canopy Pines
20. Dense-Canopy Slash	6. Dense-Canopy Pines
21. Open-Canopy Pines	5. Open-Canopy Pines
22. Dense-Canopy Pines	6. Dense-Canopy Pines
23. Evergreen Hardwoods	4. Hardwoods

APPENDIX 2 continued—Reclassification of 33 SRS habitat types[a] into 4 generalized

habitat types used in the analysis of gray fox habitat preference.

Original Classification	Reclassification
24. Upland Hardwoods	4. Hardwoods
25. Upland Oak Hardwoods	4. Hardwoods
26. Mixed-Composition Flood Plain Hardwoods	4. Hardwoods
27. Flood Plain Oak Forests	4. Hardwoods
28. Flood Plain Sweetgum Forests	4. Hardwoods
29. Mixed Bottomland Hardwoods	4. Hardwoods
30. Bottomland hardwoods and Cypress	4. Hardwoods
31. Bald Cypress/Water Tupelo	4. Hardwoods
32. Upland Scrub Forests	4. Hardwoods
33. Wetland Scrub Forests	4. Hardwoods

[a]According to Wiggins-Brown et al. 2000.

[b]Because marsh/macrophyte occurred only in small patches (0.09 ha) surrounded by

hardwoods, this habitat type was reclassified as hardwood.

APPENDIX 3—Locations of traps used all 3 years and the 1-km buffers around them.
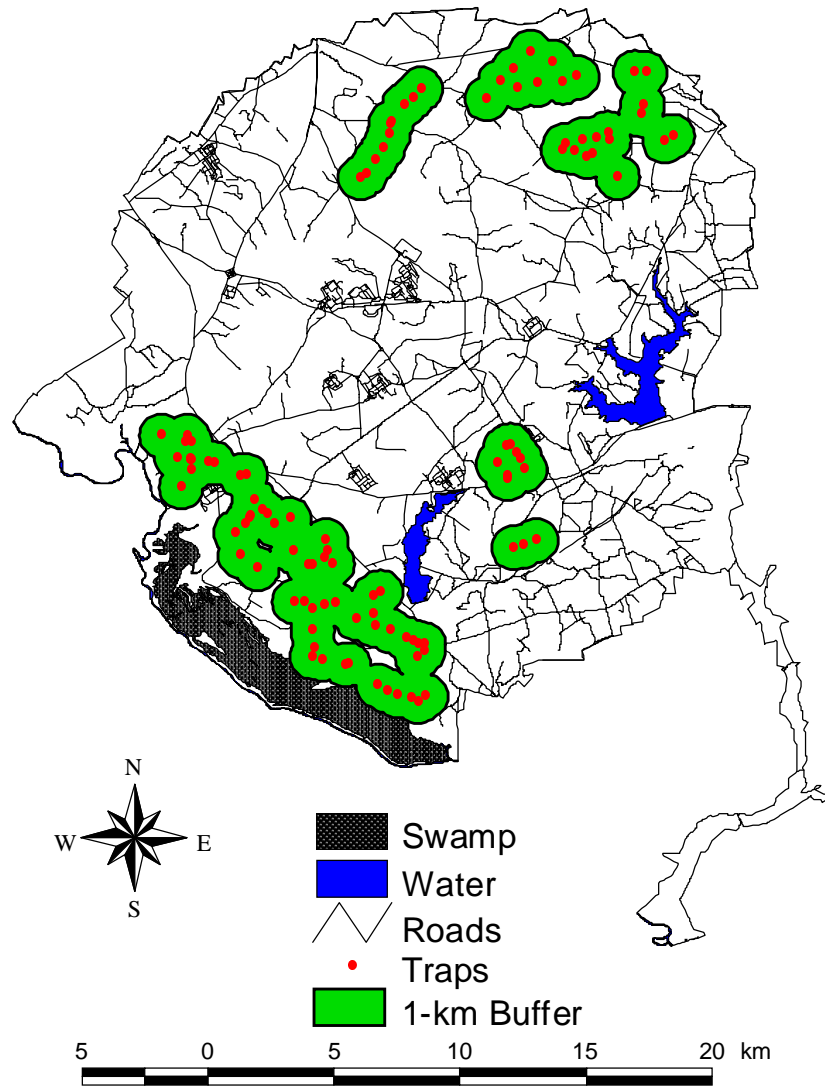
APPENDIX 4—Reproductive data for 23 gray fox females collected from the SRS.

Fox[a]	Date	Source[b]	Cementum Age[c]	# Placental Scars	# Corpora Lutea	Measurements (in cm)				Weight
						Total	Tail	Hind Foot	Ear	
GF-153	1/13/99	E	9 mos.	0	0	93.5	33.0	13.0	6.0	3.6
GF-178[d]	4/17/99	DOR	6 yrs.	≥2	—	100.0	35.0	13.4	6.1	4.6
GFE-01	12/17/99	E	1 yr. 8 mos.	0	0	98.0	37.0	13.2	6.6	4.0
GFE-02	1/17/00	E	9 mos.	0	0	106.0	37.0	13.4	7.1	4.5
GFE-04	1/27/00	E	2 yrs. 9 mos.	0	0	94.0	35.0	12.0	6.5	3.4
GFE-06	2/7/00	E	6 yrs. 10 mos.	0	0	103.0	34.0	12.8	6.6	3.4
GFE-07	2/7/00	E	6 yrs. 10 mos.	0	0	100.5	35.0	12.8	6.3	3.6
GFE-10	2/10/00	E	10 mos.	0	0	107.0	40.0	13.8	6.4	4.4
GFE-11	2/13/00	E	10 mos.	0	0	99.5	35.0	12.8	6.0	3.4
GFE-12	2/13/00	E	10 mos.	0	0	96.0	33.0	12.5	6.9	4.0
GFE-14	2/26/00	E	2 yrs. 10 mos.	0	4	100.5	35.5	13.4	6.5	3.8
GFE-15	2/27/00	E	9 yrs. 10 mos.	4	4	101.0	33.0	13.5	6.7	4.6
GFE-17	3/9/00	E	5 yrs. 10 mos.	3	3	93.0	32.0	12.0	6.2	4.2

APPENDIX 4 continued—Reproductive data for 23 gray fox females collected from the SRS.

| Fox[a]	Date	Source[b]	Cementum Age[c]	#Placental Scars	#Corpora Lutea	Measurements (in cm)				Weight (kg)
						Total	Tail	Hind Foot	Ear	
GFE-18	3/11/00	E	2 yrs. 11 mos.	4	4	101.0	34.5	13.4	6.2	3.6
GFE-19	3/11/00	E	8 yrs. 11 mos.	3	4	99.0	35.0	13.5	6.6	4.2
GFE-22	3/12/00	E	11 mos.	3	3	103.0	36.5	13.0	6.8	3.8
GFE-23	3/18/00	E	11 mos.	3	3	99.0	33.0	13.5	6.5	3.6
GFE-24	3/21/00	E	7 yrs. 11 mos.	3	4	101.0	34.0	13.2	6.1	4.8
GFE-26	3/23/00	E	2 yrs. 11 mos.	4	4	97.0	34.0	13.4	6.6	4.4
GFE-28	3/24/00	E	4 yrs. 11 mos.	5	5	104.0	37.5	13.0	6.8	3.8
GFRK-16	10/23/98	DOR	6 mos.	0	0	86.0	30.0	12.5	6.5	3.3
GFRK-25	1/16/99	DOR	2 yrs. 9 mos.	3	0	90.0	32.0	12.2	6.5	4.0
GFRK-35	5/9/98	DOR	1 yr. 1 mo.	4	4	98.0	36.0	13.2	6.2	3.8

[a]GF=Gray fox captured and released alive, later found dead; GFE=Gray fox, euthanised; GFRK=Gray fox, road-killed.

[b]DOR=Dead on Road; E=Euthanised.

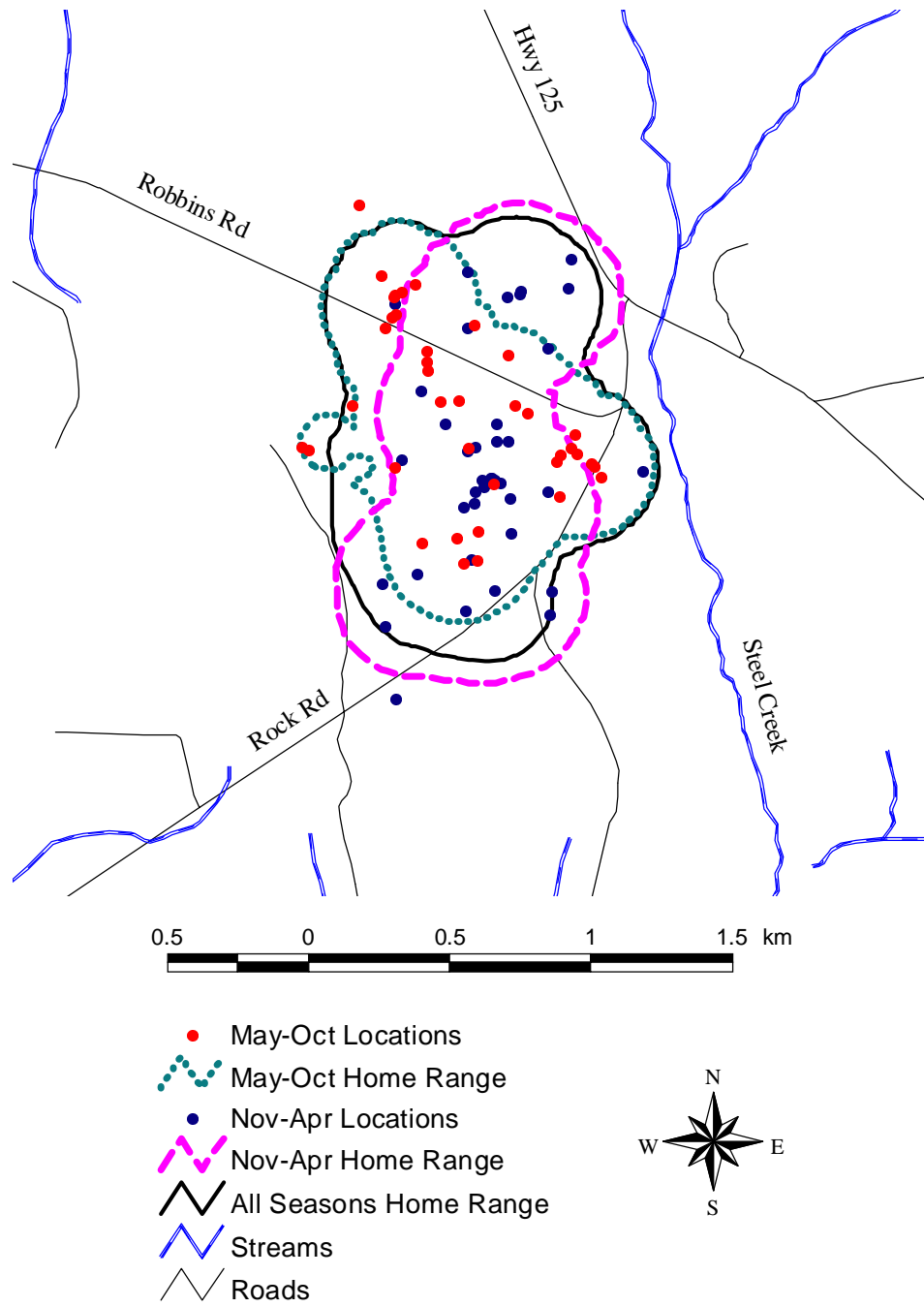[c]Age assumes all foxes were born on April 1.

[d]Hit by car, reproductive tract destroyed, ovaries destroyed, remains of at least 2 fetuses found.

APPENDIX 5—Identification codes and capture locations of 23 female gray foxes whose reproductive tracts were examined.
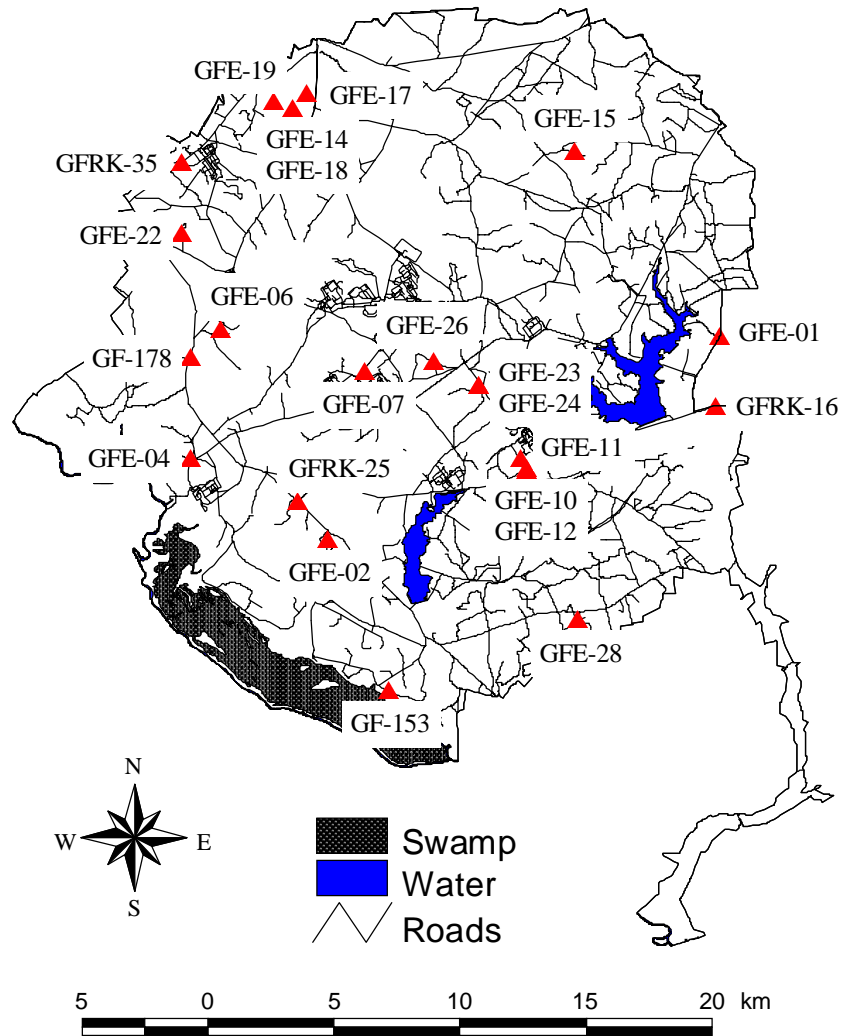
APPENDIX 6—95% adaptive kernel home range and locations for fox GF-107.

APPENDIX 7—95% adaptive kernel home range and locations for fox GF-120.

Central Shops

Rd 5

Rd C

Rd 3

0.5   0   0.5   1   1.5 km

- May-Oct Locations
- May-Oct Home Range
- Nov-Apr Locations
- Nov-Apr Home Range
- All Seasons Home Range
- Streams
- Roads

N
W E
S
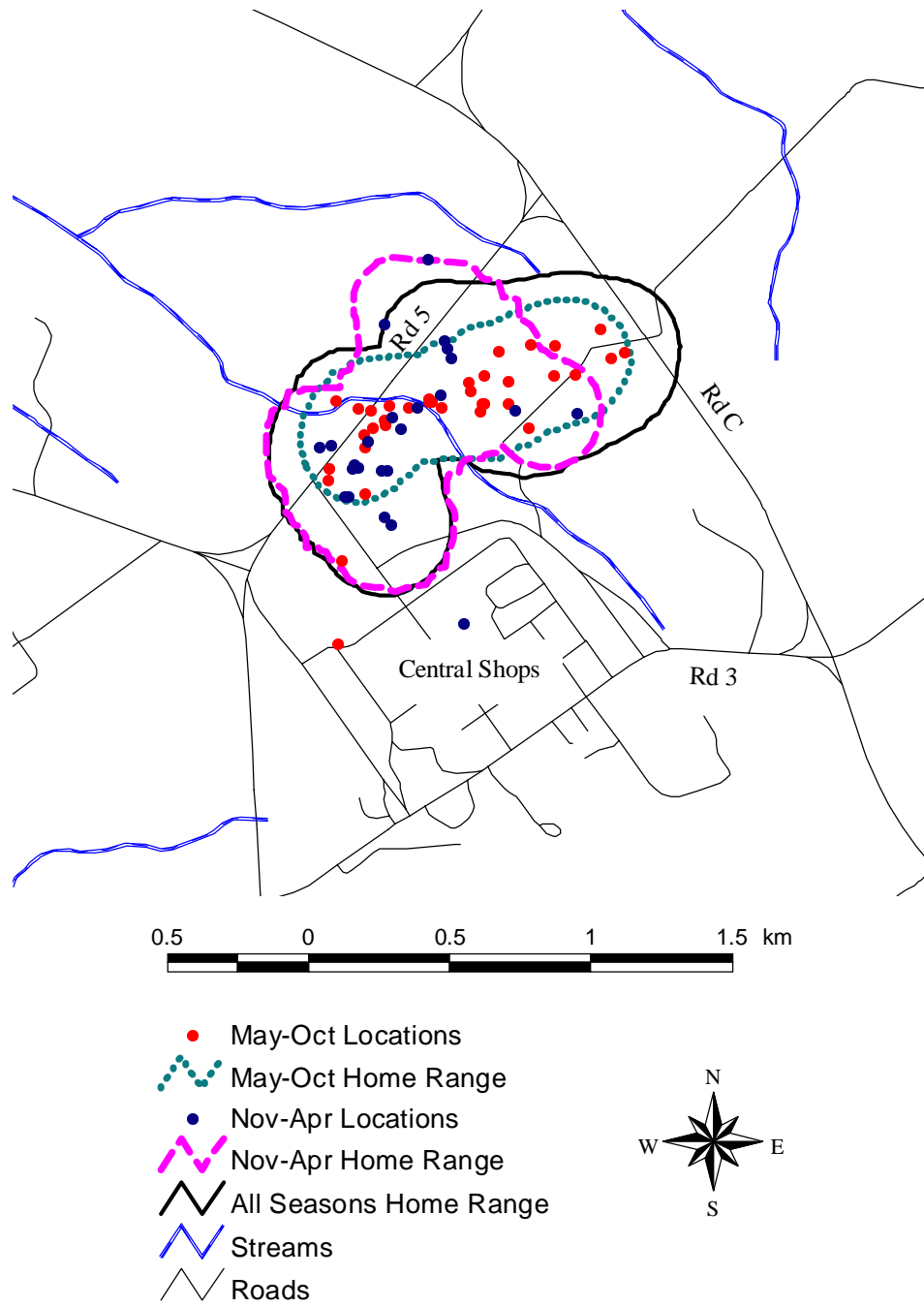
APPENDIX 8—95% adaptive kernel home range and locations for fox GF-126.

APPENDIX 9—95% adaptive kernel home range and locations for fox GF-131.

APPENDIX 10—95% adaptive kernel home range and locations for fox GF-151.

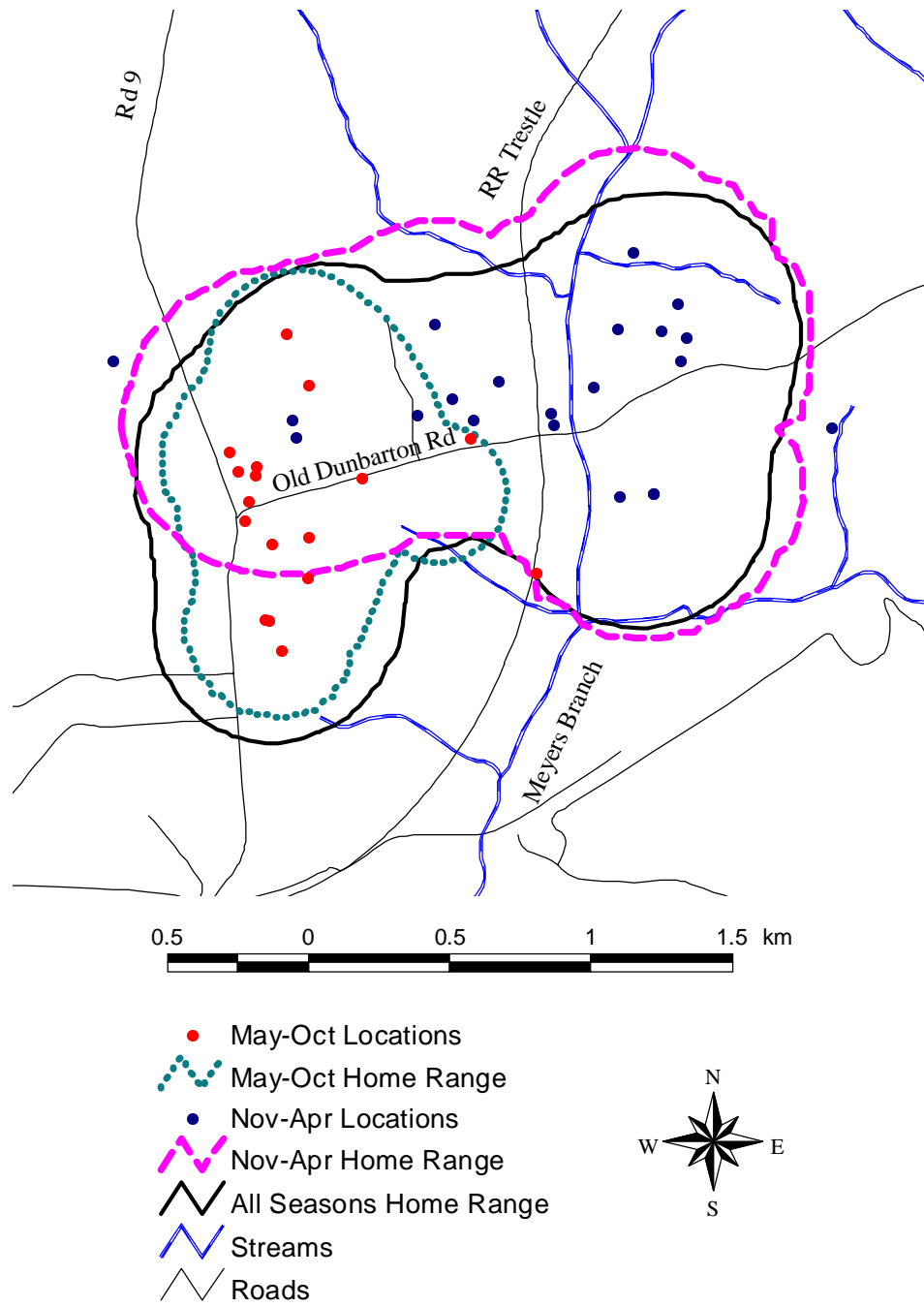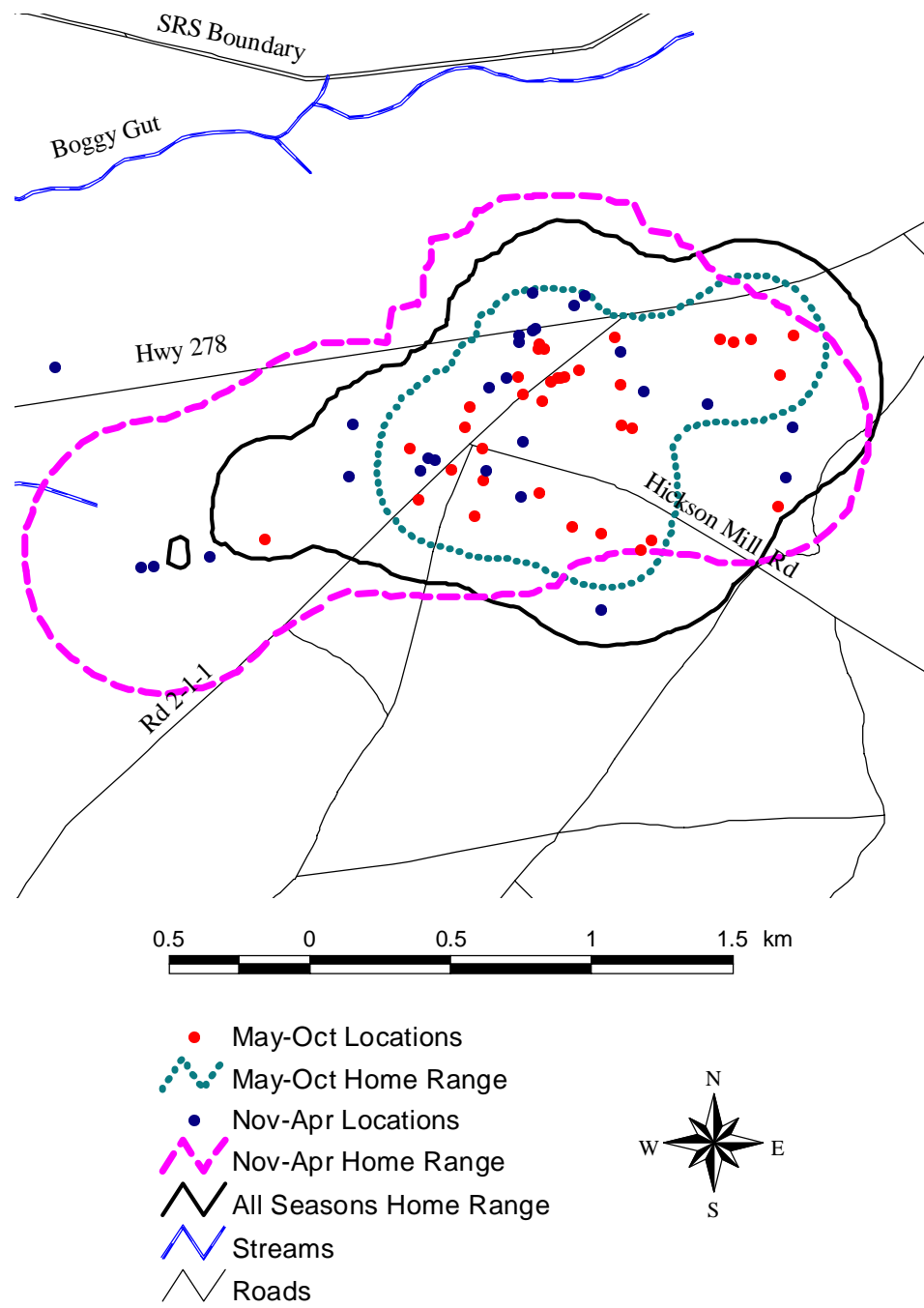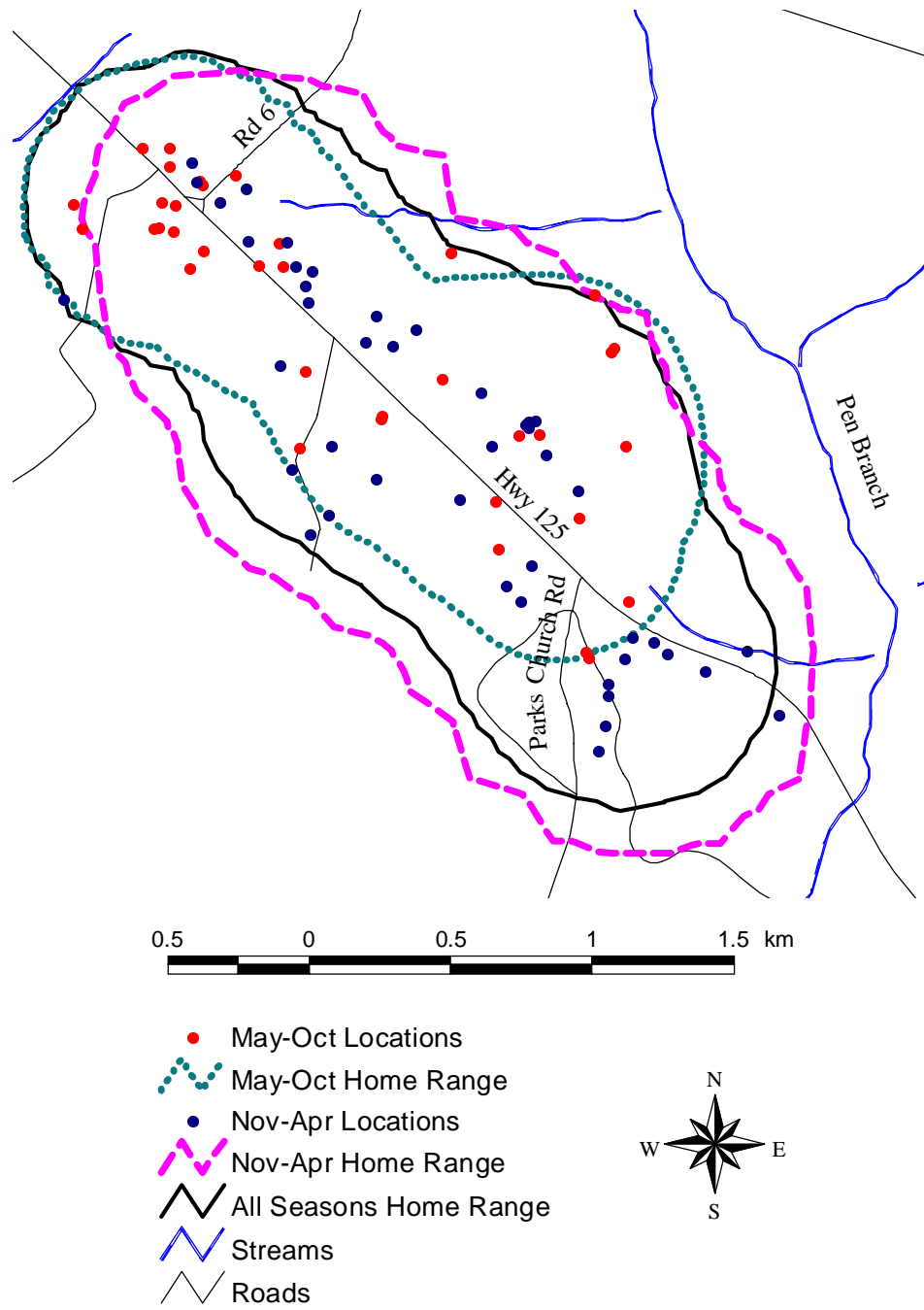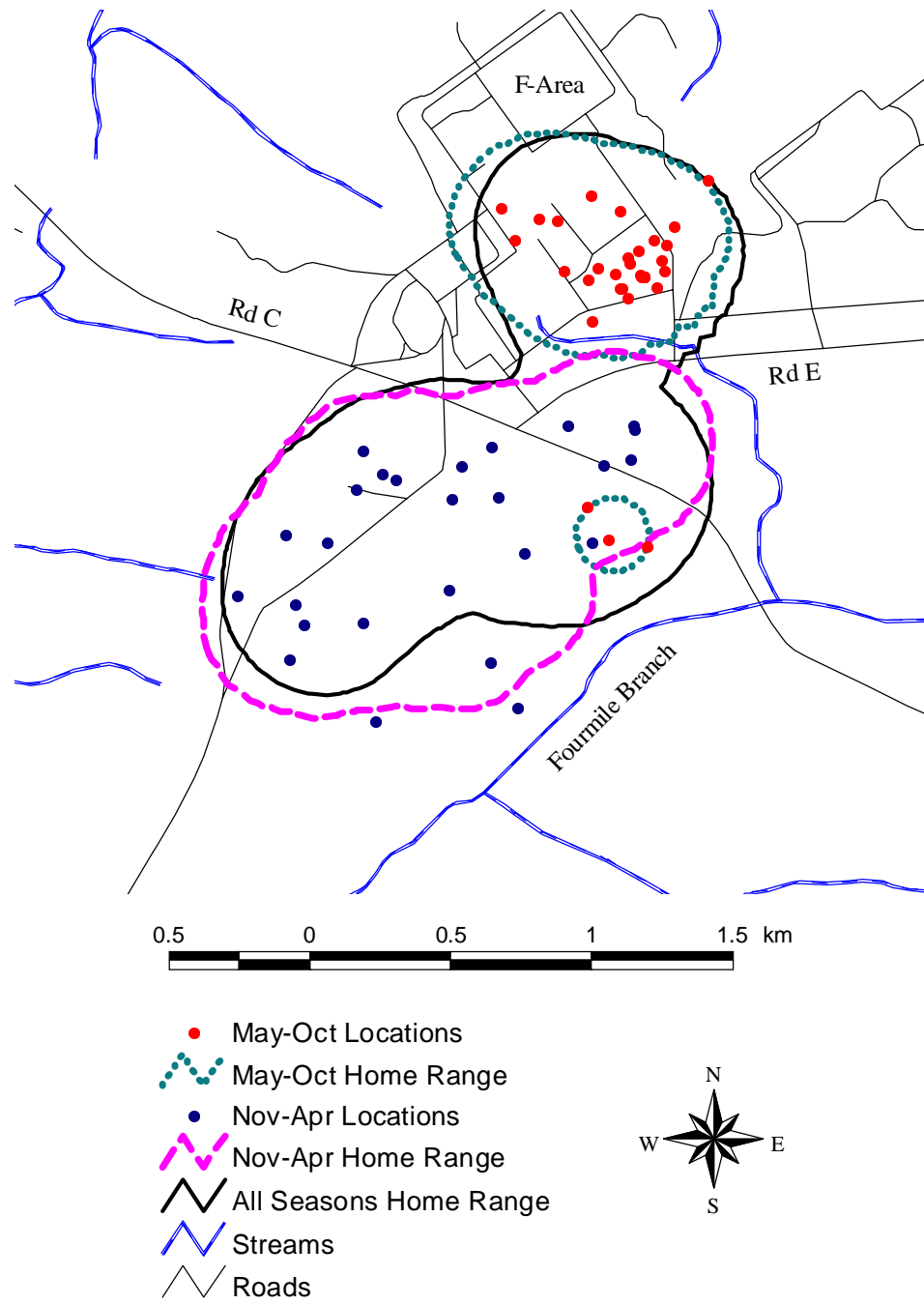APPENDIX 11—95% adaptive kernel home range and locations for fox GF-180.

APPENDIX 12—Cementum ages of 36 SRS gray foxes (male and female) rounded to the nearest year.[a]

1 yr.	2 yrs.	3 yrs.	4 yrs.	5 yrs.	6 yrs.	7 yrs.	8 yrs.	9 yrs.	10 yrs.
GFE-23									
GFE-22									
GFE-21									
GFE-16									
GFE-12									
GFE-11									
GFE-10				GFE-29					
GFE-08		GFE-26		GFE-28					
GFE-05		GFE-18		GFE-27					
GFE-02		GFE-14		GFE-25					
GF-163[b]		GFE-13		GFE-20					
GF-158	GFE-01	GFE-09		GFE-03	GFE-17	GFE-07			
GF-153	GF-150	GFE-04	GF-107[b]	GF-175	GF-178	GFE-06	GFE-24	GFE-19	GFE-15

[a]GF=Gray fox captured and released alive, later found dead and a tooth removed for cementum analysis;

GFE=Gray fox, euthanised.

[b]Ages of recaptured foxes are given as the age at first capture only.

APPENDIX 13—Cementum ages of 13 SRS gray fox males rounded to the nearest year.[a]

GFE-21									
GFE-16				GFE-29					
GFE-08				GFE-27					
GFE-05				GFE-25					
GF-163[b]		GFE-13		GFE-20					
GF-158		GFE-09		GFE-03					
1 yr.	2 yrs.	3 yrs.	4 yrs.	5 yrs.	6 yrs.	7 yrs.	8 yrs.	9 yrs.	10 yrs.

[a]GF=Gray fox captured and released alive, later found dead and a tooth removed for cementum analysis;

GFE=Gray fox, euthanised.

[b]Age of recaptured fox is given as the age at first capture only.

APPENDIX 14—Cementum ages of 23 SRS gray fox females rounded to the nearest year.[a]

1 yr.	2 yrs.	3 yrs.	4 yrs.	5 yrs.	6 yrs.	7 yrs.	8 yrs.	9 yrs.	10 yrs.
GFE-23									
GFE-22									
GFE-12									
GFE-11		GFE-26							
GFE-10		GFE-18							
GFE-02	GFE-01	GFE-14			GFE-28	GFE-17	GFE-07		
GF-153	GF-150	GFE-04	GF-107[b]	GF-175	GF-178	GFE-06	GFE-24	GFE-19	GFE-15

[a]GF=Gray fox captured and released alive, later found dead and a tooth removed for cementum analysis;

GFE=Gray fox, euthanised.

[b]Age of recaptured fox is given as the age at first capture only.

APPENDIX 15—Cementum ages of 24 gray foxes (male and female) killed on highways outside the SRS boundary rounded to the nearest year (foxes <6 months old are not considered).[a]

GFRK-46									
GFRK-44									
GFRK-43									
GFRK-41									
GFRK-40									
GFRK-39									
GFRK-37									
GFRK-36									
GFRK-31									
GFRK-30									
GFRK-28									
GFRK-24	GFRK-47								
GFRK-22	GFRK-45								
GFRK-18	GFRK-15								
GFRK-14	GFRK-13	GFRK-29	GFRK-19		GFRK-06		GFRK-07		GFRK-38
1 yr.	2 yrs.	3 yrs.	4 yrs.	6 yrs.	7 yrs.	9 yrs.	10 yrs.	12 yrs.	13 yrs.

[a]GFRK=Gray fox, road killed.

APPENDIX 16—Sex, cementum age, and distance from the SRS for 25 road-killed gray
foxes collected from outside the SRS boundary. Age assumes all foxes were born on
April 1.

Fox	Sex	Age	Distance From SRS (km)
GFRK-07	M	9 yrs. 11 mos.	19.5
GFRK-13	M	1 yr. 6 mos.	21.8
GFRK-15	M	1 yr. 6 mos.	2.3
GFRK-19	M.	3yrs. 6 mos.	22.2
GFRK-22	M	8 mos.	4.8
GFRK-29	M	2 yrs. 11 mos.	2.2
GFRK-30	M	11 mos.	16.5
GFRK-36	M	1 yr. 4 mos.	12.2
GFRK-37	M	1 yr. 4 mos.	16.9
GFRK-38	M	13 yrs. 5 mos.	16.7
GFRK-39	M	6 mos.	14.7
GFRK-41	M	7 mos.	23.0
GFRK-43	M	8 mos.	24.8
GFRK-46	M	9 mos.	32.0
GFRK-47	M	1 yr. 11 mos.	34.2
GFRK-06	F	6 yrs. 8 mos.	13.8
GFRK-14	F	6 mos.	63.3
GFRK-18	F	6 mos.	39.5
GFRK-24	F	9 mos.	6.5
GFRK-28	F	11 mos.	3.7
GFRK-31	F	1 yr. 1 mo.	10.0
GFRK-40	F	6 mos.	5.5
GFRK-44	F	8 mos.	6.7
GFRK-45	F	1 yr. 9 mos.	11.8

APPENDIX 17—Weight, measurements, and reproductive data for 6 female gray foxes killed on roads surrounding the SRS[a].

ID#	Date	Cementum Age[b]	#Placental Scars	Measurements (in cm)				Weight
				Total	Tail	Hind Foot	Ear	
GFRK-01	6/4/97	>1 yr. 2 mos.	4	88.9	29.2	13.3	6.4	3.8
GFRK-06	12/16/97	6 yrs. 8 mos.	4	100.0	35.0	13.5	6.7	4.6
GFRK-28	3/2/99	11 mos.	0	93.0	32.5	13.0	6.0	3.8
GFRK-31	5/5/99	1 yr. 1 mo.	3	96.0	37.0	13.5	6.1	4.0
GFRK-45	1/4/2000	1 yr. 9 mos.	0	96.0	37.0	13.5	6.5	3.6
GFRK-2000	4/1/2000	>1 yr.	5	92.0	32.0	13.0	5.8	3.8

[a]See Appendix 16 for distances from the SRS.

[b]Age assumes all foxes were born on April 1.

[c]D=Ovaries destroyed and corpora lutea could not be counted.

APPENDIX 18—Descriptions of the deaths of 7 radio-collared female gray foxes. Locations shown in Appendix 19.

_GF-107:_ First trapped 1/18/98 at the intersection of Robbins Road and the railroad tracks when she was 3 years 9 months old (based on cementum age obtained when she died). She was equipped with a radio-collar from AVM Instrument Company and was followed for the next several months. On 8/11/98 she was caught in a cage trap set in her home range for the purpose of evaluating her reproductive condition. She was regrowing hair on her underside, but 2 teats appeared to have been used in the last month, 2 appeared never used, and 2 were intermediate in appearance. On 12/17/98 she was trapped in a box trap set out to catch hunting hounds. At that time her collar was replaced with a radio-collar from Telonics, Inc. and she was again released. During trapping season on 1/10/99 she was suspected of having been caught in a leg-hold trap set 0.1 miles south of the corner of Robbins Road and Rock Road. This suspicion was based on the presence in the trap jaws of a cylindrical piece of plastic ca. 6 cm long which was similar to the plastic coating encasing all Telonics transmitter antennas. At that time, only one other fox carried a Telonics transmitter (GF-150, attached 12/10/98). That fox was a 1 year 8 month old female trapped 6.7 km away from the trap in question and was known to have been living in the same area on 1/4/99 and 4/7/99 when she was found dead. Her presence at that trap location, then, was unlikely. The suspicion was further confirmed when GF-107 was found dead on 7/14/99 and her collar was found to be missing a piece of antenna coating ca. 6 cm long.

Location of death was in a clearing ca. 1.3 km from the site of her first capture and 0.49 km from the trap location she was suspected of having been caught in. The last known date she was alive was 6/22/99, making her 5 years 2 months old at death. When found, her bones were ca. 60% intact but most of the soft tissue had been scavenged or decomposed. Cause of death could not be assessed. Her presence in an open area suggests that a coyote may have killed her, but no evidence of teeth marks on the bones

could be found to support this possibility. Cause of death was therefore classified as unknown.

GF-113: First trapped 1/25/98 at the intersection of Parks Church Rd and a forest road on the east 0.65 km north of Banana Road. After her release many failed attempts were made to find her signal from both the air and the ground. After an intense search, however, her signal was finally found on 4/17/98. The signal was extremely weak and indicated she had either died or pulled her collar off. The remains of her body were found 0.93 km from where she was trapped. A few scattered bones, mostly leg and foot bones, were scattered around the base of a loblolly pine while her skull with the radio-collar still attached was found buried at the base of the tree ca. 9 cm below the surface. The only two animals known to occasionally kill gray foxes are bobcats and coyotes (Fritzell and Haroldson 1982), but because bobcats are not known to dig holes the cause of death was attributed to a coyote.

GF-141: Trapped 3/27/98 at intersection of forest road 506 and a forest road 0.97 km north of Craig Road (Rd. 8-4). This female was pregnant as evidenced by the lack of fur surrounding her teats and the palpitation of at least 3 fetuses. Based on a lack of tooth wear, she was believed to be 11 months old. Her teats were ca. 3 mm long and very pink, indicative of her first litter (Layne 1958). Despite her advanced stage of pregnancy, however, she weighed only 3.0 kg (average = 3.9 kg, $n = 68$) suggesting she was very underweight and possibly unhealthy. A few days earlier on 3/24/98 an adult male raccoon was captured at the same site, which was also underweight. Though his exact weight was not taken, his pelvis and all his ribs protruded, again indicating possible disease. Although radio-collared, GF-141's transmitter was believed to have failed based on an abnormal sustained tone when tracking on 4/9/98 and a subsequent loss of any signal by 5/4/98. Her presence in the area on 4/9/98, 0.61 km from her trapped location, as well as her advanced stage of pregnancy suggest that signal loss due to emigration was

unlikely. The following year on 3/12/99, GF-179 was trapped 3.1 km away from GF-141's trap site and died of rabies 4/17/99 (see description below). The undernourished condition of both the raccoon and GF-141 despite being pregnant, along with the close proximity of GF-141 to a known rabies case the following year indicate that GF-141 likely died of rabies as well.

GF-150: Trapped in large cage trap set for hunting hounds on 12/10/98 at the intersection of Tennessee Road and Ellis Road (3.2 km east of Road 9). She was equipped with a radio-collar and released. Her radio signal was heard until 1/4/99 and then lost. When found again on 4/8/99 she was recovered dead 1.1 km from her trapped location. Her body appeared to have been scavenged because her bones were found spread over an area ca. 45 m x 18 m. If she is assumed to have died shortly after the last known date alive in January, then she died at 1 year 9 months of age. Her presence in an open area suggests she may have been killed by a coyote, but no physical evidence was found to support this possibility. The cause of death was considered unknown.

GF-175: Trapped on 2/23/99 in the woods at the intersection of Road 5 and a road leading into Central Shops 1.3 km south of Road C. She was last known alive on 4/6/99. She was recovered dead 0.82 km from her trapped location on 4/13/99 when she was determined to be 5 years old. Her body had been scavenged in that time as evidenced by her bones being found scattered across ca. 20 m^2. Her radio-collar and most of her bones were found near a blueberry bush (*Vaccinium* sp.) while her skull was found ca. 20m away in a clearing. Her rostrum had a large triangular hole in it which was the same diameter as a coyote's canine tooth, and her collar was missing a section ca. 30 mm long, which is equal to the breadth across each alveolus of the upper M^{2}s of a coyote's jaw (Hoffmeister 1989). Based on the data from this study and reports from another study (Small 1971), coyotes have not been known to eat the flesh of the foxes they kill, so they are unlikely to use them as a source of food. It seems unlikely, then, that coyotes would

scavenge a gray fox if found already dead. The coyote-sized canine hole in the rostrum of the dead fox, therefore, was likely to have been acquired from an attack rather than from scavenging. Death of this fox was attributed to a coyote.

GF-178: Trapped on 3/1/99 in a box trap placed on the shore of Caroline's Bay. She was last known alive on 4/17/99 at 2:00 AM when she spent most of 4.5 hours in one location, assumed to be a den site.   She was found that same evening at 11:30 PM dead on the highway ca. 1.3 km northeast of her site of capture. The same section of highway was passed at 8:00 PM, so death occurred sometime between 8:00-11:30 PM. When found, she was determined to be 6 years old and pregnant with 2-3 pups (one male, others unknown) as identified from the remains. Cause of death was attributed to an automobile collision.

GF-179: Trapped 3/12/99 at the intersection of forest roads 414 and 415 (road 414 is located on the north side of Road 8-11, 1.6 km west of Road 8, and road 415 bisects road 414 ca. 0.8 km north of Road 8-11). She was last known alive on 4/5/99 and was recovered dead in a thicket of blueberry (*Vaccinium* sp.) on 4/19/99, 1.8 km east of her site of capture. She appeared to have died within the previous 2 days and was in only slightly poorer health than when she was trapped (3.4 kg when trapped, 3.0 kg when recovered). The next day her body was taken to the Southeastern Cooperative Wildlife Disease Study (SCWDS) at the University of Georgia, Athens. She was diagnosed as having died of rabies. Her body was incinerated as per SCWDS protocol, so no tooth was available for cementum analysis. She was believed to be at least 2 years old, however, at the time of death due to noticeable wear on both her molars and canine teeth. Based on the 2mm-long pink teats, she was determined to have never bred. This assessment was later confirmed by an examination by SCWDS personnel. GF-179, therefore, was considered a barren female whose cause of death was rabies.

APPENDIX 19—Identification codes and locations of death for 7 female foxes that died while carrying radio-collars.
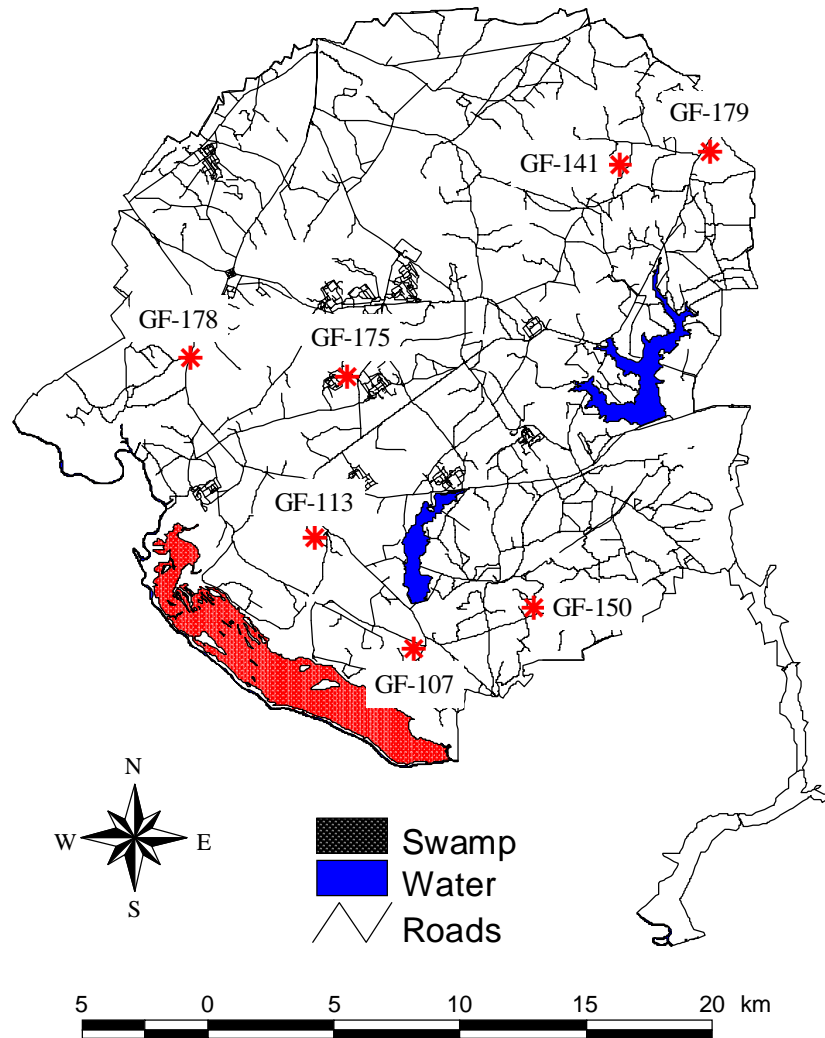
APPENDIX 20—Identification codes and locations of female gray foxes that emigrated from the site of their first capture (■) and established a home range >2 km away (✳). No home range data were available for GF-145; ● represents GF-145's site of initial capture and ■ represents the release location. Arrows show direction of travel.
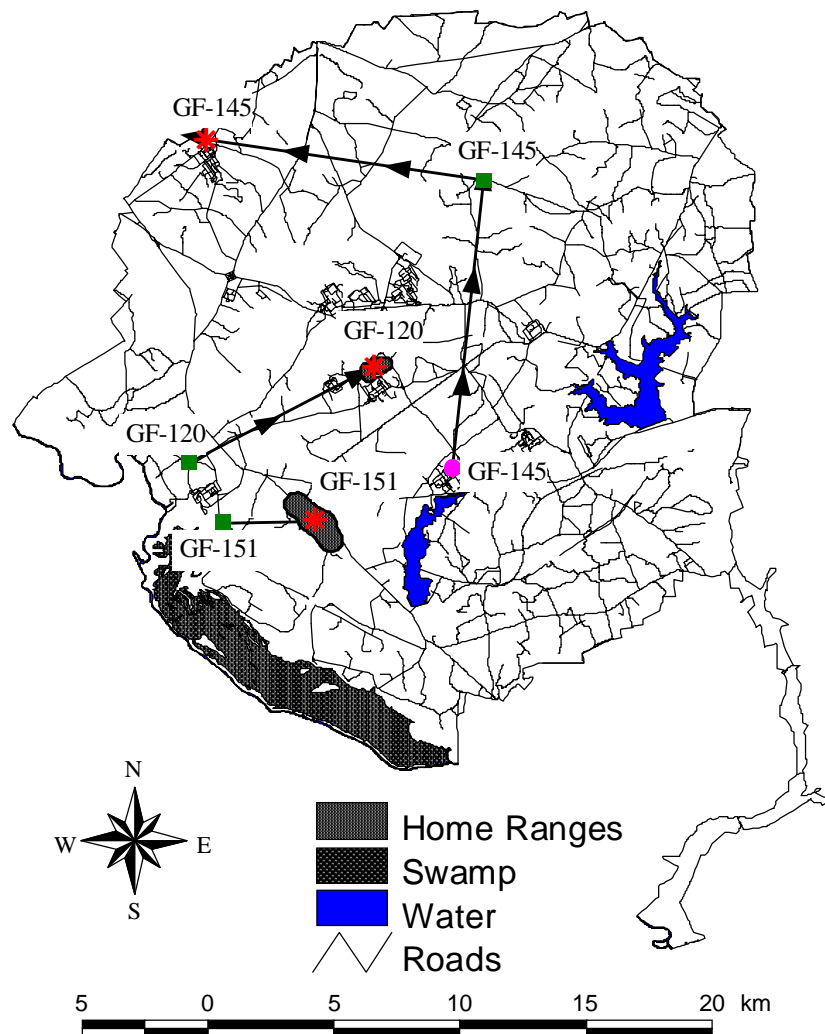
APPENDIX 21—Identification codes and locations of female gray foxes suspected of emigrating off the SRS but whose fates were unknown. Site of first capture (■) and last known location (✳) are shown. For GF-146, ● represents the fox's site of initial capture and ■ represents the fox's release location. Arrows show direction of travel.