DISTRIBUTION AND POPULATION ECOLOGY OF THE FOX SQUIRREL IN FLORIDA

By

JOHN BRUCE WOODING

A DISSERTATION PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

1997

ACKNOWLEDGEMENTS

I conducted the field work on this project while employed as a wildlife biologist with the Florida Game and Fresh Water Fish Commission. The work was fully funded by the Commission, and I appreciate the Agency's permission to use their data for this dissertation.

Many people who work for the Commission assisted with the project. Special thanks go to Tom Logan, Brad Gruver, Jim Brady, Paul Moler, and Tim Breault. Help with the field work was provided by many people, including Mark Cantrell, Dee Hungerford, Don Coyner, Bill Frankenberger, Brett Kempker, Patricia McNeill, and Vic Doig. Jeff Hamblen helped with mapping and graphics, and Steve Linda assisted with the statistical analysis.

A portion of the field work was conducted on property managed by the Florida Department of Environmental Protection. Jim Stevenson of that agency was particularly facilitative.

Field work on the Fort White study area was conducted on privately owned property. The landowners graciously allowed me access and permission to study the fox squirrels living on their farms. Special thanks go to Billy Cason, Tom Fowler, and the Gray Shadow Ranch.

My graduate committee at the University of Florida has been demanding. I have prospered from their demands, and I appreciate their commitment to quality. Steve Humphrey has been helpful during all aspects of the process.

I also thank the administrative staff at the University. This includes Cathy Ritchie, Shannon Stull, Mindy Edwards, and Cynthia Sain. I also thank the fine people working in the

Graduate School. On the numerous occasions when I've done something incorrectly (one must follow the rules without exception, no matter how trivial one believes them to be), they have helped me straighten out the mess--and they have always done it with a smile (sometimes with a strained smile, but a smile nonetheless).

On the home front, my family has been cheering me on throughout the project. From the bottom of my heart, I thank you.

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Abstract of Dissertation Presented to the Graduate School
of the University of Florida in Partial Fulfillment of the
Requirements for the Degree of Doctor of Philosophy

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John Bruce Wooding

August 1997

Chairman: Stephen R. Humphrey
Major Department: Wildlife Ecology and Conservation

Fox squirrel (Sciurus niger) distribution, movements, demographics, and management were investigated in Florida from 1989 to 1995. Fox squirrels were determined to be widespread in Florida, occurring in 65 of the state's 67 counties. There were no reported occurrences for Dade and Broward counties. The distribution, however, was patchy due to habitat loss. The largest expanses of fox squirrel habitat were found on public lands in northern Florida.

Fox squirrel movements and demographics were studied on two areas in northern Florida. Forty-four fox squirrels were monitored during the study. The density of fox squirrels on one study area was 7.4 fox squirrels/km^2; the density on the second area was 11.7 fox squirrels/km^2. Male home ranges overlapped extensively with those of females and other males, but there was little overlap in home ranges of adult females. Eight of 15 fox squirrels collared as subadults dispersed. Two older fox squirrels also dispersed. Dispersal distances ranged from 1.0 to 7.2 km. The annual mortality rate for the radio collared animals was estimated at 27-30%. Litter size ranged from 1-3. Populations had two breeding seasons per year, but the litter

frequency of radio-collared females was 1.07 litters per year.

Six radio-collared fox squirrels were translocated in 1995 to establish a breeding population in a state park. The radio signal was lost on one squirrel while it was still on the park, but the other 5 animals left the park following their release, indicating that the habitat on the park was unacceptable to fox squirrels. Dispersing squirrels settled where neighboring populations occurred, showing that local sources of fox squirrels were available that could naturally colonize the park. Further relocation of fox squirrels to the area was unwarranted under the current conditions.

CHAPTER 1
INTRODUCTION

Five hundred years ago, Florida was a wilderness. Today, it is a world famous center of urban and agricultural development. Florida's human population reached 14 million in 1995, and the population is expected to increase to 20 million by 2020 (Floyd et al. 1996). Many species of wild animals that were adapted to the Florida wilderness have declined in abundance due to the state's development (Cox et al. 1994). The fox squirrel (Sciurus niger) is one of those species.

This dissertation contains the results of an observational study on the fox squirrel in Florida. The intention of the work was to gather basic information on distribution and biology that could be applied to conserve the species. This was not a study of the theoretical or mathematical aspects of wildlife ecology. My goals for the dissertation were to present a tightly written report that contained the data I collected. Chapter 1 contains an overview on fox squirrels and it is offered as background information for the chapters that follow. The next three chapters contain the data collected in the study. Chapter 2 contains information on fox squirrel distribution in Florida, Chapter 3 contains information on the population ecology of fox squirrels in northeastern Florida as determined using radio telemetry methods, and Chapter 4 contains the results of an effort to restock fox squirrels into a state preserve.

My intentions were to keep the discussion to a bare minimum, something which I appreciate in technical reports written by others. However, dissertations are an academic exercise. I hence expanded the scope and included two discussion chapters. Chapter 5 contains a discussion on conspecific attraction and the influence this behavior has on patterns of animal distribution and conservation of populations in fragmented habitat. Chapter 6 contains a discussion on the future of fox squirrels in Florida.

Background Information on Fox Squirrels

The remainder of this chapter presents a review of fox squirrel life history and status and an overview of prior research conducted on the species. This information is offered as background for the chapters that follow.

Fox squirrels occur in most of the eastern and central portions of the United States (Koprowski 1994), and their range extends into south-central Canada. Fox squirrels have been introduced into California, Oregon, and Washington (Flyger and Gates 1982).

Fox squirrels are large tree squirrels (Silva and Downing 1995). Body mass can exceed 1.3 kg (Flyger and Gates 1982). Pelage colors range from a grizzled gray tinged with orange in the midwestern United States to black, silver, or khaki in the southeastern United States. Fox squirrels in the southeastern Coastal Plain usually have white ears and muzzles. Individuals can be a mix of colors. I have seen fox squirrels in Florida with black faces, white ears and muzzles, black shoulders and front legs, chestnut brown backs, tan flanks, and burnt orange tails. All are not this colorful, but the most colorful are striking animals.

Taxonomy

Fox squirrels are one of the world's 28 species of tree squirrels (Wilson and Reeder 1993). The genus Sciurus occurs throughout Europe, northern Asia, and North and South America (Nowak 1991). One species occurs in Japan (Wilson and Reeder 1993).

Hall (1981) recognized 10 subspecies of fox squirrel. Four of these occur in Florida: S.n. avicennia (Big Cypress fox squirrel), S.n. bachmani (Bachman's fox squirrel), S.n. shermani (Sherman's fox squirrel), and S.n. niger (Southeastern fox squirrel). The taxonomy of fox squirrels in the southeast was recently reviewed by Turner and Laerm (1993). They concluded that S.n. bachmani was not distinct enough to warrant recognition as a separate subspecies. In their opinion, S.n. bachmani, was only a clinal variation of S.n. niger. S.n. shermani and S.n. avicennia, however, were considered distinct subspecies.

The three subspecies that Turner and Laerm (1993) recognized for Florida (S.n. avicennia, S.n. shermani, and S.n. niger) differed primarily in body size: S.n. avicennia was the smallest, S.n. niger was intermediate in size, and S.n. shermani was the largest. Pelage patterns were used by Moore (1956) to help distinguish the different subspecies in Florida, but Turner and Laerm (1993) found that pelage was too subjective and varied for use as an indicator of taxonomy.

Legal Status in Florida

The Big Cypress fox squirrel is the only subspecies endemic to Florida (Turner and Laerm 1993). It occurs only in the extreme southwestern portion of the state and is listed by the Florida Game and Fresh Water Fish Commission (GFC) as a threatened species. Sherman's fox squirrel occurs throughout the peninsula and panhandle west to Okaloosa County. It also occurs in central and southern Georgia. It is considered a species of special concern by the Florida GFC. The southeastern fox squirrel only occurs in Florida in the western panhandle, but its range outside of Florida extends over much of Alabama, northern Georgia, South Carolina, and North Carolina (Turner and Laerm 1993). It is not listed.

Fox squirrels were formerly game animals in Florida, and legally hunted statewide. The season was closed in stages, beginning first in south Florida within the range of the Big Cypress fox squirrel. The season closed there in 1972. Next, the season was closed on all wildlife management areas in 1991. Fox squirrels were then legal game only on privately owned land in central and northern Florida. The season there ended in 1995. The final closure ended all legal hunting of fox squirrels in Florida.

Previous Studies

Fox squirrel research specific to Florida was begun in the 1950s by Moore (1956, 1957), who focused his attention on distribution, taxonomy, and life history. Status surveys were conducted in the 1970s by Brady (1977) and Williams and Humphrey (1979). In the late 1980s, Kantola and Humphrey (1990) investigated habitat use of radio-collared fox squirrels in northern Florida. A study of urban fox squirrels in southwestern Florida was completed in the early 1990s by Jodice and Humphrey (1992).

There have been several studies of fox squirrels in other southeastern states. In Maryland, Taylor (1973), Lustig and Flyger (1975), Dueser et al. (1988), and Larson (1990) examined the status and habitat requirements of the Federally endangered Delmarva fox squirrel (S.n. cinereus). In North Carolina, Weigl et al. (1989) conducted an 8-year study on fox squirrel population biology and habitat requirements. In South Carolina, Wood and Davis (1981) and Wood (1985a,b) investigated status and human perceptions of fox squirrels, and Edwards (1986) studied habitat selection by radio-collared fox squirrels. In Georgia, Hilliard (1979) also conducted a study of fox squirrels using radio-telemetry techniques. A similar study was completed in southern Alabama by Powers (1993).

Research on fox squirrels in the midwestern United States has been more extensive than that completed in the southeast. The first midwestern studies were completed in the 1940s (Allen 1943, Baumgartner 1943, Brown and Yeager 1945). These first studies focused on life history, habitat requirements, and management of fox squirrels as a small game species. More recent studies of midwestern fox squirrels have built on the earlier work. These include studies of behavior (Benson 1980, Koprowski 1993), food habits (Korschgen 1981, Nixon et al. 1968), ageing techniques (McCloskey 1977), and habitat management (Nixon and Hansen 1987).

There have been several general reviews of fox squirrel research and biology. Flyger and Gates (1982) and Koprowski (1994) reviewed the literature on fox squirrels for the species entire range. Weigl et al. (1989) and Loeb and Moncrief (1993) focused their literature review on fox squirrels in the southeastern United States. Kantola (1992) and Humphrey (1992) reviewed the biology and status of fox squirrels in Florida. A review of all species of tree squirrels was completed by Gurnell (1987).

CHAPTER 2
DISTRIBUTION

Two previous surveys assessed the distribution of fox squirrels in Florida. Brady (1977) used a mail survey of wildlife experts to determine the state-wide distribution of fox squirrels. He found that the species occurred throughout the state but the distribution was patchy. He identified several areas where there were large concentrations of habitat and where fox squirrels were considered common, but overall, the species was uncommon as a consequence of habitat loss. The second survey was restricted to southern Florida, within the range of the Big Cypress fox squirrel (Williams and Humphrey 1979). They determined through personal interviews that fox squirrels were present but rare in Lee, Hendry, Collier, and northern Monroe Counties

In 1989, I attempted to update the statewide survey completed by Brady (1977). To accomplish this, 437 questionnaires were mailed to field personnel employed by the Florida Game and Fresh Water Fish Commission. Respondents were provided a blank map of Florida on letter sized paper. The map showed county borders and respondents were asked to mark specific locations where populations of fox squirrels occurred. Of the 437 surveys mailed, 183 were returned. Upon review of the surveys, it was decided the information mapped was not precise enough to assess the current distribution. This was in part a fault of the small scale map mailed with the survey. It was also perhaps due to unclear instructions.

After going back to the drawing board, considering that time and manpower were limited, it was decided that personal interviews would be used to determine distribution and status. The information gathered from the interviews is presented in this chapter.

Methods

First, a GFC field employee who would serve as a local expert was identified for each of Florida's 67 counties. These people were selected by contacting regional supervisors and others in the Agency who knew which person was the best contact for each county. Criteria used in the selection included the person's time in the county and their level of knowledge. The selected employees included wildlife officers, wildlife biologists, and wildlife technicians.

These people were interviewed in person in the county of interest. The interviews were conducted while looking at a Department of Transportation county map. Each respondent was asked to share their knowledge of fox squirrel distribution and abundance in the county. Counties were examined by quarters (northeast, northwest, etc.) to keep the respondent focused. The distribution information was marked on the map as the interview progressed.

After the distribution data was mapped, the respondent was asked to drive the interviewer to specific locations in the county where fox squirrels occurred. The on-site visits allowed the interviewer to observe first-hand the characteristics of the habitat occupied. The intent was to make general observations on the habitat such as dominant plant species, vegetation structure, and land uses. Land-owners and managers encountered during the field trips were asked general questions about fox squirrels.

A county survey was normally completed in one day. However, if the respondent was unfamiliar with portions of the county, they were asked for the names and phone numbers of people who knew the area in more detail. These other people were contacted by telephone and asked to share their knowledge of fox squirrel distribution and abundance in the portion of the county in question. The information they provided was added to the county maps used in the field.

A crude estimate of habitat quantity for the larger populations was made using the section grid on the county maps. These estimates were used to assign the populations to one of three size categories: small (<1,000 ha); medium (1,000-4,000 ha); or large (4,000 ha). These estimates were only ball park approximations based on the information mapped, and they are presented with that caution in mind.

Results and Discussion

Distribution

Fox squirrels were widely distributed in Florida, but the distribution was patchy. Similar conclusions were reached by Brady (1977) and Williams and Humphrey (1979).

Fox squirrels were reported to occur in 65 of Florida's 67 counties (Table 1). There were no squirrels reported for Dade and Broward counties, although there was a possibility they occurred in the extreme western portion of both counties. They were reported to occur there in the earlier Florida surveys (Brady 1977, Williams and Humphrey 1979), and while the habitat still existed when the current survey was conducted, none of the people interviewed had seen fox squirrels in either county.

Other than the difference noted above, there were no indications from the data that there had been major changes in fox squirrel distribution in the years between the surveys. As will be discussed later, there have been changes in the quantity of fox squirrel habitat in Florida in recent years, and from that it seems reasonable to conclude that fox squirrels have declined in abundance, but the survey data did not detect those changes.

Largest Populations

The largest populations identified in the surveys are listed by county in Table 1. Several of the populations occurred in habitat that crossed county lines. If the habitat was under the control of one agency or landowner, it was counted as one fox squirrel population for the discussions that follow. As an example, the fox squirrels living in Apalachicola National Forest were considered one population, although the forest lies in three counties.

There were 59 large fox squirrel populations in Florida. Eight of the 59 populations occurred in areas were the quantity of habitat was estimated to exceed 4,000 ha. These were the largest populations in the state. Two of the largest areas were military bases (Eglin and Camp Blanding), two were National Forests (Apalachicola and Ocala), and two were State Forests (Blackwater and Withlacoochee). The habitat on these areas consisted primarily of longleaf pine (Pinus palustris) sandhill, except that on Apalachicola a large portion of the habitat was longleaf flatwoods. The forests on these areas were generally managed for timber production, and the understory vegetation was controlled by prescribed fire. Camp Blanding, which appeared to have the poorest quality habitat of the six major areas on public land, contained vast areas of cut-over sandhills that were dominated by turkey oak (_Quercus laevis_) thickets. The thickets were believed a consequence of over-logging of pines and fire suppression. My impressions were that most of the habitat on Blanding was marginal as a result of the management. However, Blanding is now under a different management approach, and the habitat for fox squirrels should improve.

The two other large populations in Florida occurred on private land. One of these occurred on the quail (_Colinus virginianus_) plantations that dominate the landscape in northern Leon and northern Jefferson Counties. The habitat on the plantations consisted of mature stands of longleaf, loblolly (_P. taeda_), and shortleaf pine (_P. echinata_), interspersed with corn (_Zea mays_) fields and food plots of various legumes planted for quail. My impressions were that the habitat was the richest in the state in terms of food abundance, partially due to quail management activities, but also due to the natural fertility of the clay soils. These soils contrast with the nutrient poor sands that characterize most of Florida's upland soils.

The second large area of privately owned habitat occurred in Osceola, Indian River, and Brevard counties, east of Kenansville and west of the St. Johns River. The area contained a series of neighboring ranches which managed their properties for cattle and wildlife. The habitat on the ranches consisted of xeric flatwoods with mature pines, scattered live oak (Q. virginian)/cabbage palm (Sabal palmetto) hammocks, and forested creek strands. Several of the ranches maintained feeding stations for wildlife, and I was told that fox squirrels were often seen at the feeders. My impressions were that this area contained one of the densest populations of fox squirrels in the state.

In addition to the eight large populations, there were 32 populations that were classified as medium-size (1,000 - 4,000 ha of habitat). Twenty one of these populations were on land privately owned. Sixteen of these occurred on ranches managed for cattle production. The habitat on the ranches consisted primarily of live oak/cabbage palm hammocks, patches of xeric longleaf and slash pine (P. elliotti) flatwoods, longleaf sandhill, and forested fencerows and strips of hardwoods along creeks and drainages. The understory on the ranches was kept low by a combination of grazing, prescribed fire, and mowing. However, in south Florida, in spite of these activities, much of the understory vegetation consisted of dense stands of saw-palmetto (Serenoa repens).

Of the other five medium-sized populations on private land, two occurred on land managed for timber, two occurred on quail plantations, and one occurred in a slowly developing residential area located in sandhill.

Eleven of the 32 medium-sized populations in the state occurred on publicly owned property. Seven of these were on state lands managed for a variety of purposes. Four were managed as wildlife management areas (Cecil Webb, Joe Budd, Apalachee, and Three Lakes), one as a state park (Wekiva and surrounding state lands), one as a state forest (Jennings), and one as a nature reserve and research center (K. Ordway). The habitat on the areas varied from primarily longleaf sandhills for the five areas in northern Florida to xeric flatwoods and live oak hammocks for the two areas in southern Florida. The understory vegetation was managed by prescribed fire, and in addition, by cattle grazing on the two areas in southern Florida.

The other four medium populations on public lands occurred on Federally owned property. Two of these were military bases (Cecil Field and Avon Park), one was a national forest (Osceola), and one was a national wildlife refuge (St Marks, Panacea Unit). The habitat on these areas was primarily xeric, longleaf flatwoods. The habitat on Avon Park consisted of native longleaf flatwoods and planted slash pine plantations.

There were 19 smaller concentrations of fox squirrels identified in the state. The habitat base for each of these populations was estimated at <1,000 ha. Thirteen of these were on private land, and six on public land. Of the 13 on private land, nine were on cattle ranches, two on timber land, two on a quail plantation, and one on a cluster of urban golf courses.

Four of the six small populations on public lands were found on state parks (Goldhead Branch, Hillsborough River, White Belt, and Suwannee River), one occurred on a state forest (Cary), and one occurred on property used for research (University of Florida, Welatka). The habitat on the areas was primarily longleaf sandhills and xeric longleaf flatwoods. The understories were managed primarily using prescribed fire.

In addition to the major concentrations mentioned above and listed in Table 1, smaller populations were scattered across the state. The smaller populations were surviving in fragmented strips and patches of habitat distributed in wooded fencerows, grazed woodlots, pecan (Carya illinoensis) groves, golf courses, and on the fringes of low density residential areas. The ground cover was managed with cattle grazing or mowing. These scattered, diffuse populations were particularly prevalent on the small farms in northern Florida. In fact, 10 of the 14 counties with fox squirrels but without a notable population occurred in northern Florida (Table 1).

Habitat Features

The vegetative structure of the forests occupied by fox squirrels in the state was consistent, and easily recognizable. The habitat was generally park-like in appearance. The forests had a grassy or otherwise low groundcover, a relatively open understory, and an overstory of large pines and oaks. The pines were usually longleaf, or in south Florida, slash pine, but there were a few sites in northern Florida were the pines were either loblolly, shortleaf, or sand pine (P. clausa).

Many wildlife professionals contacted during the surveys had the impression that fox squirrels were restricted to longleaf pine sandhills. This turned out to be a too narrow a view, because fox squirrels were found in a variety of plant communities in addition to sandhills, including xeric flatwoods, grazed woodlots, hardwood fencerows and golf courses dominated by introduced plants.

The habitat characteristics observed in this survey are well documented, both for Florida (Moore 1957, Brady 1977, Williams and Humphrey 1979, Kantola and Humphrey 1990) and for other regions of North America (Flyger and Gates 1982, Dueser et al. 1988, Koprowski 1994). Fox squirrel habitat in the midwestern United States was described as a wooded savanna (Nixon et al. 1984), a description that applies to Florida habitat as well. The plant species differ between regions, but the structure of the forest remains consistent. Dueser et al. (1988), for example, found that vegetation structure could be used to accurately predict if Delmarva fox squirrels would be found in a particular forest patch.

Habitat Trends

Fox squirrels remain widely distributed in Florida, but the distribution is patchy, and the species is locally rare in most of the state because of a lack of habitat. This situation was not always the case, because Florida once contained vast quantities of fox squirrel habitat in the form of great, open pine forests. In fact, open pine forests, dominated by longleaf pine, were until recently the major forest type in the state (Kautz 1993).

This began to change in the late 1800's when industrial logging companies moved their operations from the upper midwestern states to the southern pine forests. Certainly there had been logging, turpentining, and land clearing earlier than this, but the scale was minor in comparison to the changes that followed the arrival of the logging companies (Williams 1989). By 1916, some were lamenting the loss of the longleaf forests (Young and Mustian 1989). By 1936, although greatly depleted, longleaf forests still covered 3.09 million ha of Florida (Kautz 1993). Over the next 50 years, the coverage of longleaf fell by 88%; in 1987, only 0.38 million ha remained.

The great longleaf forests were replaced by a variety of other land uses, such as orange groves, shopping centers, pulpwood plantations, and cattle pastures. There are a few large longleaf forests protected on public lands, but most of the remaining forest patches are scattered in and around other land uses. Fox squirrels still occupy these patches, but they represent remnant populations, stranded by habitat loss. The situation is analogous to a lake drying that leaves fish stranded in pools and puddles scattered over the lake bottom.

The forest changes that have occurred in Florida in the past 100 years, for fox squirrels at least, have made a common species rare. Fox squirrels are rare mainly because their habitat is rare, and it is rare because people have made it so.

Similar trends in fox squirrel habitat have occurred in other southeastern states. Fox squirrels are rare throughout the region as a result (Weigl et al. 1989). The Delmarva fox squirrel has been particularly hard hit by habitat loss and it is currently listed as federally endangered. In contrast to the situation in the southeast, fox squirrels in the midwest have benefited from habitat changes associated with human settlement. Humans have created savannah habitat in the midwest, and fox squirrels have responded with range expansions and population increases (Flyger and Gates 1982).

The fox squirrels' future in Florida depends on the availability of their habitat, which will be influenced by a number of factors. There are several possible scenarios. These alternative futures are discussed in a later chapter of this dissertation.

Table 2-1. Distribution of fox squirrels in Florida by county. Habitat quantities estimated for notable populations: S<1,000 ha; M=1,000-4,000 ha; L>4,000 ha. Abbreviations used: National Forest (N.F.), State Forest (S.F.), State Park (S.P.), Wildlife Management Area (WMA), National Wildlife Refuge (NWR), Air Force Base (A.F.B.)

County	Notable Populations (Quantity of Habitat)	Comments
Alachua	Watermelon Pond area (S)	Most remaining habitat scattered on farms in grazed woods. A few fox squirrels present in uplands on Lochloosa WMA.
Baker	Osceola N.F. (M)	Only reports from Osceola N.F.; occur in patches of xeric flatwoods in Forest and in mowed flatwoods at Olustee Battlefield.
Bay	None	A few fox squirrels reported to occur in Pine Log S.F. and around town of Fountain in pecan groves.
Bradford	None	A few fox squirrels scattered on farms along New River and around Santa Fe Lake in grazed woodlots and pecan orchards.

Table 2-1--continued

County	Notable Populations (Quantity of Habitat)	Comments
Brevard	Cattle ranches in SW corner of county (M)	Occur on ranches in pine/oak hammocks scattered in pastures. Locally common. Also a few fox squirrels scattered in flatwoods on Farmton WMA.
Broward	None	No fox squirrels reported.
Calhoun	None	A few fox squirrels scattered in northern half of county in patches of cut-over sandhill. No reports of squirrels in southern half of county.
Charlotte	Cecil Webb WMA. (M), Babcock Ranch (M)	Fox squirrels restricted to scattered patches of xeric flatwoods and pine/oak hammocks on ranches.

Table 2-1--continued

County	Notable Populations (Quantity of Habitat)	Comments
Citrus	Withlacoochee S.F. (L), Rook Ranch (M), Hollings Ranch (M)	Fox squirrels common in southeastern part of county. A few fox squirrels occur in scattered patches of sandhill elsewhere in county.
Clay	Camp Blanding (L), Gold Head Branch S.P. (S), Jennings S.F. (M)	Habitat marginal but widespread on Camp Blanding and Goldhead. Fox squirrels occur elsewhere in sandhill patches in pastures.
Collier	Naples golf courses (S)	Common on some golf courses. A few squirrels scattered in xeric flatwoods in Golden Gate Estates, Collier Seminole S.P., Everglades City, Immokalee Ranch, and Big Cypress N.P.

Table 2-1--continued

County	Notable Populations (Quantity of Habitat)	Comments
Columbia	Ft. White area on Cason Farm (S)	Small, scattered pockets of fox squirrels; most habitat on farms in grazed woods and fencerows.
Dade	None	No fox squirrels reported
DeSoto	Carlton Ranch (M)	Bulk of habitat on Carlton Ranch. A few squirrels reported for Brighthour Ranch.
Dixie	Mature stand of slash pine--3 miles SW of Old Town (S)	Fox squirrels only reported for northeastern part of county; very rare even there. A few squirrels reported around Guaranto Springs in grazed woods.
Duval	DeeDot Ranch (M), Cecil Field Navy Base (M)	Bulk of habitat in county on DeeDot and Cecil Field. Common in suitable habitat on DeeDot.

Table 2-1--continued

County	Notable Populations (Quantity of Habitat)	Comments
Escambia	La Floresta	Fox squirrels restricted to northwestern part of county.
	Perdido, former WMA (M)	Locally common in longleaf stands managed for pole timber.
Flagler	Ranches bordering Cresent Lake (M)	Most habitat on Cresent Lake ranches in pine/oak hammocks in pastures. A few fox squirrels in pulpwood plantations in remnant patches of xeric flatwoods.
Franklin	St. James Island (S)	Only report for county from a natural longleaf stand surrounded by planted sand pine.
Gadsden	Joe Budd WMA (M)	Common on Joe Budd. A few fox squirrels elsewhere in county; restricted to grazed woods and fencerows.
Gilchrist	None	A few squirrels reported around Ginnie Springs, Pleasant Grove Church, and along S.R. 26 on the east and west side of Waccasassa Flats. Found in grazed woods and fencerows.

Table 2-1--continued

County	Notable Populations (Quantity of Habitat)	Comments
Glades	Lykes Ranch (M)	Only present in county on Lykes property in pine/oak hammocks in pasture. Rare on the property.
Gulf	None	A few squirrels reported on St.Joe seed tree orchard, on M&K Ranch near Downes Island, on along S.R. 71 south of White City.
Hamilton	Champion Quail Plantation (M)	Only reported from western half of county. Other than quail plantation, a few reported to occur along S.R. 51 on the Suwannee River.
Hardee	Carlton Ranch (M)	Bulk of habitat on Carlton Ranch in hammocks and xeric flatwoods in pastures. A few squirrels reported to occur south of Wauchula along the Peace River and on the Smoke Ranch.

Table 2-1--continued

County	Notable Populations (Quantity of Habitat)	Comments
Hendry	Alico, Hilliard, and Duda Ranches (M)	Most habitat in northwestern corner of county on ranches. A few squirrels reported for Big Cypress Indian Reservation.
Hernando	Withlacoochee S.F. (L)	Fox squirrels common on Withlacoochee S.F. Restricted elsewhere to remnant patches of sandhill forests found in subdivisions and golf courses.
Highlands	Avon Park A.F.B. (M), K-D Ranch (M)	Fox squirrels common on K-D Ranch in southeastern corner of county. A few squirrels reported for Avon Park A.F.B., on farms surrounding Highlands Hammock S.P., and along Fisheating Creek.
Hillsborough	Hillsborough River S.P. (S)	A fox squirrels on and around Hillsborough River S.P. and on ranches in southern part of county.

Table 2-1--continued

County	Notable Populations (Quantity of Habitat)	Comments
Holmes	None	Squirrels few and scattered in pecan groves and grazed woods.
Indian River	Ranches west of St. Johns River marsh (M)	Common in patches of grazed woods on ranches. No squirrels reported east of St.Johns River.
Jackson	Apalachee WMA (M)	Common on Apalachee. A few squirrels reported to occur on Florida Caverns S.P. and in scattered locations along the Apalachicola and Chipola Rivers.
Jefferson	Quail plantations (L)	Common on the numerous quail plantations scattered in northern half of county. None reported for southern half of county.
LaFayette	None	A few squirrels reported to occur in grazed woods on farms along Suwannee River.

Table 2-1--continued

County	Notable Populations (Quantity of Habitat)	Comments
Lake	Ocala N.F. (L), State lands in Wekiva River basin (M)	Bulk of habitat in Ocala N.F. and on state lands bordering Wekiva River. A few squirrels reported to occur around Astatula, Hancock Lake, and Klinger Airport.
Lee	Alico Ranch (M)	Most habitat on Alico Ranch. Also reported on golf courses and ranchettes built on western edge of Alico.
Leon	Quail plantations (L), Apalachicola N.F. (L)	Fox squirrels common in northern half of county on plantations. Widely scattered in Apalachicola in patches of sandhill and xeric flatwoods.
Levy	Williston Highlands (M)	Scattered pockets of squirrels on farms around Chiefland and in remnant longleaf stands in Williston area.

Table 2-1--continued

County	Notable Populations (Quantity of Habitat)	Comments
Liberty	Apalachicola N.F. (L)	Bulk of habitat for county in Apalachicola N.F. in vicinity of Camel Pond. Occur in patches of sandhill and xeric flatwoods.
Madison	None	Squirrels rare. Bulk of habitat along Suwannee River near I-10 rest area and along Withlacoochee River near Hickory Grove Church.
Manatee	Taylor (S), Jim Walters (S), and Drosey Ranches (S)	Bulk of habitat on ranches. Occurred in scattered locations in patches of grazed woods in pastures.
Marion	Ocala N.F. (L)	Bulk of habitat and fox squirrels occur on Ocala N.F. in longleaf islands. Fox squirrels abundant on Marion Oaks Golf Course. A few squirrels on horse ranches.

Table 2-1--continued

County	Notable Populations (Quantity of Habitat)	Comments
Martin	None	A few squirrels in grazed woods on ranches west of I-95. Reported on White Belt and Bluefield Ranchs.
Monroe	None	Only reported from Loop Road. Reportedly seen in slash pines bordering road.
Nassua	White Oak Plantation (S), Cary S.F. (S)	Most habitat along St.Marys River in patches of mature pines. Populations few and scattered.
Okaloosa	Eglin A.F.B. (L), Blackwater River S.F. (L)	This is the largest habitat block in the state.
Okeechobee	Williamson Cattle Co. (M)	A few squirrels scattered on ranches in grazed woods.

Table 2-1--continued

County	Notable Populations (Quantity of Habitat)	Comments
Orange	Leo Faurot Ranch (M), Wekiva Springs S.P. (S)	Other than Wekiva Springs S.P., most habitat scattered on ranches in eastern part of county. Common on Leo Faurot ranch located in southeastern portion of county.
Osceola	Ranches around Kenansville (L), Three Lakes WMA (M)	Fox squirrels widespread in county. Common on ranches in Kenansville area.
Palm Beach	White Belt Ranch (S) (this property is state owned)	Reportedly only occur in county in grazed woods on White Belt Ranch.
Pasco	Ranches (M)	Bulk of habitat and squirrels in central portion of county on ranches. Also reported to occur in vicinity of Big Fish Lake.

Table 2-1--continued

County	Notable Populations (Quantity of Habitat)	Comments
Pinellas	None	Reported to occur but very rare. Habitat on golf courses and grazed woods in remaining pastures.
Polk	Avon Park A.F.B. (M)	A few squirrels on Avon Park A.F.B. Also occur on ranches along Kissimmee River.
Putnam	K. Ordway Preserve (M), Fla. Rock property (M), Univ. Fla.--Welaka Unit (S)	Habitat scattered across county in remnant stands of longleaf sandhill. Locally common.
St.Johns	McCormick Ranch (S)	Bulk of habitat scattered in northwestern corner of county in grazed woods.
St.Lucie	Peacock Ranch (S)	Habitat limited to a few pine stands along Bluefield Road and on Peacock Ranch.

Table 2-1--continued

County	Notable Populations (Quantity of Habitat)	Comments
Santa Rosa	Eglin A.F.B.(L), Blackwater River S.F.(L), T.R. Miller Timber Co.(M)	Habitat abundant in eastern half of county. Fox squirrels common. No habitat or fox squirrels reported for western half of county.
Sarasota	None	Fox squirrels few and widely scattered on ranches and in new subdivisions along I-75.
Seminole	Ranches around Geneva(M), Lower Wekiva River S.P. (S)	Other than the small population on Lower Wekiva, most habitat on ranches along the St. Johns River. Common on some ranches.

Table 2-1--continued

County	Notable Populations (Quantity of Habitat)	Comments
Sumter	Ranches in NW corner of county (M)	A few squirrels on small ranches around Bushnell, but most habitat and squirrels in northwest corner of county on large ranches west of I-75 and north of S.R. 44.
Suwannee	Chinquapen quail plantation(S), Suwannee River S.P. (S)	Small pockets of squirrels widely scattered; most found in pecan groves and grazed woods on small farms.
Taylor	None	A few squirrels in remnant patches of sandhill between Perry and the Gulf.
Union	Circle S Ranch (S)	Squirrels widely scattered in grazed woods; other than Circle S Ranch, most habitat on farms along New River and Olustee Creek.

Table 2-1--continued

County	Notable Populations (Quantity of Habitat)	Comments
Volusia	Ranchs and camps around Lake Dias(M)	Bulk of habitat around Lake Dias. A few squirrels scattered in Tomoka WMA in xeric flatwoods.
Wakulla	St.Marks NWR (Panacea Unit) (M), Apalachicola N.F.(L)	Bulk of habitat in scattered patches of xeric flatwoods in Apalachicola and on St. Marks.
Walton	Eglin A.F.B. (L)	Most habitat in county on Eglin A.F.B. Elsewhere found in pecan groves and grazed woods on small farms.
Washington	None	Habitat on small farms in pecan groves and grazed woods.

CHAPTER 3
POPULATION ECOLOGY

Radio telemetry has become a standard tool for investigations of wildlife movements and demographics. It has been used in Florida on two previous studies of fox squirrels. In the first study, radio transmitters were attached to six fox squirrels on a sandhill study area in northeastern Florida (Kantola and Humphrey 1990). In the second study, five fox squirrels in Collier County were radio-collared and relocated from golf courses to the Big Cypress National Preserve (Jodice 1993). Both studies have provided valuable insight into fox squirrel biology in Florida, but both were hampered by small samples of radio-collared animals. Because of the limited data that were available on fox squirrel population ecology in Florida, the current study was initiated.

The study attempted to answer several questions on fox squirrel population ecology, including: 1. What are the home range sizes and how are the home ranges spatially distributed? 2. What are the mortality rates of radio-collared animals, and what are the important mortality factors? 3. What is the average litter size, litter frequency, and when is the breeding season? 4. What is the density of fox squirrels on the study areas? 5. What are the characteristics of subadult dispersal? and 6. How does the population ecology of fox squirrels in northern Florida compare to that observed for fox squirrels in other regions in North America?

STUDY AREAS

The first phase of the study was conducted on Goldhead Branch State Park and surrounding private property, Clay County. Field work was conducted there from January 1990 to March 1991. The 6.9 km^2 area was about 80% forested (Figure 3-1); 80% of the forest cover was longleaf pine/turkey oak) sandhill, 18% hardwood hammock (primarily oaks), and 2% sand pine scrub. The non-forested portions of the study area were open water, marsh, or uplands developed for public use or park maintenance. Hunting was prohibited on the Park, but the surrounding land was hunted.

Fox squirrels were difficult to trap on Goldhead, and because of this, the study was moved to a second area in 1991. The second study area was in southern Columbia County, about 3 km north of the town of Fort White. Field work was conducted from January 1991 to June 1994. The primary study area of 2.3 km^2 (Figure 3-2) was a patchwork of upland hardwoods (49.3 ha), pastures and row crops (144.0 ha), and clearcuts (34.3 ha). There were three residences on the study area (2.8 ha). The clearcuts were the result of a 1989 logging of planted slash pines.

The wooded portions of the Fort White area occurred as fencerows, two closed-canopy hammocks (each about 10 ha in size), and a wooded but open-canopied pasture (Figure 3-2). Tree species were predominantly laurel oak (Q. hemisphaerica) and live oak. Black cherries (Prunus serotina) and dogwoods (Cornus florida) were common in the fencerows and hammocks. Longleaf pines were scattered over the area, but they were a minor component of the forest cover. Cattle grazed most of the study

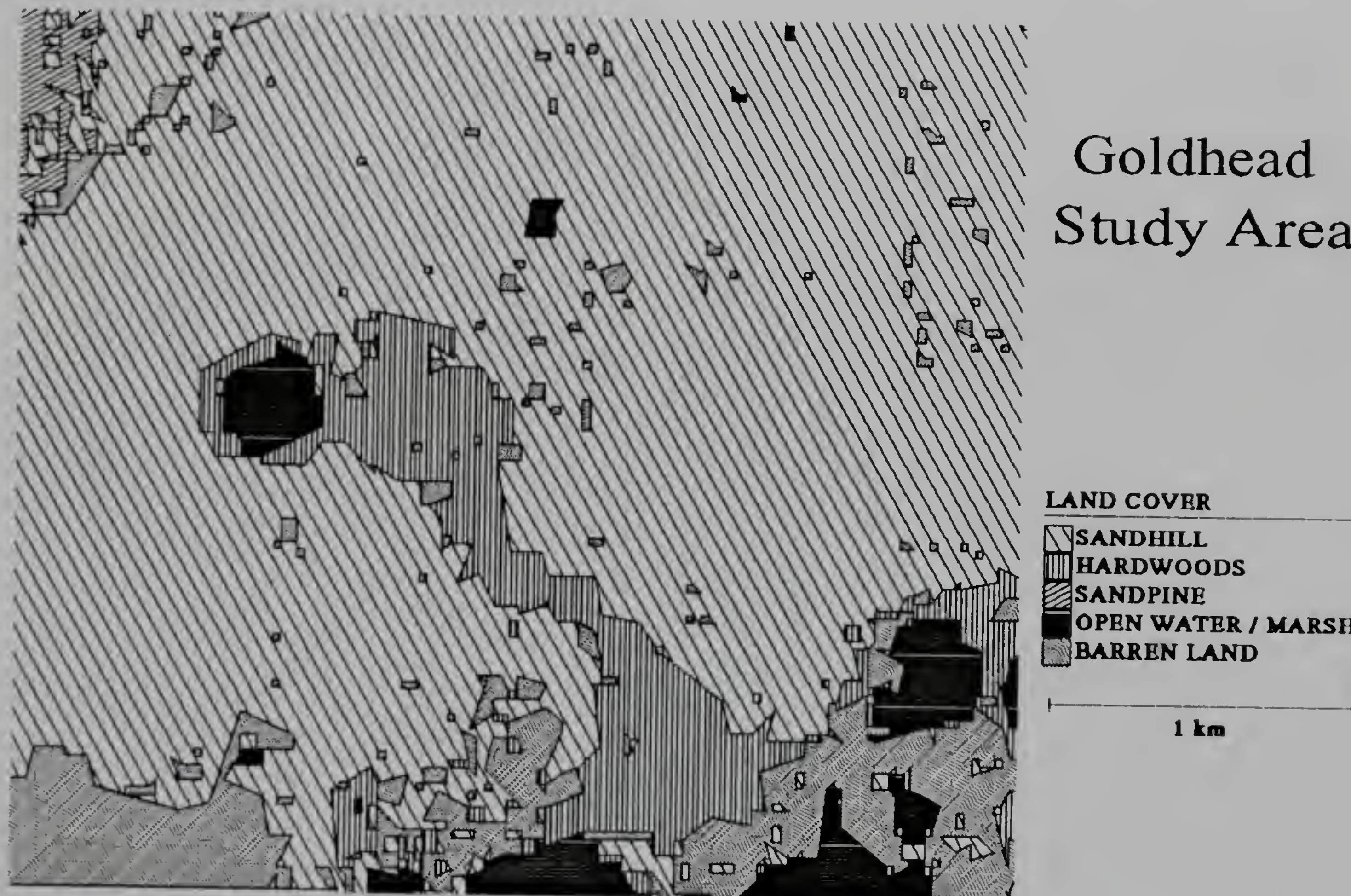

Figure 3-1. Goldhead study area, Clay County, Florida.

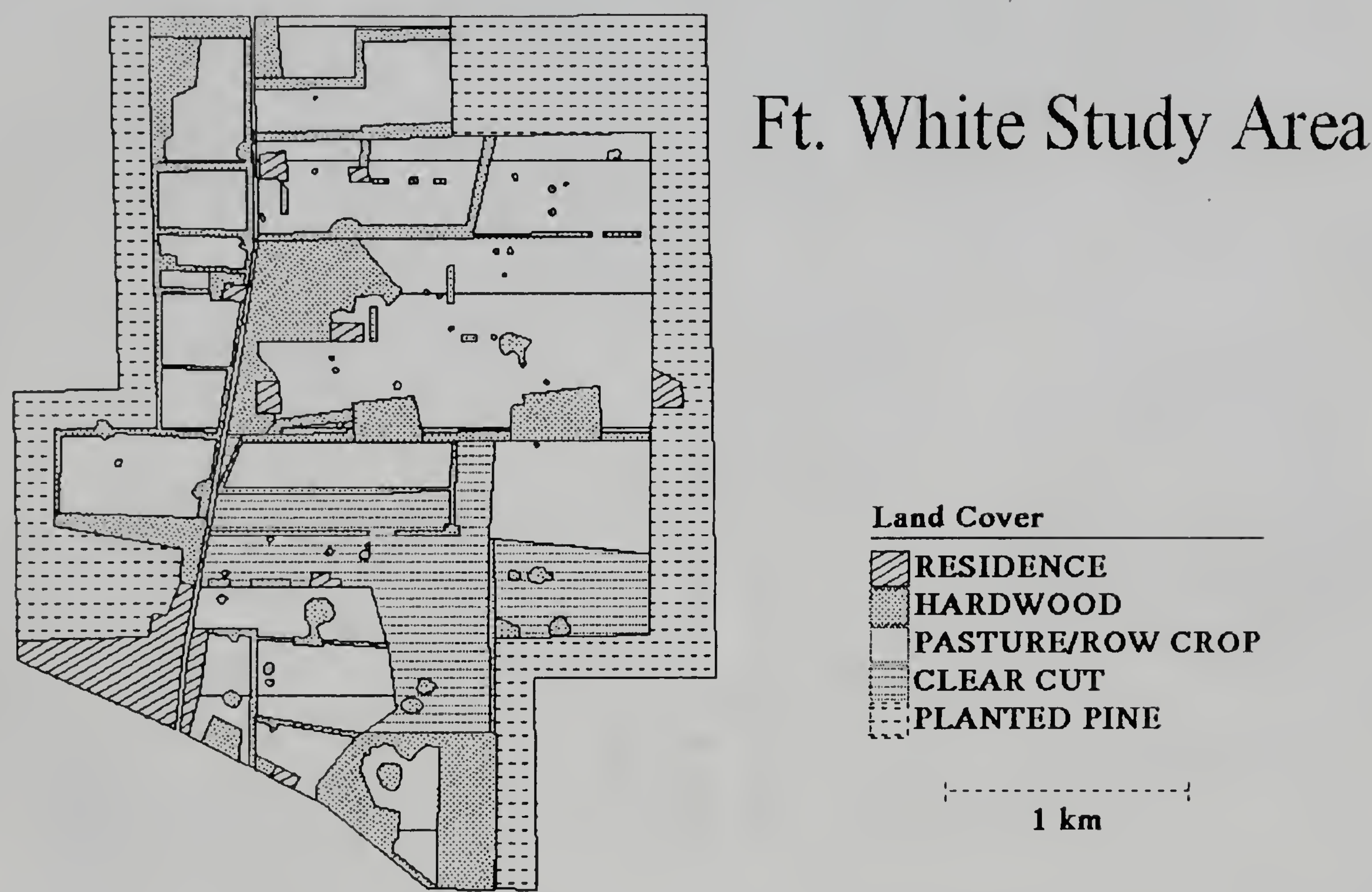

Figure 3-2. Fort White study area, Columbia County, Florida.

area, and their activity kept the hammocks and fencerows clean of undergrowth. There were four fields planted in peanuts or corn. State Road 47, a moderately traveled 2-lane highway, formed the western border of the primary study area. The landowners on the study area allowed gray squirrel (S. carolinensis) hunting, but they protected fox squirrels. This had been their practice before the study began and continued during the study.

METHODS

Capture Procedures

Adult and subadult fox squirrels were captured in live traps. Two were caught in wooden traps (61 cm long) modeled after the design of Ludwig and Davis (1975). All other trapped fox squirrels were caught in wire traps (Tomahawk brand, Models 103, 104, and 105). Raw, dried peanuts in the hull were settled on as the bait of choice, but only after using a variety of baits, including dried corn (shelled and on the cob); fresh, grocery store mushrooms; peanut butter and raisin mix, suspended in the trap in a cheese cloth sack; and scented lures, including anise and artificially flavored extracts of strawberry, banana, and walnut.

Traps were checked in the morning and again in the evening. Traps were left open overnight prior to 1993, but after that they were tripped in the evening and reset the following morning. This eliminated the capture of nontarget, nocturnal species such as raccoons (Procyon lotor), opossums (Didelphis virginiana), and striped skunks (Mephitis mephitis). It also eliminated the possibility of a fox squirrel spending the night in a trap.

Prior to handling, trapped fox squirrels were calmed by covering the trap with a jacket or towel. Next, a mesh nylon sack with a drawstring was placed over the door end of the trap. The drawstring was tightened and the door was opened with the bag in place. The jacket was then removed, and the squirrel was flushed into the bag for handling.

Animals requiring extensive handling were tranquilized with an injection in the hip of 100mg/cc ketamine hydrochloride. As a rule of thumb, all adult-sized squirrels (weight >950grams) were drugged with a dosage of 0.3 cc/squirrel. This dosage was reduced to 0.25cc/ adult squirrel in the later portions of the study. Lighter squirrels were normally given less drug, but it was found that 0.2 cc was a minimum dose for handling squirrels >800 g. The reaction of the squirrels to the tranquilizer was variable: some squirrels succumbed and were limp within 2 minutes of injection, but others never went fully under -- they continued to move and crawl but made no attempt to bite and were safely handled. Animals tranquilized in the afternoon were routinely held overnight in traps placed in a storage shed to allow them to fully recover from the drugs before their release. They were released at the capture site the next morning.

Recaptured animals that were only physically examined were processed in the mesh bag without using tranquilizers. These squirrels made no attempt to bite, but some kicked without warning with razor-clawed hind feet.

Fox squirrels were weighed to the nearest 25g with a spring scale. Body weights of adult animals were compared by sex using a nested ANOVA.

Subadults and adults were tagged in each ear with a monel tag (National Band and Tag Co., Size #1). Squirrels >700grams were radio collared. The transmitters used were either Telonics M080 or Holohil MI-2M. Fox squirrels on Goldhead were also marked by toe clipping one digit, but toe clipping was not used at Fort White. Nestlings from 2 litters handled on Fort White were marked on their leg pelage with a leather dye, and nestlings from a third litter were tagged in one ear with an adult eartag.

Estimates of Age and Sexual Maturity

Age estimates were assigned to fox squirrels based on criteria presented by Moore (1957) and Flyger and Gates (1982). Nestling fox squirrels with hair on their backs were considered at least 10 days old, and nestlings with open eyes were considered at least 4-5 weeks (Flyger and Gates 1982). The age of males caught in traps was assessed by body size, testes descent, and the amount of hair on the scrotum. Males with undescended testes and heavily furred scrotums were considered <8 months old. Males <900g with testes $\leq$3.5cm and mostly furred scrotums were aged as 8 months old; the testes on these squirrels were assumed to have just descended. Males >900g with scrotal testes and sparsely furred, black scrotums were considered >9months old. Female fox squirrels <900g were considered <5 months old.

The age in months for squirrels <9 months old was estimated by backdating from the date of capture to the appropriate winter or summer birthing periods. Animals thought born in the summer birthing period were assigned an August 1 birthday; winter born animals were assigned a January 1 birthdate.

Sexual maturity of males was assessed by testes size and scrotal characteristics. Males with undescended testes and furred scrotums were considered sexually immature. Males with large, swollen testes (>3.5 cm long) and black, mainly furless scrotums were considered sexually mature. Sexual maturity of females was assessed by nipple characteristics (McCloskey 1977). Females with nipples <1 mm long that looked like they had never been suckled were considered sexually immature. Females with nipples >3mm were considered sexually mature and thought to have bred.

Telemetry

Radio-collared fox squirrels on Goldhead were located as time permitted using triangulation procedures from fixed stations. Data were recorded by station number and azimuth. Fox squirrels on the Fort White area were normally located 2-3 times/week. All locations there were plotted in the field on aerial photographs (scale, 1cm=48m), and the data were recorded as Universal Transmercator Grid (UTM) coordinates. Squirrels were located using standard triangulation procedures or by walking or driving to the tree where the squirrel was located. A fixed-wing airplane was used to search for squirrels that could not be found from the ground. The Fort White study area was open, and visibility for seeing fox squirrels on the ground was normally unimpeded. Locations on the Fort White study area were extremely accurate because of the visibility and the attempts to pinpoint most locations to the nearest tree or clump of trees. Attempts were made on both study areas in the initial months of field work to locate animals more than once daily to obtain daily activity data. This was discontinued on Goldhead because of time constraints and on Fort White because of the influence that observers had on squirrel movements.

Home range sizes were estimated by the harmonic mean and convex polygon methods using the computer program TELEM. Pre-dispersal (natal) and post-dispersal (adult) home ranges were calculated for fox squirrels that dispersed from the study area. Transition locations between home ranges were discarded from the analysis. Home range sizes of adult males and adult females were compared using the Mann-Witney test ($p<0.01$).

<u>Habitat Use Versus Availability</u>

Habitat use was determined by assigning each location to one of the major cover types. The four habitat types used for the analysis on the Goldhead study area were sandhill, hardwood, scrub, and barren land (or non-forested land). The habitat types used on the Fort White area were hardwood, planted pine, wooded pasture, and field (includes pastures, rowcrops, and clearcuts). Habitat selection of non-dispersing squirrels was examined with Friedman's method (Alldredge and Ratti 1986). The difference between proportion used and proportion available for each habitat type was computed for each animal. These differences were ranked for each animal (lowest to highest), and the ranks were used to compute Friedman's test statistic (habitat types were considered as "treatments" and animals as "blocks"). If Friedman's test was significant, then a signed rank test was used to determine differences among use versus availability for each of the habitat types.

Mortality Rates

Annual mortality rates were calculated with the computer program MICROMORT (Heisey and Fuller 1985). The daily survival rate was assumed constant for the study period. A z-statistic was used to compare mortality rates for males and females and for residents and dispersers. In addition to the confirmed deaths of radio-collared squirrels, radio contact was lost with other squirrels for unknown reasons. It was assumed these squirrels died. Two mortality rates were calculated: one used only the confirmed deaths; the second used the number of confirmed deaths plus the number of assumed deaths.

Reproduction

Female fox squirrels have the potential for producing two litters/year, one in winter and one in summer (Flyger and Gates 1982). The frequency of litters from radio-collared females for each potential reproductive period in 1991, 1992, and 1993 was assessed using movement data, capture data, sightings of subadults, sightings of females that appeared to be nursing, and nest checks in 1992 and 1993.

Food Habits

Anecdotal data on food habits also were collected on the Fort White study area. Whenever fox squirrels were seen eating, attempts were made to identify the foods. The food habits data are presented by season using the following seasons: winter (January - February), spring (March-May), summer (June-August), and fall (September-December).

RESULTS AND DISCUSSION

Capture Success

Six adult fox squirrels (3 male:3 female) and one nestling (male) were captured on Goldhead. Five of the six adults were caught in traps (2,877 trap days, or 1 capture/575 trap days); one adult female and her nestling were caught in a nest box built by Park personnel for kestrels (*Falco sparverius*). Five of the six adults on Goldhead were radio collared. The adult not collared was caught at the end of the study during attempts to catch the radio-collared squirrels for collar removal.

Forty-four fox squirrels (27 male:17 female) were captured a total of 120 times in 3,486 trap-days on the Fort White study area (1 capture/29.1 trap days). Thirty-nine of the squirrels were radio-collared. One fox squirrel died after handling. Four squirrels caught in traps were not collared, either because they were too small (n=2) or because they were captured at the end of the study (n=2) during attempts to catch radio-collared squirrels for collar removal. Thirteen fox squirrel nestlings were also handled; 11 of these were sexed (4 male:7 female) and eight were marked with either dye or eartags.

Body Weights

Weights were taken on five adult fox squirrels (2 male:3 female) on Goldhead. The average weight of males was 1,055 grams (SE 55); the average weight of females was 1,075 grams (SE 80). The weights were not compared statistically because of the small samples.

Weights were taken on 30 adult fox squirrels (22 males:8 females) on Fort White. The average weight of males was 999 grams (SE 10); the average weight of females was 1,120 grams (SE 14). Females were significantly heavier than males (p=0.0003). Wood (1988) and Larson (1990) also reported that adult females were heavier on average than adult males, although Wood (1988) stated the differences in his data were not significant. Other studies have found no significant differences in the weights of males and females (Flyger and Gates 1982, Weigl et al. 1989).

Home Range Sizes

The minimum convex polygon home ranges on Goldhead ranged from 19.4 to 95.8 ha (Table 3-1). The average home range size for the two males (83.0 ha; SE 9.1) was over twice the mean size for the three females (35.6; SE 9.6).

The average convex polygon home range size on Fort White for 17 adult males (79.5 ha; SE 8.3) was significantly larger (p<0.01) than the average home range size for 12 females (33.0 ha; SE 4.9) (Tables 3-2 to 3-4). The natal home ranges of eight subadults averaged 6.35 ha (SE 1.76). Five animals monitored on the Fort White area did not clearly fit into the category of adult or subadult. The home ranges for these animals appears in Table 3-5.

Home ranges for both study areas also were calculated using the harmonic mean method. Based on the time I spent in the field tracking the squirrels, my opinion is that the 80% harmonic mean estimate represented the area where the squirrels were usually found. The average home range sizes using 80% of the locations were as follows: Goldhead -- adult males (n=2) 29.5 ha; adult females (n=3) 22.1 ha; Fort White -- adult males (n=17) 35.7 ha (SE 4.7); adult females (n=12) 12.8 ha (SE 2.4); subadults (n=7)

Table 3-1. Home range sizes (ha) of adult fox squirrels on the Goldhead study area by the harmonic mean (HM) and minimum convex polygon (MCP) methods.

Sex/#	Monitoring Period	# Locations	HM 65% ha	HM 80% ha	HM 95% ha	MCP ha
M390	01/25/90 - 02/12/91	134	24.1	33.0	74.7	70.3
M340	02/01/90 - 03/05/91	100	11.3	26.0	96.9	95.8
F300	02/09/90 - 08/03/90	67	6.0	9.4	25.4	19.4
F430	02/06/90 - 05/20/90	59	13.1	23.4	33.8	28.9
F410	02/02/90 - 03/05/91	104	20.5	33.7	56.6	58.4

Table 3-2. Home range sizes (ha) of subadult fox squirrels on the Fort White study area by the harmonic mean (HM) and minimum convex polygon (MCP) methods.

Sex/#	Monitoring Period	# Locations	HM 65% ha	HM 80% ha	HM 95% ha	MCP ha
F069	11/05/92 - 03/22/93	31	1.9	2.6	10.7	6.0
F630	11/04/92 - 02/24/93	42	2.7	3.5	5.6	4.1
F870	11/07/92 - 03/20/93	34	0.6	1.1	7.8	1.7
M129	10/03/91 - 05/11/92	48	1.3	2.5	5.8	3.0
M130	02/04/91 - 04/17/91	25	3.1	7.0	33.5	14.3
M150	02/05/91 - 03/06/91	18	6.0	11.9	22.9	13.6
M170	02/01/91 - 06/10/91	49	2.3	4.6	5.4	6.1

Table 3-3. Home range sizes (ha) of adult female fox squirrels on the Fort White study area by the harmonic mean (HM) and minimum convex polygon (MCP) method.

Sex/#	Monitoring Period	# Locations	HM 65% ha	HM 80% ha	HM 95% ha	MCP ha
F010	01/15/91 - 12/07/92	227	8.7	14.2	42.2	47.9
F069[a]	04/07/93 - 08/11/93	40	9.2	14.3	70.0	55.4
F070[b]	04/21/93 - 01/28/94	73	1.8	2.5	4.8	3.4
F099[b]	03/17/92 - 04/29/94	169	2.7	5.3	10.9	9.1
F100	03/18/91 - 01/28/94	318	1.4	3.3	25.5	30.7
F120	02/04/91 - 06/25/92	185	13.6	26.6	53.4	44.9
F140[a]	06/16/91 - 09/22/92	146	12.2	21.0	42.5	42.7
F260	01/18/91 - 06/23/94	325	6.9	16.4	41.2	42.4
F270	01/21/91 - 04/29/94	318	1.4	2.8	7.5	17.2
F429	02/03/93 - 04/16/94	121	11.1	22.8	42.3	47.0
F630[a]	03/11/93 - 04/29/93	22	4.6	10.0	15.8	10.4
	06/01/93 - 11/07/93	65	3.7	6.5	30.0	28.6
F870[a]	04/30/93 - 10/03/93	46	12.4	23.0	33.0	26.3
	10/17/93 - 11/19/93	13	4.2	8.7	14.9	8.9

[a] Post dispersal home ranges. F069 remained on the primary study area after dispersal, but the other three females (F140, F630, and F870) left the area.
[b] F070 and F099 attained sexual maturity during the monitoring period.

Table 3-4. Home range sizes (ha) of adult male fox squirrels on the Fort White study area by the harmonic mean (HM) and minimum convex polygon (MCP) method.

Sex/#	Monitoring Period	# Locations	HM 65% ha	HM 80% ha	HM 95% ha	MCP ha
M049	11/05/92 - 04/27/94	108	24.4	38.8	165.5	96.3
M090	02/05/91 - 08/31/92	189	39.4	72.4	183.3	134.4
M119	01/29/93 - 03/21/94	113	13.8	28.7	78.2	75.7
M128[a]	02/03/93 - 03/09/94	36	7.2	13.7	166.7	76.7
M130[a]	05/01/91 - 06/23/92	149	10.0	21.6	37.5	44.5
M150[a]	03/19/91 - 09/23/91	47	14.3	34.8	76.8	60.5
M159	03/17/92 - 04/27/94	225	3.7	8.3	53.7	38.7
M210	06/06/91 - 04/04/94	311	9.9	62.3	132.8	125.4
M239	01/29/93 - 07/19/93	54	16.2	39.0	100.2	71.5
M240	12/31/91 - 04/08/94	252	7.9	29.0	78.3	115.7

Sex/#	Monitoring Period	# Locations	HM 65% ha	HM 80% ha	HM 95% ha	MCP ha
M259	04/20/93 - 12/12/93	68	20.1	43.3	91.4	75.3
M300	11/07/91 - 04/06/92	62	30.8	51.8	167.7	101.3
M308	09/07/93 - 06/24/94	59	5.1	12.4	30.1	22.8
M368	12/31/91 - 04/27/94	263	5.4	14.8	30.5	37.1
M430	01/03/92 - 09/06/92	88	17.4	31.0	86.0	67.6
M540	01/06/93 - 07/01/93	65	16.0	38.5	126.7	75.3
M690	03/18/92 - 12/09/93	135	37.3	67.2	178.8	132.3

[a] Post-dispersal home ranges.

Table 3-5. Harmonic mean (HM) and minimum convex polygon (MCP) home range sizes (ha) of fox squirrels captured as subadults whose sexual maturity during the period of monitoring was unknown, but suspected to be that of a subadult (the possible exception is M188, who may have been sexually mature during the period shown below).

Sex/#	Monitoring Period	# Locations	HM 65% ha	HM 80% ha	HM 95% ha	MCP ha
F370	11/07/91 - 08/19/92[a]	18	7.0	8.6	12.6	11.2
F869	03/03/93 - 12/07/93	85	6.5	9.7	13.7	12.6
M128	02/03/93 - 10/12/93[b]	70	23.7	37.2	46.0	39.9
M160	02/04/91 - 09/18/91	74	2.0	3.8	10.1	8.1
M188	12/16/93 - 04/01/94	24	2.1	3.5	8.9	10.0

[a] F370 slipped her radio collar one month after capture and was last located with telemetry methods on 12/07/91. She was sighted 3 times subsequently, with the last confirmed sighting on 08/19/92.
[b] Unlike the other fox squirrels in the table, M128 dispersed from the primary study area; his post-dispersal home range appears in Table 4.

Table 3-6. Comparison of fox squirrel home ranges in the southeastern Coastal Plain (minimum convex polygon method). Data from this study are for adult squirrels only. The other studies did not report the ages or sexual maturity of the squirrels they monitored.

		Home Range Size (ha)	
Reference	Location	Males	Females
This study	Florida Goldhead	83.0 (n=2)	35.6 (n=3)
	Florida Fort White	79.5 (n=17)	33.0 (n=12)
Kantola (1986)	Florida Putnam County	40.0 (n=4)	20.6 (n=2)
Powers (1993)	Alabama Conecuh National Forest	38.0 (n=14)	11.6 (n=9)
Edwards (1986)	South Carolina Georgetown	31.6 (n=9)	19.3 (n=4)
Weigl et al. (1989)	North Carolina Coastal Plain	26.6 (n=8)	17.2 (n=14)

4.7 ha (SE 1.4). Two other harmonic mean estimates of home range size were calculated (65% and 95%). These estimates are presented in the home range tables as a reference for those who may find the information of value.

The home range sizes determined in this study were compared to those determined in other studies conducted in the southeastern United States (Table 3-6). Home ranges of males in all studies were larger than those of females.

The home ranges of both sexes on Goldhead and Fort White were almost double the size of those found in other studies. There are several possible explanations for these differences. One may be due to differences in food abundance between areas. As an example, fox squirrels on Goldhead may have had large home ranges because of low food abundance in comparison to the other study areas in the southeast. Fox squirrels on Goldhead also occurred at relatively low densities (Table 3-12), and low food abundance would explain both the low densities and large home ranges. The large home ranges on the Fort White study area were believed a result of habitat distribution. The forested habitat was distributed in fencerows and hammocks scattered in fields and pastures. The pattern may account for the large home range sizes there relative to other areas where the habitat was more continuous. Other differences in home range sizes between study areas may be due to differences in sample sizes of radio-collared animals and the duration of telemetry monitoring.

Spatial Relationship of Home Ranges

The spatial relationships of the home ranges of adult fox squirrels are illustrated in Figures 3-3 to 3-11. I tried a number of ways to depict the characteristics I observed in the field, and the method used here was the best I found. The figures contain the complete set of locations for each of the home ranges that are illustrated. The vertical spikes on the graphs represent sites with frequent locations. These normally represent locations of preferred nests. The graphics may at first glance look too "busy" to interpret, but in my opinion, they are worth taking the time to "read".

The home ranges for the three adult females tracked on Goldhead displayed minimal overlap (Figure 3-3). This pattern also observed for adult females on the Fort White study area (Figures 3-4 to 3-7).

Two males were radio-tracked on Goldhead, and although there was no overlap between them, there were too few data to evaluate the spatial arrangement of adult males on the Goldhead area (Figure 3-8). Although adult males were generally solitary, their home ranges on Fort White overlapped extensively with those of adult females and other adult males (Figures 3-9 to 3-11). The natal home ranges of subadults monitored on the Fort White area were within their mother's home ranges.

There was one exception observed regarding the separate home ranges of adult females. In this case, a subadult that did not disperse attained sexual maturity while within the range of the female believed to be her mother. The spatial arrangement of home ranges and the behavior behind the patterns is discussed in the end of this chapter.

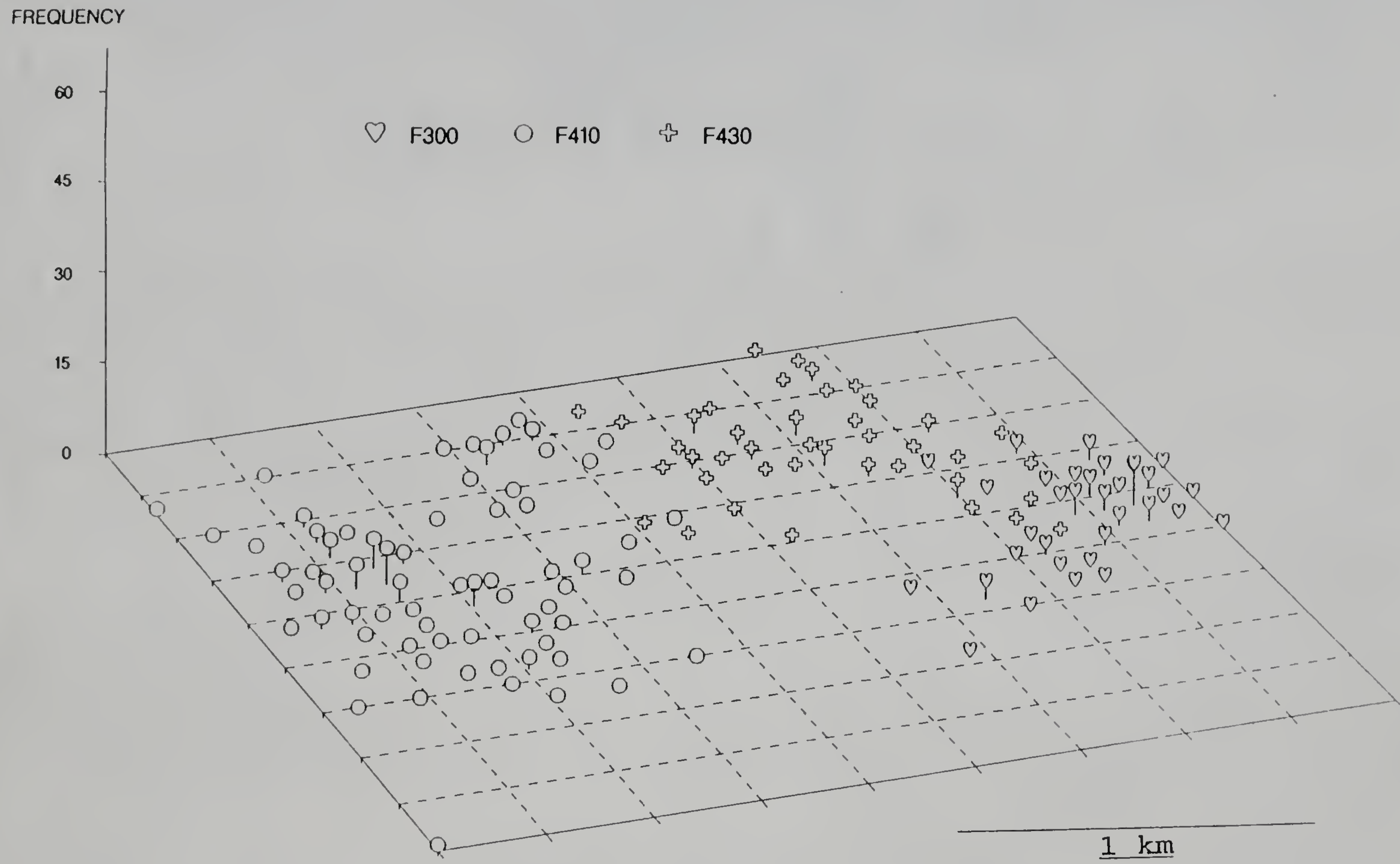

Figure 3-3. Spatial relationship of three adult female fox squirrels radio-tracked on the Goldhead study area.

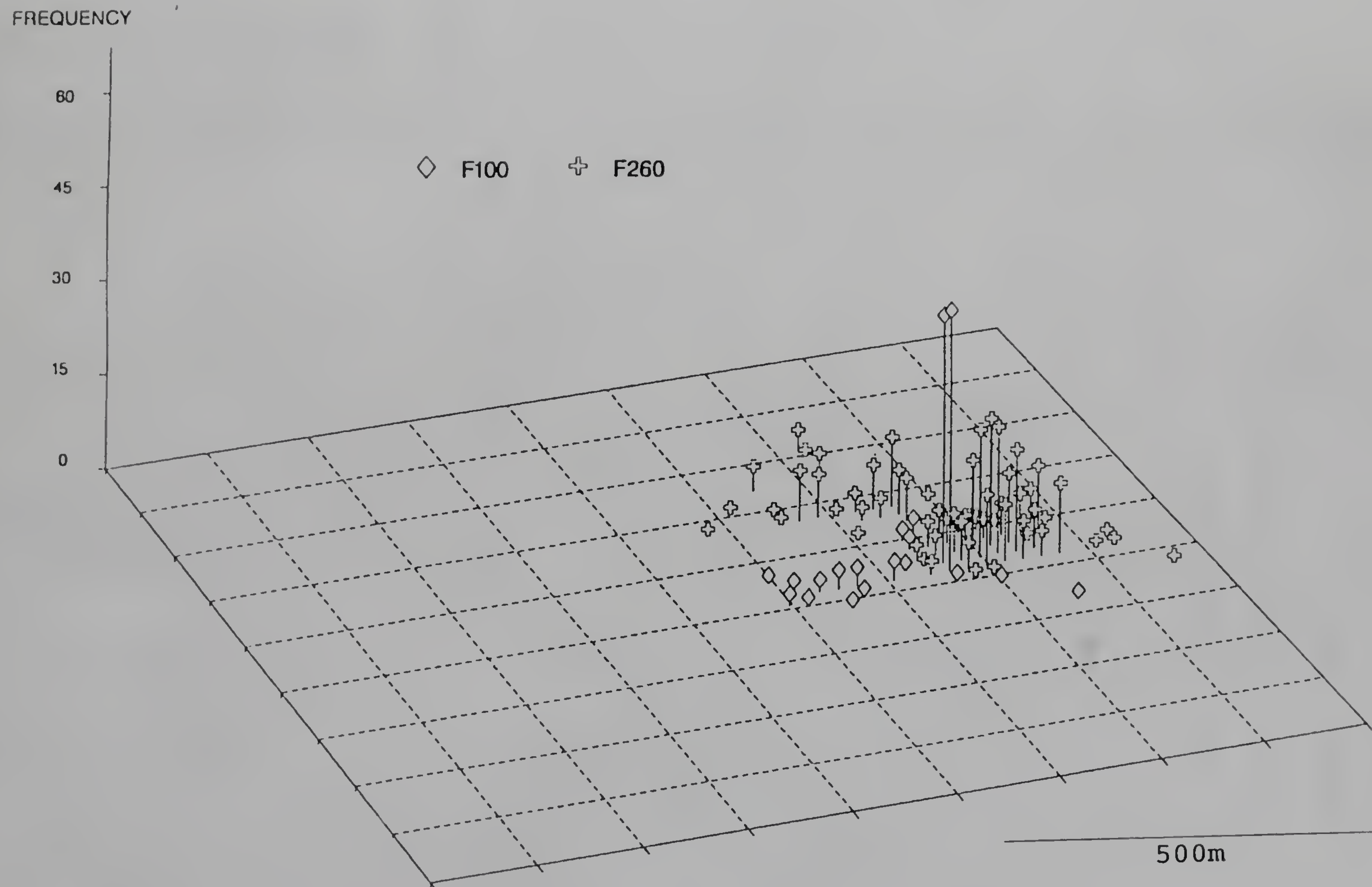

Figure 3-4. Spatial relationship of two adult female fox squirrels radio-tracked on the Fort White study area.

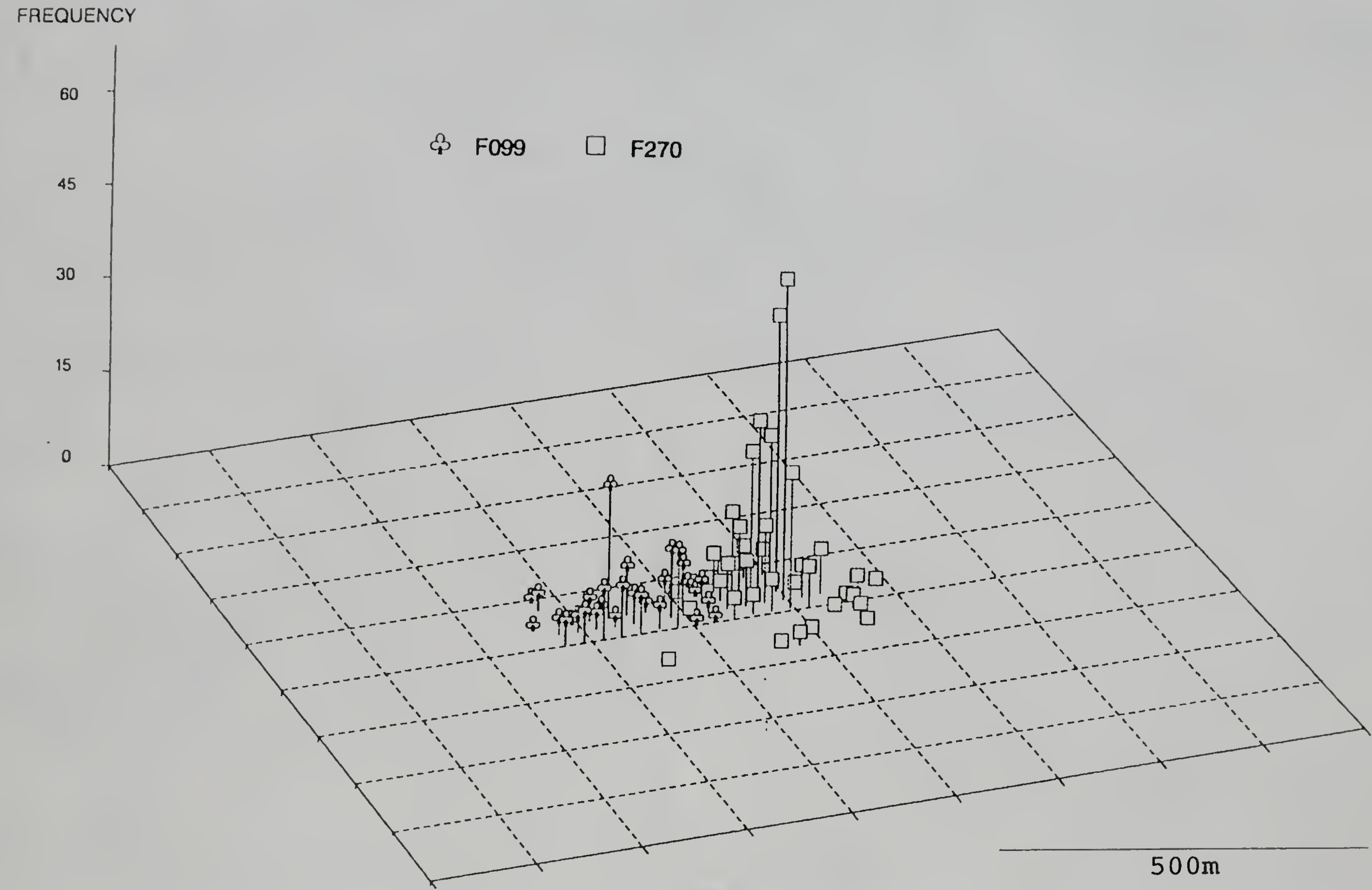

Figure 3-5. Spatial relationship of two adult female fox squirrels radio-tracked on the Fort White study area.

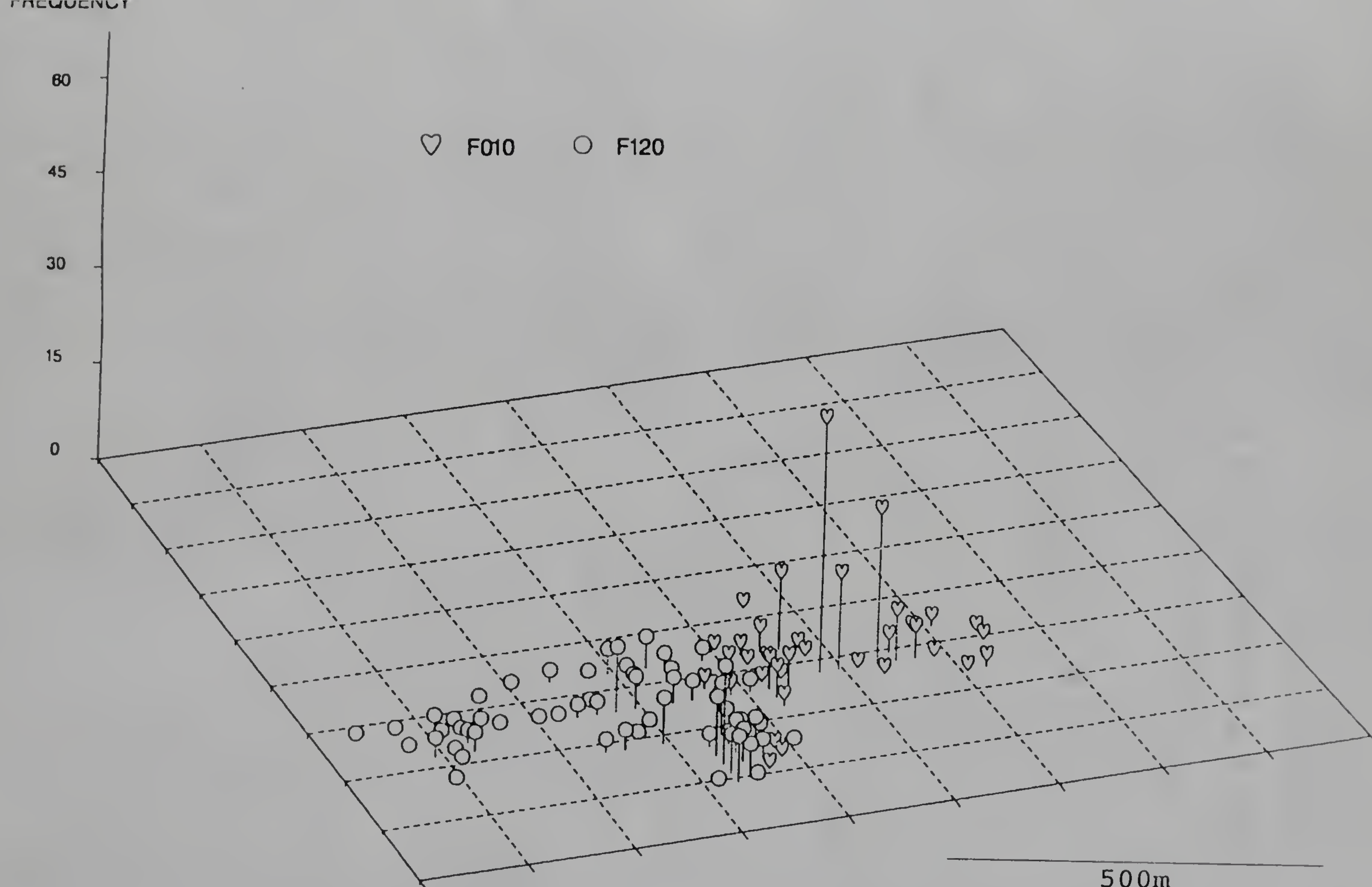

Figure 3-6. Spatial relationship of two adult female fox squirrels radio-tracked on the Fort White study area.

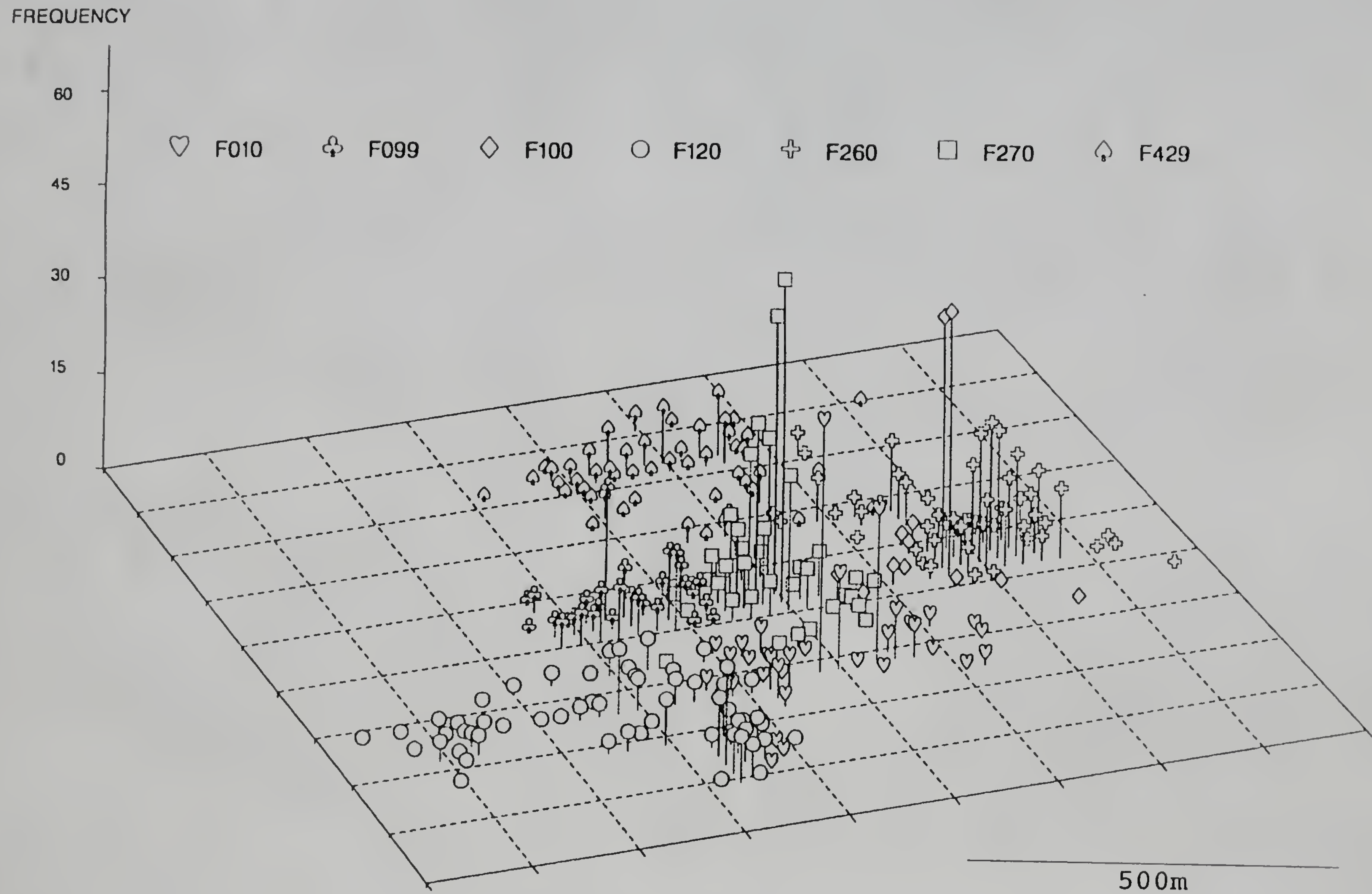

Figure 3-7. Spatial relationship of seven adult female fox squirrels radio-tracked on the Fort White study area.

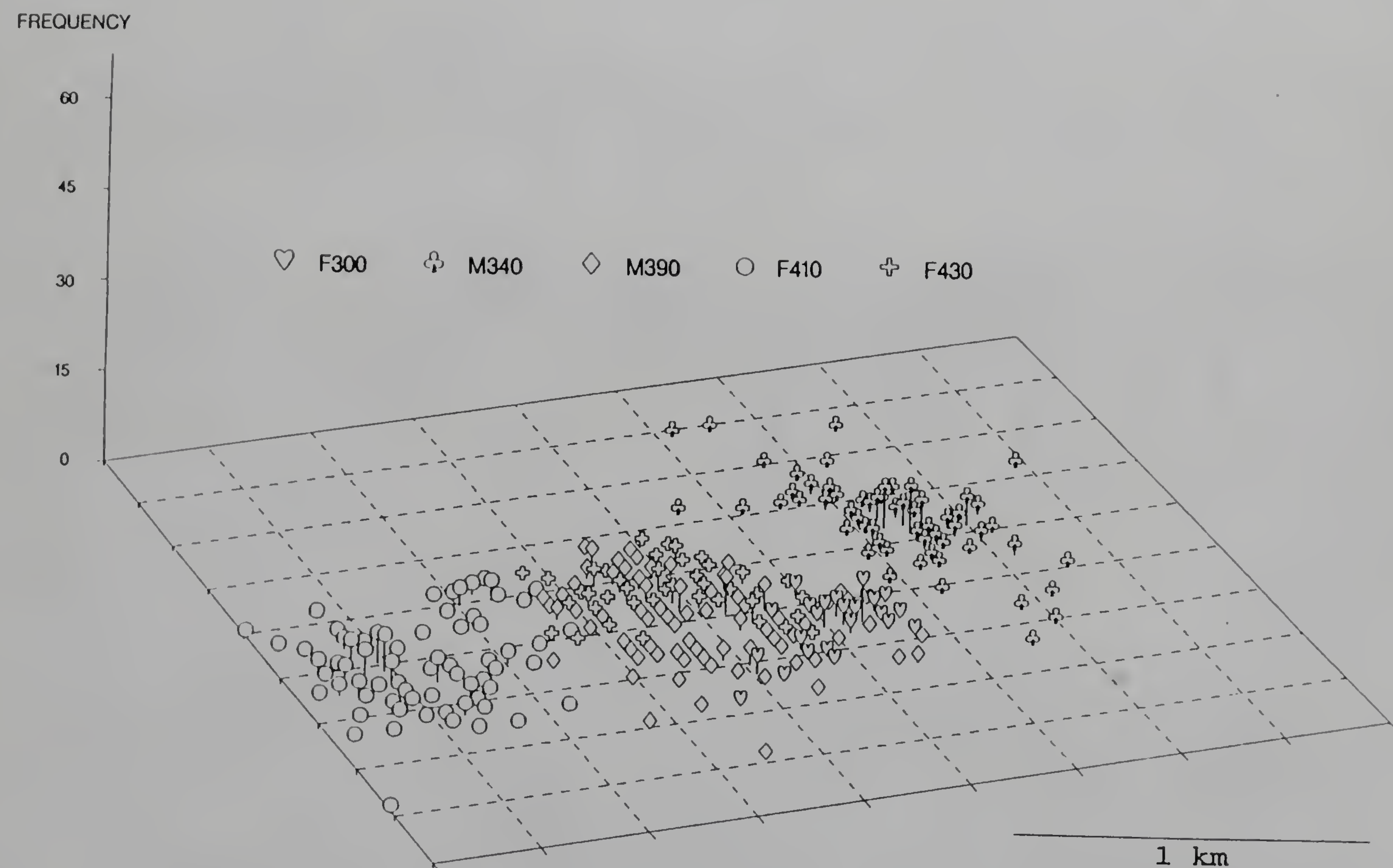

Figure 3-8. Spatial relationship of three adult female fox squirrels and two adult male fox squirrels radio-tracked on the Goldhead study area.

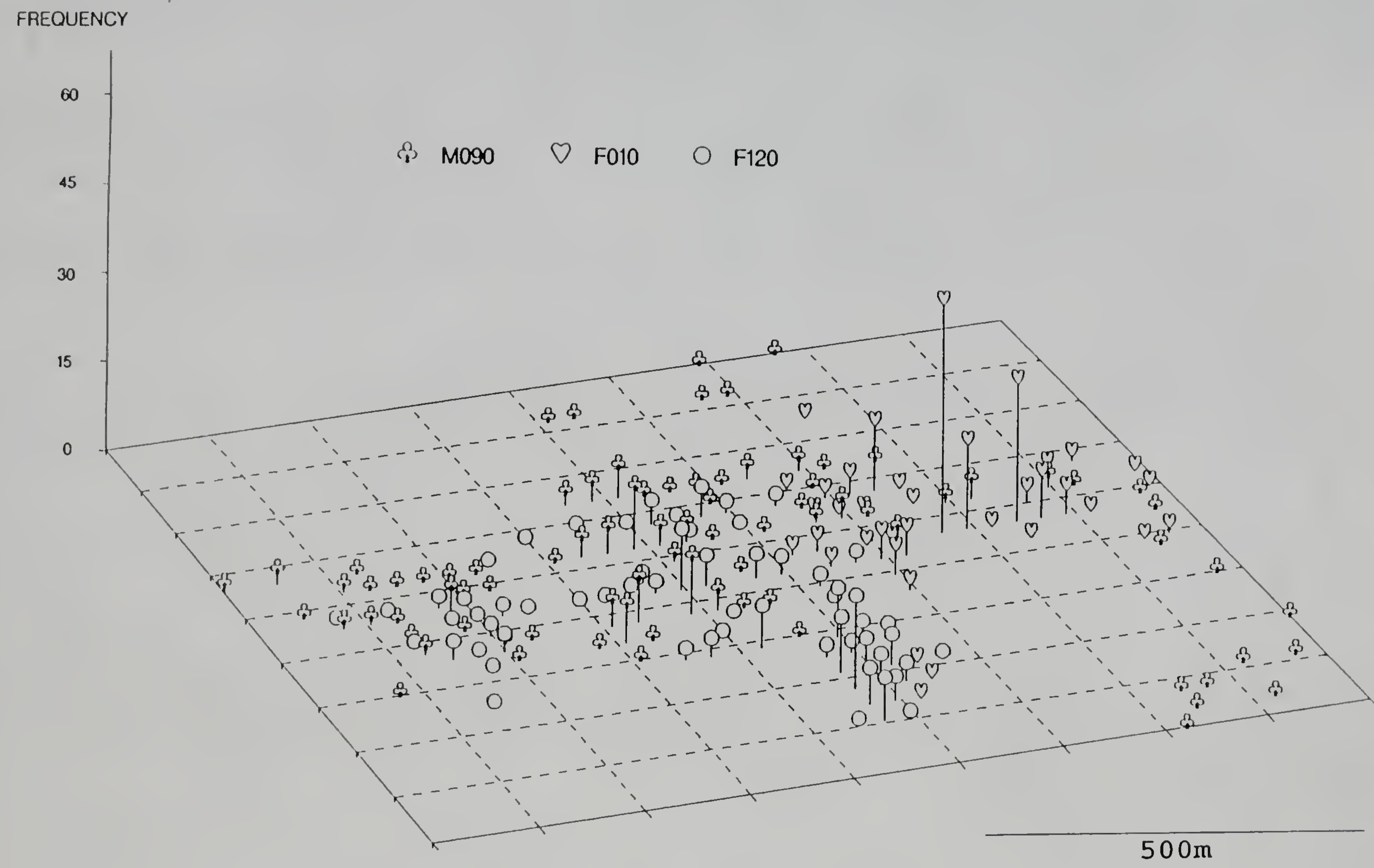

Figure 3-9. Spatial relationship of two adult female fox squirrels and one adult male fox squirrel radio-tracked on the Fort White study area.

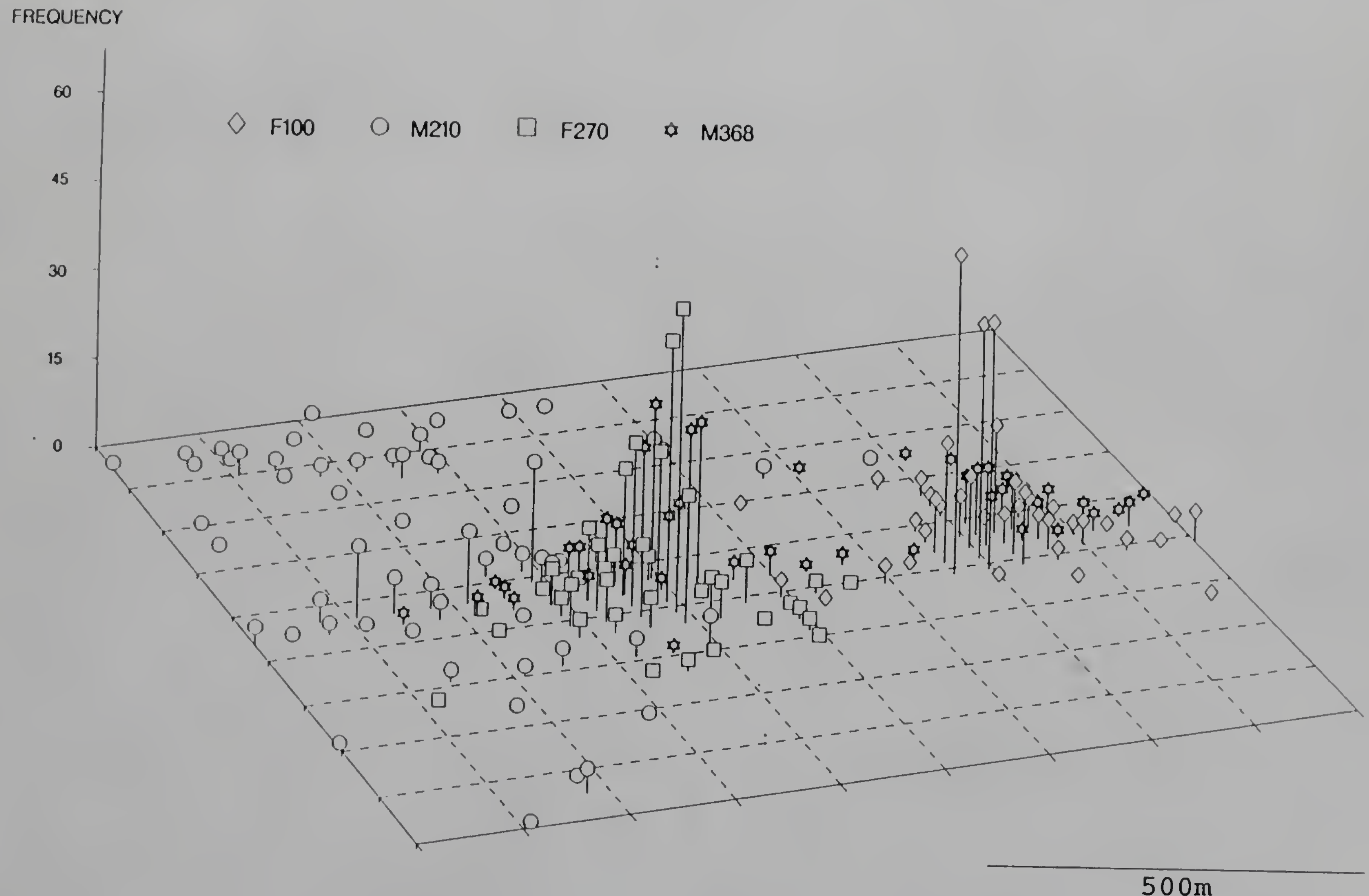

Figure 3-10. Spatial relationship of two adult female fox squirrels and two adult male fox squirrels radio-tracked on the Fort White study area.

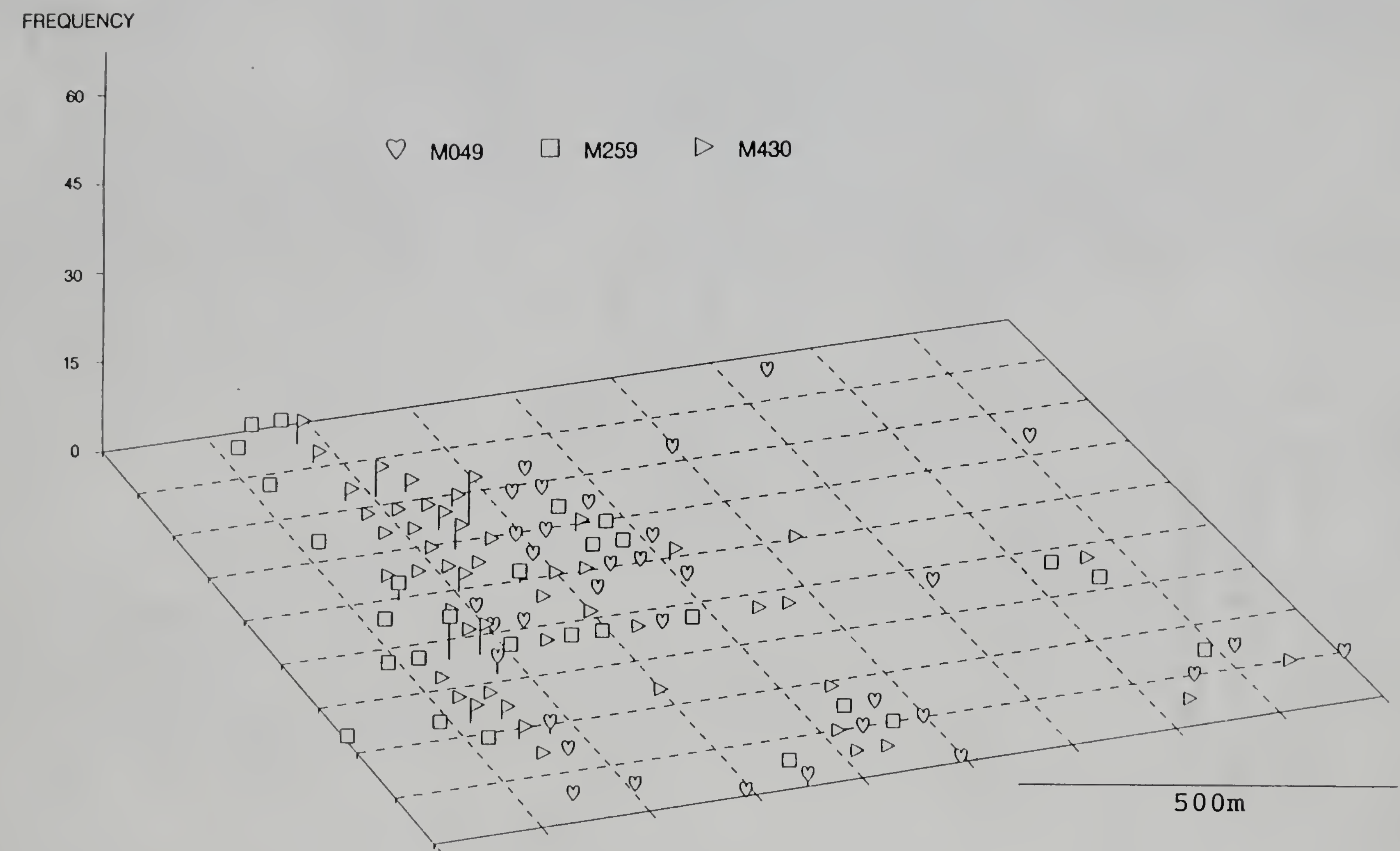

Figure 3-11. Spatial relationship of three adult male fox squirrels radio-tracked on the Fort White study area.

Habitat Use Versus Availability

Fox squirrels on the Goldhead area were located most frequently in sandhill (Figure 3-12). The second most commonly used habitat was hardwoods. There was no significant difference in habitat use versus availability ($p=0.145$).

On Fort White, fox squirrels were located most often in the hardwood fencerows and hammocks (Figure 3-13). Friedman's test indicated that habitat use on the study area was not in proportion with availability ($p=0.001$). When the four habitat types on the study area were examined individually using the signed rank test, it was found that wooded pasture was used in proportion to its availability ($p=0.795$), however, the other three habitat types were not used in proportion to their availability ($p=0.0001$ for each of the three types). Hardwood fencerows and hammocks were used in greater proportion than their availability, while planted pines and fields were used in smaller proportion than their availability.

Dispersal

Ten fox squirrels dispersed during the study (Table 3-7). Seven dispersed between the estimated ages of 7-9 months old, and one dispersed at an estimated age of 14 months. The other two dispersers were also believed to be subadults at the time of dispersal, but their exact ages were unknown. Two of the ten squirrels that dispersed left their natal home ranges in October, and the other eight dispersed between late February and mid-June (Table 3-7).

The distances between natal and adult home ranges varied from 1.0km to 7.2km. The average dispersal distance was 3.7 km

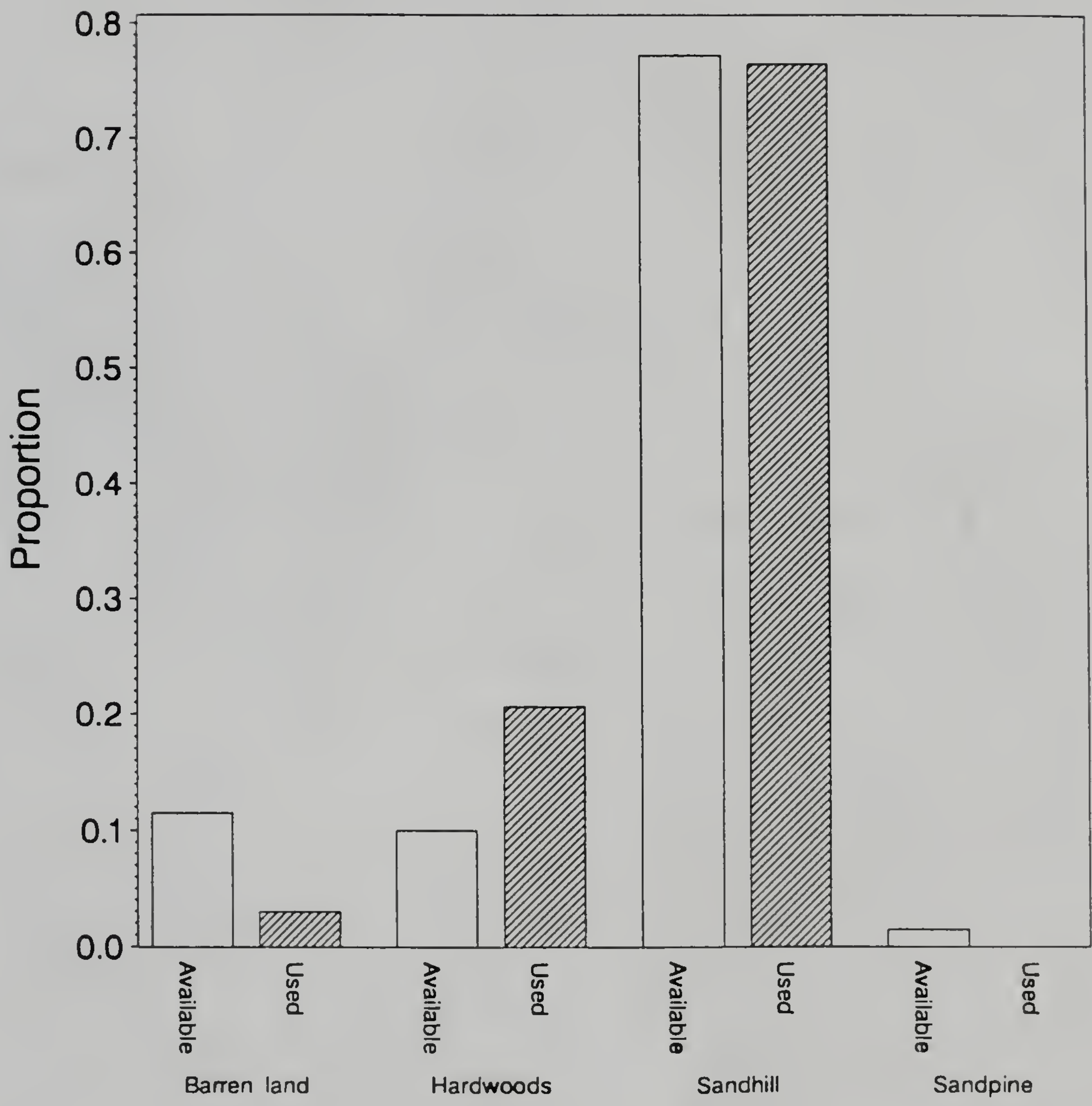

Figure 3-12. Habitat available versus habitat used by fox squirrels radio-tracked on the Goldhead study area.

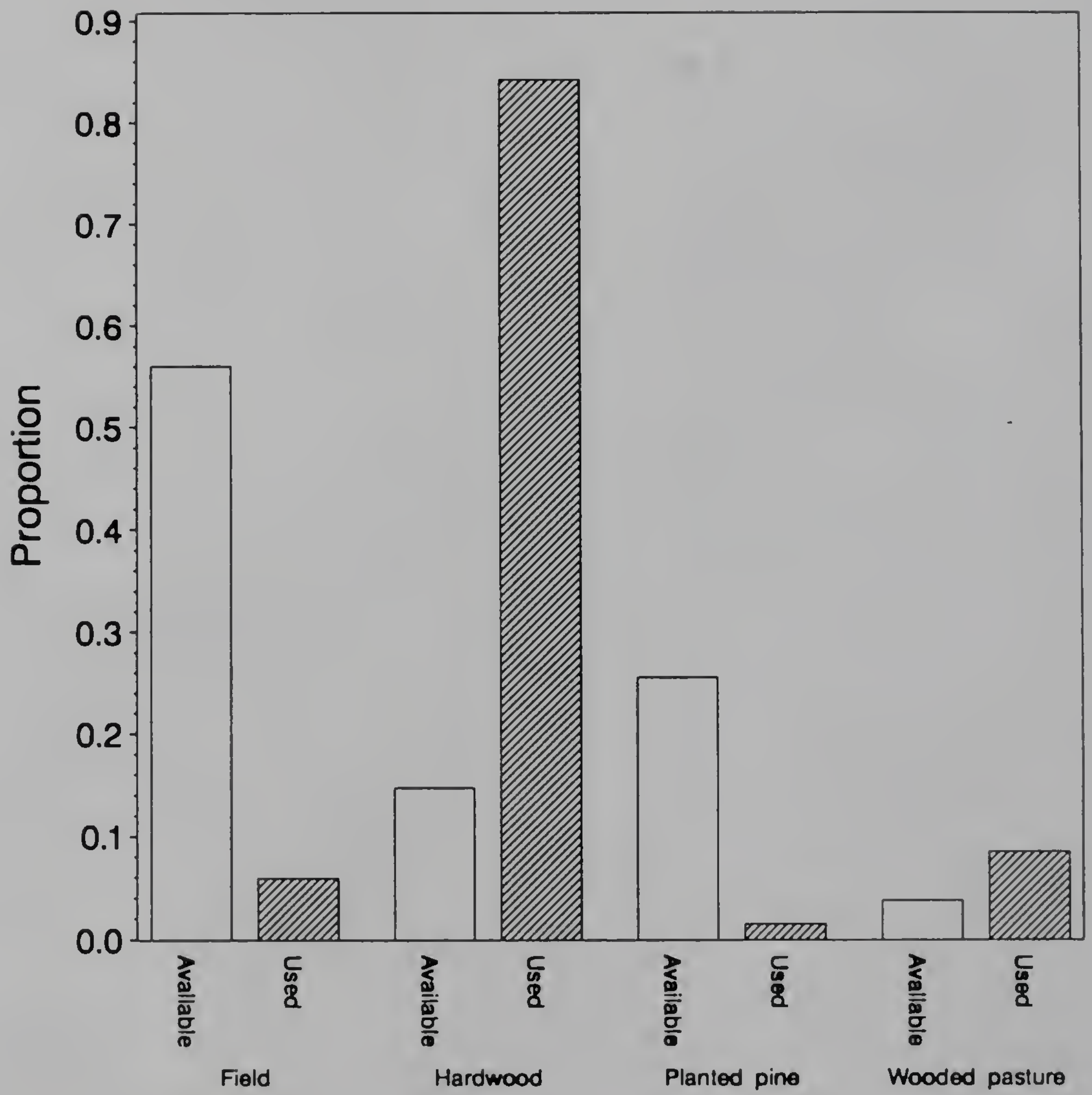

Figure 3-13. Habitat available versus habitat used by fox squirrels radio-tracked on the Fort White study area.

for males and 3.3 km for females. Two females moved from their first adult home range to a second adult home range. The distances between the two adult home ranges were 5.4km for F630 and 2.0km for F870. The second adult home ranges were 3.1 km (F630) and 3.6 km (F870) from the natal home ranges.

Two of the ten squirrels that dispersed were killed or their radio signals were lost during dispersal. Seven of the eight that seemed to have completed their dispersal movements during the monitoring period settled in areas that contained other fox squirrels, based on subsequent sightings of fox squirrels in their adult home ranges. No other fox squirrels were sighted in the adult home range of one of the eight squirrels, but the post-dispersal monitoring period for this squirrel was brief because he was killed by a bobcat (Lynx rufus) about one month after dispersal.

Fox squirrels dispersing from the Fort White study area had a limited choice of habitats within the distances they dispersed. Basically, they could choose agrarian land, either in row crops or pastures, with scattered hardwood hammocks and fencerows, or they could choose planted slash pine plantations. Seven of the eight chose habitat that was primarily agrarian and, thus, similar in composition and structure to the habitat in their natal home ranges. The one exception occurred with a female fox squirrel that dispersed to a 15-20 year old slash pine plantation.

Several of the radio-collared subadult fox squirrels did not disperse. Five females captured as subadults were monitored for

Table 3-7. Summary of subadult fox squirrel dispersal, Fort White study area: January 1991-June 1994.

Sex/#	Date of First Capture	Estimated Age at First Capture (Months)	Last Known Date in Natal Home Range	First Known Date in Adult Home Range	Estimated Age at Dispersal	Dispersal Distance (km)
F140	04/23/91	Unknown[a]	05/07/91	06/16/91	Unknown	5.5
F630	11/04/92	3 months	02/24/93	03/11/93[b]	7 months	2.0
F870	11/07/92	3 months	03/20/93	04/30/93[c]	7 months	5.6
F069	11/05/92	3 months	03/22/93	04/07/93	7 months	1.0
M130	02/04/91	6 months	04/17/91	05/01/91	9 months	1.1
M170	02/01/91	>9 months	06/10/91	06/15/91[d]	>13 months	7.2
M150	02/05/91	8 months	03/06/91	03/19/91	>10 months	6.5
M129	01/03/92	5 months	05/11/92	05/19/92	9 months	4.0
M630	10/01/92	8 months	10/16/92	10/19/92[e]	8 months	1.3

Table 3-7--continued.

Sex/#	Date of First Capture	Estimated Age at First Capture (Months)	Last Known Date in Natal Home Range	First Known Date in Adult Home Range	Estimated Age at Dispersal	Dispersal Distance (km)
M128	02/03/93	6 months	10/12/93	10/29/93	14 months	2.4

[a] F140's small nipples suggested she was a sexually immature, and therefore a subadult when captured.
Her exact age at the time of capture was not known.
[b] F630 remained in this area from 03/11/93 to 04/29/93. She then traveled 5.4km to her second post-dispersal home range. She remained there from 06/01/93 to 01/17/94, at which time the battery in her transmitter failed. The second post-dispersal home range was 3.1 km from her natal home range.
[c] F870 remained in this area from 04/30/93 to 10/03/93. She then moved 2km to her second post-dispersal home range. She occupied this second area from 10/17/93 to at least 11/19/93. She was killed by a vehicle sometime in the week after her last location. The second post-dispersal home range was 3.6 km from her natal home range.
[d] M170 was last located 06/18/91, after which the signal was lost. An aerial search was conducted 06/27/91, without success, and it was concluded the transmitter had failed.
[e] M630's carcass was found 10/20/92, the day after he was located in the new area. It is unknown how far he would have gone had he survived.

>300 days; three of the five dispersed. Nine males captured as subadults were monitored for >133 days; five of the nine dispersed.

Young fox squirrels of both sexes dispersed. Koprowski (1996) also observed that both sexes of fox squirrels dispersed. These observations are unusual in that the normal pattern in mammals is for males only to disperse (Greenwood 1980). The fact that female fox squirrels dispersed may be related to the intolerance that adult females have towards other females.

Recruitment

There were two sources of recruitment into the adult segment of the Fort White population. The first were animals born on the study area. As previously noted, six of the 14 radio-collared subadults did not disperse. Recruitment was documented for three of the six. One of these was a female, and the other two were males. Both males participated in breeding activities as they grew older. Sexual maturation of the female was assessed by nipple characteristics observed through binoculars. As she matured, her nipples enlarged and darkened. This was taken as evidence that she reached sexual maturity on the study area. The other three non-dispersing squirrels either died or were lost from radio contact before they reached sexual maturity.

The second source of recruits were animals that immigrated to the study area. I did not have proof of immigration, but, in two instances, I suspected that "new squirrels" were recent immigrants to the study area. In both instances the squirrels were males which suddenly appeared. Both squirrels had descended testes when they arrived on the study area, and both were captured soon after being first sighted. They remained in the capture area during the period they were monitored (six months for one squirrel and nine months for the other).

Mortality

One of the five squirrels monitored on Goldhead died during the study. The squirrel, an adult female, was believed killed by a raptor based on the condition of the carcass. When the body was found, the skin of the legs was turned inside out. The sign was indicative of raptor feeding (B. Millsap, GFC, personal communication).

Nineteen fox squirrel deaths were documented on Fort White (16 squirrels were radio-collared and three were unmarked). Nine deaths were due to predation, one death was due to unknown causes, and nine deaths were due to human-related factors (six to vehicles, one to a steel trap set by the landowner for coyotes, one to drowning in a metal drum, and one to capture stress). A total of 16 of the 39 animals radio-collared died during the study (Table 3-8).

Two instances of nest predation were observed at Fort White. During the winter of 1991-92, the leaf nests of two radio-collared females were found destroyed. Both females were thought to have had young when the nests were destroyed. Large buteo hawks have been observed attacking squirrels that were hiding in leaf nests (B. Millsap, M. Cantrell, GFC, personal communication). Based on these observations, and the fact that red-tailed hawks (Buteo jamaicensis) were the only large hawk seen on the study area, I suspect that the nests were destroyed by a red-tailed hawk that was digging after the nestling squirrels. Nest loss of this type was seen only twice, and, if a red-tail was responsible, it may have been a transient bird that had learned the technique of hunting squirrels in their nests.

Although red-tailed hawks were year-round residents on the Fort White area and suspected of destroying these two nests, their impact on radio-collared squirrels was less than I expected. I had been anticipated that they would be a significant predator of the fox squirrel. They are known to prey on fox squirrels in Florida (B. Millsap) and they were commonly seen hunting on the area. In addition, the habitat was open, providing good hunting conditions for the hawk, both species were active at similar times, and furthermore, the squirrels were often seen foraging or traveling across open pastures where they seemed extremely vulnerable. However, only three fox squirrel deaths could be attributed to raptors (all believed due to red-tailed hawks, the only large raptors seen on the study area).

The minimal impact of red-tailed hawks to fox squirrels on the Fort White area may be due to two factors. One may be that they normally select smaller prey than fox squirrels, and the second may be that fox squirrels have excellent defenses against hawk attacks. Regarding the latter, fox squirrels crossing open pastures ran with a loping, stop-and-go pattern of travel. They sat up on their haunches when they stopped and scanned the area for a fewseconds before loping off again. Fox squirrels foraging on the ground behaved similarly in that they stopped frequently, sat on their haunches, and looked around. The squirrels often flicked their tails above their backs when running and foraging, a behavior which might attract the attack to the tail rather than to the body. These behaviors, in addition to the squirrel's large body size, may have reduced their vulnerability to red-tailed hawk predation.

Other predators that were seen on the study area included bobcats, coyotes, domestic dogs (Canis familiaris), gray foxes (Urocyon cinereoargenteus), and diamondback rattlesnakes (Crotalus adamanteus). Owls were not seen or heard on the study area.

Bobcats were thought responsible for three deaths of radio-collared squirrels and canids for three deaths (Table 3-8). Two of the squirrels that canids killed were found buried. When the carcasses were found, they were intact, and it looked like the uneaten bodies had been cached. The size of the bite marks on the dead squirrels suggested the predator was either a small domestic dog or coyote.

Mammalian predators seemed to be rare on the primary study area based on sightings and tracks, yet they killed twice as many radio-collared animals as the more common red-tail hawks. This suggests that fox squirrels may be more vulnerable to predation by bobcats and canids than to predation by red-tailed hawks. Several factors may have reduced the fox squirrel's vulnerability to mammalian predators and thus kept the mortality within sustainable limits. One was that contact was reduced by activity periods with minimal overlap, in that the fox squirrels were diurnal whereas the mammalian predators were generally nocturnal. A second factor was that fox squirrels seemed to minimize the time spent foraging or traveling in open areas more than 20m from trees where they were vulnerable to being chased and caught;

normally they tended to stay close to the safety of the trees. A third factor that may minimize mammalian predation is that fox squirrels seemed to prefer habitats with low ground cover. There may be two advantages to the low groundcover: first, it was easier to traverse to escape a pursuer and second, in low ground cover, the squirrel's vision was unimpeded by vegetation, making escape from approaching predators more probable. An unsustainable vulnerability to mammalian predation may be a primary reason why fox squirrels do not inhabit forests with a dense understory.

Mortality Rates

Annual mortality rates were calculated for the radio-collared fox squirrels on Fort White (Table 3-9). There were 10 confirmed male deaths and five confirmed female deaths (the one death due to capture stress was excluded from the calculations). In addition to the confirmed deaths, radio contact was lost on three other males. The possibility that they died is reflected in the bracketed values presented in Table 3-9.

The annual mortality rate for all radio-collared squirrels was about 30% (Table 3-9). Similar mortality rates were observed by Nixon et al. (1986) for an unexploited fox squirrel population in Illinois.

Mortality rates of resident and dispersing squirrels were compared by sex, with the expectation that dispersing squirrels would suffer higher mortality rates than resident animals. Although the average mortality rates were higher for squirrels that dispersed (Table 3-9), the differences were not significant ($p>0.05$). A comparison also was made between the mortality rates

Table 3-8. Summary of fox squirrel mortality, Fort White study area: January 1991 -June 1994.

Sex/#	Last Date Known Alive	Date Carcass Found	Cause of Death
F120	06/23/92	06/25/92	Predation, red-tailed hawk
F069	08/09/93	08/11/93	Predation, bobcat
F870	11/19/93	Nov.,93	Roadkill
F869	12/09/93	12/13/93	Predation, canid
F100	01/28/94	01/31/94	Predation, canid
M300	04/06/92	04/08/92	Predation, raptor
M090	08/31/92	Sept.,92	Roadkill
M289	05/10/93	05/11/93	Roadkill
M260	02/11/91	02/12/91	Drowned in a barrel
M160	09/16/91	09/18/91	Predation, suspect canid
M150	09/20/91	09/25/91	Predation, raptor
M129	06/19/92	06/23/92	Predation, bobcat
M630	10/19/92	10/20/92	Predation, suspect bobcat
M890	01/05/93	01/06/93	Capture stress
M239	07/16/93	07/19/93	Unknown
M259	12/17/93	12/21/93	Roadkill

Table 3-9. Annual mortality rate of fox squirrels radio monitored on the Fort White study area, 1991-94. Rates calculated by the methods of Heisey and Fuller (1985). Contact was lost with three radio collared males, one for unknown reasons, and the other two because they lost their collars, perhaps after death. These three males represent the assumed deaths in the table below.

Group	Radio Days	Confirmed Deaths (Assumed Deaths)	Mortality Rate - Confirmed Deaths (Confirmed + Assumed Deaths)	95% CI -Confirmed Deaths (Confirmed + Assumed Deaths)
Males				
Residents	7,321	7 (2)	0.29 (0.36)	0.09 - 0.45 (0.14 - 0.52)
Dispersers	1,462	3 (1)	0.53 (0.63)	0.00 - 0.80 (0.02 - 0.86)
All Males	8,783	10 (3)	0.34 (0.42)	0.15 - 0.49 (0.21 - 0.57)
Females				
Residents	6,780	3	0.15	0.00 - 0.29
Dispersers	1,615	2	0.36	0.00 - 0.66
All Females	8,395	5	0.20	0.03 - 0.34
All Squirrels	17,178	15 (3)	0.27 (0.32)	0.15 - 0.38 (0.19 - 0.43)

of males and females, with the expectation that the wider ranging males would suffer higher mortality rates than the more sedentary females. Males did suffer higher mortality rates (Table 3-9), but the differences were not statistically significant ($p>0.05$).

<u>Reproduction</u>

Information on reproduction on Goldhead was restricted to the capture of a nestling male fox squirrel. At the time of its capture on 2 February, 1990, it weighed 100 grams, its dorsal surface was furred, and its eyes were closed. The squirrel was estimated to be about 3 weeks old based onthese characteristics. By back-dating and assuming a 45-day gestation period (Flyger and Gates 1982), the squirrel would have been conceived in the last week of November 1989 and born in the second week of January 1990.

Five litters were found on the Fort White area (Table 3-10). All were in leaf nests in oaks. There were 2-3 young/litter. By back-dating, three of the litters were conceived in the period 31 May - 4 August and the other two litters in the period 15 December - 2 February.

The summer breeding season on Fort White began as early as 17 April, based on observations of an adult male chasing an adult female on that date, and extended until 4 August, based on the back dating of one litter. The winter breeding began as early as 12 October, based on observations of an adult male pursuing an adult female on that date, and extended until 2 February, the estimated date of conception for one of the litters handled.

Radio-collared males on Fort White expanded their home ranges during the breeding seasons, when some were located about

Table 3-10. Fox squirrel litters found in nests on the Fort White study area.

Date Examined	# Young	Sex	Weight (g)	Estimated Age	Estimated Birthday	Estimated Date of Conception
26 Feb 92	2	---	---	28 days	29 Jan 92	15 Dec 91
10 Apr 91	3	2M:1F	---	21 days	20 Mar 91	2 Feb 91
5 Aug 92	2	0M:2F	110/each	21 days	15 July 92	31 May 92
19 Aug 93	3	1M:2F	150/each	21 days	29 July 93	14 June 93
9 Oct 92	3	1M:2F	150/each	21 days	18 Sept 92	4 Aug 92

Table 3-11. Litter frequency for female fox squirrels monitored on the Fort White study area. A "Y" indicates there was evidence that a litter was born during the breeding season. A "N" indicates there was no evidence a litter was born.

	1991		1992		1993	
Animal #	Winter	Summer	Winter	Summer	Winter	Summer
F010	N	Y	Y	Y	---	---
F140	---	---	N	---	---	---
F120	Y	Y	---	---	---	---
F100	Y	Y	---	Y	N	N
F260	Y	N	N	Y	N	Y
F270	N	Y	N	N	Y	---
F099	---	---	---	---	Y	N
F429	---	---	---	Y	N	N
Total	3Y:2N	4Y:1N	1Y:3N	4Y:1N	2Y:3N	1Y:3N

1.0 km outside of their normal home ranges. Females remained in their normal home ranges during the breeding season. This is the normal fox squirrel breeding pattern (Koprowski 1994). Seven radio-collared males were observed on one occasion clustered within 50m of a radio-collared female. All of the males were 0.5 to 1 km outside of their normal home ranges.

The frequency of litters for adult females on Fort White appears in Table 3-11. Sufficient data were available to evaluate the productivity of these females for 28 reproductive periods. Litters were produced in 15 of the 28 potential reproductive periods. The females averaged about one litter/year. Nine of the 15 litters were born in the summer period and six in the winter period.

Scent Marks

Fox squirrels often were seen climbing trees with their noses to the trunk or limb, apparently sniffing the bark as they traveled. They also were seen rubbing their faces on the bark, a method fox squirrels use to scent mark (Benson 1980).

Adult male fox squirrels were seen on three occasions rubbing their faces on trees in spots where the outer bark had been chewed away. Two of the squirrels first bit at the spot before they rubbed their faces on the tree. In one instance, the squirrel pressed his abdomen to the mark point after he had rubbed his face on it. The points were on the trunk but immediately under an overhanging branch or knot and sheltered from rain. One of the marked trees was a southern red oak (_Q. falcata_). This tree had at least four different spots marked. The spots ranged in size from about 5 by 15 cm to 10 by 30 cm.

All were under the lower most branches on the tree and clearly visible from the ground. The highest mark seen was about 10m above the ground. The other two trees where males were seen marking were pecans. Additional marks were seen on laurel oaks and live oaks. No effort was made to systematically survey the study area for mark trees, however, mark trees were observed scattered across the study area. Similar marking behavior and mark points have been observed in other studies; both gray squirrels and fox squirrels have been observed exhibiting this behavior (Taylor 1968, 1976; Koprowski 1993).

Density

Ten fox squirrels were sighted on the Goldhead study area during two months of intensive field work in January and February, 1990. A 95 ha portion of the study area was trapped more intensely than any other, and, within this area, seven adult-sized fox squirrels were sighted. Five of the seven were captured and radio collared. The collared squirrels restricted most of their activity to the 95-ha area, and it is assumed the 2 uncollared fox squirrels did also. The minimum fox squirrel density for this 95-ha area is therefore 7.4 fox squirrels/km^2. This was the best quality fox squirrel habitat in the study area, and based on sightings and trapping results, it contained the highest density of fox squirrels.

The primary Fort White study area was 2.3 km^2; 27 fox squirrels lived on the area in April-May 1993: 20 were radio collared (11 adult males, 5 adult females, 1 subadult male, 3 subadult females); two were ear-tagged only (both subadult females); and five were unmarked (age and sex unknown). The unmarked squirrels were assumed residents. The density was therefore 11.7 fox squirrels/km^2.

Fox squirrels on Fort White restricted most of their activity to the wooded portions of the study area, an area of 49.3 ha. This was their primary habitat. Their density in the wooded areas was or 54.8 fox squirrels/km^2.

Estimates of fox squirrel density from this and other studies appear in Table 3-12. Density estimates for the southeastern Coastal Plain range from 5 - 39 fox squirrels/km^2. This compares to an estimated density for a study area in Illinois of 153-314 fox squirrel/km^2. The striking difference in densities between the southeast and midwest is believed due to habitat quality. Even the best fox squirrel habitat in the Coastal Plain is of marginal quality compared to the habitat in the midwest.

Foods

Anecdotal observations were made on food habits of fox squirrels on the Fort White area. They are reported only because there is little information on the food habits of fox squirrels in the southeast. The following items were eaten by fox squirrels on the Fort White area (the season the items were eaten follows the item): acorns (WI,SP,SU,FA); newly emergent herbaceous growth (WI,SP); hardwood buds (WI,SP); oak flowers (SP); mushrooms (WI,SP,SU,FA); mistletoe (*Phoradendron serotinum*) berries (WI); field corn (FA); pecans (WI,SU,FA); jelly fungi (*Auricularia sp*.) (WI); peanuts (WI,SU,FA); black cherries (SU); lichens (SU,WI); longleaf and slash pine seeds (SU,FA); magnolia (*Magnolia grandiflora*) fruit (SU); and oak galls (FA). Though

Table 3-12. Density estimates for fox squirrels.

Reference	Location	Method	Density Squirrels/km^2
Weigl et al. 1989	North Carolina	Nest Count	5
This study	Florida Goldhead	Complete Count	7.4
Humphrey et al. 1985	Florida Putnam County	Line Transect	8.4
This study	Florida Fort White	Complete Count	11.7
Kantola 1986	Florida Putnam County	Nest Count	12.3
Tappe et al. 1993	Georgia	Captures	15.3-17.7
Moore 1957	Florida Putnam County	Complete Count	38
Larson 1990	Virginia	Captures	39
Nixon et al. 1986	Illinois	Captures	153 - 314
Benson 1980	Illinois	Sightings	720-1,000

not observed, fox squirrels also may have eaten wild grapes (Vitus sp.) and blackberries; both fruits were common on the area in the summer. Evidence of squirrels eating pear seeds was found, but the sign could have been that of gray squirrels.

Fox squirrels were seen caching food items on 10 occasions. Food caching was also observed in Florida by Moore (1957) and Jodice (1990). The items cached on the Fort White study area were pecans, acorns, peanuts, and, in one instance, an immature puff ball (Order Lycoperdales). On one occasion I observed a fox squirrel moving a pecan and an acorn that had been cached previously. The items were reburied about 7m from where they were previously cached.

It is common knowledge that squirrels cache food items, and it was only mentioned here because of speculation that southeastern fox squirrels do not cache foods (Loeb and Moncrief 1993). Fox squirrels in Florida cache foods, but perhaps less frequently than fox squirrels in other areas. The infrequency of the behavior may have caused other researchers in the southeast to miss it, thus leading to the statements made by Loeb and Moncrief (1993).

Fox squirrels supplemented their diet with peanuts and corn. The importance of these crops varied by year and by squirrel. Peanuts, for example, were planted on a 2-4 year rotation. They grew as volunteers in the off-years, but they were only abundant in the years when planted. Fox squirrels ate the crops available within their home range, but there were no observed instances of fox squirrels traveling outside of their normal home range to exploit crops.

Pine trees were uncommon on the Fort White study area, and although the squirrels ate the pine mast that was available, it was a minor component of their diet. This contrasts to the Goldhead study area and other areas in the Coastal Plain were pine mast was a critical component of the summer and early fall diet (Kantola 1986, Weigl et al. 1989). Fox squirrels on the Fort White area successfully substituted other foods for pine mast.

Concluding Discussion

In the past 10 years, our knowledge of fox squirrel population ecology in northern Florida has increased considerably, both with the study reported here and with the work of Kantola and Humphrey (1990). Prior to these studies, our knowledge of fox squirrel biology in northern Florida was based primarily on a two year study conducted in the 1940s (Moore 1957). In some aspects, the new information has changed our understanding of fox squirrels, whereas in other areas additional study has only strengthened Moore's (1957) conclusions. I have tried to summarize our knowledge of fox squirrel biology in northern Florida in the discussion that follows. Sample sizes remain small for many aspects of their biology, and our knowledge remains limited. However, we know more than we did. When necessary, I have compared and contrasted the Florida observations to those made on fox squirrels in other parts of the species's range in an attempt to clarify the discussion.

Mortality

The only data on fox squirrel predation for northern Florida were the observations reported earlier from the Fort White study area. The important predators on the Fort White study area were raptors, canids, and bobcats. This probably applies throughout the state, but other predators, such as great horned owls (Bubo virginianus), gray and red foxes (Vulpes vulpes), rattlesnakes, and domestic dogs, may be locally important predators on fox squirrels. Moore (1957) considered that bald eagles might be a significant predator of fox squirrels. This seems unlikely. Eagles are relatively uncommon, they tend to hunt around lakes or scavenge along highways (Wood 1992), and because of these traits, I doubt if they encounter fox squirrels often enough, or are proficient enough at hunting them, to be an important predator.

Human predation on fox squirrels may have been significant in the past, but interest in fox squirrel hunting in Florida has been low in recent times (Wooding 1990). The lack of interest was one of the factors which lead to the season closure on fox squirrels in northern Florida. This took affect beginning with the 1996-97 season. Fox squirrels were legal game on Fort White study area during the time of the field work, but no one hunted them.

A number of fox squirrels on the Fort White study area were killed by vehicles while crossing S.R. 47, a two-lane highway that formed the western border of the study area. Roadkill mortality was not observed on the Goldhead study area, and it was not mentioned by Moore (1957) or Kantola and Humphrey (1990). There may be areas in Florida where roadkill mortality is so severe that it limits fox squirrels, such as in urban areas or subdivisions with a high road density, but these conditions did not exist on any of the northern Florida study areas.

The only data available on mortality rates for Florida were obtained on the Fort White study area. The annual mortality rate of radio collared squirrels was about 30%. The rate included mortality by vehicles and predators. Similar rates were observed by Hansen et al. (1986) for an unhunted fox squirrel population in Illinois. Moore (1957) had speculated that predators would only kill an occasional fox squirrel. The Fort White data supported his suspicions. Weigl et al. (1989) believed that coastal plain fox squirrels were too rare to become a major food item, and as a result, no predator could afford to hunt specifically for them.

Before concluding this section on mortality, I want to comment on one of Moore's (1957) observations on fox squirrel behavior. He reported several incidents in which fox squirrels that were fleeing for their lives ran down gopher tortoise (Gopherus polyphemus) burrows. Moore (1957) believed that the behavior was common, but it was not observed by myself or Kantola and Humphrey (1990). My interpretation of the events Moore (1957) described were of desperate animals taking desperate actions, and I believe if given a choice between a tree or a hole in the ground, a fox squirrel will tree every time. While there are a number of species that depend on gopher tortoise burrows for their survival, the data suggest that fox squirrels are not one of them.

Reproduction

Moore (1957) identified 2 breeding seasons per year for fox squirrels, a pattern that is consistent throughout the species range (Koprowski 1994). The first data for the state on litter frequency was collected at Fort White. Several females produced two litters per year, but the overall litter frequency was 1 per year. Similar litter frequencies have been observed elsewhere (Harnishfeger et al. 1978).

Knowledge of litter size in northern Florida is based on a sample of 17 litters; 11 were examined by Moore (1957), and six were examined in the current study). Litter size ranged from 1 to 4, with a mean of 2.3. Fox squirrels usually have 2-3 young per litter throughout their range (Koprowski 1994).

Weigl et al. (1989) studied fox squirrel reproduction in coastal North Carolina in habitat similar to that found in northern Florida. He reported rather emphatically that the winter breeding season was the major period of reproduction. His data were based almost exclusively on examinations of nest boxes. In Florida, data are available on the period of birth for 27 litters; 11 in Moore (1957) and 16 in this study. Fourteen of the litters were born in the winter breeding season, and 13 in the summer season. Only one of the Florida litters was found in a nest box, and it was a winter litter. I believe that the Florida data more accurately represent the breeding characteristics of fox squirrels, and until further data show otherwise, that the two breeding seasons are of equal importance. I believe the North Carolina observations (Weigl et al. 1989) were biased by their study methods. Fox squirrels use nest boxes mainly during cold weather (Nixon et al. 1989), and I think the summer litters were missed because they were not checking leaf nests.

Nesting Habits

Much of Moore's (1957) field effort was spent in studying fox squirrel nesting habits. Among other observations, Moore (1957) concluded that leaf nests were used more often than were tree cavities. This conclusion was also reached by Kantola and Humphrey (1990). My observations are largely anecdotal, but they support the other studies. I can only remember 4 occasions when I located a radio collared fox squirrel in a tree cavity, compared to hundreds of locations when the squirrels were in leaf nests.

Edwards (1986) believed that litters born in tree cavities were safer from predators than those born in leaf nests. This is probably true, and even though nest predation was suspected at Fort White, there are no indications that the availability of cavities limits fox squirrels in Florida. Kantola and Humphrey (1990) observed abundant cavities on their study area, yet they observed little cavity use. Cavities may be needed at times in northern areas as a thermal refuge, but Florida winters are mild and it is unlikely that cavities are needed for warmth. The conclusion of this is that cavities, or artificial cavities such as nest boxes, are not a necessary component of fox squirrel habitat in Florida.

Normally when we think of cavities for a tree squirrel, we think of above ground cavities in standing trees. Moore (1957) made a number of unusual observations on his study area, one of which was of fox squirrels nesting in tree stumps. He found 5 such underground dens. I never saw this behavior, nor did Kantola and Humphrey (1990), and nor have any other studies with which I am familiar. It thus seems, based on the evidence, that underground nesting is not a common event in fox squirrels. This topic was mentioned because of a current debate underway among management area biologists over the value of pine stumps for wildlife in northern Florida. For fox squirrels at least, pine stumps do not appear to be a limiting factor, and the removal of the stumps for the turpentine they contain will not impact fox squirrels.

Food Habits and Habitat Use

There have been no detailed studies of fox squirrel food habits in northern Florida. However, certain conclusions can be reached with the data that are available. One conclusion is that acorns are probably a major component of the diet. Important oak species include live oak, turkey oak, southern red oak, and laurel oak. No research has been conducted in xeric flatwoods habitat on fox squirrels, however, the runner oaks (Q. *minima* and Q. *pumila*) may be an important source of acorns.

The importance of a particular species will vary with its abundance and the quantity of seeds it produces. Moore (1957) believed that turkey oak was a major producer of acorns, but Umber (1975) demonstrated that turkey oak only occasionally produces large quantities of mast. In an average year in sandhill habitat, live oak may be more important than turkey oak (Kantola and Humphrey 1990).

Pine mast is another important food for fox squirrels in northern Florida. In certain habitat types, such as longleaf sandhill, longleaf pine seeds are a primary summer food (Moore 1957, Kantola and Humphrey 1990). Fox squirrels will also eat the seeds of other pines. I have seen them eat seeds from loblolly, slash, and sand pine. My impressions are that fox squirrels relish pine seeds, which are an energy rich source of food (Weigl et al. 1989). However, if other foods are available, fox squirrels can survive in northern Florida without pine mast. Mast bearing pines were rare on the Fort White area, and although fox squirrels ate the pine mast that was available, they subsisted on other foods in the summer.

Under most conditions, oak and pine seeds appear to be the staple foods of fox squirrels in northern Florida. Other foods that may be seasonally or locally important include leaf buds, oak flowers, row crops, pecans, and wild fruits, such as black cherries.

Fox squirrels also ate a mystery food on the Fort White study area. I often saw fox squirrels eating items which they dug from the ground. The foods were occasionally acorns, but on a number of occasions, the foods were not acorns or other nuts. I was never able to identify the food, but it was darkly pigmented and appeared to be soft in texture because they ate it with minimal chewing. My suspicions were that it was the fruiting body of a subterranean fungi. Weigl et al. (1989) suggested that fungi may be an important food item for fox squirrels in the southeastern coastal plain.

<u>Habitat Use and Quality</u>

Fox squirrels in northern Florida are normally associated with mature longleaf pine forests. As discussed in Chapter 2, my impressions are that it is not the pines that draw the squirrels, but it is the structure of the habitat. Fox squirrels are especially adapted for life in wooded savannahs (Nixon et al. 1984, Weigl et al. 1989). The savannahs occupied by fox squirrels in Florida are pine dominated, whereas those occupied in the midwestern United States are hardwood dominated. The longleaf savannah is the natural habitat of the fox squirrel in Florida, and still the animal's predominate habitat. Fox squirrels have adapted to man-made savannahs, such as those found on the Fort White study area, demonstrating that it is not the pines but the structure. Longleaf pine forests just happen to be the most common forests in northern Florida with the required structure.

Fox squirrel studies conducted in northern Florida have revealed that fox squirrels here occur at low densities and occupy the largest home ranges determined for the species. In comparison to Florida, fox squirrel densities in the midwestern United States were up to 90 times greater than those in Florida (Table 3-12), and home ranges have been observed there that were 90% smaller than those in Florida (Adams 1976).

Difference in carrying capacity and reproductive potential between the midwest and Florida can be clearly demonstrated by comparing data collected on the Fort White study area to that collected on a study area in Illinois (Hansen et al. 1986). If we assume a litter frequency of 1/year, an average litter size of 2.5 for both study areas, and use the adult female density estimates of 77/km^2 for Illinois and 2.2/km^2 for Fort White, the annual production of offspring per km^2 is 192 for Illinois and 5.5 for Florida.

Differences in fox squirrel abundance between Florida and the midwest are believed a consequence of differences in the abundance of hardwood seeds. Midwestern savannahs contain an assortment of hardwood tree species that produce highly digestible, energy rich seeds that are easily stored, or cached for later use (Nixon et al. 1968, Korschgen 1981). The best seeds in terms of energy and digestibility are hickories (Carya sp.) and black walnuts (Juglans niger) (Smith and Follmer 1972, Havera and Smith 1978).

Florida pine savannahs typically contain a low diversity of mast producing species. Pine seeds are one of the richest foods produced in the habitat (Weigl et al. 1989), but they are only available for about 4 months of the year, and they are not storable. Oaks are the primary hard mast producer in Florida fox squirrel habitat. Acorns are lower in calories and less digestible than hickories and walnuts (Havera and Smith 1979). Acorns also have less storage potential than the other seeds, which limits the period they are available as a food source. Smith and Follmer (1972) have shown the nutritional value of acorns decreases after germination. Acorns of the white oak group, which includes live oak, tend to germinate soon after falling, which makes them undesirable for storage. Acorns of the red oak group, such as turkey oak, have delayed germination, which would increase their value for caching. However, Florida's winters are mild, which could lead to quicker germination of these seeds, thus decreasing the length of time they are available. These factors relating to seed storage may be the reason that seed caching has been observed infrequently in the southeastern coastal plain (Loeb and Moncrief 1993).

A lack of high quality, storable seeds, coupled with periodic failures of the seeds crops that are available (Kantola and Humphrey 1990), may explain the low carrying capacity of Florida fox squirrel habitat. The species is able to survive in Florida, but only at low densities and by foraging over large areas, perhaps persisting in lean times on fungi or some other low quality food.

Female Behavior

The spacing behavior of female fox squirrels observed in this study and by Kantola and Humphrey (1990) suggested that females were territorial to other females. Territories are normally defined as an exclusive area that is maintained by aggression or advertizement (Wilson 1975, Maher and Lott 1995). I did not observe fights, but I did observe females marking trees by "face wiping" (Benson 1980), which is both a visual and olfactory form of marking. The act of marking and the odors left behind are believed to function in mammals as threat displays, and individuals can recognize each other by their scent (Halpin 1987). I assume scent marking was the method used by females to advertize, and thus defend the boundaries of their territories.

Female fox squirrels tend to avoid each other throughout the species range, a behavior which may have evolved as a means to prevent infanticide by other females (Wolff 1997). However, the degree of avoidance varies between areas, suggesting that other factors are involved. At the one extreme, females have overlapping home ranges and show no sign of territoriality, even though they avoid close contact (Benson 1980, Armitage and Harris 1982, Koprowski 1996). A moderate level of spacing between female home ranges was observed by Havera and Nixon (1978), who found that females had over-lapping home ranges, but that the main den sites and centers of activity were no closer than 50m to the centers of activity of another female. At the opposite extreme, such as observed in Florida, the females occupied home ranges that were nearly exclusive of other females.

The variation in avoidance between areas is believed resource related, and the territorial behavior exhibited by female fox squirrels in Florida is believed a behavioral adaptation to low food supplies. Benson (1980) speculated that territoriality in tree squirrels may be an adaptation to habitat which contained a low diversity of foods that were evenly dispersed. This aptly describes the typical pine forests occupied by fox squirrels in northern Florida. Nixon et al. (1986) theorized that female fox squirrels exclude other females from their ranges to decrease competition for food, and thereby increase their nutritional levels and improve their chances for reproducing. Adult females were heavier on average than adult males, perhaps indicating that the strategy was working at least from a nutritional standpoint.

By spacing themselves, females limit their numbers. On the Fort White area, females comprised 30% of the adult population. Similar sex ratios have been observed in South Carolina (Woods 1988) and Virginia (1990), but they have not been observed in the midwest, where adult sex ratios are considered to be 1:1 (Koprowski 1994).

Male Behavior

On the Fort White area, males had overlapping home ranges, suggesting a greater tolerance of each other than demonstrated by females. Other studies have shown that males are more tolerant of each other than are females of each other (Nixon et al. 1986, Koprowski 1996). Koprowski (1996), for example, found that nest sharing occurred much more frequently among adult males than among adult females. Nixon et al. (1986) found that females tended to be evenly dispersed across their study area, but that males showed an aggregate or random dispersal. Within the male segment of the population, however, there are dominance hierarchies (Benson 1980), which may be maintained in part by the scent marks placed on the underside of branches.

Reproductive Strategies

The contrasting social systems of male and female fox squirrels are believed a consequence of different reproductive strategies. The female strategy involved establishing a territory and securing adequate food resources. Other females were excluded from the territory, perhaps to reduce competition, but also as a means of eliminating the chances that those females would kill the other female's offspring.

Males, on the other hand, had a different strategy. They had overlapping home ranges and displayed no signs of territoriality. They minimized the energy expended on day-to-day squabbles with a dominance hierarchy (Benson 1980). Their main period of competition was during the mating seasons, when they gathered around a female in estrous, and tried to insure that their genetic code was passed on. The large home ranges displayed by males are largely a result of travels made during the mating seasons. After the males had participated in the mating game, they returned to their normal home ranges and presumably settled back into the dominance hierarchy, with perhaps some adjustment in status depending on recent events.

Conclusion

The picture that has emerged from the studies done on fox squirrels in Florida is of a species scratching out a living on marginal habitat. Considering the natural infertility of their habitat, and the tremendous losses it has suffered in Florida in the past 100 years, it is little wonder that fox squirrels are imperiled in the state. The species future in Florida, and possible conservation measures, are addressed in Chapter 5.

CHAPTER 4
REINTRODUCTION

Animal translocation, or stocking, is a tool commonly used to supplement or establish animal populations (Griffith et al. 1989, Wolf et al. 1996). The method has been successfully used with fox squirrels to establish populations of the endangered Delmarva fox squirrel in Maryland and Virginia (Bendel and Therres 1994). The method has been used in Florida in an experiment conducted on fox squirrels in southern Florida to learn more about habitat use of Big Cypress fox squirrels (Jodice 1993).

Translocation of fox squirrels was used in this study in an attempt to establish the species on San Felasco Hammock State Preserve, a 24-km^2 mosaic of upland hardwoods and pines located in western Alachua County. Park rangers had been told by "old timers" familiar with the natural history of the area that fox squirrels once occurred on the Preserve. The sightings were during a period when the area was grazed and burned. The state purchased San Felasco in 1976, and up until the early 1990's, only one fox squirrel had been seen on the Preserve by rangers.

Park rangers began an aggressive prescribed burning program in the mid-1980's. Fire opened the understory and improved the suitability of the area for fox squirrels. In the early 1990's the Preserve biologist investigated the possibility that fox squirrels would naturally colonize San Felasco. Land surrounding the preserve was surveyed for fox squirrels, but no concentrations were found that could serve as a source of colonizers. Given that the habitat on San Felasco appeared suitable, that it was publicly owned and thus secure from development, and that natural stocking seemed unlikely, the preserve seemed an ideal location to translocate fox squirrels.

Methods

The site chosen to establish fox squirrels was a 6-km^2 stand of upland pines and hardwoods. The topography was gently rolling. Longleaf and loblolly pine dominated the hill tops; hickory, magnolia, and spruce pine (*P. glabra*) dominated the bottoms. The stand had been managed with prescribed fire since the mid-1980's. The ground cover was the most sparse on the ridge tops where wiregrass (*Aristida beyrichiana*) predominated, but it became progressively thicker down-slope where dense thickets of dwarf wax myrtle (*Myrica* sp.) covered the ground. The ground cover in the hardwood bottoms was leaf litter.

Six fox squirrels (4 male: 2 female) were translocated to the release site. Three of the squirrels were captured on Marion Oaks golf course in southern Marion County. These tame squirrels were captured with a dip net using cheese crackers as bait. The other three "wild" squirrels were captured in live traps baited with raw peanuts. One of the three was caught on a horse farm in northern Marion County, and the other two were caught on a cattle ranch in southwestern Alachua County.

All captured squirrels were tranquilized with injections of ketamine hydrochloride (the drugging procedure is described in detail in Chapter 3). They were then eartagged, radio collared with Holohil MI-2M transmitters, and transferred to holding cages located on a longleaf pine/wiregrass ridge top. The rectangular cages were 1.8m by 1.8m by 1.2m. Each cage was equipped with climbing posts and a nest box. Squirrels were housed one to a cage. Fox squirrels were housed from 4 to 15 days. Food and water were provided daily.

Fox squirrels were released in two batches. There were four squirrels in the first release, and two in the second. In the first release, four fox squirrels were moved from their cages while they were in their nest box. The nest boxes were secured to nearby trees at a height of about 3m. The squirrels were allowed to leave the nest box at will. It was hoped that the fox squirrels would remain in the area of their nest box. However, no squirrels used their nest boxes after release, and the method was abandoned. In the second release, the doors to the cages were simply opened and the two squirrels were allowed to leave the cages at will. The nest boxes were not disturbed under the second method.

Attempts were made to locate the fox squirrels once per day until they settled in a home range. They were then located 2-3 times per week. Monitoring was conducted for a 90 day post-release period. Squirrels were located using ground and aerial tracking methods. Locations were plotted in the field on 1:24000 topographic maps and recorded to the nearest 10m.

Results and Discussion

The first four squirrels were released 18 April 1995 (Table 4-1). The nest boxes were secured to trees between the hours 0800 to 0900 h, and the squirrels were allowed to leave at will.

The squirrels were located that afternoon between the hours of 1600 to 1800 h. The distance traveled from the release site in that 8-10 hour interval ranged from 0.3 to 1.5 km.

One of the four squirrels returned to the release site three days after being released. On 20 April 1995 (about 48 hours after release), the squirrel was 3 km from the release site, but by the next afternoon, it was back at the release site. It remained there for about two weeks (21 April to 5 May). It then left the preserve, and, two days later, was located 3 km south of the release site. It remained in this area through the study.

None of the other three squirrels released 18 April returned to the release site. One of the squirrels (M346) was killed on Interstate 75 two days after release. The radio signal was lost on another squirrel one day after release (F127). Her last location was on the preserve and about 1.6 km from the release site. Her status remains unknown.

The fourth squirrel established a temporary home range located off the preserve and about 2 km west of the release site. She remained in this area for about three weeks (20 April to 12 May). She then traveled further west, establishing a home range located 4.5 km from the release site, where she remained through the study period. The landowner of the ranch where the squirrel settled told me that she had seen other fox squirrels on the ranch.

The other two fox squirrels translocated in the study were released on 23 May 1995 between the hours of 0800 to 0900. They were located that afternoon between the hours of 1600 to 1630. The distance traveled from the cages ranged from 100-500m.

Table 4-1. Status of fox squirrels translocated to San Felasco Hammock State Preserve.

Sex/ Animal #	Capture Date/ Location	Release Date	Status
M346	3 April 1995 Marion Oaks Golf Course, Marion Co.	18 April 1995	Roadkill, 20 April 1995, 1 km west of the release site
F127	"	"	Lost radio signal. Last location, 19 April 1995, 1.6 km southwest of the release site
M047	"	"	Established home range, beginning 7 May 1995, 3.0 km south of the release site. Carcass found 17 Aug. 95, cause of death unknown
F166	14 April 1995, horse farm, Orange Lake, Marion Co.	"	Established home range, beginning 16 May 1995, 4.5 km wes of the release site

Sex/ Animal #	Capture Date/ Location	Release Date	Status
M308	18 May 1995, cattle ranch, Watermelon Pond, Alachua Co.	23 May 1995	Established home range, beginning 28 May 1995, 4.9 km south of the release site
M290	19 May 1995, cattle ranch, Watermelon Pond, Alachua Co.	"	Status unknown. Collar found 3 July 1995, 7 km north of the release site, fate unknown.

One of the squirrels (M290) remained within 200m of the cages for at least one more day. He then left the preserve and established a temporary home range located about 3 km north of the release site, where he stayed for about 2.5 weeks (28 May to 15 June). He left this area and traveled north for a two week period without settling in a particular area. He was last located alive on 30 June at a location 7 km north of the release site. His collar was found lying on the ground at this location on 3 July. The carcass was not found, and the squirrel's fate could not be determined.

The second squirrel released on 23 May traveled for five days before establishing a home range located off the preserve and 5 km from the release site. The squirrel remained in this area through the study period.

In summary, six fox squirrels were released on San Felasco. The radio signal was lost on one squirrel while it was still on the preserve, but the other five animals were documented leaving the preserve. One of these was killed by a vehicle on Interstate 75 two days after release (two other squirrels successfully crossed the interstate).

Three of the four squirrels that left the Preserve established home ranges where they remained during the study period. One of the squirrels that successfully established a home range was a "tame" golf course squirrel, and the other two were "wild" squirrels that had been captured on ranches. The home ranges of the relocated squirrels were scattered such that there was no contact between the squirrels after their release. However, there were other fox squirrels in the areas where the study animals settled. This was similar to the behavior of dispersing subadults in that both selected habitat containing other fox squirrels, and the apparent attraction of fox squirrels for conspecifics is discussed in Chapter 5.

The habitat conditions where the squirrels settled was similar. The squirrels established their home ranges on farms containing mature pines and oaks with a grassy ground cover kept low by grazing and/or mowing. Each home range contained a rural human residence, and the fox squirrels occasional foraged in the yards around the houses.

The condition of the habitat where the squirrels settled was similar to that on the preserve in that both contained a mixture of upland oaks and pines. The difference between the habitats was primarily in the understory and ground cover. The understory where the squirrels settled was open and grassy; on the preserve, it was mostly overgrown and shrubby due to the wide spread stands of dwarf wax myrtle.

The undesirable condition of the habitat on the preserve was in part a consequence of an infestation of the southern pine beetle that lead to a prohibition of prescribed fire beginning in the winter of 1994-95. Managers on the preserve were afraid that fire would stress the pines and decrease their natural resistance to a beetle attack. The stand where the squirrels were released had been scheduled for fire in the winter of 1994-95. Had it been burned as planned, it is believed that the squirrels would have found the habitat more acceptable.

There were two major assumptions involved in this project. One was that the preserve contained suitable fox squirrel habitat. This did not appear to be the case judging from the behavior of the released squirrels -- none of them settled on the preserve. The reason for the poor quality of the habitat was probably the over-grown condition of the understory, the result of an unanticipated prohibition on burning caused by the beetle infestation. Preserve personnel expect that it will be years before they burn the woods again because of the infestation. The consequence is that the understory vegetation will continue to thicken, and accordingly, the habitat quality for fox squirrels will continue to decline.

The second major assumption of the project was that there was not a local source of fox squirrels to colonize the preserve. This assumption was also incorrect. Three of the released squirrels traveled from the release site to neighboring habitat that contained resident fox squirrels. The trip could presumably be made in reverse, suggesting that local fox squirrels could colonize the preserve if habitat conditions were suitable, negating the need for imported squirrels.

CHAPTER 5
CONSPECIFIC ATTRACTION

Fox squirrel habitat surrounding the Fort White and San Felasco study areas was a mosaic of forest patches scattered among fields and pastures. One of the observations made during the study was that radio-collared animals that left the primary study areas tended to settle in habitat patches which contained other fox squirrels. The attraction to conspecifics was one of the reasons that attempts to stock San Felasco were unsuccessful. The purpose of this chapter is to discuss this behavior in terms of its survival value and in terms of its practical applications in wildlife conservation.

The basic social systems among rodents are solitary and communal (Eisenberg 1967). Prairie dogs (Cynomys ludovidianus) are a well known example of a communal rodent. Prairie dogs live in family groups called coteries, which are typically composed of an adult male, 3-4 adult females, and their juvenile offspring (Hoogland 1995). The coteries are organized into wards, or groups of coteries, and the wards are organized into towns.

Tree squirrels, on the other hand, display a solitary social system. Fox squirrels are solitary animals, and the territorial behavior exhibited by adult females towards other females places Florida fox squirrels among the least social members of their genus (Gurnell 1987).

In spite of the fact that fox squirrels are solitary animals, I observed several incidents of transient fox squirrels settling in habitat patches that contained conspecifics. It occurred with animals that dispersed from the Fort White study area, and it occurred with the squirrels that were translocated to San Felasco. Given the fox squirrels' solitary social system, it was a surprise that the transients chose to settle with conspecifics. Although I did not measure fox squirrel abundance or habitat quality outside the primary study areas, my impressions, based solely on anecdotal observations, were that suitable but unoccupied habitat existed. If these impressions were correct, and there were vacant patches of suitable habitat, the observations suggest that fox squirrels chose habitat with conspecifics over similar habitat that did not contain fox squirrels.

On the surface, the concept that animals are attracted to members of their own species is to be expected, and there seems little value in discussing it. We have all heard the expression "birds of a feather flock together". Although we expect communal species to form groups, the claim expressed here is that solitary species are also attracted to one another. A consequence of the attraction is that solitary species also tend to occur in groups.

Group formation as a consequence of conspecific attraction was suggested in the data collected on fox squirrels. The attraction, and its consequences on distribution patterns, have been observed with other solitary vertebrates. Stamps (1988), for example, studied the attraction of conspecifics in a territorial lizard, Anolis aeneus. In a controlled experiment, juvenile lizards demonstrated a preference for habitat occupied by conspecifics over identical habitat without conspecifics.

In another example, Sherry and Holmes (1985) observed that habitat selection in Least Flycatchers (Empidonax minimus) was controlled by a strong urge to aggregate, and this behavior overrode vegetation characteristics. The result was a clumped distribution.

A third example of group formation by a solitary species was observed in a study of mountain lions (Felis concolor) released into unoccupied habitat in northern Florida (Belden and McCown 1995). The cats wandered over large portions of north Florida and southern Georgia, but the majority ultimately settled in northern Florida, where they formed a local population with adjoining territories. One exception to this behavior was displayed by a young male cat that settled apart from the group. However, upon reaching the age of sexual maturity, the lone cat traveled across the state of Georgia and joined the others living in northern Florida.

Other examples of conspecific attraction are provided as case studies by Smith and Peacock (1990). Their examples support the claim that conspecifics of solitary species are attracted to each other.

The observations that solitary animals tend to settle with conspecifics seems odd considering their social systems. Solitary animals do not need each other as do communal animals. Solitary animals do not hunt or forage cooperatively, or depend on one another for safety, so there seems little advantage for group formation. It would seem, that if given a choice, a dispersing solitary animal would prefer to settle in unoccupied habitat. This would free the individual from intraspecific competition for resources, and it would eliminate the social stresses and fighting associated with that competition. Danielson and Gaines (1987) observed that immigrating *Microtus ochrogaster* received a hostile greeting from residents, and that the residents hampered settlement. This behavior was also observed in fox squirrels by Hansen and Nixon (1985) who found that resident females limited recruitment into the study areas. Dispersing Florida panthers are often met with hostility from residents, and several incidents have been observed in southern Florida where residents killed the immigrants (J. Roof, GFC, personal communication).

The fact that solitary animals appear to be drawn together in spite of these hostilities suggests that the benefits of the behavior may offset the costs. There appear to be two primary benefits. The first, and most obvious advantage of settling with conspecifics is for mating (Stamps 1988). This almost goes without saying, however, settling with conspecifics is not a necessity for mating, because the animals could live apart and converge only when necessary to breed. This strategy works for toads (*Bufo* sp.), but for an animal such as a fox squirrel, it is probably advantageous to settle with potential mates. The close proximity to mates would reduce the dangers associated with traveling to a distant breeding ground. It would also increase the likelihood that a male, for example, would be near enough to detect an estrous female, and not miss out on the brief period she was receptive.

The second advantage of conspecific attraction is for habitat selection. One of an individuals most important decisions in life is where to settle (Orians and Wittenberger 1991). If the animal chooses correctly, there will be adequate food, safety from dangers, and an opportunity to pass on one's genes. If the animal makes a poor decision, it not only loses its life, but its genetic code dies as well.

Choosing a quality location could take years of study. For a fox squirrel, data would be needed on reliability of mast crops, location of alternative foods in event of a mast failure, bobcat abundance, food preferences of resident red-tailed hawks, the farmer's attitude towards fox squirrels in the pecan grove, and if the farmer is intolerant, how good is his aim. All these factors could affect the animal's chances for survival, and a wise decision maker would want to consider each one.

Yet the observations on fox squirrel dispersal suggest that the decision on where to settle was not a drawn out process. The long distance movements of dispersing and relocated fox squirrels were characterized by a sudden, one-way movement from their natal home range or release site to the area where they ultimately settled. The entire process of dispersing and establishing a home range was generally completed in 2-3 weeks. A similar time frame was observed in the two instances when fox squirrels moved from their first adult home range to their second.

This brings us to the advantage of conspecific attraction and habitat selection. I can think of no other cue that offers as much data as quickly about a site as the easily observed fact that conspecifics live there. There are no formulas involved, or drawn out assessments of mast crops. The value of conspecifics as a cue to habitat quality has been previously noted by Keister (1979) and Stamps (1988).

An innate attraction to conspecifics would be especially valuable to animals in transition, such as dispersing subadults. An animal that used a simple gauge of habitat quality, such as presence or absence of conspecifics, could quickly settle and avoid the dangers of prolonged travel through unfamiliar territory. The ability to make the decision quickly would be a distinct advantage to a transient.

Certainly there are situations when an animal will not encounter conspecifics in its travels, and will be forced to use other cues to assist it in choosing a place to settle. The cues might include food abundance, vegetative structure, or some other environmental variable that suggests to the animal that the habitat is appropriate. Or, it is possible that the animal will choose to return to its natal region, or to the last place it encountered conspecifics. This was observed with one of the fox squirrels released on San Felasco. The squirrel left San Felasco upon release, but it returned a few days later. By the time it returned, the three fox squirrels it had been released with had left San Felasco. After a few days alone, it left the site for a second time, but heading in a new direction. The squirrel ultimately settled in an area that contained other resident fox squirrels, none of which had been released for the project.

Conservation and Conspecific Attraction

Considering the interests in metapopulation dynamics, it seems that conspecific attraction would be a "hot" topic. The idea is not new (Keister 1979), and it was even incorporated into a model (Ray et al. 1991), but the topic is not in vogue. For example, recent studies on habitat selection and colonization of habitat patches have focused on variables such as resource abundance, interspecific competition, and resource distribution (Fahrig and Merriam 1994, Gustafson and Gardner 1996, Hartman 1996, Lima et al. 1996, Miller et al. 1996, Schneider 1997). The social aspect of habitat selection was not discussed. Conspecific attraction has also been ignored in recent studies on dispersal, where the topics of interest have included inbreeding depression, kinship, and reproductive success (Jones 1987, Doolan and MacDonald 1996, and Gese et al. 1996). There almost appears to be a silent assumption that dispersers will settle with conspecifics, and therefore the topic is not discussed.

Conspecific attraction warrants more attention for two reasons. One is that the concept is testable and should be of interest to the research community. To my knowledge, only two studies have tested the role of conspecific attraction on habitat selection, and both were conducted on lizards in a laboratory setting (Keister 1979, Stamps 1988).

The second reason the concept should receive more attention is because it has practical significance for wildlife conservation. One application of the idea involves the colonization of vacant habitat patches. As was witnessed on San Felasco with fox squirrels, if conspecifics are nearby, it may be a waste of time and animals to relocate animals to habitat within easy dispersal distances of resident populations.

Conspecific attraction may also limit natural colonization of suitable habitat patches. In cases where this is noticed by wildlife managers, translocation could possibly be used to form a starter population that would draw immigrants to the habitat. This could perhaps be done by holding the translocated animals in captivity, and using them as decoys to trick dispersers into settling the vacant habitat. Stamps (1988) suggested luring songbirds to vacant habitat by playing tape recordings of their mating songs.

Another practical application of conspecific attraction is that radio-collared animals could be used as field assistants for help in locating hard to find species. I mention this partially in jest, but it actually happened in the fox squirrel introduction in San Felasco. About 1 year before the fox squirrels were released into the Preserve, the area biologist conducted a survey of the local habitat to determine if there were resident fox squirrels that could naturally colonize the area. He did not find them. However, the fox squirrels that were translocated to the Preserve left the area and within weeks they settled with fox squirrels that were missed by the biologist.

A third practical application is related to the fact that not all occupied habitats are of equal value. Some habitats are optimal, while others are marginal. The marginal habitats may even function as population sinks. If the main attraction to the sink is due to its occupation by a few resident animals, these individuals could be removed and thus remove the habitat's main drawing power. This application would probably only merit consideration for intensive endangered species management, but there may be situations where such actions would be warranted.

Conclusion

The basic idea that animals are attracted to conspecifics is not new, or as Keister (1979; 328) pointed out, "for communal animals, the idea that conspecifics are important as cues in habitat selection is as old as the first use of duck decoys." However, wildlife biologists may have overlooked that conspecific attraction applies to solitary animals as well, and that conspecifics may play an important role in an animal's decision on where to settle. The attraction that solitary animals have for one another, and the consequences of this attraction on patterns of distribution, have changed my perceptions of fox squirrel societies. I now perceive them as living in colonies. The members of the colony are widely spaced, and the colony is not easy to see from a human perspective, as a prairie dog colony is easy to see, but nonetheless, it is a colony. The colony was formed, and is maintained, by the power of conspecific attraction.

CHAPTER 6
FUTURE OF FOX SQUIRRELS IN FLORIDA

Fox squirrel's are rare in most of Florida. One of the reasons for their rarity is due to the low productivity of their habitat, as discussed in Chapter 3. This factor is responsible for the low densities, the large home range sizes, and the low production of young per unit area.

The second, and most important reason they are rare is because of habitat loss (Moore 1957, Brady 1977, Kantola 1992, Humphrey 1992). As discussed in Chapter 2, longleaf pine forests are one of the fox squirrels primary habitats. Historically, the forests covered 2.8 million ha of the state; by 1988, there were only 0.34 million ha remaining (Kautz 1993, Cox et al. 1994), which represented an 88% reduction from historic levels. There is no comparable data on fox squirrel populations, but it seems reasonable to assume that their numbers have declined in proportion with declines in the habitat.

The precarious status of fox squirrels in Florida has been recognized by the Florida Game and Fresh Water Fish Commission's listing of *S. n. shermani* as a species of special concern and of *S. n. avicennia* as a threatened species. The third subspecies in the state, *S. n. niger*, is also rare, but it is not on the state's list of imperiled species.

There seems to be legitimate reason for concern over the fox squirrel's future in Florida. This brings us to the point of this chapter, which is to discuss the factors which will influence the species' future, and to try to predict the most likely scenario.

Minimum Population Size

Cox et al.(1994) used computer simulations for estimating the survival potential of various sized fox squirrel populations in Florida. The model challenged the populations with environmental fluctuations that affected survival and fecundity. The process identified the population sizes most likely to survive the next 200 years. The simulations indicated that populations of at least 200-300 individuals occupying contiguous habitat stood the best chance for survival. Smaller populations did not handle the environmental fluctuations as well, and they were less likely to survive.

Cox et al.(1994) then used various estimates of fox squirrel density and estimated that a population of 200-300 fox squirrels would require 2,000-4,000 ha of suitable habitat. The habitat estimates give us a criteria to use to search the state for habitat blocks of the required size.

Population Identification

There are two estimates of fox squirrel habitat in Florida, both of which are imperfect. One of these is based on Landsat data, and it was used by Cox et al.(1994) to identify important wildlife habitats in the state. The Landsat data are technically advanced, but only portions of the data are published (Cox et al. 1994). A second drawback of the Landsat data are that it cannot detect certain types of fox squirrel habitat, such as that found on ranches and on farms (Cox et al. 1994).

The second estimate of fox squirrel habitat was calculated from coarsely mapped distribution data. These data were described in Chapter 2. The data are technically impaired, and provide only a crude estimate of habitat quantity. However, it has two important advantages over the Landsat data. One is that the habitat on ranches and farms was detected. The second reason is that the complete data set is in hand and available for use. For these reasons, the cruder estimates of habitat were used for the discussions that follow.

Based on the habitat estimates, there were eight areas in Florida where the quantity of suitable fox squirrel habitat exceeded 4,000 ha. These areas are capable of supporting fox squirrel population with the best chances for long-term persistence. There were also 36 areas in the state where the habitat patches range in size from 1,000 to 4000 ha. Recognizing the crudeness of the habitat estimate, I am willing to assume that each of the smaller areas had sufficient habitat to support a population with chances for long-term persistence. By combining the two habitat size categories, there were 44 areas of the state with sufficient habitat to support fox squirrel populations with a chance for long term persistence.

If all the small populations are lost, 44 populations potentially will be left in the state. If the habitat in these 44 areas persists, and if the population model is correct, these populations could survive indefinitely. However, a goal of this discussion is to be realistic, and there are a number of reasons to doubt the assumption that the habitat will remain in its current state.

Reasons to Expect Change

One reason to expect changes in the habitat is because Florida's human population is expected to continue growing. The population in 1995 was estimated at 14 million (Floyd et al. 1996). It is expected to increase to 20 million in the next 25 years. These increases will result in the loss of wildlife habitat as Florida further develops to accommodate the growth, some of which will be habitat occupied by fox squirrels.

A second reason to anticipate change in habitat quantities is that Florida's forests continue to change in directions unfavorable to fox squirrels. For example, in the period 1988-95, longleaf forests declined by an additional 22% (Brown 1996). Pine plantations, on the other hand, a habitat typically not used by fox squirrels, increased during the same period by 15%.

A third reason to anticipate change is that logging of Florida's forests continues. Logging has been the traditional cause of habitat changes for fox squirrels. In the period 1987-95, the harvests of Florida hardwoods increased by 33% (Brown 1996). Timber prices for southern pines have increased in recent years, providing people a greater incentive to harvest mature trees. Prices for southern pine saw timber, for example, increased from $103/1000 board feet in 1986 to $246/1000 board feet in 1995 (USDA 1997).

A fourth reason to expect change in the quantity of habitat is that forest regeneration is absent from much of the areas occupied by fox squirrels. The forests contain mature trees, but the saplings are missing. The mature trees that die are not being replaced by reproduction, and as a result, the forests are slowly dying. These conditions are especially noticeable in forests with heavy cattle grazing. They have also been observed on quail plantations (Kantola and Humphrey 1990).

A final reason to expect change is that the quantity of habitat being burned is declining (Brenner and Wade 1992), and it is expected that this trend will continue. Prescribed fire is a primary tool for controlling under growth in the forests occupied by fox squirrels. Less burning means thicker, more overgrown understories, which diminishes the value of the habitat for fox squirrels.

Public versus Private

After considering these recent trends, it seems likely that the quantity of fox squirrel habitat will experience further declines. As a result, it seems unlikely that each of the 43 populations will persist. The question now to consider is which of the 43 populations will be lost. A criterion which has been used in Florida to predict the future of wildlife habitat is whether the habitat occurs on private or public lands (Cox et al. 1994). The assumption is that habitat on private land will eventually be converted to some other land use, such as a residential development or a pulpwood plantation.

If the habitat on private land is made unsuitable for fox squirrels, 26 of the 43 populations will be lost. The remaining 17 populations occur on publicly owned land, and as a result, their future may be secure. All things considered, these populations probably stand a better chance of long-term persistence than any in the state. They are the largest in Florida, and they occur on habitat secured in public ownership. If the habitat in these areas is managed appropriately for fox squirrels, such as with frequent burns and long rotation timber management, and the squirrels are protected from poaching, the species should not go extinct in Florida.

Status of Subspecies

The story changes slightly, though, when the fox squirrel's future is examined at the subspecies level. This is the traditional taxonomic level for fox squirrel management in Florida. The future of each of Florida's three subspecies is briefly discussed below.

The southeastern fox squirrel (*S. n. niger*) ranges across much of the southeastern United States. In Florida it occurs in the western Panhandle, from Okaloosa county west to the Alabama line (Turner and Laerm 1993). The two largest concentrations of fox squirrel habitat in Florida occur in the range of this subspecies, and both concentrations are publicly owned (Eglin A.F.B. and Blackwater River State Forest). The subspecies' future in Florida appears secure.

Sherman's fox squirrel (S.n. shermani) occupies the peninsula and the panhandle east of Okaloosa county. Its range extends into the Georgia piedmont (Turner and Laerm 1993). Fifteen of the 17 large concentrations of habitat on public land in Florida occur in the range of this subspecies. As a result, its future in the state seems secure. The largest blocks of habitat occur on Apalachicola National Forest, Ocala National Forest, Camp Blanding Military Reserve, and Withlacooche State Forest. The smaller blocks of habitat occur on the following areas: Osceola National Forest, Cecil Webb WMA, Jennings S.F., Cecil Field Naval Air Station, Joe Budd WMA, Avon Park AFB, Apalachee WMA, 3 Lakes WMA, St. Marks NWR, K. Ordway Preserve, and Wekiva River SP and surrounding properties.

The Big Cypress fox squirrel (S.n. avicennia)is endemic to southwestern Florida. None of the state's 17 largest concentrations of habitat on public land were within the range of this subspecies. If the population model is correct, and only the largest populations living on public land survive, then the future of this subspecies is questionable.

The criteria used above in forecasting the fox squirrel's future were based on a worst case scenario. It was assumed that only the largest populations would persist, and that all privately owned habitat would be lost. The result was that

Florida was left with 17 isolated fox squirrel populations restricted to the largest pieces of publicly owned property. Under that scenario, S.n. avicennia went extinct.

Alternative Futures

As we all know, the problem with forecasting is that we really do not know what the future holds. The fox squirrels' future could be drastically different in Florida with different forest management. As an example, Florida contained 1.84 million ha in pine plantations in 1995 (Brown 1996). If private and industrial tree farmers where to manage their plantations for saw logs instead of pulpwood, and they were to control the understory with frequent burns, there could be a tremendous quantity of habitat created within a few years.

In central and southern Florida, much of the habitat is on ranches. If the ranchers were to plant fencerows in pines and oaks, they could substantially increase the amount of habitat on the ranches. Second, if they could take steps to encourage tree regeneration they could improve the long-term potential of the habitat for fox squirrels. Third, if they were to control saw-palmetto growth in the pine flatwoods they could substantially improve the quality of the habitat for fox squirrels.

In northern Florida, if landowners were to take the simple step of controlling undergrowth there would be a notable increase in the quantity of habitat available. Northern Florida is dotted with small woodlots and striped with fencerows. Many of the patches contain large oaks and seed bearing pines, but the understories are overgrown with shrubs and vines and thus the stands are poor habitat for fox squirrels.

The few steps mentioned above could greatly increase the numbers of fox squirrels in Florida. If the habitat changes became permanent, the fox squirrel's future would be substantially brighter. However, it is important to point out that there is a time element involved if we expect the new habitat to be naturally colonized. In the farm country of northern Florida, for example, fox squirrels are widespread, but the populations are small and diffuse. These are the sources of squirrels for natural colonization. If the positive habitat changes were to occur soon, natural colonization would be more likely now than in the future when many of the smaller populations may be extinct.

Economic Reality

Although positive changes could occur in the habitat, it seems unlikely they will, mainly because the actions require money and manpower. We are a profit driven society, and there are no direct profits in fox squirrels. Granted, there could be profits in a shift to longer pine rotations, but the forest industry does not appear to be headed in that direction (Brown 1996). Therefore, while there are steps which could be taken to change the fox squirrels future, it does not seem likely that the steps will be taken.

An example of the relationship between profits, fox squirrels, and land management was observed on the Fort White study area. The Fort White landowners appreciated fox squirrels. One landowner had even named one of fox squirrels that lived on his farm (he called him Rusty). But even though the farmers enjoyed seeing fox squirrels, and protected them from hunting, they managed their farms for economic reasons. Fox squirrels were just a by-product of that management.

One year before the study began, a stand of mature pines was clear-cut from one of the farms because the owner needed money for retirement. Fox squirrels were known to occupy the stand, but the landowner did not consider them in his decision to cut the trees. I captured three adult fox squirrels on fencerows that ran through the clearcut (Rusty was one of the squirrels), and my suspicions were that they were former occupants of the pine stand. Two of the squirrels were killed during the study (Rusty was run-over where the fencerow met the highway), and the third squirrel disappeared with its fate unknown. By the end of the study, there were no fox squirrels living on the farm.

Another farm on the study area was sold during the study to a church based in Miami. The former owner was protective of the fox squirrels, as expressed in his initial reluctance to allow me to trap on his property. He was worried that the fox squirrels might be injured in the traps. Concerned as he was with the treatment of the fox squirrels, he still sold the farm to the church, knowing that the church intended to develop the farm as a retreat and retirement village for church members, and that this would likely impact the farm's fox squirrels. Fox squirrels were important to him, but not that important. The landowner's priorities were understandable and perfectly normal.

Best Guess on the Future

Fox squirrels have expensive tastes in their choice of habitat due to their dependence on mature trees and upland areas. This is unfortunate for them. It is also unfortunate that fox squirrels require open understories with low ground cover. This requires active management, which requires time and money. It seems that only an eccentric landowner would spend money and forego profits because of fox squirrels.

This brings us back to the point of this discussion, which was to attempt to predict the fox squirrels future in Florida. The species' future on private lands seems questionable considering the economic incentives to harvest mature trees and subdivide and develop Florida's remaining uplands. This leaves the fox squirrel dependent on habitat in public ownership. If the smaller population on government land are unable to survive, as predicted by the population model, then only the largest fox squirrel populations will persist. This was described earlier as the worst case scenario, and while it does not have to occur, it seems likely that it will.

CHAPTER 7
SUMMARY AND CONCLUSIONS

This was an observational study on fox squirrels in Florida. The first phase of the study determined the distribution of the species in the state. The survey revealed that fox squirrels remain widely distributed in Florida, occurring in 65 of Florida's 67 counties (there were no reported occurrences for Dade and Broward counties). The primary habitat of the fox squirrel in Florida is open, mature, pine-oak forests. These habitat features were found under a variety of land-uses. They occurred on public lands in longleaf pine sandhills and xeric flatwoods managed as natural areas. The features were also found on privately owned land in grazed woodlots and forested fencerows. The features were also present on quail plantations, golf courses, and long-rotation pine stands managed for poles and saw logs.

The largest expanses of fox squirrel habitat were found on the following areas: Blackwater River State Forest, Eglin Air Force Base, Apalachicola National Forest, the quail plantations in northern Leon and Jefferson counties, Ocala National Forest, and the Croom and Citrus districts of the Withlacoochee State Forest.

Fox squirrels remain widely distributed in Florida, but the distribution has been severely fragmented by habitat loss.

Except for local areas of concentration, the species is rare across the state.

The second phase of the study used radio telemetry to investigate the population ecology of fox squirrels on two study areas in northern Florida. Forty-four fox squirrels were monitored during the study. This was the largest sample of radio-collared fox squirrels for any study yet conducted on the species in the southeastern United States. The density of fox squirrels on one north Florida study area was 7.4 fox squirrels/km^2; the density on the second area was 11.7 fox squirrels/km^2. These were among the lowest densities reported for the species. Male home ranges overlapped extensively with those of females and other males, but there was little overlap in home ranges of adult females. These spatial patterns were hinted at in an earlier study on fox squirrels in northern Florida (Kantola and Humphrey 1990), but the larger sample sizes in the current study provide more conclusive evidence that female fox squirrels are territorial towards other females. This degree of intolerance between females has not been observed elsewhere, and it is believed a behavioral adaptation to low food supplies. Eight of 15 fox squirrels that were collared as subadults dispersed. Two older fox squirrels also dispersed. Dispersal distances ranged from 1.0 to 7.2 km. This is the only dispersal data available for fox squirrels in the south, and it is the only dispersal data for the species that was obtained using radio telemetry methods. The annual mortality rate for the radio collared animals was estimated at 27-30%, a figure that is comparable to that observed for fox squirrels in the midwestern

United States (Hansen et al. 1986). Litter size ranged from 1-3. Populations had two breeding seasons per year, but the litter frequency of radio-collared females was 1.07 litters per year. This is the first data available on litter frequency for fox squirrels in the south, and it halves the production levels suspected by Moore (1957) for northern Florida.

Fox squirrels on the study areas had the largest home ranges reported for the species. All characteristics of fox squirrels in northern Florida indicate that the habitat is marginal quality, and that the squirrels are only able to survive at low densities by foraging over large areas.

A third phase of the investigation was an attempt to establish a breeding population of fox squirrels in a state park. Six squirrels were released into the park. When the study was first planned, the habitat appeared to be suitable, and there did not appear to be a local source of animals to colonize the area naturally. However, a planned burn did not take place because of an infestation of pine beetles, and because of this, the understory vegetation was believed too overgrown at the time of the releases. The squirrels were released anyway, and they immediately fled the release site. Those that survived settled in habitat surrounding the preserve that contained resident fox squirrels. This indicated that fox squirrels could naturally colonize the preserve if they chose, and there was no reason to relocate fox squirrels to the area. A second observation made during the study was that transient animals seemed to be attracted to members of their own species.

The topic of conspecific attraction was discussed in Chapter 5. The conclusions reached in that discussion were that even solitary animals were drawn towards members of their own species, and that the attraction led to group formation, causing animals to be distributed in clusters. The attraction between animals is believed innate, and it is common because of the advantages the attraction offers its practitioners. One advantage is mating, but a second advantage is that conspecifics offer a quick and easy method for habitat assessment. The attraction has practical significance for conservation, as witnessed in the unexpected movements of relocated fox squirrels towards resident animals off the park.

Chapter 6 contained a discussion on the future of fox squirrels in Florida. It was noted that fox squirrels were rare for two reasons. One was due to the low productivity of their habitat, and the second was due to the conversion of their habitat to other land uses. I expect that significant losses will occur in their habitat as Florida further develops, and that all will remain are a few isolated populations restricted to the largest parcels of publicly owned property.

Over the years, I have developed a great appreciation for fox squirrels. I hunted them when I lived in Mississippi, but I have no desire to shoot one now. They are gorgeous animals, and they make a living in some of the poorest woods in the south. They have style. I love to hear them bark and see them whip their tails in defiance at an intruder. They have gone the way of so much of Florida, and while they do not seem at risk of extinction, their days of prominence are over. I am reminded of the title to an article on the endangered Delmarva fox squirrel, a huge, light-colored squirrel of northern Virginia, which is affectionately known as "Big Silver". The title was "Is Big Silver Really Gone for Good?". Southeastern fox squirrels, like the Delmarva in Virginia, and those in Florida, are a gift from the past, and I feel most fortunate to have gotten to know them.

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BIOGRAPHICAL SKETCH

I was born in Honolulu, Hawaii, in 1957, the third child of a Marine Corp Sergeant from rural Virginia and his wife from Philadelphia. I was raised in North Carolina. I graduated with a B.S. in wildlife ecology from North Carolina State University in 1980, and a M.S. in wildlife ecology from Mississippi State University in 1984. Between degrees I worked in coastal North Carolina as a wildlife and fisheries technician in the Young American Conservation Corp.

I began work with the Florida Game and Fresh Water Fish Commission in 1984 as a wildlife biologist assigned to three wildlife management areas in the panhandle. I transferred to Gainesville in 1986 where I worked as a research biologist in the Agency's wildlife research office. I left the Agency in 1996 to complete the requirements for my Ph.D.

I have been married since 1982 to Terry L. Moir. We have two children, Frank, age 12, and Sara, age 8.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Stephen R. Humphrey

Steve Humphrey, Chair
Professor of Wildlife Ecology and Conservation

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Franklin Percival
Associate Professor of Wildlife Ecology and Conservation

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

George W. Tanner

George Tanner
Professor of Wildlife Ecology and Conservation

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Melvin E. Sunquist

Melvin Sunquist
Associate Professor of Wildlife Ecology and Conservation

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Louis Guillette
Professor of Zoology

This dissertation was submitted to the Graduate Faculty of the College of Agriculture and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

December, 1997

Dean, College of Agriculture

Dean, Graduate School