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Supplemental Information for the Big Cypress Fox Squirrel

Biological Status Review Report

The following pages contain peer reviews received from selected peer reviewers and the draft report that was reviewed before the final report was completed.

March 31, 2011

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Peer review #1 from William Giuliano

From: Giuliano,William M
To: Imperiled
Cc: Garrison, Elina; Giuliano,William M
Subject: Big Cypress & Sherman''s fox squirrel Draft BSR Report
Date: Wednesday, December 29, 2010 11:03:27 AM

FWC:

I have reviewed the Draft BSRs for the Big Cypress Fox Squirrel and Sherman's Fox Squirrel. Based on my review, I believe that for both subspecies, the Biological Review Groups were thorough, accurate, and complete in their use of the biological information available and data analyses, and were reasonable and justified in their assumptions, interpretations of the data, and conclusions in the respective BSRs. I concur with the recommendations made for each subspecies based on my own review of the data, and also make note that a lack of data/knowledge for both subspecies led to some uncertainty in conclusions.

Bill

William M. Giuliano
Undergraduate Program Coordinator
Professor & Extension Specialist
Certified Wildlife Biologist
Department of Wildlife Ecology & Conservation
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University of Florida
308 Newins-Ziegler Hall
PO Box 110430
Gainesville, FL 32611-0430

Peer review #2 from Deborah Jansen

From: Deborah_Jansen@nps.gov
To: Imperiled
Cc: Ron_Clark@nps.gov
Subject: Re: Deadline reminder for peer reviews of BSR reports
Date: Tuesday, January 11, 2011 1:53:19 PM
Attachments: Biological Status Review of the BICY Fox Squirrel Jan 2011 DJansen.docx

Attached is my review of the Big Cypress fox squirrel BSR. I will submit the Sherman's fox squirrel review yet today.

Deborah

(See attached file: Biological Status Review of the BICY Fox Squirrel Jan 2011 DJansen.docx)

Deborah Jansen
Wildlife Biologist
Big Cypress National Preserve
33100 Tamiami Trail East
Ochopee, FL 34141

Biological Status Review of the Big Cypress Fox Squirrel—Reviewer Comments

Prepared 10 Jan 2011 by Deborah Jansen, Wildlife Biologist, National Park Service

I have reviewed the document "Biological Status Review for the Big Cypress fox squirrel (Sciurus niger avicennia). I concur with the findings that this species meets the criteria for listing as threatened. I have a few comments on the document:

1) There is no mention of the fact that this species was once legally hunted and then taken off the list of "legal to hunt" species, nor an explanation of when and why this decision was made. Nor is there any data on how many were harvested and where. What impact did hunting have on the population and its distribution? Did it show recovery after legal hunting ended?

2) Brown (1978) emphasizes pinelands as important habitat and the ongoing work in Big Cypress has found that cypress are an important component of their habitat. Other habitats are also mentioned in earlier documents. What isn't known, however, is what composition of these habitats is critical for occupancy. This may be a limiting factor.

3) The review states that the core of the range is in Big Cypress and Everglades so it is assumed that they are not faring well on private property including open agricultural or cattle lands. The review should expand on the status of fox squirrels in open range habitat that may provide nesting habitat in cabbage palms and food in hammocks, cabbage palms and the open range itself. Have surveys been done on private property in south Florida?

4) A study funded by USFWS on the status and abundance of the Big Cypress fox squirrel was initiated in 2006 and conducted by Reed Noss, Jane Waterman, and Danielle Munim. This study is not cited and I recommend that its results be included in this document, especially since it is one of the most recent studies undertaken.

5) I have an unpublished report done by my technicians in Big Cypress in 1996-97 in which we had an opportunity to collar and track a fox squirrel that we received from the Conservancy's Animal Rehabilitation Center in Naples, Florida. Although the movements were influenced by the fact that it was a translocated and habituated animal, the report offers some insight into fox squirrel food habits. I'll send a copy to you for possible inclusion into your file of fox squirrel information.

Thank you for your agency's efforts in determining the status of the Big Cypress fox squirrel and the opportunity to review these efforts.

Deborah

Peer review #3 from Dr. Jack Stout

From: Jack Stout
To: Imperiled
Subject: review
Date: Tuesday, January 11, 2011 2:35:11 PM
Attachments: Big Cypress Fox Squirrel Final Draft BSR 11-17-10.docx_.renamed_size=56849; creation-date=_Wed, 22 Dec
2010 15_48_20 GMT.docx

I agree with the analysis and decision to recommend threatened status be retained. Data are lacking to support a more optimistic view of the status of this subspecies. Climate change and the future of fire management add to the uncertainty surrounding this assessment.

Jack Stout

Biological Status Review
for the
Big Cypress fox squirrel
(*Sciurus niger avicennia*)

EXECUTIVE SUMMARY

The Florida Fish and Wildlife Conservation Commission (FWC) directed staff to evaluate all species listed as Threatened or Species of Special Concern as of September 1, 2010. Public information on the status of the Big Cypress fox squirrel was sought from September 17 to November 1, 2010. The members of the biological review group (BRG) met on November 3-4, 2010. Group members were Elina Garrison (FWC lead), Bob McCleery (University of Florida), and John Kellam (National Park Service). In accordance with rule 68A-27.0012 Florida Administrative Code (F.A.C.), the BRG was charged with evaluating the biological status of the Big Cypress fox squirrel using criteria included in definitions in 68A-27.001(3), F. A. C., and following the protocols in the *Guidelines for Application of the IUCN Red List Criteria at Regional Levels (Version 3.0)* and *Guidelines for Using the IUCN Red List Categories and Criteria (Version 8.1)*. Please visit http://www.myfwc.com/WILDLIFEHABITATS/imperiledSpp_listingprocess.htm to view the listing process rule and the criteria found in the definitions.

The Big Cypress fox squirrel Biological Review Group concluded from the biological assessment that the Big Cypress fox squirrel met criteria for listing. Based on the literature review, information received from the public, and the biological review findings, FWC staff recommends retaining the species on the FWC list of threatened species.

This work was supported by a Conserve Wildlife Tag grant from the Wildlife Foundation of Florida.

BIOLOGICAL INFORMATION

Taxonomic Classification – The Big Cypress fox squirrel (*Sciurus niger avicennia*), one of 3 subspecies of the fox squirrel occurring in Florida, is defined on the basis of size (it is smaller than both *S. n. niger* and *S. n. shermani*; Moore 1956; Turner and Laerm 1993 as cited in Wooding 1997). *Sciurus n. a.* has been variously known as the Big Cypress fox squirrel, mangrove fox squirrel, Everglades fox squirrel, and south Florida fox squirrel (Hafner *et al*. 1998).

Life History – Big Cypress fox squirrels are large tree squirrels with variable dorsal fur color. Most commonly, individuals have a black head and dorsal fur with buff sides and belly, buff and black tail, and white nose and ears (Florida Natural Areas Inventory 2001). They are a primarily ground-dwelling species that inhabits stands of cypress, slash pine savanna, mangrove swamps, tropical hardwood forests, live oak woods, coastal broadleaf evergreen hammocks, and suburban habitats including golf courses, city parks, and residential areas (Hafner *et al.* 1998; Humphrey and Jodice 1992; Jansen 2008; Williams and Humprey 1979). In Big Cypress National Preserve, one of the most important habitat components is the presence of large cypress domes with good adjacent foraging habitat (Jansen 2008; Kellam and Jansen 2010). Optimum habitat for *S. n. avicennia* includes an open understory free of bushes and undergrowth (Brown 1978 as cited in Hafner *et al*. 1998).

Reproductive behaviour of *Sciurus niger* is summarized as follows for the species in general (see Koprowski 1994 for additional citations). Fox squirrels can mate at any time of the year but most breeding occurs between November and February with a peak in December and between April and July with a peak in June. On a golf course in western Collier County, more reproduction was observed in the warm summer/autumn season than in the winter/spring season because exotic foods supplemented a limited summer native diet (Ditgen and Shepherd 2007). *Sciurus niger* females go into estrus for only one day during which several males aggregrate on a female's home range and form linear dominance hierarchies. Females mate with more than one of these males. Average litter size is generally 2 or 3 offspring. Females can become sexually mature at 8 months of age, but more generally wait to reproduce until they are over a year old and then may breed for more than 12 years.

Territorial behaviour of *Sciurus niger* is also summarized as follows for the species in general (see Koprowski 1994 for additional citations). *Sciurus niger* adults, especially females, defend exclusive core areas but home ranges of individuals overlap and territoriality is not observed. Average home ranges are 0.85-17.2 ha for females and 1.54-42.8 ha for males. All juveniles disperse from their natal area but some may remain with their mother during the first winter.

Big Cypress fox squirrels translocated from Naples, Florida, to Big Cypress National Preserve exhibited inconsistent site fidelity and movements of up to 32km that could be attributed to dispersal, post-release investigative behavior, or long-distance foraging (Jodice 1993). Crude estimates of Big Cypress fox squirrel population densities have been calculated at 0.0009 squirrels/ha in typical Big Cypress Swamp habitat in Corkscrew Swamp Sanctuary and 0.0192 squirrels/ha in ranchland woodlots (Jodice and Humphrey 1993). Humphrey and Jodice (1992) stated that these densities are probably much too low, however, because they included some unoccupied habitat. Densities estimated for other squirrels in the southeastern United States are 0.05 squirrels/ha for *S. n. niger* (as summarized in Koprowski 1994) and a range of 0.04 to 0.38 squirrels/ha for *S. n. shermani* (Kantola and Humphrey 1990; Wooding 1997; Humphrey et al. 1985, Kantola 1986, and Moore 1957 as cited in Kantola 1992).

Big Cypress fox squirrels have been documented eating java plum, *Ficus* sp., fig fruit, Bischofia berries, acorns, red maple samaras, bottlebrush and silk oak flowers, insects, fungi, bromeliad buds, thistle seed, pond apple fruit, cabbage palm fruit, holly fruit, queen palm fruit, ~~palmetto~~ saw palmetto fruit, pine seeds, slash pine cones, and cypress cones (Ditgen and Shepherd 2007; Jansen 2008; Jodice and Humphrey 1992; Kellam and Jansen 2010). Pine cones, cypress cones, and queen palm fruits are scatter hoarded (Ditgen and Shepherd 2007; Jodice and Humphrey 1992).

Nests of individuals translocated into Big Cypress National Preserve were either stick structures or were nestled among the leaves of bromeliads in co-dominant or dominant cypress trees in cypress or mixed-swamp habitat (Jodice 1993). Fox squirrels living in Big Cypress National Preserve have been found to build nests in bald cypress trees (98% of nests), cabbage palm trees, and slash pine trees (only 1 nest; Kellam and Jansen 2010). Four types of nest are built: (1) stick nests, (2) stick nests that also contain thinly stripped cypress bark, (3) bromeliad nests with stripped bark, or (4) cabbage palm nests with stripped bark.

Geographic Range and Distribution – The Big Cypress fox squirrel is the only species of fox squirrel endemic to Florida (Turner and Laerm 1993 as cited in Wooding 1997). It can be found in the southwestern tip of peninsular Florida, in Hendry and Lee Counties south of the Caloosahatchee River, Collier County, mainland northern Monroe County, and extreme western Miami-Dade County (a strip of land that is largely in Big Cypress National Preserve; Williams and Humphrey 1979; Moore 1956;

see summary in FWS 2002). *Sciurus niger avicennia* occupies "the mangrove, the pinelands, and the Big Cypress west of the Everglades and south of the Caloosahatchee River" (Moore 1956).

Population Status and Trend –The status of Big Cypress fox squirrels in the core of their range in Big Cypress National Preserve and the Everglades is largely unknown because of the difficulty of studying and observing squirrels in such habitat (Jansen 2008; Jodice and Humphrey 1992; Jodice and Humphrey 1993; Maehr 1993). According to Humphrey and Jodice (1992), "since the Big Cypress National Preserve was established in 1974, preserve staff have recorded progressively fewer fox squirrels, concluding that the population is not prospering there." Furthermore, according to the IUCN Rodent Specialist Group, *S. n. avicennia* has not been seen recently in the Everglades and is currently restricted in distribution to Big Cypress Swamp and its adjacent pinelands (Brown 1978). In particular, the Big Cypress fox squirrel is no longer present at the Cape Sable coast of Everglades National Park in the vicinity of Flamingo, Monroe County (FWS 2002). Big Cypress fox squirrels have also been completely extirpated from Corkscrew Swamp Sanctuary and Everglades City (Jodice and Humphrey 1992). Isolation of Big Cypress fox squirrel populations has occurred in western Lee and Collier counties due to rapid urbanization (Ditgen and Shepherd 2007; Endries *et al*. 2009; Kellam and Jansen 2010).

In the future, the Big Cypress fox squirrel is likely to lose some habitat to urbanization, agriculture, and mining. Furthermore, although at least fifty-five percent of potential Big Cypress fox squirrel habitat exists in conservation lands and is therefore protected from development (FWS 2002, Endries *et al*. 2009), analyses by Florida's Wildlife Legacy Initiative indicate that the majority of *S. n. avicennia*'s habitat (natural pineland and pine rockland) is both poor in quality and declining (FWC 2005). Big Cypress fox squirrels are, however, fairly adaptable; they can be found in disturbed/transitional habitat such as on private ranches and in urban areas like golf courses (Ditgen and Shepherd 2007; FWC 2005; FWS 2002; Jodice and Humphrey 1992).

Quantitative Analyses – A population viability analysis was carried out on the Big Cypress fox squirrel using demographic information from the species as a whole (Root and Barnes 2006; Endries *et al*. 2009). The baseline model estimated juvenile survivorship at 0.5, adult survivorship at 0.66, adult fecundity at 0.4125, and juvenile survivorship to adulthood at 0.25, resulting in a growth rate of 0.9725. Distance between populations was estimated at 5km. Initial abundance was estimated at 0.025 while carrying capacity was estimated at 0.18. Results revealed that small changes in the model had large impacts on population trends. Risk of extinction in the next 100 years was found to be zero for both managed habitat and all potential habitat. The risk of large declines, however, was quite large. The probability of a 95% decline in abundance in the next 100 years was about 50%. Abundance was particularly reduced when only managed habitat was considered. The model was sensitive to changes in the adult survival value and adult fecundity. Only the largest populations containing at least 200 individuals survived throughout the 100 year simulation indicating that smaller populations will not persist without dispersal into the population.

BIOLOGICAL STATUS ASSESSMENT

Threats – The biggest threat to Big Cypress fox squirrels on the periphery of their range is destruction of habitat and habitat fragmentation due to encroaching development (FWC 2005; FWC 2008; Jansen 2008; Jodice and Humphrey 1992; Koprowski 1994; Zwick and Carr 2006). Rapid urbanization has isolated Big Cypress fox squirrel populations in fragmented habitat in western Lee and Collier counties (Ditgen and Shepherd 2007). Similarly, the conversion of rangeland to citrus groves has destroyed Big Cypress fox squirrel habitat in the flatwoods region of Hendry County

(Ditgen and Shepherd 2007) while fire suppression has led to the decline of Big Cypress fox squirrel numbers in seasonally inundated areas of Big Cypress Swamp and the Everglades because extensive understory growth makes forests uninhabitable (Ditgen and Shepherd 2007).

A skin fungus is known to cause mortality of Big Cypress fox squirrels in urban areas but no researchers have indicated that this fungus could be a major threat to populations as a whole (as summarized in FWS 2002). In 2010, a Big Cypress fox squirrel was found in the summer to be infected with Squirrel Poxvirus (J, Kellam, unpublished data). Squirrel Poxvirus has a 75-100% mortality rate in squirrels infected with the disease which can spread throughout a population through contact among conspecifics (NPS 2010). The US National Park Service is currently monitoring Big Cypress fox squirrels in Big Cypress National Preserve for an outbreak of Squirrel Poxvirus (NPS 2010).

Although some authors believe that illegal poaching in Big Cypress National Preserve may be having an impact on Big Cypress fox squirrel numbers (Humphrey and Jodice 1992), the US Fish and Wildlife Service states that it does not have evidence to support this claim (FWS 2002).

The US Fish and Wildlife Service reviewed the status of the Big Cypress fox squirrel in 2002 and concluded that this subspecies does not qualify for listing as an endangered or threatened species due to any of the five factors as defined in the Endangered Species Act (FWS 2002).

Sciurus niger avicennia is currently listed as Lower Risk, conservation dependent by the IUCN Rodent Specialist Group "based on the historical loss of habitat and restricted number and distribution of populations of *S. n. avicennia*, probably including Big Cypress National Preserve" (Hafner *et al.* 1998).

Recommended actions of the IUCN Rodent Specialist Group (Hafner *et al.* 1998) are:

- "Conduct studies to determine the optimum habitat requirements of *S. n. avicennia*, and survey for presence of populations in Big Cypress National Preserve
- Conduct controlled burns to open up the understory for better foraging areas for *S. n. avicennia*
- Set aside remaining occupied habitat as refuges for *S. n. avicennia* (Brown 1978)"

Statewide Population Assessment – Findings from the Biological Review Group are included in a Biological Status Review information table.

LISTING RECOMMENDATION – Staff recommends that the Big Cypress fox squirrel be listed as a Threatened species because the species met two of the criteria for listing as described in 68A-27.001(3), F. A. C.

SUMMARY OF THE INDEPENDENT REVIEW

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Peer review #4 from Dr. Pat Jodice

From: Patrick Jodice
To: Imperiled
Cc: Garrison, Elina
Subject: RE: Big Cypress Draft BSR Report
Date: Monday, February 07, 2011 12:01:03 PM

I have very few comments. I found the report thoroughly researched and well-reasoned. I agree that the data support a threatened listing.

Page 3, Population status and trends:
I would suggest toning down the concept of fox squirrels being highly adaptable – I think that is somewhat misleading. Fox squirrels are able to exist in urban and developed habitats apparently as long as there is sufficient food and open understory. They are prone to predation and car mortality, two factors that can play an important role in these urban habitats.

BSR Information findings:
I understand that guidelines were provided for the scoring of these factors. I would like to see it made very clear that there is a severe lack of information on population characteristics of BCFS and therefore that many of the categories are difficult to address. For example, in section (C) Population size and trend, it is stated that no estimates of decline are available (true) but perhaps more relevant is the fact that no estimates of population trends are available at all (and that documenting a declining trend in a rare and secretive species is statistically very challenging).

Please let me know if I can provide any additional information

Pat

Patrick Jodice, Ph.D.
Leader, South Carolina Cooperative Fish & Wildlife Research Unit
Associate Professor
Clemson University
Clemson, SC 29643, USA

Peer review #5 from Dr. Reed Noss

From: Reed Noss
To: Imperiled
Subject: Re: Deadline reminder for peer reviews of BSR reports
Date: Tuesday, December 28, 2010 3:34:54 PM

Dear Elisa,

After reading these two reports, I have decided not to provide a detailed review. Basically, the reports are not substantial enough at this time to warrant peer review. Much more field data (i.e., collected as part of a comprehensive status survey) and a more thorough literature review and consultation with experts, are needed before the biological status of these two subspecies (which are probably not genetically distinct, i.e., see Moncrief et al. 2010, Journal of Mammalogy 91:1112-1123) can be determined with any accuracy. Since these species have also been proposed for federal listing by the USFWS, and earlier petitions (such as the one I submitted for the Shermans's fox squirrel in 1987, here listing was found to be "warranted") are being reconsidered for these taxa, I strongly recommend that the FFWCC and USFWS jointly fund thorough status surveys for fox squirrels throughout Florida. In the meantime, the precautionary principle suggests that both taxa be listed as Threatened until or unless substantial further study finds them much more abundant and stable than existing evidence suggests.

Sincerely,

Reed

Reed F. Noss, Ph.D.
Davis-Shine Professor of Conservation Biology
University of Central Florida
Department of Biology
4000 Central Florida Blvd.
Orlando, FL 32816-2368

Peer review #6 from Dr. Brad Bergstrom

From: Bradley J. Bergstrom
To: Imperiled
Subject: RE: Deadline reminder for peer reviews of BSR reports
Date: Friday, January 28, 2011 11:48:12 AM
Attachments: Peer review of Florida Mouse BSR.docx
Peer review of BigCypress Fox Squirrel BSR.docx
Peer review of Sherman"s Fox Squirrel.docx

Please find attached three separate Word files, which are my peer reviews of the BSRs for:
1) Florida mouse
2) Big Cypress fox squirrel
3) Sherman's fox squirrel

____
Brad Bergstrom, Ph.D., Professor
Department of Biology
Valdosta State University
Valdosta, GA 31698-0015 USA

Peer review of ―Biological Status Review for the Big Cypress fox squirrel (*Sciurus niger avicennia*)"

Reviewer: Dr. Brad Bergstrom, Biology Dept., Valdosta State University, Valdosta, GA
e-mail: bergstrm@valdosta.edu
Date of Review: 26 January 2011

The Big Cypress fox squirrel (*Sciurus niger avicennia*) is a subspecies endemic to forested habitat in the northwestern part of the Everglades ecosystem of south Florida. It is currently listed as a state Threatened species. The subspecies has a small extent of occurrence and a small area of occupancy, and its population is currently declining, just as there are indications of past episodes of extreme fluctuations in abundance. Its current population may number as few as a few hundred and at most a few thousand individuals. Population viability analysis indicates high probabilities of precipitous declines. Serious threats include loss and fragmentation of remaining habitat, succession of habitat due to fire suppresssion, and possibly disease.

The above listed threats to this endemic population are summarized in the BSR as meeting two of the criteria for listing as a Threatened species. From this, it is clear that the Big Cypress fox squirrel is a species that is imperiled in Florida, in serious need of concerted recovery efforts, without which its long-term survival would be threatened and therefore deserving of continued Threatened status.

Peer review #7 from John Wooding

From: Wooding, John B
To: Imperiled
Cc: Garrison, Elina
Subject: RE: Deadline reminder for peer reviews of BSR reports
Date: Wednesday, January 05, 2011 11:16:15 AM

Hi Dr. Haubold, I read the Biological Status Reports for Sherman's fox squirrel and the Mangrove fox squirrel, and I am in concurrance with the findings. Ms. Garrison did an excellent job (and if possible, she should mail me a check for $20.00).

Best Regards,
John Wooding

Letters and emails received during the solicitation of information from the public period of September 17, 2010 through November 1, 2010

Email from Dick Kempton

From: HowardR85@aol.com
To: Imperiled
Subject: Big Cypress fox squirrel
Date: Wednesday, October 06, 2010 12:38:27 PM

There is a thriving population of fox squirrels in the pine lands, about 11- 14 miles north of US 41, off sand road. I have observed as many as 10 at one location, along with others in the area..Several color variations.

Dick Kempton

Email from Paula Halupa

From: Paula_Halupa@fws.gov
To: Imperiled; Garrison, Elina
Cc: Dana_Hartley@fws.gov
Subject: Re: Big Cypress fox squirrel - part 1 of x
Date: Tuesday, November 02, 2010 3:04:26 PM
Attachments: 1978 Brown.pdf
1990 Jodice.pdf
Importance: High

Hi Elina,

We have a large amount of information that does not appear to be on the FWC's sharepoint. I will send you the reports / information in a series of emails (due to size restrictions).

Thanks,

-Paula
(See attached file: 1978 Brown.pdf)(See attached file: 1990 Jodice.pdf)
^^^
Paula J. Halupa
Fish and Wildlife Biologist
Listing, Candidate Conservation, and Recovery
U.S. Fish and Wildlife Service
South Florida Ecological Services Office
1339 20th Street
Vero Beach, FL 32960-3559

ECOLOGY AND TRANSLOCATION OF URBAN POPULATIONS OF BIG CYPRESS FOX SQUIRRELS (*Sciurus niger avicennia*)

BY

PATRICK G. R. JODICE

A THESIS PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

UNIVERSITY OF FLORIDA

1990

ACKNOWLEDGEMENTS

This project was funded by the National Park Service, Big Cypress National Preserve.

As I think back on the 18 months I spent in Big Cypress I realize how many people contributed their talents, ideas, and assistance to this project; its completion is due in no small part to all of them.

Good teachers, I was once told, should be nothing more than a finger pointing out interesting items. It is the students job to explore, develop and test ideas, and draw conclusions. By this definition, Steve Humphrey was an excellent teacher. He allowed me the opprtunity to develop many facets of this project, and his confidence in my skills as field researcher, data analyzer, and writer were always appreciated.

Committee members Mel Sunquist and C. S. Holling helped develop ideas for the golf course study. They provided efficient readings of the thesis and a much appreciated realistic outlook for accomplishements.

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Caramouche; Wyndemere and Mr. Mark Hampton; Country Club of Naples and Mr. E. J. Thompkins.

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Laura L. Williams, a fine naturalist and teacher in her own right, deserves special thanks for her patience, faith, and sense of humor (as unexplainable as it is). Good things do come to those who wait.

The final and most deep felt acknowledgement is extended to my family,and especially my parents, Pat and Mary Ann Jodice. All I have accomplished or ever will accomplish is due to your perserverance, love, and sacrifice. This thesis is as much yours as it is mine. And Jody helped too.

TO DO SOMETHING MORE IN LIFE
THAN IS WISE, PRUDENT, OR NECESSARY

Jean Louie Etiene
Trans-Antarctica Expedition, 1989.

TABLE OF CONTENTS

Abstract of a Thesis Presented to the Graduate School
of the University of Florida in Partial fulfillment of the
Requirements for the Degree of Master of Science

ECOLOGY AND TRANSLOCATION OF AN URBAN POPULATION OF
BIG CYPRESS FOX SQUIRRELS
(Sciurus niger avicennia)

By

PATRICK G. R. JODICE

December 1990

Chairman: Dr. Stephen R. Humphrey
Major Department: Wildlife and Range Sciences (Forest Resources and Conservation)

The Big Cypress fox squirrel (Sciurus niger avicennia) is previously unstudied and listed as threatened by the state of Florida. A population of fox squirrels was studied in an urban setting, and 5 individuals were radio-collared and translocated to the Big Cypress National Preserve.

Activity patterns and diet of fox squirrels on four golf courses in Naples, Florida, were studied for 1 year. Percentage of time spent foraging and inactive varied seasonally. Diets among all 4 seasons also varied. Time spent active was not significantly affected by climate or seasonal differences in diet. Mating behavior and young-rearing may have the strongest effect on seasonal activity

patterns. Fox squirrels concentrated feeding on seasonally ripe foods and included native and exotic species in their diet.

Densities of fox squirrels on golf courses appear to be higher than in natural habitats. Availability of a temporally stable food source may be the cause.

Five fox squirrels translocated to the Big Cypress National Preserve shifted habitat use between seasons. Home-ranges were established in two locations. Home-range size was larger than that reported for fox squirrels elsewhere in the southeastern U. S.

Very few resident fox squirrels were observed in Big Cypress National Preserve. Observations were inconsistent with respect to location, indicating that use-areas of fox squirrels may be quite large. Most resident fox squirrels were observed in open-understory pinelands.

Further study and monitoring of fox squirrel populations on golf courses in Naples is critical. As development in urban areas of southwestern Florida continues, fox squirrel populations on golf courses could easily become isolated from one another and locally extirpated. Additional distribution data are needed on fox squirrels in Big Cypress. Management for open-understory, mature pinelands would probably benefit populations of fox squirrels in Big Cypress National Preserve.

INTRODUCTION

The Big Cypress fox squirrel is one of ten subspecies of fox squirrel, three of which occur in Florida. Big Cypress fox squirrels (*Sciurus niger avicennia*) inhabit the Big Cypress Swamp ecosystem of southwestern Florida, a seasonally flooded mosaic of cypress, pinelands, hardwood hammocks, and prairies.

Densities of fox squirrels in Big Cypress National Preserve (BICY) appear to be low (Williams and Humphrey 1979). Since the establishment of the Preserve in 1974, preserve staff have recorded progressively fewer fox squirrel sightings. Populations of fox squirrels have become locally extirpated from some areas (Corkscrew Swamp Sanctuary, Everglades City), while other suitable habitats are being altered or becoming isolated through development.

Early reports (Brown 1973, 1978) considered habitat lost the most serious threat to Big Cypress fox squirrels. Although large areas of land in Florida's southern peninsula are protected from development (Big Cypress National Preserve, Water Conservation Areas, Panther National Wildlife Refuge, Corkscrew Swamp Sanctuary), urban sprawl continues at a rapid pace along the gulf coast and nearby inland areas. Florida is one of the fastest growing states in the U.S., and southwestern Florida is one of the fastest growing regions in the state (Duda, 1987). Populations of fox squirrels in this area remain predominantly on golf courses and temporarily undeveloped lands.

The Big Cypress fox squirrel is listed as threatened by the Florida Game and Freshwater Fish Commission. Some protective measures, such as the prohibition of hunting since 1972, have been initiated. Unfortunately, few other steps have been taken to ensure survival of this subspecies.

Understanding the ecology of fox squirrels in anthropogenic habitats will be critical to creating effective management plans and protective measures. With that goal in mind, our objectives were 1) to conduct distribution surveys of Big Cypress fox squirrels in Big Cypress National Preserve, 2) to determine activity patterns and diets of fox squirrels on golf courses, and 3) to translocate urban fox squirrels to Big Cypress National Preserve (BICY) to, a) access the feasibility of this technique should it become necessary, and b) obtain some information on habitat use and movement.

STUDY ANIMAL

S. n. avicennia was described from a single specimen by Howell (1919), and the taxon was re-evaluated by Moore (1956) based on 56 specimens. The subspecific name and often used common name of "mangrove fox squirrel" incorrectly imply restriction to the mangrove habitat. To reflect its approximate distribution, the common name "Big Cypress fox squirrel" is preferable (Humphrey and Jodice, in press).

The Big Cypress fox squirrel is distinctly smaller than Sherman's fox squirrel, its adjacent cogener (Moore 1956). Like other subspecies of fox squirrel in the southeastern United States, the Big Cypress fox squirrel is highly variable in color, ranging from buff to black.

The subspecies occurs in the Immokalee Rise, Big Cypress Swamp, and Devil's Garden areas of Lee, Hendry, Collier, Monroe, and extreme western Dade counties in southwestern Florida. The distribution is south of the Caloosahatchee River and west of the Everglades, and it is disjunct from the range of other subspecies of fox squirrels.

Little is known about the ecology of fox squirrels in BICY. Open understory (i.e., frequently burned) pinelands, cypress domes and strands with large trees, and hardwood hammocks are thought to be important habitats. Habitat loss, hunting, improper burning regime, and logging (Duever et al. 1986) may have depressed fox squirrel populations. Habitat loss is by far the most critical factor outside of the BICY.

STUDY AREAS

Golf Course Population

The golf course study area was approximately 55 km west of BICY, along the Gulf of Mexico, in Naples, Florida. Observations of fox squirrels were conducted on four golf courses: 1) Royal Poinciana, 2) Hole-in-the-Wall, 3) Country Club of Naples, and 4) Wyndemere. Houses were present on courses number three and four. Courses one, two, and three were adjacent and totaled about 330 ha. Course four was about 200 ha and was separated from the other three by 2000 m of undeveloped pinelands and agricultural fields. An 800-ha area within these pinelands was scheduled for development as a golf course community.

Vegetation on golf courses was a mix of remnant native species and planted natives and exotics. South Florida slash pine (Pinus elliotti var. densa), cabbage palm (Sabal palmetto), and cypress (Taxodium distichum) were the dominant native species. Queen palm (Cocos pamosa), Ficus spp., melaleuca (Melaleuca quinquenervia), silk oak (Grevillea robusta), and bottlebrush (Callistemon spp.) were common planted species. Vegetation usually occurred in thin (< 30 m), sparsely stocked strips ("roughs") separating fairways. The understory was usually very open.

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Courses 1 and 2 were separated by a 20 by 1000 m long remnant of a mixed-swamp strand. Course 2 had a 10 ha undeveloped, mixed-swamp strand with dense understory. Each golf course had ponds and was watered daily. Various fertilizers, pesticides, and fungicides were routinely applied. Golf courses experienced the most human activity from December through April.

Big Cypress National Preserve

Big Cypress National Preserve was created by law in 1974 (PL93-440). The Preserve is located in southwestern Florida and covers 230,000 ha of Collier, Monroe, and extreme western Dade counties. The acquisition of an additional 59,000 ha adjacent to the northeast corner of BICY is being negotiated.

Big Cypress is part of the large watershed that feeds the Everglades. The area has a tropical savanna climate (Hela 1952) with a spring drought, heavy summer rains, and mild, dry winters. Average annual rainfall is 1,360 mm. Mean annual temperature is 23° C, with a mean low of 14° C in January and a mean high of 28° C in August (Duever et. al. 1979). Natural fires are most frequent in the late dry season (March - May) and early wet season (June - August), the time of highest lightning strikes, when there is little or no accumulated groundwater. Arson fires occur throughout the year.

Duever et. al. (1979) give an extensive description of vegetation types in BICY, and the following information is condensed from that report. The dominant vegetation types were pinelands, cypress and mixed-swamp strands and domes, marshes, hardwood hammocks, and prairies. Areal extent of each habitat type is given in parentheses.

Pine forests (18%) often occur as islands. South Florida slash pine dominates the overstory, often occurring with cabbage palm in the mid-story. Canopy cover is often less than 20%. Understory is dominated by saw palmetto (Serenoa repens), and its density is typically determined by fire frequency. Grasses in the genera Muhlenbergia, Andropogon, and Paspalum, and herbs of the genera Sabatia, Polygala, and Asimina are also common in the understory. Pinelands occur on elevated sites (often less than 1 m above cypress elevation) that are inundated for at most 2 months/year.

Cypress (43%) occur at lower elevations and are characterized by small trees occurring in relatively open stands (dwarf cypress prairies). Larger cypress occur at higher densities in areas of poorer drainage to form domes and strands. Hydroperiod averages about 250 days/year. Saw grass (Cladium jamaicensis) is common in the understory.

Red maple (Acer rubrum), pop ash (Fraxinus caroliniana), willow (Salix caroliniana), and swamp bay

(Persea palustris) occur with cypress to form mixed swamp forests (6.5%). Hydroperiod averages 290 days/year. Many species of bromelliads occur in the cypress and mixed-swamps.

Wetter habitats also include prairies (24%), marshes (4.2%), and ponds, in associations of mixed grasses, sedges, and other herbaceous plants. These occur on a continuum of sites ranging from hydroperiods of less than 50 days for dry prairies, 250 days for marshes, and nearly year round inundation for ponds.

Hardwood hammocks (1.5%) occur on the driest sites, are frequently dry all year, and have a closed canopy (75 - 90%). Common tree species are red maple, laurel oak (Quercus laurifolia), strangler fig (Ficus aurea), wild tamarind (Lysiloma latisiliqua), gumbo limbo (Bursera simaruba), poison wood (Metopium toxiferum), red bay (Persea burbonia), and coco plum (Chrysobalanus icaco) (Belden et. al. 1988).

The Big Cypress receives year-round human use. The Preserve is divided into 6 management units and managed as a multiple-use area. Intensive uses include hunting (320 days of the year, 130 of which are raccoon-only), fishing, off-road vehicle (ORV) use, and oil and gas production. Native Americans participate in traditional activities within the Preserve as well. Additionally, over 200 inholdings in the form of back-country camps are scattered throughout the Preserve. The Corn Dance Unit contains the Dade-Collier Transition and training airport, with 81 ha of runways. Major roads (and associated canals) crossing or bordering BICY include I-75 (4 lanes), U.S. 41 (2 lanes), and S.R. 29 (2 lanes).

Surveys for fox squirrels occurred throughout the Preserve. Relocation occurred in the south-central Turner River Unit. This area is characterized by cypress strands with second-growth pinelands, mixed swamp strands, and prairies. Hunting, ORV use, and arson fires are high in this area. There are 55 back-country inholdings as well as front-country homes in this area.

METHODS

Golf Course Population

Questionnaires were mailed to 27 golf courses in the Naples area to determine presence of fox squirrels. Ten golf courses responded and four golf courses were chosen for fox squirrel observations.

Activity Patterns

Observations of fox squirrels on golf courses were conducted from May 1989 through May 1990. Individual fox squirrels were not identified due to similarity of color patterns and inability to consistently sex or age animals. Binoculars and a spotting scope were used to observe fox squirrels from golf carts. Observations were conducted between sunrise and sunset with time recorded as hours since sunrise. Daylight was divided into three periods; T1 - first 4 hours after sunrise, T2 - second 4 hours after sunrise, and T3 - remaining hours until sunset. At the start of each hour I recorded temperature, cloud cover, wind, and precipitation.

Temperature was recorded using an inexpensive outdoor thermometer. Cloud cover was estimated and categorized as follows: 0) no cloud cover; 1) 1-25% cloud cover; 2) 26-50% cloud cover; 3) 51-75% cloud cover; 4) 76 - 100% cloud cover. Wind was categorized as 1-light, 2-medium, or 3-strong. Precipitation was recorded as minutes of rain/hour. Based on local temperature and precipitation patterns I grouped months into the following four seasons: early wet season (EW, June -August), late wet season (LW, September - November), early dry season (ED, December - February), and late dry season (LD, March - May).

Activity was recorded using focal-animal sampling (Altmann 1974). Upon arrival at a golf course I surveyed the area by golf cart until a fox squirrel was seen. Behavioral observations then began at the start of the next minute, and behavior was recorded each minute. Behavioral activities recorded were as follows:

Inactive (IA): squirrels sitting or lying still, grooming.
Foraging (FO): squirrels feeding, searching for food, caching food.
Travelling (TR): squirrels moving from one place to another.
Other Active (OA): squirrels vocalizing, alert, or disturbed; interspecific interactions.
Social Interactions (SI): any intraspecific interaction.

"Activity" was defined as the sum of FO, TR, OA, and SI.

Fox squirrels were observed as long as possible. If more than one squirrel was visible, data were collected on all squirrels. Where possible, sex of squirrels was noted. A map of use areas was sketched.

Data from all four golf courses were combined, as were daily behavioral data from all observed fox squirrels (daily pooled data). For each time period, fox squirrel behaviors were calculated as percentage of total recorded activity. Daily pooled data were used to calculate seasonal means for each behavioral category during each time period. Means were transformed to arcsine square roots for statistical analyses; actual means are reported for ease of comparison.

Activity data were analyzed using an ANOVA test for unbalanced design with weighted variables (Proc GLM, SAS Institute 1985) for the following sources of variation: 1) within behavioral categories among seasons and time blocks and 2) within seasons and time blocks among behavioral categories. A least square means with paired difference test (PDIFF) was used to identify means that were significantly different.

Climate data collected hourly during observation periods were tested for correlation with hourly inactivity for each season. A stepwise procedure multiple linear regression was performed with transformed percent inactive data to determine significance of the three climate variables.

Feeding Observations and Diet

Diet was determined by observation of foraging animals at distances of less than 50 m. At each 1-minute interval during an observation I recorded the food item, position of the squirrel (arboreal or terrestrial), number of squirrels foraging nearby, and their estimated distances from each other. These data were pooled on a daily basis. An intensive measure of food use (I) was calculated for each food item as daily mean percentage of total time spent feeding in a given season. Intensive feeding data were analyzed for variation 1) within food items among seasons and 2) within seasons among food items, using the same design described for activity data. An extensive measure of food use (E) was calculated for each food item as the percentage of foraging squirrels observed feeding on each item for each season.

Food items that were not significantly different based on PDIFF results were grouped together and ranked by mean daily percent use. Primary food items had the highest mean daily percent use, secondary items the next highest, and so forth.

Diet similarity among seasons and throughout the year was calculated using Schoener's similarity index (SSI) (Schoener 1970, Linton et. al. 1981, Spowart and Hobbs 1985) and the von Mises distribution (Stephens 1964, 1982, Mulholland 1983). The von Mises distribution was used to test the null hypothesis that diets among all four seasons and diets between each pairwise seasonal comparison were not significantly different.

Translocated Fox Squirrels

Translocation and Telemetry

Five fox squirrels were translocated from Naples to BICY, a distance of about 55 km. Squirrels were captured from September 1989 through February 1990. Fox squirrels were captured from golf courses and residential areas. Squirrels in these areas often approached humans if food was offered, so trapping success was high. Squirrels were baited using bird seed, peanuts, and bananas, and captured in either a live trap or cloth sack. Squirrels were not anesthetized. Animals were transported to a laboratory at BICY where they were radio collared. The following information was recorded: weight, sex, standard mammal measurements, and age (juvenile or adult) (Appendix 6.) Photographs were taken.

Radio collars were built by Dr. Kenneth Meyer (University of Florida, Gainesville). Collars were single-stage units with external whip antennas and weighed less than 20 g, or about 2.2% of average body weight of the 5 captured squirrels. Collars were fastened with super glue. After collaring, squirrels were taken to a site in BICY and released. All squirrels were released within 2 hours of capture.

I attempted to visually locate instrumented animals daily. If squirrels were not observed, locations were classified as either habitat positive (individual not observed, but signal pinpointed to a particular habitat), triangulated, or approximated during fixed-wing flight. Squirrel locations were recorded in UTMs and plotted on 1:24,000 orthophoto maps.

At each squirrel location, habitat type was classified and understory density was visually estimated and recorded as open, medium, or dense. Fox squirrel position in the vegetation strata was recorded as either ground, mid-canopy, or canopy. Behavior was recorded using the same categories described under activity pattern methods. Time of day, weather, surrounding habitat type, and ground water level were also recorded.

Translocated fox squirrels were classified as residents if they occupied a fixed home range for >1 month, temporary residents if present in a range $\geq$ 1 week but $\leq$ 1 month, or transients if they were present in an area < 1 week (Slough 1989). Home ranges were calculated for resident animals using the HOME RANGE program (Ackerman et al. 1990). Two measures were calculated: 1) the minimum area or minimum convex polygon (MCP) (Mohr 1947), and 2) the harmonic mean (HM) and corresponding core area (Dixon and Chapman 1980). The first measure is presented to allow comparisons with other studies. Discussion will focus on the HM core area.

Nest Data

The following data were recorded at fox squirrel nest sites in BICY and on golf courses: habitat, nest type (stick, drey, cavity, airplant), nest-tree species, nest height, nest orientation (if applicable), nest location on tree (trunk, limb), tree height, diameter at breast height of nest tree, crown dominance of nest tree, nest-tree distance to nearest edge, nest-tree distance to nearest tree, understory density (open, medium, dense), understory-species composition, and presence/absence of cavities in nest tree. I also noted if the nest tree or surrounding trees had bark stripped from them.

Fox Squirrel Surveys in BICY

Field surveys were conducted for fox squirrels in BICY. Surveys were conducted by walking or driving all-terrain vehicles. Squirrel locations were recorded using the same categories described under the telemetry section. Reported observations of fox squirrels by non-project individuals were recorded using the same categories.

Questionnaires aimed at obtaining information on distribution, habitat use, and historic population trends of fox squirrels were sent in return addressed, stamped envelopes to 130 individuals who owned camps in BICY. Questionnaires were provided at hunter-check stations. Hunter-exit interviews were conducted periodically.

RESULTS

Golf Course Population

Seasonal Activity Patterns

Fox squirrels were observed for 334.2 hours between May 1989 and May 1990 (Appendix 1). Behavior varied widely among individuals and seasons. Fox squirrels spent more time active than inactive in each season. Daily mean time active ranged from a low of 62.4% during the late dry season to a high of 84.5% during the late wet season (Table 1).

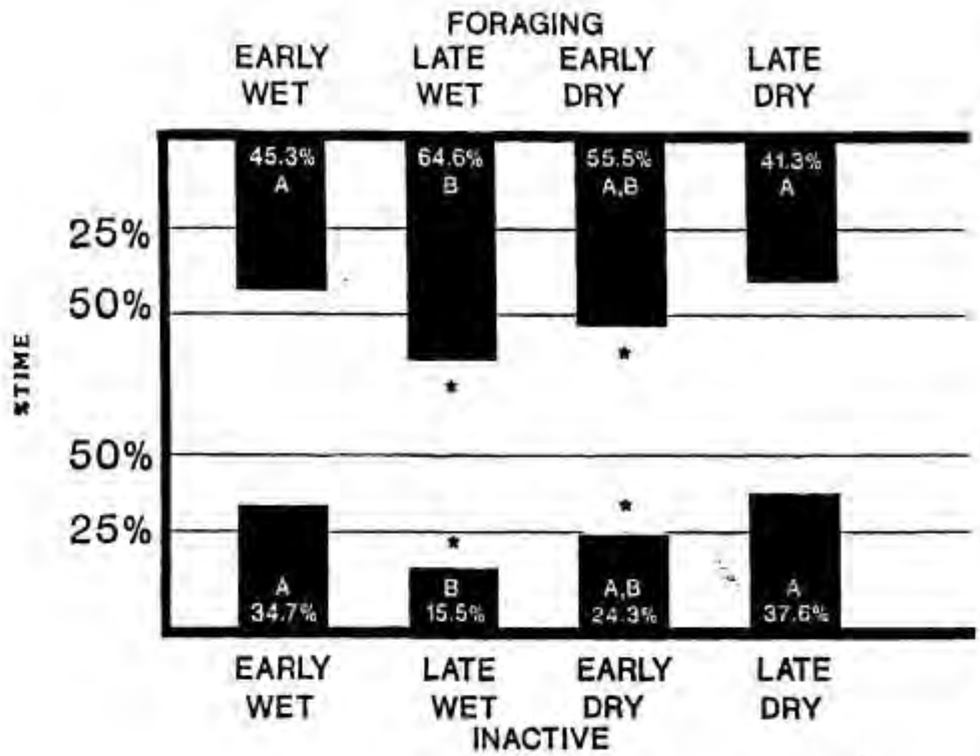
There were significant differences in daily means among seasons for the following behavior categories; foraging, inactive, and other active (Appendix 2). Mean daily foraging and inactivity had the largest single-season change in frequency (19.3% and 19.2% respectively) between the early and late wet seasons (Fig. 1). The daily mean maximum for foraging (64.6%) and minimum for inactivity (15.5%) occurred in the late wet season. Other active daily mean ranged from 4.3% (early wet) to 9.0% (early dry). Travelling showed the least variation among seasons, ranging from 8.8% to 10.4%. Social interaction was always low, but did vary among seasons relative to other behaviors (Table 1).

Table 1. Daily mean percent of behaviors by time of day and season.

Seasons/ Time of day	Behaviors*				
	FO	IA	TR	OA	SI
Early wet	45.3	34.7	10.2	4.3	5.5
T1	51.5	17.8	15.0	6.7	9.6
T2	41.0	42.1	8.4	3.6	4.5
T3	42.0	51.4	4.8	1.4	0.5
Late wet	64.6	15.5	8.8	8.7	2.3
T1	67.1	22.4	11.2	10.1	2.2
T2	60.1	12.8	7.1	8.5	2.0
T3	69.3	9.0	7.9	6.4	3.5
Early dry	55.5	24.3	10.4	9.0	0.8
T1	54.5	16.6	14.0	13.6	1.3
T2	54.7	31.5	7.4	5.7	0.6
T3	58.4	25.1	9.4	6.8	0.2
Late dry	41.3	37.6	9.1	6.3	5.5
T1	44.0	36.8	6.2	6.3	6.6
T2	45.9	36.7	7.2	4.3	5.8
T3	26.7	41.2	18.9	10.4	2.8

* Active = foraging + travelling + other active + social interaction

Fig. 1. Foraging and inactivity budget (mean percent/day) of Big Cypress fox squirrels on four golf courses in Naples, Florida, 1989-1990. Seasonal effects are illustrated (means within a behavior sharing common letter are not significantly different, $P > 0.05$; vertically opposing bars with * are significantly different, $P < 0.05$).


FORAGING
EARLY WET
LATE WET
EARLY DRY
LATE DRY
45.3% A
64.6% B
55.5% A,B
41.3% A
25%
50%
%TIME
50%
25%
A 34.7%
B 15.5%
A,B 24.3%
A 37.6%
EARLY WET
LATE WET
EARLY DRY
LATE DRY
INACTIVE

20

There was a significant difference among behaviors within each season (Fig. 2, Appendix 3). Mean percent time foraging was significantly different from mean percent time inactive during the late wet and early dry seasons (Fig. 1). Mean percent time foraging was always significantly different from the remaining active behavior categories. Inactivity was significantly different from travelling, other active, and social interaction except during the late wet season. Travelling was never significantly different from other active. Social interaction was not significantly different from other active and travelling during the early wet and late dry seasons.

Diel Activity Patterns

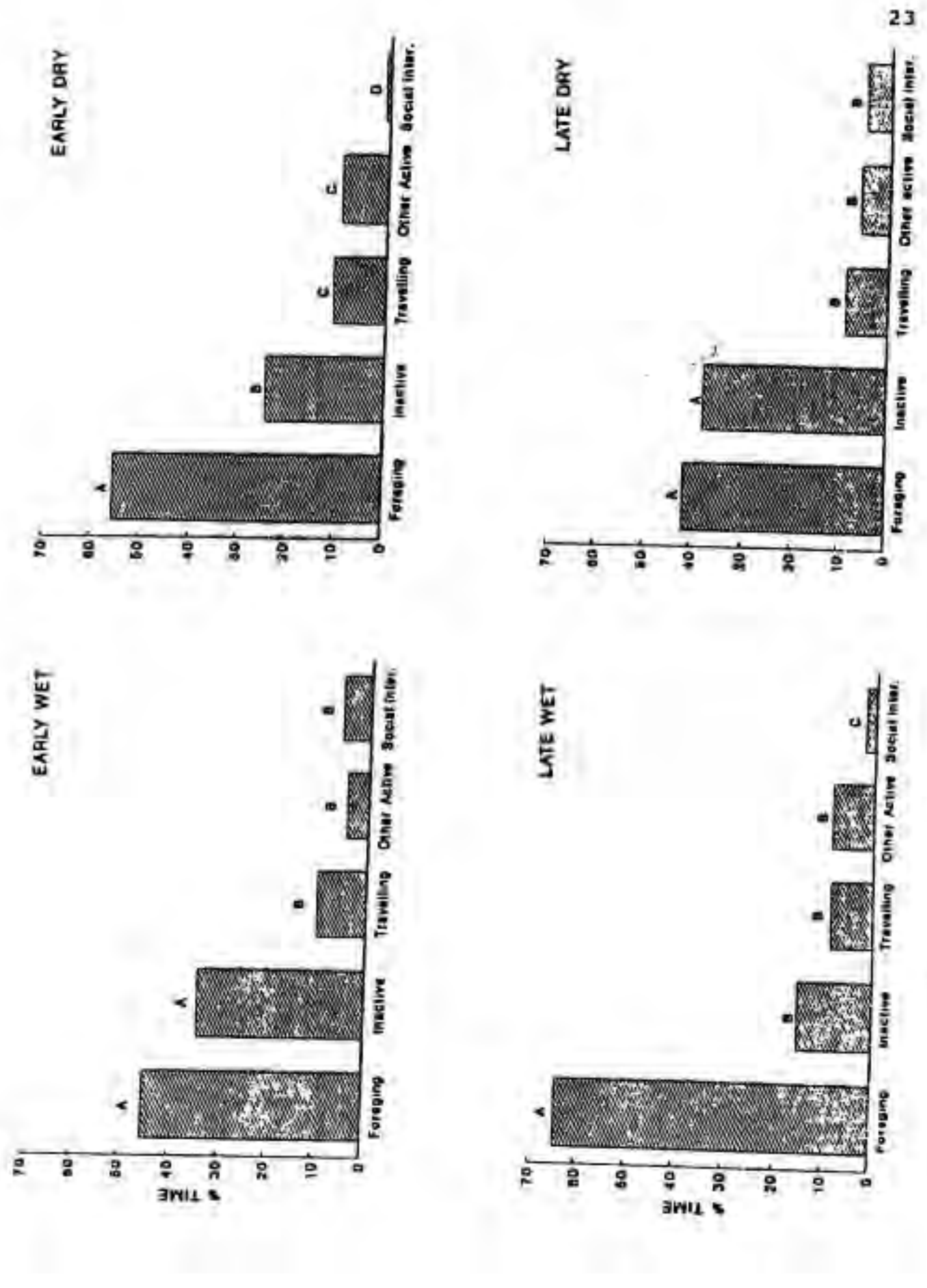
Fox squirrel behavior varied significantly ($P < 0.05$) among times of day only during the early wet season (Fig. 3). Pairwise contrasts showed that time period 1 was significantly different from time periods 2 and 3 for both inactive and travelling.

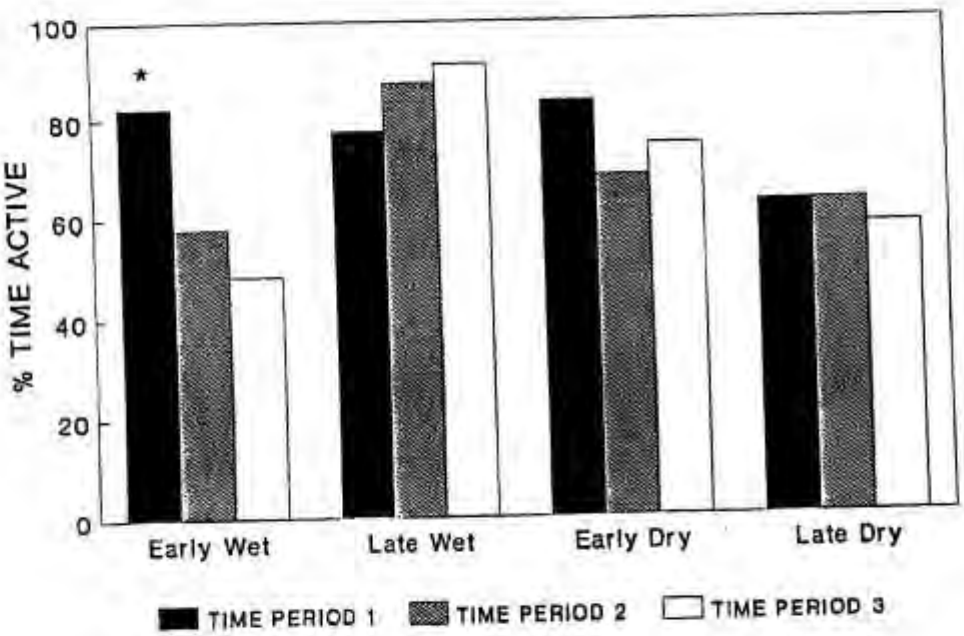
Influence of Weather

Climate data collected hourly from golf courses are shown in Table 2. The proportion of within season variation in fox squirrel activity accounted for by weather variation was low each season, with model R^2 ranging from 0.08 (late dry) to 0.19 (early wet) (Table 3). Slope was significantly different from zero ($P < 0.05$ for seasonal models) during all but the late dry season.

Fig. 2. Time budgets (mean percent/day) of Big Cypress fox squirrels on four golf courses in Naples, Florida, 1989-1990. Seasonal effects are illustrated (means within each seasonal graph sharing common letter are not significantly different, $P > 0.05$).

Fig. 3. Activity budget (mean percent/day) for Big Cypress fox squirrels on four golf courses in Naples, Florida, 1989-1990. Time of day effects for each season are illustrated; time of day was only significant for the early dry season. (* indicates time period 1 is different from time period 2 and time period 3, $P > 0.05$).F4


23
EARLY WET
EARLY DRY
LATE WET
LATE DRY
% TIME
70
60
50
40
30
20
10
0
Foraging
Inactive
Travelling
Other Active
Social Inter.
A
B
C
D


100
80
60
40
20
0
% TIME ACTIVE
*
Early Wet
Late Wet
Early Dry
Late Dry
TIME PERIOD 1
TIME PERIOD 2
TIME PERIOD 3

25

Table 2. Summary of climate data collected hourly during behavioral observation of fox squirrels on four golf courses in Naples, Florida, 1989-1990.

	Early wet	Late wet	Early dry	Late dry	Annual
Temperature					
Mean	31.2	29.3	25.1	28.3	28.7
Maximum	36	34	31	35	36
Minimum	23	20	15	21	15
Cloud Cover					
Mean	1.2	1.4	2.2	0.8	1.4
Maximum	4	4	4	4	4
Minimum	0	0	0	0	0
Wind					
Mean	1.0	0.9	1.7	1.3	1.1
Maximum	4	2	3	2	4
Minimum	0	0	0	0	0

* Cloud cover units of measure are: 1 = 0-24%, 2 = 25-49%, 3 = 50-74%, and 4 = 75-100%.
Wind units of measure are: 1 = light, 2 = medium, and 3 = strong.

Table 3. Regression coefficients and P-values for weather variables influencing mean percent of time inactive per day, in each season, for fox squirrels on four golf courses in Naples, Florida, 1989-1990. Significance level for variable entry into stepwise model < 0.15. Variables listed in order of entry.

Season	$\bar{x}$ % inactive	Model R^2	Variable	Partial R^2	Partial P - value
Early wet	34.7	0.171			
			Temperature	0.171	0.0001
			Cloud cover	NE[*]	
			Wind	NE	
Late wet	15.5	0.096			
			Temperature	0.048	0.07
			Wind	0.047	0.07
			Cloud cover	NE	
Early dry	24.3	0.174			
			Cloud cover	0.144	0.001
			Temperature	0.031	0.11
			Wind	NE	
Late dry	37.7	0.078			
			Temperature	0.078	0.07
			Cloud cover	NE	
			Wind	NE	

[*] NE = Variable not entered

Multiple linear regression with the stepwise method entered temperature as a variable each season and as the first variable during all but the early dry season, when cloud cover was entered first. The early dry season had the highest mean cloud cover and lowest mean temperature (Table 2). Wind was entered as a variable only during the late wet season. The greatest partial $\underline{R}^2$ (0.17), model $\underline{R}^2$ (0.19), and most significant variable and model $\underline{P}$ values occurred during the early wet season with temperature as the only variable in the model; it was only during the early wet season that time of day had a significant effect on behavior.

Diet Composition

Foraging totaled 173.6 hours for the year. Number of food items observed eaten each season were: early wet = 13, late wet = 11, early dry = 16, late dry = 8, annual total = 22. Fox squirrels consumed plant material from 10 families and 13 genera (Table 4). Plant food types included seeds, nuts, soft fruits, and possibly pollen and nectar. Animal matter was observed being eaten only once. Consumption of fungi was observed, but a true measure of its importance was difficult to obtain solely from visual observations. Ground foraging on unknown items occurred throughout the year. The seven most frequently consumed food items were identified and all feeding analyses were carried out on these: cabbage palm fruits, seeds from cypress cones,

Table 4. Foods of fox squirrels from four golf courses in Naples, Florida, 1989-1990.

Aquifoliaceae
holly (*Ilex* spp.)
Soft fruit

Araucariaceae
Norfolk Island pine (*Araucaria excelsa*)
Seeds from female cones

Arecaceae
queen palm (*Cocos pamosa*) = (*Arecastrum romanzoffianum*)
Soft edible pulp surrounding nutshell
cabbage palm (*Sabal palmetto*)
Soft fruit

Fabaceae
royal poinciana (*Delonix regia*)
Seeds in pods
earleaf acacia (*Acacia auriculaeformis*)
Seeds in pods

Fagaceae
live oak (*Quercus virginiana*)
Acorns, leaves

Moraceae
strangler and benjamin fig (*Ficus* spp.)
Soft fruit

Myrtaceae
(*Melaleuca quinquenervia*)
Nut like fruit or seed??
bottlebrush (*Callistemon* spp.)
Nectar or pollen from flowers

Pinaceae
South Florida slash pine (*Pinus elliottii* var. *densa*)
Seeds from female cones; male cones

Proteaceae
silk oak (*Grevillea robusta*)
Nectar or pollen from flowers

Taxodiaceae
cypress (*Taxodium distichum*)
Seeds from female cones

Fungi

Animal material
Cuban tree frog (*Hyala septentrionalis*)

Bird seed from bird feeders

fruits of Ficus spp., flowers of silk oak and bottlebrush, seeds from slash pine cones, queen palm fruits,and ground foraging on unknown food items. Other foods are used for intensivity data to total foraging to 100%.

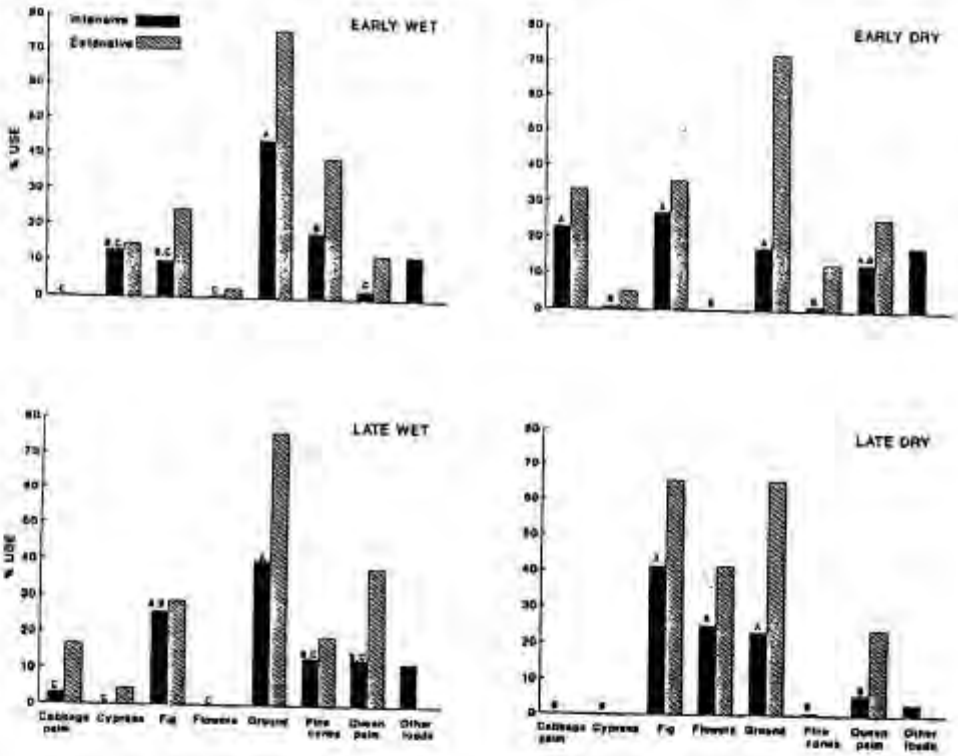
A generalized fruiting phenology of the golf courses was as follows: early wet - pine cones ripening, queen palm ripening; late wet - pine cones still available, queen palms peaking, cypress cones ripening, and during the end of the late wet season cabbage palms ripening; early dry - cabbage palms peaking, some queen palms still available; late dry - bottle brush and silk oak in flower during the end of the late dry. Ficus, which fruits asynchronously, was available throughout the year.

Fox squirrels foraged singly and in groups. Two or more fox squirrels were observed foraging within 25 m of each other during 33.6% of foraging observation time. Two or more fox squirrels were often observed foraging at figs, queen palm, bottlebrush, and silk oak, but less frequently in pine trees.

Seasonal Feeding Patterns

Figure 4 shows intensive and extensive seasonal use of the 7 major food groups. Either ground foraging or figs accounted for greatest use intensively and extensively each season. The only identifiable items eaten each season were queen palm and fig. Fox squirrels also foraged along the ground on unknown items each season. Fox squirrels were

Fig. 4. Intensive and extensive use of food items (mean percent/day) by Big Cypress fox squirrels on four golf courses in Naples, Florida, 1989-1990. Seasonal effects are illustrated (means within each seasonal graph sharing a common letter are not significantly different, $P > 0.05$; other foods not included in analyses).



Intensive
Extensive
EARLY WET
EARLY DRY
LATE WET
LATE DRY
% USE
Cabbage palm
Cypress
Fig
Flowers
Ground
Pine cones
Queen palm
Other foods

observed caching queen palm more frequently than any other food item, and this may account for its year-round use.

Only two food items, cabbage palm and flowers, were significantly different ($\underline{P} < 0.05$) in daily mean percent use among seasons (Appendix 4). Use of each was confined predominantly to one season. Other food items showing intensive use ranges of 30% (fig) and 20% (pine cones) over 3 or 4 seasons showed no significant differences among seasons. This is unexpected especially for pine cones, which show a limited seasonal availability. There was a significant difference among food items within each season (Fig 4., Appendix 5).

The primary food item for the early wet season was ground foraging (intensivity (I) = 43.9%, extensivity (E) = 75.6%), which was significantly different from all other food items (Fig. 4). Secondary food items were pine seeds cones (I = 18.1%, E = 39.0%), fig (I = 10.0%, E = 24.4%), and cypress (I = 12.8%, E = 14.6%). Extensive use of pine seeds was at a maximum and figs at a minimum this season.

The primary food items for the late wet season were ground (I = 43.9%, E = 76.2%) and fig (I = 25.8%, E = 28.6%). Secondary food items were queen palm (I = 13.0%, E = 38.1%) and pine seeds (I = 13.1%, E = 19.1%). Extensive use of queen palm was at its annual maximum this season. Extensive use of pine seeds was 50% less in the late wet season than the early wet season.

The greatest number of food items were observed being eaten during the early dry season (N = 16). Intensive use of cabbage palm was significantly different between the early dry and all other seasons. Intnesive use of cabbage palm increased from 3.4% during the late wet season to 22.7% during the early dry season. Extensive use doubled during this same period. The primary food items were; fig (I = 27.0%, E = 35.9%), cabbage palm (I = 23.0%, E = 33.3%), ground (I = 17.35, E = 71.8%), and queen palm (I = 13.0%, E = 25.6%). Although squirrels were investing little time foraging on seeds from pine cones, extensive use was still apparent (12.8%) as individuals were still examining cones for ripe seeds. An addition to the diet during the early dry season was microstrobolii from slash pine, with an extensivity measure of 15%. Royal poinciana seeds were also consumed during this season by 2 fox squirrels.

Fox squirrels consumed the fewest number of food items during the late dry season (N = 8). Intensive use of flowers was significantly higher in the late dry season (25%) compared to all other seasons (0.6% total). Squirrels were observed licking flowers and may have been obtaining nectar or pollen. Squirrels would visit a tree for up to 2 hours and it was not unusual for more than one squirrel to be feeding in the same tree.

Primary foods during the late dry season were fig (I = 41.0%, E = 65.5%), flowers (I = 25.0%, E = 41.4%), and ground (I = 23.0%, E = 65.5%). Extensive use of fig was greatest this season. The only queen palm eaten were those that had been cached earlier in the year. Squirrels did not forage on seeds from pine cones this season.

Similarity of Seasonal Diets

Two measures of dietary similarity among seasons were calculated. Schoener's similarity index (SSI) provides an estimate of percent overlap (diet similarity) for pairwise comparisons between seasons. The von Mises (VM) distribution tests for significant differences in diets among all seasons and for seasonal pairwise comparisons. Both were conducted using intensivity data. Diets differed significantly among all four seasons ($P < 0.001$; Table 5). Percent overlap (SSI) ranged from 74.05% (early wet*late wet) to 44.85% (late dry*early wet). Only two pairwise comparisons, early wet*late wet (SSI = 74.05%) and late wet*early dry (SSI = 72.3%), were not significantly different ($P > 0.05$) (VM). Each were consecutive season comparisons.

Table 5. Similarity index and differences between seasonal diets based on intensivity feeding data of seven major food items by fox squirrels on four golf courses in Naples, Florida, 1989-1990.

Seasonal comparison	Schoener's similarity index (%)	P-value from von Mises test
EW*LW*ED*LD		***
EW*LW	74.05	NS
LW*ED	72.30	NS
ED*LD	61.80	*
LD*LW	60.10	*
ED*EW	47.05	***
LD*EW	44.85	***

* $P < 0.05$
** $P < 0.01$
*** $P < 0.001$

Translocated Fox Squirrels

Capture, Release, and Survival

Five fox squirrels (four males (M) and one female (F); Appendix 6) were captured in Naples, Florida, fitted with radio collars and then released in BICY. Fox squirrel M3 died from predation 1 week after release.

Squirrel F1 was not included in movement data because she slipped her radio collar within two days of release. Squirrel M2 was transferred 4.5 km WNW from the original release site after 108 days because he continually frequented a house that provided food. M2a refers to data before the transfer, and M2b to data after the transfer.

Movements

The mean maximum distance fox squirrels travelled from release sites was 11,620 m (SD=11,786; Table 6). The longest movement from a release site was 32,000 m by M4 (travelling in the direction of the original capture location). The longest movements in the shortest time were 3,227 m between sunset and 0800 hrs the following day (M2b) and 2,236 m in <7 hours (M2a). The mean final distance fox squirrels were observed from release sites was 9,390 m (SD = 13,357).

Fox squirrels travelled on the ground and through the trees. When any standing water was present at a site, 98% of locations were above ground. When no standing water was present at a site, 63% of locations were above ground.

Table 6. Movements of Big Cypress fox squirrels translocated from Naples to Big Cypress National Preserve, Florida, September 1989 - April 1990.

Squirrel number	Date released	Days of contact	No. of relo-cations	Maximum dist. from release site (m)	Final dist. from release site (m)
M1	12 SEP 90	50	40	4,700	200
M2a	10 OCT 90	108	75	7,400	750
M2b	01 FEB 90	76	70	11,000	11,000
F1	13 JAN 90	2	3	—	25
M3	14 JAN 90	7	6	3,000	3,000
M4	19 FEB 90	55	12	32,000	32,000

M = males, F = females

Squirrel M2a made its longest movement within 1 week of the subsidence of standing water. Squirrel M1 travelled extensively through the trees while water levels were high during the late wet season, making use of dense cypress strands and woodlands.

A total of 203 radio locations was obtained between 12 September 1989 and 17 April 1990. Fox squirrel movement patterns varied among individuals. Squirrel M2a was a resident in the release area (Fig. 5). Squirrel M2b was a resident <2000 m north of his release area for 48 days before dispersing northeastward (Fig. 6). Squirrel M2b was a temporary resident in the new area and slipped his collar soon after arrival.

Squirrels M3 and M4 dispersed from their release sites. Squirrel M4 was last located 32,000 m NW of the release site. Squirrel M3 was found dead within 1 week of dispersal, apparently from predation. M3 was released where F1 had been released the previous day. F1 was still located at this site when M3 dispersed.

Fox squirrel M1 also dispersed from the release site, but returned within 200 m of the release site after a 50-day transient period (Fig. 7). M1 travelled in an ellipse with a maximum distance from the release site of 4,700 m after 35 days. Mean distance travelled per day was 270 m. M1 returned to within 200 m of the release site in another 14 days. No signal was received after this return.

Fig. 5. Telemetry locations of translocated fox squirrel M2a, October 1989 - January 1990, Big Cypress National Preserve, Florida. Solid line indicates boundary of harmonic mean core area representing 66.1% of utililization volume. + indicates telemetry locations, O indicates outlying locations, * indicates harmonic mean.

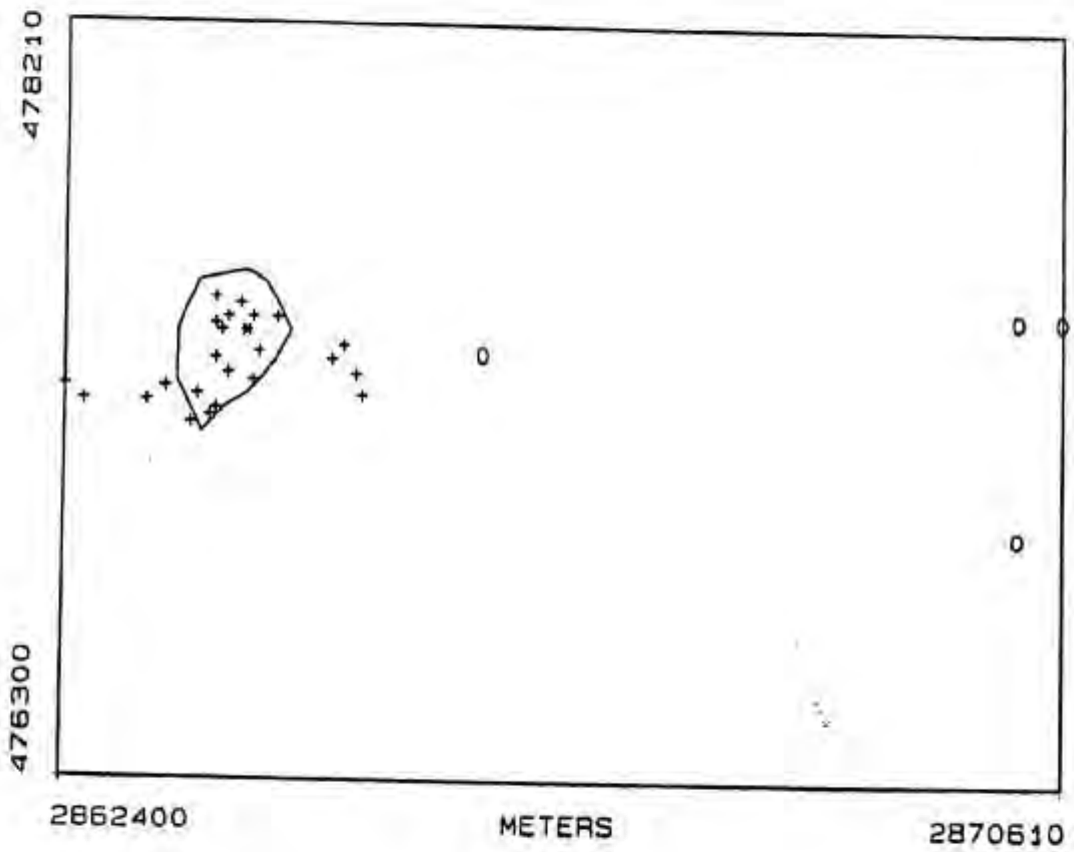

478210
476300
2862400
METERS
2870610

Fig 6. Telemetry locations of translocated fox squirrel M2b, January 1990 - April, 1990, Big Cypress National Preserve, Florida. Solid line indicates boundary of harmonic mean core area representing 62.1% of utilization volume. + indicates telemetry locations, O indicates outlying locations, * indicates harmonic mean.

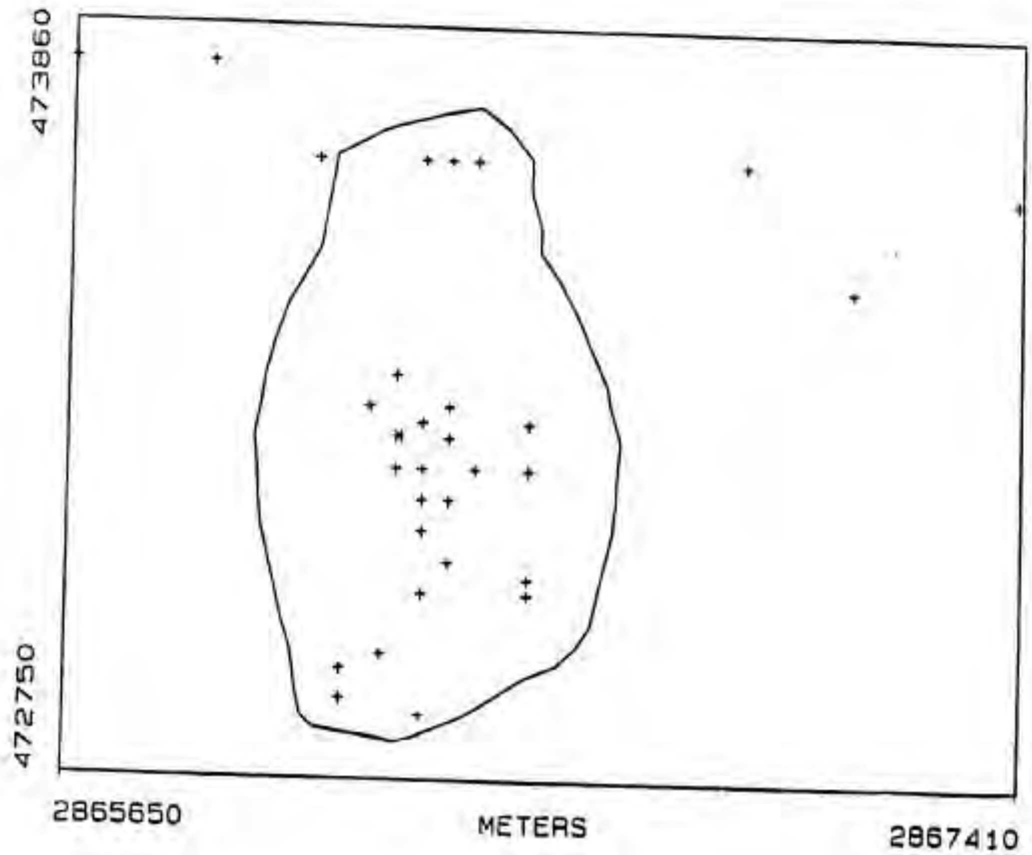


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Fig. 7. Movement pattern of translocated fox squirrel M1, September 1989 - October 1989, Big Cypress National Preserve, Florida.

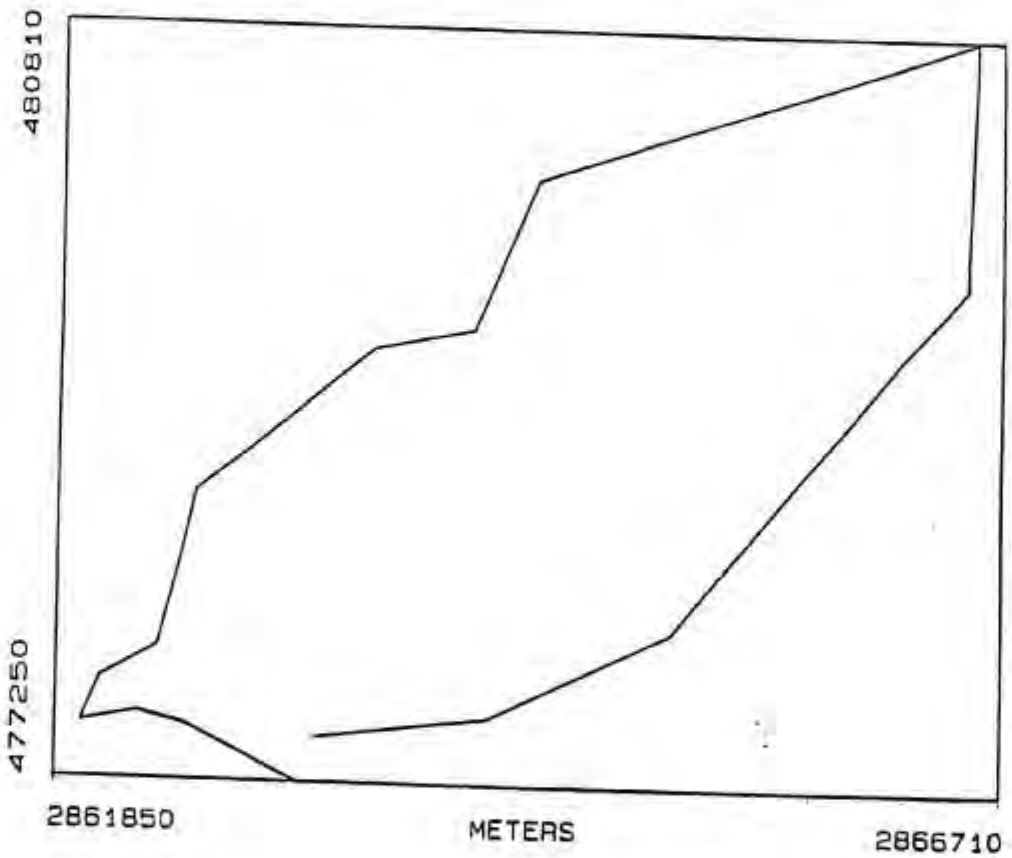

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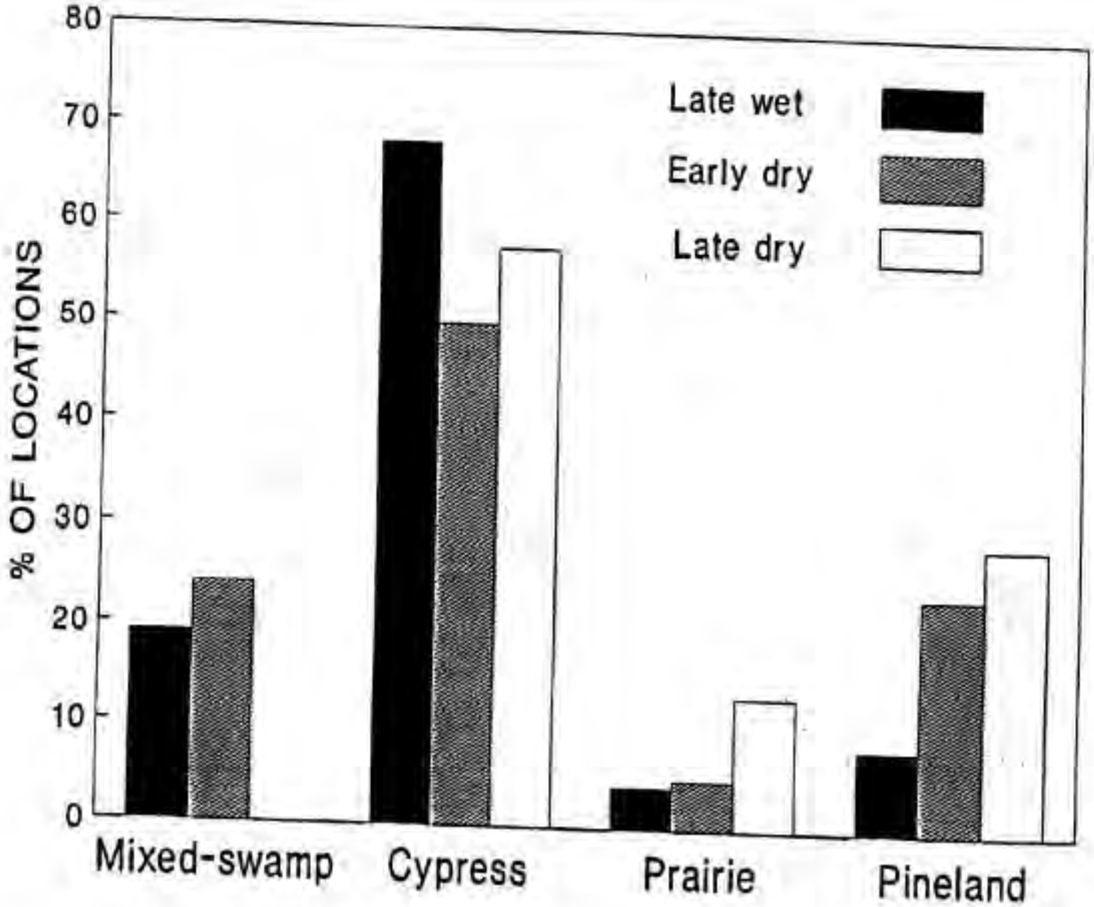
Fig. 8. Seasonal variation in use of habitat types by translocated Big Cypress fox squirrels in Big Cypress National Preserve, Florida, September 1989-April 1990.



80
70
60
50
40
30
20
10
0
% OF LOCATIONS
Late wet
Early dry
Late dry
Mixed-swamp
Cypress
Prairie
Pineland

51

Home Range

Squirrel M2a stayed within 1,600 m (linear distance) of the release site for 108 days, except for a short-duration (9 days) excursion 7,400 m north (Fig. 5). During the last month of this time M2a was residing near a house where food was available. Home range area was estimated for squirrel M2a while resident there. The harmonic mean (Dixon and Chapman 1980) estimate for a core area representing 66% of utilization volume was 67.0 ha for this 108-day period (Table 7).

Squirrel M2 exhibited movements characteristic of a residential home range after being transferred on 1 February. Within 9 days of release, M2b established a nest and remained in that area, using the nest on a daily basis for 45 days (Fig. 6). Home-range area was estimated for squirrel M2b during this period. The harmonic-mean for a core area representing 62.1% of utilization volume was 52.3 ha (Table 7). Table 8 shows home-range estimates of fox squirrels from other areas in the southeastern U.S. for comparison.

Habitat Use

Habitat overlap for pair-wise seasonal comparisons using Schoener's similarity index was 51.6% for late dry * late wet, 65.6% for early dry * late dry, and 69.2% for early dry * late wet.

Table 7. Harmonic-mean home-range estimates from two locations for a translocated fox squirrel in Big Cypress National Preserve, Florida, 1990.

Squirrel number	Number of relo-cations	95% Utilization distribution (ha)	Core area (ha)	MCP 95% (ha)
M2a	75	223.6	67.0*	128.7
M2b	45	270.6	52.3*	71.9

* Core area as determined from harmonic mean values: M2a 66.1% of utilization volume; M2b 62.1% of utilization volume.

Table 8. Comparison of home range means (ha) for southeastern fox squirrels.

Source/ state	MCP		95 % MCP		JT		95 % HM		HM CORE AREA	
	Male (N)[1]	Female (N)	Male	Female	Male	Female	Male	Female	Male	Female
Jodice (FL)	--	--	100.3 (2)	--	--	--	246.8	--	59.6	--
Weigl et al. (NC)	26.6 (8)	17.2 (12)	--	--	43.7	25.0	--	--	--	--
Hilliard (GA)	26.4 (1)	13.0 (3)	--	--	--	--	--	--	--	--
Edwards (SC)	31.6 (9)	19.3 (4)	25.4	13.3	47.8	25.0	--	--	--	--
Kantola (FL)	40.0 (4)	20.6 (2)	--	--	--	--	42.8 (4)	16.7 (2)	8.5 (2)	2.95 (2)

1 = number of fox squirrels used for estimate

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It was difficult to detect differences in seasonal habitat use for translocated squirrels on an individual basis because of small sample size. However, by combining animals within a season, some basic trends become apparent (Fig. 8). During the late wet season (number of locations = 73) collared fox squirrels used the wetter cypress (68.5%) and mixed-swamp habitats (19.2%) most. Standing water was present here, and squirrels were spending much time in the trees foraging on cypress cones. Airplant buds were consumed infrequently, and it is probable that squirrels obtained some water from the leaves (Duever et al. 1979).

During the early dry season (number of locations = 42) and the late dry season (number of locations = 38) use of pinelands increased (23.8% and 28.9%, respectively). Cypress was still used during the early and late dry seasons (50% and 57.9%, respectively) for nesting areas, resting locations during mid-day, and travelling. Mixed-swamp forests were not used during the late dry season. Squirrels were observed foraging on the ground during the early and late dry seasons.

Nest Data

Fourteen fox squirrel nests were found in BICY. Squirrels typically nested around sunset and emerged from nests within an hour after sunrise. All nests were in cypress trees. Eighty-six percent (12) of fox squirrel nests were airplants, either in the long leaves of the airplant or in the organic matter at the base of the plant. The other two nests were stick nests. No cavity nests were found in BICY.

Most nests were located low in the canopy, where most of the airplants grow. Mean nest height was 9.6 m, mean nest tree height 13.1 m, and mean nest tree diameter at breast height (DBH) 28.3 cm. The mean distance of nest trees to the next nearest tree was 1.4 m. Seventy-nine percent of nest trees had co-dominant crowns, and the remaining nest trees had dominant crowns.

One nest was found in each of the following habitats: mixed-swamp strand, cypress strand, and cypress woodland. Dome-shaped habitats (cypress and mixed swamp) had the remaining 76% of squirrel nests. Fifty-seven percent of nest trees were located at least 16 m from the nearest edge. Three nests were located on the edge of a dome (within 5 m). Understory density below nests was evenly divided between sparse, medium, and dense cover.

Five fox squirrel nests were found on golf courses. Structurally these were more varied than BICY nests. Three nests were found in cabbage palms, 1 leaf nest in a small sapling, and 1 cavity nest in a large cypress.

Mean nest height at golf courses was 5.9 m, mean nest tree height 7.9 m, and mean DBH of nest trees 27.8 cm. Mean nest tree distance to the next nearest tree was 3.7 m.

Squirrels tended to enter nests at sunset. Time schedules of golf courses precluded recording emergence time of fox squirrels from nests.

Fox Squirrel Surveys in BICY

Between January 1989 and May 1990, 27 observations of fox squirrels were recorded, representing approximately 23 animals. Individuals were recorded in pinelands with relatively open understory, pine/prairie that was recently burned, and at the edges of cypress strands. These observations represent countless hours in the field by park rangers, biologists, fire fighters, hunters, and resident oil-workers in Raccoon Point.

Questionnaires were sent to 130 BICY users. Twenty-three (17.7%) were completed and returned. Responses to most questions were too inconsistent to evaluate answers. However, questions concerning habitat use and population trends were answered frequently. Preferred habitat use was answered (N = 22) as: cypress = 45% (N = 10), pine = 18% (N = 4), Hardwood hammocks = 27% (N = 6), and ranchland and prairie 4.5% each (N = 1 each).

Regarding population trends, 54% (N = 7) of respondents answered that populations of fox squirrels had decreased between 1960 and 1980, and 28% (N = 4) answered that fox squirrel populations decreased between 1980 and 1989. The following reasons were given by those who thought squirrel populations had declined: overhunting, change in food supply, change in water level, and increased use of I-75.

DISCUSSION

Golf Course Population

By examining a species' population in a situation unlike its natural habitat, we may be able to ascertain which aspects of the species' ecology are variable under differing ecological conditions (Tamura et. al. 1989). This information can be used to better understand the adaptability of the species in question and thus to manage it more efficiently. Results from observations of fox squirrels on golf courses in southwestern Florida indicate that activity patterns, social structure, breeding cycles, and diets are traits that may shift with varying ecological parameters.

Seasonal activity patterns

Seasonal activity patterns of fox squirrels vary throughout their range, as would be expected for such a vast area. Sharp seasonal peaks in activity as well as periods of apparent disappearance are common traits of the species, especially in the southeastern United States (Weigl et al. 1989, Williams and Humphrey 1979). Seasonal activity patterns of fox squirrels may be guided by seasonal food resources climate, or reproductive activity (Allen 1943, Baker 1944, Brown and Yeager 1945, Hicks 1949, Nelson 1981, Packard 1956, Weigl et al. 1989)

The greatest shift in seasonal activity patterns for fox squirrels on golf courses was observed between the early wet and late wet seasons. The observed differences in foraging and inactivity are not sufficiently explained by seasonal differences in either diet or weather. Differences in diets among seasons did not match shifts in time spent foraging. Unlike fox squirrels in other areas of the southeastern U.S., fox squirrels on golf courses did not show a surge in activity with the onset of the pine cone crop (Weigl et al. 1989). These data indicate that seasonal activity of fox squirrels on golf courses may not be dominated by food availability to the same degree as populations without supplemental food.

A plausible explanation for the behavioral shifts (i.e., foraging) between the early wet and late wet seasons may be related to social interaction during the late dry and early wet seasons. During these two seasons social interaction was not significantly different from other active and travelling behaviors; during the remaining two seasons social interaction was less than these two behaviors. An increase in the number of squirrel chases, indicating an increase in mating activity (Benson 1980), was observed from mid-June through late July. Copulation was observed in early and mid-July, 1989. With a 42-day gestation period, these females would bear young in mid-August through September. Females would be lactating for the remainder of the late wet season. During lactation, energy needs of female fox squirrels increases by >200% (Havera 1979), resulting in an increase in foraging time (Weigl et al. 1989). Collection of further data comparing foraging time of males vs. females during this season would be informative.

Daily Activity Patterns

Daily activity patterns of fox squirrels, like seasonal patterns, vary with geographical location and season. Moore (1957) classified Sherman's fox squirrels as "late risers", becoming active well after sunrise. Weigl et al. (1989) found initiation of activity for North Carolina fox squirrels between 0800 and 0900 hrs (varying with season) and daily activity patterns that were unimodal in winter, bimodal in early summer, and evenly distributed in late summer. Daily activity patterns have been attributed to day length and food resources. Midwestern fox squirrels are reported to become active earlier than southeastern fox squirrels. In Illinois, Brown and Yeager (1945) found fox squirrels most active between 0600 and 0800 hours. In North Dakota, Nelson (1981) found a bimodal pattern with midmorning and afternoon peaks and a mid-day lull. Nelson suggested that temperature was the causal factor.

Little variation was observed in daily activity patterns for fox squirrels on golf courses. Relatively stable daily climate patterns throughout the year may reduce daily variation in activity. Only during the hottest season (early wet) did activity decrease through the day.

Food Resources

Food resources influence animal populations in a variety of ways, especially when food availability reaches extreme highs or lows. Squirrel populations (gray and fox) undergo declines (resulting from decreased or ceased reproduction, emigration, high infant/juvenile mortality, and adult mortality) following poor food years (Kantola 1986, Weigl et al. 1989, Gorman and Roth 1989). Good food years are marked by the opposite occurrences (Gurnell 1983). Good and poor food-year patterns typically fluctuate in time and space and with them so do squirrel populations.

Supplemental food has the same effects as good food years. Gregory et al. (1988) document increases in number of females, recruitment of females, and overwintering survival of females for eastern chipmunks (*Tamias striatus*) supplied with food for 2 years. Golf courses in southwestern Florida, with their planted exotic species and artificially maintained habitats, provide fox squirrels with a relatively stable food source. A poor crop one year for one food item is compensated for by a greater diversity of food items. Different items are used in different seasons, with no season without a new food. Extreme reliance on one food item for a season was not observed, unlike the case for palms in Panama eaten by S. granatensis (Glanz, 1984) and for fox squirrels and pine seeds throughout the southeastern U.S. (Kantola 1986, Weigl et al. 1989).

Understanding the effects of supplemental food on diet, population density, social behavior, and reproduction are important facets of fox squirrel management in a growing urban area.

Diet Composition and Seasonal Feeding Patterns

Seasonal feeding patterns of fox squirrels on golf courses reflect a diet of seasonally available foods. Because different foods are available during different seasons, similarity among seasons is not great. Diets among seasons may differ because of changes in relative abundance of food items or temporal and spatial changes in forage quality (Gillingham and Bunnell, 1989).

Figs, considered a keystone plant species in the new world because of their asynchronous fruiting pattern (Terborgh 1986), provide a year-round fresh food for fox squirrels. Their importance is reflected in their occurrence as a primary food item in 3 of 4 seasons. Palms (both native cabbage and exotic queen) and seeds from pine cones also dominate extensivity data for particular seasons. Palm fruits, figs (or year-round fruiting trees in general), and pine seeds have all been identified as important food items for various species of tree squirrels. Glanz (1984) found one species of palm (Scheelea zonensis) to be 71% of Sciurus granatensis diet in Panama. Ficus insipida also was used over a 6-month period there. Emmons (1980) identified year-round reliance of tree squirrels in Gabon, Africa, on Raphia, an asynchronously fruiting tree. Fox squirrels in the southeastern U.S. rely on pine seeds in the summer months (Weigl et al. 1989).

The only important food item of southeastern fox squirrels that was consumed by fox squirrels on golf course was pine seeds. The appearance of pine seeds in the diet coincides with breeding in the early wet season and may provide females with an important, high-energy food during lactation in the late wet season. Acorn crops from oaks, which were available on golf courses, were rarely eaten. Use of hypogeous fungi, an important food source for many sciurids, was difficult to gauge through visual observations. Seeds from cypress cones were consumed rarely, although abundant throughout the golf courses.

Extensivity and Intensivity Data

For most seasons and food items extensivity and intensivity data seem similar. However, in some instances one is out of proportion to the other. Two examples (cabbage palm and seeds from pine cones) may indicate use of an item out of its peak season and may reflect its relative importance as measured by search effort. For example, while time invested in foraging on pine seeds decreased from 13.1%

in the late wet season to 1.3% in the early dry season, over 12% of the squirrels were still observed foraging on seeds. Pine seeds' high energy yield (5,500 calories/gram; Weigl et al. 1989) may maintain the desire of squirrels to seek and consume pine seeds before switching to another less preferred food (Gillingham and Bunnell, 1989). Similarly, squirrels may have been examining cabbage palm during the late wet season as it approached ripening. Extensive ground foraging each season is difficult to interpret because of the lack of information on items being eaten.

Food Resources and Fox Squirrel Ecology

Fox squirrels are considered an asocial species. However, when food is abundant they have been reported to gather at food sources in larger numbers than typically observed (Weigl et al. 1989, Gurnell 1987, Mollar 1983). Tamura et al. (1989) found that female Formosan squirrels were more tolerant of other females and young when food resources were higher in quality. Weigl et al. (1989) further state that if the supplemental food is not widely dispersed, an individual squirrel may be able to monopolize the food source. In these situations, linear dominance hierarchies and agonistic interactions are common (Benson 1980). A brief increase in the number of fox squirrels may occur, but its duration varies with the longevity and distribution of the food source.

Observations of two or more fox squirrels foraging at the same food source indicate that changes in typical social behvior may be occurring. Two or more squirrels were often observed at figs, queen palm, bottlebrush, and silk oak, but less frequently in pine trees. Each of these food items has the potential to produce large quantities of fruit or seed during short time periods. Agonistic interactions were rare and those that did occur during these foraging observations were brief. Food items were often too scattered and numerous on the ground or within the tree for one fox squirrel to successfully exclude others.

Defense of food by fox squirrels in food rich situations is uneconomical (Armitage and Harris 1982). Because the supplemental food on golf courses is not a point source, but dispersed throughout the course in time and space, squirrels do not attempt to drive away other individuals. Individuals will tolerate other squirrels foraging as close as 2 or 3 m. The few agonistic encounters that were observed usually occurred as one squirrel approached another feeding squirrel, with the approached squirrel moving a few m away and the approaching squirrel taking over the former feeding position. Agonistic encounters were frequent at bird feeders. Such a point source can easily be monopolized on a short-term basis.

One possible benefit derived from group feeding may be predator detection and avoidance (Tamura 1989). Foraging squirrels often reacted to an alarm call or disturbance behavior of a nearby squirrel. In one instance, five fox squirrels took refuge in a fig tree they had been feeding under when one of the five reacted to an unidentified disturbance and fled up the tree. Young fox squirrels seemed to react more strongly to alarm calls than adults.

Another aspect of squirrel ecology that varies with food quantity and quality is reproduction. Food affects reproduction by influencing litter size, number of litters per year, juvenile breeding, length of breeding season, and survival of young (Gurnell 1983).

Fox squirrels may have the opportunity to extend their breeding season with the occurrence of supplemental food (Gurnell 1983). Mating behavior (males chasing females) was observed on the golf courses each season, although most of this activity (including the only observations of copulation) occurred in the early wet season. However, one litter of two was observed emerging from a nest in late February 1990, indicating that mating took place during the late wet season, probably in mid- to late October 1989. The occurrence of a year-round food source might allow this type of reproductive behavior. For example, fox squirrels in North Carolina have two breeding seasons during good food years (Weigl et al. 1989), so it would be feasible for fox squirrels with supplemental foods to extend their breeding seasons beyond the typical peak month(s).

Unfortunately, no data are available on juvenile breeding, number of litters per year, or litter size. Each of these does increase with supplemental food (Brown and Yeager 1945).

Population density, social behavior, feeding, and activity patterns of fox squirrels on golf courses in Naples all seem to vary when compared to fox squirrels throughout the southeastern United States. The availability of a stable spatio-temporal food source may be the most important factor contributing to the occurrence of fox squirrels on golf courses throughout the region.

Translocation

Habitat Use

Translocated fox squirrels shifted habitats as water levels and food availability changed. Shifting use of habitats to compensate for seasonally available foods is common in fox squirrels throughout the Southeast (Edwards 1986, Weigl et al. 1989).

Wetter habitats (cypress and mixed-swamp forests) were used until water levels receded midway through the early dry season. Squirrels fed on cabbage palm and cypress cones during this time. Cypress is an uncommon food in other parts of the range of this squirrel (as well as on golf courses in Naples); acorns from oaks and other hardwood seeds are typically used during these late fall and winter months. However, in BICY, hardwoods occur only in the scattered hammocks (1.5% of BICY habitat) and mixed-swamp forests. Although the later habitat is used by fox squirrels, foraging for acorns on the ground is not possible because of sustained flooding.

As water levels decreased, fox squirrels foraged predominantly on the ground. Beginning late in the early dry season and continuing through mid-April (the termination of telemetry locations), fox squirrels were often observed digging shallow pits at the base of pine trees. This behavior indicates that fox squirrels were obtaining hypogeous fungi, an important winter and early spring food item for other southeastern fox squirrels (Weigl et al. 1989). Few other foods are available during these months. Pine seeds do not become available until the early wet season.

Movements and Home Range

Relocated fox squirrels covered large areas in short periods of time and made long journeys into previously unused areas. Although much of this movement may be attributed to relocation to a new area (Bertram and Moltu 1986), it demonstrates a strong ability to travel.

Seasonally variable and widely spaced food resources influence home-range size, movement patterns, and habitat use of fox squirrels (Kantola 1986, Weigl et al. 1989). In a naturally fragmented landscape, such as BICY, where food items are variable within and between patches and habitats, a fox squirrel might need to use several habitat islands or patches to supply itself with the necessary amount of food (Weigl et al. 1989). Consequently, in comparison to more food abundant or food stable areas, home-ranges of animals might be expected to be larger and densities lower in BICY.

Movement data from translocated fox squirrels indicate the ability of animals to move great distances in short periods and/or long durations on the ground or through the trees. Although comparisons with other studies are difficult because of differences in estimating home-range size, it is apparent that avicennia may use a larger home range than fox squirrels in other areas.

The mean core area (59.6 ha; approximately 66% of utilization volume) of fox squirrel M2a and M2b was 10 ha larger than a 95% utilization area of S. n. shermani in north-central Florida (Kantola 1986). Other estimates (MCP) indicate that home ranges of avicennia are larger than those of S. n. niger as well (Edwards 1986, Weigl et al. 1989).

One reason for the differences is home range sizes among regions may be food availability and diversity (Weigl et al. 1989). Habitats of shermani and niger are predominantly longleaf pine/turkey oak. This mosaic of pine/hardwood presents fox squirrels with a greater diversity of food spatially and temporally than the BICY habitat of slash pine/cypress. For example, hardwood habitats were rare in

BICY, and thus the fall hardwood mast absent throughout most of the Preserve. Consequently, because food is not as scattered for niger and shermani, home-range sizes and movements may be smaller than those of avicennia. Similarly, fox squirrels in the mid-western U.S., where a greater variety of hardwood mast is available, show smaller home ranges than S. n. niger (Weigl et al. 1989).

Although these home-range data describe activities of translocated animals, it is likely that resident animals would display similar habits. Inability to locate resident animals consistently in any natural area, combined with large home-range areas of translocated fox squirrels working out of one or several nests, indicate large use-areas for avicennia.

Although no density estimates of fox squirrels were made, telemetry data indicate low squirrel densities. During 8 months of telemetry only one uncollared fox squirrel was observed in the vicinity of a translocated individual. Squirrel M2b was observed chasing a female fox squirrel in early April after he dispersed from his previous home-range.

Based on the above information, and a lack of observations of resident animals in the release area, the release area may be considered as suitable but not ideal. Squirrel M2a was able to find enough food in the area to survive and the return of M1 to the release area suggests suitable habitat (Slough 1989). Releasing translocated animals into areas with known fox squirrel populations would provide more information on population density, social interactions, dispersal, and breeding.

Nest Data

Fox squirrels in BICY, like Sherman's fox squirrel in northern Florida, do not use cavity nests to the degree of their midwestern counterparts, probably because of a milder climate (Moore 1957, Kantola 1986). Instead, Big Cypress fox squirrels made use of the unique vegetation by nesting in a locally common bromelliad, quill-leaf or stiff-leafed wild pine (*Tillandsia fasciculata*). Quill-leaf is a frequent perennial on cypress. These bromelliads (airplants) typically grow near the base of the crown. Bromelliad nests seem structurally similar to leaf nests, yet require little to no maintenance or construction. Squirrels may add some sticks to the nest, but this seems to be rare. Stripped cypress bark from nearby trees is often carried up to the nest. This may be similar to Sherman's fox squirrel using Spanish moss (*Tillandsia usneoides*) in nests (Kantola 1986).

Nest locations within the tree are similar to those reported for other southeastern fox squirrels (Hilliard 1979, Edwards 1986). However, nest tree species and habitats were not similar to other reports (Hilliard 1979, Edwards 1986); these authors report heavy use of pines and oaks, while all fox squirrel nests observed in BICY were in cypress trees located most often in domes. Hardwoods may be used in mixed-swamp strands or tropical-hardwood hammocks, but this was not observed. Squirrels may prefer cypress habitats over pinelands for the following reasons: presence of bromelliads and denser canopy cover (Duever et al. 1979), which would provide more shade and protection from rain, and more closely spaced trees providing abundant travel routes to and from the nest.

It was not possible to get a count on the number of nests each squirrel used. Squirrel M2b used an airplant nest for 35+ days. However, squirrel M1, while travelling out and back from the release site probably used many different nests. Rapid long-distance movements into previously unused areas may be made easier for the squirrels by the abundance of "pre-fabricated" airplant nests. It is impossible to use airplant nests as a measure of fox squirrel density because of the difficulty in distinguishing airplants from airplant nests.

Squirrels strip cypress bark from nest trees or adjacent trees. This occurs on a regular basis, not just during the initial use of a nest. Stripped cypress bark may provide an important field sign in identifying possible squirrel use areas. Freshly stripped cypress trees show a deep red color at the site of bark removal, while less recent strippings appear light tan. Each color is recognizable against the gray cypress bark. Stripped trees were located in the vicinity of observed resident fox squirrels.

Fox Squirrel Surveys in BICY

Questionnaire Responses

Returns from questionnaires were low but did provide some useful information on past and present fox squirrel locations. Sample size was too small to provide any accurate information concerning population trends. All of the questionnaire responses indicated that fox squirrels were presently scarce and difficult to sight, and most agreed that fox squirrels were always difficult to find. One response was "There are not enough fox squirrels in the Big Cypress to do research."

Distribution and Observations of Fox Squirrels in BICY

Observations of native (i.e. non-translocated) fox squirrels were uncommon and inconsistent. Habitat use of native fox squirrels is impossible to determine by these scattered observations. However, based on observation locations of native fox squirrels, it seems that open understory may be an important habitat feature. A female fox squirrel was observed at a recently burned area (dispersal area of M2b) and feeding behavior of radio-collared fox squirrels indicate that ground foraging is important for at least 4 months per year.

Location of fox squirrels at back-country camps seems to be relatively common. Some of these camps have small gardens, citrus trees, and bird feeders. Others may provide food directly to squirrels; many camp owners seem to like having "camp squirrels". It is also probable that squirrels have been extirpated near some camps by hunting.

Native fox squirrels were observed throughout the Preserve during this study, indicating widespread populations. Most observations were recorded in the Raccoon Point area. Although this may be due to the heavy use of the area by researchers and resident oil workers, the area does contain potentially good habitat for fox squirrels including much second-growth and some old-growth pine interspersed with cypress domes. The understory is mostly saw palmetto or grasses. The area provides good red-cockaded woodpecker (Picoides borealis) habitat. Habitat needs of these two species seem to be similar, and it has been suggested that management for one benefits the other (Weigl et al. 1989). In fact, native fox squirrels have been observed in woodpecker colonies in BICY. Ongoing red-cockaded woodpecker research and management in BICY may present the best opportunity to search and manage for fox squirrels. Surveying cypress domes around colonies for stripped trees, indicating squirrel nesting activity, could provide useful information on fox squirrel presence. Searching for remains of eaten pine seeds (i.e., cone remains) along the ground in woodpecker colonies would also be beneficial.

It is very difficult to define any trend in native fox squirrel populations in BICY. What does seem apparent is that fox squirrels are not abundant in BICY. Local abundance has been recorded in the past (Duever et al. 1979) but was not observed during this project. Based on telemetry data from translocated animals and life history traits of fox squirrels throughout the Southeast, low densities and large use areas should be expected. Squirrel hunting, opportunistic hunting during the 1930 - 1950 deer/tick eradication (Derr 1989), logging of virgin pine and cypress, and poor burning strategies have all been considered as detriments to fox squirrel populations.

Other reasons for low densities were discussed in detail in the telemetry section. Temporally and spatially variable food supplies may limit local densities and overall abundance. Lack of a large fall acorn crop may also inhibit population size.

SUMMARY AND CONCLUSIONS

Social behaviors, breeding cycles, and diets of fox squirrels on golf courses in southwestern Florida seem to be atypical of the species. Individuals are less asocial, and often forage within a few meters of other squirrels. Mating may take place throughout the year. Diets include many of the planted species throughout the golf courses; no one food item is relied on exclusively in a season.

Populations of fox squirrels on golf courses may denser than in natural habitat in BICY. However, little is known of the effects of isolation of golf courses (i.e., many courses are becoming surrounded by uninhabitable areas such as parking lots, malls, or roads). There is some indication that populations of fox squirrels on golf courses in central Florida may be dwindling as development increases (L. Williams, pers. comm.).

Translocation of fox squirrels from Naples to BICY indicates that translocation/reintroduction of fox squirrels would be feasible. Four of five squirrels survived the translocation. Problems occurred with individuals dispersing long distances from release sites, and radio signals were often difficult to receive. One solution may be to release animals during the early wet season, when seeds from pine cones are available. This may limit the need for squirrels to range widely in search of food.

Telemetry data of translocated fox squirrels indicate that habitat use changes on a seasonal basis. Food availability and water levels are two factors influencing seasonal habitat use. Translocated fox squirrels foraged on the ground during the early dry and late dry seasons and on seeds from cypress cones and cabbage palm during the late wet and beginning of the early dry season.

Resident fox squirrels were located throughout BICY, so it does not seem that the population is isolated to one or two quality areas. Natural populations seem to be rare. A population decline is suspected, but no data exist to determine its validity. Questionnaire responses from BICY were of little value because of low returns. Habitat-use data from telemetry of translocated fox squirrels and information from other southeastern fox squirrels indicate that a more controlled natural cycle in pinelands may improve habitat conditions.

MANAGEMENT RECOMMENDATIONS AND RESEARCH NEEDS

1. Developing golf courses should leave as much native vegetation in place as possible. Open understories beneath pines is preferable. Mature pines provide valuable foods. Cypress, although not eaten extensively on golf courses, should also be left. Cypress provide nesting sites (bromelliads), daily resting sites, and nesting material (stripped cypress bark). Cabbage palm is an important food and nest tree on golf courses.
2. Planted species provide important supplemental foods that may be necessary for occurrence of fox squirrels on golf courses. Figs, queen palm, bottlebrush, and silk oak are all important foods for fox squirrels.
3. If urban populations of fox squirrels are becoming isolated from each other, preserving habitat to retain corridors between fox squirrel habitat (other golf courses or undeveloped lands) may provide a critical element in maintaining the long-term viability of golf courses as fox squirrel habitat.
4. Maintaining a naturally open understory in pinelands in BICY through proper fire management may enhance habitat conditions (and cone production) for fox squirrels.
5. Information is needed about use of adjoining habitats by fox squirrels on golf courses. Dispersal, immigration,

and emigration of fox squirrels around golf courses, and a census of golf course populations all would be valuable. Surveying for fox squirrels in areas scheduled for development to provide a before/after picture is important.

6. Distribution of fox squirrels in BICY still needs to be researched. Two methods are: 1) surveying for stripped cypress trees that indicate squirrel (gray or fox) nesting. More recently stripped trees appear very red, while older stripped trees appear as a fainter tan or gray. 2) Surveying during the months of July, August, and September for cut pine cones beneath pine trees. This indicates squirrel feeding activity. Combining the information from the above two surveys could yield valuable squirrel use area data. Locating nest sites may develop ideas for capturing resident squirrels for telemetry at or near nests.

7. Big Cypress fox squirrels are currently listed as threatened by the Florida Game and Fresh Water Fish Commission and should remain listed as such.

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Appendix 1. Percent frequency of behavior of fox squirrels on four golf courses in Naples, Florida, 1989-1990.

Season/ Time	Hours of observa- tion	Squirrels observed per hour	Foraging	Inactive	Travel.	Other active	Social inter.
Early wet	95.6	1.7	42.7	36.5	8.6	4.2	7.8
Time period 1	28.6		54.7	19.9	11.5	5.3	8.5
Time period 2	53.2		35.4	44.0	7.9	3.8	8.9
Time period 3	13.8		46.1	42.5	5.1	3.3	1.6
Late wet	78.9	2.2	61.8	16.3	7.9	8.7	3.3
Time period 1	23.6		66.3	9.7	7.8	11.1	5.2
Time period 2	38.8		56.8	24.4	7.9	8.7	2.2
Time period 3	16.5		67.0	16.3	8.1	5.3	3.3
Early Dry	88.9	1.7	52.8	32.2	8.0	6.1	0.9
Time period 1	20.4		49.9	28.8	11.0	8.8	1.6
Time period 2	57.2		55.0	32.9	6.6	4.8	0.8
Time period 3	11.3		47.4	34.7	10.1	7.6	0.3
Late dry	70.9	2.9	52.2	30.1	5.5	5.2	7.0
Time period 1	20.2		52.0	24.2	6.4	8.9	8.5
Time period 2	37.7		55.2	28.3	5.2	3.5	7.7
Time period 3	13.0		44.7	44.0	4.3	4.5	2.6
Annual	334.3	2.0					

Appendix 2. P-values from paired comparisons of LSMEANS for differences among seasons within a behavior.

Foraging Model P = 0.0192

	EW	LW	ED	LD
EW	--	.0093	.0881	.5380
LW	--	--	.3186	.0124
ED	--	--	--	.0704

Inactive Model P = 0.0182

	EW	LW	ED	LD
EW	--	.0054	.1040	.7007
LW	--	--	.2124	.0149
ED	--	--	--	.1249

Other active Model P = 0.0175

	EW	LW	ED	LD
EW	--	.0049	.0136	.2177
LW	--	--	.5926	.3121
ED	--	--	--	.5394

Social interaction Model P = 0.2109

	EW	LW	ED	LD
EW	--	.5964	.1110	.4089
LW	--	--	.3762	.2505
ED	--	--	--	.0541

Travelling Model P = 0.9741

	EW	LW	ED	LD
EW	--	.8145	.8565	.7926
LW	--	--	.7069	.9478
ED	--	--	--	.7028

Appendix 3. P - values from paired comparisons of LSMEANS for differences among behaviors within a season.

Early dry Model P = 0.0001

	FO	IA	OA	SI	TR
FO	--	.0001	.0001	.0001	.0001
IA	--	--	.0011	.0001	.0094
OA	--	--	--	.0005	.4857
SI	--	--	--	--	.0001

Early wet Model P = 0.0001

	FO	IA	OA	SI	TR
FO	--	.0798	.0001	.0001	.0001
IA	--	--	.0001	.0001	.0094
OA	--	--	--	.4661	.0746
SI	--	--	--	--	.0125

Late dry Model P = 0.0001

	FO	IA	OA	SI	TR
FO	--	.9246	.0001	.0001	.0005
IA	--	--	.0001	.0001	.0006
OA	--	--	--	.5430	.6082
SI	--	--	--	--	.2639

Late wet Model P = 0.0001

	FO	IA	OA	SI	TR
FO	--	.0001	.0001	.0001	.0001
IA	--	--	.3807	.0001	.4101
OA	--	--	--	.0004	.9576
SI	--	--	--	--	.0004

Appendix 4. P-values from paired comparisons of LSMEANS for differneces among seasons within a food item with model P values < 0.05.

Cabbage palm Model P = 0.0053

	EW	LW	ED	LD
EW	--	.2847	.0009	1.000
LW	--	--	.0184	.4429
ED	--	--	--	.0131

Flowers Model P = 0.0001

	EW	LW	ED	LD
EW	--	.6608	.6639	.0001
LW	--	--	1.0000	.0001
ED	--	--	--	.0001

Cypress Model P = 0.1366

	EW	LW	ED	LD
EW	--	.0475	.0750	.1093
LW	--	--	.8492	.8880
ED	--	--	--	.7782

Fig Model P = 0.1098

	EW	LW	ED	LD
EW	--	.1399	.0814	.0302
LW	--	--	.7755	.2647
ED	--	--	--	.3671

Ground Model P = 0.2036

	EW	LW	ED	LD
EW	--	.7536	.0514	.3020
LW	--	--	.1098	.4291
ED	--	--	--	.6720

Pine Cone Model P = 0.1281

	EW	LW	ED	LD
EW	--	.6095	.0407	.1077
LW	--	--	.1289	.2200
ED	--	--	--	.9341

Appendix 4 (cont.)

Queen Palm Model $\underline{P}$ = 0.2210

	EW	LW	ED	LD
EW	--	.0602	.0976	.4542
LW	--	--	.8325	.5223
ED	--	--	--	.6312

Appendix 5. P-values from paired comparisons of LSMEANS for differences among food items within a season.

Early wet Model P = 0.0001

	CP	CY	FG	FW	GR	PC	QP
CP	--	.067	.092	.855	.0001	.007	.592
CY	--	--	.876	.098	.0001	.360	.190
FG	--	--	--	.133	.0001	.285	.248
FW	--	--	--	--	.0001	.011	.724
GR	--	--	--	--	--	.0009	.0001
PC	--	--	--	--	--	--	.028

Late wet Model P = 0.0001

CP	--	.477	.018	.395	.0001	.291	.242
CY	--	--	.003	.888	.0001	.079	.063
FG	--	--	--	.002	.088	.177	.215
FW	--	--	--	--	.0001	.059	.046
GR	--	--	--	--	--	.003	.004
PC	--	--	--	--	--	--	.909

Early dry Model P = 0.0001

CP	--	.007	.427	.003	.85	.009	.269
CY	--	--	.0007	.762	.004	.919	.099
FG	--	--	--	.0002	.545	.0009	.060
FW	--	--	--	--	.002	.686	.052
GR	--	--	--	--	--	.005	.196
PC	--	--	--	--	--	--	.121

Late dry Model P = 0.0001

CP	--	1.0	.0001	.003	.001	.800	.227
CY	--	--	.0001	.003	.001	.800	.227
FG	--	--	--	.121	.185	.0001	.001
FW	--	--	--	--	.813	.005	.047
GR	--	--	--	--	--	.003	.028
PC	--	--	--	--	--	--	.335

Appendix 6. Weights and measurements of Big Cypress fox squirrels captured in Naples, FL, and translocated to Big Cypress National Preserve, FL. A=adult, I=immature.

Fox squirrel no.	Body weight (g)	Body length (cm)	Tail length (cm)	Total length (cm)	Neck girth (cm)	Chest girth (cm)
M1(A)	900	32	23	55	--	19
M2(A)	940	28	--	--	--	--
M3(I)	800	23	34	57	12	--
M4(A)	940	33	30	63	--	--
F1(A)	960	28	28	56	--	--
mean	908	28.8	28.8	57.7	--	--

BIOGRAPHICAL SKETCH

Patrick G. R. Jodice was born on 6 December 1961. He was raised in New Milford, New Jersey, and graduated from St. Joseph High School in Montvale, New Jersey. He attended the University of Maine at Orono and received a Bachelor of Science in wildlife in May of 1983. Previous to enrolling at the University of Florida in September of 1988, he worked on wildlife projects on common loons in remote northern Maine, bald eagles in the Sonoran desert of Arizona, and songbird communities in central Maine. Patrick also taught at various environmental education centers in New England and for two years with the New York Zoological Society.

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Rare and Endangered Biota of Florida

Peter C. H. Pritchard, SERIES EDITOR

Brown, L.N
1978

Volume One

MAMMALS

Edited by James N. Layne

Chairman, Special Committee on Mammals

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Sponsored by the FLORIDA AUDUBON SOCIETY and FLORIDA DEFENDERS OF THE ENVIRONMENT

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Sylvia J.
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Endangered
MANGROVE FOX SQUIRREL

Sciurus niger avicennia Howell
Family Sciuridae
Order Rodentia

OTHER NAMES: Everglades Fox Squirrel; South Florida Fox Squirrel.

DESCRIPTION: The pelage of the large-bodied Mangrove Fox Squirrel grades from black on the head and shoulders to brown with an orange wash on the sides, rump, and tail. The belly is orange or black washed with orange. This color combination differs markedly from the fox squirrels of central and northern Florida which are paler on the belly and back. A melanistic phase of the Mangrove Fox Squirrel is prevalent in some areas, with the entire pelage being black except for a white patch on the nose.

3. Mangrove Fox Squirrel, *Sciurus niger avicennia*. (Photo by R.S. Palmer)

RANGE: Formerly this Fox Squirrel was found across all of southern Florida south of Lake Okeechobee in suitable habitat. The type locality is Everglades, Collier County. It was present in both Dade and Broward counties until the early 1900's when it disappeared there. Today it occurs only in the Big Cypress Swamp and the adjacent pinelands of southwestern Florida (in Collier County and northwestern Monroe County). There are no recent records of its occurrence in habitats now preserved in Everglades National Park where it was found until the early 1900's.

HABITAT: The Mangrove Fox Squirrel occurs in several types of south Florida woodlands, including open pinelands, dry cypress strands, and coastal broad-leaf tropical evergreen hammocks. It appears to be most abundant in mature pinelands having an open understory relatively free of brush and palmetto clumps. In coastal locations it occasionally ventures into the mangrove zone where it was first recorded by Howell (1919), but due to the absence of nesting cavities or suitable food in that habitat, this squirrel should not be considered a permanent resident of the mangrove zone.

LIFE HISTORY AND ECOLOGY: As in all tree squirrels, the Mangrove Fox Squirrel is diurnally active. Both tree hollows and leaf nests are utilized for shelter. Food sources vary greatly with the habitat and season, but include seeds, nuts, fruits, and buds of many native south Florida trees. The seeds of Slash Pine (*Pinus elliottii*) are heavily utilized when available. The presence of freshly chewed pine cones under the trees is often a tell-tale sign of Fox Squirrel residency in an area. These squirrels spend a great deal more time on the ground foraging for food than do Gray Squirrels.

Very little is known about the breeding cycle of the Mangrove Fox Squirrel. Generally one or two litters per year of two to four young each are produced by adult females. The primary sources of predation in young squirrels appear to be large snakes, hawks, and Bobcats.

The Mangrove Fox Squirrel seldom tolerates man to the extent of persisting in residential areas of towns. The only notable exception to this were the famous "town-squirrels" in the Everglades City area reported by Moore (1954). Hurricane Donna in 1960 decimated this population, and the squirrels did not repopulate to any extent during the subsequent decade. This probably demonstrates the susceptibility of the species to severe hurricanes.

BASIS OF STATUS CLASSIFICATION: Habitat destruction as a result of logging the mature pine and cypress forests in south Florida apparently brought on the early decline in Mangrove Fox Squirrel populations in the late 1800's and early 1900's. The rapid development and urbanization of the coastal portions of south Florida have greatly accelerated habitat destruction and further contributed to the population decline. Today the continued bulldozing of forests and development of natural habitats in and around the Big Cypress Swamp are rapidly eliminating remaining Fox Squirrel habitats. Also, complete fire protection in pine woodlands has resulted in the growth of dense understory vegetation which is not suitable as Fox Squirrel habitat. The Fox Squirrel does not appear to fare well anywhere in Florida unless the understory vegetation is open and sparse.

The only protected population of the Mangrove Fox Squirrel presently known to exist is located in the Corkscrew Swamp Sanctuary of the National Audubon Society, situated in northern Collier County. This refuge contains only a few dozen individuals at most. It is also possible that some small isolated Fox Squirrel populations remain in the remote northern portions of Everglades National Park, but this has not been verified in recent years.

RECOMMENDATIONS: Studies should be initiated to determine the optimum habitat requirements of the Mangrove Fox Squirrel and appropriate habitat management steps taken to insure its survival. An obvious need is to conduct "control burning" in the south Florida pinelands to open up the understory vegetation and promote better Fox Squirrel foraging areas.

A major refuge should also be established under state or federal ownership in the Big Cypress Swamp. With proper management and protection, the remnant Mangrove Fox Squirrel population present in that area would gradually increase.

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PREPARED BY: Larry N. Brown, *Department of Biology, University of South Florida, Tampa, Florida 33620.*

Endangered
GOFF'S POCKET GOPHER

Geomys pinetis goffi Sherman
Family Geomyidae
Order Rodentia

OTHER NAMES: None.

DESCRIPTION: Like other eastern Pocket Gophers, *G. p. goffi* is a small rodent with short fur and a nearly naked tail. The head is large and characterized by external fur-lined cheek pouches and large, permanently exposed incisors. The eyes and ears are small and the forefeet are equipped with long, robust claws. The pelage of the dorsum is a rich reddish-yellow brown which shades to "orange-cinnamon" on the sides. A white blaze extends from the forehead to the nose in most specimens, and there are white markings on the forelimbs and throat. The venter is gray. This subspecies is distinguished from others in peninsular Florida by a body that is longer in proportion to the length of the skull and by the fact that unsuitable soils isolate it geographically from other populations.

RANGE: G. p. goffi is known only from Pineda Ridge, a high sandy ridge bordering the Indian River in the region of the type locality, which was given as "Eau Gallie, Brevard County, Florida," by H.B. Sherman, who described the subspecies. It is important to note that in 1970 the cities of Eau Gallie and Melbourne, formerly 6.4 km (4 mi) south of Eau Gallie, merged to form one city and adopted the name "Melbourne." Sherman found evidence of Pocket Gophers about 3.2 km (2 mi) north and south of Eau Gallie and about 3.2 km (2 mi) inland from the Indian River.

HABITAT: G. p. goffi is restricted to the deep, friable Norfolk and St. Lucie fine sands of the Pineda Ridge. Sand Pine scrub and scrub mixed with elements from the nearby flatwoods and coastal dune scrub characterize the ridge.

cox et al. 1994

contain. We conclude that current conservation areas provide the minimum habitat requirements sought for populations of scrub lizards. However, this does not imply that other elements of the scrub community are adequately protected.

Section 6.2.18. Fox Squirrels

Three subspecies of fox squirrel occur in Florida (Moore 1956, Turner and Laerm 1993). The Big Cypress fox squirrel (*Sciurus niger avicennia*) occurs south of the Caloosahatchee River and is ecologically and morphologically distinct (Turner and Laerm 1993). Sherman's fox squirrel (*S. n. shermani*) occupies a broad range extending north from southeastern Florida to central Georgia and west to approximately Walton County (Turner and Laerm 1993). The *shermani* subspecies appears to intergrade with the *niger* (or *bachmani*) subspecies (Turner and Laerm 1993) in the panhandle north and west of Walton County.

The *niger* and *shermani* subspecies appear to have similar ecological requirements (Weigl et al. 1989). Potential habitat for these subspecies was estimated using a similar habitat model. The sandhill, mixed pine-hardwood, and dry prairie land-cover types were consolidated into a single class categorized as appropriate land cover (Moore 1957, Kantola 1992). The pineland land cover in the Tampa Bay, Central Florida, Southwest Florida, and Treasure Coast regions was also categorized as appropriate habitat since these areas tend to consist of open pine flatwoods where fox squirrels may occur. The pineland class on public lands in north and northwest Florida was also treated as appropriate fox squirrel habitat. However, the pineland land cover on private lands in northwest Florida was excluded since these areas typically consist of commercial pine plantations that are not used frequently by fox squirrels (Weigl et al. 1989).

We isolated individual patches of these "preferred" cover types, calculated their sizes, and eliminated patches smaller than 10 ha (25 acres), an approximate home range size (Kantola 1986, Weigl et al. 1989). A 120-m zone was then created around the remaining large patches. Small patches of preferred cover, and infrequently used land-cover types, such as hardwood hammock and cypress swamp, within this 120-m zone were included as potential habitat for fox squirrels. A final stipulation was that potential habitat be located at least 60 m away from barren land cover, which is generally avoided by fox squirrels. This last condition produces a conservative estimate of potential habitat areas.

The map of potential fox squirrel habitat represents only a portion of the total habitat occupied by these subspecies. Both *shermani* and *niger* inhabit rangeland areas interspersed with oak trees and the edges of forested wetlands and rangeland. These conditions are difficult to model using only the land-cover map. However, the model of potential habitat can be used to estimate the habitat provided by current conservation areas and to identify many of the remaining habitat areas on private land.

We used a density of 0.05-0.10/ha (Kantola 1986, Weigl et al. 1989) to estimate the security of habitat capacity in current conservation areas. Based on the analysis of population viability performed in Section 5.1., we estimate that secure fox squirrel populations require approximately 2,000-4,000 ha (4,940-9,880 acres) of appropriate habitat. However, habitat and population management within conservation areas of these general sizes is especially critical to ensuring fox squirrel persistence (see Section 5.1).

A cross-tabulation of potential habitat by current conservation areas indicates that conservation areas within the range of *shermani* support at least 10 populations > 200 individuals. The largest blocks of habitat on conservation areas within the range of *shermani* occur on the Ocala National Forest, Apalachicola National Forest, Osceola National Forest, Withlacoochee State Forest, and Camp Blanding Military Reserve. The geographic distribution of habitat on conservation areas also extends throughout the range of the subspecies in Florida, and we conclude that the *shermani* race has the minimum base of habitat needed for long-term security.

A similar cross-tabulation performed for conservation areas within the range of the *niger* subspecies shows sufficient habitat to support at least two very large populations (> 200 individuals). And two populations in the range of 25-200 individuals. The largest habitat areas are found on Eglin Air Force Base and Blackwater River State Forest. These conservation areas provide an estimated 2,432 km^2 (600,800 acres) of potential habitat, which could support approximately 12,000-24,000 fox squirrels. The recent acquisition of approximately 210 km^2 of potential fox squirrel habitat in Walton County may establish a third potentially secure population in west Florida. However, current habitat conditions on this site are largely unsuitable, and an undetermined portion of this area may be returned to private ownership. Given the fact that this subspecies has a very limited range in northwest Florida (Turner and Laerm 1993) and is represented by at least two very large populations, we conclude that it has sufficient representation on the existing system of conservation areas in Florida.

Identification of habitat features important to the *avicennia* subspecies focussed on the pineland and dry prairie land cover in southwestern Florida. Habitat requirements of this subspecies are not well known (Humphrey and Jodice 1992), but open pinelands and prairies (with interspersed pines) appear to be a primary habitat requirement. Based on food preference studies (Humphrey and Jodice 1992), slash pine forests appear to be important in spring and early summer, and the edges of cypress swamps appear to be important in fall and early winter. However, this subspecies has been found in many different habitat types, including hammocks, mangrove swamps, and hardwood swamps. Only the interiors of cypress and hardwood swamps seem to be avoided. Since Big Cypress fox squirrels (as well as the other subspecies of fox squirrel) spend much of their time on the ground, an open understory is important regardless of the dominant tree species. Such habitat requirements are difficult to evaluate using the land-cover map.

Within the known range of the Big Cypress subspecies (Williams and Humphrey 1979, Humphrey and Jodice 1992), we consolidated the pineland and dry prairie land cover into a single land-cover class. Individual patches < 100 ha (247 acres) were eliminated to focus attention on large patches of habitat that might support a stable population. The contiguous patches of hardwood hammock, mixed hardwood-pine, cypress swamp, hardwood swamp, and mangrove land cover occurring within 300 m of the edges of these large patches of pine and prairie land cover were also incorporated as appropriate land cover.

The habitat distribution map (Figure 90) developed for this subspecies shows several large blocks of habitat in Glades, Hendry, Charlotte, and Collier counties. The largest contiguous patch of habitat on private land occurs around Devil's Garden in Hendry County, with two other large patches of habitat occurring in southwest Collier County (north of Belle Meade) and northeast Lee County (north of Lehigh Acres). Large portions of the habitat areas in Lee, Collier, and Charlotte counties are undergoing development. This habitat distribution map corresponds well with the range of the subspecies described by Humphrey and Jodice (1992).

Average densities of the Big Cypress fox squirrel are not well known (Humphrey and Jodice 1992). **However, it is apparent that the species lacks an adequate habitat base in current conservation areas.** Only five conservation areas currently provide habitat for distinct populations of this subspecies, and the population associated with the Corkscrew Sanctuary may be extirpated (Humphrey and Jodice 1992). A total of 1,676 km^2 of potential habitat was identified, with only 347 km^2 (21%) in current conservation areas. If densities of the Big Cypress fox squirrel are comparable to those reported for other subspecies, these acreage totals imply a population of about 1,000-4,000 individuals in current conservation areas.

Most of the major blocks of habitat described for the Big Cypress fox squirrel on private lands are incorporated in the Strategic Habitat Conservation Areas recommended for other species (see sections on Florida black bear, Florida panther, and red-cockaded woodpecker). The habitat conservation areas described for these other species will, to a large degree, umbrella the habitat requirements of fox squirrels. The Strategic Habitat Conservation Areas provided for other species will increase the quantity of fox squirrel habitat on conservation areas by 153% and establish at least three potentially secure populations. However, one area of extensive fox squirrel habitat may not be adequately conserved through conservation of habitat for other species. A large tract of fox squirrel habitat occurs in northern Lee County around Hickey Creek and southwest Charlotte County. This area (Area 1, Figure 90) was also identified as an important habitat area for the Florida scrub jay (Section 6.2.16). Because of its importance to these two unique components of Florida's biological diversity, a Strategic Habitat Conservation Area is proposed for this area totalling 3,104 ha (7,667 acres). We estimate that a habitat conservation area of this size is capable of supporting 155-310 fox squirrels, a population capable of long-term survival under favorable management conditions.

Section 6.2.19. Gopher Tortoise

Although gopher tortoises occur in a variety of disturbed and natural areas, our model of potential gopher tortoise habitat emphasizes patches of "natural" habitat that have the capacity to support persistent populations. We isolated xeric land-cover types (sandhill, oak scrub, and sand pine scrub) in which gopher tortoises might occur. We also imposed a map of xeric soils over other land cover types (pineland, dry prairie, and mixed-hardwood pine) and added these to the map of xeric land-cover types to create an initial map of potential gopher tortoise habitat.

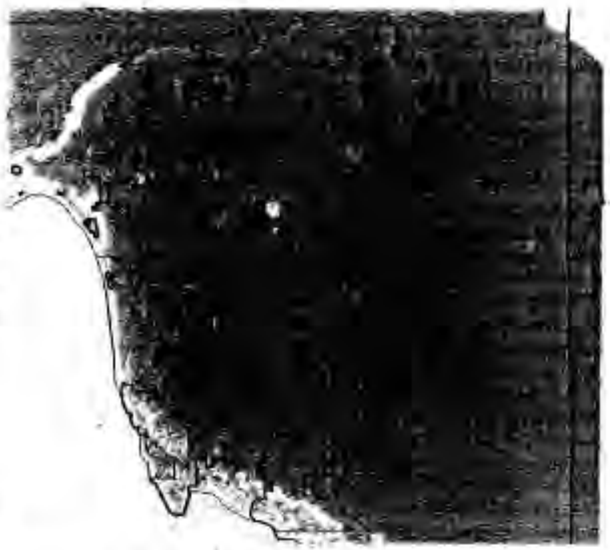

Figure 90. Potential habitat and proposed Strategic Habitat Conservation Area for the *avicennia* subspecies of fox squirrel.

This initial map was then refined by identifying contiguous patches of appropriate land cover and eliminating patches < 20 ha (50 acres). This minimum size criterion resulted in moderately sized blocks of potential gopher tortoise habitat that have the potential of supporting stable populations (Cox et al. 1987). We then generated a 60-m zone surrounding these larger blocks of potential habitat and incorporated the smaller patches of potential habitat found within this distance and eliminated initially because of their small sizes. In the end, this model produces a map of moderately sized patches of potential gopher tortoise habitat and smaller patches of potential habitat that occur within 60 m of larger patches.

We used a density estimate of 3/ha (Cox et al. 1987) to determine the base of habitat provided by current conservation areas in Florida. There are an estimated 93 conservation areas with sufficient habitat to support populations > 200 individuals. While we do not believe that adequate protection is necessarily provided to species that utilize gopher tortoise burrows (Jackson and Milstrey 1989), and thus require stable populations of tortoises in order to survive, we conclude that the current system of conservation areas in Florida provides the minimum level of habitat protection required to maintain gopher tortoises.

Section 6.2.20. Limpkin

The map of potential limpkin habitat was created using information stored by the Florida Natural Areas Inventory and occurrences reported in the Atlas of Florida Breeding Birds (Kale et al. 1992). A small-radius circle (250 m) was generated around occurrence records stored by the Florida Natural Areas Inventory. Within the area defined around point data, and in atlas blocks where limpkins were recorded as "proba-

APPENDIX A

Data sheets used in food surveys during the eight years of the fox squirrel study.

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Observer:

Vegetation and Food Survey

Date:

Location:

Road or transect:

Distance and end points:

General description and seral stage:

Numbers (stems)	Dominance (canopy)	Distribution
I Pure 95-100%	A Predominant	1 Continuous
II Abundant >40%	B Substantial	2 Abundant uniform
III Common 20-39%	C Moderate	3 Scattered
IV Some 5-15%	D Minor	4 Clumped L=large c=close s=small d=distant
V Few <5%	E Minimal	5 Occasional

Food	Food Distribution
a Prodigious	+++ All trees
b Abundant	++ Most
c Common	+ Some
d Some	- Few
E Scarce	

Species

Comments

93

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THE ECOLOGY OF
FOX SQUIRREL
(SCIURUS NIGER)
IN NORTH CARO
IMPLICATIONS FOR
SURVIVAL IN THE
SOUTHEAST

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The gray color phase of the southeastern fox squirrel. The ecology of these populations is closely linked to the food resources of their pine-oak habitat.

THE ECOLOGY OF THE FOX SQUIRREL (*SCIURUS NIGER*) IN NORTH CAROLINA: IMPLICATIONS FOR SURVIVAL IN THE SOUTHEAST

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CONTENTS

ABSTRACT

The fox squirrels of North Carolina are one of a group of ecologically and morphologically similar squirrels occupying the Atlantic and Gulf Coastal Plains. Unlike the flourishing and well-studied reddish forms west of the Appalachian Mountains, these large, variably-colored fox squirrels have remained largely unstudied and seem to be declining over much of their range. Thus, over an 8-year period (1979–1986) fox squirrel populations in the Sandhills area and one coastal county of North Carolina were studied to obtain basic information on population biology and habitat requirements. Regular monitoring of 550 nest boxes led to 271 captures of 218 fox squirrels, with capture success being associated with food supply and seasonal weather conditions. Density estimates averaged 0.05 squirrels/ha and ranged from 0.01–0.17 at different sites for the 8-year period. Almost all reproduction occurred in the spring. Litter size averaged 2.5/breeding female and ranged from 1–5. Large numbers of litters, large litters and fall litters were observed only after successive periods of good food supplies. No evidence of more than one litter per female per year was found. Nestling weights suggest an approximate growth rate of 4.6 g/day during the 90-day dependency on the mother. The sexes were equally represented in all age groups. The apparent high adult representation in the age structure of most populations may reflect both the superior survivorship and the dominance of this group in the better habitats. Life span for the southeastern fox squirrel is unknown. Nestling mortality may be heavy at times, but adults appear to have few predators in today's forests. Adult body weight is a reasonably good indicator of population condition and future reproductive output and averaged 1006 g during the study. Recaptures were relatively infrequent (53) but almost always at, or very near, sites of initial capture. On the basis of nest box and telemetry data it was clear that these squirrels are largely solitary; only a few male-female and adult-juvenile pairs were found together in boxes. Laboratory studies revealed high levels of intraspecific aggression. Finally, the overall frequency of gray and melanistic color morphs was the same for both adults and nestlings, indicating little selective pressure against any particular morph. However, different proportions of the color variants at different study sites suggest the possible importance of dispersal, colonization, inbreeding and perhaps genetic drift in the squirrels' biology.

A total of 4040 nest box checks and 2008 radio locations provided data on habitat requirements and responses. Fox squirrels showed a marked preference (>80%) for open, mature, pine-oak habitat, especially longleaf pine-turkey oak (*Pinus palustris-Quercus laevis*), and the ecotones between pine and other vegetation types. In the summer, they used hardwood and wetland forests more often than would be predicted on the basis of availability. Climatic factors and fire appear to have profound effects on squirrel habitat and food resources. Temperature extremes partly regulate nest and food demands. Food supply was the most important determinant of fox squirrel biology in this study. Food supplies in today's pine-oak habitats are unpredictable, patchy and limited in

diversity. Acorns, longleaf pine cones, vegetative plant parts and fungi are the more important foods. Southeastern fox squirrels may have special evolved relationships with both longleaf cones and certain hypogeous, mycorrhizal fungi. Nesting sites, especially tree cavities or nest boxes, appear critical for reproduction and refuge, but natural hollows are scarce in today's relatively young forests. Squirrel activity was influenced by photoperiod, food supply and weather conditions. Home range estimates are among the largest for any tree squirrel: males 26.8 ha and females 17.2 ha (minimum convex polygon); males 43.7 ha and females 25.0 ha (95% ellipse). Seasonal ranges and activity levels vary with food availability. During late June and July, the period of lowest food supply, animals reduce activity and use of their ranges and seem to "disappear". They "reappear" in August when longleaf pine seed becomes available.

The present decline of the fox squirrel over much of its range can be attributed to habitat destruction and modification which reduces food supply and possibly favors the more competitive gray squirrel (*Sciurus carolinensis*). The mature forest to which this animal is adapted has been progressively reduced to mere remnants since the late 19th century, and only the squirrel's extreme vagility has allowed it to persist. Regional concern, additional study, and large-scale habitat acquisition and management will be required to stem the present decline.

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The interest, hospitality and support of the people of North Carolina is gratefully acknowledged, with special thanks going to K. Sprunt, H. Bellamy, P. Marshburn, J. Harper and the owners of Overhills, Inc. In the course of the study many people from the Coastal Plain provided assistance and encouragement, and we thank them for their interest and kindness.

Finally, special thanks are due to spouses and families whose assistance and sacrifices were crucial to the completion of this work.

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INTRODUCTION

Problem

The fox squirrels (*Sciurus niger*) of the southeastern coastal plain are the largest tree squirrels in the western hemisphere (Nowak and Paradiso 1983) and the most variably colored mammals in North America (Cahalane 1961). They were among the first species to greet European settlers of the tidewater South, were described by Catesby (1771), Bartram (1791), Audubon and Bachman (1849), and other early American naturalists and have been hunted for food and sport for generations. Yet, with very few exceptions they have received almost none of the attention, study, and solicitude usually granted to species of such attributes. It is almost as if long familiarity has actually bred a kind of disinterest among public and professional admirers of wildlife. Perhaps then, it is not surprising that the steady decline of these squirrels has generally gone unnoticed and that today they occupy only a fraction of their former range. It is also clear that there are only limited relevant biological data to help counteract this decline. Thus, the present study represents an attempt to reverse this process by bringing together pertinent background information on these animals, by presenting the results of our recent field and laboratory work, and by suggesting some elements of a management plan. It is hoped that this study will provide a basis for both additional research and some urgently needed conservation measures.

Background and Rationale

Perhaps nothing can bring the status of the fox squirrel into focus more sharply than a short account of the factors which led up to the present study. In 1977, as part of a behavioral and physiological study of the feeding energetics of tree squirrels, we needed live fox squirrels as the largest representatives of the nut-eating guild which, in the east, also includes the flying (*Glaucomys volans*), red (*Tamiasciurus hudsonicus*), and gray (*Sciurus carolinensis*) squirrels (Weigl et al. 1983). Numerous works on mammals and a variety of state and regional field guides described the fox squirrel's wide range, abundance, and basic biology. Since fox squirrels were known from eastern North Carolina, we attempted to capture animals in areas of the Coastal Plain where the species was reputed to be abundant (F. Barkalow, pers. comm. 1977). The fact that no one in the region seemed to have any first-hand experience with fox squirrels or really knew how to trap them, however, should have alerted us to potential difficulties. When several months of work yielded no animals, few sightings, and only limited signs of feeding and nesting activity, we were forced to choose between giving up or expanding our knowledge of the species.

Extensive exploration of the literature revealed that no ecological study of the fox squirrel had ever been conducted in North Carolina, and the total

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research effort expended on the species in the Southeast before 1978 consisted of an old study from Florida (Moore 1957), several short papers by Flyger and his associates (e.g. Flyger and Lustig 1976) on the Delmarva subspecies, master's thesis research in Georgia (Hilliard 1979), and incidental information from state and taxonomic literature (e.g. Bangs 1896, Lowery and Davis 1942, Moore 1956, Williams and Humphrey 1979). There was voluminous literature on the species west of the Appalachian Mountains (ex. Allen 1942, Baumgartner 1943, Brown and Yeager 1945, Bakken 1952, Packard 1956, Madson 1964, Nixon et al. 1975, 1984, Havera and Smith 1979) and it was soon evident that data from these western animals were being used to describe and manage fox squirrels in the Southeast. By implication, southeastern fox squirrels were being considered southern outliers or variants of the main populations of the U.S. heartland.

Examination of fox squirrel specimens at the American and National Museums provided some idea of the species' geographic variation. The differences between the eastern and western squirrels were spectacular. Fox squirrels from the west were the reddish, moderately large (generally less than 900 g) animals well described in the literature. The eastern animals were huge (up to 1400 g) and strikingly colored—silver, gray, black, gold—often with black masks and with distinct white markings on nose, ears, and feet. Not only were the two groups very different in color and size but the fact that western squirrels generally inhabited deciduous forests while those of the East occupied mature pine-oak woodlands suggested some major ecological differences between the two forms. Thus, our preliminary research at this time indicated that little data existed on southeastern fox squirrels, that the eastern and western populations differed in morphology and ecology, and that the eastern forms were being managed on the basis of data from the West.

The status of the fox squirrel in the Southeast became another factor in our study. The Coastal Plain of North Carolina and other southern states is undergoing rapid deforestation and forest modification, due on one hand to accelerated residential and agricultural development, and on the other to the implementation of intensive management techniques in commercial forests. While deforestation associated with development has a clear impact on wildlife, it has not always been recognized that current timber practices—replacement of native species by nursery seedlings (mostly loblolly pine, *Pinus taeda*), large scale monoculture, early harvesting (25–30 year rotations), and vigorous control of hardwoods, especially oaks—can have an equally profound effect on wild populations. A number of animal species appears to be dependent on the mature pine-oak regions of the South and East and two in particular, the red-cockaded woodpecker (*Picoides borealis*) and pine barrens tree frog (*Hyla andersonii*), are already considered endangered or of special concern (Cooper et al. 1977). The fox squirrel of the Southeast is also particularly vulnerable, for we quickly came to realize that, in North Carolina at least, it is abundant only in or near mature pine-oak habitat. As a relatively large mammal (approximately 1000 g) in a low diversity and often trophically unpredictable environment, the fox squirrel might well require large areas for support and thus might be

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considered a good indicator of the quality of oak-pine habitat for other wildlife. A three-page survey sent to all wildlife biologists and game officers in the southeastern sector of North Carolina revealed that only a few areas supported substantial fox squirrel populations and that the perceived decline in the species was in some way associated with habitat modification. Three other groups of eastern fox squirrels are at present considered of special concern or endangered, due mainly to changes in habitat: the Delmarva fox squirrel, *S. niger cinereus* (Taylor and Flyger 1974, Taylor 1973) and two subspecies in Florida, *S. niger shermani* and *S. niger avicennia* (James Layne, per. comm. 1979, Williams and Humphrey 1979). In addition, a recent survey of fox squirrel populations in South Carolina (Wood and David 1981) indicates a general decline of the species in yet another area. In sharp contrast with the plight of the eastern fox squirrels, those of the West have generally maintained their numbers and expanded their range to the Rocky Mountains (Hibbard 1956, Madson 1964).

The fox squirrel is a game animal in those states where it is not protected. In the past few years, because of its size and spectacular color variation, it has become a trophy animal, hunted more for taxidermy than for food. In terms of hunter participation, squirrels are among the more popular game species in the eastern United States (Barkalow and Shorten 1973). While less numerous than the wide-ranging gray squirrel, the fox squirrel has been the dominant squirrel species in the southeastern pine forest.

The present study thus grew out of an initial need for fox squirrel specimens in 1977, followed by a growing awareness of the southeastern fox squirrel's uniqueness, precarious status, and virtual omission from the wildlife literature. Two years of preliminary work during 1978 and 1979, subsequently helped to define the following objectives and constraints of our research. First, given the limited nature of past work, our study would have to be broad in scope and stress basic biology. Second, we needed to build on the few earlier studies (not repeat them) and concentrate on those aspects of fox squirrel biology, such as demography, habitat utilization, and behavior, which we considered most critical to the animal's survival and conservation. Third, because of the relative rarity and high dispersion of fox squirrels and the problems inherent in studying them, we realized that only a long-term study would begin to describe their ecology. Most previous studies had been short-term or intermittent—some just a few months—and the total number of animals observed or collected less than thirty (Lustig and Flyger 1975, Hilliard 1979, Flyger and Smith 1980). The present study presents data taken over a 10-year period, with an intensive phase of 8 years. Finally, since our research subject was rare and apparently declining over much of its remaining range, we ruled out many techniques involving high risks to, or destruction of numbers of squirrels. With trapping ineffective at most study areas and shooting inappropriate, we were forced to develop and rely upon procedures which permitted the accumulation of data with minimal disturbance to squirrel populations. The following study is thus an attempt to define (in the broad sense) the fox squirrels of the Southeast, to summarize several years of research on their population biology and habitat requirements, and to suggest some steps necessary to manage the species if it is to remain part of the eastern fauna.

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DEFINITION OF THE SOUTHEASTERN FOX SQUIRREL

Although the present study has concentrated on the fox squirrels of eastern North Carolina, *Sciurus niger niger*, we believe that our findings largely apply to a whole group of southeastern populations. It is thus important at the outset to define a little more precisely the identity, approximate range, and characteristics of the animals we are lumping into the "southeastern fox squirrel" category. Studies of almost 700 museum specimens from the entire range of the species suggest the existence of three morphologically and ecologically different but intergrading groups of fox squirrels (Williams 1977, Sherman et al. 1984, and Weigl et al. in prep.). The southeastern fox squirrels of our study are very large (900-1200 g), gray, agouti, and black animals, often with black markings on the head and with white noses, ears, and paws. At present they are largely confined to open pine or pine-oak habitats of the Atlantic and Gulf Coastal plains from the Delmarva Peninsula to central Florida and from there to the edge of the Mississippi River flood plain (Fig 1). Included in this group are Hall's (1981) *S. n. cinereus*, *S. n. niger*, *S. n. shermani*, and *S. n. bachmani*. "Western" fox squirrels are smaller (600–900+ g), reddish forms, generally inhabiting deciduous and mixed forests, from the valleys of south central Pennsylvania, the Appalachian Mountains and the uplands of the Gulf states, west to the prairie and more recently to the front range of the Rocky Mountains (Fig. 1). The subspecies *S. n. rufiventer*, *S. n. vulpinus*, *S. n. ludovicianus* and *S. n. limitis* are included in this group (Hall 1981). While eastern and western forms are now widely separated in the Atlantic states, considerable gene flow is possible in the Gulf region. A third but strictly artificial group is composed of two small, variably colored, and isolated forms, occupying what appear to be trophically poor and often wet habitats: *S. n. avicennia* of southern Florida and *S. n. subauratus* of the Mississippi flood plain.

The coloration, habitat, and size differences of eastern and western fox squirrels suggest some type of long-term or repeated isolation in the past history of the species (Weigl and Steele 1986). Prior to European settlement the total species range was much more extensive (Taylor and Flyger 1974) and may have included sizeable zones of intergradation in the Northeast and south of the Appalachian Mountains. Squirrels occupying western Pennsylvania, New York and New England were reddish or tawny colored forms (Bangs 1896, Poole 1944), often assigned to the subspecies *S. n. vulpinus* (Flyger and Lustig 1976). The white belly of southern members of the *vulpinus* group is very likely the result of interbreeding between western-type squirrels and the northern extension (eastern Pennsylvania, New Jersey) of the gray and white Delmarva form. In parts of northern Georgia, Alabama, Mississippi, and Louisiana more extensive interbreeding occurred, producing reddish or tan squirrels with some of the black and white markings of the southeastern populations (Moncrief 1987). It is not clear whether the different coloration of southeastern and western squirrels is the result of selection in pine forest and hardwood habitats respectively, or merely the result of random processes in isolated regions during the

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Figure 1. Range map of the fox squirrel, *Sciurus niger* (modified from Hall, 1981). 1. *S. n. avicennia*. 2. *S. n. bachmani*. 3. *S. n. cinereus*. 4. *S. n. limitis*. 5. *S. n. ludovicianus*. 6. *S. n. niger*. 7. *S. n. rufiventer*. 8. *S. n. shermani*. 9. *S. n. subauratus*. 10. *S. n. vulpinus*.

late Pleistocene. The rather distinct habitat differences of the two forms and their very different responses to human modification of these habitats may indicate considerable isolation and specialization in the past.

Our studies of museum specimens have pointed to another major difference between the southeastern and western populations of fox squirrels. Western populations follow "Bergmann's Rule;" that is, they show a size cline, with larger squirrels in the north and progressively smaller animals occupying zones of decreasing latitude (Weigl et al. in prep.). On the other hand, fox squirrels of the Atlantic Coastal Plain not only are absolutely larger than their conspecifics to the west but also show a "reverse Bergmann" size cline, with the largest animals inhabiting northern Florida (Williams 1977). Of particular significance to these size considerations is the unique status of the fox squirrel population (*S. n. ludovicianus*) of western Louisiana and eastern Texas. Inhabiting the western extension of the longleaf pine forest—the common habitat of the southeastern forms—these typically reddish squirrels are distinctly larger than any surrounding populations. Taken together, these clines and the distinctiveness of the *ludovicianus* animals implicate some habitat factor as an explanation of this size variation, and at the same time provide additional evidence for past separation of eastern and western populations in different habitats. Thus, on the basis of differences in coloration, range, habitat, and size variation it is quite likely that southeastern and western fox squirrels evolved in isolation in separate refugia during some portion of the Pleistocene, eventually colonized different regions and habitats in the North, and subsequently established variable zones of overlap and interbreeding (Weigl and Steele 1986, Moncrief 1987).

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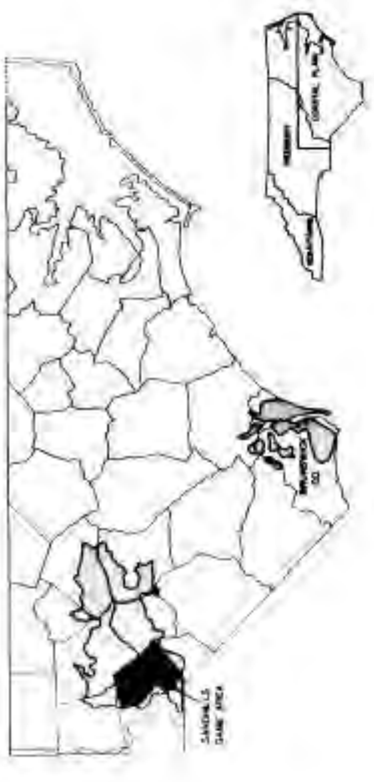

Figure 2: Locations of study sites in Sandhills Game Area and Brunswick County. Stippled areas show extent of longleaf pine-turkey oak-wiregrass habitat (Modified from Clay et al. 1975).

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STUDY AREAS

The study was conducted in the North Carolina Sandhills (Moore, Richmond, Scotland and Harnett counties) and in eastern Brunswick County, two areas of the Coastal Plain known to support fox squirrel populations and representative of habitat conditions for the species over much of the Southeast (Fig. 2). The Sandhills region is located in the south central part of North Carolina near the boundary between the Piedmont uplands and the Coastal Plain. It consists of rolling hills (100 m or more above sea level) with coarse sands underlain by clays and dissected by slow-flowing streams. Brunswick County is a tidewater coastal area of low relief in the extreme southeastern section of North Carolina. Here low sand ridges and flats are interspersed among a great variety of wetlands from blackwater and tidal streams to flood plains, swamps, pocosins, bays, and cypress (*Taxodium*) ponds.

The climate of much of North Carolina is considered "humid subtropical" with mild winters and long, hot, and humid summers (Clay et al. 1975). While westerly winds and fronts dominate much of the state's weather patterns, in the Coastal Plain maritime influences moderate winter and summer extremes. Mean minimum January temperatures are above 0°C in the Sandhills and above 4°C in Brunswick County. Mean maximum July temperatures are 32–33°C and 29–30°C respectively. Winter extremes below -12°C and summer extremes over 38°C were not uncommon during the eight years of the study. Precipitation which averages between 112 and 140 cm annually, is fairly uniform, with small peaks in summer and winter.

Apart from the general effects of climate, elevation, and geologic substrate, the soils and vegetation of the Sandhills and Brunswick areas are largely products of the water table—of its proximity to the surface and seasonal variation. Coarse sands, especially on the higher ridges and slopes, retain little water and generally have lower water tables and more xeric conditions. Clay substrates, lower slopes, flats, and flood plains are usually associated with higher water tables, better water retention, and mesic or hydric conditions. Water availability and periodicity have also affected rates of accumulation and decomposition of organic matter derived from vegetation, and thus, soils may range from largely inorganic sands, through reasonably fertile loams, to pure peat. Finally, the position of the water table has marked effects on the frequency, extent and severity of natural or human-caused fires. Upland and sandy areas burn frequently and extensively; pocosins and flood plains only during periods of drought.

Only a few of the many plant communities of the Coastal Plain are known to support substantial fox squirrel populations. Mature, open, pine-oak forests of the sandy ridges and slopes were the core areas of our study sites. These areas vary widely in size but are usually surrounded by, or interspersed with, more mesic hardwoods or mixed woodlands, or various kinds of wetlands. The core areas themselves are dominated by only a few species, typically longleaf pine, turkey oak, some bluejack oak (*Quercus incana*), and a groundcover of

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wiregrass (*Aristida stricta*) and dwarf huckleberry (*Gaylussacia dumosa*). This "fire climax" community commonly consists of large (18–30 m), well-spaced pines and an understory of scattered or clumped oaks. Moister slopes or areas with better soils and less frequent fires support patches or belts of such species as blackjack oak (*Q. marilandica*), post oak (*Q. stellata*), southern red oak (*Q. falcata*) and sometimes loblolly pine and hickory (*Carya* spp.). Here the trees are taller and closer together and the groundcover of grasses, ericaceous shrubs and ferns more dense and continuous. Still moister conditions near streams or in floodplains produce dense stands in which the longleaf pine and xeric oaks have been replaced by pond pine (*P. serotina*), willow oak (*Q. phellos*), water oak (*Q. nigra*), live oak (*Q. virginiana*—coastal regions only), tulip poplar (*Liriodendron tulipifera*), sweetgum (*Liquidambar styraciflua*), blackgum (*Nyssa sylvatica*), red maple (*Acer rubrum*), holly (*Ilex opaca*), and dogwood (*Cornus florida*). Such areas have lush ground covers of shrubs (e.g. *Myrica, Ilex*), greenbriar (*Smilax*), grape (*Vitis*) and cane (*Arundinaria gigantea*). Two special types of wetlands, cypress-gum swamps and pocosins or bays, commonly border on the longleaf pine-oak habitats. In regions of frequently standing water—along floodplains, blocked channels, and ponds—tall, dense stands of cypress, tupelo gum (*Nyssa aquatica*) and swamp gum (*Nyssa biflora*) form a sharply defined community with only a narrow shrub zone separating it from the pine-oak forest. In poorly drained, peat-lined flats and depressions, pocosins or the famous oblong bays of the Carolinas abut against the drier forests. These are impenetrable shrub bogs consisting of scattered pond pine and vast arrays of evergreen shrubs and small trees—*Persea, Gordonia, Lyonia, Myrica, Cyrilla, Zenobia, Magnolia,* and *Ilex*. The vegetation described above represents the more common and extensive plant communities available to fox squirrels in our study areas.

In addition to the array of natural plant communities, fox squirrels have access to a number of human-modified habitats. Since colonial times the pine-oak forests of the Southeast have been exploited for wood products, naval stores, agriculture, and settlement. Later, the swamp forests were harvested and many of the wetlands drained and converted to farmland. All of our study sites thus represent naturally-regenerated forest and sometimes some of the successional stages following agriculture, timber harvest, or human occupation. Among the more common man-made habitats in or near our study areas are oak scrub, pine plantation, abandoned field, clear cut, live oak park, and roadside. An oak scrub community is the product of complete pine harvest, fire exclusion, and rampant sprouting and spreading of the remaining oaks. The characteristic dense stands of stunted oak trees inhibit pine regeneration and, without thinning, produce little mast. Pine plantations, usually of loblolly pine, are little more than heavily managed monoculture. Most are cut before they produce any appreciable quantity of seed, and, while they may provide some nesting sites and fungi for squirrels, they are not suitable long-term habitat. Live oak avenues and parks are expanses of open ground with well-spaced, planted live oaks and other trees. They usually flank long, sandy roads or surround old

house or plantation sites. The oaks, pecan (*Carya illinoensis*) trees, and other species can be a major source of food for squirrels. Roadsides, clear cuts, fields, and human habitations round out the available habitats on our study areas. All are used or at least traversed by fox squirrels. Unlike many other fox squirrel studies (Hilliard 1979, Flyger and Smith 1980), the major sites selected for this research lacked agricultural land, picnic areas, trash heaps and other potential sources of supplementary food.

Table 1. General description of the 12 major study sites.

Site	Abbreviation	Location	Approximate area (ha)	Number of boxes	Box arrangement	Major Plant communities
Gum Swamp	GS	Sandhills	77	13	lines	Pine-oak, hardwood, wetland
Gardner Farm	GF	Sandhills	40	26	line	Pine-oak, oak scrub
Laurel Hill-A	LH-A	Sandhills	27	26	grid	Pine-oak
Laurel Hill-B	LH-B	Sandhills	103	28	line	Pine-oak, hardwood
Indian Camp	IC	Sandhills	130	47	line	Pine-oak, hardwood, wetland
Block L	BL-L	Sandhills	135	37	line	Pine-oak, hardwood
Block O	BL-O	Sandhills	202	40	line	Pine-oak, hardwood, wetland
Block W	BL-W	Sandhills	17	18	grid	Pine-oak, hardwood
Camp MacKall	CM	Sandhills	36	50	grid	Pine-oak, hardwood, wetland
Overhills	OH	Sandhills	116	14	lines	Pine-oak, hardwood, wetland
Single Pond	SP	Brunswick Co.	107	31	lines	Pine-oak, wetland
Pleasant Oaks	PO	Brunswick Co.	387	23	line	Pine-oak, oak scrub, wetland

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MATERIALS AND METHODS

Study Sites

Specific sites were selected for intensive study from the available pine-oak forests of the Sandhills and Brunswick County. In the Sandhills, nine sites were established in the Sandhills Game Lands, a 22,000-hectare wildlife management area of the North Carolina Wildlife Resources Commission (Fig. 2). One additional area was chosen from a private estate (Overhills, Inc.) 50 km to the northeast (Table 1). In Brunswick County, two major study sites were selected after preliminary work in eight areas; both were parts of large private estates near the Cape Fear River.

Capture Techniques

During the early part of the study (1977 and 1978) and at intervals throughout the next eight years, trapping with Tomahawk live-traps (#201, #202 and #206) was attempted for periods of up to 10 days and for a total of 900 trap nights. Because trap success was poor (only 8 animals captured), even with prebaiting, this technique was abandoned.

The need for nesting, reproductive and other population data led to the use of nest boxes as the primary capture method. Not only have nest boxes proven useful in studying a number of squirrel species (Barkalow and Soots 1965, Goetz et al. 1975, Pederson 1978, Nixon et al. 1984, Doby 1984), they have also been found to be more attractive than natural cavities to gray and fox squirrels (Barkalow and Shorten 1973, McComb and Noble 1981a). Two kinds of nest structures were used: wooden boxes (35 x 25 x 25 cm) and folded tire halves (Burger 1969). By the second year of the study a total of 550 nest boxes had been erected in the 12 major study sites and for varying periods at 11 additional areas (hereafter referred to as minor sites). These were checked either at dawn, dusk or at night, 2-3 times per year: once in late fall, once in late February to early April, and often again in late April and May. Each summer, the boxes at a few of the major sites received an additional check in an attempt to obtain animals for telemetry studies.

No systematic check of leaf nests was attempted, although the abundance and location of such nests were noted and many were examined, especially in the early part of the study. Because few animals were ever found in leaf nests in the study areas and because checks resulted in considerable disruption of the nests themselves, leaf nest monitoring received little emphasis during most of the study. Squirrels in nest boxes were first driven into a cage with a sliding door and then transferred to Tomahawk traps prior to examination. Filling the trap with leaves and pine needles was found to have a calming effect on the captives and prevented injury and gnawing. Squirrels were then shunted into a tapered cloth cone (zippered at both ends for easy access), weighed, marked in each ear with No. 1 monel fingerling tags (National Band and Tag

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Co.) and examined to determine reproductive condition, age, nutritional state, coloration and any identifying marks. In the course of the study only one recaptured squirrel was observed to have lost both tags, but because scars from the tags were obvious and many animals could be identified by color pattern alone such losses were of little significance in recognizing individuals. Pink, hairless young were not marked and were handled as little as possible. Animals were assigned to one of three age categories: nestling, i.e. dependent on the mother; juvenile, independent individuals under 800 g; and adult. All squirrels were released at their site of capture either immediately after marking or, if radio-collared, within 8–12 hours of capture. During the last six years of the study, gray squirrels also were weighed, marked, and sexed and flying squirrels counted and sexed. Fourteen fox squirrels were removed for behavioral studies and maintained in outdoor cages (2 × 2 × 4 m) at Wake Forest University. Captives received a variety of nuts, seeds, and fruit in addition to Purina lab chow and a vitamin-mineral supplement mixed into peanut butter. Low densities (two squirrels per cage) and individual nest boxes seemed necessary to maintain the health of captives.

Food Studies

Surveys of available foods were carried out on each visit to major study sites. At each nest box or at intervals along a transect through a site each of the following food-related characteristics was rated on a 5-point scale and recorded on a special data sheet (See Appendix A): frequency and dominance of each food plant species, its distribution, its current food production, and the plant-to-plant variability of production. Incidental food resources were listed. The resulting semiquantitative estimate of food availability was sufficiently accurate to establish the food categories "none", "low", "moderate" and "high" used to interpret the other findings of this study.

In June, July, and August of 1983 and 1984, green longleaf pine cones were collected from trees near the study areas and their seeds extracted, dried at NPC and (in 1983) analyzed for total energy content in a Gentry bomb calorimeter (Gentry Instruments, Inc., Aiken, S.C.). Cone samples were taken at two-week intervals and consisted of three cones from each of 10 trees. Such a procedure provided information on the nutritional status of these cones prior to and after fox squirrel use of this food source in early August.

Fox squirrels were too scarce to permit much collecting for analysis of gut contents but roadkills and hunter kills were examined qualitatively using the study by Smith (1970) as a guide. In the summer of 1984, stomach and fecal samples were analyzed for fungi by C. Maser and J. Trappe and their associates at the Forestry Sciences Laboratory at Corvallis, Oregon. When all guts tested were found to contain fungal spores, two investigators from that laboratory, M. Castellanos and Y. Wang, visited the Sandhills study area to help locate and identify representative hypogeous fungi.

On the basis of estimates of available foods, observations of feeding behavior, and study of the remains of materials eaten, it was possible to obtain an idea of both the food habits and the seasonal and annual resource base of the fox squirrels. Food availability varied greatly from year to year largely because of the limited number of potential food sources and the high variability in food production. Thus, early in the study we came to recognize five distinct food seasons: 1) spring (March 15–May 31), a period of diverse and relatively abundant foods; 2) early summer (June 1–July 31), a hot, dry time with very limited food resources; 3) late summer (August–September), the season of longleaf cone harvest; 4) fall (October–January 14), potentially the best food period, combining the end of the longleaf seed supply and the major acorn crop; 5) winter (January 15–March 14), a season of variable and declining food resources depending on fall crops. Annual and seasonal food estimates over the eight years of the study were used to evaluate variations in population parameters, habitat use, and behavior.

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Telemetry

Twenty adults exceeding 935 g in weight were radio-collared for study of activity patterns, movement and home range. Animals were anesthetized with methoxyflurane (Metofane, Pitman-Moore, Inc., Washington Crossing, NJ, 08560; Barry 1972) and collared with either a Dav-tron model SL-502 transmitter (Dav-tron, Inc., 400 Penn Avenue South, Minneapolis, MN 55405) or after May, 1982, a Telonics model 090 unit (Telonics Inc., Mesa, AZ 85201). The larger-than-expected home ranges of these fox squirrels made the > 1 mile range of the Telonics equipment essential for the study. Dav-tron transmitters had a life span of 6 weeks; Telonics, 3–4 months. The Dav-tron unit weighed 28 g and the Telonics, 38 g; thus, on the basis of squirrel weights of 935–1250 g, the maximum load of the collar and transmitter unit was never more than 4.1% of an animal's body weight. Two receiving systems were employed: a Dav-tron model RMX receiver and later two Telonics TR-2 receivers. All receivers were used with a hand-held yagi antenna.

After radio collaring, squirrels were monitored three days at a time at two- to three-week intervals during the life of the transmitter or, in a few cases, until the squirrel slipped the collar. Because our goal was the acquisition of data on habitat use, movement, and other activities in addition to home range determination, locations were determined every 60–90 minutes during daylight hours. Each location was obtained from 2 or 3 bearings from fixed points or, in some cases, from direct observations of an animal or nest. Time, weather conditions, and levels of activity (active or inactive) were recorded at each check.

Locations from radio tracking were plotted on maps drawn from aerial photographs (scale 1:2490). The X and Y coordinates for each point were entered in a microcomputer file, and home range and movement statistics were calculated by means of a BASIC program written for this study (Ha 1983). In order to render the telemetry results comparable to other such studies, both the minimum convex polygon ([illegible]) and the 95% probability ellipse (PE) were

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calculated (Jennrich and Turner 1969). In addition, the distance moved per hour (D/T) was used as a measure of activity and movement within the home range. The D/T represents the distance (in meters) between two sequential locations divided by the time elapsed (in hours) between those locations. If the elapsed time was greater than 4 hours, the observation was omitted from the analysis. The median D/T (MD/T) was calculated for each squirrel. Large MD/T values were characteristic of highly active squirrels which covered much of their range each day; small values generally indicated low levels of activity and movements confined to a limited part of the range. Finally, to obtain an additional measure of the use of the home range the MAP (minimum area vs. probability) index (Ford and Krumme 1979) was calculated with the aid of a computer program written by Anderson (1982). The MAP(50) used in this study is the minimum area required to encompass 50% of the telemetry locations. The ratio of the MAP(50) to the MCP thus provided a measure of the intensity and evenness of space use within a given home range. Ratios near zero indicate uneven use of the home range, higher values more even use of the range.

Habitat Preference

Three measures of habitat preference were determined from the habitat use patterns of the squirrels studied. First, the location of the most heavily-used nest boxes provided an indication of areas preferred for nesting. It was clear early in the study that only a small percentage of the available boxes were used by fox squirrels. Accordingly, point-quarter vegetation analyses were performed for the 25 most-used fox squirrel boxes, 25 most-used gray squirrel boxes, and 25 boxes chosen at random. Such measures could be used to construct hypothetical (composite) stands for each group of boxes. At the time of the vegetation analyses, each of the 75 boxes was also rated for 30 additional site characteristics. These data, placed in fox squirrel, gray squirrel, and random groupings, were compared by chi square and factor analysis to determine the nest box variables which might define the requirements of the two species. Second, since many boxes were set out at fixed intervals along forest roads which traversed many plant communities, use of boxes in one habitat type or another was a further indication of habitat preference. Finally, from telemetry data it was possible to discover the areas used for nesting, feeding, and other activities and compare patterns of use of different habitat types with the overall availability of these habitats in the study site. To carry out this analysis, radio locations were plotted on vegetation maps drawn from aerial photographs and ground surveys. Three inclusive plant communities were recognized: longleaf pine-oak forest, bottomland habitat (including stream borders and bays) and scrub oak-field vegetation. Since all the study sites consisted of large blocks of pine-oak forest and contiguous areas of the other plant communities, a special "edge" habitat 50 m wide (25 m into each adjacent habitat) was drawn along the pine boundary. This procedure was prompted by repeated mention of edge use in the literature (Smith and Follmer 1972, Flyger and Smith 1980, Nixon et al.

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1984) and by the apparent clustering of radio locations along ecotones in our study. For each site the area of each vegetation type was determined from the maps with the aid of an Apple II Graphics Tablet. The number of radio locations in each plant category provided a measure of squirrel habitat use. The proportions of different vegetation types within the study site represented the habitat "available" to a squirrel and permitted the calculation of "expected" values for habitat use. (The "available" habitat was actually limited to a rectangle drawn around all home ranges within a study site such that no home range was closer to the edge of the rectangle than one-half the longest-observed range length.)

Experimental Studies

In order to obtain more accurate and reliable interpretations of phenomena noted in the field during the early years of the study, several experiments were carried out in both the field and the laboratory. Some of these have been reported elsewhere (Steele et al. 1984 and 1985) and will be summarized later in the monograph. Two additional studies are outlined briefly here.

1. The effect of supplemental food. Because of our increasing awareness of the influence of food supplies on fox squirrel numbers and behavior, supplemental food was provided to two of the nest box grids from summer, 1983 to winter, 1985. Four hopper-type feeders (spaced evenly on the grids) were attached to trees 3–4 m above the ground and kept filled with a mixture of corn, soybeans, and sunflower seeds. Welded wire cages were fastened to the hoppers to exclude animals larger than fox squirrels. We predicted that the population size and number of captures would increase at these sites as the combined result of the added food and the unusually low mast crop during the fall of 1983.

2. Longleaf pine cone use and body size in seed predators. In August, the large (200–400 g), green cones of the longleaf pine become a major, if not the sole food of the fox squirrel in the Coastal Plain. The use of this critical resource may not only provide some insight into the fox squirrel's exceptional size but also reveal the potential outcome of competition for this resource where the fox and gray squirrel occupy contiguous habitats. In order to explore the relationship between body size and cone handling ability we studied the feeding behavior of three groups of squirrels: gray squirrels weighing approximately 500 g, midwestern fox squirrels at about 800 g and North Carolina fox squirrels at 1000 g. Each group was provided with longleaf pine cones for four weeks in addition to their normal diet. All ate the cones readily. Thereafter, the squirrels were timed eating cones of known weight 2–3 times per week for four weeks. After each feeding trial the cone cores were removed and weighed. Thus it was possible to obtain both feeding times and rates of cone bract removal with different sized cones. In addition, the handling and feeding behavior were videotaped to see if there were differences in handling behavior.

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RESULTS AND DISCUSSION

Population Biology

General

Nest box checks in both major and minor study sites during the period 1979–1986 resulted in the capture of 218 individual fox squirrels, 271 total captures, and 193 animals which were marked and released at the site of capture. Thus there were 53 recaptures. Twenty-five squirrels remained unmarked either because they were too small for tagging at the time of capture or because they were among the 14 animals taken to the laboratory for behavioral studies. In all, 4040 nest box checks were made during the study. Generally more squirrels were captured in the spring than in the fall and early winter season (160 vs. 61). This difference is at least partially due to the presence of non-mobile nestlings during the spring months. Fox squirrels, like gray and flying squirrels rarely use boxes in the summer (Barkalow and Soots 1965, Doby 1980) and thus the capture data represent fall, winter and spring only.

A better representation of these fox squirrel populations can be obtained from a consideration of the major sites alone, since these areas received the greatest attention and produced the majority of the captures. Table 2 summarizes pertinent data for the 12 major sites. Although all but three of the sites had been established before 1979, because of initial manpower limitations and the large number of other nest box locations, systematic checking was at first confined to five (Spring 1979), and then eight (1979–80) of the major areas which, on the basis of squirrel sign and sightings, were considered the best potential capture sites. However, captures, signs of activity and food supplies were so low during the early years of the study (1977–1979) that no extra nest box surveys were attempted. Since the nest boxes had been in place for considerable periods of time by the spring of 1979 it is highly unlikely, in light of later capture success, that the low capture rate can be attributed to anything but low squirrel numbers. It is also clear that the presence of the boxes themselves prior to 1979 did not increase the resident populations. Capture success showed improvement only after 1979–80 in association with better food supplies. As can be seen from the data on captures and active nests per 100 boxes checked, increased box checks and the inclusion of more sites (1981–83) did not after a certain point produce either higher capture or active nest discovery rates. Nest box data for the entire study period describe squirrel populations which were depressed initially, grew steadily for 4–5 years and then levelled off toward the end of the study. However, when the low food, body weight, and reproductive levels of 1983–84 are also taken into consideration (see below), it becomes evident that the increase in captures in that year might also be attributed to greater box use for energy conservation (escape from the cold by lean animals) rather than to continued population growth. Thus, while nest box data provided reasonable indices

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Table 2. Summary (fall to summer) of fox squirrel captures (no. cap.) (excluding nestlings) and active boxes (act. b) for the 12 major study sites (Sp = spring).

Site	Year								Total captures	Total individuals	Captures per 100 boxes checked	Index per 100 boxes checked
CA no. cap.	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	12	[illegible]	[illegible]
no. act. b	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]			
CP no. cap.	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
no. act. b	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]			
[illegible] no. cap.		[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
no. act. b		[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]			
[illegible] no. cap.	[illegible]		[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
no. act. b	[illegible]		[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]			
[illegible] no. cap.			[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
no. act. b			[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]			
[illegible] no. cap.		[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
no. act. b		[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]			
[illegible] no. cap.				[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
no. act. b				[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]			
[illegible] no. cap.			[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
no. act. b			[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]			
[illegible] no. cap.	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
no. act. b	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]			
[illegible] no. cap.		[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
no. act. b		[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]			
SP no. cap.	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]			27	[illegible]	[illegible]	[illegible]
no. act. b	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]			[illegible]			
[illegible] no. cap.		[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
no. act. b		[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]			
Total no. cap.	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
no. act. b	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]			

of squirrel numbers, they were much more reliable and useful if combined with other measures of animal and environmental conditions.

In addition to providing a measure of general population trends, the capture data raise some interesting questions about the relationship between squirrel numbers and special features of various habitats. While the values for number of individuals and number of captures per 100 boxes for the 12 sites are quite similar there appears to be no clear correlation between squirrel numbers and either area of a site or number of available nest boxes (Table 1). In fact, small to moderate sized sites with relatively few boxes often produced the most squirrels. These findings imply that some quality of the better sites themselves was important in maintaining fox squirrels. As it turns out, the 6 best sites are narrow strips or irregular patches of open forest surrounded

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by water, wetlands, plantations, successional forest, or dense hardwoods.

A comparison of captures and active nests for each site suggests considerable variation in squirrel numbers and activity over the eight-year period. Because the number of boxes did not change, some factor or factors at each site must have affected the survival or residence of the fox squirrel populations. In some cases, especially early in the study and at some sites later, low capture success can be attributed to the virtual absence of food. There was also some indication that warm weather and abundant food in the fall retarded the reoccupation of the nest boxes. On the other hand, good food supplies at a site were a reasonably good predictor of increased activity and box use later in the year. Whatever the apparent variation by site and year, the capture data make it very clear that fox squirrels occupying these Coastal Plain habitats are exceedingly rare in comparison to almost any other squirrel population studied in recent years (Gurnell 1983).

Density

The ability to recognize active nests was critical for estimating the size of fox squirrel populations. Active fox squirrel nests could be identified on the basis of the size, contour and "neatness" of the cavity left behind in the nesting material upon the animal's departure. Nesting material in older nests showed distinctive types of disarray. Gray squirrel nest cavities were characteristically smaller and narrower. Years of removing squirrels from nest boxes provided a continuous review of species-specific nesting habits.

In spite of site and yearly differences in numbers, there is a great similarity in the capture:active nest ratio for all sites. The average ratio of 2.8 active nests per squirrel permitted the estimation of population size even if no animals were actually caught in a particular box check. Estimates of squirrel numbers at our major sites, based on actual captures and active nests, are shown in Table 3. The estimates are generous (i.e., rounded upward) on the assumption that we were likely to miss a few squirrels which did not regularly use the nest boxes or whose ranges only marginally included our study areas. When these estimates are expressed in terms of the areas of each site (Table 3) the resulting density approximations clearly reveal the extremely low values characteristic of our study areas. The mean density of 0.05 squirrels per hectare is lower than all but two of the 31 density values cited by Gurnell (1983) in his review of seven tree squirrel species, and the two low values mentioned, one for *S. niger* on the prairie (0.05) and one for *S. vulgaris* in Spain (0.03), were atypical for the species or subspecies under consideration. Densities for eastern fox squirrels recalculated from Moore (1957) and Hilliard (1979) were approximately 0.33 and 0.26 squirrels per hectare respectively. Moore's study was approximately two years in duration; Hilliard's was based on one winter–spring season and one April a year later. The highest annual densities from our 12 study sites during an eight-year period were 0.35, 0.28, 0.22—values comparable to those of the above researchers. More recently, on the basis of surveys in a pine forest in northern Florida, S. Humphrey

Table 3. Estimates of fox squirrel numbers (no. sq.) and densities (per hectare) from squirrel captures (including sightings) and the number of active boxes at the 12 major study sites (Sp = spring).

Site	Sp 1978	1978-80	1980-81	1981-82	1982-83	1983-84	1984-85	1985 sp	Mean density
[illegible] no. sq.	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	
density	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible] no. sq.	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	
density	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible] no. sq.		[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	
density		[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible] no. sq.	[illegible]		[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	
density	[illegible]		[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible] no. sq.			[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	
density			[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible] no. sq.		[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	
density		[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible] no. sq.				[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	
density				[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible] no. sq.			[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	
density			[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible] no. sq.	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	
density	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible] no. sq.		[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	
density		[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible] no. sq.	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	
density	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible] no. sq.		[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	
density		[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Mean density	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

of the University of Florida calculated a density of 0.084 (pers. comm. 1985). No density estimates are available for the Delmarva fox squirrel, but Flyger and Smith (1980) captured 24 fox squirrels in two years on a 261 hectare farm. Lustig and Flyger (1975) observed even lower numbers: they captured 26 fox squirrels in an 11-year study of four areas in Maryland. Since typical densities for western fox squirrels range from 1.2 to 6.9 animals per hectare, it is clear that even under the best conditions southeastern fox squirrels are scarce throughout their range. Although some areas may temporarily maintain relatively large numbers of animals, and sightings of aggregations of squirrels during the breeding season or near a seasonal food source give the impression of abundance, those conditions are probably atypical and poor indicators of the overall status of the species. Only areas with widely dispersed supplemental food appear to support higher densities. For example, woodland with access to agricultural crops and residential or picnic areas seem to have larger squirrel populations (Flyger and Smith 1980, M. A. Steele unpublished study, J. W. Edwards pers. comm.). In contrast to these fox squirrel densities those for the gray squirrel—a potential competitor—can reach 15 animals per hectare (Gurnell 1983). Although these density figures for eastern fox squirrels are approximations, they effectively reveal the precarious status of these animals and the necessity for large areas of habitat to support viable populations.

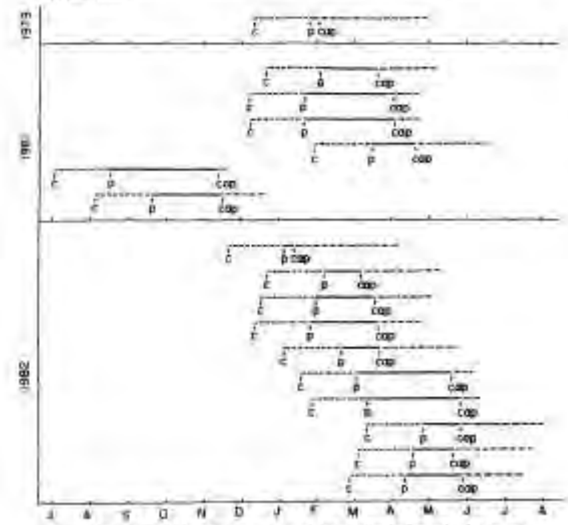

Figure 3. Estimated breeding seasons of fox squirrels for calendar years 1980-1986, based on 37 litters captured at both major and minor sites. (c = conception, p = parturition, cap = capture date.) Line is extended to estimated time of weaning.

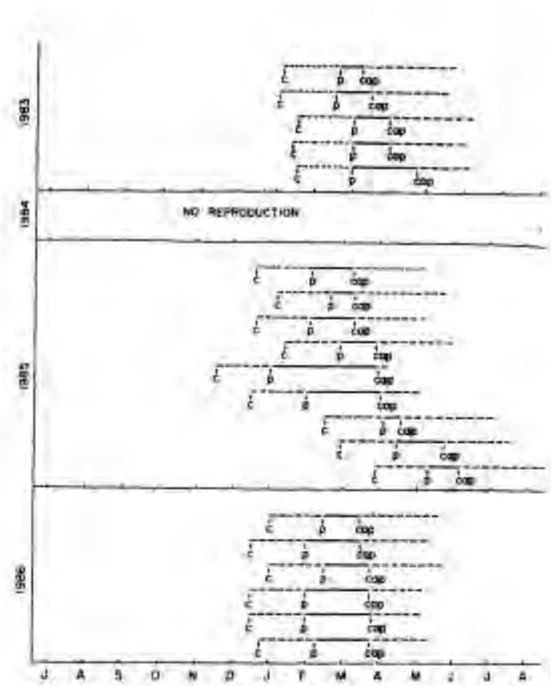

Figure 3 continued.

Reproduction

Eastern fox squirrels are known to have two breeding seasons (Moore 1957, Lustig and Flyger 1975, Lowery 1974). In the present study the reproductive schedule was estimated from the age of litters found in nests, assuming a 44-day gestation period and a 90-day dependency on the mother (Fig. 3; Moore 1957). The winter–spring breeding season is of overwhelming importance to fox squirrels at this latitude, while summer–fall breeding is an infrequent phenomenon. Mating behavior was only rarely observed, but appears to be most prevalent from December to early February and in late July and August. Most young are born in late February and March, but in 1982 and 1985 a bimodal birth schedule was observed with one-third of the litters appearing in April (Fig. 3). While most researchers state that two litters per year are common under normal conditions, we have no record of any individual female producing more than one litter in a year, nor can we find any such evidence from the literature for southeastern fox squirrels. Only four instances of summer breeding were observed in the present study. The rarity of summer breeding was further indicated by the almost complete absence of young animals of the appropriate age and size from the late fall and winter box check records.

There was great year-to-year variability in reproductive activity (Fig. 3; Table 4): no litters in 1980, 6 in 1981, 10 in 1982, 5 in 1983, 0 in 1984, 9 in 1985 and 6 in 1986. Food supply appeared to be the critical factor in reproductive performance. There was a significant positive association between the number of females reproducing in a given spring and the food supplies of the late summer and fall of the previous year ($X^2 = 8.7$, DF = 1; $p < 0.005$). No litters and few reproductively active squirrels were seen in the springs of 1980 and 1984, following periods of extremely poor food conditions. Overall, during times of limited food availability 90% of females produced no spring litters while only 12% failed to reproduce during good food years. The combined reproduction of late 1981 and spring, 1982—12 litters —occurred after unusually good seed and nut crops (Fig. 4).

Litter size varied greatly over the eight-year period and also showed a strong response to food conditions. Litter size averaged 2.5 (SD = 0.83) and ranged from 1 to 5. The same year that produced the greatest number of litters produced the larger litters. During the 1981–82 period of food abundance, litters of 4, 4 and 5 were recorded and an average litter size of 2.7 (second highest in the study). If one compares the average litter size of 2.3 with published values for the western fox squirrel, gray squirrel, European red squirrel (*S. vulgaris*), Abert's squirrel (*S. aberti*) and red squirrel, it becomes obvious that the North Carolina value is equal to or well below the lowest litter sizes recorded for these other tree squirrels (Farentinos 1972, Gurnell 1983). In an eleven-year study of the Delmarva fox squirrel Lustig and Flyger (1975) observed 12 litters (8 spring and 4 fall) ranging from 1–4 young and with a mean litter size of 2.38.

Since all squirrels were weighed at the time of capture during the last 7 1/2 years of the study and since weight may be an indicator of food conditions as well as relative age, it is useful to compare the weights of reproductive females with other females. In general, females with litters were larger

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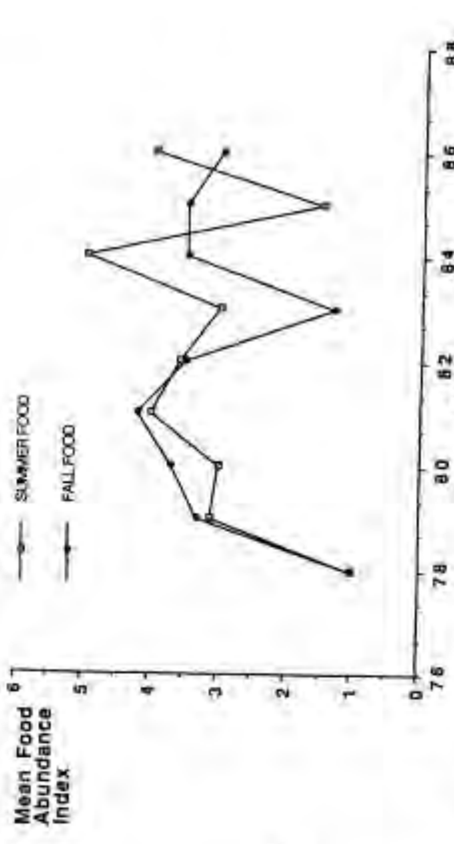

Figure 4. Estimated age-body weight curve for nestling fox squirrels. Points which fall well below curve represent individuals (runts) much smaller than littermates.

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Table 4. Summary (fall or summary) of fox squirrel reproduction for the 12 major study sites (Sp. = spring).

Site	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	Total	Litters per 100 [illegible]	Young per 100 [illegible]	Young per litter
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

than their nonreproductive counterparts ($t = 3.07$; $p < .003$) and there was a strong positive relationship between the weight of reproductive females and the size of their litters (Spearman Rank, $r = .66$, $p < 0.0001$). Only under exceptional food conditions did squirrels smaller than 960 g reproduce. Since the age of these females was not known, it is possible that such breeding at small size represents either early age of first reproduction or a special case of energy allocation to breeding associated with a particularly good food supplies. Thus, overall, data from this study suggest that food supplies (as well as age) affect body weight (energy reserves) and in turn both litter size and

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frequency of reproduction.

Just as most reproduction was confined to certain years, it was also largely concentrated in particular areas (Table 4). Sixty-eight percent of all litters and 72% of all offspring were found in just four of the 12 sites. The Gardiner Farm Site had the highest reproductive output as well as a high number of adult captures during the eight-year period. On the other hand, the Single Pond site had the second largest number of individual animals but one of the lowest reproductive rates and thus seems to be very similar to the area studied by Hilliard (1979) in Georgia. What makes certain areas so important for the rearing of young is unclear.

Using Moore's (1957) descriptions of young fox squirrels we were able to estimate the ages of our nestlings by their stage of development and to construct an age-body weight curve (Fig. 5). A linear regression on these points suggests a mean growth rate of 4.6 g per day for nestling animals ($r = .96$, $p < 0.001$). The points that fall well below the line represent unusually small members (runts) of particular litters. Such weight discrepancies among litter mates appeared more common in older litters and those born later in the spring. Since food supplies late in the spring may be limited or declining, differential growth and perhaps survival might be considered an effective strategy for adjusting reproductive output to prevailing resource conditions (Gurnell 1987). Such a strategy might take the form of one or two young dominating the available milk supply or of a female favoring the more vigorous over the weaker offspring. In either case the fitness of mother and remaining young would be enhanced. Similar strategies have been described for birds and other vertebrates inhabiting trophically unpredictable environments (Eisenberg 1981, Mock 1985).

Sex Ratio and Age Structure

The population sex ratio and age structure for the North Carolina fox squirrels over the eight-year period are indicated in Tables 5 and 6. In an age group

Table 5. Sex and age composition of fox squirrel populations from the 12 major sites for all years combined.

Age class	Females	Males
Nestling	40	42
Juvenile	15	7
Adult	50	55
Total	109	106

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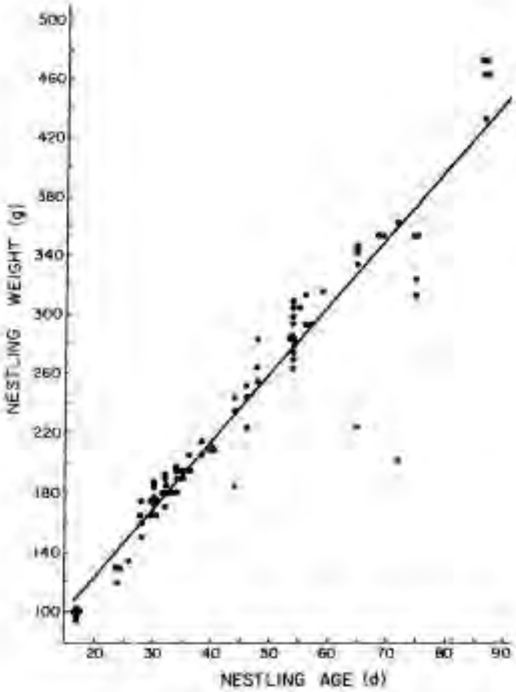

Figure 5. Average food supplies at 12 major study sites, 1978-1986. Late summer food mostly longleaf pine cones; fall food mostly oak mast.

Table 4. Age structure of fox squirrel populations from the 12 major study sites by season (Sp = spring, F = fall) and year.

	Proportion of different age classes													
Age class	Sp 79	F 80	Sp 81	F 81	Sp 82	F 82	Sp 83	F 83	Sp 84	F 84	Sp 85	F 85	Sp 86	Total
Nestling	0.30	0.09	0.13	0.64	[illegible]	0.00	0.29	0.00	0.00	0.00	[illegible]	0.00	[illegible]	[illegible]
Juvenile	[illegible]	0.27	[illegible]	0.07	[illegible]	[illegible]	0.07	0.21	0.00	0.00	0.00	0.50	0.11	0.11
Adult	0.60	0.73	[illegible]	0.29	[illegible]	[illegible]	0.65	0.79	[illegible]	1.00	[illegible]	0.50	0.19	[illegible]
Number	10	11	17	14	36	[illegible]	29	19	35	1	[illegible]	4	27	[illegible]

is the sex ratio significantly different from one. Such an observation tends to rule out a male-female bias in box use.

The age structure appeared to vary considerably during the study, although the small number of captures each year permit only a limited assessment of trends. Nestlings were generally well represented in the spring, but during two years of poor food conditions none were produced. Only in late 1981 were fall nestlings observed. Juvenile squirrels were more common in the boxes in the fall, but they were never very abundant. They increased after the high reproductive output of 1981 and 1982 and as adults contributed to the larger populations of 1983-1986. Their generally low representation may indicate either their subordinate position within populations or their tendency to disperse or occupy peripheral areas. Adults were usually the dominant animals in terms of numbers, but, if natural cavities and nest boxes are indeed particularly desirable resources, then the concept of "dominance" might apply equally to the behavioral cause of their numerical superiority.

Mortality

Except for data from captives and from midwestern populations nothing is known of the longevity of fox squirrels. Moore (1957) mentions captives living 10 years. Barkalow and Soots (1975) present data on gray squirrels living for 20 years in captivity and 12 years in the field. Midwestern fox squirrels might live 13 years in captivity (Flyger and Gates 1982) and may live 6-7 years under natural conditions. Gurnell (1987) suggests that the maximum life span for Holarctic tree squirrels is 5-10 years. Gray and midwestern fox squirrels are smaller than the eastern fox squirrel and have much higher reproductive rates. If size is directly and fecundity inversely related to longevity (Eisenberg 1981) then the fox squirrels of our study might have slightly longer life spans than other North American tree squirrels. In the Sandhills, where the population seems to be holding its own at a characteristically sparse level, the low recruitment rate, already discussed, must approximate the death rate. In other words fox squirrels in such a habitat might live a long time, perhaps 7 years or more after the first year.

Much more is known about the sources of mortality for fox squirrels. Without a doubt, one of the major squirrel "predators" today is often the automobile. The increase in paved roads, traffic, and high automobile speeds in many parts of the Coastal Plain may well have had a considerable impact on these animals. Many of the specimens we have recovered for stomach analysis or study skins have been road kills. Apparently, relatively few natural predators can regularly capture adult fox squirrels, and most of these seem to take them opportunistically (Flyger and Gates 1982). Bobcats (*Felis rufus*), foxes (*Vulpes*, *Urocyon*), red-tailed hawks (*Buteo jamaicensis*), and great horned owls (*Bubo virginianus*) are among the few potential or reported predators (Moore 1957, Kantola 1986). Nestlings and young squirrels are particularly vulnerable to climbers, such as raccoons (*Procyon lotor*), opossums (*Didelphis virginiana*) and especially rat snakes (*Elaphe obsoleta*) and pine snakes (*Pituophis melanoleucus*). They may also suffer high mortality in high winds if occupying leaf nests (Madson 1964). In considering predation, it is necessary to recall the low density estimates (0.05 squirrels per hectare) mentioned earlier. No predator could concentrate on fox squirrel prey without patrolling a truly vast home range. Natural predation thus should be confined to incidental removal of members of this scattered population or to occasional multiple captures near a nest or a particularly good food source. Only if alternate prey were available in sufficient quantity to support a predator near fox squirrel habitat, should the predation pressure reach appreciable levels. Such a situation is unlikely in large tracts of open pine-oak forest where small mammal populations are usually low. However, small areas of fox squirrel habitat adjacent to large closed-canopy hardwood stands or overgrown pine-oak forest (because of the absence of fire) tend to support substantial populations of gray squirrels. Abundant gray squirrels might well permit the establishment of a resident predator population and thus markedly increase the predation pressure on the fox squirrel. Just such a phenomenon has been advanced to explain the caribou (*Rangifer tarandus*) decline in Newfoundland where abundant alternate prey have permitted lynx (*Felis lynx*) populations to remain at high levels and periodically switch to caribou fawns (Bergerud 1983). Thus, it is possible that changes in habitat which favor the gray squirrel and perhaps other prey species have a strong negative impact on the relatively less vulnerable fox squirrel. Interestingly, the only place known to us with appreciable fox squirrel predation is the study area of J. W. Edwards in South Carolina (Edwards 1986). Here the fox squirrel population is relatively large due to the availability of agricultural crops and, with other prey species, may provide a predictable food supply for local predators.

Although the subject of human hunting will receive greater attention later in this paper, the parallels between the alternate prey model just described and the behavior of human hunters are obvious. Except for those people

desiring trophy specimens for mounting, few hunters with whom we have talked specialize in hunting fox squirrels. While fox squirrels were evidently abundant enough to be hunted with dogs and to be considered a reliable food source in the past, most hunters today hunt squirrels opportunistically, choosing areas which might harbor both species or more commonly, the more numerous gray squirrel. Therefore, in regions of good pine-oak habitat fox squirrels are able both to maintain their population and, perhaps because of their natural rarity, to escape some of the pressure from human hunting.

Body weight

One measure of the condition of a population and its capacity to cope with stresses such as reproductive costs, adverse weather, temporary food shortages or intense interspecific interactions is the body weight of its members. Weights above the average for members of a population indicate energy reserves; below average, marginal conditions which may be associated with reproductive failure, emigration, or mortality. One exception to this pattern of weight variation involves the very few observed cases of low body weight and high fecundity during periods of food abundance (see section on reproduction); in such a case, high energy turnover and perhaps early reproduction might best explain such weight records. With this caution, it is clear that seasonal weight data over an eight-year period provide additional insights into the population biology of these fox squirrels.

The mean weight of adult fox squirrels from all sites and during the entire study was 1006 g (SD = 109.4). This can be compared with a mean weight of 962 g (SD = 91.9) for 44 museum specimens from the Carolinas and northern Georgia. Male and female weights were not significantly different and thus have been considered together.

Squirrel weight showed much variation seasonally in apparent response to food conditions. Fall weights were often the highest at 1017 g (SD = 182.1) reflecting the best food supplies of the year. During the winter, weights appeared to fall in response to the previous fall's mast crop. The mean value 992 (SD = 210.6) is not significantly different from the fall mean but was highly variable during the study and needs further explanation. For example, at the end of the 1982-83 winter, the mean weight in March was 956 g (SD = 80) and was followed by some reproduction (Fig. 3). At the end of the 1983-84 winter—after a fall mast failure—the March mean was 905 g (SD = 36) and the population experienced complete reproductive failure. The monthly weight data for 1983-84 (Table 7) show a progressive decline in squirrel weight from fall to late winter and then an increase due to the abundant food supplies of spring. Thus, winter weights tend to vary considerably according to both nutritional and perhaps climatic conditions. Spring (late March through May) weights averaged 1005 g (SD = 160.5) and are essentially the same as those of the fall. Few data are available for summer, since squirrels then tend to abandon boxes in favor of leaf nests. Captures in the summer consisted of small adults (935, 915 g) or young animals (668, 685, 690 g). It is possible that these captures represent subordinate animals or temporary occupancies, but low weight levels in summer are consistent with our estimates of summer food supplies, squirrel behavior, and the poor condition of some of the animals handled or observed at this time of year. Goodrum (1972), working with the reddish fox squirrels which occupy similar pine-oak habitats in eastern Texas, also noted a marked weight drop in the summer.

Table 7. Mean body weights of fox squirrels after mast failure in fall 1983.

	Nov 83	Dec 83	Jan 84	Feb 84	Mar 84	Apr 84
Number	4	8	3	7	6	15
Mean (g)	1130	1107	988	986	905	1012
SD (g)	95	128	46	77	35	117

Recaptures

Recaptures have traditionally provided the data for estimates of population size and longevity, lifetables and various behavioral analyses (Barkalow et al. 1970, Schemnitz 1980). Unfortunately the low population densities and resulting slow accumulation of marked squirrels on our study areas limited the number of recaptures and thus the use of various demographic procedures. However, available recapture data (Table 8), especially from the last half of the study, gave some clues to the biology of the fox squirrel in North Carolina. Forty squirrels (out of the 218) were accounted for in the 53 recaptures observed. Males and females were about equally represented (19 versus 21) and animals marked as adults were most often recaptured. A disproportionate number of the recaptures occurred in the spring (60%) and within the first 14 months after initial capture (83%). One male caught as a nestling was retaken 35 months later in a box a short distance from its original brood nest. This represents the longest recapture interval in the study. There is some evidence that the recapture rate began to level off once 80–90 squirrels had been marked and released (1983) but a definitive evaluation of these capture trends will require many more years of data. When compared with gray or midwestern fox squirrels (Mosby 1969, Barkalow et al. 1970, Nixon et al. 1975), Coastal Plain fox squirrels generally fail to provide large sam-

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Table 8. Summary of fox squirrel recaptures (excluding nestlings) from the 12 major study sites for all years combined.

Site	Total recaptures	Recaptures per 100 boxes checked
CS	7	1.5
CF	11	7.8
LH-A	0	0.0
LH-B	0	0.0
JC	4	1.4
BL-L	7	4.3
BL-O	1	0.3
BL-W	1	0.3
CM	18	3.7
OH	2	0.6
SP	3	1.8
PG	1	0.7
Total	53	Mean = 1.95

ple sizes and abundant demographic data.

Recapture data reveal two interesting aspects of the fox squirrel's relationship with its habitat. First, it is evident that some study sites had much higher recapture rates than others—once again an indication perhaps of some special quality of these particular habitats. Secondly, an analysis of the location of each recapture reveals that in 35 of 53 cases squirrels were recaught in either the same or a adjacent nest boxes (within 70 m). Since the time interval between captures was often many months, since recaptures were relatively rare, and since repeated checks of sites often failed to locate any animals, it is likely that marked animals were either away from study sites or using other nests between captures. The absence of sightings or sign in some of these sites, however, suggests that these squirrels might be using distant areas where food or nesting resources were temporarily better before returning to their home areas. The low recapture rate might also indicate that many initial captures were temporary occupants or vagrants, away from their own home areas and thus unlikely candidates for future recapture. Much additional data on

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dispersal and behavior are needed, but the above information clearly reveals a capacity to return to a "home" nest after a long interval, and the possibility of a population structure based on the opportunistic use of and movement among large habitat islands like our study sites.

Social Behavior

Southeastern fox squirrels are generally described as solitary animals, interacting socially only during mating, young rearing, or around temporarily abundant food resources. Since social behavior or intraspecific antagonism can have a direct effect on population levels and stability, it is necessary to deal with this subject in some detail. In the course of the present study, several kinds of observations provided insight into this aspect of the squirrel's biology. First of all, except for females and dependent nestlings, use of nest boxes by more than one squirrel was rare. Only nine multiple occupancies were observed. In the five instances where all the occupants were captured, four were male-female pairs, and the other an adult female and a young-of-the-year female. At least one of the remaining double occupancies involved an adult-juvenile combination. Thus, while cohabitation of nests is rare, it is most common among males and females or adults and juveniles.

A second line of evidence bearing on social behavior comes from the location of squirrel captures within a given site at the time of a nest box check. Occupation of adjacent boxes might indicate a degree of mutual tolerance or some relationship between individuals. Omitting cohabitation of boxes, there were 44 instances of multiple capture during checks of particular sites. Eleven pairs of squirrels occupied adjacent boxes (within 70 m of each other); 9 of these (82%) were male-female combinations. Seventeen pairs were a moderate distance (several box intervals) apart; 10 (59%) of these were male-female pairs. Sixteen pairs were separated by a considerable distance; 6 (38%) were male-female combinations. The above data suggest that close proximity is relatively uncommon except among male-female groupings and thus reinforce the general asocial picture of these animals.

Telemetry studies of fox squirrels occupying the same areas are an additional source of information on social behavior. On the basis of 6 years of radio tracking we have little evidence of social interaction among fox squirrels. Such findings are in keeping with current information on tree squirrel dominance hierarchies (Havera and Nixon 1978, Thompson 1978) and observations on midwestern fox squirrels (Bakken 1952, Armitage and Harris 1982). Although fox squirrels are not territorial, there is some evidence for individual control of nesting areas, especially during the breeding season (Brown 1984, Nixon et al. 1984).

Finally, laboratory experiments by Steele et al. (1984) point to a potentially high degree of antagonism among southeastern fox squirrels. In studies of nest box competition between both North Carolina and midwestern fox squirrels and gray squirrels, Steele found that control pairings of southeastern

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fox squirrels showed much higher levels of aggression and even wounding than bouts between midwestern fox squirrels or between gray squirrels. While the intensity of the interactions may have been influenced to some extent by confinement of the animals to large outdoor cages for such experiments, the unexpected levels of aggression by the southern fox squirrels might well represent a real regional and species difference in intraspecific tolerance. Thus, the nest box, telemetry, and experimental data suggest a limited degree of sociality in southeastern fox squirrel behavior and are consonant with the low population levels observed in this study. Such solitary behavior and intolerance are not really surprising considering the widely dispersed and often limited nest and food resources for which these squirrels must compete.

Color Variation and Population Distinctness

Fox squirrels are perhaps the most polymorphic mammals in the United States (Cahalane 1961). In North Carolina most fox squirrels are a salt and pepper gray, or agouti, but this basic grayish color is often modified by a gold, tan or reddish wash, especially on the legs, sides, and tail. Most squirrels have varying amounts of black across the face and crown and distinctive white noses, ears, and paws. Some animals are melanistic—either totally black with white noses and ears or black with saddles of dark gray. While most gray fox squirrels have a whitish belly and melanistic forms are black ventrally, squirrels in the Sandhills were often gray with a distinct gold or reddish belly. Table 9 gives the percentages of the four most commonly observed color variants for all individuals captured. If gray/gold belly is included with the other gray forms, then North Carolina fox squirrels are seen to be 74% gray and 26% melanistic. Although such color variation is highly reminiscent of a 3:1 Mendelian ratio, the genetic basis of this polymorphism is presently unknown. It was not uncommon to find various color morphs sharing nest boxes and litters consisting of both melanistic and gray individuals. The morphs of offspring from mothers of known and unknown coloration are shown in Table 10. The fact that an identical 3:1 ratio also occurs in nestlings may indicate the absence of strong selection later in life for or against either of the two major color phases. In his study of fox squirrel coloration, Moore (1956) recognized several color phases, but if one recalculates his proportions on the basis of our dorsal coloration categories, his animals are seen to be 74.1% gray to 25.9% melanistic, once again 3:1.

The causes and nature of this color polymorphism are poorly understood. Why are eastern and western fox squirrels so different in coloration and why are the eastern forms so variable? The Abert's squirrel—a pine forest species of the Rocky Mountains—also has grey and melanistic morphs, with differing amounts of light marking (Farentinos 1972). Dark-colored populations of the gray squirrel and the European squirrel (Voipio 1969) occupy the northern parts of their respective ranges. None of these color polymorphisms, however, have been adequately explained. To a human observer both gray

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Table 9. Summary of color variation in fox squirrels from the 11 major study sites.

		Percent in each color class				Combined	
		Gray		Melanistic			
Site	n	White Belly	Gold Belly	Saddleback	Black	Gray	Melanistic
[illegible]	[illegible]	45.4	18.2	27.3	9.1	[illegible]	[illegible]
[illegible]	35	[illegible]	[illegible]	[illegible]	21.8	73.9	26.1
[illegible]	8	[illegible]	37.5	0.0	12.5	87.5	12.5
[illegible]	1						
[illegible]	15	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	7	[illegible]	[illegible]	0.0	[illegible]	100.0	0.0
[illegible]	17	[illegible]	13.3	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	28.6
CM	15	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	17	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
SP	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	8	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Total	[illegible]						
Mean		[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

Table 10. Color morphs of offspring from fox squirrel mothers of known and unknown coloration.

	Percent offspring	
Mother (n)	Gray (n)	Melanistic (n)
Gray (15)	[illegible]	[illegible]
Melanistic (16)	53.3 (8)	46.7 (7)
Unknown ([illegible])	[illegible]	[illegible]
Total	[illegible]	[illegible]

and black fox squirrels are exceptionally difficult to see in the contrasting dark and bright backgrounds of southern pine-oak forests, especially if the ground and tree stems have been blackened or blotched by fire. A gray squirrel is much more visible in such a setting. Thus, it is possible that the basic colors of southeastern fox squirrels represent a form of camouflage and the markings of light and dark a kind of disruptive coloration to elude predators. It is also possible that the colors may be in some way associated with radiation balance and thermoregulation, as has been suggested for both the Abert's squirrel (Golightly and Ohmart 1978) and the gray squirrel in Canada (Innes and Lavigne 1979).

Whatever the cause of this color polymorphism, natural selection has apparently not favored any single color variant and thus greater population uniformity. In our study the proportions of the color variants at different study sites were highly variable (Table 9). For example, Camp Mackall (CM) has a relatively large number of gold-bellied squirrels; Single Pond (SP) animals are almost exclusively gray; Indian [illegible] (IC) supports large numbers of melanistic squirrels; and at the new Boiling Springs site eight of the nine animals observed in a mating chase had a distinctive white-tipped tail—a trait not seen elsewhere in this study.

While genetic and evolutionary explanations of this polymorphism may not be forthcoming, the site-by-site variation observed in this study may provide important clues to other aspects of the fox squirrel's biology. Taken together, the data on coloration, sociality, recaptures, and density provide an outline of a possible dynamic distribution and way of life. In response to the low carrying capacity of their habitat, its resource patchiness in space and time, and perhaps the current human dissection of the eastern Coastal Plain, fox squirrels at different times may live as disperser-colonizers or as resident inbreeders. Because of their high mobility, some young or subordinate individuals may leave "crowded" or low resource areas and occupy either nearby or distant islands of suitable but vacant habitat. Some return to their former home areas—often to the same nest cavity. Others may provide a nucleus for a new squirrel colony in a new core area. Semipermanent residents of core areas may never be very numerous, and it is likely that periods of inbreeding, genetic drift and one-way dispersal could lead to the numerical dominance or fixation of certain color characteristics, different for each island of habitat. It is also possible that the few founders of a new breeding population would carry only a small sample of the total color genes, and fixation would again result. Finally, periodic local extinctions of adjacent populations could promote increased isolation, reduced gene exchange, and once again a local set of color characteristics. Such a dynamic pattern of colonization, drift, inbreeding and local extinction need not change the overall color proportions of a large region but could account for the site-by-site color differences and the somewhat greater similarities of adjacent populations seen in this study.

Response to Habitat Factors

Climate

Climatic factors have far-reaching effects on the fox squirrels of North Carolina and the Southeast and provide the background conditions against which this species and the other organisms of its habitat have evolved. Certainly seasonal variation in temperature and rainfall are major determinants of soils, moisture conditions, and vegetation. The vegetation in turn, especially the longleaf pine-turkey oak woodland and adjacent wetlands, provide natural nest cavities and certain foods, such as pine cones and fungi, which are used by fox squirrels. So far the relationship between squirrel and climate is obvious. However, when one considers these indirect factors more closely, it is clear that they may be associated with some of the special characteristics of these southeastern populations. For example, the generally mild climate of the Coastal Plain and the kinds and patchy distribution of food resources, so typical of these forests, may help explain the unusually large size of these animals relative to their western conspecifics. Large size may be partially attributable to a release from extreme and long-term winter thermoregulatory costs and to the kinds of food supplies provided by certain southern tree species. Large size is a definite advantage in moving long distances between patchy food sources, in carrying stored fat (Linstedt and Boyce 1985), and in extracting seeds from large woody cones and nuts (Weigl et al. 1981).

Climatic factors may have more direct effects on fox squirrel behavior and ecology (Carroll 1987). Some of these effects have been enumerated by Hicks (1949) for midwestern fox squirrels and by other researchers using nest boxes to study tree squirrel biology (Barkalow and Soots 1965, McComb and Noble 1981b). In the present study temperature and perhaps rainfall appeared to have the greatest influence on squirrel behavior. Monthly temperature and degree-day data for the winters 1978 to 1984 were available from a weather station at Hamlet, North Carolina, 20 km from most of our Sandhills study sites and from Southport, North Carolina, 15 km from our Brunswick County areas (NOAA 1978–84). The temperature conditions in the two areas were comparable but less extreme in Brunswick County due to their proximity to the ocean. Temperature conditions combined with food supply appeared to affect box use in the fall and winter. If temperatures were mild and food supplies relatively abundant, fox squirrels were slow to occupy nest boxes in the fall. Only after the onset of fairly continuous cold weather did box use increase. At this time, low temperatures and reduced or more highly dispersed food supplies may have caused squirrels to construct thick, leaf-lined nests within the nest boxes. Thus, energy demand imposed by temperature and food conditions may affect the nesting habits of fox squirrels.

Low temperatures had another more lasting effect on the squirrels. Sub-

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freezing temperatures in April, such as occurred during 1982 and 1983, destroyed the flowers of the oaks and perhaps some of the hickories. These freezes, like that reported by Nixon and McClain (1969), resulted in mast failures in white oaks the following fall and in red oaks a year later. The loss of these food supplies appeared to have profound effects on the population size and behavior of fox squirrels; they searched out alternate energy sources, covered large areas, and used nest boxes more frequently. The reproductive failure and high capture rate of spring 1984 are probably attributable to these conditions.

Hot weather during the summer months may also have an impact on the species. Most squirrels reduce activity in the summer months, abandon nest boxes for leaf nests, and use adjacent wetlands more frequently. Some researchers have blamed heat or a buildup of ectoparasites in the boxes for this change in nest preference (Barkalow and Soots 1965, Goetz et al. 1975, Havera 1979, McComb and Noble 1981b). Since, in the South, late June and July are also periods of low food supply and often low weight in fox squirrels (Goodrum 1972), it is difficult to separate the role of high temperature from these other factors. However, intense activity follows the ripening of the seed in green longleaf pine cones in August—an extremely hot month—so heat alone cannot explain the apparent lethargy and "disappearance" of fox squirrels earlier in the summer.

Based on observations of wild fox squirrels and radio tracking we have developed some additional impressions about activity and weather conditions. While activity may be inhibited by extremely hot or cold temperatures, high winds or violent storms, there is good evidence that activity actually increases during light rain. At such times animals spend considerable time moving along the ground either foraging or exploring. Following Cahalane's (1942) suggestion that squirrels could locate buried nuts more rapidly when these items were wet, Steele (unpublished data) examined the ability of fox and gray squirrels to detect wet and dry nuts buried at various depths in a sand substrate. Both species showed a marked improvement in foraging success when locating wet nuts. Thus, it is possible that nuts and perhaps other foods, such as fungi, provide more olfactory cues during wet weather or in wet soils and that moisture conditions can influence both the time and location of squirrel activity. It has also been suggested (Landers pers. comm.) that rainfall may not only facilitate the location of foods but may also make the digging of nuts, fungi and tubers easier by changing the consistency of the soil.

Fire

The mature pine-oak forest of the southeastern Coastal Plain has often been described as a fire climax community, and many species such as longleaf pine and wiregrass seem to thrive only with frequent fires (Waggoner 1975, Boyer and Peterson 1983, Christensen 1988, Platt et al. 1988). While the present investigation did not specifically set out to study the influence of fire on fox

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squirrel habitat, working in the same areas over an 8-year period produced a certain awareness of community change and the impact of fire on squirrel biology. Fire not only maintains the pine-oak habitat but seems to have a more direct effect on animal foods and competitive interactions (Kantola 1986).

Mature longleaf pine-turkey oak forests are usually burned at frequent intervals as the result of lightning or human carelessness or, more commonly today, as part of a timber or wildlife management plan. The effects are well known (Christensen 1981, Wade, Ewel and Hofstetter 1980, Wallach 1981). Fire prevents fuel accumulation which can lead to crown fire and forest destruction. It releases nutrients which are rapidly taken up by the living trees and their mycorrhizal fungi. It destroys a certain percentage of the hardwood competition, to the advantage of the fire-resistant pines and some of the larger oaks. It reduces the incidence and severity of certain pathogens. Fire tends to maintain the stand size by burning back encroaching hardwood communities and by exposing mineral soil needed for pine seed germination. Thus the extent, vitality, and perpetuation of the pine-oak forest habitat are dependent on fire factor.

These and other effects of fire have special implications for fox squirrel survival. Our observations of many areas suggest that the very open stands produced by fire result in better pine cone and mast production. Like orchard trees, pines and oaks growing in the open receive more light, maintain more branches at lower levels, and produce heavier crops of cones and nuts (Goodrum 1938, Smith and Follmer 1972). In crowded stands cones and nuts are confined to the tops of trees and are often less abundant. It could also be argued that nutrient availability and the enhanced vigor of burned pine forest are associated with larger crops of hypogeous fungi and mushrooms, foods of considerable importance to squirrels (see Food Habits). Perhaps of equal significance is the effect of fire on competition between fox and gray squirrels. Fires tend to produce very open forest with widely spaced trees. The fox squirrel's large size, running proficiency, and tendency to escape along the ground permit it to exploit extensive areas of such habitat. In unburned areas hardwoods become more abundant, the canopy starts to close and the community merges with adjacent wetland or deciduous forest. Such areas favor the gray squirrel, a species of closed forest and heavier undergrowth which tends to move through the canopy or among closely-spaced trees (Smith and Follmer 1972, Taylor 1973, Korschgen 1981). Gray squirrels are common in the bottomland and deciduous forests contiguous to our study sites, and their numbers and range have increased in those areas that have remained unburned. To the degree that the fox and gray squirrel compete, fire could be a deciding factor in determining the availability of suitable habitat and resources to one or the other species.

Vegetation

In combination with climatic and pyric factors, certain plant communities of the Coastal Plain seem to play a critical role in maintaining fox squirrel

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populations. These communities not only provide necessary food and nesting resources but by their structure, age, diversity, and size supply a whole array of additional subtle requirements. When we started our study, we already knew that the pine-oak forest of the Coastal Plain was a major habitat of the fox squirrel in North Carolina, but it remained our task to study this and adjacent habitats and to determine any patterns or preferences in habitat use.

One method of determining the preferred habitat and at the same time characterizing its major features was by analyzing the arboreal vegetation around the nest boxes used more frequently by fox squirrels or gray squirrels and around a group of boxes chosen at random. Such a comparison was carried out in two ways: by conducting a point-quarter analysis at each box and creating a hypothetical, composite forest-type based on these data; and by scoring 36 site and habitat variables and, by means of chi square and factor analysis, determining those variables most important to each species. A summary of the vegetation data for the 25 most used fox squirrel boxes (Table 11) essentially is a description of a typical longleaf pine-turkey oak forest (Wells and Shunk 1931, Braun 1964, Waggoner 1975). Such a forest is dominated by large well-spaced pines and smaller turkey and other oaks and typically has a low species diversity (H = 2.309). Since the more famous and endangered red-cockaded woodpecker often uses essentially the same habitat, additional characteriza-

Table 11. Point quarter analysis at the 25 nest boxes most commonly used by fox squirrels.

Species	Number of Individuals	Density (Ind./ha)	Dominance (cm^2/ha)	Frequency	Important value
Longleaf pine	50	118.8	17554.8	0.68	1.39
Turkey oak	17	40.4	10439.4	0.40	0.65
Blackjack oak	14	33.2	9544.0	0.24	0.35
Bluejack oak	4	9.5	3613.4	0.12	0.11
Live oak	4	9.5	9699.5	0.08	0.17
Loblolly pine	3	7.1	9717.4	0.08	0.14
Dogwood	3	7.1	4126.6	0.12	0.15
Mockernut hickory	2	4.8	1488.0	0.08	0.08
Post oak	1	2.4	236.4	0.04	0.03
Red maple	1	2.4	1455.9	0.04	0.06
Southern red oak	1	2.4	852.2	0.04	0.04
Total	100	237.7	108597.2	1.88	

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tions of this forest type can be found in the studies of Van Balen and Doerr (1978), Delorelle et al. (1983), and Carter et al. (1983). Results from a similar analysis of the 25 most used gray squirrel boxes describe a forest of much greater diversity (H′ = 3.459), stem density and overall dominance (Table 12). Such a forest generally possesses a closed canopy, abundant undergrowth and numerous hardwood and mesic species. The hypothetical stand derived from 25 boxes chosen at random reflects our predisposition at the beginning of the study to place boxes in or near longleaf forests. Thus while somewhat intermediate between the other groups in number of species, dominance and density, it is more like the fox squirrel habitat in species diversity (H′ = 2.420) and importance values. On the basis of these comparisons of forest characteristics, it is clear that open pine-oak areas are favored by fox squirrels

Table 12. Point quarter analysis at the 25 nest boxes most commonly used by gray squirrels.

Species	Number of Individuals	Density (ind./ha)	Dominance (cm²/ha)	Frequency	Importance value
Longleaf pine	36	52.8	47431.3	0.58	0.88
Blackjack oak	18	47.5	17242.5	0.38	0.46
Loblolly pine	13	34.3	20192.7	0.24	0.39
Turkey oak	11	29.0	5892.8	0.24	0.26
Bluejack oak	9	23.7	4050.3	0.24	0.22
Post oak (mixed)	7	18.5	9841.9	0.16	0.20
Tulip poplar	4	10.6	7783.3	0.04	0.09
Sand post oak	4	10.6	1286.8	0.08	0.08
Mockernut hickory	3	7.9	3260.7	0.08	0.09
Pond Pine	2	5.3	3842	0.04	0.04
Spruce pine	2	5.3	5483.5	0.08	0.08
Water oak	2	5.3	3723.3	0.08	0.08
Dogwood	2	5.3	1178.1	0.08	0.06
Southern red oak	2	5.3	130.3	0.08	0.06
Southern magnolia	1	2.6	1544.3	0.04	0.04
Live oak	1	2.6	368.6	0.04	0.03
Slash pine	1	2.6	3251.0	0.04	0.06
Total	100	269.4	129827.6	2.44	

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for nest box use. It is our belief that the size and spacing of pines and oaks are among the important features of their habitat but that, as shown by Taylor (1973) and Hilliard (1979), the actual species of pines and oaks themselves may not always be a major consideration in defining fox squirrel habitat.

Factor analysis was used to group and evaluate the importance of vegetation and site variables measured at the fox squirrel and gray squirrel boxes. The first three factors together accounted for 88% of the variance in the model. The first factor was loaded primarily by measurements of understory characteristics (number of species, density, number of parent tree species in the overstory, and escape routes through the understory). The second factor reflected overstory conditions (density, escape routes, Bitterlich measurements). The third factor provided a measure of moisture conditions and resulting stem dominance and density. Thus the factor analysis reinforced many of our earlier ideas about the habitat differences of the two species. The preferred nest box habitat for the fox squirrel consists of an open, low diversity, mature forest with little understory and rather xeric conditions. For the gray squirrel, this habitat is typically a closed-canopy, relatively diverse forest with a dense understory, good moisture conditions, and ample arboreal escape routes. Random box sites resembled fox rather than gray squirrel areas.

Another measure of habitat preference was the analysis of box use in areas where nest boxes were laid out in lines at fixed intervals without regard to vegetational considerations. Such an analysis involved 6 study sites and a total of 102 nest boxes set out at approximately 350-m intervals through a full range of plant communities. Each box was assigned to either pine-oak or hardwood-bottomland vegetation types. While the proportion of boxes ever used by fox squirrels in each habitat was essentially equal to box availability ($X^2 = 2.56$, $p > 0.10$), the number of occupancies in nest boxes of the two habitat-types showed the animals' distinct preference for the pine-oak forest ($X^2 = 4.2$, $p < 0.05$). Thus, fox squirrels seem to have a predisposition for using nest boxes in longleaf-turkey oak forests during the cooler parts of the year. Perhaps then, it is reasonable to assume that, if tree cavities were abundant in these forests, they too would be used by squirrel populations and there would be less dependence on nesting sites in neighboring hardwood and wetland habitats.

Telemetry provided a third source of information about the plant communities important to the fox squirrel. Fairly extensive tracking data for 11 squirrels and a smaller number of radio locations for 6 more animals—in all, representing 6 study sites—made it possible to determine both a general habitat preference and the identity of vegetation-types of special significance. The percentage of telemetry locations in each vegetation type, either collectively or on a squirrel by squirrel basis (Tables 13 and 14), demonstrates an overwhelming amount of time spent in pine-oak forest and, to a lesser degree, edge. If radio locations are summed for each vegetation-type (Table 15), pine-oak and edge (part of which contains some pine-oak) are found to be used at least 80% of the time.

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Table 13. Percent of telemetry locations in different habitat types during the fall and winter.

ID	Sex	Site	Tracking period	Number of locations	% Pine-oak	% Edge	% Bottomland	% Field and oak scrub
[illegible]	Male	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	Male	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
			[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
			[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	Male	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	Male	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	Female	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	Female	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
			[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
			[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	Female	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	Female	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

Table 14. Percent of telemetry locations in different habitat types during the summer.

ID	Sex	Site	Tracking period	Number of locations	% Pine-oak	% Edge	% Bottomland	% Field and oak scrub
[illegible]	Male	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
			[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
			[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
			[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	Female	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
			[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	Female	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	Female	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
			[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
			[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	Female	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
			[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
			[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	Female	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
			[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
			[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	Female	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
			[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
			[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
			[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

Table 15. Percent of active and inactive telemetry locations in different vegetation types during fall-winter and summer. (Total = % of all locations in particular vegetation type.)

Activity	% Pine-oak	% Edge	% Bottomland	% Field and oak scrub
		Fall-Winter		
Active	63.9	28.1	6.4	2.0
Inactive	61.1	37.8	1.6	0.0
Total	62.2	33.9	4.4	1.0
		Summer		
Active	38.3	51.4	[illegible]	2.0
Inactive	50.4	34.3	13.7	1.6
Total	45.0	42.6	10.1	2.3

A more detailed analysis of the radio locations of 13 squirrels from 3 sites with especially diverse vegetation reveals use patterns related to season, activity, and community availability. During the winter, fox squirrels spend much more time (than expected on the basis of habitat availability) in the edge and somewhat more time in the bottomland forest ($X^2 = 171.2$, d.f. = 2, $p < 0.001$). The majority of the radio locations in the edge areas are associated with inactivity while those in the bottomland are "active" points ($X^2 = 7.9$, d.f. = 2, $p < 0.025$). Active and inactive points are equally represented in the longleaf pine habitats. Such a pattern of habitat utilization is consistent with our observations of increased nest use in edge areas and extensive foraging along the ground in all habitats. During the summer, fox squirrels show a shift in their activity away from open pinelands and sand ridges toward the moister lowlands. Both edge and bottomland areas are used much more intensively relative to availability ($X^2 = 808.1$, d.f. = 2, $p < 0.001$). Squirrels show considerable activity in the edge, but only half of the radio locations are "active points" in the bottomland region. It is during the first half of the summer that we notice large numbers of leaf nests in the hardwood, cypress and bottomland forest adjacent to pinelands. This is also a period of food scarcity, inactivity, and smaller ranges. With the ripening of the longleaf cones at the beginning of August, fox squirrels start to move up from the lowlands. The cones in the edge areas are attacked first, then those on the slopes and ridges. Thus a pattern of plant community use emerges which centers on pine-oak forests and involves a summer shift to moister habitats and edge, bottomland,

and wetland vegetation. These summer areas may have more favorable microclimates, better sites for leaf nest construction, more food (especially on the ground), and easier access to water. Their use may also partially reflect the second growth and disturbed nature of the pine woodlands of the present-day Coastal Plain which are much less mature than the forests described by Moore (1957) and Wells and Shunk (1931).

While mature pine-oak and, to some degree, open edge and bottomland forests may be necessary for the maintenance of viable fox squirrel populations, it is evident that such a wide-ranging and opportunistic species can exploit a number of other plant communities for food and nesting sites and as thoroughfares between preferred habitat. Since fox squirrels are not limited to progression through the canopy or along heavily timbered corridors, even treeless areas might be incorporated into their annual ranges. During the present study squirrels were observed in swamps, scrub oak woodlands, pine plantations, housing developments, on golf courses and near agricultural land. Because of their mobility, squirrels can nest in one habitat, feed in others, and traverse many more. However, while a mosaic of different plant communities might provide an adequate resource base, it appears that such composite areas must be sufficiently large to supply basic needs, have a large percentage of prime pine-oak habitat, or provide some sort of subsidy in the form of nests and food supplies. Strips or islands of mature forest among fields planted in grain, corn and soybeans are one example of a subsidized habitat. Another might be low density residential and recreational areas which provide food in the form of birdseed, fruit and ornamental plantings and a variety of artificial nest sites such as bird houses, and wood duck (*Aix sponsa*) boxes. While fox squirrels are known to use such habitats, their survival would ultimately depend on the persistence of these subsidies and the control of potential threats like domestic dogs and traffic (see Problems of Conservation and Management).

Food Habits

Of all the factors which influence the ecology of the southeastern fox squirrel, one—the food supply—has assumed the paramount position in our attempts to understand this species. The scope of the fox squirrel's relationship with the food resources of the mature pine-oak forest is so all-encompassing that it might be considered coevolutionary in nature. It is thus important to review the seasonal food habits of these squirrels and some of their special responses to various dietary items. The diet of the fox squirrel has been the subject of intensive study (Baumgartner and Martin 1939, Baumgras 1944, Brown and Yeager 1945, Weeks and Kirkpatrick 1978, Havera and Smith 1979, Korschgen 1981). Many regional faunal works have assumed that these animals consumed the same foods as other squirrels, especially the gray and western fox squirrel, and placed little emphasis on this aspect of their ecology. Details of seasonal food use in pine forests date from the work of Goodrum (1938), Baker (1944), Martin et al. (1951), Moore (1957), Taylor (1973), Lowery (1974),

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and Hilliard (1979). The following qualitative seasonal summary is thus based on the literature, direct observation of squirrels, examination of food remains in the field and stomach contents of 20 animals shot by hunters or killed on the road.

Spring (March 15–June 1): This is a period of relatively abundant food supplies especially if appreciable quantities of mast remain from the previous fall. Pine buds, staminate cones, flowers, maple samaras, corms, bulbs, both hypogeous and epigeous fungi, insects—in short, a whole assortment of emerging plant and animal material—make up the spring diet. This is a time of weight gain and young-rearing, and most squirrels appear in good condition.

Early summer (June and July): These two months usually represent the poorest food supplies of the year. The increasing temperature and aridity of the sandy habitats are associated with declining quantities of succulent plant parts and emerging insects. Old mast supplies are exhausted, and the berries, fruits and fungi that are available are patchy in distribution. Squirrels are often thin and in poor condition at this time of year. This is the "disappearance" period when fox squirrels seem to "shut down", i.e. become inactive and remain in or near the nest.

Late summer (August and September): As soon as the seeds in the closed green cones of the longleaf pine have filled out (but not fully ripened) in late July or early August, the fox squirrel population experiences a resurgence of activity—in fact, a complete behavioral reversal of the progressive inertia of the preceding months. Squirrels appear to sample the majority of pines within their habitat and later concentrate their feeding on certain trees (Steele 1988, Steele and Weigl 1987). Such concentration may be a function of seed ripening or some energetic characteristic of the trees themselves, as has been observed in the Abert squirrel-ponderosa pine (*Pinus ponderosa*) relationship (Capretta et al. 1980, Farentinos et al. 1981). If the pine cone crop is abundant, fox squirrels can gain weight rapidly while covering only a small area. More commonly (5 out of 7 years) the crop is small and patchy (USDA 1948) and the squirrels move from area to area cutting and eating cones. No attempt to cache or defend cones has been observed. Once the cones open in late September, fox squirrels and many other seed eaters forage along the ground for the dispersed seeds. In addition to this pine seed staple, squirrels have a large variety of berries (holly, bay, grape, greenbriar), fruits (e.g. persimmon (*Diospyros*)) and fungi to add to their diet.

Fall (October–January 15): This time interval is the major mast season and the most critical food period of the year. Although acorns and hickory nuts may be exploited to varying degrees in September, especially if the cone crop is poor, these foods later make up the bulk of the diet during the fall, winter, and even the following spring. The turkey-oak, southern red oak, blackjack oak, and bluejack oak are among the most important mast trees of the red oak group. These oaks produce acorns of high lipid and tannin content the second fall after flowering. Among the white oak group, which develop acorns

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of lower energy and tannin content the first fall after flowering, the post oak and live oak make up the bulk of the fox squirrel diet. Many pine-oak habitats support relatively few oak species and of these the turkey oak is often the dominant hardwood. Thus, because of the flowering phenology of the two oak groups and their low species diversity, one severe spring frost can destroy much of the acorn crop over a two-year period. Another significant characteristic of these Coastal Plain oaks and one which we have not found discussed in the literature is their tendency to drop acorns over a long period of time. In good mast years it is not unusual to find considerable quantities of nuts on trees well into January. This phenomenon contrasts with the rapid acorn drop observed in Piedmont, North Carolina and obviously places a climbing mammal at an advantage in harvesting these foods.

Among the other foods of lesser importance are hickories: mockernut, pignut and pecan. These are commonly found in moister forests, and unless present in isolated groves within the pine-oak habitats, have to be shared with gray squirrels and other seed eaters. Chinquapin (*Castanea pumila*) nuts, cypress cones, sweetgum seeds, tupelo drupes, tulip poplar samaras, and the cones of the pond pine are also eaten in varying quantities along with a variety of fungi.

Winter (January 15–March 15). Winter food supplies are largely dependent on fall mast production and thus vary from year to year. If that crop fails, fox squirrels are reduced to tearing apart fallen longleaf pine cones, searching for scattered pine seed and samaras, harvesting the small pond pine cones, or digging a multitude of small pits around the bases of longleaf pines for hypogeous fungi such as *Elaphomyces* or *Rhizopogon*. With some mast from the previous fall, especially after a good pine cone season, the squirrels survive the winter in good condition and produce litters in late February and March.

The food supply in our Sandhills and Brunswick County study sites varied greatly over the 10 years of our study. Recognition of this variation provided the impetus for repeated monitoring of these supplies during box checks over an 8-year period and drew our attention to the potentially dominant role of this factor in fox squirrel biology. A summary of late summer and fall data for the years 1978–1986 provides a good picture of average overall food conditions (Fig. 4). Fall and spring are usually times of food abundance; early summer (June and especially July) and sometimes late winter represent the worst food conditions. Late summer supplies vary with the longleaf crop. Fall mast failures as in 1978 and 1983 are often associated with late spring frosts and result in poor conditions the following winter and spring. Such frosts affect low-lying areas and some sites more than others and thus produce much among-site variation in food levels. However, in spite of some site-by-site variation, food supplies seemed to fluctuate similarly over much of the Coastal Plain. Accordingly, food availability during the study could be described as 1) very poor initially, 2) improving slowly and variably through the spring of 1983, 3) then declining to a low in the fall and winter 1983–84, and 4) finally recovering

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in late summer and fall of 1984 and remaining relatively stable in 1985 and 1986 (Fig. 4).

One aspect of the food supply which is not apparent from Figure 4 is its distribution at different seasons. "High" levels of longleaf cones or acorns usually imply that most trees of the appropriate species are producing appreciable quantities of food and that these items are fairly widely distributed throughout the study site. "Moderate" and "low" designations indicate both reduced supply and increasing patchiness in food distribution. Often only one species of tree will produce nuts or seed during a particular season; at other times, isolated, widely-spaced groups of trees will bear cones or mast; and sometimes both conditions occur. In a low diversity, open forest, low or moderate conditions are the rule, and extensive travel within and, probably at times, outside the stand are a necessity.

Although the effect of variation in food supply on the biology of the fox squirrel was often difficult to interpret, certain patterns were evident. First of all, most changes in populations seemed to be associated with successive seasons of low or high food conditions. The long period of low food supply at the beginning of the study (1977–78) at least partly accounted for the low population size as indicated by number of captures at the time, the low recruitment of 1979, and the slow increase in squirrel numbers in the following years. The reproductive failure of spring 1984, followed several seasons of relatively poor food conditions. While the fox squirrel's large body size permits the storage of appreciable fat reserves which can buffer the effects of short-term deprivation (Linstedt and Boyce 1985), the squirrels cannot cope with prolonged marginal conditions. Similarly, several good food seasons may be required for the kind of energy accumulation favoring unusually high fecundity. The spectacular reproduction of 1981–82 was associated with at least 4 better-than-average food seasons. Secondly, food supplies interacted in a complex fashion with low temperature to affect nest box use. Good food supplies appeared to counteract the effects of low temperatures and tended to reduce the need for energy conservation through box use. Thus, our capture records alone, separate from weight and reproductive data, do not tell the whole story about population trends. Third, extreme conditions, particularly the complete absence of food at a site, were invariably accompanied by low levels of squirrel activity or in some cases the complete absence of animals. Finally, given the large number of nest boxes in the study sites, it is clear that nest availability was not the factor limiting population size. Because of the strong association between squirrel population parameters and both natural food levels (present study) and agricultural food sources (J.W. Edwards pers. comm., Fryger and Smith 1980), it is likely that food supplies are a critical limiting factor for fox squirrel populations of the Coastal Plain.

Because of the apparent limiting nature of the food supply we attempted to assess the impact of supplemental food on the populations of two of our sites during the fall, winter, and spring of 1985–86. Corn, soybeans and

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sunflower seeds were provided at each site in 4 large hoppers which excluded mammal species larger than a fox squirrel. The food provided was used rapidly, possibly due to the poor mast crop that fall, but nest box checks revealed no increase in numbers at either site. However, squirrels were observed near the hoppers, and oddly enough, all the animals captured were males. One possible explanation of these findings is that at each site one or two males dominated the easily-defended point sources of food and effectively kept other squirrels away. Since fox squirrels are generally asocial animals accustomed to patchy indefensible food supplies, it is conceivable that a localized and predictable food supply elicited dominance behavior and prevented any population buildup. Such male dominance has been reported by Nixon et al. (1984) in the nest box use of midwestern fox squirrels. Thus, one would predict that supplemental food would increase population levels only if it was widely dispersed throughout the habitat so that it would not be monopolized by a few animals.

The relationships between fox squirrels and certain foods of the longleaf pine-oak forest not only demonstrate the importance of this factor in the animals' ecology but also hint at the special nature of the squirrel-food interaction in the evolution of the species. Two foods are of particular significance, pine cones and fungi, and will be discussed in turn.

We have already discussed the "disappearance period" in June and July. This is a time of predictably low food supplies, low body weight, reproductive quiescence, infrequent fox squirrel sightings, and, as we can show from the telemetry data, reduced activity and movement. This period comes to an abrupt end with the development of the green cones of the longleaf pine. These cones are critical. They are practically the only resource available until the fall mast crop, and their highly nutritious seeds appear crucial to recovery from the scarcity of early summer, initiation of a second breeding season, and preparation for winter. Perhaps it is not surprising that so much of the fox squirrel's activity and behavioral repertoire are associated with this food source.

During the summers of 1983 and 1984 cone collections were made at two-week intervals, and the seeds analyzed for energy and water content. Young seeds contain small quantities of watery endosperm. Older seeds are solid, oily in consistency, and much higher in energy content (Fig. 6). Although a few cut cones are found at intervals in June and July, it appears that such feeding represents a kind of sampling (Steele 1988). Only at the very end of July or early August does the harvest begin in earnest. Suddenly large numbers of cone cores appear at the bases of pines and the squirrels are once again more active. The harvest appears to be very closely linked to developmental stage of the pine seed—a time when the seeds are nearing maturity (of reduced water content) and the energy content, at 5500 cal/g, is above almost all other squirrel foods. Thereafter, longleaf cones become the major food source for the rest of the summer.

Longleaf pine cones are spectacular energy packages. Cones may contain 100 seeds and a total energy content of 47000 cal. But they are also difficult

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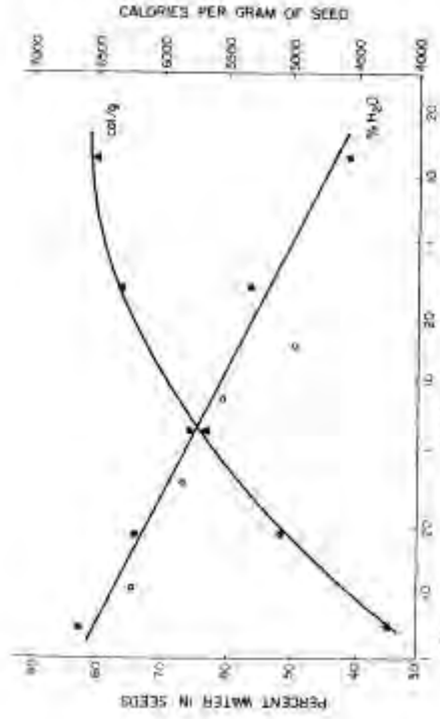

Figure 6. Analysis of longleaf pine seeds from 1983 (closed circles) and 1984 (open circles). Calorimetry was performed only on seeds collected in 1983.

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to exploit. First, green longleaf cones are large—up to 29 cm in length and 490 g in weight. Secondly, they do not dry out and open until late September and thus can be used only by an animal that can handle the bulky weight of the cone and chew off the fibrous bracts protecting the seeds. Finally, except in mast years, many pines produce few cones or none at all and the rare trees with large cone crops may be long distances apart. A squirrel that could deal with these exploitation problems would have exclusive control of a rich energy source at a critical time of year. The fox squirrel, because of its size and locomotor capacities, seems uniquely adapted to this situation.

In order to assess the importance of body size on cone use, North Carolina fox and gray squirrels and western fox squirrels were timed and videotaped while feeding on longleaf cones of different sizes. Differences in feeding ability among the three groups were pronounced. Comparisons of total feeding times per cone and rates of bract removal for the three squirrel groups clearly show the superiority of the North Carolina fox squirrels in feeding on this food and the relative importance of body size in cone handling (Table 16). When the feeding times of each group are plotted against cone size (Fig. 7), it is immediately apparent that large cones represent more time and work than smaller cones and that, on the basis of the steeper slopes of the curves for the gray and western fox squirrels, increasing food size has a greater effect on the feeding times of the smaller squirrels than on those of the larger North Carolina fox squirrels. Finally, videotapes of feeding revealed that these differences in feeding were only partially related to gnawing ability. The most pronounced advantage of the larger fox squirrels' size was their greater strength and dexterity in carrying and handling such food items. In the wild these animals normally cut cones and carry them along a branch to a stable feeding site near the trunk or retrieve them from the ground and eat them near the base of the tree. The strength required is considerable. Western fox squirrels moved cones with difficulty. Gray squirrels dragged cones along the ground and straddled them awkwardly while feeding. While small size alone does not prevent gray squirrels from using this resource, it does have an effect on the time, location

Table 16. Feeding performance of fox and gray squirrels on cones of *Pinus palustris* (cone weight ranged from 90 g to 300 g)

Species (habitat)	n (squirrels)	Approximate squirrel weight (g)	Handling time in min (SE)	Rate of removal of cone material (g/min)
S. niger (NC)	[illegible]	1000	13.0 (0.6)	11.2
S. niger (IN)	3	800	17.2 (2.3)	9.8
S. carolinensis (NC)	7	500	20.9 (1.2)	7.6

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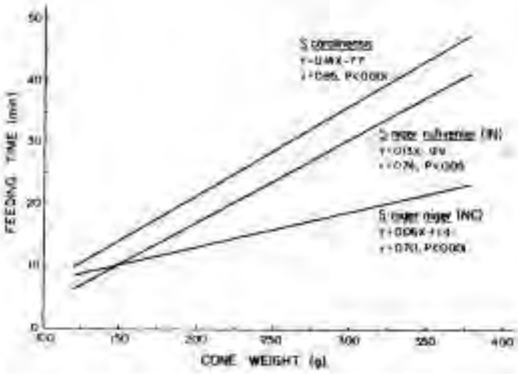

Figure 7. Feeding times of fox and gray squirrels on different sized cones of longleaf pine trees.

and perhaps the risk associated with this food. On the other hand, the crucial nature of this resource to the fox squirrel, especially after a period of food scarcity, may partially account for the evolution of a body size which would permit its rapid and relatively safe use.

We have repeatedly alluded to the patchy nature of longleaf pine and mast production in pine-oak habitats and thus, the importance of locomotor ability in exploiting these foods. Throughout their range, fox squirrels spend considerable time on the ground in open woodland or at some kind of forest-grassland interface (Taylor 1973, Armitage and Harris 1982, Nixon et al. 1984). Large size may well reduce arboreal agility, and the discontinuous canopy of many habitats make a partially cursorial existance a necessity. North Carolina fox squirrels usually run out of sight along the ground on release from a trap or hits. Animals elude a human climber by leaping from the home tree and running along the ground rather than escaping through the branches. In fact, we have often observed fox squirrels, when pursued, leaping from near the top of pine trees, landing on the ground with a loud "thump" and running off

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unimpaired. Thus cursorial behavior is critical to food acquisition, escape, and general movement through the pine-oak habitat. Large body size permits greater velocities and greater efficiency for running animals (Calder 1984). Interestingly, Gauthreaux (1980) suggests that only mammals of a kilogram or more are capable of long distance movement or migration. North Carolina and other southeastern fox squirrels are often a kilogram or more in weight, and thus may represent the lower end of the spectrum of long distance runners. Reports of fox squirrel sightings in forests miles from any known population seem to substantiate this capacity and indicate the importance of dispersal and colonization in their adjustment to Coastal Plain conditions. However, it is highly likely that at the heart of this squirrel's mobility are years of natural selection for the ability to use critical patchy resources like longleaf pine.

Having stressed the importance of food scarcity and patchiness in the pine-oak forests of North Carolina, we need to compare our study region with other parts of the eastern Coastal Plain. Unfortunately, with two exceptions comparative data are nonexistant. Moore (1957) described a different schedule of food availability that can be linked to latitude. The fox squirrels of northern Florida, the largest of this species, experience a more moderate winter climate; a short, but apparently not extreme, period of food shortage in the spring, the onset of the longleaf seed harvest in June, and thereafter pine seed availability into September (Moore 1957). Since Moore's study lasted two years it is not possible to judge if these conditions were typical. However, both the milder conditions and absence of any long summer food shortage are energetically consistent with the larger size of his squirrels, and the higher incidence of summer litters. The squirrels of northern Florida, while still occupying the longleaf pine-turkey oak forest, have lower costs and better food conditions than those of the Carolinas. On the other hand, the Delmarva fox squirrels studied by Flyger, Taylor, and their colleagues must cope with more costly winter conditions and a loblolly pine-oak habitat more like the North Carolina Piedmont than the Coastal Plain. The absence of a special resource like longleaf pine, the closed nature of many forests, and the abundance of the gray squirrel, in addition to a demanding climate, may partially account for the smaller size of these populations.

Fungi are another resource that suggest the existence of a special relationship between the fox squirrel and its pine-oak habitat. During the early years of the study we had often observed mushrooms of several species with distinctive toothmarks and had found areas of dug-up pine straw which were underlain by fungal mycelia. Later, especially during periods of low food supply, we started to notice large numbers of small pits 3–6 cm deep in the pine needles and duff around longleaf pines. Because such pits very rarely yielded any part of a fungal fruiting body, it was not immediately evident that most or all of these excavations were associated with fungi. However, results of an analysis of stomach and fecal samples in the laboratory of Maser, Trappe, and their colleagues at the Forest Sciences Laboratory in Corvallis, Oregon, revealed the spores of eight

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genera of hypogeous fungi and a substantial fungal component in the diets of the animals represented. A visit by two mycologists from this laboratory in the fall of 1984 confirmed the suspected association of pit digging and fungi acquisition and revealed an abundance of fungi in 5 areas of the Sandhills. Hypogeous fungi, such as the genera *Elaphomyces* and *Rhizopogon* found in our study sites, form subterranean or subsurface fruiting bodies whose spores are exclusively animal dispersed (Trappe and Maser 1977). The fruiting bodies are a source of food and nutrients (sodium, phosphorous) for many mammal species (Maser et al. 1978) but their spores are indigestible and thus are dispersed whenever and wherever these mycophagists defecate. Many of these fungi, like the truffle of culinary fame, produce volatile substances which attract animal dispersers and thus guarantee the fungus' perpetuation.

Hypogeous fungi are also mycorrhizal. Their hypae form mutualistic associations with the roots of certain tree species. As a result, the tree effectively increases the surface area and nutrient absorption of its roots, while the fungus receives a source of carbohydrate and a place to live. Recent work by Li et al. (1986) indicates that some of these fungi contain mutualistic bacteria which can fix nitrogen, some of which may be available to the host tree. Finally, other studies (Slankis 1973) have shown that many mycorrhizal fungi produce plant hormones, auxins and cytokinins, and thus may influence plant growth directly.

While many of the details are in need of study, the foregoing information raises the possibility of a complex interdependent relationship among the fox squirrel, longleaf pine, and one or more species of hypogeous fungus. One and perhaps several of the fungi so far identified are closely associated with the roots of longleaf pine. The fox squirrel uses fungi for food and thus acts as a dispersal agent for fungal spores. Recently, Castellano (1988) has shown that mycorrhizae become established on the roots of longleaf seedlings after exposure to fecal material from fox squirrels fed *Elaphomyces* sporocarps. Although other mammals may eat these fungi, few travel the distances over open ground that the fox squirrel does. And the bare, mineral soil of burns and clearcuts, so necessary for pine seed germination, would require a new fungal inoculum to promote vigorous longleaf growth. Thus it appears that the fitness of all three partners—squirrel, tree, and fungus—is potentially enhanced by this relationship, which begins to appear coevolutionary in nature. Similar relationships have been described for the Abert's squirrel (States 1984), western gray squirrel, and flying squirrel, *Glaucomys sabrinus* (Maser et al. 1985) and their respective forests, but in none of these cases does the interdependence of all the components seem so strong.

Nests

Nests are critical resources for squirrel survival and have received a great deal of attention in other studies of southeastern fox squirrels (Moore 1957, Hilliard 1979, Flyger and Smith 1980), western fox squirrels (Nixon et al. 1984)

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and tree squirrel species in general (Flyger and Gates 1982, Gurnell 1987). The efficacy of using nest boxes to study squirrels is well documented in the literature and provides another measure of the importance of cavity-type nests in the biology of various species. Leaf nests, or dreys, and occasional underground refuges (Moore 1957) are frequently occupied during warmer months or in the more southerly parts of the squirrels' range. Because of the extensive work of Moore and Hilliard and the high level of disturbance resulting from leaf nest checks no systematic research on nests was conducted in the present study. However, 3 years of field work and 4 years of telemetry data provide additional information on nest use and its relation to other aspects of fox squirrel biology.

Investigators have pointed out the critical importance of tree hollows for the rearing of young and protection from severe winter conditions (Madson 1964, Barkalow and Soots 1965, McComb and Noble 1981a). Such natural hollows were generally scarce in the pine-oak vegetation of our study sites. Most of these forests were too young with too few really large, old trees to supply many such cavities. Most cavities are found in large storm- or fire-damaged oaks scattered among the pines, but a high proportion of such trees are currently removed by timber operations, firewood gathering or management techniques directed at oak suppression. Hollows in longleaf pines most often occur in ancient flat-topped trees and are frequently the result of fire, injury associated with commercial resin collection or the nest building of red-cockaded woodpeckers. The scarcity of both the endangered woodpecker and suitable pines currently restricts this source of nesting sites. While hollows appear to be limited in many present-day pinelands, they are much more abundant in the moister habitats adjacent to the pine-oak forest. Large tulip poplars, oaks, maples, and hickories of hardwood areas, and cypresses and gums of floodplains and swamps provide numerous cavities which can be used by fox squirrels, even though much of their foraging (as determined by telemetry) is carried out in pine-oak woodlands. Occupation of these areas also tends to increase the zone of overlap with the gray squirrel, another cavity nester.

During the summer and any period of mild weather and/or abundant food, fox squirrels build and use leaf nests. These are usually constructed in the crotch of an oak or pine or among a tangle of vines growing on some large tree. The height and size of nests vary greatly. Fox squirrels have been shaken out of leaf nests only 30–40 cm in diameter and only 4 meters from the ground. Some nest in what appear to be inappropriately small and flexible trees (10–20 cm dbh). More commonly, leaf nests are fairly massive aggregations of twigs, grass, leaves, pine needles and spanish moss (*Tillandsia*) with lateral entrances and large 20–30 cm interior cavities. The size, height, and quality of the nest lining appear to be associated with its function. Day rests, feeding stations, and short term refuges are often little more than platforms while cold weather and rearing nests are more elaborate, well insulated structures. Generally, leaf nests are found wherever appropriate trees occur. However, during the hottest part of

the summer, leaf nests are more often located in moist forests or at the edge of wetlands. It is not clear whether the choice of nesting sites is dependent on microclimate, proximity of water, available food or some combination of factors.

The nest boxes used in the present study presumably supplemented the numbers of natural cavities. Boxes were more often used during cold weather, periods of low food supply and young rearing. In some areas fox squirrels showed a distinct preference for boxes in ecotones or moist forests. Box use occurred only in sites with some observable food supply. When food was excessively scarce or absent, as was the case at a few sites during the eight-year period, the presence of nest boxes failed to attract and hold the squirrel population.

Nest use by southeastern fox squirrels has been intensively studied by Moore (1957) and Hilliard (1979). Moore found that each fox squirrel averaged 3–6.6 nests, depending on the season. Hilliard's animals averaged 9 nests each but only 3 were used intensively and constituted primary nests. In the present study we averaged 2.6 active nest boxes per squirrel capture and 3.2 nests per squirrel during periods of radio tracking. Multiple nest use is common in North American squirrels (Jackson 1961) and insures both rapid concealment and protection for adults and young if occupied nests are threatened or disturbed.

Nesting sites, at least in the form of nest boxes, are in great demand by a number of species besides fox squirrels. Gray squirrel use in and near dense stands of hardwoods has already been mentioned. Many nest boxes were occupied by the southern flying squirrel. Like the fox squirrel this small glider was often found far into the open park-like pine-oak forest, away from groves of deciduous trees. While the fox squirrel traverses such open-canopy woodland by running along the ground, the flying squirrel can glide across the often considerable distances between trees. Up to 21 flying squirrels were taken from a single box, and it was not unusual to find these animals in the abandoned nests of the larger squirrels. Other mammal species occasionally taken from nest boxes include raccoons, opossums, and mice (*Peromyscus* spp.). Screech owls (*Otus asio*) occupied boxes throughout the year but were especially abundant during nesting in the spring. Great crested flycatchers (*Myiarchus crinitus*) often nested in boxes, their presence revealed by the pieces of snake skin incorporated into the nest. Black rat snakes (*Elaphe obsoleta*) were common in the study areas and a few were captured in boxes. These large, predatory, climbing snakes are a potential threat to small mammals, squirrel nestlings and many birds. Other box occupants include lizards (*Eumeces* spp. and *Anolis carolinensis*), the tree frog (*Hyla squirella*), and a variety of wasps, bees, and ants. Repeated checks of nest boxes clearly demonstrate the importance of the artificial cavities provided by nest boxes to many species of vertebrates, but especially to the sciurids which routinely use them for energy conservation and reproduction.

Because of the critical nature of nesting sites to the biology of the fox squirrel and the possibility of nest competition between the fox and gray squirrel, Steele et al. (1985) initiated a study of nest box interactions between these species in the laboratory. Pairs of squirrels were released in large outdoor cages containing two identical nest boxes, one on the side of the cage and one on the floor. Earlier work and studies of other species (Ackerman and Weigl 1970, Weigl 1978) had revealed a strong preference for nesting above ground. Pairs of fox squirrels would not share the upper box; pairs of gray squirrels almost always did so. When one fox and one gray squirrel were introduced into the cage, the fox squirrels clearly dominated the preferred boxes. Thus in direct interactions for this important resource, the fox squirrel appears to have a distinct advantage. However, in areas of predominantly hardwood vegetation and higher gray squirrel numbers, the outcome of such confrontations may be less one-sided. The greater abundance of natural cavities in or near gray squirrel habitat in today's forests suggests that this interaction is now played out with increasing frequency.

Activity Patterns

Moore (1957) and Hicks (1949) have documented many aspects of the daily and seasonal activity patterns of eastern and western fox squirrels respectively. The squirrels of northern Florida were classified as "late risers" by Moore, but were considered exceptionally active within the first two hours of leaving the nest. Telemetry and various other technological advances (Kramm 1975, Hokkanen et al. 1977, Tomsala et al. 1980, Ferron 1983) have permitted the collection of such data with more precision and less physical exertion and have provided additional information on the annual variation in activity. Although the study of activity was secondary to that of space utilization, radio tracking of 21 fox squirrels over the past three years provided some indication of seasonal activity patterns. Two aspects were investigated: seasonal variation in onset and cessation of activity and seasonal changes in daily activity patterns.

Mean onset and cessation times during telemetry periods throughout the year (Fig. 8) demonstrate the fox squirrel's response to photoperiod and the influence of differing seasonal conditions. During the winter months, squirrels generally left the nest between 0900 and 1100 and returned by 1600. During May, June, and July activity began earlier, 0700-0900, and ended later, 1700-1800. In August and early September both onset and cessation times were highly variable. Activity started as early as 0600 and sometimes continued until after sunset. Such long days are associated with the period of longleaf cone use and perhaps the beginning of the mast harvest. Thus, winter activity periods of 7–8 hours, midsummer periods of 10-11 hours, and long bouts, up to 14 hours, in late summer may be typical of North Carolina squirrels. However, it is important to add that these periods represent the potential duration of activity only, bracketed by the onset and cessation times, not the actual time spent moving in the habitat.

Daily patterns of activity also varied seasonally. During the winter,

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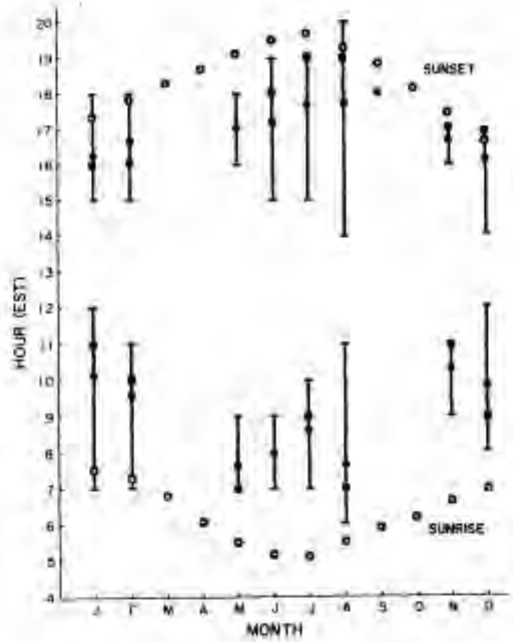

Figure 8. Times of onset and cessation of fox squirrel activity in relation to times of sunrise and sunset (open circles). Closed circles represent the mean, squares indicate the mode, and bars indicate the range.

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December-February, fox squirrel activity was high and mostly confined between 1000 and 1600 (Fig. 9). A few animals exhibited some activity between 0800 and 1000, and 1600 and 1800. Thus, limited day length and perhaps winter conditions commonly produce a short, sustained pattern of activity.

Summer activity patterns were much more complex (Fig. 10). During June, fox squirrels were active most of the daylight hours. A bimodal pattern with additional minor peaks was typical, with major activity peaks falling between 0600 and 1200 and between 1400 and 1800. In July, both the duration and intensity of activity were greatly reduced. Most squirrels were moving in midmorning and late afternoon. This is the so-called "disappearance" period when food supplies are at their lowest and squirrel sightings relatively rare. August provides a marked contrast with both June and July. The bimodal pattern is replaced by a series of roughly equal peaks. Activity is generally high and spread throughout the day. Observations during data collection reveal that this burst of activity may be largely attributed to the longleaf cone harvest, a period of intense feeding after the July food shortage.

The limited data presented here suggest that squirrel activity is linked to a variety of factors, but especially day length and food supply. It could be argued also that the peaks of activity in the winter and summer to some degree reflect the most favorable temperature conditions for moving about these open forests. The July decline in activity is perhaps the most interesting finding. Assuming that both food supply and squirrel activity are low, what are these animals doing during this period? One would expect high activity and large range at times of low food supply if such behavior would produce a net gain in...

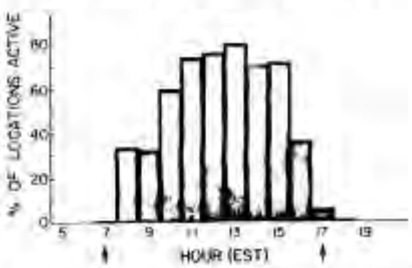

Figure 9. Daily activity patterns of radio-collared fox squirrels (n = 7) during fall and winter (December, January, and February combined). Arrows indicate hours of sunrise and sunset.

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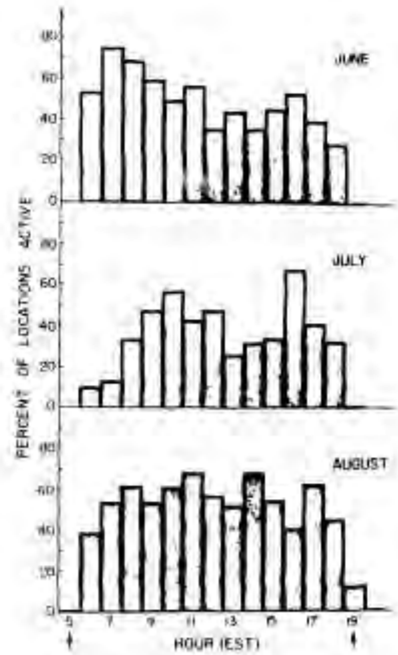

Figure 10. Daily activity patterns of radio-collared fox squirrels (n = 6) during the summer. Arrows indicate hours of sunrise and sunset.

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tionally. Since we often find the opposite, we have to assume that the squirrels are sitting in or near nests and waiting out the food shortage utilizing stored fat and whatever foods are available locally. Such an interpretation is consistent with Goodrum's (1972) description of light body weights in the mixed forests of eastern Texas during the summer and our own impressions of the relatively poor condition of summer squirrels. If fox squirrels are waiting out the food shortage, could they extend their energy reserves by letting their body temperature drop to ambient—by becoming heterothermic or estivating? While an answer to this question will require further study, it is worth noting that the Abert's squirrel in the ponderosa pine forests of the west has been found to use heterothermy to survive adverse conditions in winter (Golightly and Ohmart 1978). Since the summer food scarcity is a predictable event in the life of North Carolina fox squirrels, it would not be surprising if they had evolved physiological as well as behavioral responses to insure survival.

Home Range and Habitat Use

Home range, use of space, and movements of a species are basic to any understanding of its ecology since they integrate the varying influences of size, population parameters, habitat variables, and behavior (McNab 1963, Peters 1983, Calder 1984). A recent review of home range characteristics of tree squirrels (Don 1983) has summarized much of the available information on these animals and pointed out theoretical and methodological concerns which have greatly influenced our own research. In order to evaluate an animal's home range it is necessary to consider the total size of its range, seasonal variations in area and movement, and actual utilization of space within the range (Sanderson 1966, Adams and Davis 1967, Jones 1984). Most previous studies of the fox squirrel have concentrated on determining the overall range of the species, often on the basis of data from single seasons (Baumgartner 1943, Bernard 1972, Donohoe and Beal 1972, Adams 1976, Havera and Nixon 1978, Hilliard 1979). However, early in our research Ha's (1983) two-year study of the influence of season and food supply on home range size revealed some of the complexities in the fox squirrel's use of space and provided a basis for the more fine-grained analyses we have used subsequently.

Recent telemetry studies, plus those of Ha (1983), document the range and movements of 21 fox squirrels (Table 17). Twenty of these were located frequently enough (18–168 times each) to obtain good estimates of their home range and activity. The other six, with fewer radio locations, provide approximations of the same parameters. Although many past studies, especially those involving trapping, have used small numbers of points in range calculations (see Don 1983, for a review), the resulting ranges often underestimate (MCP) the area actually used by an animal. Table 17 is based on 229 days of telemetry and a total of 2008 radio locations. On the basis of these data we calculated minimum convex polygon (MCP) and 95% ellipse home ranges (Jennrich and Turner 1969). The mean values for the 20 most-studied squirrels are males 26.6 ha, females 17.2 ha (MCP) and males 43.7 ha, females 25.0 ha (ellipse). These

Table 17. Home range estimates based on all radio locations for individual fox squirrels. (Second group represents animals for which only limited data are available, see text.)

ID	Sex	Age	Tracking Interval	Number of Locations	MCP (ha)	95% Ellipse (ha)
[illegible]	Male	[illegible]	Nov-Jan 83	46	11.7	7.1
111	Male	[illegible]	Dec-Feb 84	98	20.6	36.7
31	Male	[illegible]	Jan-Feb 84	[illegible]	11.8	22.8
107	Male	[illegible]	Feb 84	51	14.7	18.6
81	Male	[illegible]	May-Aug 84	123	43.7	79.5
84	Female	[illegible]	Nov 82	12	3.0	15.1
113	Female	[illegible]	Dec-Feb 84	96	15.1	17.6
[illegible]	Female	[illegible]	Jan-Feb 84	86	17.6	19.1
[illegible]	Female	[illegible]	Feb 84	45	[illegible]	[illegible]
[illegible]	Female	[illegible]	Jun-Aug 83	38	25.1	21.9
[illegible]	Female	[illegible]	Aug 83	46	1.6	1.3
[illegible]	Female	[illegible]	Jun-Aug 83	168	20.0	19.2
[illegible]	Female	[illegible]	Jun-Aug 83	[illegible]	[illegible]	[illegible]
[illegible]	Female	[illegible]	May-Aug 84	112	18.1	11.9
[illegible]	Female	[illegible]	Jun-Aug 84	[illegible]	12.2	24.4
[illegible]	Male	[illegible]	Jun-Aug 84	146	24.6	79.2
[illegible]	Female	[illegible]	Jul-Aug 84	95	—	42.0
[illegible]	Female	[illegible]	Jul-Sept 85	166	15.7	25.1
[illegible]	Male	[illegible]	Jan-Mar 86	103	40.9	100.6
[illegible]	Female	[illegible]	Jan-Mar 85	105	[illegible]	41.1
[illegible]	Female	[illegible]	Dec-Jan 85	71	15.1	41.1
[illegible]	Male	[illegible]	Dec 85	21	17.1	29.8
[illegible]	Female	[illegible]	Dec 85	21	3.1	49.1
			Mean	91.1	17.9	39.1
61	Male	[illegible]	Jan 82	4	7.1	11.4
62	Male	[illegible]	Apr 81	8	7.8	31.8
58	Female	[illegible]	May 82	11	3.3	3.8
59	Female	[illegible]	Apr 81	11	1.1	1.8
[illegible]	Female	[illegible]	Mar 82	11	[illegible]	3.3
56	Female	[illegible]	Jul-Aug 82	18	4.7	12.7

home ranges represent different seasons, food conditions and study sites and provide only an approximation of the total area familiar to the squirrels studied. While these mean values are comparable to those of Hilliard (1979) for animals in a complex habitat mosaic in Georgia (males 26.4 ha, females 13.0 ha, MCP), they are somewhat smaller than the ranges reported by Edwards (1986) in pine plantation and hardwood "runners" in South Carolina (males 31.6 ha, females 19.3 ha) and by Kantola (1986) for the large *S. n. shermani* in longleaf pine-oak woodland in Florida (males 40.0 ha, females 20.6 ha). In contrast, these southeastern home ranges are substantially greater than the 0.8–7.0 ha (MCP) ranges reported by Baumgartner (1943), Bernard (1972), Adams (1976), and Havera and Nixon (1978) for western fox squirrels. Only the ranges of Donohoe and Beal (1972) approach the values for southeastern fox squirrels, and this similarity may be the result of both a small sample size (4) and the predominance of male squirrels in the study (Ha 1983). Southeastern fox squirrels also have much larger home ranges than would be predicted on the basis of body size and diet (McNab 1963, Harestad and Bunnell 1979, Peters 1983), and it is likely that such unexpected ranges result from the resource patchiness of their habitat (Mace and Harvey 1983). In sharp contrast to these fox squirrel data are the home range estimates for gray squirrels ($\bar{x}$ = 3.5 ha MCP) occupying the hardwood and bottomland forests at our study sites. Obviously these smaller animals can survive with less space both individually and as a population.

While general home range statistics provide a measure of the area covered by an individual, they ignore much of the ecological and seasonal variation in both range size and area utilization. Thus in the present study, telemetry data for each squirrel were analyzed for each 3-day radio tracking session, each month, and each season, and the resulting records combined in various ways to obtain some idea of the annual variation in use of space. Two other statistics —the MD/T (median distance moved per hour) and the MAP(50)/MCP index—provided measures of activity and evenness in the use of the home range.

Telemetry results reveal considerable variation in space use associated with sex, season and food supply. Male home ranges were usually much larger than those of females, especially during periods of winter food scarcity (Table 18). Home ranges of both sexes were generally consistent throughout the year, but showed indicates of some seasonal variation. Activity levels (MD/T) varied considerably with food availability (Fig. 11, Table 19). During periods of food abundance (most of the data is from the spring) females were more active than during times of scarcity, while males showed a reduction in activity. In the case of the females, this change may be associated with the energy demands of young rearing. Males, on the other hand, probably can meet their energy requirements with less activity.

Space use during periods of winter and summer food scarcity also showed some interesting contrasts (Fig. 12). While home ranges were similar in both seasons or slightly smaller for males in summer, activity levels were markedly

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Table 18. Comparison of mean activity, home range size, and 50 percent utilization distribution between low food and moderate or high food availability (number of telemetry sessions is in parentheses).

	Sex	Low food	Moderate or high food
% Active locations	Combined	46.0 (37)	46.0 (10)
MD/T (m)	Female	85.4 (24)	106.2 (14)
MD/T (m)	Male	112.8 (9)	80.0 (8)
MCP (ha)	Female	9.2 (24)	10.2 (14)
MCP (ha)	Male	13.9 (9)	18.0 (8)
MAP(50)/MCP	Combined	0.14 (14)	0.19 (5)

Table 19. Comparison of mean activity, home range size, and 50 percent utilization distribution among winter low food (Dec 83–Feb 84), summer low food, and summer low to moderate food (Jun–Aug 84; number of telemetry sessions is in parentheses).

	Sex	Winter low	Summer low	Summer low to moderate
% Active locations	Combined	32.0 (10)	49.0 (7)	44.0 (6)
MD/T (m)	Female	99.0 (5)	88.1 (15)	34.4 (4)
MD/T (m)	Male	146.2 (5)	68.5 (2)	73.8 (2)
MCP (ha)	Female	8.9 (5)	9.4 (15)	8.9 (4)
MCP (ha)	Male	19.0 (5)	14.9 (2)	15.2 (2)
MAP(50)/MCP	Combined	0.02 (6)	0.25 (10)	0.09 (6)

lower for all squirrels during the predictably low food conditions of the summer "disappearance period". At this time squirrels used their ranges more evenly possibly searching for food. During an unusually wet summer when food supplies appeared more abundant, squirrel ranges were more like those of winter and female activity dropped even further.

On the basis of the above telemetry data, the activity patterns described in the previous section, and eight years of behavioral observations, we would offer the following explanation of the fox squirrel's varied use of space. During

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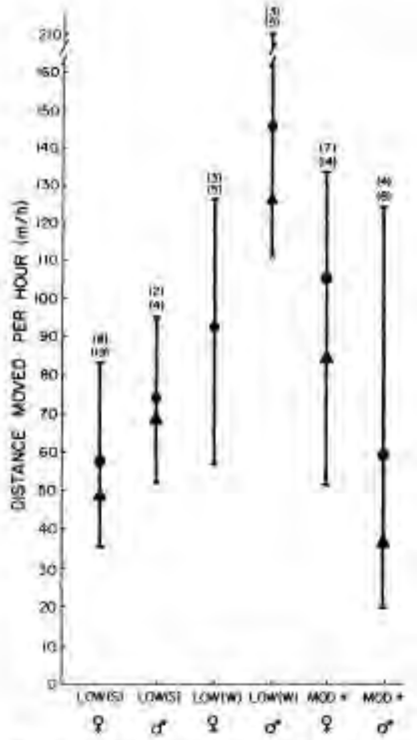

Figure 11. Distance moved per hour plotted against food supply. S = summer; W = winter, MOD. + represents food supplies ranked at moderate or above; numbers in parantheses are number of individuals and number of telemetry sessions respectively. Circles indicate the mean; triangles, the median; bars, the range.

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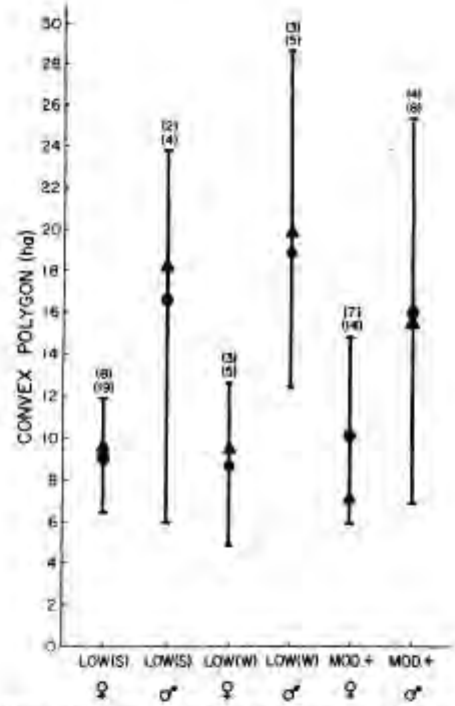

Figure 12. Minimum convex polygon home range estimates plotted against food supply. S = summer, W = winter; MOD. + represents food supplies ranked at moderate or above; numbers in parentheses are number of individuals and number of telemetry sessions, respectively. Circles indicate the mean; triangles, the median; bars, the range.

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periods of food abundance — the cone harvest in late summer or the mast harvest in the fall — squirrels (both male and female) are generally active throughout most of the daylight hours, but partly because of mild temperature conditions can obtain sufficient food from relatively small areas. When food supplies are scarce in the winter, animals must cope with increasing competition and exceedingly patchy resources in addition to higher thermoregulatory costs. Under such conditions, stored fat and food may well be inadequate to meet energy requirements for extended periods, and the males, especially, are forced to expand their ranges and increase their activity to locate food (Fig. 13). From the telemetry data and direct observation it is apparent that this is a time of foraging along the ground and a time of digging for hypogeous fungi. The much larger home ranges of males (compared to females) at this time may be largely a function of food availability. With their smaller ranges a number of females might occupy a particular habitat, exploit it thoroughly, and in the process limit the availability of food and nesting sites to males. If these females also defended the areas around nests, as has been reported for midwestern fox squirrels (Havera and Nixon 1978), it is likely that males would be forced to cover much larger areas to meet their energy requirements. The males' tendency toward greater activity and slightly larger ranges in times of food shortage parallels their habit of covering large areas during the breeding season. It is

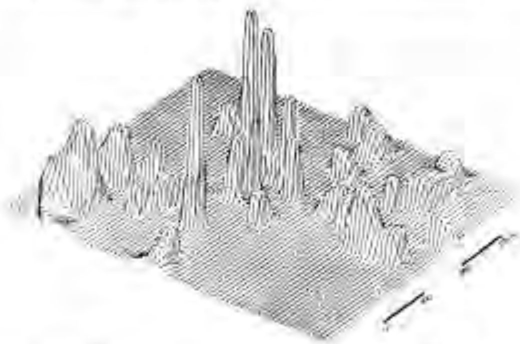

Figure 13. Three-dimensional representation of the home range of a female fox squirrel (n = 55) during December and January indicating increased activity and use of the home range area.

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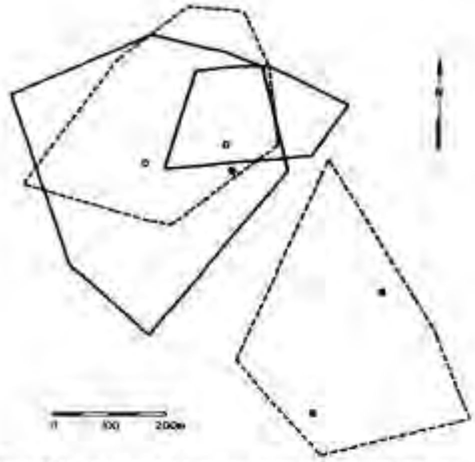

Figure 14. Minimum convex polygon home ranges for four fox squirrels tracked at CM study site during February 1984. Male ranges are indicated by broken lines and female ranges by solid lines. Closed stars represent nests of males and open stars represent female nests.

not uncommon to find a male home range overlapping the ranges of several females, but we have yet to discover any overlap among male ranges (Fig. 14). Thus a combination of female occupancy, male reproductive strategy, and heightened energy demands may be the basis of the special home range response seen in our fox squirrels during winter food scarcity.

Unlike the occasional and usually brief periods of food shortage in winter, the scarcity of summer food is a predictable annual event. With the previous fall's mast crop exhausted, the spring bloom of plant and animal foods suppressed by hot, dry conditions, and the longleaf pine seed several weeks from maturity, both adult fox squirrels and their spring litters face the most severe conditions of the year. Fox squirrels respond by moving down from ridges and pinelands to the edges of bottomlands and swamps. Fortunately, low

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Figure 15. Three-dimensional representation of the home range of a female fox squirrel (n = 50) during the summer low food period (June-July 1983) indicating low activity and home range usage.

thermoregulatory costs, favorable microclimates of refuges and nests, and easy access to water may reduce energy costs and permit the use of fat reserves at minimal rates. The animals become less active but may use their ranges more evenly (Fig. 15). Ranges for females may increase slightly but rarely equal those of the males. To an observer accustomed to fox squirrel behavior during the rest of the year, the animals seem to have "shut down", to have "disappeared"! Evidence of digging in moist soils indicates that hypogeous fungi are again an important part of the diet. Occasional longleaf cone cores suggest that squirrels, in effect, keep track of the seed ripening process (Steele 1988). When seed in the green cones has matured sufficiently, squirrels often show a spectacular increase in activity, especially in trees, and cone cores litter the ground under pines. Although home range use reflects cone availability and harvest, the size of the range does not increase unless the cone supply is low and very patchy. Once again, food is relatively abundant and the squirrels return to a pattern of space use more typical of such conditions. Longleaf pine cone ripening may have an additional effect in that it may trigger the mating activity which produces fall litters. The one year (1981) in which fall litters were detected in this study followed several seasons of good food supplies and a better-than-average longleaf crop. Calculation of the time of conception from litter age estimates

reveals that mating must have taken place around the time of cone ripening. Thus, the large ranges of the males in late summer may at times serve both an energetic and reproductive function.

The above scenario reflects our present understanding of fox squirrel ranges and habitat use. In keeping with the admonitions of Don (1983) and others, we have found that careful examination of fine-grained temporal and spatial patterns is much more useful than the documentation of overall ranges. Study of data from each radio tracking session, each month, or some other time interval revealed that the size and location of an animal's home range often changed markedly and was invariably smaller than the overall range. By examining ranges at different intervals, we were often able to document changes in food habits, nesting sites and habitat as well as seasonal shifts. The differences in the ratios of short-term MCPs to overall MCPs for summer and winter clearly show the distinctly seasonal aspects of squirrel spatial use (Table 19). Thus, using a series of short-term ranges to interpret large-scale patterns was found to be more effective than the reverse approach.

GENERAL DISCUSSION

Synthesis and Conclusions

The fox squirrels of North Carolina are one of a group of ecologically and morphologically similar squirrels occupying much of the Atlantic and Gulf Coastal Plains. Until recently, this group has remained virtually unstudied while the smaller, reddish forms west of the Appalachian Mountains have been the subject of repeated investigations and form the basis for most of our understanding of the species as a whole. While the western populations have thrived and extended their range (Hibbard 1956, Madson 1964, Wrigley et al. 1973, Wright and Weber 1979), those of the Southeast are faced with an increasingly precarious status, with three subspecies now considered of special concern or endangered. The present study represents one of the first attempts to acquire long-term demographic data on a Coastal Plain population and to analyze closely some of the habitat factors which might explain population trends and patterns. In spite of the obvious limitations of our data and the need for further research we would like to summarize some of our findings and ideas about North Carolina fox squirrels, briefly contrast these with certain aspects of the ecology of western animals, and suggest some general guidelines for managing the fox squirrels of the Southeast.

Study of approximately 220 fox squirrels over the past 8 years has begun to provide a clearer picture of the species' population biology in the present-day Coastal Plain—a picture quite different from that emanating from midwestern research. The fox squirrels of eastern North Carolina are elusive, large tree squirrels occupying disjunct stands or expanses of pine-oak forest at densities well below those of most other North American squirrel populations (Gurnell 1983). Recruitment—litter size, litter frequency and perhaps even litter survival—is low and highly variable from year to year, once again approaching the minimal values cited for other species. Longevity for these animals is unknown, but may be appreciable after the first year of life, considering the limited sources of mortality, preponderance of adult age classes and low reproductive rate of relatively stable populations. In the course of a single year or several years, all population parameters including body weight, seem to fluctuate with the food supply. The large home ranges of these squirrels, their cursorial proficiency and their occasionally sporadic presence at particular sites suggest an extremely high level of mobility and the capacity to respond to resource conditions by movement or even long-distance dispersal. The long-term residence of small populations at certain sites appears to be directly linked to the quality of the habitat rather than any social bonding among individuals; for, except for breeding and young-rearing, fox squirrels are largely solitary. Finally, the site-specific proportions of the different color variants and the sudden but often temporary appearance of fox squirrels in distant areas hint at a survival strategy involving small, sedentary, inbreeding populations at the better sites and younger, dispersing founder populations in new islands of habitat.

Our research to date suggests that the observed population characteristics of North Carolina fox squirrels are best explained by certain habitat factors and the impact of human activities on these factors. Figure 16 describes our understanding of the major components of the fox squirrels' habitat and, by means of the width of the arrows, the relative importance which we attach to various factors affecting population size, recruitment and survival. At this point we believe that the food supply, the habitat which produces it, and human influences on this habitat are the critical factors for squirrel survival. Using the diagram as an outline, we consider each of its parts separately and summarize our findings and interpretations.

The primary habitat of the fox squirrels of North Carolina and much of the Southeast is open, mature, pine-oak forest, especially longleaf pine-turkey oak, along with some adjacent hardwoods, bottomlands, or swamp woodlands. Although the actual species composition of the habitat can vary, it must provide a minimum array of foods and preferably some cavities for reproduction and protection. Only stands with large mature trees seem to provide adequate food supplies and nesting sites. The southeastern fox squirrel's large size and unusual clinal variation appear to be related to the presence of longleaf pine, the openness of the forest, and perhaps the arrangement of available habitats in the Coastal Plain. Large body size is a definite advantage in the exploitation of bulky longleaf cones and in locomotion along the ground between trees,

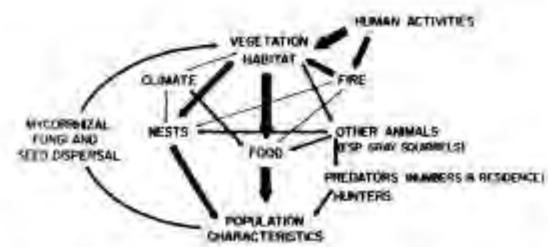

Figure 16. Diagram indicating the relationship between habitat factors and population characteristics. Width of arrows drawn to suggest relative importance of various factors.

food sources, and distant blocks of habitat. The openness and harshness of the habitat also seems to limit the number of other small mammals (such as the gray squirrel) which might enter this forest and potentially compete for food and nesting sites. During the eight years of the study the progressive closure of the canopy of a site and the development of the understory led to increased gray squirrel and fewer fox squirrel captures. Finally, as in an orchard the open nature of oak-pine forests may promote greater tree crown development and higher production of squirrel foods due to reduced competition for light, nutrients and water (Goodrum 1938, Flyger and Gates 1982). And the critical determinant of the open character of this habitat is fire. Fire not only thins the forest and suppresses the understory but eliminates all but the most fire tolerant species and individuals which typically make up this community.

In addition to the species composition and open nature of this pine-oak habitat, its size and distribution in the Coastal Plain are potentially important factors in squirrel survival. Because of the low diversity and seasonality of resources in typical habitat, large areas are required to support a population of fox squirrels. The sparseness, low demographic statistics, and large home ranges of these animals clearly are their response to the relatively meager resource base of pine-oak forests. The needs of these squirrels might be met by either large expanses of habitat or by a mosaic of pine-oak islands enclosed in a wetland or hardwood matrix. The mobility of the fox squirrel permits easy exploitation of either area. In fact, given the dissected physiography of the southeastern Coastal Plain, it could be argued that the fox squirrel is specifically adapted to using such habitats. However, if the pine forests and islands become too small, due to fire suppression or certain types of land use, or too far apart, the total remaining habitat in a region may be inadequate to support a breeding population of fox squirrels. And even though some small, disjunct populations may continue to breed, complete isolation from other such populations could lead to progressive inbreeding, homozygosity, and the inability to adapt to changing conditions.

Any consideration of the vegetational component of the fox squirrel's habitat would be incomplete without the addition of some historical perspective. Such an assertion stems from our belated realization that the declining range, numbers, and density of the eastern fox squirrel are perhaps the result of the animals' current occupation of marginal habitat and habitat remnants. In other words, the habitat in which the eastern fox squirrel evolved may have already disappeared. Even a casual reading of the early naturalists such as Catesby, Bartram, and Audubon invokes a picture of the southeastern Coastal Plain quite different from the reality today. The longleaf pine-oak woodlands of today are mostly small, disjunct, second growth pygmy stands in comparison with past forests. In their study of the North Carolina Sandhills 50 years ago, Wells and Shunk (1931) comment on the status of the longleaf forests as follows (p. 487):

> In its pristine condition with millions of trees measuring a yard or more in basal diameter, the *Pinus palustris* consocies unquestionably presented one of the most wonderful forests in the world. And today hardly an acre is left in North Carolina to give its citizens a conception of what nature had wrought in an earlier day. The complete destruction of this forest constitutes one of the major social crimes of American history.

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Moore (1957, p. 8) describes similar forests in his study of the fox squirrels of Florida:

> Before white man brought his cross-cut saw into Florida, great longleaf pines (*Pinus australis*) stood majestically aloof from one another in sunny, open forests which covered the sandhills. Inconspicuously, 40- or 50-foot turkey oaks (*Quercus laevis*) sporadically formed a scanty understory beneath the towering pines.

Clearly these are not the pine-oak forests of the present Coastal Plain in either structure or extent. Both the longleaf pine forest and adjacent bottomland and swamp vegetation have largely been modified, destroyed, or replaced. It is likely then that the decline in the squirrels of the Southeast has been going unnoticed for some time and that the rather anemic demographic characteristics of most present populations reflects their precarious hold on survival in the existing habitat. Perhaps only their exceptional vagility—the legacy of their evolutionary history in the Coastal Plain—has permitted them to persist at all in their current range and numbers.

In marked contrast to the fox squirrels' history in the Southeast, settlement and agriculture in the midwestern states so favored the fox squirrel that during the 1940s and 1950s many people feared for the survival of the gray squirrel (Madson 1964). The conversion of large expanses of deciduous forest to woodlots and grain fields, development of fence row and shelterbelt vegetation, and settlement of the prairie seemed to benefit the larger semiterrestrial fox squirrel. Only relatively large, continuous tracts of closed canopy woodland, usually with well-developed understories, are likely to be the exclusive domain of the gray squirrel. Coexistence is common only in the open food-rich stands of mature hardwoods like those of the midwest (Nixon and McClain 1969, Hanera and Nixon 1978 and 1980), in woodlands adjacent to agriculture, or in man-made habitats such as cities (Fogl 1982), graveyards (Bakken 1952), and college campuses (Armitage and Harris 1982). If settlement favored the fox squirrel in the West, why has it not had a positive effect in the East? The answer to this question may involve both habitat and mobility factors. First of all, because of its large body size the fox squirrel requires substantial food supplies and relatively large cavities for nesting sites. These needs are best supplied by open stands of mature mast-producing trees or woodlots adjacent to small grain cropland. When such forests are logged, the subsequent second-growth woodland, often with a dense understory, provides less of both resources and may place a cursorial species like the fox squirrel at greater risk of predation (Taylor 1973). If the fox squirrel must also share this habitat with the more arboreal gray squirrel, competition for the same but reduced food supply, especially during poor mast years or in the absence of agricultural crops, might favor the energetically cheaper, smaller species. The second factor, mobility,

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is closely related to these habitat considerations. If islands of good squirrel habitat are widely separated by open terrain, as in much of the settled Midwest, the greater capacity of the fox squirrel to cross such barriers would give it a definite advantage in locating and colonizing isolated farms, towns, and woodlots. In the presence of agriculture and the absence of its congener, even small stands might support fox squirrel populations. Such a mobility-habitat relationship has been invoked by Hibbard (1956) to explain the expansion of fox squirrels along river valleys in the Rocky Mountains. On the other hand, in the eastern Coastal Plain the removal of mature forests, fire suppression, secondary succession in old fields, current timber practices, and residential development have resulted in an abundance of habitat and migration corridors for the gray squirrel and loss of isolated habitat for the fox squirrel. The mature longleaf pine-oak and other open forests of the past were to a large extent the exclusive domain of the fox squirrel. Both habitat and squirrel are thus disappearing together.

While habitat considerations may well be the ultimate determinant of fox squirrel survival in the eastern Coastal Plain, the food supply is certainly the most critical proximate factor in its ecology. In the present study many of the major demographic characteristics of our populations and much of their behavioral repertoire are clearly related to some aspect of the food supply. Even our relatively crude estimates of food availability permitted an unexpected degree of interpretation and prediction of ecological parameters such as density, reproduction, body weight, home range and habitat use. Compared with the food supplies of the deciduous forests of the North Carolina Piedmont or the Midwest, those of the pine-oak forests are exceedingly limited and unpredictable. Since the fox squirrel's large size is a pronounced advantage in exploiting widely dispersed foods and handling the massive longleaf cones, they have an almost exclusive resource base as long as sufficiently extensive and mature tracts of this habitat exist. When food supplies reach critical levels, the squirrel "disappears" by moving into the pine-bottomland ecotone and remaining inactive for extended periods of time each day. The scarcity and limited range of foods has favored considerable specialization in feeding behavior (Steele 1988) and may account for both the high level of aggressiveness observed in our laboratory studies and the limited sociality seen in the wild. Finally, the potentially mutualistic relationship among the fox squirrel, certain hypogeous mycorrhizal fungi, and longleaf pine may point once again to a long evolutionary history in this habitat.

In light of the fox squirrel's high degree of dependence and specialization on the limited food supplies of its habitat, it is not surprising that anything which diminishes these resources in quantity, quality, or predictability can have grave effects on the health of squirrel populations. While spring frosts, insect infestations and poor mast years have definite but usually temporary effects on food availability, major natural or human alteration of the habitat produces a largely irreversible and devastating reduction of the resource base. In addi-

tion to the habitat lost to development and agriculture, the virtual replacement of natural pine-oak forest by large scale, heavily managed, short rotation, pine monoculture has virtually sealed the fate of the fox squirrel in much of North Carolina and the Southeast. Such areas may provide some cover and nesting sites but rarely any appreciable quantities of food. Of the remaining longleaf or other pine forests, most are too small, too young, or too disturbed to provide an adequate food supply.

Compared to food conditions in Coastal Plain habitats, nest availability is a secondary but still important factor in fox squirrel ecology. Although these squirrels can always build and use leaf nests, at least in the cooler parts of their range, they seem to prefer natural cavities or nest boxes for young rearing and as refuges during severe weather. The marked success of nest box studies with a variety of sciurids clearly indicates the importance of natural and artificial cavities to this group of animals. However, many present day pine-oak forests are too young to have any appreciable number of cavities, and most of the resident squirrels are thus forced to raise young in the more vulnerable leaf nests or to move to bottomland habitats possessing more cavities, but perhaps more competitors (e.g. gray squirrel) and predators as well. Timber management techniques aimed at eradicating all hardwoods from commercial forests and the encouragement of firewood cutting on private and public lands has also reduced the number of nesting sites available to squirrels. Only changes in land management and timber rotation intervals will guarantee an adequate supply of natural cavities and an improvement in fox squirrel recruitment and survival.

While a number of other species of wildlife use or pass through the pine-oak forest of the Coastal Plain, very few seem to have much impact on the fox squirrel. Many species of birds and mammals eat acorns, fruits and shed pine seed and thus could be considered potential competitors. However, we have no evidence that these relatively rare and opportunistic animals present a major threat to the arboreal and highly mobile fox squirrels. Many other species use nest cavities, but with the exception of the flying squirrel, screech owl, and great crested flycatcher, most of these nest competitors are more common near the wetland-pine ecotone than in the open forest itself. While the fox squirrel can dominate the majority of nest competitors because of its size, the small size of most natural cavities would effectively exclude it from many nesting sites. Predators, especially nest predators, may have an impact on fox squirrel populations but the low densities and wide distribution of squirrels in pine-oak habitat should make such losses an occasional occurrence, and prevent predators from specializing on this species. Only in areas of seasonally abundant food or near agricultural land are fox squirrel populations likely to reach levels which would favor heavy predation.

The above account of the potential effect of competitors and predators on fox squirrel populations assumes the existence of the squirrel's primary habitat. If pine-oak and other habitats are marginal in quality and restricted in size, the whole formula for survival for this species changes. Limited open and mature woodland forces squirrels into bottomland and successional forests, pine plantations, or settled areas. Apart from the resource limitations of these areas, such habitats may also increase the competitive and predation pressures on the fox squirrel. These are the habitats of the gray squirrel, a species which uses most of the same foods and nesting sites as the fox squirrel. While the fox squirrel might dominate suitable nesting sites and forage as efficiently as the gray squirrel, it would still be at a competitive disadvantage. Because of its smaller size and lesser energy demands the gray squirrel can maintain larger populations on a given resource base and is more likely to survive mast failures than the energetically more costly fox squirrel. In addition, the greater abundance of smaller cavities in such forests and the greater availability of certain foods to the arboreally more agile gray squirrel might hasten the elimination of the fox squirrel from such areas of overlap. Added to this possible competitive scenario is the increased threat of predation. Not only is the semiterrestrial fox squirrel more vulnerable to ambush in dense forest (Taylor 1973), but the greater abundance of squirrels and other small mammals in such habitats might favor the establishment of a resident predator population. The resulting increase in predation pressure could have a disproportionate impact on species with low reproductive rates or near the lower critical population size for effective breeding. Thus, although the fox and gray squirrel can exist in adjacent natural habitats of the Coastal Plain, destruction of the mature pine-oak forest and the restriction of the fox squirrel to the bottomland and successional habitats favored by the gray squirrel, especially if these are of small size, could potentially lead to increased competition, predation and elimination of the larger species.

The foregoing analysis of fox squirrel ecology represents our current understanding of both the biology and plight of this species in North Carolina and the southeastern Coastal Plain. It also provides a basis for comparing the differences between eastern and western populations. The smaller, reddish squirrels of the Midwest commonly occupy diverse, food-rich hardwood forest and agricultural land, attain high population densities, and seem to be limited primarily by intraspecific interactions and, to some degree, by predation and disease. Human settlement has generally enhanced both their ecological success and their range. On the other hand, the large, multicolored, fox squirrels of our study require large tracts of pine-oak forest, maintain dispersed low-density populations, and are usually resource limited. Human activity has destroyed much of the habitat and food supply of these populations, forced them into marginal habitats and improved conditions for both their competitors and predators. We believe these differences represent both a summary and a prediction of the present and future status of the fox squirrels in the two parts of the country. In the Southeast only a change in certain human activities will permit this unique and colorful squirrel to remain a member of the regional fauna.

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Problems of Conservation and Management

Because of the current uncertain status of the fox squirrel in the Southeast, its long years of relative obscurity, and some of our recently acquired data on its demography and habitat requirements, it is appropriate to discuss a few aspects of its conservation and management. In reality two issues need to be addressed. First, why has the southeastern fox squirrel, until recently, remained virtually unstudied and unmanaged for such a long time? Second, what concepts and practices can help preserve these animals in the future?

The first question—that of oversight—is perhaps the central problem in any consideration of future management. No amount of biological data or list of management recommendations will help preserve this animal unless there is a desire on the part of the public and various organizations to do so. As widespread, abundant, and visible mammals, squirrels have been popular with both urban and rural people and figure widely in art and folklore. They are important game animals which can be hunted at little cost by a large segment of the public. Their popularity has led to vast numbers of studies in almost all parts of the eastern United States and Canada. Given the above, why has the largest and most spectacularly colored squirrel in the United States received so little attention from both the public and the research community? This silence is especially baffling when one considers the number of research institutions and biologists in the Southeast, the concerns and recommendations expressed in the few earlier studies, and the well-publicized endangered status of the Delmarva population.

The answer to this question, like almost everything else about the southeastern fox squirrel, may be closely linked to its habitat and the geographical distribution of this habitat. The pine-oak forests favored by this species occupy the Atlantic and Gulf Coastal plains—a predominantly agricultural region distant from most large population centers. Few people today have seen a fox squirrel and many consider its habitat an unavoidable "wasteland" which surrounds some favorite resort or separates their home city from the beach areas of the coast. A disproportionate number of both conservationists and hunters reside in the population centers of the coast or Piedmont. Although the hunting community may have grown up with squirrels, many hunters later move on to game birds, deer and other species. Hunting squirrels for food no longer assumes the importance it had in the past. Finally, because of the ongoing conversion of the Coastal Plain vegetation to agriculture and managed forest, the people of this region are less and less likely to be familiar with the fox squirrel and less likely to influence wildlife policy in its behalf. Thus, given the current lack of familiarity with the fox squirrel, public attitudes toward the Coastal Plain and popular interests in other species, it is not too surprising that, until recently, many wildlife agencies have concentrated on the animals and geographic areas important to their strongest constituencies.

The lack of interest in this species by the scientific community also needs

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some explanation. In spite of its special biological interest, game status, and proximity to research centers the fox squirrel has largely been ignored. Several factors may be responsible for this situation. The vast literature on western fox squirrels and the assumption that the eastern and western forms are similar ecologically may in part explain the lack of interest in additional research in the South. The tendency to view the endangered Delmarva fox squirrel as a distinct ecological entity, rather than one of a group of Coastal Plain populations also may account for the low level of concern about the rest of the group. The priorities of other research and scarcity of any baseline data by which to gauge the status of the fox squirrel populations may also have inhibited needed work. Perhaps the most important constraints on fox squirrel research, however, are the problems of studying the squirrel in the first place. Compared to many other small mammals, fox squirrels are relatively rare, widely dispersed, and often difficult to trap and observe. Such characteristics restrict both the techniques available for study and sample sizes attainable in a short time. In an era where rapid periodic sampling, large sample sizes, and short-term studies are both in demand and in vogue, most researchers cannot afford the time and risk involved in studying a species like the fox squirrel. In addition, during the summer when many biologists concentrate on field studies, fox squirrels are often particularly difficult to locate and collect. And while Coastal Plain swamps and forests are pleasant, open environments in the winter, they can be exceptionally hot, humid, and tick- and chigger-infested in the summer months. With the exception of an occasional ornithologist, botanist or unwilling military recruit, we rarely encountered anyone in our study areas during eight summers of work.

A number of recent developments have begun to change attitudes toward both the fox squirrel and its habitat. Most important of these developments is the national concern and enthusiasm for the endangered red-cockaded woodpecker, a species with habitat requirements similar to those of the fox squirrel. The interest of the conservation community and later the public at large in this bird species, and the resulting massive research program in several southeastern states has awakened concern for mature pine-oak habitat. Somewhat later, knowledge of the size, attractive color variation and relative rarity of the fox squirrel transformed it from an incidental food item to a trophy animal and taxidermist's prize, attractive to hunters from both within and outside the Coastal Plain. The renewed interest among hunters has become increasingly evident during the eight years of the present study and has often included verbal support for conservation measures. Finally, among the scientific community the development of improved telemetry equipment and techniques has begun to counteract the habitat avoidance of past years. Such remote sensing permits the acquisition of quantities of data with minimal intrusion into squirrel habitat. Of the 7 field studies (known to the authors) on southeastern fox squirrels initiated in the last 10 years all have been largely based on telemetry techniques. However, with the exception of the ongoing

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Delmarva studies no additional demographic investigations of Coastal Plain populations are apparently being attempted. While the developing interest in the fox squirrel, its habitat, and other pine forest species are encouraging signs of possible commitment to future study, management and protection, most of the activity surrounding this species is still rather tenuous and indirect. Only a broadly conceived program of research and management directed at the fox squirrel itself will provide the necessary information and impetus to preserve both animal and habitat.

The task of developing a generalized management plan for the fox squirrel in North Carolina and perhaps other areas of the Southeast has been somewhat simplified by the availability and consistency of a wide array of published material, much of very recent origin. First the suggestions and ideas of Moore (1957), Taylor (1973), Flyger and Lustig (1975), Hilliard (1979) and Kantola (1986) provide both an outline of the squirrel's habitat requirements and some concrete recommendations for preserving its habitat. Second, the present study complements this earlier work and extends the idea of habitat dependence and the pervasive influence of food identity and supply on the evolution and survival of these squirrels. For the first time, certain demographic trends have been linked to habitat characteristics in such a way that the implications for habitat management seem inescapable. If, after additional study, it is also shown that the fox squirrel-hypogeous fungi-longleaf pine relationship plays an important part in the productivity of Coastal Plain forests, then there will be an economic as well as an ecological rationale for preserving this habitat and its constituent species.

A third source of information for managing the fox squirrel is the recent detailed management plan for the red-cockaded woodpecker issued March, 1985, as part of the Wildlife Habitat Management Handbook. Many of the concrete recommendations outlined in that study would apply equally well to the fox squirrel. A few exceptions, however, should be noted. First and most importantly, any action that removes all or most of the larger oaks (or hickories) from among the pines of the preferred pine-oak habitat will have a devastating effect on the food supply and nest cavity availability for the fox squirrel and many other kinds of wildlife. The continuous thinning of dense small hardwoods by fire or other means would be highly beneficial in most forests, but the management goal should be an open stand of large pines and scattered 30+ year-old oaks or oak groves. We believe that the invasion of woodpecker trees by flying and other squirrels may often be caused by a lack of alternate nesting sites or by hardwood removal, and that under natural conditions squirrels and woodpeckers normally coexist and have done so for thousands of years. A second exception to this management plan is our recognition that while the mature pine-oak forest represents the major habitat of the fox squirrel, this is not the only vegetation type which this animal can use, nor does such prime habitat have to occur in single large units. A mosaic of habitats with substantial pine-oak representation, large areas of edge, some open land, and access

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in bottomland seems to support squirrels as well as larger pine tracts. A third consideration in fox squirrel management—not applicable to the red-cockaded woodpecker—is the relationship between conservation and hunting. In large areas of good habitat the fox squirrel can probably tolerate a short hunting season with moderate bag limits, providing this activity is confined to late fall and is monitored carefully by wildlife authorities. However, as areas of squirrel habitat become smaller, more disjunct, and of lower quality, there is a real danger that hunting pressure could wipe out some of the small remaining populations and thereby threaten species survival in a whole region.

A final consideration in fox squirrel management concerns the arrangement, size, and age of habitat units within the Coastal Plain and the need for managing these forests for both wildlife and wood products. We have repeatedly stressed the importance of stand maturity and habitat size and complexity in this study and have suggested that the fox squirrel was well adapted for exploiting habitat mosaics and islands providing these were sufficiently close to permit colonization and some minimal gene exchange. Several papers and a recent book by L.D. Harris (1984) of the School of Forest Resources and Conservation at the University of Florida advance a model for forest and wildlife management which, although devised in the northwestern United States, is remarkably well-suited to both fox squirrel and forest management in the Coastal Plain. Using MacArthur and Wilson's (1967) theory of island biogeography as an inspiration and starting point, Harris discusses the conflicting needs of forestry and wildlife in terms of economics, stand rotation, species diversity, population genetics, and critical habitat size, and comes up with an "island archipelago" model which would perpetuate a dynamic system of old-growth islands scattered among different aged stands and other habitats. If adequate dispersal corridors were maintained, such a system would permit island replacement and interisland movement in response to changing conditions. It might well preserve species and genetic diversity better than the current large park and fixed boundary schemes and protect large or highly mobile animals. Thus, just as the detailed red-cockaded woodpecker management plan provides a basis and a beginning for managing habitats for fox squirrels, Harris' model could represent a critical step in the regional planning necessary for any long-term management and preservation effort.

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United States
Department of
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Forest Service

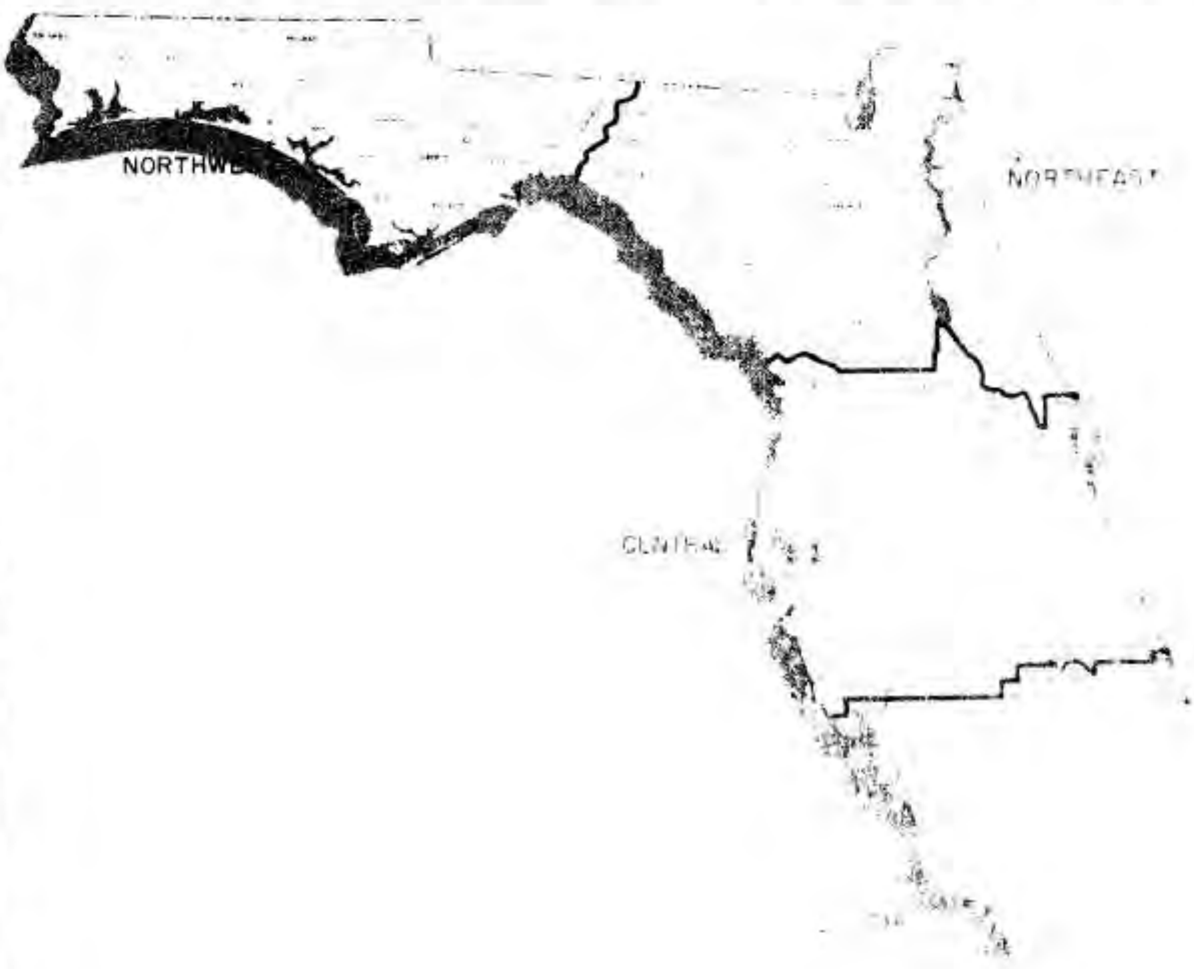
Southeastern Forest
Experiment Station

Resource Bulletin

Forest Statistics for Florida, 1987

Mark J. Brown

Michael T. Thompson



Forest Statistics for Florida, 1987

Mark J. Brown, Forester
and
Michael T. Thompson, Forester
Forest Inventory and Analysis
Asheville, North Carolina

F reword

This report highlights the principal findings of the sixth forest survey in Florida. Field work began in September 1986 and was completed in October 1987. Five previous surveys, completed in 1936, 1949, 1959, 1970, and 1980, provide statistics for measuring changes and trends over the past 51 years. The primary emphasis in this report is on the changes and trends since 1980. Previously reported figures have been adjusted to provide the best estimate of change.

Periodic surveys of the forest resource are authorized by the Forest and Rangeland Renewable Resources Research Act of 1978. These surveys are a continuing, nationwide undertaking by the Regional Experiment Stations of the USDA Forest Service. In Florida, Georgia, North Carolina, South Carolina, and Virginia, these surveys are administered by the Forest Inventory and Analysis (Forest Survey) Research Unit at the Southeastern Forest Experiment Station, with headquarters in Asheville, NC. The primary objective of the survey is to periodically inventory and evaluate all forest and related resources. These multiresource data help provide a basis for formulating forest policies and programs and for the orderly development and use of the resources. This report deals only with the extent and condition of forest land, associated timber volumes, and rates of timber growth and removals.

Reports have been issued for the Northwest, Northeast, and Central Survey Units in Florida as USDA Forest Service Resource Bulletins SE-96, SE-97, and SE-99. A similar report for South Florida, SE-100, is being released with this report. An indepth analytical report for the State should be avaliable in late 1988.

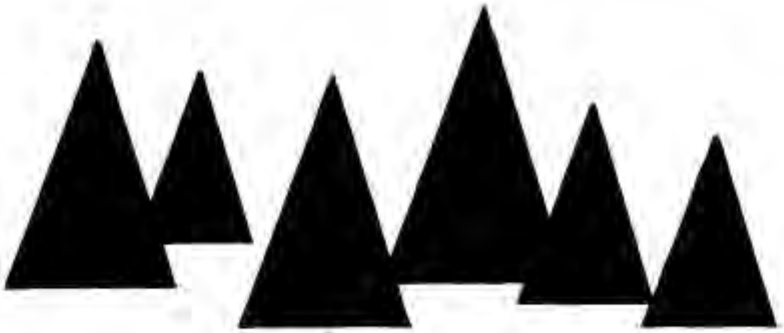
The Southeastern Station gratefully acknowledges the cooperation and assistance provided by the Florida Division of Forestry, Department of Agriculture and Consumer Services in collecting field data. Appreciation is also expressed for the excellent cooperation of other public agencies, forest industry, and other private landowners in providing information and access to the sample locations.

Joe P. McClure

JOE P. McCLURE
Project Leader

Contents

*Tables 1-12, 27, 29-33, 35-38, 41, 42, and 44 are common to all Forest Inventory and Analysis forest resource statistical reports of the Eastern United States.



Since the fifth inventory of Florida's forest resources was completed in 1980--

• area of timberland decreased almost 682,000 acres, or by more than 4 percent. Timberland in Florida now totals less than 15.0 million acres, or 43 percent of the total land area. Timberland decreased in each Survey Unit. Almost 1.3 million acres were diverted to some ther land use, while another 609,000 acres were added to the timberland base. Almost 55 percent of the diversions went to urban and related land uses, 25 percent to agriculture, and 20 percent to a reserved timberland status.

• area of nonindustrial private forest (NIPF) land decreased 12 percent to 7.1 million acres. Farmer-owned NIPF timberland declined nearly 43 percent to 1.1 million acres. Timberland owned by corporations (excluding forest industry) declined 15 percent, while that owned by other individuals increased 9 percent. Timberland owned or leased by forest industry remained about the same at 5.4 million acres. Public timberland rose 12 percent to 2.4 million acres, primarily due to increases in State-owned timberland.

• area in pine plantations has increased 23 percent to more than 4.0 million acres. Pine plantations account for 27 percent of Florida's timberland, the highest proportion of any State in the Southeast. The area in natural pine stands is down 22 percent to 3.5 million acres. All three broad management classes of pine, oak-pine, and hardwood decreased in area. Of the 7.5 million acres classed as pine forest types, slash pine decreased 2 percent to 5.2 million acres. Loblolly pine increased 40 percent to almost 0.6 million acres, and sand pine was up 14 percent to 0.6 million acres. Longleaf pine declined 23 percent to 951,000 acres, and p nd pine fell 32 percent to 158,000 acres. Oak-pine forest type declined 15 percent to 1.2 million acres. Of the 6.2 million acres classed as hardwood forest types, oak-hickory was down 7 percent to less than 1.1 million acres, whereas oak-gum-cypress changed little at 4.3 million acres. Scrub oak dropped by 17 percent to 0.8 million acres.

• area receiving a final harvest and retained in timberland averag d 296,000 acres annually. Pine plantations accounted for 32 percent of the final harvest area, and natural pine stands accounted for 45 percent. About 7 percent came from oak-pine stands and 16 percent from hardwoods. Lands controlled by forest industry accounted for 54 percent of the area receiving a final harvest. About 36 percent of the final harvest occurred on NIPF lands; the remainder took place on public lands. Selective cutting and thinning occurred on an average of almost 83,000 acres each year. Natural agents such as fire, weather, insects, and diseases damaged an average of 113,000 acres annually.

• area of timberland regenerated both artificially and naturally averaged 272,000 acres annually. Artificial methods of regeneration accounted for more than 196,000 acres of this total, up 52 percent from that in 1980. About 60 percent of the artificial regeneration took place on areas controlled by forest industry, 32 percent on NIPF land, and 8 percent on public land. Although artificial regeneration increased across all major ownerships, it more than tripled on NIPF lands. About 40 percent of NIPF artificial regeneration occurred on previously nonforest land. New pine stands were established on 219,000 acres--equivalent to 97 percent of the area of pine stands harvested.

• average basal area of live trees 5.0 inches d.b.h. and larger increased from 53 to 55 square feet per acre. Net volume per acre averaged 1,120 cubic feet. The average number of saplings per acre decreased from 404 to 375 trees. Numbers of softwood trees decreased in all diameters below 14 inches, and hardwoods declined in all diameters less than 12 inches. Softwood declines were greatest in the 4-inch diameter class, whereas hardwood trees declined most in the 2-inch class. Stands classified as fully stocked increased by more than 5 percent; medium-stocked stands decreased nearly 3 percent. Poorly stocked and nonstocked areas declined by 12 percent, but they still comprise almost 37 percent of Florida's timberland.

• volume of softwood growing stock changed little, increasing 1 percent to 9.3 billion cubic feet. The inventory for yellow pine decreased more than 2 percent to 6.5 billion cubic feet, while that of other softwoods increased more than 10 percent to nearly 2.8 billion cubic feet. Softwood volume rose 15 percent on public lands to 2.0 billion cubic feet, and by 4 percent on forest industry land to 3.1 billion cubic feet. It decreased 7 percent on NIPF properties to 4.2 billion cubic feet. About 22 percent of the softwood volume is located in pine plantations. Slash pine, relatively unchanged at 4.0 billion cubic feet, remains the predominant species. Cypress species contain n arly 2.7 billion cubic feet, up by 10 percent. Longleaf pine declin d more than 19 percent to less than 1.2 billion cubic feet. Loblolly pine increased 8 percent to 675 million cubic feet, and sand pine volume increased 23 percent to nearly 426 million cubic feet. Softwood volume was up in all diameter classes 14 inches and greater. Volume of softwood sawtimber increased more than 6 percent to 28.4 billion board feet.

• volume of hardwood growing stock increased 11 percent to almost 5.7 billion cubic feet. Inventory of hardwoods on public lands nearly doubled t 1.0 billion cubic feet as a result of increased State ownership of wetlands and reclassification of some reserved timberland. Hardwood volume is down 3 percent to less than 1.6 billion cubic feet on areas controlled by forest industry, and up 5 percent t 3.1 billion cubic feet on NIPF lands. Collectively, oaks accounted for nearly 1.7 billion cubic feet, up 10 percent. Tupelo and blackgum volume rose more than 8 percent to 1.5 billion cubic feet. Bay and magnolia species increas d 22 percent to 765 million cubic feet. Sweetgum was up 11 percent to 528 million cubic feet, and soft maple increased 9 percent to 412 million cubic feet. Hardwood volume increased in all diameters except the 14-inch class. Volume of hardwood sawtimber rose more than 16 percent to 16.5 billion board feet.

• net annual growth of growing stock averaged 628 million cubic feet, down 20 percent since the last survey. Net growth per acre averaged 42 cubic feet, down 16 percent from more than 50 cubic feet. Softwood growth declined almost 20 percent to less than 488 million cubic feet. About 51 percent of current softwood growth occurred on pine plantations. Almost 47 percent of softwood growth occurred on forest industry lands. Softwood growth was down across all major ownership categories. On forest industry land, softwood growth declined by 9 percent. On public and NIPF lands, it was down 23 and 28 percent, respectively. Hardwood growth was down 22 percent to 141 million cubic feet. About 58 percent

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of hardwood growth took place on NIPF lands. Hardwood growth increased 28 percent on public land, but decreased 34 percent on forest industry and by 22 percent on NIPF ownerships. Altogether, net annual growth of growing stock includes nearly 2.0 billion board feet of sawtimber, down 24 percent.

• annual removals of growing stock remained fairly stable overall at nearly 541 million cubic feet. Softwood removals, however, increased almost 5 percent to 474 million cubic feet, accounting for 88 percent of all removals. Hardwood removals decreased almost 25 percent to more than 66 million cubic feet. Pine plantations now provide about 40 percent of the annual softwood removals. Almost 47 percent of the softwood removals were from forest industry lands, 43 percent from NIPF, and 10 percent from public lands. Nearly 47 percent of the softwood removed came from the 8- and 10-inch diameter classes. Half of the hardwood removals came from NIPF lands, 48 percent from industry, and less than 2 percent from public ownerships. Annual removals of yellow pine exceeded their net growth by 3 percent. Hardwood removals totaled less than one-half of their growth. Total annual removals of growing stock included more than 1.4 billion board feet of sawtimber.

• annual mortality of growing stock averaged 122 million cubic feet, up 16 percent. Although softwoods and hardwoods each accounted for about half of the mortality, the percentage of losses were greater for hardwoods than for softwoods. Softwood mortality increased just over 2 percent, whereas hardwood mortality was up 35 percent. The leading identifiable cause of death to softwoods was fire, followed by insects. Causes f hardwood mortality were less distinguishable, with weather being the most prominent. Softwood mortality increased on public and NIPF lands but decreased about 20 percent on forest industry lands. Hardwood mortality increased on all major ownerships. Altogether, annual mortality of growing stock included 376 million board feet of sawtimber. Mortality reduced gross growth of softwoods by 11 percent and gross growth of hardwoods by 30 percent.

How the Invent ry is Made

The method of the inventory is a sampling procedure designed to provide reliable statistics primarily at the State and Survey Unit levels. Individual county statistics are presented so that any combination of counties may be added together until a total is large enough to meet the desired degree of reliability. Procedures were as follows:

1. In the Northwest, Northeast, and Central Units, initial estimates of forest and nonforest areas were based on the classification of 90,378 sample clusters systematically spaced on the latest aerial photographs available. A subsample of 10,746 of the 16-point clusters was ground checked, and a linear regression was fitted to the data to develop the relationship between the photo and ground classification of the subsample. This procedure provides a m ans for adjusting the initial estimates of area for change in land use since date of photography and for photo misclassifications. In the South Florida Unit a different method of land use classification was employed. There, estimates of forest and nonforest areas were determined from direct aerial observations along 27 east-west flight lines spaced at 5-mile intervals. The flight lines were selected systematically from random start and flown perpendicularly to the direction of primary drainage. From an altitude of 500 feet above the ground, observers classified the land use at 28,299 sample points along the flight lines. An interval tim r was used to locate the sample points. This direct aerial method was not used in the Keys because of their unique geographical layout. In the Keys, gross area estimates were made by planimeter of the U.S. Geological Survey boundaries as transferred from maps onto aerial photographs. The breakdown of gross acreage into detailed land use was based upon the ground classification of 45 sample locations.

2. Estimates of timber volume and forest classifications were based on measurements recorded at 5,487 ground sample locations systematically distributed on timberland. The plot design at each location was based on a cluster of 10 points. In most cases, variable plots, established by using a basal-area factor of 37.5 square feet per acre, were systematically spaced within a single forest condition at 5 of the 10 cluster points. Trees less than 5 inches d.b.h. were tallied on a fixed-radius plot ar und each point center.

3. Equations prepared from detailed measurements collected on standing trees in this Survey Unit, and similar measurements taken throughout the Southeast, were used to compute the volume of individual tally trees. A mirror caliper and sectional aluminum poles were used to obtain the additional measurements on these standing trees required to construct volume equations.

4. Felled trees were measured at 100 active cutting operations. These data will supplement the standing-tree volume data and be used to generate utilization factors for product and species gr ups. Forest biomass estimates were made from equations developed by the Utilization of Southern Timber Research Work Unit of the Southeastern Forest Experiment Station in Athens, GA.

5. Estimates of growth, removals, and mortality were determined from the remeasurement of 4,803 permanent sample plots established in the fourth survey.

6. Ownership information was collected from correspondence, public records, and local contacts. In those counties where the sample missed a particular wnership class, temporary sample plots were added.

7. All field data were sent to Asheville for editing and were entered into disk and magnetic-tape storage for processing. Final estimates were based on statistical summaries of the data.

Reliability of the Data

Statistical analysis of these data indicates the following sampling errors in terms of one standard error (two times out of three):

	Percent
Per million acres of timberland	1.63
Per billion cubic feet of growing stock	6.54
Per billion cubic feet of net annual growth	1.32
Per billion cubic feet of annual removals	2.84

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Sampling errors for county and unit totals,[a] in terms of one standard error, Florida, 1987

County	Timberland area	Cubic-foot volume of growing stock		
		Inventory	Growth	Removals
	- - - - - - - Sampling error[b] - - - - - - -			
Alachua	2.32	11.34	11.37	28.08
Baker	.88	10.43	10.23	23.53
Bay	1.37	13.45	10.75	17.57
Bradford	2.35	20.31	20.32	30.08
Brevard	6.32	18.59	21.88	37.94
Broward	0.00	0.00	0.00	0.00
Calhoun	1.47	11.50	11.94	24.88
Charlotte	6.91	31.52	29.60	56.83
Citrus	2.74	15.87	16.23	38.93
Clay	2.31	11.73	11.09	27.64
Collier	11.19	17.48	17.95	57.73
Columbia	2.03	9.35	10.30	19.45
Dade	0.00	0.00	0.00	0.00
De Soto	7.62	27.93	24.84	100.29
Dixie	.87	9.35	9.11	19.61
Duval	2.60	12.71	12.29	21.48
Escambia	2.50	12.10	9.47	23.71
Flagler	1.59	11.93	10.15	29.11
Franklin	1.17	15.27	12.53	30.89
Gadsden	1.83	13.60	11.86	27.42
Gilchrist	3.30	22.67	21.30	25.05
Glades	16.41	32.33	29.46	102.21
Gulf	1.27	16.40	13.05	32.80
Hamilton	2.37	12.50	11.44	27.31
Hardee	4.98	21.31	19.47	48.13
Hendry	15.71	30.99	27.01	55.11
Hernando	3.56	14.59	13.11	48.95
Highlands	7.33	23.96	21.43	55.31
Hillsborough	5.51	18.51	16.53	52.75
Holmes	2.43	13.83	15.62	30.75
Indian River	11.91	35.29	33.64	.00
Jackson	2.69	10.58	10.47	26.03
Jefferson	1.76	10.47	9.28	23.06
Lafayette	1.85	10.43	12.80	26.90
Lake	2.92	11.33	10.94	39.02
Lee	15.88	35.71	28.95	82.37
Leon	1.93	9.17	9.35	26.03
Levy	1.63	9.48	9.81	22.22
Liberty	.40	8.39	8.61	20.63
Madison	2.02	12.27	11.47	30.82
Manatee	9.53	30.36	25.17	55.45
Marion	1.70	8.15	7.95	17.93
Martin	20.22	38.47	41.85	103.22
Monroe	0.00	0.00	0.00	0.00
Nassau	1.32	9.93	10.98	21.97

Continued

Sampling errors for county and unit totals,[a] in terms of one standard error, Florida, 1987--Continued

County	Timberland area	Cubic-foot volume of growing st ck		
		Inventory	Growth	Removals
	- - - - - - - - Sampling error[b] - - - - - - -			
Okaloosa	1.67	8.56	9.36	27.89
Okeechobee	10.34	22.77	20.25	.00
Orange	4.37	14.28	14.10	30.51
Osceola	4.16	11.85	11.76	71.56
Palm Beach	0.00	0.00	0.00	0.00
Pasco	4.03	14.11	12.99	49.71
Pinellas	20.51	34.51	37.82	77.33
Polk	3.88	12.50	11.65	30.98
Putnam	1.95	13.38	10.21	20.13
Santa Rosa	1.69	7.62	7.29	17.72
Sarasota	9.01	21.89	28.28	61.93
Seminole	5.82	23.22	21.24	42.60
St. Johns	2.24	10.79	10.63	22.81
St. Lucie	14.24	25.75	36.53	56.39
Sumter	2.99	14.52	12.13	43.14
Suwannee	3.20	15.99	14.22	26.02
Taylor	.75	9.11	8.72	15.43
Union	3.17	17.54	17.43	29.48
Volusia	1.81	8.22	8.88	24.96
Wakulla	1.38	11.09	11.02	26.95
Walton	1.56	8.93	8.27	19.88
Washington	1.64	14.77	12.57	28.94
Total	.42	1.69	1.66	3.86

[a]Sampling error of breakdowns of county and State totals may be computed with the following formula:

$$E = \frac{(SE)\sqrt{(\text{Specified volume or area})}}{\sqrt{(\text{Volume or area total in question})}}$$

Where: E = Sampling error of the volume or area total in question

SE = Specified sampling error in table.

[b]By random-sampling formula (in percent).

Definiti ns of Terms

Allowable cut. The volume of timber that could be cut on timberland during a given period under specified management plans aimed at sustained production of timber products.

Basal area. The area in square feet of the cross section at breast height of a single tree or of all the trees in a stand, usually expressed as square feet of basal area per acre.

Biomass. The aboveground green weight of solid wood and bark in live trees 1.0 inch d.b.h. and larger from the ground to the tip of the tree. All foliage is excluded. The weight of wood and bark in lateral limbs, secondary limbs, and twigs under 0.5 inch in diameter at the point of occurrence on sapling-size trees is included but is excluded on poletimber and sawtimber-size trees.

Bole. That portion of a tree between a 1-foot stump and a 4-inch top diameter outside bark (d.o.b.) in trees 5.0 inches d.b.h. and larger.

Br ad management class. A classification f timberland based on forest type and stand origin.

Pine plantation. Stands that have been artificially regenerated by planting or direct seeding and with a southern yellow pine, white pine-hemlock, or other softwood forest type.

Natural pine. Stands that have not been artificially regenerated and with a southern yellow pine, white pine-hemlock, or other softwood forest type.

Oak-pine. Stands with a forest type of oak-pine.

Upland hardwood. Stands with a forest type of oak-hickory, chestnut oak, southern scrub oak, or maple-beech-birch.

Lowland hardwood. Stands with a forest type of oak-gum-cypress, elm-ash-cottonwood, palm, or other tropical.

Bureau of Land Management lands. Federal lands administered by the Bureau of Land Management.

Census water. Streams, sloughs, estuaries, canals, and other moving bodies of water one-eighth of a statute mile in width and greater, and lakes, reservoirs, ponds, and other permanent bodies of water 40 acres in area and greater.

Commercial forest land. (see: Timberland).

Commercial species. Tree species conventionally regarded as being able to develop into trees suitable for the manufacture of industrial timber products. Species that typically exhibit small size, poor form, or inferior quality are excluded.

Cropland. Land under cultivation within the past 24 months, including orchards and land in soil-improving crops but excluding land cultivated in developing improved pasture. Also includes idle farmland.

D.b.h. Tree diameter (outside bark) at breast height (4.5 feet above the ground).

Diameter class. A classification f trees based on tree d.b.h. Two-inch diameter classes are commonly used by Forest Inventory and Analysis, with the even inch as the approximate midpoint for a class. For example, the 6-inch class includes trees 5.0 through 6.9 inches d.b.h.

Farm. Land on which agricultural operations are being conducted and sale of agricultural products totaled $1,000 or more during the year.

Farm operator. A person who operates a farm, either doing the work or directly supervising the work.

Farmer-owned land (see: Other private land).

Forest industry land. Land owned by companies or individuals operating wood-using plants.

F rest industry-leased land. Land leased or under management contracts to forest industry from other owners for periods of one forest rotation or longer. Land under cutting contracts is not included.

Forest land. Land at least 16.7 percent stocked by forest trees of any size, or formerly having had such tree cover, and not currently developed for nonforest use.

F rest type. A classification of forest land based on the species forming a plurality of live-tree stocking.

<u>White pine-hemlock</u>. Forests in which eastern white pine, red pine, or jack pine, singly or in combination, constitute a plurality of the stocking. (Common associates include hemlock, birch, and maple.)

<u>Spruce-fir</u>. Forests in which spruce or true firs, singly or in combination, constitute a plurality of the stocking. (Common associates include maple, birch, and hemlock.)

<u>Longleaf-slash pine</u>. Forests in which longleaf or slash pine, singly or in combination, constitute a plurality of the stocking. (Common associates include oak, hickory, and gum.)

<u>Loblolly-shortleaf pine</u>. Forests in which loblolly pine, shortleaf pine, or other southern yellow pines, except longleaf or slash pine, singly or in combination, constitute a plurality of the stocking. (Common associates include oak, hickory, and gum.)

<u>Oak-pine</u>. Forests in which hardwoods (usually upland oaks) constitute a plurality of the stocking but in which pines account for 25 to 50 percent of the stocking. (Common associates include gum, hickory, and yellow-poplar.)

<u>Oak-hickory</u>. Forests in which upland oaks or hickory, singly or in combination, constitute a plurality of the stocking, except where pines account for 25 to 50 percent, in which case the stand would be classified oak-pine. (Common associates include yellow-poplar, elm, maple, and black walnut.)

<u>Oak-gum-cypress</u>. Bottom-land forests in which tupelo, blackgum, sweetgum, oaks, or southern cypress, singly or in combination, constitute a plurality of the stocking, except where pines account for 25 to 50 percent, in which case the stand would be classified oak-pine. (Common associates include cottonwood, willow, ash, elm, hackberry, and maple.)

<u>Elm-ash-cottonwood</u>. Forests in which elm, ash, or cottonwood, singly or in combination, constitute a plurality of the stocking. (Common associates include willow, sycamore, beech, and maple.)

<u>Maple-beech-birch</u>. Forests in which maple, beech, or yellow birch, singly or in combination, constitute a plurality of the stocking. (Common associates include hemlock, elm, basswood, and white pine.)

<u>Palm, other tropical</u>. Forests in which palms and other tropicals constitute a plurality of the stocking.

Gross growth. Annual increase in merchantable volume of trees in the absence of cutting and mortality. (Gross growth includes survivor growth, ingrowth, growth on ingrowth, growth on removals prior to removal, and growth on mortality pri r to death.)

Growing-stock trees. Live sawtimber-size trees of commercial species containing at least a 12-foot log, or two noncontiguous saw logs each 8 feet or longer, meeting minimum grade requirements (hardwoods must qualify as a log grade of either 3 or 4; softwoods must qualify as a log grade 3) with at least one-third of the gross board-foot volume (International 1/4-inch rule) between a 1-foot stump and the minimum saw-log top being sound, or a live tree below sawtimber size that will prospectively qualify under the above standards.

<u>Desirable tree</u>. A tree that qualifies as growing stock and has no serious defects in quality limiting present or prospective use; is of relatively high vigor (30 percent or more live crown ratio); is compatible with the site and

physiographic class; has a total board-foot loss not to exceed 15 percent in softwoods or 25 percent in hardwoods as a result of severe sweep, crook, or lean; and has a relatively clear bole.

Acceptable tree. A tree that qualifies as growing stock but does not meet the minimum requirements to qualify as a desirable tree. Included are sawtimber-size trees that do not contain a 12-foot saw log because of excessive, natural taper in the butt log but have the potential to produce a 12-foot saw log as diameter increases.

Growing-stock volume. Volume (cubic feet) of solid wood in growing-stock trees 5.0 inches d.b.h. and larger, from a 1-foot stump to a minimum 4.0-inch top diameter, outside bark, on the central stem. Volume of solid wood in primary forks from the point of occurrence to a minimum 4.0-inch top diameter outside bark is included.

Hardwoods. Angiosperms; dicotyledonous trees (including all palm species which are monocotyledonous), usually broadleaf and deciduous.

Soft hardwoods. Soft-textured hardwoods such as boxelder, red and silver maples, hackberry, loblolly-bay, sweetgum, yellow-poplar, magnolia, sweetbay, water tupelo, blackgum, sycamore, cottonwood, black cherry, willow, basswood, and elm.

Hard hardwoods. Hard-textured hardwoods such as sugar maple, birch, hickory, dogwood, persimmon (forest grown), black locust, beech, ash, honeylocust, holly, black walnut, mulberry, and all commercial oaks.

Idle farmland. Land including former cropland, orchard, improved pasture, and farm sites not tended within the past 2 years, and currently less than 16.7 percent stocked with live trees.

Improved pasture. Land currently improved for grazing by cultivation, seeding, irrigation, or clearing of trees or brush.

Indian land. All lands held in trust by the United States for individual Indians or tribes, or all lands, titles to which are held by individual Indians or tribes, subject to Federal restrictions against alienation.

Industrial wood. All roundwood products except fuelwood.

Ingrowth. The number or net volume of trees that grow large enough during a specified year to qualify as saplings, poletimber, or sawtimber.

Inhibiting vegetation. Cover sufficiently dense to prevent the establishment of tree seedlings.

Land area. The area of dry land and land temporarily or partly covered by water such as marshes, swamps, and river flood-plains (omitting tidal flats below mean high tide), streams, sloughs, estuaries, and canals less than one-eighth of a statute mile in width, and lakes, reservoirs, and ponds less than 40 acr s in area.

Live trees. All trees 1.0 inch d.b.h. and larger which are not dead at the time of inventory.

Live-tree volume. Volume (cubic feet) of wood above the ground line in live trees 1.0 inch d.b.h. and larger. The volume in twigs and lateral limbs smaller than 0.5 inch in diameter at the point of occurrence on sapling-size trees is included but is excluded on poletimber and sawtimber-size trees.

Log grade. A classification of logs based on external characteristics as indicators of quality or value.

Logging residues. The unused merchantable portion of growing-stock trees cut or destroyed during logging operations.

Logging slash. The unmerchantable portion of growing-stock trees (including saplings) plus all cull trees 1.0 inch d.b.h. and larger cut or destroyed during logging operations and not used.

Manageable stand. Timberland at least 60 percent stocked with growing-stock trees that can be featured together under a management scheme.

Merchantable portion. That portion of live trees 5.0 inches d.b.h. and larger between a 1-foot stump and a minimum 4.0-inch top diameter outside bark on the central stem. That portion of primary forks from the point of occurrence to a minimum 4.0-inch top diameter outside bark is included.

Merchantable volume. Solid-wood volume in merchantable portion of live trees.

Miscellaneous Federal land. Federal land other than national forests, land administered by the Bureau of Land Management, and land administered by the Bureau of Indian Affairs.

Miscellaneous private land. (see: Other private land).

Mortality. The merchantable volume in trees that have died from natural causes during a specified period.

National forest land. Federal land that has been legally designated as national forests or purchase units, and other land under the administration of the Forest Service, including experimental areas and Bankhead-Jones Title III land.

Net annual growth. The net change in merchantable volume for a specific year in the absence of cutting (gross growth minus mortality for that specified year).

Net volume. Gross volume of wood less deductions for rot, sweep, or other defect affecting use for timber products.

N ncommercial species. Tree species of typically small size, poor form, or inferior quality which normally do not develop into trees suitable for industrial wood products.

Nonforest land. Land that has never supported forests and land formerly forested where timber production is precluded by development for other uses.

Nonindustrial private f rest (NIPF) land. (see: Other private land).

Nonstocked f rest land. Timberland less than 16.7 percent stocked with growing-stock trees.

Other private land. Privately wned land excluding forest industry land or forest industry-leased land. Also referred to as nonindustrial private forest (NIPF) land.

Farmer-owned land. Owned by farm operators, excluding incorporated farm ownerships.

Other individual land. Owned by individuals other than farm operators.

Other corporate land. Owned by corporations, including incorporated farm ownerships.

Other removals. The growing-stock volume of trees removed from the inventory by cultural operations such as timber stand improvement, land clearing, and ther changes in land use that result in the removal of the trees from the timberland.

Plant residues. Wood material generated in the production of timber products at primary manufacturing plants.

Coarse residues. Material, such as slabs, edgings, trim, veneer cores and ends, which is suitable for chipping.

Fine residues. Material, such as sawdust, shavings, and veneer chippings, which is not suitable for chipping.

Plant byproducts. Residues (coarse or fine) utilized in the further manufacture of industrial products or for consumer use, or utilized as fuel.

Unused plant residues. Residues (coarse or fine) that are not used for any product, including fuel.

Poletimber-size trees. Live trees at least 5.0 inches d.b.h. but smaller than sawtimber size.

Productive-reserved forest land. (see: Reserved timberland).

Quality class. A classification of sawtimber volume by log or tree grades.

Rangeland. Land on which the natural vegetation is predominantly native grasses, grasslike plants, forbs, or shrubs valuable for forage, not qualifying as timberland and not developed f r another land use. Rangeland includes natural grassland and savannah.

Reserved timberland. Forest land sufficiently productive to qualify as timberland, but withdrawn from timber utilization through statute or adminstrative designation.

R tten trees. Live trees of commercial species that do not contain at least one 12-foot saw log, or two noncontiguous saw logs, each 8 feet or longer, now or prospectively, primarily because of rot or missing sections, and with less than one-third of the gross board-foot tree volume in sound material.

R ugh trees. Live trees of commercial species that do not contain at least one 12-foot saw log, or two noncontiguous saw logs, each 8 feet or longer, now or prospectively, primarily because of roughness, poor form, splits, and cracks, and with less than one-third of the gross board-foot tree volume in sound material; and live trees of noncommercial species.

Roundwood (roundwood logs). Logs, bolts, or other round sections cut from trees for industrial or consumer uses.

Roundwood chipped. Any timber cut primarily for pulpwood, delivered to nonpulpmills, chipped, and then sold to pulpmills as residues, including chipped tops, jump sections, whole trees, and pulpwood sticks.

Roundwood products. Any primary product such as lumber, poles, pilings, pulp, or fuelwood which is produced from roundwood.

Salvable dead trees. Standing or down dead trees considered utilizable by Forest Inventory and Analysis standards.

Saplings. Live trees 1.0 to 5.0 inches d.b.h.

Saw log. A log meeting minimum standards of diameter, length, and defect, including logs at least 8 feet long, sound and straight, and with a minimum diameter inside bark for softwoods of 6 inches (8 inches for hardwoods).

Saw-log portion. That part of the bole of sawtimber trees between a 1-foot stump and the saw-log top, including the portion of forks large en ugh to contain a saw log.

Saw-log top. The point on the bole of sawtimber trees above which a conventional saw log cannot be produced. The minimum saw-log top is 7.0 inches in diameter outside bark (d.o.b.) for softwoods and 9.0 inches (d.o.b.) for hardwoods.

Sawtimber-size trees. Softwoods 9.0 inches d.b.h. and larger and hardwoods 11.0 inches d.b.h. and larger.

Sawtimber volume. Growing-stock volume in the saw-log portion of sawtimber-size trees in board feet (International 1/4-inch rule).

Seedlings. Live trees of commercial species less than 1.0 inch d.b.h. that are expected to survive and develop.

Site class. A classification of forest land in terms of inherent capacity to grow crops of industrial wood based on fully stocked natural stands, by annual production capacity.

<u>Class 1</u>. 165 or more cubic feet per acre.

<u>Class 2</u>. 120 to 164 cubic feet per acre.

<u>Class 3</u>. 85 to 119 cubic feet per acre.

<u>Class 4</u>. 50 to 84 cubic feet per acre.

<u>Class 5</u>. 20 to 49 cubic feet per acre.

Softwoods. Gymnosperms; in the order Coniferales, usually evergreen (includes the genus *Taxodium* which is deciduous), having needles or scalelike leaves.

Pines. Yellow pine species which include loblolly, longleaf, slash, pond, shortleaf, pitch, Virginia, sand, spruce, and Table Mountain pines.

Other softwoods. Cypress, eastern redcedar, white cedar, eastern white pine, eastern hemlock, spruce, and fir.

Stand-size class. A classification of forest land based on the diameter class distribution of growing-stock trees in the stand.

Sawtimber stands. Stands at least 16.7 percent stocked with growing-stock trees, with half or more of total stocking in sawtimber and poletimber trees, and with sawtimber stocking at least equal to poletimber stocking.

Poletimber stands. Stands at least 16.7 percent stocked with growing-stock trees of which half or more of total stocking is in poletimber and sawtimber trees, and with poletimber stocking exceeding that of sawtimber.

Sapling-seedling stands. Stands at least 16.7 percent stocked with growing-stock trees of which more than half of total stocking is saplings and seedlings.

State, county, and municipal land. Land owned by States, counties, and local public agencies or municipalities, or land leased to these governmental units for 50 years or more.

Stocking. The degree of occupancy of land by trees, measured by basal area or the number of trees in a stand and spacing in the stand, compared with a minimum standard, depending on tree size, required to fully utilize the growth potential of the land.

Fully stocked. 100 percent or more stocking.

Medium stocked. 60 to 99 percent stocking.

Poorly stocked. Less than 60 percent stocking.

Survivor gr wth. The merchantable volume increment on trees 5.0 inches d.b.h. and larger in the inventory at the beginning of the year and surviving to its end.

Timberland. Land at least 16.7 percent stocked by forest trees of any size, or formerly having had such tree cover, not currently developed for nonforest use, capable of producing 20 cubic feet of industrial wood per acre per year and not withdrawn from timber utilisation by legislative action.

Timber products. Roundwood products and byproducts.

Timber removals. The merchantable volume of trees removed from the inventory by harvesting, cultural operations such as stand improvement, land clearing, or changes in land use.

Top. The portion of the main stem and forks from a 4.0-inch diameter outside bark to the tips of the main stem and forks, plus all other limbs above the 4.0-inch top at least 0.5 inch in diameter at their point of occurrence.

Treatment opportunity. A classification of the management or treatment that would most improve for timber production the existing condition of the stand being sampled.

Tree grade. A classification of sawtimber trees based on the log grade of the butt log in the tree.

Unproductive forest land. (see: Woodland).

Upper-stem portion. That part of the main stem or fork of sawtimber trees above the saw-log top to minimum top diameter 4.0 inches outside bark or to the point where the main stem or fork breaks into limbs.

Urban and other areas. Areas developed for residential, industrial, or recreational purposes, school yards, cemeteries, roads, railroads, airports, beaches, powerlines and other rights-of-way, or other nonforest land not included in any other specified land use class.

Woodland. Forest land incapable of producing 20 cubic feet per acre per year of industrial wood under natural conditions, because of adverse site conditions.

Stocking Standard

D.b.h. class	Minimum number of trees per acre for full stocking	Minimum basal area per acre for full stocking
Seedlings	600	—
2	560	—
4	460	—
6	340	67
8	240	84
10	155	85
12	115	90
14	90	96
16	72	101
18	60	106
20	51	111

Conversion factors

Cubic feet of wood per average cord (excluding bark)

D.b.h. class	All species	Pine	Other softwood	Hardwood
6	61.6	61.0	68.2	60.0
8	69.5	68.1	76.0	68.4
10	74.7	73.1	81.4	73.4
12	77.9	76.7	85.2	76.4
14	80.4	79.4	88.2	78.4
16	82.0	81.6	90.4	79.8
18	83.2	83.3	92.3	80.8
20	84.0	84.8	93.8	81.5
22	84.3	86.0	95.1	82.1
24+	85.7	87.7	98.2	83.2
Average	74.8	72.2	82.5	74.6

Metric equivalents of units used in this report

1 acre = 4,046.86 square meters or 0.404686 hectare
1 cubic foot = 0.028317 cubic meter
1 inch = 2.54 centimeters or 0.0254 meter
Breast height (4.5 feet) = 1.4 meters above ground level
1 square foot = 929.03 square centimeters or 0.0929 square meter
1 square foot per acre basal area = 0.229568 square meter per hectare
1 pound = 0.454 kilogram
1 ton = 0.907 metric ton

County Tables

The county tables are intended for use in compiling forest resource estimates for groups of counties. Because the sampling procedure used by the Forest Survey was intended primarily to furnish inventory data for the survey unit as a whole, individual county estimates have limited and variable accuracy. As county totals are broken down by various subdivisions, the possibility of error increases and is greatest for the smallest items. The order of this increase can be computed with the formula on page 6.

Table 1.--Area, by county and land class, Florida, 1987

County	All land[a]	Forest land				Nonforest land[b]
		Total	Timberland	Woodland	Reserved timberland	
	Acres					
Alachua	576,941	307,773	297,262	—	10,511	269,168
Baker	374,509	338,624	327,657	—	10,967	35,885
Bay	484,858	402,062	400,032	2,030	—	82,796
Bradford	187,373	130,077	130,077	—	—	57,296
Brevard	637,062	118,545	109,806	8,739	—	518,517
Broward	775,213	35,666	—	35,666	—	739,547
Calhoun	363,392	298,800	298,800	—	—	64,592
Charlotte	441,613	54,217	33,838	20,379	—	387,396
Citrus	402,330	232,125	226,973	5,146	6	170,205
Clay	379,008	289,812	289,812	—	—	89,196
Collier	1,276,224	745,852	309,023	266,917	169,912	530,372
Columbia	509,728	364,523	357,298	1,096	6,129	145,205
Dade	1,251,366	240,537	—	207,661	32,876	1,010,829
De Soto	406,867	48,176	48,176	—	—	358,691
Dixie	448,826	396,866	396,866	—	—	51,960
Duval	496,954	262,713	261,242	1,359	112	234,241
Escambia	422,682	250,847	246,116	4,357	374	171,835
Flagler	314,099	255,897	253,247	1,345	1,305	58,202
Franklin	348,698	312,324	309,773	2,440	111	36,374
Gadsden	331,264	242,495	242,495	—	—	88,769
Gilchrist	226,413	138,145	138,145	—	—	88,268
Glades	488,301	91,189	79,469	11,720	—	397,112
Gulf	357,523	294,176	293,027	1,149	—	63,347
Hamilton	331,193	228,055	228,055	—	—	103,138
Hardee	407,968	90,844	90,844	—	—	317,124
Hendry	744,013	94,282	85,487	8,795	—	649,731
Hernando	305,421	170,299	170,299	—	—	135,122
Highlands	658,310	84,688	84,202	486	—	573,622
Hillsborough	673,830	131,354	121,406	9,948	—	542,476
Holmes	312,000	184,977	184,664	—	313	127,023
Indian River	318,118	36,513	29,367	7,146	—	281,605
Jackson	602,611	284,617	284,617	—	—	317,994

Continued

Table 1.--Area, by county and land class, Florida, 1987--Continued

County	All land[a]	Forest land: Total	Timberland	Woodland	Reserved timberland	Nonforest land[b]
	Acres					
Jefferson	389,933	281,815	279,715	--	2,100	108,118
Lafayette	348,928	286,790	286,790	--	--	62,138
Lake	610,790	258,234	239,716	5,698	12,820	352,556
Le	513,952	181,037	120,398	60,639	--	332,915
Leon	432,582	295,031	294,872	--	159	137,551
Levy	703,718	496,965	486,570	895	9,500	206,753
Liberty	535,814	508,591	500,791	--	7,800	27,223
Madison	454,618	310,381	310,381	--	--	144,237
Manatee	478,163	49,249	43,563	5,666	20	428,914
Marion	1,030,195	576,799	563,237	302	13,260	453,396
Martin	355,002	37,892	30,485	7,407	--	317,110
Monroe	661,824	420,634	--	331,583	89,051	241,190
Nassau	415,386	335,452	334,940	512	--	79,934
Okaloosa	598,918	429,121	428,524	597	--	169,797
Okeechobee	493,114	33,366	31,780	1,586	--	459,748
Orange	582,714	175,071	172,515	2,556	--	407,643
Osceola	863,795	186,501	183,545	2,556	400	677,294
Palm Beach	1,275,590	82,691	--	82,691	--	1,192,899
Pasco	472,224	150,790	150,455	157	178	321,434
Pinellas	179,315	19,594	11,541	7,677	376	159,721
Polk	1,166,803	288,235	263,571	24,664	--	878,568
Putnam	469,043	351,426	348,923	--	2,503	117,617
Santa Rosa	655,053	476,441	475,212	--	1,229	178,612
Sarasota	366,810	57,182	56,050	1,132	--	309,628
Seminole	190,739	76,704	74,953	--	1,751	114,035
St. Johns	395,059	270,465	267,741	2,672	52	124,594
St. Lucie	371,840	34,853	33,267	1,586	--	336,987
Sumter	359,174	178,938	173,311	5,567	60	180,236
Suwannee	441,388	211,231	211,231	--	--	230,157
Taylor	676,813	592,791	586,127	6,664	--	84,022
Union	157,286	118,903	118,903	--	--	38,383
Volusia	707,198	482,229	467,605	11,017	3,607	224,969
Wakulla	384,845	337,567	311,635	--	25,932	47,278
Walton	682,080	510,924	508,291	2,633	--	171,156
Washington	377,427	288,049	287,894	--	155	89,378
Total	34,652,841	16,549,012	14,982,607	1,162,836	403,569	18,103,829

[a]From U.S. Bureau of the Census, 1980.

[b]Includes 121,108 acres of water according to Forest Survey standards of area classification, but defined by the Bureau of Census as land.

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Table 2.--Area of timberland, by county and ownership class, Florida, 1987

County	All ownerships	Ownership class							
		National forest	Miscellaneous Federal	State	County and municipal	Forest industry[a]	Other private		
							Farmer	Corporate	Individual
	Acres								
Alachua	297,262	—	10	5,053	1,560	125,026	37,965	41,403	66,245
Baker	327,657	87,249	3,678	382	10	207,641	4,669	24,349	19,479
Bay	400,032	—	21,410	4,542	285	267,747	4,865	68,116	51,087
Bradford	130,077	—	—	12,936	929	83,356	13,529	3,798	13,529
Brevard	109,806	—	10,738	205	2,484	1,920	18,406	44,557	30,496
Calhoun	398,800	—	—	33	85	198,688	21,620	24,323	54,051
Charlotte	33,838	—	—	6,827	288	—	—	16,702	10,021
Citrus	226,973	—	2,704	46,597	678	8,763	—	64,234	103,997
Clay	289,812	—	640	46,341	1,138	86,192	7,068	68,326	80,207
Collier	309,023	—	—	1,950	2,720	—	44,639	24,348	235,366
Columbia	357,298	74,145	10	4,356	185	151,818	45,451	28,706	52,627
De Soto	48,376	—	38	1,040	198	—	9,380	18,761	18,761
Dixie	396,866	—	4,827	1,177	245	322,742	2,262	33,938	31,675
Duval	261,242	—	15,015	2,020	1,334	48,530	3,037	85,025	106,281
Escambia	246,116	—	2,360	5,404	90	100,721	15,548	62,192	59,601
Flagler	253,247	—	—	767	415	150,339	11,301	36,727	53,678
Franklin	309,773	21,170	7,293	17,380	690	253,184	—	3,016	7,038
Gadsden	242,495	—	1	12,383	145	88,654	19,784	33,915	87,413
Gilchrist	138,145	—	—	5	280	32,336	35,125	15,075	65,326
Glades	79,469	—	205	—	25	73,337	1,475	4,427	—
Gulf	293,027	—	753	39,392	87	210,535	3,817	16,903	22,538
Hamilton	228,035	—	—	2,486	390	148,038	29,572	11,376	36,357
Hardee	90,844	—	—	1,018	80	—	8,158	40,794	40,794
Hendry	85,487	—	8,809	460	40	30	19,032	42,822	14,274
Hernando	170,299	—	3,806	45,978	1,715	410	2,631	42,094	73,665
Highlands	84,202	—	22,500	4,213	140	—	13,034	26,068	18,247
Hillsborough	121,406	—	135	19,125	2,917	—	30,177	38,520	30,532
Holmes	184,664	—	500	2,432	337	69,725	77,105	—	34,565
Indian River	29,367	—	—	583	764	—	7,642	12,735	7,641
Jackson	284,617	—	5,209	2,809	83	84,941	88,379	42,850	80,345
Jefferson	279,715	—	2,200	4,338	412	119,270	60,393	35,008	78,094
Lafayette	286,790	—	—	90	323	214,077	18,861	15,717	37,722
Lake	239,716	69,712	280	15,684	454	305	11,270	60,863	81,149
Lee	120,398	—	—	200	2,133	—	4,723	18,892	94,460
Leon	294,872	101,538	20	8,528	1,918	56,677	17,319	39,586	69,276
Levy	486,370	—	7,070	9,840	1,256	281,017	18,475	52,785	116,127
Liberty	500,791	252,135	—	23,452	40	167,578	10,969	8,227	38,392
Madison	310,381	—	955	1,061	47	161,966	45,226	10,644	90,472
Manatee	43,563	—	—	5,270	2,086	—	2,262	10,362	13,575
Marion	363,237	244,691	—	28,905	1,309	94,078	36,293	48,429	107,532
Martin	30,485	—	—	8,988	275	—	—	8,843	12,379
Nassau	334,940	—	3	3,298	599	197,370	9,326	21,760	102,582

Continued

Table 2.--Area of timberland, by county and ownership class, Florida, 1987—Continued

County	All ownerships	Ownership class							
		National forest	Miscellaneous Federal	State	County and municipal	Forest industry[a]	Other private		
							Farmer	Corporate	Individual
	Acres								
Okaloosa	428,524	—	211,478	39,859	748	54,823	15,133	10,810	75,671
Okeechobee	31,780	—	—	192	100	—	10,494	10,498	10,496
Orange	172,515	—	278	34,309	11,238	—	5,067	81,082	40,341
Osceola	183,545	—	850	12,412	350	215	21,513	112,349	35,856
Pasco	150,455	—	20	30,109	4,096	28,757	6,900	34,529	46,038
Pinellas	11,541	—	—	600	1,026	—	—	3,949	3,966
Polk	263,571	—	15,000	20,793	1,881	—	35,296	98,830	91,771
Putnam	368,923	19,037	4,443	3,868	397	110,909	11,034	110,342	88,273
St. Johns	267,741	—	—	4,201	120	139,252	12,670	32,943	78,555
St. Lucie	33,267	—	—	535	358	—	2,490	17,432	12,452
Santa Rosa	475,212	—	36,033	132,525	809	171,004	27,647	10,633	76,561
Sarasota	56,050	—	—	8,749	3,492	—	2,434	26,772	14,603
Seminole	74,953	—	160	180	1,269	—	15,944	25,511	31,889
Sumter	173,311	—	—	54,545	5	18,990	15,350	46,048	38,373
Suwannee	211,231	—	40	3,681	626	24,486	17,490	29,983	134,925
Taylor	586,127	—	—	280	224	546,082	2,551	3,827	33,163
Union	118,903	—	—	5,210	280	76,141	14,365	2,869	20,080
Volusia	467,605	—	1,220	2,715	740	78,986	22,922	180,510	180,510
Wakulla	311,635	139,880	31,732	6,729	175	56,765	12,220	15,275	48,879
Walton	508,291	—	137,233	18,687	209	128,721	58,520	42,560	122,361
Washington	287,894	—	10	13,869	178	42,236	43,882	102,392	85,327
Total	14,982,607	990,155	579,910	813,602	59,432	5,466,419	1,114,908	2,360,155	3,618,026

[a]Includes 676,795 acres of other private land under long-term lease.

Table 3.—Area of timberland, by county and forest-type group, Florida, 1987

County	All type groups	Forest-type group								
		White pine-hemlock	Spruce-fir	Longleaf-slash	Loblolly-shortleaf	Oak-pine	Oak-hickory	Oak-gum-cypress	Elm-ash-cottonwood	Maple-beech-birch
	Acres									
Alachua	297,262	—	—	160,367	9,652	17,026	55,669	54,548	—	—
Baker	327,637	—	—	230,162	—	16,349	—	81,146	—	—
Bay	400,032	—	—	283,724	20,903	15,559	46,318	33,528	—	—
Bradford	130,077	—	—	68,173	6,951	21,617	3,865	29,471	—	—
Brevard	109,806	—	—	40,237	11,091	—	4,923	53,555	—	—
Calhoun	298,800	—	—	142,360	28,442	41,842	23,733	54,582	7,841	—
Charlotte	33,838	—	—	21,838	—	—	—	11,980	—	—
Citrus	226,973	—	—	50,992	9,175	44,238	66,324	53,185	3,059	—
Clay	289,812	—	—	129,665	27,549	10,723	52,731	69,144	—	—
Collier	309,023	—	—	44,678	—	24,348	4,058	235,979	—	—
Columbia	357,298	—	—	188,322	12,833	20,586	47,257	88,302	—	—
De Soto	48,176	—	—	11,723	198	2,345	9,381	24,527	—	—
Dixie	396,866	—	—	177,390	11,424	21,314	41,963	144,775	—	—
Duval	261,242	—	—	122,097	18,218	34,901	33,475	52,551	—	—
Escambia	246,116	—	—	138,565	18,761	31,857	24,468	29,873	2,592	—
Flagler	253,247	—	—	156,036	7,810	16,275	7,395	65,731	—	—
Franklin	309,773	—	—	202,582	14,452	21,805	4,138	66,796	—	—
Gadsden	242,495	—	—	31,470	65,878	34,081	19,951	91,115	—	—
Gilchrist	138,145	—	—	69,382	5,026	10,049	43,372	10,316	—	—
Glades	79,469	—	—	42,306	—	1,475	—	35,688	—	—
Gulf	293,027	—	—	145,022	2,818	19,441	2,817	120,111	2,818	—
Hamilton	228,055	—	—	115,134	15,754	12,697	30,752	53,718	—	—
Hardee	90,844	—	—	21,415	80	4,079	12,237	44,873	8,160	—
Hendry	85,487	—	—	33,766	—	4,758	4,758	42,205	—	—
Hernando	170,299	—	—	34,002	21,048	15,122	74,639	25,488	—	—
Highlands	84,202	—	—	25,534	—	5,214	15,674	37,780	—	—
Hillsborough	121,406	—	—	12,721	2,544	12,720	21,001	72,420	—	—
Holmes	184,464	—	—	48,140	46,909	16,655	27,289	45,671	—	—
Indian River	29,367	—	—	16,048	—	5,095	2,547	5,677	—	—
Jackson	284,017	—	—	56,687	47,627	33,368	26,780	114,656	5,501	—
Jefferson	279,715	—	—	48,179	46,092	27,334	30,026	127,184	—	—
Lafayette	286,790	—	—	138,327	16,942	17,423	32,661	81,437	—	—
Lake	239,716	—	—	57,893	42,080	19,102	28,360	87,793	4,508	—
Lee	120,398	—	—	56,876	—	14,169	4,723	44,630	—	—
Leon	294,872	—	—	103,241	57,696	27,868	61,920	44,147	—	—
Levy	486,570	—	—	175,609	44,807	37,586	109,361	116,277	2,730	—
Liberty	500,791	—	—	236,421	29,105	38,089	31,392	153,363	12,021	—
Madison	310,381	—	—	102,888	36,384	16,732	59,819	91,642	2,916	—
Manatee	43,563	—	—	9,806	4,349	—	9,049	20,361	—	—
Marion	563,237	—	—	119,134	195,816	46,712	134,134	67,431	—	—
Martin	30,683	—	—	15,105	6,263	1,769	—	7,348	—	—
Nassau	334,940	—	—	179,007	17,513	17,893	14,786	105,741	—	—

Continued

Table 3.--Area of timberland, by county and forest-type group, Florida, 1987--Continued

County	All type groups	Forest-type group								
		White pine-hemlock	Spruce-fir	Longleaf-slash	Loblolly-shortleaf	Oak-pine	Oak-hickory	Oak-gum-cypress	Elm-ash-cottonwood	Maple-beech-birch
	Acres									
Okaloosa	428,524	—	—	199,512	55,872	64,529	50,256	58,355	—	—
Okeechobee	31,780	—	—	10,595	—	—	—	19,086	2,099	—
Orange	172,515	—	—	27,873	34,042	3,119	18,014	89,467	—	—
Osceola	183,345	—	—	40,023	2,390	11,951	17,382	111,599	—	—
Pasco	150,455	—	—	39,387	—	6,906	41,809	62,353	—	—
Pinellas	11,561	—	—	4,992	1,983	1,983	—	2,583	—	—
Polk	263,571	—	—	50,395	2,599	14,119	59,095	126,773	10,590	—
Putnam	348,923	—	—	163,577	28,606	29,099	70,782	54,100	2,759	—
St. Johns	267,761	—	—	124,485	23,793	33,571	10,136	70,688	5,068	—
St. Lucie	33,267	—	—	22,771	2,491	2,490	—	5,515	—	—
Santa Rosa	475,212	—	—	258,759	12,106	57,889	60,907	85,551	—	—
Sarasota	56,050	—	—	20,636	—	8,749	7,301	19,364	—	—
Seminole	74,953	—	—	14,025	—	5,189	23,511	32,228	—	—
Sumter	173,311	—	—	63,503	11,511	8,032	44,668	59,661	5,936	—
Suwannee	211,231	—	—	99,081	2,499	20,305	64,158	22,490	2,498	—
Taylor	586,127	—	—	305,501	44,122	17,647	18,141	200,716	—	—
Union	118,903	—	—	79,834	2,869	2,429	7,726	26,045	—	—
Volusia	467,605	—	—	193,679	28,651	57,069	25,214	160,126	2,866	—
Wakulla	311,635	—	—	145,781	47,621	34,689	10,527	73,017	—	—
Walton	508,291	—	—	172,476	114,005	30,640	81,451	109,719	—	—
Washington	287,894	—	—	69,855	58,213	21,942	52,951	84,933	—	—
Total	14,982,607	—	—	6,149,924	1,376,843	1,210,769	1,890,375	4,271,134	85,742	—

Table 4.--Area of timberland, by county and stand-size class, Florida, 1987

County	All stands	Stand-size class			Nonstocked areas
		Sawtimber	Poletimber	Sapling-seedling	
	Acres				
Alachua	297,262	85,105	89,983	107,442	14,732
Baker	327,657	85,908	104,146	116,544	21,059
Bay	400,032	34,177	117,716	173,299	74,840
Bradford	130,077	13,805	34,887	60,362	21,023
Brevard	109,806	45,241	24,951	10,980	28,634
Calhoun	298,800	91,329	72,651	98,382	36,438
Charlotte	33,838	6,681	15,179	3,340	8,638
Citrus	226,973	79,645	47,053	61,713	38,562
Clay	289,812	73,122	83,037	80,188	53,465
Collier	309,023	140,693	60,870	40,581	66,879
Columbia	357,298	101,366	118,702	125,387	11,843
De Soto	48,176	15,147	11,923	—	21,106
Dixie	396,866	103,605	155,613	117,828	19,820
Duval	261,242	81,588	49,377	100,174	30,103
Escambia	246,116	100,523	63,060	79,560	2,973
Flagler	253,247	82,727	94,645	59,287	16,588
Franklin	309,773	59,430	74,554	153,982	21,807
Gadsden	242,495	79,672	51,520	102,723	8,580
Gilchrist	138,145	10,187	43,235	56,427	28,296
Glades	79,469	21,221	36,666	7,118	14,464
Gulf	293,027	80,286	58,298	122,315	32,128
Hamilton	228,055	53,554	78,811	81,644	14,046
Hardee	90,844	44,874	24,556	4,080	17,334
Hendry	85,487	36,332	31,944	12,453	4,758
Hernando	170,299	76,529	35,581	35,174	23,015
Highlands	84,202	37,779	10,214	10,354	25,855
Hillsborough	121,406	68,216	29,648	13,364	10,178
Holmes	184,664	60,169	35,601	83,226	5,668
Indian River	29,367	19,179	2,547	—	7,641
Jackson	284,617	102,053	63,199	97,796	21,569
Jefferson	279,715	129,953	39,214	77,289	33,259
Lafayette	286,790	65,587	101,843	97,478	21,882
Lake	239,716	94,320	70,467	35,298	39,631
Lee	120,398	23,615	56,876	14,169	25,738
Leon	294,872	129,712	45,818	109,056	10,286
Levy	486,570	137,393	133,067	150,036	66,074
Liberty	500,791	223,244	95,326	126,875	55,346
Madison	310,381	93,773	76,448	99,543	40,617
Manatee	43,563	18,100	8,873	—	16,590
Marion	563,237	166,800	162,838	143,276	90,323
Martin	30,485	9,800	—	11,569	9,116
Nassau	334,940	89,765	119,041	105,322	20,812

Continued

Table 4.--Area of timberland, by county and stand-size class, Florida, 1987--Continued

County	All stands	Stand-size class			Nonstocked areas
		Sawtimber	Poletimber	Sapling-seedling	
	Acres				
Okaloosa	428,524	181,735	95,261	98,380	53,148
Okeechobee	31,780	21,284	6,298	—	4,198
Orange	172,515	76,732	51,261	20,272	24,250
Osceola	183,545	99,996	34,176	22,227	27,146
Pasco	150,455	73,363	26,136	27,502	23,454
Pinellas	11,541	7,575	1,983	1,983	—
Polk	263,571	118,685	64,610	29,179	51,097
Putnam	348,923	79,779	94,275	111,738	63,131
St. Johns	267,741	78,058	94,939	84,608	10,136
St. Lucie	33,267	18,326	7,471	4,980	2,490
Santa Rosa	475,212	189,743	131,071	134,727	19,671
Sarasota	56,050	26,368	10,317	3,598	15,767
Seminole	74,953	52,472	3,349	3,188	15,944
Sumter	173,311	81,000	43,953	22,312	26,046
Suwannee	211,231	60,389	45,960	92,388	12,494
Taylor	586,127	124,635	161,768	226,971	72,753
Union	118,903	28,385	46,458	41,631	2,429
Volusia	467,605	182,399	106,997	133,172	45,037
Wakulla	311,635	151,571	34,875	106,812	18,377
Walton	508,291	145,357	117,766	145,083	100,085
Washington	287,894	56,518	73,896	105,214	52,266
Total	14,982,607	4,926,575	3,882,798	4,401,599	1,771,635

Table 5.—Area of timberland, by county and site class, Florida, 1987

County	All classes	Site class (cubic feet per acre per year)				
		>164	120-164	85-119	50-84	20-49
	Acres					
Alachua	297,262	—	5,986	109,752	152,059	29,465
Baker	327,657	—	9,508	46,664	249,844	21,641
Bay	400,032	—	—	10,693	223,650	165,689
Bradford	130,077	—	758	16,212	102,163	10,944
Brevard	109,806	—	—	8,317	56,330	45,159
Calhoun	298,800	—	7,641	33,580	202,845	54,734
Charlotte	33,838	—	—	1,670	23,529	8,639
Citrus	226,973	—	—	4,395	89,429	133,149
Clay	289,812	—	4,712	42,410	172,732	69,958
Collier	309,023	—	—	4,058	107,458	197,507
Columbia	357,298	—	7,505	95,153	226,227	28,413
De Soto	48,176	—	—	198	22,183	25,795
Dixie	396,866	—	5,119	48,032	281,818	61,897
Duval	261,242	—	6,074	43,503	142,891	68,774
Escambia	246,116	2,592	—	24,847	199,167	19,510
Flagler	253,247	—	5,287	17,005	191,050	39,905
Franklin	309,773	—	1,924	3,648	116,604	187,597
Gadsden	242,495	—	5,954	53,933	157,036	25,572
Gilchrist	138,145	—	2,644	7,948	87,352	40,201
Glades	79,469	—	—	—	49,424	30,045
Gulf	293,027	—	—	5,587	140,779	146,661
Hamilton	228,055	—	—	32,844	181,739	13,472
Hardee	90,844	—	—	12,317	36,715	41,812
Hendry	85,487	—	—	—	57,556	27,931
Hernando	170,299	2,631	2,631	16,961	101,715	46,361
Highlands	84,202	—	—	140	47,888	36,174
Hillsborough	121,406	—	—	7,633	72,048	41,725
Holmes	184,664	—	—	47,303	112,730	24,631
Indian River	29,367	—	—	766	8,225	20,376
Jackson	284,617	—	14,473	46,903	189,732	33,509
Jefferson	279,715	—	13,465	48,810	188,614	28,826
Lafayette	286,790	—	—	30,587	205,427	50,776
Lake	239,716	2,255	11,806	33,854	128,500	63,301
Lee	120,398	—	—	—	19,092	101,306
Leon	294,872	—	7,422	39,864	159,176	88,410
Levy	486,570	—	2,639	73,136	298,850	111,945
Liberty	500,791	—	—	45,482	269,770	185,539
Madison	310,381	—	—	64,012	218,228	28,141
Manatee	43,563	—	—	4,349	13,574	25,640
Marion	563,237	6,169	20,155	126,503	287,501	122,909
Martin	30,485	—	—	—	9,801	20,684
Nassau	334,940	—	5,838	59,594	191,458	78,050

Continued

Table 5.--Area of timberland, by county and site class, Florida, 1987—Continued

County	All classes	Site class (cubic feet per acre per year)				
		>164	120-164	85-119	50-84	20-49
	Acres					
Okaloosa	428,524	—	—	31,782	170,806	225,936
Okeechobee	31,780	—	—	100	19,084	12,596
Orange	172,515	—	—	10,135	108,891	53,489
Osceola	183,545	—	—	12,300	99,649	71,596
Pasco	150,455	—	—	9,583	90,786	50,086
Pinellas	11,541	—	—	1,026	6,549	3,966
Polk	263,571	—	—	940	171,777	90,854
Putnam	348,923	—	—	76,082	191,648	81,193
St. Johns	267,741	—	2,534	29,230	197,042	38,935
St. Lucie	33,267	—	—	358	12,986	19,923
Santa Rosa	475,212	—	22,300	99,353	243,070	110,489
Sarasota	56,050	—	—	—	27,248	28,802
Seminole	74,953	—	—	14,025	51,361	9,567
Sumter	173,311	3,837	2,098	5,935	134,221	27,220
Suwannee	211,231	—	—	22,487	138,256	50,488
Taylor	586,127	—	—	75,202	360,434	150,491
Union	118,903	5,210	—	26,046	79,480	8,167
Volusia	467,605	2,865	8,596	57,544	298,490	100,110
Wakulla	311,635	—	—	34,533	156,678	120,424
Walton	508,291	—	—	23,410	263,911	220,970
Washington	287,894	—	4,192	26,453	110,717	146,532
Total	14,982,607	25,559	181,261	1,825,187	8,725,993	4,224,607

Table 6.--Area f timberland, by county and stocking class of growing-stock trees, Florida, 1987

County	All classes	Stocking class (percent)[a]				
		>130	100-130	60-99	16.7-59	<16.7
	Acres					
Alachua	297,262	20,254	99,905	108,594	53,777	14,732
Baker	327,657	31,550	130,394	89,400	55,254	21,059
Bay	400,032	8,262	118,052	116,581	85,211	71,926
Bradford	130,077	13,513	27,177	51,994	16,370	21,023
Brevard	109,806	11,294	13,009	24,844	32,025	28,634
Calhoun	298,800	—	85,148	122,757	54,457	36,438
Charlotte	33,838	3,341	11,837	5,011	5,011	8,638
Citrus	226,973	9,573	14,553	35,454	128,831	38,562
Clay	289,812	13,728	77,998	91,564	53,057	53,465
Collier	309,023	16,233	60,870	71,706	93,335	66,879
Columbia	357,298	16,515	110,596	132,088	86,256	11,843
De Soto	48,176	36	3,386	9,578	14,070	21,106
Dixie	396,866	20,576	80,281	161,042	115,147	19,820
Duval	261,242	6,545	102,601	79,080	42,913	30,103
Escambia	246,116	21,335	79,725	102,070	40,013	2,973
Flagler	253,247	15,143	69,544	107,753	44,219	16,588
Franklin	309,773	10,627	97,709	121,649	57,981	21,807
Gadsden	242,495	11,673	62,718	107,979	51,545	8,580
Gilchrist	138,145	7,675	48,737	25,668	27,769	28,296
Glades	79,469	5,641	5,641	25,386	28,337	14,464
Gulf	293,027	14,296	67,029	98,508	81,066	32,128
Hamilton	228,055	16,845	80,761	66,679	49,724	14,046
Hardee	90,844	—	16,319	24,556	32,635	17,334
Hendry	85,487	14,324	8,155	26,766	31,484	4,758
Hernando	170,299	2,298	17,828	70,679	56,479	23,015
Highlands	84,202	7,713	10,321	17,032	23,281	25,855
Hillsborough	121,406	20,995	5,224	44,914	40,095	10,178
Holmes	184,664	2,659	65,129	70,625	40,583	5,668
Indian River	29,367	583	3,313	2,547	15,283	7,641
Jackson	284,617	8,035	103,370	113,715	37,928	21,569
Jefferson	279,715	12,822	45,081	136,936	51,617	33,259
Lafayette	286,790	15,984	84,635	93,429	70,860	21,882
Lake	239,716	10,683	42,870	61,760	84,772	39,631
Lee	120,398	4,723	23,815	9,446	56,676	25,738
Leon	294,872	2,475	77,222	145,785	59,104	10,286
Levy	486,570	34,426	105,863	173,703	106,504	66,074
Liberty	500,791	18,523	96,738	205,213	124,971	55,346
Madison	310,381	28,141	74,229	117,659	49,735	40,617
Manatee	43,563	—	—	11,138	15,835	16,590
Marion	563,237	7,003	139,019	183,168	143,724	90,323
Martin	30,485	—	6,263	7,075	8,031	9,116
Nassau	334,940	22,214	120,769	123,841	47,304	20,812

Continued

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Table 6.--Area of timberland, by county and stocking class of growing-stock trees, Florida, 1987--Continued

County	All classes	Stocking class (percent)[a]				
		>130	100-130	60-99	16.7-59	<16.7
	Acres					
Okaloosa	428,524	14,759	43,639	151,809	165,169	53,148
Okeechobee	31,780	2,292	12,695	6,298	6,297	4,198
Orange	172,515	18,322	26,508	42,883	60,552	24,250
Osceola	183,545	28,683	49,086	42,061	36,569	27,146
Pasco	150,455	22,524	33,858	27,064	43,555	23,454
Pinellas	11,541	600	6,975	—	3,966	—
Polk	263,571	30,838	53,484	66,571	61,581	51,097
Putnam	348,923	19,595	59,874	109,645	99,436	60,373
St. Johns	267,741	13,348	81,033	106,648	56,576	10,136
St. Lucie	33,267	535	2,848	4,981	22,413	2,490
Santa Rosa	475,212	32,278	138,885	172,246	114,800	17,003
Sarasota	56,050	—	—	17,037	23,246	15,767
Seminole	74,953	180	4,457	19,133	35,239	15,944
Sumter	173,311	21,900	26,045	42,313	57,007	26,046
Suwannee	211,231	—	68,673	84,465	45,599	12,494
Taylor	586,127	14,987	175,423	178,409	144,555	72,753
Union	118,903	20,221	49,325	26,359	20,569	2,429
Volusia	467,605	25,695	122,295	123,799	150,779	45,037
Wakulla	311,635	10,215	63,132	112,920	106,991	18,377
Walton	508,291	18,937	70,323	202,478	116,468	100,085
Washington	287,894	2,438	70,591	105,152	57,447	52,266
Total	14,982,607	786,603	3,652,983	5,037,643	3,742,083	1,763,295

[a]See stocking standards on page 13.

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Table 7.--Volume of growing stock and sawtimber on timberland, by county and species group, Florida, 1987

County	Growing stock					Sawtimber				
	All species	Pine	Other softwood	Soft hardwood	Hard hardwood	All species	Pine	Other softwood	Soft hardwood	Hard hardwood
	Thousand cubic feet[a]					Thousand board feet				
Alachua	321,961	151,985	51,525	52,054	66,397	847,699	269,927	197,442	139,553	260,777
Baker	393,443	253,061	67,886	70,760	1,736	1,082,496	711,739	203,613	164,291	2,853
Bay	168,861	133,873	8,741	17,235	9,012	289,017	204,467	23,163	54,131	7,256
Bradford	87,065	54,778	6,688	14,283	11,316	189,348	99,946	12,673	21,878	54,851
Brevard	102,020	52,946	14,313	15,937	18,824	276,963	93,162	40,887	59,204	83,710
Calhoun	247,070	141,938	19,176	52,030	33,926	757,979	383,980	84,074	166,237	123,688
Charlotte	28,257	11,047	15,848	277	1,085	62,415	24,512	32,804	—	5,099
Citrus	154,888	62,509	39,615	23,979	28,785	309,420	193,390	173,024	67,269	75,737
Clay	257,201	148,711	11,437	48,772	48,281	686,941	393,937	41,628	108,206	143,170
Collier	306,580	47,000	213,950	28,970	16,660	877,153	143,422	601,680	78,857	53,196
Columbia	366,963	208,923	50,077	76,253	31,710	1,065,519	694,807	169,345	124,139	77,228
De Soto	35,809	6,092	5,776	15,877	8,064	126,212	29,158	23,663	43,323	30,068
Dixie	438,281	148,291	103,414	95,130	91,446	1,132,383	315,760	318,244	250,144	248,235
Duval	281,941	128,484	14,346	83,432	55,679	865,189	428,259	38,918	215,663	182,349
Escambia	322,810	177,563	5,671	106,152	33,424	1,138,189	615,946	22,974	390,774	108,495
Flagler	294,892	141,004	91,378	43,984	18,526	757,384	302,216	257,331	116,921	80,916
Franklin	223,161	108,866	46,106	60,526	7,663	668,255	293,853	139,351	211,770	23,281
Gadsden	235,374	93,291	—	72,935	69,148	802,131	360,491	—	211,514	230,126
Gilchrist	82,278	54,581	16,643	3,794	8,260	185,615	104,310	48,712	4,073	28,520
Glades	67,212	34,841	27,755	3,369	1,247	207,038	92,972	103,430	4,637	5,999
Gulf	220,673	57,806	58,632	85,083	19,152	655,935	131,429	182,153	269,331	73,022
Hamilton	246,355	105,708	30,977	60,699	48,971	604,846	241,046	69,858	117,036	176,906
Hardee	97,301	27,496	28,117	13,897	27,791	375,538	137,141	105,517	29,542	103,338
Hendry	121,746	25,672	85,713	4,607	5,754	395,640	78,318	277,564	19,682	20,076
Hernando	176,404	50,057	5,448	58,974	61,925	571,602	180,736	24,287	166,150	200,429
Highlands	89,409	16,153	34,507	28,983	9,766	321,114	58,384	146,011	75,901	40,618
Hillsborough	204,390	24,585	102,628	31,591	45,586	641,067	116,102	278,864	80,314	165,787
Holmes	167,021	68,039	8,662	68,736	21,584	512,960	263,285	36,071	143,459	70,145
Indian River	27,548	16,490	8,470	267	2,321	110,307	76,008	24,232	—	10,067
Jackson	328,367	116,200	21,101	103,980	87,086	1,074,208	451,855	79,731	254,487	288,135
Jefferson	345,506	88,676	40,431	130,731	85,668	1,213,020	402,779	162,196	365,248	282,797
Lafayette	241,050	120,181	48,759	36,377	35,733	583,575	268,830	120,069	57,735	136,941
Lake	277,521	97,532	74,279	72,500	33,210	871,810	373,741	199,179	178,974	119,916
Lee	85,523	33,004	52,519	—	—	183,339	46,105	137,234	—	—
Leon	314,153	160,318	6,202	78,104	69,529	1,109,015	632,840	16,045	223,254	236,876
Levy	515,926	218,455	97,012	98,755	101,704	1,428,263	547,116	277,991	280,713	322,443
Liberty	542,876	230,902	94,064	152,652	65,258	1,913,295	786,016	387,126	476,004	264,149
Madison	316,917	98,333	61,374	122,317	34,893	903,319	312,305	198,347	299,364	93,303
Manatee	27,861	7,299	—	13,404	7,158	106,374	32,403	—	49,901	24,070
Marion	492,341	335,883	20,422	54,932	81,104	1,390,207	888,150	64,362	136,578	301,117
Martin	10,539	10,313	226	—	—	40,631	40,631	—	—	—
Nassau	394,980	189,941	40,833	110,209	53,997	1,021,708	505,141	134,937	216,758	164,872

Continued

Table 7.—Volume of growing stock and sawtimber on timberland, by county and species group, Florida, 1987—Continued

County	Growing stock					Sawtimber				
	All species	Pine	Other softwood	Soft hardwood	Hard hardwood	All species	Pine	Other softwood	Soft hardwood	Hard hardwood
	Thousand cubic feet[a]					Thousand board feet				
Okaloosa	387,051	292,081	15,448	51,167	28,355	1,349,401	1,082,601	71,811	98,163	96,826
Okeechobee	58,351	12,921	16,423	24,352	4,655	203,725	45,467	66,346	77,282	14,630
Orange	232,202	51,547	92,295	65,841	22,519	700,659	149,603	281,753	185,388	83,915
Osceola	316,504	60,584	168,126	60,832	26,962	970,242	287,565	439,028	180,957	62,292
Pasco	215,159	31,327	86,848	45,456	51,528	661,477	115,272	236,141	122,562	187,502
Pinellas	15,000	8,889	3,329	2,266	516	53,222	37,553	7,467	6,729	1,473
Polk	387,694	70,170	167,830	104,271	45,423	1,147,375	278,496	430,017	272,713	166,149
Putnam	333,237	174,093	11,725	91,694	55,725	943,442	428,231	42,717	276,696	195,798
St. Johns	278,033	138,937	29,618	67,272	42,206	705,229	364,571	90,895	125,754	124,009
St. Lucie	20,785	18,291	2,494	—	—	79,465	69,389	9,876	—	—
Santa Rosa	568,392	356,429	50,534	124,259	37,170	1,769,373	1,179,542	190,253	300,831	98,747
Sarasota	24,532	16,612	—	3,404	4,516	73,329	48,126	—	8,345	16,858
Seminole	65,279	19,666	477	15,163	29,973	266,765	84,865	2,117	57,419	122,164
Sumter	257,161	38,857	87,007	57,984	73,313	831,490	121,583	284,775	167,295	257,837
Suwannee	139,596	47,436	219	23,887	68,054	497,905	147,778	—	88,183	261,944
Taylor	430,431	173,754	69,131	97,125	90,421	1,072,135	350,249	203,919	232,940	285,027
Union	124,806	57,467	16,378	45,033	5,928	282,650	109,296	50,346	108,202	14,806
Volusia	487,843	201,479	138,264	101,040	47,060	1,453,766	715,077	328,202	242,573	167,914
Wakulla	306,381	172,923	7,412	69,522	56,524	1,153,274	733,552	30,474	206,309	182,939
Walton	424,410	280,951	11,695	103,363	28,401	1,349,353	943,836	50,457	290,896	64,166
Washington	236,240	63,217	50,421	77,647	44,955	727,786	206,545	253,473	147,188	122,780
Total	14,969,561	6,344,458	2,758,397	3,641,125	2,225,581	44,887,182	19,824,410	8,544,797	9,069,640	7,448,335

[a]Factors for converting to cords are shown on page 13.

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Table 8.--Average net annual growth of growing stock and sawtimber on timberland, by county and species group, Florida, 1980-1986

County	Growing stock					Sawtimber				
	All species	Pine	Other softwood	Soft hardwood	Hard hardwood	All species	Pine	Other softwood	Soft hardwood	Hard hardwood
	Thousand cubic feet					Thousand board feet				
Alachua	17,011	13,233	857	1,167	1,754	63,094	46,649	3,848	4,992	7,605
Baker	20,168	17,390	1,237	1,438	123	39,604	33,403	4,351	1,778	72
Bay	14,398	13,784	194	296	324	16,497	14,878	243	731	643
Bradford	5,308	4,405	212	497	194	13,698	11,791	296	497	1,112
Brevard	4,179	3,165	273	383	359	16,955	12,748	1,248	1,661	1,298
Calhoun	12,169	9,807	325	1,149	888	32,332	23,162	2,402	3,440	3,328
Charlotte	1,042	633	351	18	40	3,683	3,612	851	—	219
Citrus	6,954	3,979	1,020	877	1,078	25,790	12,724	5,563	2,365	5,138
Clay	14,589	11,920	182	1,350	1,137	38,147	30,688	481	3,216	3,762
Collier	8,300	2,340	4,438	1,008	514	26,897	6,991	15,275	2,932	1,699
Columbia	16,645	11,869	666	2,927	1,183	42,815	35,116	2,249	2,900	2,550
De Soto	1,093	204	122	496	271	5,087	1,918	689	1,766	714
Dixie	23,475	16,070	2,399	2,201	2,805	56,956	31,567	7,910	6,575	10,904
Duval	12,646	9,132	240	2,125	1,149	45,073	30,864	961	7,066	6,186
Escambia	11,614	8,889	140	1,516	1,069	46,460	36,243	613	5,351	4,253
Flagler	14,432	11,417	1,889	877	249	41,386	30,276	7,152	2,825	1,333
Franklin	10,990	9,583	715	593	99	18,663	13,061	2,423	2,682	494
Gadsden	9,116	5,461	—	1,780	1,873	32,525	15,596	—	7,277	9,652
Gilchrist	6,209	5,510	301	99	299	19,438	17,565	1,017	48	808
Glades	2,465	1,918	438	73	36	9,871	6,468	2,322	873	208
Gulf	5,927	3,577	1,136	905	310	15,353	5,893	4,431	3,603	1,424
Hamilton	14,241	10,829	675	1,525	1,212	24,263	15,374	2,054	3,574	3,261
Hardee	2,743	784	843	373	743	10,610	4,994	3,061	628	1,927
Hendry	2,881	952	1,708	83	138	15,005	5,759	6,685	435	2,126
Hernando	6,837	3,559	166	1,479	1,633	24,796	12,598	771	6,364	5,063
Highlands	2,477	778	686	741	272	10,317	1,926	3,804	3,216	1,371
Hillsborough	6,125	916	2,898	793	1,518	26,227	4,297	14,088	3,660	4,172
Holmes	6,571	4,096	164	1,402	911	18,919	12,924	930	2,696	2,369
Indian River	883	539	279	15	50	4,632	3,221	1,261	—	150
Jackson	10,008	5,221	487	2,003	2,297	42,032	23,954	1,715	5,340	11,023
Jefferson	9,973	3,880	615	2,996	2,481	42,071	16,670	4,366	10,748	10,287
Lafayette	12,955	10,319	846	1,053	737	26,793	21,544	2,185	958	2,106
Lake	11,023	5,466	2,092	2,499	966	45,144	22,392	7,319	10,343	5,090
Lee	2,869	2,014	855	—	—	9,919	5,830	4,089	—	—
Leon	11,100	7,017	134	1,865	2,084	47,880	31,500	293	6,485	9,602
Levy	23,826	16,751	2,263	2,139	2,673	80,748	55,248	9,422	6,291	9,787
Liberty	14,429	9,718	1,145	2,309	1,257	48,702	27,290	5,819	8,247	7,346
Madison	11,429	6,936	856	2,373	1,266	33,708	18,608	3,465	8,126	3,509
Manatee	835	263	—	265	307	3,553	1,465	—	1,178	910
Marion	26,516	22,257	310	1,681	2,268	73,884	58,848	1,168	5,634	8,234
Martin	461	423	38	—	—	1,170	1,170	—	—	—
Nassau	21,121	16,547	686	2,612	1,276	56,159	43,467	1,924	6,718	4,050

Continued

Table 8.--Average net annual growth of growing stock and sawtimber on timberland, by county and species group, Florida, 1980-1986--Continued

County	Growing stock					Sawtimber				
	All species	Pine	Other softwood	Soft hardwood	Hard hardwood	All species	Pine	Other softwood	Soft hardwood	Hard hardwood
	Thousand cubic feet					Thousand board feet				
Okaloosa	14,473	12,137	245	1,310	781	54,517	46,785	1,475	2,802	3,455
Okeechobee	1,803	631	370	637	165	7,612	2,091	1,975	2,791	755
Orange	8,180	3,339	2,379	1,915	547	40,812	19,765	11,551	6,268	3,228
Osceola	9,367	2,040	4,720	1,867	760	39,951	11,623	20,466	6,201	1,621
Pasco	6,219	1,251	2,238	1,223	1,507	29,551	6,598	10,539	4,118	8,296
Pinellas	392	351	128	94	19	3,309	2,315	671	276	47
Polk	13,636	3,667	5,479	3,585	905	54,455	13,599	23,784	11,974	5,098
Putnam	15,175	11,626	205	2,354	990	43,930	32,165	960	7,234	3,571
St. Johns	15,254	11,269	643	2,367	975	35,096	25,105	2,086	5,050	2,855
St. Lucie	1,098	1,037	61	—	—	3,990	3,650	340	—	—
Santa Rosa	21,635	16,438	1,064	2,558	1,375	85,310	69,405	5,728	6,653	3,724
Sarasota	1,655	1,201	—	107	347	6,112	5,179	—	560	373
Seminole	1,661	658	33	345	625	10,481	3,682	193	3,389	3,218
Sumter	8,356	3,819	2,229	1,461	1,853	29,494	7,103	11,070	4,690	6,631
Suwannee	6,432	3,830	12	486	2,104	19,052	9,779	—	2,004	7,269
Taylor	25,385	19,294	1,589	2,338	2,164	57,001	37,766	5,374	6,203	7,658
Union	5,979	4,548	359	945	127	14,370	10,520	747	2,787	316
Volusia	17,953	11,887	2,400	2,750	918	54,926	36,524	7,241	7,302	3,859
Wakulla	10,332	7,114	221	1,367	1,630	35,780	24,710	543	4,406	6,121
Walton	16,703	14,008	234	1,480	981	73,094	60,615	1,116	6,634	4,729
Washington	8,366	4,609	708	1,670	1,379	24,058	10,867	4,322	4,943	3,926
Total	628,306	427,177	60,371	80,733	60,025	1,980,110	1,249,121	248,948	249,528	232,513

Table 9.—Average annual removals of growing stock and sawtimber on timberland, by county and species group, Florida, 1980-1986

County	Growing stock					Sawtimber				
	All species	Pine	Other softwood	Soft hardwood	Hard hardwood	All species	Pine	Other softwood	Soft hardwood	Hard hardwood
	Thousand cubic feet					Thousand board feet				
Alachua	20,148	18,380	—	354	1,414	46,376	41,182	—	1,353	3,841
Baker	14,152	14,028	66	—	58	40,577	40,577	—	—	—
Bay	12,015	11,891	—	—	124	25,953	25,953	—	—	—
Bradford	11,535	10,603	89	384	459	35,859	32,374	333	971	2,181
Brevard	2,937	2,937	—	—	—	11,922	11,922	—	—	—
Calhoun	9,499	9,044	—	271	184	28,800	27,327	—	806	667
Charlotte	1,358	1,320	—	—	38	2,751	2,751	—	—	—
Citrus	1,984	1,034	605	295	52	5,674	2,089	2,376	953	256
Clay	10,151	8,925	977	249	—	22,923	19,576	2,707	640	—
Collier	1,262	1,088	174	—	—	3,198	3,198	—	—	—
Columbia	16,339	14,425	984	609	321	48,133	41,123	2,785	2,723	1,502
De Soto	33	—	—	—	33	—	—	—	—	—
Dixie	9,380	6,406	513	921	1,540	14,913	9,883	1,453	1,691	1,886
Duval	13,535	12,077	203	911	342	33,450	30,641	532	1,467	810
Escambia	8,815	8,815	—	—	—	24,208	24,208	—	—	—
Flagler	12,925	11,958	888	79	—	28,117	24,515	3,602	—	—
Franklin	6,377	6,199	178	—	—	17,872	17,464	408	—	—
Gadsden	12,377	8,626	—	2,203	1,548	43,961	28,433	—	8,844	6,664
Gilchrist	14,075	11,676	779	176	1,453	23,934	16,315	3,165	544	3,910
Glades	58	56	—	—	—	—	—	—	—	—
Gulf	7,702	6,386	54	967	295	30,925	27,391	—	2,203	1,331
Hamilton	12,060	10,470	689	587	316	28,600	27,405	312	616	267
Hardee	3,467	2,552	850	65	—	13,635	11,052	2,583	—	—
Hendry	1,483	1,683	—	—	—	5,473	5,473	—	—	—
Hernando	1,470	986	—	59	425	5,838	4,292	—	222	1,324
Highlands	1,399	1,399	—	—	—	4,806	4,806	—	—	—
Hillsborough	2,386	699	1,028	301	358	8,203	1,294	4,906	821	1,182
Holmes	9,435	7,714	—	409	1,312	23,996	19,876	—	261	3,859
Indian River	—	—	—	—	—	—	—	—	—	—
Jackson	10,436	7,851	—	166	2,419	26,703	21,535	—	—	5,168
Jefferson	16,580	14,013	—	484	2,083	64,680	57,865	—	1,637	5,178
Lafayette	10,166	7,784	1,019	750	593	20,089	15,216	3,326	1,096	451
Lake	4,006	1,345	1,366	1,069	226	13,372	5,821	3,682	3,133	736
Lee	724	224	—	—	—	663	663	—	—	—
Leon	11,125	9,108	—	734	1,283	39,303	32,723	—	2,607	3,973
Levy	19,106	15,099	1,130	1,358	1,519	41,927	29,892	4,361	2,471	5,202
Liberty	11,919	9,960	200	836	923	37,721	29,766	188	3,055	4,714
Madison	11,842	6,554	345	2,723	2,220	34,244	16,398	1,515	10,506	5,825
Manatee	173	173	—	—	—	874	874	—	—	—
Marion	25,269	21,394	346	1,131	2,398	83,918	73,457	1,230	1,228	8,003
Martin	30	—	—	—	30	105	—	—	—	105
Nassau	17,565	13,634	—	2,832	1,099	46,601	38,778	—	4,910	2,912

Continued

Table 9.—Average annual removals of growing stock and sawtimber on timberland, by county and species group, Florida, 1980-1986—Continued

County	Growing stock: All species	Growing stock: Pine	Growing stock: Other softwood	Growing stock: Soft hardwood	Growing stock: Hard hardwood	Sawtimber: All species	Sawtimber: Pine	Sawtimber: Other softwood	Sawtimber: Soft hardwood	Sawtimber: Hard hardwood
	Thousand cubic feet					Thousand board feet				
Okaloosa	5,733	4,937	—	394	402	19,645	17,793	—	1,206	646
Okeechobee	—	—	—	—	—	—	—	—	—	—
Orange	5,066	2,497	2,226	237	106	19,106	10,346	7,236	1,113	411
Osceola	2,814	284	2,487	43	—	10,446	618	9,828	—	—
Pasco	3,200	2,427	773	—	—	15,270	12,551	2,719	—	—
Pinellas	775	190	585	—	—	3,090	919	2,171	—	—
Polk	6,227	1,503	3,917	807	—	15,264	5,913	8,854	497	—
Putnam	20,541	19,642	—	407	492	48,426	45,151	—	1,964	1,311
St. Johns	17,362	12,952	561	2,721	1,158	40,948	28,541	1,109	7,321	3,977
St. Lucie	319	157	—	—	162	1,003	800	—	—	203
Santa Rosa	14,675	14,278	273	124	—	43,479	42,717	762	—	—
Sarasota	771	771	—	—	—	2,573	2,573	—	—	—
Seminole	2,467	1,960	—	396	111	10,128	8,698	—	1,430	—
Sumter	4,012	1,340	2,161	318	193	11,307	2,015	6,807	1,477	1,008
Suwannee	14,437	14,013	73	118	233	20,240	19,837	403	—	—
Taylor	35,320	25,528	3,499	3,295	2,998	68,057	36,475	15,089	7,596	8,897
Union	9,634	9,634	—	—	—	20,386	20,386	—	—	—
Volusia	14,260	9,398	3,769	1,048	45	43,239	24,083	16,097	3,059	—
Wakulla	10,123	8,197	—	276	1,650	29,789	24,031	—	1,451	4,307
Walton	10,460	8,673	260	557	970	28,131	22,931	1,166	1,651	2,383
Washington	5,519	4,662	44	65	748	8,728	8,060	—	—	668
Total	540,687	441,241	33,003	31,745	34,899	1,449,952	1,158,767	111,704	83,523	95,958

Table 10.--Area of timberland, by forest type and ownership class, Florida, 1987

Forest type	All ownerships	Ownership class				
		National forest	Other public	Forest industry	Forest industry-leased	Other private
	Acres					
Softwood types						
White pine-hemlock	—	—	—	—	—	—
Spruce-fir	—	—	—	—	—	—
Longleaf pine	950,946	178,595	239,202	144,353	5,607	383,189
Slash pine	5,198,978	315,002	332,016	2,276,953	432,229	1,842,778
Loblolly pine	578,472	4,667	28,965	253,749	32,537	258,554
Shortleaf pine	30,061	—	937	8,691	—	20,433
Virginia pine	—	—	—	—	—	—
Sand pine	610,277	192,574	96,304	138,507	—	182,892
Eastern redcedar	—	—	—	—	—	—
Pond pine	157,833	34,308	20,796	25,466	5,269	71,994
Spruce pine	—	—	—	—	—	—
Pitch pine	—	—	—	—	—	—
Table Mountain pine	—	—	—	—	—	—
Total	7,526,567	725,146	718,220	2,847,719	475,642	2,759,840
Hardwood types						
Oak-pine	1,210,769	71,762	127,719	311,009	23,707	676,572
Oak-hickory	1,053,868	8,225	68,123	202,232	15,772	759,516
Chestnut oak	—	—	—	—	—	—
Southern scrub oak	836,507	36,334	99,323	83,049	9,070	608,731
Oak-gum-cypress	4,271,134	148,688	430,761	1,306,927	152,604	2,232,154
Elm-ash-cottonwood	83,762	—	8,798	18,688	—	56,276
Maple-beech-birch	—	—	—	—	—	—
Total	7,456,040	265,009	734,724	1,921,905	201,153	4,333,249
All types	14,982,607	990,155	1,452,944	4,769,624	676,795	7,093,089

Table 11.--Area of timberland, by ownership and stocking classes of growing-stock trees, Florida, 1987

Ownership class	All classes	Stocking class (percent)[a]				
		>130	100-130	60-99	16.7-59	<16.7
	Acres					
National forest	990,155	31,098	200,020	367,325	297,647	94,065
Other public	1,452,944	105,223	260,960	476,252	459,367	151,142
Forest industry	4,769,624	275,116	1,469,078	1,654,816	934,849	435,765
Forest industry-leased	676,795	36,332	265,354	260,516	71,748	42,845
Other private	7,093,089	338,834	1,457,571	2,278,734	1,970,132	1,047,818
All ownerships	14,982,607	786,603	3,652,983	5,037,643	3,733,743	1,771,635

[a] See stocking standards on page 13.

Table 12.—Area of timberland, by forest type and stand-size class, Florida, 1987

Forest type	All stands	Stand-size class			Nonstocked areas
		Sawtimber	Poletimber	Sapling-seedling	
	Acres				
Softwood types					
White pine-hemlock	—	—	—	—	—
Spruce-fir	—	—	—	—	—
Longleaf pine	950,946	552,924	99,298	203,847	94,877
Slash pine	5,198,978	927,836	1,837,511	2,121,158	312,473
Loblolly pine	578,472	149,967	125,602	295,706	7,197
Shortleaf pine	30,061	21,370	8,691	—	—
Virginia pine	—	—	—	—	—
Sand pine	610,277	119,848	191,863	275,432	23,134
Eastern redcedar	—	—	—	—	—
Pond pine	157,833	61,138	66,900	13,187	16,608
Spruce pine	—	—	—	—	—
Pitch pine	—	—	—	—	—
Table Mountain pine	—	—	—	—	—
Total	7,526,567	1,833,083	2,329,865	2,909,330	454,289
Hardwood types					
Oak-pine	1,210,769	491,341	211,570	412,570	95,288
Oak-hickory	1,053,868	430,776	193,926	285,151	144,015
Chestnut oak	—	—	—	—	—
Southern scrub oak	836,507	42,678	29,445	131,623	632,761
Oak-gum-cypress	4,271,134	2,065,437	1,105,722	654,693	445,282
Elm-ash-cottonwood	83,762	63,260	12,270	8,232	—
Maple-beech-birch	—	—	—	—	—
Total	7,456,040	3,093,492	1,552,933	1,492,269	1,317,346
All types	14,982,607	4,926,575	3,882,798	4,401,599	1,771,635

Table 13.--Area of timberland, by stand-age and broad management classes, all ownerships, Florida, 1987

Stand-age class (years)	All classes	Broad management class				
		Pine plantation	Natural pine	Oak-pine	Upland hardwood	Lowland hardwood
	Acres					
0-10	2,373,358	1,677,281	244,741	129,747	143,971	177,618
11-20	1,647,856	1,170,375	197,563	75,831	70,737	133,350
21-30	1,487,976	900,138	349,998	45,336	27,853	164,651
31-40	1,102,383	124,180	551,483	80,917	61,884	283,919
41-50	1,004,559	10,496	395,879	128,097	74,655	395,432
51-60	931,097	4,112	279,044	71,722	56,765	519,454
61-70	581,173	2,617	93,847	36,335	35,475	412,899
71-80	406,826	—	57,937	28,701	25,321	294,867
81+	503,086	—	18,188	16,458	37,631	430,809
No manageable stand	4,944,293	136,613	1,312,075	597,625	1,356,083	1,541,897
All classes	14,982,607	4,025,812	3,500,755	1,210,769	1,890,375	4,354,896

Table 14.--Area of timberland, by stand-age and broad management classes, public ownerships, Florida, 1987

Stand-age class (years)	All classes	Broad management class				
		Pine plantation	Natural pine	Oak-pine	Upland hardwood	Lowland hardwood
	Acres					
0-10	221,798	145,496	48,491	8,051	17,155	2,605
11-20	167,846	115,961	35,644	4,768	1,227	10,246
21-30	179,501	93,506	62,993	7,043	--	15,959
31-40	193,980	19,759	136,669	18,655	3,526	15,371
41-50	206,323	4,661	162,654	--	4,086	34,922
51-60	272,405	4,112	175,777	14,866	2,056	75,594
61-70	157,796	--	54,399	5,547	3,188	94,662
71-80	112,297	--	39,197	--	6,669	66,431
81+	114,429	--	15,644	5,457	--	93,328
No manageable stand	816,724	17,673	310,730	135,094	174,098	179,129
All classes	2,443,099	401,168	1,042,198	199,481	212,005	588,247

Table 15.--Area of timberland, by stand-age and broad management classes, forest industry,[a] Florida, 1987

Stand-age class (years)	All classes	Broad management class				
		Pine plantation	Natural pine	Oak-pine	Upland hardwood	Lowland hardwood
	Acres					
0-10	1,213,770	1,012,763	40,530	56,388	37,272	66,817
11-20	1,017,870	871,707	33,079	40,338	11,360	61,386
21-30	712,445	567,473	71,259	14,754	--	58,959
31-40	331,712	56,757	148,955	12,045	10,543	103,412
41-50	293,049	3,132	74,934	48,130	11,283	155,570
51-60	284,598	--	47,349	20,133	16,417	200,699
61-70	123,615	2,617	16,624	9,700	7,932	86,742
71-80	92,615	--	8,077	5,394	--	79,144
81+	145,694	--	--	11,001	--	134,693
No manageable stand	1,231,051	79,209	288,896	116,833	215,316	530,797
All classes	5,446,419	2,593,658	729,703	334,716	310,123	1,478,219

[a]Includes 676,795 acres of other private land under long-term lease.

Table 16.--Area of timberland, by stand-age and broad management classes, other private ownerships,[a] Florida, 1987

Stand-age class (years)	All classes	Broad management class: Pine plantation	Natural pine	Oak-pine	Upland hardwood	Lowland hardwood
	Acres					
0-10	937,790	519,022	155,720	65,308	89,544	108,196
11-20	462,140	182,707	128,840	30,725	58,150	61,718
21-30	596,030	239,159	215,746	23,539	27,853	89,733
31-40	576,691	47,664	265,859	50,217	47,815	165,136
41-50	505,187	2,703	158,291	79,967	59,286	204,940
51-60	374,094	—	55,918	36,723	38,292	243,161
61-70	299,762	—	22,824	21,088	24,355	231,495
71-80	201,914	—	10,663	23,307	18,652	149,292
81+	242,963	—	2,544	—	37,631	202,788
No manageable stand	2,896,518	39,731	712,449	345,698	966,669	831,971
All classes	7,093,089	1,030,986	1,728,854	676,572	1,368,247	2,288,430

[a]Excludes 676,795 acres of other private land under long-term lease to forest industry.

Table 17.—Area of timberland, by broad management and stand-volume classes, Florida, 1987

Broad management class	All classes	Stand-volume class (cubic feet of growing stock per acre): 0-499	500-999	1000-1499	1500-1999	2000+
	Acres					
Pine plantation	4,025,812	2,540,961	604,664	381,911	269,220	229,056
Natural pine	3,500,755	1,344,210	736,397	477,207	395,708	547,233
Oak-pine	1,210,769	595,924	195,919	139,596	100,313	179,017
Upland hardwood	1,890,375	1,323,255	201,321	134,878	127,255	103,666
Lowland hardwood	4,354,896	1,237,064	629,176	590,044	430,607	1,468,005
All classes	14,982,607	7,041,414	2,367,477	1,723,636	1,323,103	2,526,977

Table 18.--Volume of growing stock on timberland, by broad management class, species group, and stand-age class, Florida, 1987

Broad management class and species group	All classes	No manageable stand	Stand-age class (years)								
			0-10	11-20	21-30	31-40	41-50	51-60	61-70	71-80	81+
	Thousand cubic feet										
Pine plantation											
Softwood	2,013,045	15,977	35,353	651,287	1,092,138	190,554	17,365	5,491	4,880	—	—
Hardwood	36,153	408	6,114	6,853	19,728	2,322	728	—	—	—	—
Total	2,049,198	16,385	41,467	658,140	1,111,866	192,876	18,093	5,491	4,880	—	—
Natural pine											
Softwood	3,485,205	481,068	53,561	97,806	377,921	845,636	759,210	513,260	184,885	134,153	37,705
Hardwood	191,095	15,789	3,780	6,337	17,659	37,928	61,884	15,139	12,434	16,427	3,718
Total	3,676,300	496,857	57,341	104,143	395,580	883,564	821,094	528,399	197,319	150,580	41,423
Oak-pine											
Softwood	775,130	195,878	16,235	20,006	32,579	85,087	189,250	101,097	53,327	47,009	34,662
Hardwood	368,983	42,641	4,266	4,685	17,700	51,932	108,614	63,318	36,857	21,999	16,971
Total	1,144,113	238,519	20,501	24,691	50,279	137,019	297,864	164,415	90,184	69,008	51,633
Upland hardwood											
Softwood	128,309	67,773	6,772	9,358	4,789	8,269	13,091	7,742	5,300	2,260	2,957
Hardwood	791,344	231,188	15,248	31,163	27,627	71,976	122,288	101,536	66,468	45,985	78,063
Total	919,653	298,961	22,020	40,521	32,416	80,245	135,379	109,278	71,768	48,245	81,020
Lowland hardwood											
Softwood	2,903,166	177,928	13,344	20,005	69,321	159,693	284,188	518,793	473,109	390,566	796,219
Hardwood	4,276,931	504,946	37,244	46,991	97,098	328,964	579,022	790,374	718,940	539,087	634,265
Total	7,180,097	682,874	50,588	66,996	166,419	488,657	863,210	1,309,167	1,192,049	929,653	1,430,484
All types											
Softwood	9,304,855	938,624	125,265	798,460	1,576,748	1,289,239	1,263,104	1,146,383	721,501	573,988	871,543
Hardwood	5,664,706	794,972	66,652	96,031	179,812	493,122	872,536	970,367	834,699	623,498	733,017
Total	14,969,561	1,733,596	191,917	894,491	1,756,560	1,782,361	2,135,640	2,116,750	1,556,200	1,197,486	1,604,560

Table 19.--Average net annual growth of growing stock on timberland, by broad management class, species group, and stand-age class, Florida, 1980-1986

Broad management class[a] and species group	All classes	No manageable stand	Stand-age class[a] (years) 0-10	11-20	21-30	31-40	41-50	51-60	61-70	71-80	81+
	Thousand cubic feet										
Pine plantation											
Softwood	247,242	2,197	16,432	117,170	98,666	11,143	1,074	428	132	—	—
Hardwood	3,016	5	127	1,125	1,444	290	25	—	—	—	—
Total	250,258	2,202	16,559	118,295	100,110	11,433	1,099	428	132	—	—
Natural pine											
Softwood	135,293	18,843	3,352	8,435	24,359	36,790	23,134	12,529	4,564	2,551	736
Hardwood	7,753	876	95	218	994	1,690	2,535	454	348	395	148
Total	143,046	19,719	3,447	8,653	25,353	38,480	25,669	12,983	4,912	2,946	884
Oak-pine											
Softwood	29,801	7,887	1,698	2,454	1,938	3,141	6,685	2,871	1,368	1,056	703
Hardwood	12,065	1,961	146	586	858	2,132	3,595	1,375	661	398	353
Total	41,866	9,848	1,844	3,040	2,796	5,273	10,280	4,246	2,029	1,454	1,056
Upland hardwood											
Softwood	3,881	3,249	317	547	220	321	474	196	190	73	94
Hardwood	21,687	6,440	809	1,935	1,364	2,256	3,090	2,332	1,344	832	1,285
Total	27,568	9,689	1,326	2,482	1,584	2,577	3,564	2,528	1,534	905	1,379
Lowland hardwood											
Softwood	69,331	6,239	620	862	2,161	4,822	7,489	12,620	11,682	8,101	14,735
Hardwood	96,237	14,350	1,151	2,732	4,305	9,247	14,488	17,140	14,376	9,533	8,914
Total	165,568	20,589	1,772	3,594	6,466	14,069	21,977	29,760	26,058	17,634	23,649
All types											
Softwood	487,548	38,415	22,619	129,468	127,344	56,217	38,856	28,644	17,936	11,781	16,268
Hardwood	140,758	23,632	2,329	6,596	8,965	15,615	23,733	21,301	16,729	11,158	10,700
Total	628,306	62,047	24,948	136,064	136,309	71,832	62,589	49,945	34,665	22,939	26,968

[a]Classifications at the end of the remeasurement period.

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Table 20.--Average annual removals of growing stock on timberland, by broad management class, species group, and stand-age class, Florida, 1980-1986

Broad management class[a] and species group	All classes	No manageable stand	Stand-age class[a] (years) 0-10	11-20	21-30	31-40	41-50	51-60	61-70	71-80	81+
	Thousand cubic feet										
Pine plantation											
Softwood	189,158	1,802	1,775	82,177	96,173	6,700	--	531	--	--	--
Hardwood	971	--	--	287	453	231	--	--	--	--	--
Total	190,129	1,802	1,775	82,464	96,626	6,931	--	531	--	--	--
Natural pine											
Softwood	219,215	20,090	1,659	9,540	42,253	72,687	42,791	19,382	4,960	1,646	4,207
Hardwood	5,468	532	68	498	903	1,602	1,459	264	--	63	79
Total	224,683	20,622	1,727	10,038	43,156	74,289	44,250	19,646	4,960	1,709	4,286
Oak-pine											
Softwood	23,226	7,692	307	791	3,338	4,034	1,343	3,949	1,109	313	150
Hardwood	8,725	1,758	285	51	2,077	1,480	1,136	1,938	--	--	--
Total	31,951	9,450	592	842	5,415	5,514	2,479	5,887	1,109	313	150
Upland hardwood											
Softwood	4,991	2,951	450	118	368	184	920	--	--	--	--
Hardwood	14,393	3,241	702	475	2,139	2,636	1,746	1,208	659	629	958
Total	19,384	6,192	1,152	593	2,507	2,820	2,666	1,208	659	629	958
Lowland hardwood											
Softwood	37,653	2,265	660	373	2,594	4,319	3,328	7,278	7,714	5,168	3,954
Hardwood	36,887	6,659	197	592	1,347	5,918	7,693	4,364	6,465	3,537	115
Total	74,540	8,924	857	965	3,941	10,237	11,021	11,642	14,179	8,705	4,069
All types											
Softwood	474,243	34,800	4,851	92,999	144,726	87,924	48,382	31,140	13,783	7,327	8,311
Hardwood	66,444	12,190	1,252	1,903	6,919	11,867	12,034	7,774	7,124	4,229	1,152
Total	540,687	46,990	6,103	94,902	151,645	99,791	60,416	38,914	20,907	11,556	9,463

[a]Classifications before timber removals.

Table 21.—Merchantable volume of live trees and growing stock on timberland, by forest-type and species groups, Florida, 1987

Forest-type group	Live trees					Growing stock				
	All species	Pine	Other softwood	Soft hardwood	Hard hardwood	All species	Pine	Other softwood	Soft hardwood	Hard hardwood
	Thousand cubic feet									
White pine-hemlock	—	—	—	—	—	—	—	—	—	—
Spruce-fir	—	—	—	—	—	—	—	—	—	—
Longleaf-slash pine	4,777,961	4,479,843	66,982	102,075	129,061	4,688,049	4,469,874	61,512	92,375	64,288
Loblolly-shortleaf pine	1,076,715	976,077	2,476	32,245	65,917	1,037,449	964,388	2,476	27,955	42,630
Oak-pine	1,282,527	657,021	126,790	240,595	258,121	1,144,113	652,687	122,443	207,805	161,178
Oak-hickory	1,320,051	128,150	3,863	197,388	990,650	919,853	126,264	2,043	176,879	614,665
Oak-gum-cypress	8,112,350	334,731	2,650,868	3,341,076	1,785,675	7,001,587	331,889	2,559,413	2,856,438	1,253,847
Elm-ash-cottonwood	212,256	1,356	10,508	94,409	105,983	178,510	1,356	10,508	79,673	86,973
Maple-beech-birch	—	—	—	—	—	—	—	—	—	—
All types	16,781,860	6,577,178	2,861,487	4,007,788	3,335,407	14,969,561	6,546,458	2,758,397	3,441,125	2,223,581

Table 22.--Area of timberland treated or disturbed annually and retained in timberland, by treatment or disturbance and ownership class, Florida, 1980 to 1987

Treatment or disturbance	All ownerships	Ownership class			
		Public	Forest industry	Forest industry-leased	Other privat
	Acres[a]				
Final harvest	296,052	28,483	139,159	21,337	107,073
Partial harvest[b]	37,181	6,026	9,493	3,446	18,216
Commercial thinning	45,454	13,156	16,519	3,734	12,045
Other stand improvement	6,524	1,006	1,915	—	3,603
Site preparation	196,418	19,847	112,337	19,627	44,607
Artificial regeneration[c]	196,470	15,999	97,700	19,728	63,043
Natural regeneration[c]	75,589	7,990	13,809	1,503	52,287
Other treatment	13,476	2,483	1,722	—	9,271
Natural disturbance	113,166	12,707	33,302	4,022	63,135

[a]Since some acres experience more than one treatment or disturbance, there are no column totals.

[b]Includes high grading and some selective cutting.

[c]Includes establishment of trees for timber production on forest and nonforest land.

Table 23.--Area of timberland treated or disturbed annually and retained in timberland, by treatment or disturbance and broad management class, Florida, 1980 to 1987

Treatment or disturbance	All classes	Broad management class[a]				
		Pine plantation	Natural pine	Oak-pine	Upland hardwood	Lowland hardwood
	Acres[b]					
Final harvest	296,052	93,319	132,573	21,567	19,177	29,416
Partial harvest[c]	37,181	1,751	11,865	5,018	1,700	16,847
Commercial thinning	45,454	28,012	15,831	322	299	990
Other stand improvement	6,524	1,418	3,583	—	774	749
Sit preparation	196,418	65,690	83,930	11,745	21,866	13,187
Other treatment	13,476	670	4,668	1,872	3,060	3,206
Natural disturbance	113,166	30,756	33,763	7,956	8,650	32,041

[a]Classification before treatment or disturbance.

[b]Since some acres experience more than one treatment or disturbance, there are no column totals.

[c]Includes high grading and some selective cutting.

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Table 24.--Area f timberland regenerated annually, by type of regeneration and broad management class, Fl rida, 1980 to 1987

Type of regeneration	All classes	Broad management class[a]				
		Pine plantation	Natural pine	Oak-pine	Upland hardwood	Lowland hardwo d
	Acres					
Artificial regeneration following harvest	118,374	114,040	—	3,253	717	364
Natural regeneration following harvest	36,476	322	9,079	2,898	9,377	14,800
Other artificial regeneration on forest land	51,098	46,292	—	3,850	592	364
Other natural regeneration on forest land	25,896	—	13,981	4,673	2,150	5,092
Artificial regeneration on nonforest land	26,998	26,329	—	669	—	—
Natural reversion of nonforest land	13,217	—	9,085	1,369	1,291	1,472
Total	272,059	186,983	32,145	16,712	14,127	22,092

[a]Classification after regeneration.

Table 25.--Area of timberland, by treatment opportunity and broad management class s, Florida, 1987

Treatment opportunity class	All classes	Broad management class				
		Pine plantation	Natural pine	Oak-pine	Upland hardwood	Lowland hardwo d
	Acres					
Salvage	33,548	5,402	16,321	3,119	—	8,706
Harvest	545,274	2,617	89,033	39,862	57,694	356,068
Commercial thinning	468,451	398,362	49,488	2,759	—	17,842
Other stand improvement	605,925	63,389	174,327	77,635	76,882	213,692
Stand conversion	141,466	10,608	8,933	22,394	33,935	65,596
Regeneration	4,698,887	133,671	1,300,957	582,483	1,353,142	1,328,634
Stands in relatively good condition	7,436,549	3,408,821	1,845,655	442,887	365,781	1,373,405
Adverse sites[a]	1,052,507	2,942	16,041	39,630	2,941	990,953
All classes	14,982,607	4,025,812	3,500,755	1,210,769	1,890,375	4,354,896

[a]Areas where management opportunities are severely limited because of steep sl pes or poor drainage.

Table 26.--Area of timberland, by treatment opportunity and ownership classes, Florida, 1987

Treatment opportunity class	All ownerships	Ownership class			
		Public	Forest industry	Forest industry-leased	Other private
	Acres				
Salvage	33,548	6,306	12,141	—	15,101
Harvest	545,274	123,422	124,688	3,707	293,457
Commercial thinning	468,451	17,985	217,728	79,762	152,976
Other stand improvement	605,925	89,686	144,734	36,688	334,817
Stand conversion	141,466	15,632	42,598	6,863	76,373
Regeneration	4,698,887	780,681	1,051,003	85,727	2,781,476
Stands in relatively good condition	7,436,549	1,212,009	2,835,369	441,885	2,947,286
Adverse sites[a]	1,052,507	197,378	341,363	22,163	491,603
All classes	14,982,607	2,443,099	4,769,624	676,795	7,093,089

[a]Areas where management opportunities are severely limited because of steep slopes or poor drainage.

Table 27.--Merchantable volume of live trees and growing stock on timberland, by ownership class and species group, Florida, 1987

Ownership class	Live trees					Growing stock				
	All species	Pine	Other softwood	Soft hardwood	Hard hardwood	All species	Pine	Other softwood	Soft hardwood	Hard hardwood
	Thousand cubic feet									
National forest	1,165,172	763,768	127,374	205,486	72,544	1,087,057	760,049	113,042	172,248	41,718
Other public	2,194,242	844,062	332,336	581,653	436,191	1,906,454	839,926	322,590	483,890	260,048
Forest industry	4,515,128	1,985,064	731,644	1,168,786	649,634	4,163,590	1,978,477	708,266	1,002,020	474,827
Forest industry-leased	523,952	316,033	72,209	94,472	40,238	500,125	315,129	70,763	85,607	28,626
Other private	8,380,366	2,668,251	1,597,924	1,977,391	2,136,800	7,312,335	2,652,877	1,543,736	1,697,360	1,418,362
All ownerships	16,781,860	6,577,178	2,861,487	4,007,788	3,335,607	14,969,561	6,546,458	2,758,397	3,441,125	2,223,581

Table 28.--Volume of sawtimber on timberland, by ownership class and species group, Florida, 1987

Ownership class	Small sawtimber[a]					Large sawtimber[b]				
	All species	Pine	Other softwood	Soft hardwood	Hard hardwood	All species	Pine	Other softwood	Soft hardwood	Hard hardwood
	Thousand board feet									
National forest	2,402,718	2,028,956	199,005	132,265	42,492	1,206,460	627,695	180,436	305,400	92,929
Other public	3,440,990	2,163,303	524,120	506,690	246,877	3,492,923	1,168,609	683,966	1,004,307	636,041
Forest industry	5,731,695	3,019,937	1,225,929	1,028,927	456,902	4,701,498	1,138,755	981,145	1,482,038	1,099,560
Forest industry-leased	533,703	307,782	125,994	75,722	24,205	401,200	189,123	44,249	88,139	79,669
Other private	11,831,040	5,921,469	2,768,425	1,868,568	1,272,578	11,124,955	3,258,781	1,811,528	2,557,564	3,497,082
All ownerships	23,940,146	13,441,447	4,843,473	3,612,172	2,043,054	20,927,036	6,382,963	3,701,334	5,437,448	5,405,281

[a]Volume of sawtimber trees less than 15.0 inches at d.b.h.

[b]Volume of sawtimber trees 15.0 inches and larger at d.b.h.

Table 29.--Average net annual growth and removals of growing stock on timberland, by ownership class and species group, Florida, 1980-1986

Ownership class	Net annual growth					Annual timber removals				
	All species	Pine	Other softwood	Soft hardwood	Hard hardwood	All species	Pine	Other softwood	Soft hardwood	Hard hardwood
	Thousand cubic feet									
National forest	35,659	30,010	1,364	3,332	953	32,031	31,980	—	51	—
Other public	58,727	35,601	6,795	9,305	7,026	17,513	16,176	352	391	594
Forest industry	229,825	180,479	14,145	22,997	12,204	219,001	183,324	7,859	13,533	14,285
Forest industry-leased	36,512	31,919	1,243	2,557	793	37,206	28,277	4,616	2,858	1,457
Other private	267,583	149,168	36,824	42,542	39,049	234,936	181,484	20,175	14,914	18,363
All ownerships	628,306	427,177	60,371	80,733	60,025	540,687	441,241	33,002	31,745	34,699

Table 30.--Average net annual growth and removals of sawtimber on timberland, by ownership class and species group, Florida, 1980-1986

Ownership class	Net annual growth					Annual timber removals				
	All species	Pine	Other softwood	Soft hardwood	Hard hardwood	All species	Pine	Other softwood	Soft hardwood	Hard hardwood
	Thousand board feet									
National forest	111,896	93,716	5,437	8,279	4,464	99,360	99,360	—	—	—
Other public	240,932	148,504	31,550	31,327	29,551	52,199	48,396	888	1,463	1,452
Forest industry	543,973	381,138	53,429	61,912	47,294	550,265	444,071	29,077	35,399	41,718
Forest industry-leased	76,969	65,576	4,732	4,623	2,038	74,062	51,131	12,269	7,105	3,557
Other private	1,006,340	560,187	153,600	143,387	149,166	674,066	515,809	69,470	39,556	49,231
All ownerships	1,980,110	1,249,121	248,948	249,528	232,513	1,449,952	1,158,767	111,704	83,523	95,958

Table 31.--Volume of timber on timberland, by class of timber and species group, Florida, 1987

Class of timber	All species	Pine	Other softwood	Soft hardwood	Hard hardwood
	Thousand cubic feet				
Sawtimber trees					
Saw-log portion	8,517,216	3,670,993	1,739,694	1,749,476	1,357,053
Upper-stem portion[a]	1,185,172	390,165	240,269	342,256	212,482
Total	9,702,388	4,061,158	1,979,963	2,091,732	1,569,535
Poletimber trees	5,267,173	2,485,300	778,434	1,349,393	654,046
All growing-stock trees	14,969,561	6,546,458	2,758,397	3,441,125	2,223,581
Rough trees					
Sawtimber size	831,268	17,546	32,193	222,139	559,390
Poletimber size	769,982	12,224	37,667	256,898	463,193
Total	1,601,250	29,770	69,860	479,037	1,022,583
Rotten trees					
Sawtimber size	186,603	950	30,245	74,234	81,174
Poletimber size	24,446	—	2,985	13,392	8,069
Total	211,049	950	33,230	87,626	89,243
Salvable dead trees					
Sawtimber size	24,405	13,441	2,552	4,255	4,157
Poletimber size	14,360	8,052	1,986	2,485	1,837
Total	38,765	21,493	4,538	6,740	5,994
Total, all timber	16,820,625	6,598,671	2,866,025	4,014,528	3,341,401

[a]Includes cull sections in the saw-log portion.

Table 37.--Number of live trees on timberland, by species and diameter class, Florida, 1987

Species	All classes	Diameter class (inches at breast height) 1.0–2.9	3.0–4.9	5.0–6.9	7.0–8.9	9.0–10.9	11.0–12.9	13.0–14.9	15.0–16.9	17.0–18.9	19.0–20.9	21.0–28.9	29.0 and larger
	Thousand trees												
Softwood													
Longleaf pine	171,291	56,833	28,985	18,452	17,403	19,211	16,585	9,229	3,316	908	257	110	3
Slash pine	1,624,998	497,005	507,133	342,978	165,846	61,060	27,537	13,373	6,082	2,653	948	494	11
Shortleaf pine	8,408	2,263	2,003	1,086	1,125	893	435	428	207	80	18	36	4
Loblolly pine	176,227	71,917	45,169	26,593	13,209	6,936	4,285	3,000	2,064	1,458	802	745	26
Pond pine	32,172	6,301	8,070	5,646	5,417	2,716	1,954	1,049	507	148	106	63	—
Virginia pine	—	—	—	—	—	—	—	—	—	—	—	—	—
Pitch pine	—	—	—	—	—	—	—	—	—	—	—	—	—
Table Mountain pine	—	—	—	—	—	—	—	—	—	—	—	—	—
Spruce pine	6,198	2,582	1,308	1,163	208	273	231	161	111	89	46	36	—
Sand pine	257,939	140,856	54,662	33,217	17,115	6,569	3,671	1,090	325	171	65	—	—
Eastern white pine	—	—	—	—	—	—	—	—	—	—	—	—	—
Eastern hemlock	—	—	—	—	—	—	—	—	—	—	—	—	—
Spruce and fir	—	—	—	—	—	—	—	—	—	—	—	—	—
Baldcypress	75,131	20,821	14,386	11,680	8,782	5,946	4,108	2,863	1,963	1,325	938	1,080	271
Pondcypress	732,893	331,640	163,261	96,371	61,563	38,376	20,784	11,369	4,751	2,377	938	1,126	137
Cedars	35,396	20,010	5,506	3,096	2,595	1,799	1,012	681	438	133	80	38	—
Total softwoods	3,120,653	1,150,407	830,483	540,289	293,254	144,581	80,652	43,302	19,956	9,338	4,205	3,760	452
Hardwood													
Select white oaks	9,381	4,242	2,463	1,102	548	416	276	250	118	82	46	36	4
Select red oaks	551	331	—	—	127	41	—	18	—	11	18	5	—
Chestnut oak	—	—	—	—	—	—	—	—	—	—	—	—	—
Other white oaks	270,686	140,256	55,432	18,232	11,051	6,987	4,719	3,470	2,758	2,344	1,406	3,064	1,079
Other red oaks	714,394	478,258	110,807	50,241	26,767	17,998	12,164	6,722	4,630	2,375	1,461	2,289	482
Hickory	35,248	19,117	6,617	3,239	1,866	1,148	934	860	553	294	191	224	4
Yellow birch	—	—	—	—	—	—	—	—	—	—	—	—	—
Hard maple	5,388	3,367	523	328	420	133	197	77	49	33	21	40	—
Soft maple	280,310	177,765	49,106	19,655	12,828	8,285	5,437	3,151	2,103	1,327	432	491	30
Beech	1,703	324	824	111	133	—	102	60	29	36	48	32	4
Sweetgum	220,900	136,081	44,617	19,708	10,530	8,740	5,198	2,818	1,588	835	417	346	16
Tupelo and blackgum	758,315	410,531	173,910	72,407	41,380	22,562	14,823	9,382	5,281	3,167	1,933	2,509	365
Ash	293,039	172,962	63,747	28,265	11,038	7,234	4,265	2,136	1,584	844	498	410	58
Cottonwood	12	—	—	—	—	—	—	—	—	—	—	12	—
Basswood	4,584	3,285	322	224	249	107	88	163	66	36	36	8	—
Yellow-poplar	15,203	7,479	2,551	2,365	760	321	695	282	286	77	89	116	4
Bay and magnolia	584,898	348,081	128,739	52,090	26,053	16,297	8,737	4,008	2,223	1,307	632	665	56
Black cherry	21,344	14,446	4,499	1,216	673	303	160	102	15	34	—	—	—
Black walnut	162	162	—	—	—	—	—	—	—	—	—	—	—
Sycamore	394	—	156	—	51	—	61	19	14	47	8	14	4
Black locust	—	—	—	—	—	—	—	—	—	—	—	—	—
Elm	45,147	33,887	10,086	4,861	2,332	1,711	884	640	421	136	106	83	6
Other eastern hardwoods	1,129,134	843,052	191,150	58,511	21,005	9,348	2,841	1,348	363	378	218	263	37
Total hardwoods	4,391,193	2,793,826	843,727	332,541	167,817	99,909	61,597	35,722	22,261	13,181	7,758	10,687	2,167
All species	7,511,846	3,944,233	1,674,210	872,823	461,071	244,490	142,239	79,023	42,213	22,519	11,967	14,447	2,619

Table 33.—Number of growing-stock trees on timberland, by species and diameter class, Florida, 1987

Species	All classes	1.0–2.9	3.0–4.9	5.0–6.9	7.0–8.9	9.0–10.9	11.0–12.9	13.0–14.9	15.0–16.9	17.0–18.9	19.0–20.9	21.0–28.9	29.0 and larger
	Diameter class (inches at breast height)												
	Thousand trees												
Softwood													
Longleaf pine	166,215	52,697	38,673	18,128	17,339	19,131	16,486	9,211	3,391	897	257	110	3
Slash pine	1,590,867	472,325	499,889	361,533	165,484	80,730	37,505	13,230	6,053	2,042	938	487	41
Shortleaf pine	8,082	1,917	2,003	1,084	1,123	693	495	428	207	80	18	30	4
Loblolly pine	170,425	47,820	44,136	26,459	12,893	6,733	4,233	3,000	2,064	1,458	803	738	20
Pond pine	27,607	3,924	6,668	5,325	5,291	2,646	1,880	1,049	507	148	106	63	—
Virginia pine	—	—	—	—	—	—	—	—	—	—	—	—	—
Pitch pine	—	—	—	—	—	—	—	—	—	—	—	—	—
Table Mountain pine	—	—	—	—	—	—	—	—	—	—	—	—	—
Spruce pine	5,191	1,613	1,308	1,163	208	273	221	418	98	89	66	56	—
Sand pine	249,306	136,688	53,721	32,814	16,022	6,309	3,370	1,070	486	171	65	—	—
Eastern white pine	—	—	—	—	—	—	—	—	—	—	—	—	—
Eastern hemlock	—	—	—	—	—	—	—	—	—	—	—	—	—
Spruce and fir	—	—	—	—	—	—	—	—	—	—	—	—	—
Baldcypress	68,381	16,536	12,769	11,577	8,613	6,727	4,057	2,806	1,912	1,272	901	1,004	207
Pondcypress	646,479	276,160	147,301	89,092	57,522	36,569	20,105	11,064	4,512	2,152	901	994	107
Cedars	30,546	17,710	4,293	2,545	2,085	1,722	864	645	411	133	80	58	—
Total softwoods	2,963,097	1,045,168	800,783	529,714	287,180	141,573	79,436	42,641	18,549	9,042	4,115	3,538	356
Hardwood													
Select white oaks	8,177	3,266	2,151	1,103	472	416	242	250	118	82	46	28	6
Select red oaks	380	160	—	—	127	41	—	18	—	11	18	5	—
Chestnut oak	—	—	—	—	—	—	—	—	—	—	—	—	—
Other white oaks	37,868	24,583	11,388	4,149	3,768	1,964	1,114	1,249	1,141	825	857	1,472	558
Other red oaks	489,056	304,155	81,582	40,449	22,188	14,989	10,147	5,517	3,765	1,989	1,319	1,661	315
Hickory	20,377	8,344	4,001	2,887	1,374	1,025	848	785	491	247	174	197	4
Yellow birch	—	—	—	—	—	—	—	—	—	—	—	—	—
Hard maple	1,588	338	551	223	298	133	31	71	49	33	21	33	—
Soft maple	136,378	72,619	28,766	11,648	6,471	5,675	3,995	2,295	1,437	891	342	309	22
Beech	958	161	336	111	133	—	76	40	13	12	38	18	4
Sweetgum	155,401	75,136	34,192	17,543	9,685	8,244	4,920	3,688	1,500	796	395	286	12
Tupelo and blackgum	439,990	172,073	124,485	59,048	34,017	19,100	12,240	8,021	4,549	2,639	1,630	1,981	207
Ash	106,068	50,155	22,608	16,256	6,540	4,874	3,373	1,555	1,280	725	412	319	35
Cottonwood	6	—	—	—	—	—	—	—	—	—	—	6	—
Basswood	1,232	1,299	160	224	109	107	56	143	66	26	36	8	—
Yellow-poplar	11,618	4,436	2,228	2,233	760	521	646	282	251	77	71	111	4
Bay and magnolia	360,576	190,792	83,821	39,469	20,096	11,814	7,078	3,312	1,986	1,097	908	561	42
Black cherry	13,355	7,926	3,355	1,102	498	201	133	102	13	23	—	—	—
Black walnut	—	—	—	—	—	—	—	—	—	—	—	—	—
Sycamore	394	—	156	—	51	—	81	19	14	47	8	14	4
Black locust	—	—	—	—	—	—	—	—	—	—	—	—	—
Elm	23,585	10,278	5,917	2,543	1,887	1,030	676	587	365	136	88	73	4
Other eastern hardwoods	28,738	18,686	5,043	2,144	1,222	725	334	313	121	119	35	16	—
Total hardwoods	1,851,765	964,405	411,537	199,133	111,696	70,837	45,896	27,273	17,101	9,773	5,803	7,098	1,215
All species	4,814,862	1,989,573	1,212,320	728,847	398,876	212,410	125,332	69,914	36,650	18,815	9,918	10,636	1,571

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Table 34.--Merchantable volume of live trees on timberland, by species and diameter class, Florida, 1987

Species	All classes	Diameter class (inches at breast height)									
		5.0–6.9	7.0–8.9	9.0–10.9	11.0–12.9	13.0–14.9	15.0–16.9	17.0–18.9	19.0–20.9	21.0–28.9	29.0 and larger
	Thousand cubic feet										
Softwood											
Longleaf pine	1,183,944	53,756	122,429	245,734	319,734	256,301	119,726	41,246	14,886	9,572	370
Slash pine	4,008,701	861,447	1,039,845	725,516	531,611	376,895	230,795	132,453	62,466	44,378	2,195
Shortleaf pine	39,797	3,484	8,171	9,078	9,362	12,723	8,233	3,927	1,592	2,519	708
Loblolly pine	679,440	38,720	72,844	75,605	86,636	87,933	85,049	77,705	36,296	75,910	4,740
Pond pine	172,714	13,847	29,949	29,685	35,068	26,448	18,125	7,224	6,833	5,535	—
Virginia pine	—	—	—	—	—	—	—	—	—	—	—
Pitch pine	—	—	—	—	—	—	—	—	—	—	—
Table Mountain pine	—	—	—	—	—	—	—	—	—	—	—
Spruce pine	38,533	4,302	1,697	3,494	4,359	4,187	4,962	5,486	3,430	5,616	—
Sand pine	434,049	109,378	117,455	83,238	67,091	27,976	17,834	7,158	3,719	—	—
Eastern white pine	—	—	—	—	—	—	—	—	—	—	—
Eastern hemlock	—	—	—	—	—	—	—	—	—	—	—
Spruce and fir	—	—	—	—	—	—	—	—	—	—	—
Baldcypress	616,401	36,642	57,459	76,898	70,433	67,798	65,128	37,259	50,753	84,839	47,192
Pondcypress	2,142,784	298,923	403,996	430,559	352,279	272,051	148,829	93,284	67,309	77,881	17,613
Cedars	104,302	8,433	13,633	19,344	18,237	16,313	14,362	6,783	4,508	4,609	—
Total softwoods	9,438,465	1,449,132	1,867,478	1,699,151	1,491,882	1,148,725	713,043	432,515	252,562	311,459	73,018
Hardwood											
Select white oaks	39,049	2,826	2,884	4,641	4,549	6,397	4,636	3,690	3,333	2,203	770
Select red oaks	4,161	—	682	333	—	561	—	481	1,275	849	—
Chestnut oak	—	—	—	—	—	—	—	—	—	—	—
Other white oaks	853,011	40,784	46,169	53,388	55,628	64,927	72,654	74,407	67,228	212,145	170,501
Other red oaks	1,443,987	136,098	159,595	194,282	203,669	160,572	147,258	101,392	88,345	179,635	74,137
Hickory	133,846	7,433	10,167	11,509	18,885	21,740	19,832	13,026	12,060	19,874	720
Yellow birch	—	—	—	—	—	—	—	—	—	—	—
Hard maple	17,020	1,231	2,038	1,679	2,953	2,051	1,799	1,397	1,090	2,782	—
Soft maple	554,291	54,932	73,146	83,811	90,457	74,182	64,832	47,995	24,781	35,996	4,059
Beech	12,574	203	1,086	—	1,406	1,507	790	855	2,834	2,847	824
Sweetgum	556,167	64,736	44,402	101,319	101,572	79,068	61,271	42,331	26,647	29,448	3,375
Tupelo and blackgum	1,757,715	193,344	237,736	233,676	241,960	224,595	188,095	126,279	94,596	170,989	46,465
Ash	483,151	63,352	61,868	75,840	74,326	50,605	51,619	38,727	27,409	32,196	7,389
Cottonwood	753	—	—	—	—	—	—	—	—	753	—
Basswood	16,098	600	1,392	1,289	1,342	3,411	2,185	1,055	2,192	632	—
Yellow-poplar	70,328	8,308	5,297	6,325	12,587	7,351	10,699	4,020	5,513	9,629	599
Bay and magnolia	904,101	140,446	149,095	150,908	147,283	97,608	73,869	55,684	33,881	49,313	6,024
Black cherry	16,874	3,479	4,173	2,068	2,881	2,445	674	1,354	—	—	—
Black walnut	—	—	—	—	—	—	—	—	—	—	—
Sycamore	7,893	—	270	—	1,406	519	623	2,461	376	1,301	737
Black locust	—	—	—	—	—	—	—	—	—	—	—
Elm	108,660	11,181	12,390	13,044	14,840	16,028	14,506	7,313	6,498	7,917	943
Other eastern hardwoods	388,516	100,266	87,722	70,350	36,120	28,772	14,837	13,555	9,885	15,938	6,871
Total hardwoods	7,363,395	816,217	920,112	1,008,662	1,009,224	842,419	708,999	536,622	403,257	774,669	323,214
All species	16,781,860	2,265,349	2,787,590	2,707,813	2,501,106	1,991,144	1,422,043	989,167	655,309	1,086,128	396,232

Table 35.--Volume of growing stock on timberland, by species and diameter class, Florida, 1987

Species	All classes	5.0-6.9	7.0-8.9	9.0-10.9	11.0-12.9	13.0-14.9	15.0-16.9	17.0-18.9	19.0-20.9	21.0-22.9	29.0 and larger
	Diameter class (inches at breast height)										
	Thousand cubic feet										
Softwood											
Longleaf pine	1,179,882	53,231	122,121	245,016	318,618	255,945	118,993	40,930	14,886	9,372	570
Slash pine	3,998,887	858,696	1,037,771	723,406	532,216	376,588	229,953	131,909	62,194	43,959	2,195
Shortleaf pine	59,797	3,484	8,171	9,078	9,362	12,723	8,233	3,927	1,592	2,519	708
Loblolly pine	674,808	58,599	71,483	73,525	84,343	87,933	85,049	77,705	56,296	75,135	4,740
Pond pine	170,091	13,250	29,461	28,980	34,235	26,448	18,125	7,224	6,833	5,535	—
Virginia pine	—	—	—	—	—	—	—	—	—	—	—
Pitch pine	—	—	—	—	—	—	—	—	—	—	—
Table Mountain pine	—	—	—	—	—	—	—	—	—	—	—
Spruce pine	37,398	4,302	1,697	3,494	4,339	3,603	4,349	5,486	3,430	6,616	—
Sand pine	425,595	108,095	114,939	81,256	65,724	27,687	17,017	7,158	3,719	—	—
Eastern white pine	—	—	—	—	—	—	—	—	—	—	—
Eastern hemlock	—	—	—	—	—	—	—	—	—	—	—
Spruce and fir	—	—	—	—	—	—	—	—	—	—	—
Baldcypress	593,824	36,394	56,639	75,083	69,957	67,407	64,129	36,011	50,011	81,623	36,570
Pondcypress	2,066,435	281,679	384,756	416,831	345,278	266,487	145,839	89,296	46,510	73,862	15,917
Cedars	98,118	7,353	11,613	18,898	14,723	15,677	13,956	6,783	4,508	4,609	—
Total softwoods	9,304,855	1,425,083	1,838,651	1,675,567	1,478,815	1,140,560	705,641	426,429	249,979	303,430	60,700
Hardwood											
Select white oaks	35,359	2,826	2,725	4,641	4,140	6,397	4,656	3,690	3,233	2,081	770
Select red oaks	4,161	—	682	333	—	541	—	481	1,275	849	—
Chestnut oak	—	—	—	—	—	—	—	—	—	—	—
Other white oaks	405,502	10,042	17,284	17,605	15,788	26,835	34,431	32,944	33,076	118,302	99,195
Other red oaks	1,235,329	112,710	138,746	169,592	176,570	140,069	129,351	90,222	75,023	144,603	36,443
Hickory	120,992	6,816	8,069	10,374	15,373	20,098	18,012	12,335	11,111	18,084	720
Yellow birch	—	—	—	—	—	—	—	—	—	—	—
Hard maple	13,260	491	1,456	1,679	584	2,051	1,799	1,397	1,090	2,713	—
Soft maple	412,419	34,298	52,633	61,645	69,725	57,251	48,681	30,779	20,473	25,504	3,430
Beech	10,705	205	1,086	—	1,416	1,507	551	406	2,565	2,145	824
Sweetgum	527,787	41,939	60,492	97,343	97,491	76,543	58,745	41,169	25,756	26,170	2,137
Tupelo and blackgum	1,519,532	161,995	204,158	206,760	211,479	203,047	151,731	113,017	85,168	146,941	35,236
Ash	378,894	36,678	43,942	56,133	64,361	42,409	43,433	35,008	24,494	27,898	4,538
Cottonwood	294	—	—	—	—	—	—	—	—	294	—
Basswood	12,967	600	832	1,289	1,133	3,142	2,185	962	2,192	632	—
Yellow-poplar	67,610	7,942	5,297	6,325	12,213	7,351	9,962	4,020	4,734	9,165	599
Bay and magnolia	765,094	109,405	120,015	130,465	123,811	83,619	68,635	49,443	29,645	44,268	5,788
Black cherry	14,395	3,246	3,035	2,068	2,371	2,445	474	756	—	—	—
Black walnut	—	—	—	—	—	—	—	—	—	—	—
Sycamore	7,893	—	270	—	1,406	519	623	2,461	576	1,301	737
Black locust	—	—	—	—	—	—	—	—	—	—	—
Elm	88,113	5,861	10,545	11,535	12,173	15,129	12,808	6,631	5,728	6,960	743
Other eastern hardwoods	46,400	3,618	6,551	7,162	6,384	7,996	3,915	5,618	2,234	922	—
Total hardwoods	5,664,706	540,672	677,818	784,949	816,420	697,151	589,992	439,339	328,373	578,832	211,160
All species	14,969,561	1,965,755	2,516,469	2,460,516	2,295,235	1,837,711	1,295,633	865,768	578,352	882,262	271,860

Table 36.—Volume of sawtimber on timberland, by species and diameter class, Florida, 1987

Species	All classes	Diameter class (inches at breast height) 9.0–10.9	11.0–12.9	13.0–14.9	15.0–16.9	17.0–18.9	19.0–20.9	21.0–28.9	29.0 and larger
	Thousand board feet								
Softwood									
Longleaf pine	4,493,564	498,560	1,330,397	1,368,871	684,388	248,663	94,326	64,248	4,104
Slash pine	9,907,449	3,650,020	2,466,525	1,975,176	1,313,956	884,335	398,594	298,702	16,161
Shortleaf pine	303,028	56,336	42,086	65,430	66,193	23,407	9,993	35,315	5,070
Loblolly pine	2,945,172	267,263	381,799	453,428	481,716	468,386	356,309	500,643	36,430
Pond pine	827,033	110,591	157,832	136,282	101,567	42,621	42,416	35,724	—
Virginia pine	—	—	—	—	—	—	—	—	—
Pitch pine	—	—	—	—	—	—	—	—	—
Table Mountain pine	—	—	—	—	—	—	—	—	—
Spruce pine	173,171	14,182	20,412	18,983	24,437	31,974	20,763	41,442	—
Sand pine	836,993	318,363	308,659	147,265	97,726	43,428	23,550	—	—
Eastern white pine	—	—	—	—	—	—	—	—	—
Eastern hemlock	—	—	—	—	—	—	—	—	—
Spruce and fir	—	—	—	—	—	—	—	—	—
Baldcypress	2,354,560	237,717	266,550	294,096	303,955	287,211	269,198	473,591	235,236
Pondcypress	5,196,360	1,307,458	1,346,896	1,184,985	709,236	442,652	153,604	430,253	101,216
Cedars	383,877	73,362	67,381	80,022	76,638	39,820	27,219	29,465	—
Total softwoods	28,369,207	5,991,861	4,568,543	5,724,536	3,842,060	2,452,477	1,495,972	1,897,161	398,417
Hardwood									
Select white oaks	113,697	—	14,100	26,368	31,047	18,258	16,946	11,830	3,148
Select red oaks	16,234	—	—	2,299	—	2,591	6,532	4,812	—
Chestnut oak	—	—	—	—	—	—	—	—	—
Other white oaks	1,789,356	—	55,129	106,800	149,563	150,556	159,585	613,533	557,186
Other red oaks	3,938,280	—	672,725	610,448	615,715	457,401	399,295	828,461	354,055
Hickory	437,112	—	52,775	81,392	81,420	60,041	57,195	99,866	4,423
Yellow birch	—	—	—	—	—	—	—	—	—
Hard maple	43,334	—	1,899	8,097	7,801	6,487	5,248	13,822	—
Soft maple	1,077,967	—	230,100	318,186	305,329	175,433	98,307	131,358	19,254
Beech	37,411	—	5,205	5,664	3,157	1,600	10,370	8,927	3,488
Sweetgum	1,489,381	—	351,150	329,016	281,592	224,513	163,474	155,409	14,227
Tupelo and blackgum	4,170,473	—	700,095	801,203	664,469	539,207	429,643	811,806	224,070
Ash	1,026,821	—	209,068	163,916	188,140	164,385	121,696	150,758	28,858
Cottonwood	1,491	—	—	—	—	—	—	1,491	—
Basswood	43,916	—	3,313	12,228	9,213	4,667	10,857	3,238	—
Yellow-poplar	232,549	—	63,336	31,341	48,577	21,753	17,341	55,731	4,071
Bay and magnolia	1,853,103	—	614,630	323,896	391,217	223,232	142,042	226,713	33,355
Black cherry	23,927	—	8,139	9,852	2,156	3,780	—	—	—
Black walnut	—	—	—	—	—	—	—	—	—
Sycamore	34,389	—	4,314	1,937	2,765	11,464	2,928	6,889	4,392
Black locust	—	—	—	—	—	—	—	—	—
Elm	252,209	—	61,605	59,110	54,499	34,123	27,365	15,414	4,093
Other eastern hardwoods	113,603	—	22,535	32,249	17,158	27,141	11,728	4,792	—
Total hardwoods	16,497,975	—	2,830,718	2,824,508	2,642,798	2,112,650	1,670,552	3,162,230	1,256,518
All species	44,867,182	5,991,861	7,399,261	8,549,044	6,484,858	4,565,129	3,166,524	5,059,391	1,650,935

Table 37.--Volume of sawtimber on timberland, by species, size class, and tree grade, Florida, 1987

Species	All size classes					Trees 15.0 inches d.b.h. and larger				
	All grades	Tree grade				All grades	Tree grade			
		1	2	3	4		1	2	3	4
	Thousand board feet									
Softwood										
Yellow pines[a]	19,824,410	5,594,330	4,247,287	9,982,793	—	6,382,963	2,734,715	1,510,540	2,137,708	—
Eastern white pine[b]	—	—	—	—	—	—	—	—	—	—
Spruce and fir[b]	—	—	—	—	—	—	—	—	—	—
Cypress[c]	8,150,920	1,989,756	2,139,992	3,950,811	70,361	3,528,212	1,989,756	1,149,796	369,330	19,330
Other eastern softwoods[b]	393,877	115,877	118,060	148,373	13,567	173,112	77,285	58,525	37,302	—
Total	28,369,207	7,697,963	6,505,339	14,081,977	83,928	10,084,287	4,801,756	2,718,861	2,544,340	19,330
Hardwood[c]										
Select white and red oaks	129,931	35,744	40,966	49,066	4,155	87,164	35,744	27,431	21,361	2,628
Other white and red oaks	5,727,638	1,108,903	1,603,279	2,446,811	566,645	4,282,528	1,108,903	1,413,381	1,443,165	317,079
Hickory	437,112	107,049	155,647	149,369	25,047	302,945	107,049	118,719	62,431	14,746
Yellow birch	—	—	—	—	—	—	—	—	—	—
Hard maple	43,356	—	10,826	18,200	14,328	33,358	—	8,427	15,906	9,025
Sweetgum	1,489,581	290,572	534,488	616,827	47,696	809,415	290,572	333,998	165,134	19,711
Ash, walnut, and black cherry	1,050,748	227,050	318,303	471,104	34,291	657,773	227,050	227,623	187,486	15,614
Yellow-poplar	232,549	56,010	67,634	102,796	6,109	157,472	56,010	56,140	45,322	—
Other eastern hardwoods	7,387,062	1,591,065	2,370,738	3,138,738	286,521	4,512,094	1,591,065	1,725,559	1,062,022	133,448
Total	16,497,975	3,416,393	5,101,879	6,994,911	984,792	10,842,749	3,416,393	3,911,278	3,002,827	512,251
All species	44,867,182	11,114,356	11,607,218	21,076,888	1,068,720	20,927,036	8,218,149	6,630,139	5,547,167	531,581

[a]For yellow pines, tree grade is based on "Southern Pine Tree Grades for Yard and Structural Lumber," Research Paper SE-40, published by the Southeastern Forest Experiment Station, Asheville, NC, 1966. Tree grade 4 does not apply to yellow pine.

[b]For other softwoods (excluding cypress), tree grade is based on "Tree Grades for Eastern White Pine," Research Paper NE-214, published by the Northeastern Forest Experiment Station, Broomall, PA, 1971.

[c]For hardwoods and cypress, tree grades 1, 2, and 3 are based on "Hardwood Tree Grades for Factory Lumber," Research Paper NE-333, published by the Northeastern Forest Experiment Station, Broomall, PA, 1976. Grade 4 tre s are sawtimber trees not qualifying as tree Grades 1, 2, or 3. The butt log of these trees qualify as construction (tie and timber) 1 as based on "A Guide to Hardwood Log Grading (revised)," General Technical Report NE-1, published by the Northeastern Forest Experiment Station, Broomall, PA, 1973.

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Table 38.--Cubic volume in the merchantable saw-log portion of sawtimber trees on timberland, by species and diameter class, Florida, 1987

Species	All classes	Diameter class (inches at breast height)							
		9.0-10.9	11.0-12.9	13.0-14.9	15.0-16.9	17.0-18.9	19.0-20.9	21.0-28.9	29.0 and larger
	Thousand cubic feet								
Softwood									
Longleaf pine	917,792	202,985	291,245	243,378	115,342	40,110	14,691	9,477	564
Slash pine	1,872,566	571,316	482,294	358,079	223,614	129,993	61,376	43,521	2,173
Shortleaf pine	44,694	7,427	8,475	12,119	8,027	3,875	1,575	2,495	701
Loblolly pine	509,790	56,909	75,926	83,174	82,547	76,428	55,729	74,385	4,692
Pond pine	117.507	23,776	31,410	25,259	17,693	7,174	6,765	5,478	—
Virginia pine	—	—	—	—	—	—	—	—	—
Pitch pine	—	—	—	—	—	—	—	—	—
Table Mountain pine	—	—	—	—	—	—	—	—	—
Spruce pine	29,730	2,761	3,926	3,473	4,234	5,391	3,395	6,550	—
Sand pine	178,914	66,007	59,548	26,249	16,451	6,997	3,662	—	—
Eastern white pine	—	—	—	—	—	—	—	—	—
Eastern hemlock	—	—	—	—	—	—	—	—	—
Spruce and fir	—	—	—	—	—	—	—	—	—
Baldcypress	445,139	52,826	59,081	60,406	59,124	52,577	47,404	78,267	35,454
Pondcypress	1,222,253	320,926	302,552	244,840	137,146	85,052	44,664	71,533	15,540
Cedars	72,302	15,218	13,319	14,750	13,436	6,602	4,426	4,551	—
Total softwoods	5,410,687	1,320,151	1,327,776	1,071,727	677,614	414,151	243,887	296,257	59,124
Hardwood									
Select white oaks	21,543	—	2,868	5,402	4,104	3,378	3,030	1,998	763
Select red oaks	2,864	—	—	442	—	445	1,174	803	—
Chestnut oak	—	—	—	—	—	—	—	—	—
Other white oaks	327,012	—	11,690	22,160	29,978	29,440	30,140	109,911	93,693
Other red oaks	694,518	—	129,103	115,455	112,672	80,850	68,431	134,559	53,448
Hickory	82,312	—	11,056	16,516	15,741	11,127	10,220	16,962	690
Yellow birch	—	—	—	—	—	—	—	—	—
Hard maple	8,413	—	383	1,675	1,566	1,259	998	2,532	—
Soft maple	214,165	—	48,214	45,445	41,311	34,081	18,431	23,463	3,220
Beech	8,073	—	1,048	1,194	473	352	2,289	1,957	760
Sweetgum	274,313	—	69,023	63,408	52,079	37,994	24,399	25,294	2,116
Tupelo and blackgum	800,396	—	150,673	166,178	131,944	101,700	78,182	137,895	33,824
Ash	202,783	—	44,773	34,789	37,893	31,731	22,693	26,504	4,400
Cottonwood	280	—	—	—	—	—	—	280	—
Basswood	8,771	—	832	2,566	1,883	869	2,030	591	—
Yellow-poplar	40,884	—	8,399	6,020	8,806	3,727	4,498	8,843	393
Bay and magnolia	337,991	—	86,740	68,815	60,644	45,416	27,951	42,697	5,728
Black cherry	4,805	—	1,720	1,994	411	680	—	—	—
Black walnut	—	—	—	—	—	—	—	—	—
Sycamore	6,385	—	862	394	535	2,164	526	1,204	700
Black locust	—	—	—	—	—	—	—	—	—
Elm	49,470	—	8,547	12,116	10,851	5,806	5,117	6,344	689
Other eastern hardwoods	21,551	--	4,488	6,298	3,266	4,779	1,906	814	--
Total hardwoods	3,106,529	--	580,419	570,867	514,155	395,798	302,015	542,651	200,624
All species	8,517,216	1,320,151	1,908,195	1,642,594	1,191,769	809,949	545,902	838,908	259,748

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Table 39.--Total volume of live trees on timberland, by species and diameter class, Florida, 1987

Species	All classes	Diameter class (inches at breast height)											
		1.0-2.9	3.0-4.9	5.0-6.9	7.0-8.9	9.0-10.9	11.0-12.9	13.0-14.9	15.0-16.9	17.0-18.9	19.0-20.9	21.0-28.9	29.0 and larger
	Thousand cubic feet												
Softwood													
Longleaf pine	1,614,696	11,797	36,143	74,063	147,247	184,142	363,785	389,086	134,358	46,176	16,626	10,660	633
Slash pine	5,341,831	130,367	369,145	1,207,976	1,258,376	839,626	604,637	426,205	258,361	147,779	89,563	49,290	2,432
Shortleaf pine	72,225	486	2,528	4,594	9,901	10,515	10,703	16,408	9,280	4,413	1,786	2,823	790
Loblolly pine	852,098	15,876	41,382	83,905	89,001	88,241	98,816	99,675	93,846	87,296	63,107	84,874	5,283
Pond pine	211,732	1,345	7,898	18,398	36,037	34,574	40,294	30,198	20,602	8,199	7,733	6,234	—
Virginia pine	—	—	—	—	—	—	—	—	—	—	—	—	—
Pitch pine	—	—	—	—	—	—	—	—	—	—	—	—	—
Table Mountain pine	—	—	—	—	—	—	—	—	—	—	—	—	—
Spruce pine	46,710	333	1,610	3,493	2,028	4,062	4,998	4,751	3,596	6,178	3,856	7,415	—
Sand pine	642,907	32,374	67,767	138,846	145,233	97,475	77,058	31,782	20,161	8,057	4,174	—	—
Eastern white pine	—	—	—	—	—	—	—	—	—	—	—	—	—
Eastern hemlock	—	—	—	—	—	—	—	—	—	—	—	—	—
Spruce and fir	—	—	—	—	—	—	—	—	—	—	—	—	—
Baldcypress	788,870	4,612	21,565	54,012	74,060	95,518	85,878	82,067	78,590	66,806	40,876	101,840	59,048
Pondcypress	3,334,688	102,835	236,318	503,447	540,996	560,288	452,810	346,038	188,220	117,782	59,786	98,111	22,637
Cedars	135,971	3,994	6,930	11,485	16,894	23,034	15,177	19,136	16,749	7,946	5,231	5,357	—
Total softwoods	13,961,748	306,117	972,403	2,121,621	2,339,785	2,043,473	1,756,326	1,341,386	827,343	502,628	292,738	366,624	90,823
Hardwood													
Select white oaks	50,371	1,173	3,286	4,186	5,766	5,881	5,705	8,221	5,765	4,568	3,993	2,873	954
Select red oaks	5,213	43	—	—	883	423	—	688	—	591	1,369	1,038	—
Chestnut oak	—	—	—	—	—	—	—	—	—	—	—	—	—
Other white oaks	1,168,294	34,511	57,394	70,526	63,663	69,007	69,785	80,178	89,048	91,116	75,802	257,977	208,889
Other red oaks	2,117,993	97,920	141,428	210,083	213,999	250,203	237,242	302,536	183,409	126,920	110,088	226,383	94,284
Hickory	178,019	3,393	7,809	11,876	13,331	14,493	20,760	26,443	33,983	18,507	14,532	23,061	859
Yellow birch	—	—	—	—	—	—	—	—	—	—	—	—	—
Hard maple	23,753	780	793	1,807	3,624	2,064	3,661	2,485	2,163	1,080	1,308	3,443	—
Soft maple	799,816	41,925	72,355	78,388	92,619	102,829	109,602	89,198	78,207	57,681	28,501	43,307	4,906
Beech	16,798	308	659	313	1,446	—	2,078	1,871	1,004	1,141	2,522	3,650	1,008
Sweetgum	740,755	25,832	52,060	68,623	79,950	119,922	117,044	90,764	69,989	48,134	30,258	33,621	3,958
Tupelo and blackgum	2,589,028	126,436	249,885	390,268	309,031	292,051	297,778	274,693	205,916	134,901	116,787	313,289	59,953
Ash	709,395	45,733	80,230	90,668	76,398	90,057	66,757	58,501	59,366	44,395	31,484	37,140	8,666
Cottonwood	889	—	—	—	—	—	—	—	—	—	—	889	—
Basswood	17,538	680	413	806	1,455	1,696	1,558	3,929	2,501	1,268	2,514	720	—
Yellow-poplar	87,110	1,738	3,001	10,907	6,275	7,308	16,378	8,320	12,053	4,529	4,209	10,823	669
Bay and magnolia	1,388,584	84,689	173,205	207,099	188,634	183,603	176,253	115,987	87,405	65,887	40,221	58,310	7,089
Black cherry	31,730	3,154	3,905	4,678	5,186	2,477	3,410	2,880	358	1,586	—	—	—
Black walnut	79	79	—	—	—	—	—	—	—	—	—	—	—
Sycamore	9,399	—	431	—	325	—	1,649	605	723	2,448	566	1,503	869
Black locust	—	—	—	—	—	—	—	—	—	—	—	—	—
Elm	130,095	3,398	12,153	18,393	15,533	20,656	17,675	18,816	17,077	8,558	7,822	8,234	863
Other eastern hardwoods	864,728	158,490	185,694	139,563	114,959	89,535	45,026	35,692	17,432	16,833	12,420	20,056	9,128
Total hardwoods	10,948,809	632,323	1,046,999	1,226,882	1,190,383	1,252,001	1,230,899	1,021,988	858,999	649,023	489,496	948,139	402,075
All species	23,910,557	938,440	2,019,485	3,348,503	3,530,168	3,295,474	2,987,225	2,363,374	1,686,342	1,151,651	782,234	1,314,763	492,898

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Table 40.--Green weight of forest biomass on timberland, by species and diameter class, Florida, 1987

Species	All classes	1.0-2.9	3.0-4.9	5.0-6.9	7.0-8.9	9.0-10.9	11.0-12.9	13.0-14.9	15.0-16.9	17.0-18.9	19.0-20.9	21.0-28.9	29.0 and larger
	Hundred thousand pounds												
Softwood													
Longleaf pine	1,108,675	9,311	30,673	53,439	111,907	220,343	287,135	229,706	107,384	37,130	13,388	8,566	505
Slash pine	4,305,888	96,003	508,830	883,169	981,003	847,856	489,350	329,618	101,105	114,932	53,920	38,243	1,857
Shortleaf pine	50,796	286	1,522	2,893	6,667	7,481	7,717	10,393	6,728	3,253	1,270	2,058	568
Loblolly pine	416,198	7,711	25,085	61,657	67,187	65,772	71,042	73,157	69,744	63,739	45,856	61,414	3,830
Pond pine	150,771	862	4,448	13,175	30,185	26,853	28,962	21,768	14,862	5,803	5,468	4,408	—
Virginia pine	—	—	—	—	—	—	—	—	—	—	—	—	—
Pitch pine	—	—	—	—	—	—	—	—	—	—	—	—	—
Table Mountain pine	—	—	—	—	—	—	—	—	—	—	—	—	—
Spruce pine	32,302	398	1,465	3,282	1,351	2,755	3,471	3,332	2,976	4,360	2,733	5,233	—
Sand pine	438,088	22,953	55,425	97,371	96,856	68,768	55,783	21,296	14,118	5,684	2,836	—	—
Eastern white pine	—	—	—	—	—	—	—	—	—	—	—	—	—
Eastern hemlock	—	—	—	—	—	—	—	—	—	—	—	—	—
Spruce and fir	—	—	—	—	—	—	—	—	—	—	—	—	—
Baldcypress	591,619	3,729	13,615	27,740	46,171	45,597	43,767	53,683	82,111	55,497	50,062	86,463	53,304
Pondcypress	1,986,987	55,691	148,820	220,054	307,426	346,702	301,125	242,086	136,490	87,704	45,494	76,962	18,635
Cedars	105,926	2,818	4,490	8,773	13,033	17,485	15,380	15,229	13,656	6,175	4,288	4,387	—
Total softwoods	9,387,246	199,330	794,371	1,370,535	1,637,796	1,465,792	1,301,702	1,011,264	630,374	384,436	225,325	287,716	78,397
Hardwood													
Select white oaks	43,639	847	2,481	2,859	3,098	4,877	4,810	5,876	4,845	4,011	3,391	2,591	853
Select red oaks	4,489	33	—	—	487	369	—	381	—	568	1,358	893	—
Chestnut oak	—	—	—	—	—	—	—	—	—	—	—	—	—
Other white oaks	1,063,101	25,786	43,376	40,834	30,936	60,058	63,796	74,756	63,944	87,201	73,004	230,804	208,388
Other red oaks	1,712,209	86,321	107,137	161,076	178,847	204,123	210,308	166,122	151,717	103,946	90,287	180,234	72,881
Hickory	148,074	2,884	6,800	8,176	10,821	11,468	16,800	22,053	20,299	14,144	12,534	21,008	786
Yellow birch	—	—	—	—	—	—	—	—	—	—	—	—	—
Hard maple	20,335	639	855	1,455	2,376	1,823	3,254	2,201	1,939	1,575	1,233	3,183	—
Soft maple	594,062	31,872	50,852	55,601	71,655	78,300	82,071	66,895	38,179	42,806	23,255	33,175	3,401
Beech	13,837	96	382	327	917	—	1,711	1,325	880	1,008	2,952	3,023	810
Sweetgum	543,544	17,179	34,711	45,981	57,401	87,485	87,020	88,372	53,129	38,974	23,623	26,425	3,236
Tupelo and blackgum	1,741,221	82,011	168,730	148,125	188,316	188,237	198,161	191,121	168,592	116,096	90,193	172,158	52,591
Ash	462,395	27,951	50,833	72,732	55,951	60,350	54,618	34,271	35,628	21,609	17,850	30,126	4,467
Cottonwood	723	—	—	—	—	—	—	—	—	—	—	723	—
Basswood	12,554	442	287	439	1,133	1,022	1,113	2,881	1,762	923	1,820	312	—
Yellow-poplar	61,494	1,299	2,572	6,688	4,335	3,057	10,246	6,088	8,692	3,327	4,615	8,073	516
Bay and magnolia	865,150	52,545	103,041	110,825	116,999	116,031	113,610	76,329	57,958	44,108	27,828	88,693	4,977
Black cherry	20,231	2,588	3,944	2,793	3,380	1,652	2,301	2,004	359	1,172	—	—	—
Black walnut	71	71	—	—	—	—	—	—	—	—	—	—	—
Sycamore	7,094	—	385	—	245	—	1,149	434	518	2,124	313	1,154	662
Black locust	—	—	—	—	—	—	—	—	—	—	—	—	—
Elm	100,233	3,956	8,563	9,931	10,484	15,516	11,823	12,696	11,483	5,633	3,263	6,289	593
Other eastern hardwoods	730,469	135,877	174,693	143,233	103,676	79,051	38,768	27,303	13,546	11,626	7,187	11,240	4,071
Total hardwoods	8,160,707	473,499	759,401	811,013	859,278	913,631	901,564	764,698	654,534	502,031	384,106	779,324	358,428
All species	17,547,953	673,049	1,553,772	2,181,568	2,497,044	2,379,423	2,203,266	1,775,962	1,284,908	886,467	609,431	1,067,038	436,825

Table 41.--Average net annual growth and removals of live timber and growing stock on timberland, by species, Florida, 1980-1986

Species	Live timber[a]		Growing stock	
	Net annual growth	Annual timber removals	Net annual growth	Annual timber removals
	- - - - - Thousand cubic feet - - - - -			
Softwood				
Yellow pines	428,125	443,305	427,177	441,241
Eastern white pine	---	---	---	---
Spruce and fir	---	---	---	---
Cypress	57,888	32,306	57,340	31,872
Other eastern softwoods	3,107	1,130	3,031	1,130
Total softwoods	489,120	476,741	487,548	474,243
Hardwood				
Select white and red oaks	968	821	964	703
Other white and red oaks	56,688	36,223	47,938	28,669
Hickory	2,750	3,145	2,622	2,981
Yellow birch	---	---	---	---
Hard maple	435	---	406	---
Sweetgum	14,533	9,460	14,057	8,946
Ash, walnut, and black cherry	9,919	2,850	8,250	2,374
Yellow-poplar	2,783	1,193	2,736	1,193
Tupelo and blackgum	26,771	12,405	24,844	11,191
Bay and magnolia	25,600	6,565	23,175	5,085
Other eastern hardwoods	24,784	12,866	15,766	5,302
Total hardwoods	165,231	85,528	140,758	66,444
All species	654,351	562,269	628,306	540,687

[a]Merchantable portion only.

Table 42.--Average net annual growth and removals of sawtimber on timberland, by species, Florida, 1980-1986

Species	Net annual growth	Annual timber removals
	Thousand board feet	
Softwood		
Yellow pines	1,249,121	1,158,767
Eastern white pine	---	---
Spruce and fir	---	---
Cypress	235,638	107,499
Other eastern softwoods	13,310	4,205
Total softwoods	1,498,069	1,270,471
Hardwood		
Select white and red oaks	3,808	2,412
Other white and red oaks	186,630	80,125
Hickory	11,068	8,632
Yellow birch	---	---
Hard maple	2,073	---
Sweetgum	56,099	26,591
Ash, walnut, and black cherry	28,174	4,789
Yellow-poplar	7,684	3,878
Tupelo and blackgum	75,800	32,378
Bay and magnolia	62,078	10,182
Other eastern hardwoods	48,627	10,494
Total hardwoods	482,041	179,481
All species	1,980,110	1,449,952

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Table 43.--Average annual removals of growing stock on timberland, by species and diameter class, Florida, 1980-1986

Species	All classes	Diameter class (inches at breast height)									
		5.0-6.9	7.0-8.9	9.0-10.9	11.0-12.9	13.0-14.9	15.0-16.9	17.0-18.9	19.0-20.9	21.0-28.9	29.0 and larger
	Thousand cubic feet										
Softwood											
Yellow pines	441,241	75,036	118,626	91,808	68,125	41,627	22,222	11,797	6,620	5,241	139
Eastern white pine	--	--	--	--	--	--	--	--	--	--	--
Spruce and fir	--	--	--	--	--	--	--	--	--	--	--
Cypress	31,872	3,299	3,768	6,089	5,157	4,640	3,391	1,814	1,437	2,083	194
Other eastern softwoods	1,130	161	99	275	132	390	73	--	--	--	--
Total softwoods	474,243	78,496	122,493	98,172	73,414	46,657	25,686	13,611	8,057	7,324	333
Hardwood											
Select white and red oaks	703	--	111	99	--	108	101	105	179	--	--
Other white and red oaks	28,669	3,147	4,073	4,479	3,477	3,699	3,353	1,910	1,142	2,320	1,069
Hickory	2,981	253	247	447	663	781	244	85	--	126	135
Yellow birch	--	--	--	--	--	--	--	--	--	--	--
Hard maple	--	--	--	--	--	--	--	--	--	--	--
Sweetgum	8,946	846	1,011	1,173	1,810	1,868	919	214	679	426	--
Ash, walnut, and black cherry	2,374	616	298	366	212	301	80	87	89	325	--
Yellow-poplar	1,193	--	192	205	--	478	200	--	118	--	--
Tupelo and blackgum	11,191	1,309	990	1,284	2,343	1,637	1,095	812	571	1,150	--
Bay and magnolia	5,085	1,085	718	760	979	604	171	263	167	338	--
Other eastern hardwoods	5,302	549	1,131	1,095	828	582	436	97	451	133	--
Total hardwoods	66,444	7,805	8,771	9,908	10,312	10,058	6,599	3,573	3,396	4,818	1,204
All sp cies	540,687	86,301	131,264	108,080	83,726	56,715	32,285	17,184	11,453	12,142	1,537

Table 44.--Average annual mortality of live timber, growing stock, and sawtimber on timberland, by species, Florida, 1980-1986

Species	Live timber[a]	Growing stock	Sawtimber
	- - Thousand cubic feet - -		Thousand board feet
Softwood			
Yellow pines	52,853	51,419	161,946
Eastern white pine	---	---	---
Spruce and fir	---	---	---
Cypress	11,457	10,163	24,037
Other eastern softwoods	833	693	3,085
Total softwoods	65,143	62,275	189,068
Hardwood			
Select white and red oaks	617	371	1,433
Other white and red oaks	33,808	23,592	87,889
Hickory	897	596	2,074
Yellow birch	---	---	---
Hard maple	---	---	---
Sweetgum	5,150	4,411	12,792
Ash, walnut, and black cherry	5,357	2,971	6,835
Yellow-poplar	527	423	1,139
Tupelo and blackgum	10,846	8,519	27,008
Bay and magnolia	15,462	11,292	29,535
Other eastern hardwoods	22,734	7,607	18,346
Total hardwoods	95,398	59,782	187,051
All species	160,541	122,057	376,119

[a]Merchantable portion only.

Table 45.—Change in number of live trees on timberland, by species group, survey completi n date, and diameter class, Florida

Species group and year	All classes	Diameter class (inches at breast height) 1.0-2.9	3.0-4.9	5.0-6.9	7.0-8.9	9.0-10.9	11.0-12.9	13.0-14.9	15.0 and larger
	- - - - - - - -	- - - - - - - -	- - - - - - - -	- - - -	Thousand trees	- - - -	- - - - - - - -	- - - - - - - -	- - - - - - - -
Yellow pine									
1980	2,471,599	786,135	762,024	480,100	224,775	110,118	60,561	28,284	19,602
1987	2,277,233	777,936	647,330	429,137	220,314	97,458	54,748	28,208	22,102
Change	-194,366	-8,199	-114,694	-50,963	-4,461	-12,660	-5,813	-76	+2,500
Other softwood									
1980	967,401	443,066	207,646	128,511	83,821	49,747	26,540	14,413	13,657
1987	843,420	372,471	183,153	111,145	72,940	47,123	25,884	15,093	15,611
Change	-123,981	-70,595	-24,493	-17,366	-10,881	-2,624	-656	+680	+1,954
Hardwood									
1980	4,883,719	3,237,417	881,121	345,331	172,444	100,049	60,786	36,733	49,838
1987	4,391,193	2,793,826	843,727	332,541	167,817	99,909	61,597	35,722	56,054
Change	-492,526	-443,591	-37,394	-12,790	-4,627	-140	+811	-1,011	+6,216

Table 46.--Land area, by land use class, major forest type, and survey completion date, Florida

Land use class	Survey completion date 1970	1980	1987	Change 1980-1987
	Acres			
Forest land				
Timberland:				
Pine and oak-pine types	9,567,984	9,193,657	8,737,336	-456,321
Hardwood types	6,693,255	6,470,520	6,245,271	-225,249
Total	16,261,239	15,664,177	14,982,607	-681,570
Reserved timberland	94,200	411,844	403,569	-8,275
Woodland	1,590,744	1,057,868	1,162,836	+104,968
Total forest land	17,946,183	17,133,889	16,549,012	-584,877
Nonforest land				
Cropland	3,671,347	3,784,515	3,937,202	+152,687
Pasture and range	6,456,018	6,991,503	6,324,067	-667,436
Other	6,464,601	6,622,456	7,721,452	+1,098,996
Total	16,591,966	17,398,474	17,982,721	+584,247
All land[a]	34,538,149	34,532,363	34,531,733	-630

[a]Excludes all water areas.

Brown, Mark J.; Thompson, Michael T.

Forest statistics for Florida, 1987. Resour. Bull. SE-101. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station; 1988. 61 pp.

Since 1980, area of timberland in Florida has decreased by 4 percent to less than 15.0 million acres. Area of nonindustrial private forest land has declined 12 percent to 7.1 million acres. Area harvested and retained in timberland averaged 196,000 acres annually. An average of 272,000 acres regenerated annually, 72 percent of which occurred through artificial methods. The area in pine plantations rose 23 percent to 4.0 million acres. Volume of softwood growing stock increased only 1 percent to 9.3 billion cubic feet, whereas volume of hardwood growing stock increased 11 percent to 5.7 billion cubic feet. Average basal area of live trees 5.0 inches d.b.h. and larger increased from 53 to 55 square feet per acre. Average net annual growth decreased 20 percent to 628 million cubic feet. Softwood removals increased 5 percent to 674 million

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Population Estimates, Habitat Requirements, and Landscape Design and Management for Urban Populations of the Endemic Big Cypress Fox Squirrel (*Sciurus niger avicennia*)

FINAL REPORT

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Abstract: The Big Cypress fox squirrel (*Sciurus niger avicennia*), listed as threatened by the state of Florida, is endemic to open forested habitats of southwest Florida. While considered to be increasingly rare in the wild lands of southwest Florida, its remains on certain golf courses in Lee and Collier counties. This study was carried out from August 1995 to December 1997 to document status and population levels in a variety of golf course landscapes, to determine habitat use and requirements of golf course populations, and to provide guidelines for favorable landscape design and management in urban and developing areas.

Sixty golf courses in western Lee and Collier counties were visited. Elements of vegetation composition and structure, and landscape configuration within and around courses were recorded. Repeat counts of squirrels were made at each course to determine the fox squirrel population levels. Cluster and factor analyses were used to identify landscape features favorable to squirrel habitation. A Landscape Evaluation Index (LEI), developed from these features, allowed ranking of the 60 courses in terms of their suitability for fox squirrels.

Radio-telemetry was used to examine home range size, habitat use within and around golf courses, and population dynamics at 2 courses, Royal Poinciana Cypress Course and Royal Palm County Club.

Tracking studies indicate a density of 42.4-49.8 squirrels/ha at the Cypress course and a density of 6.3-8.2 squirrels/ha at the Royal Palm course. At Cypress, squirrels fed heavily on pine and cypress from late summer to mid-winter, and relied on a mixture of native and exotic species between March and May. At Royal Palm, squirrels showed a heavy reliance on feeders between January and July.

The LEI identified 7 courses with high quality landscapes. All were part of 36 hole courses, contained large stands of open pine and cypress, and had contiguous areas free of automobile traffic. The remaining courses had combinations of unfavorable landscape elements: isolation within developed landscapes, poor quality tree stands, heavy understory vegetation, and complex development patterns. Twenty-three courses offer little opportunity for habitat improvement. The remaining 30 courses can improve habitat for present fox squirrel residents, but do not contain the landscape features required for long-term stable populations.

Landscape design and placement are the most crucial elements in creating potential fox squirrel habitat. Courses, or groups of courses, must contain large areas free of roadways and intense development to allow safer and less stressful movement within large home ranges. Large stands of pine, cypress, cabbage palms and associated native trees with open understories are required. Areas of pine litter ground cover promote fungi feeding.

ACKNOWLEDGMENTS

We thank the Florida Fish and Wildlife Conservation Commission, Nongame Wildlife Division, for their continuing attention to the pressures and consequences of rapid landscape change in southwest Florida. We are grateful for their funding and the support which made this project possible. We thank the staff of the Florida Museum of Natural History for administration of the funding.

Our work relied on access to the private property of over 60 golf courses in Lee and Collier counties. We thank the golf course superintendents, staffs and members of these courses for their generous contributions to our work. Special thanks and deep appreciation goes to the 2 clubs which facilitated the radio-telemetry studies centered on their property. At Royal Poinciana Golf Club, Gary Grigg, CGCS, and his staff provided assistance and access for 2 years of work, while Dale Walters, CGCS, and his staff at Royal Palm County Club, assisted in our work for the final year of the field study. Courses adjoining these main sites also permitted frequent visits to locate collared fox squirrels. These clubs included Hole in the Wall, Wilderness, Country Club of Naples, Quail Run, Bear's Paw, Hibiscus, and Royal Wood. We would also like to thank Tim Hiers and Mike Mongoven for their contributions to our understanding of the management and history of golf courses in southwest Florida.

Hardy thanks go to colleagues in the field and office. Joys and challenges of trapping and collaring were shared by 2 excellent field assistants Audrey Grieser and John Pamilio. Jay Harrison helped with the analysis of the data on the 60 course sites. John Shepherd gave generous assistance with vegetation sampling and mapping, GIS quagmires and all around support and enlightenment. For lively discussions, timely and invigorating e-mail, and a shared passion for work in the mammal world, thanks go to Lisa Molloy, Susan Walker, Deb Jansen, Kae Kawanishi, Laura Farrell, and Candace McCaffery.

And most importantly, we thank the 38 fox squirrels whose fondness for peanut butter and pecans lead them to carry radio-transmitters for up to 20 months as they moved, mated, fought and played. We won't forget you.

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INTRODUCTION

Fox squirrels (*Sciurus niger*) are a diurnal, arboreal species inhabiting open forests of the eastern and central United States (Hall 1981). The 4 subspecies of the southeastern states are larger and more varied in color than those to the north and west and prefer open pine forests with oaks and associated hardwoods (Kantola and Humphrey 1990, Moore 1957, Weigl et al. 1989). Of these, the Big Cypress fox squirrel (*S. n. avicennia*) is the most restricted, found only in the southwest tip of Florida, south of the Caloosahatchee River and west of the true Everglades. Native to open stands of slash pine, cypress, and tropical hardwoods, these squirrels frequently feed and move on the ground. Their relatively large size and habits of ground use make them especially vulnerable to the widespread landscape changes promoted in recent decades (Humphrey and Jodice 1992, Moore 1956, Williams and Humphrey 1979).

Human activities affecting fox squirrel populations are widespread and varied in southwest Florida. Changes in fires cycles on large preserves and privately owned forests have allowed development of heavy understory vegetation not conducive to fox squirrel movement and ground feeding. Conversion of range lands to citrus groves in northern and central agricultural areas has eliminated open, parklike habitat favorable to fox squirrels. Rapid urbanization of coastal property from Naples to Ft. Myers has created fragmented habitat with serious obstructions to squirrel movement, resulting in isolated populations amid shrinking green space (Moore 1954, Williams and Humphrey 1979, Jodice and Humphrey 1993). Current demographic trends predict that Lee County will grow from 410,000 people in 1999 to 940,800 in 2020 (Lee County DCD 1998) and Collier County will increase from 245,000 in 1995 to between 508,000 and 770,000 in 2020 (Collier County 1996). Most of the development will be concentrated in the western edge of the counties, with Collier County expecting full development west of highway 951 by 2050 (D. Weeks, person. commun.).

While fox squirrel populations have apparently declined in the preserves such as Big Cypress and Corkscrew Swamp and have vanished from dense housing developments and commercial areas, they remain obvious on certain golf courses within and near the burgeoning developments of western Lee and Collier counties (Deborah Jansen pers. commun., Jodice 1990, Jodice and Humphrey 1992, 1993). Golf courses with remmant open pine and cypress stands preserve fragments of suitable habitat within a swirl of traffic and commerce.

In an effort to understand the ecology of these golf course fox squirrel populations, Jodice (Jodice and Humphrey 1992) undertook a study of their diet and activity patterns on 4 Naples courses in 1989-1990. His work relied on focal-animal sampling of individuals located visually rather than by radio-telemetry, undoubtedly allowing bias in a species which is often difficult to see. His work successfully highlighted questions of population levels and stabilty of golf course habitats (Jodice and Humphrey 1993, Maehr 1993). It became clear that little is known about spatial needs, movements, habitat requirements, or population trends of these urban populations and still less about the prevalence of these golf course populations and the landscape configurations which might promote their survival. Insights into these questions could show whether golf courses might play roles as refugia for urban populations and how courses might be designed and managed to promote fox squirrel survival. The goal of this project was to address location and size of golf course populations, habitat use and population dynamics. Specifically, the goals were:

1. To survey the status of golf course populations and the landscape elements and configuration of a range of golf course types. Sixty courses in western Lee and Collier counties will be considered.
2. To gather data on home range size, dispersal, habitat use, and population dynamics through the use of radio-telemetry. Two golf course populations in Collier County will be studied, 1 with high numbers of squirrels and 1 with lower numbers of squirrels.
3. To evaluate the role of golf courses as refugia for urban populations of fox squirrels and to provide recommendations for design and management of golf course landscapes based on the analysis of the golf course surveys and the data on home range, movements, habitat use and population dynamics.

STUDY AREA

All study sites were located in the western half of Collier and Lee counties in southwest Florida (Fig.1). The area has a humid subtropical climate with heavy influence from the surrounding warm waters and the seasonal changes in the Bermuda high (Chen and Gerber 1990). These features give rise to cool dry winters and warm, rainy summers and autumns, with extreme events such as occasional hard frosts and hurricanes playing a strong role in the composition of the vegetation community. Native vegetation of the flatwoods physiographic region in which the sites were located includes pine flatwoods, cypress domes, and mangroves. The presence of Entisols, Histosols, and Spodosols reflect a mixed terrain of high, relatively dry, sandy ridges, and low, poorly drained swamps (Brown et al. 1990).

Patterns of temperature and precipitation varied from year to year in the 3 calendar years of the study, with wide deviations from normal in summer precipitation (NOAA, 1995-97). Summer and fall of 1995 were extremely wet. Stations at Ft. Myers and Naples reported 1.7 m or more of precipitation between June 1 and October 31, more than 0.76 m above normal. Flooding and long-term standing water were common on most sites during late summer and fall 1995. In the same months of 1996 the stations received only 0.56 m of rain, a 0.36 m deficit. January 1997 to August 1997, when the tracking studies ended, had normal levels of precipitation. The winter of 1995-1996 had at least 2 cool periods, with 4 nights of 0 C , and widespread damage to the more tropical flora. The winter of 1996-1997 was warmer than normal. An average January, with warm weather (19 C) and 1 light frost, was followed by 2 months of high temperatures. February averaged 22 C, 3.5 C above normal, and March 24 C, 3 C above normal.

Landscape Study

Of the 60 golf courses selected for the landscape analysis and fox squirrel censusing, 18 were in Lee County, south of the Caloosahatchee River, and 42 were in Collier County. Course landscapes ranged from undeveloped, with large tracts of native vegetation, to intensely developed courses having close-set, multiple story condominiums on both sides of the fairways. Highly developed courses usually allowed for few trees, native or exotic, in the roughs. Courses ranged in age from over 40 years to those recently opened and still under development. The oldest courses in the study, located near the Gulf Coast, commonly were isolated from other clubs and were surrounded by development. On the eastern edge of development courses tended to be newer, often grouped together, and were located within a mixture of increasing development and remnants of pine and cypress stands.

Radio-Telemetry Study

Two 18-hole golf courses in Collier County, Florida, were selected for the radio-telemetry studies (Figs. 2,3). Site 1, the 18-hole Royal Poinciana Cypress Course, was half of a 36-hole private Royal Poinciana Golf Club built in 1971 in central Naples. Royal Poinciana has no residential development within the 135 ha of the golf course grounds. Fairways are bordered by open stands of moderate-size pines (*Pinus elliottii* var. *densa*), cypress (*Taxodium ascendens* and *T. distichum*) and cabbage palms (*Sabal palmetto*), and plantings of non-native broad-leafed evergreens (Appendix A).

Automobile traffic around the Cypress Course is limited to a short segment of private entrance roadway on the north side of the Cypress Course, with no public roadways on the boundaries of the course. Three golf courses, including the 18-hole Pines Course within the same club, comprise the western, northern and part of the eastern boundaries. The south boundary is an undeveloped pine stand of 115 ha and the remaining eastern boundary is residential development of varying density. Royal Poinciana and the neighboring clubs are located within a tract of approximately 1020 ha, which contains 6, 18-hole golf courses, of which 3 are undeveloped, 2 moderately developed, and 1 heavily developed. The tract contains 230 ha of forested land, ranging from drier pine to swampy cypress stands. The 1020 ha tract is bordered by 4 extremely busy roadways, Goodlette-Frank, Pine Ridge, Airport-Pulling, and Golden Gate Parkway.

Known predators at the site included eagles, bobcats, great horned owls, raccoons, rat snakes, and the club house cat which was allowed to roam the course at night.

Site 2, Royal Palm Country Club, is a developed 18-hole course near the eastern limit of intense suburban development along Highway 41 East (Figs. 4 & 5). The club, built in 1970, and the adjoining housing development cover 150 ha, of which 75 ha are private homes, condominium property and roadways. The club lies within a landscape currently undergoing rapid and dense development. All the fairways have development on both sides, either single family homes or large condominiums. When I began research at this site in 1996, 8 undeveloped, pine-covered lots remained along the fairways. In the next 12 months at least 4 of these were developed, with all of the pines being cut. The dominant vegetation of the Royal Palm roughs and the surrounding condominiums is open pine stands. Non-native trees of a limited variety are scattered around the course and are common in the small lots of the surrounding private homes. Cypress trees are present but are not common and generally small. The southwest boundary of Royal Palm adjoins the public 18-hole Hibiscus Golf Course. The Hibiscus course and surrounding dense development, together 132 ha, have few native tree species and narrow, open roughs with only small and scattered stands of trees (Appendix A). Busy 2-lane and 4-lane roadways border Royal Palm on the north, east and south, and Augusta Boulevard bisects the course from north to south. Known predators at the site included: eagles, raccoons, and a domestic cat.

Activity on the courses changed with the seasons. Golf play was heavy on both courses from December until April, with Royal Palm frequently having play on every hole from 0730 until late afternoon. Royal Poinciana was generally less crowded. Summer play was light, with each course closing 1 day a week for intensive maintenance work on the course and roughs. Daily maintenance work began at 0530 or 0600 and continued until late afternoon. In winter, maintenance crews worked on the courses every day, 0630 until 1430 weekdays, and 0630 until noon on weekends. Maintenance for the removal of vegetation in the understory of tree stands included mowing, hand removal of shrubs and

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herbaceous plants, the addition of pine straw and the use of herbicides. Both clubs irrigated the fairways, greens and tees in the early morning and often again in the early evening. Cone production on the study courses was noticeably higher in 1996 than 1997. In the summer and fall of 1996, following a wet 1995 summer and fall, cone production on both pine and cypress trees appeared to be high, with both species heavily laden throughout the Cypress Course. In 1997, little cone production was evident on pines and the cypress suffered an infestation of tent caterpillars in the late spring, resulting in widespread defoliation of cypress and lower early season cone production.

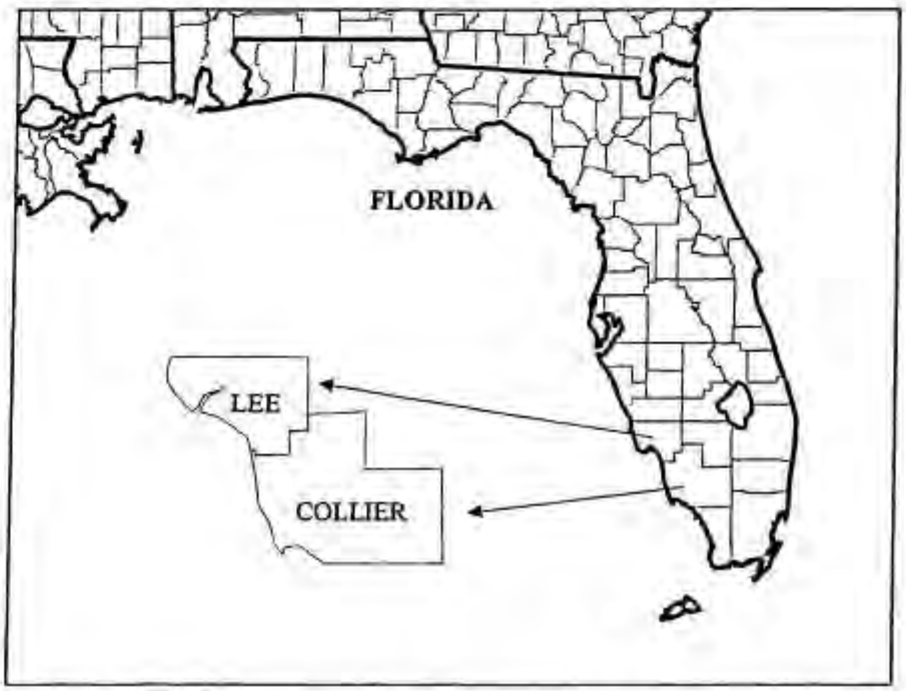

Figure 1. Locator map showing Lee and Collier counties in the southwest corner of Florida.

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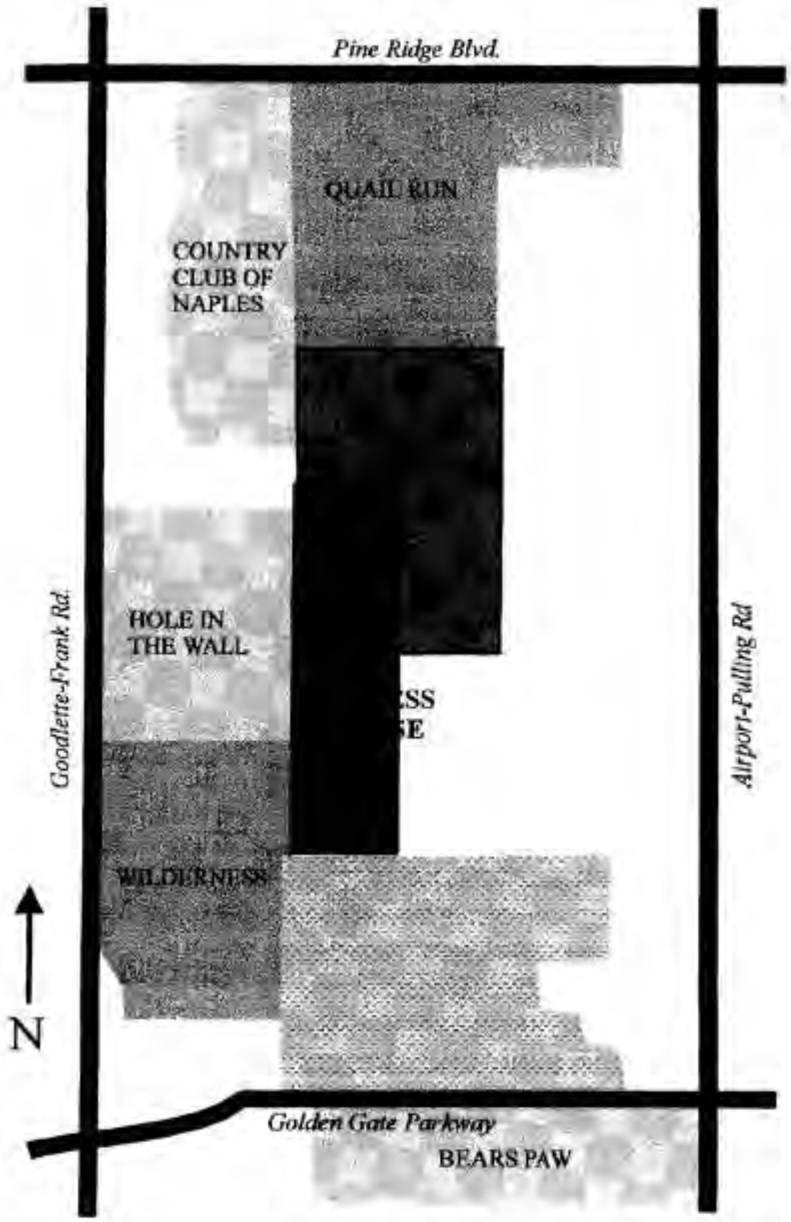

Figure 2. Identification of golf courses known to be used by fox squirrels from Site 1, Royal Poinciana Golf Club, Cypress Course. Five courses adjoin Site 1, including the Pines Course in the same club. Bear's Paw is south across Golden Gate Parkway. Stippled area is pine forest.

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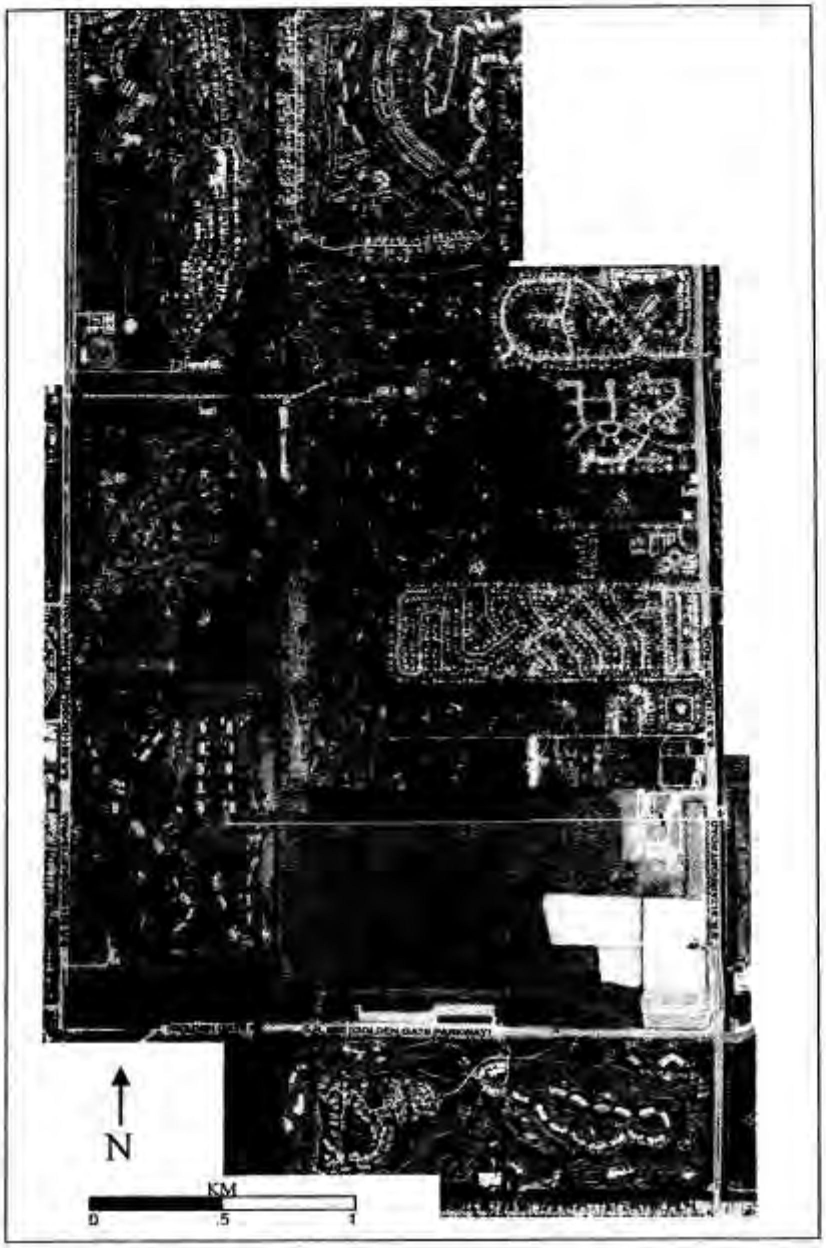

Figure 3. Site 1 and configuration of the surrounding landscape. Royal Poinciana Cypress Course is located in the center, with 6 other 18-hole courses nearby. Names on Fig. 2.

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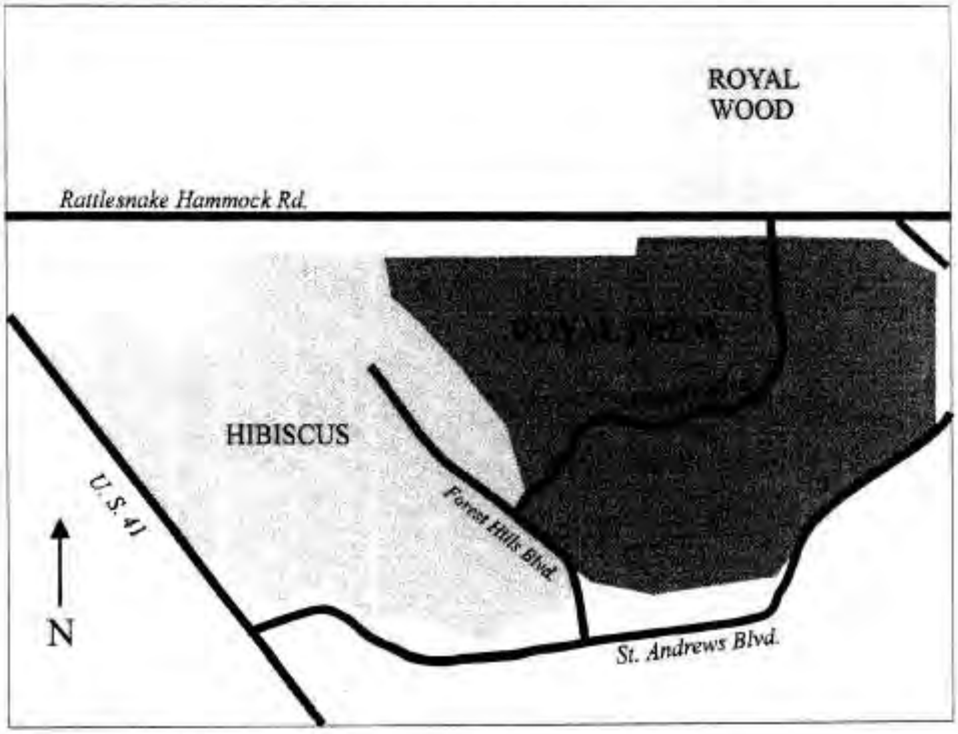

Figure 4. Landscape position of Site 2, Royal Palm Country Club, and 2 neighboring 18-hole courses.

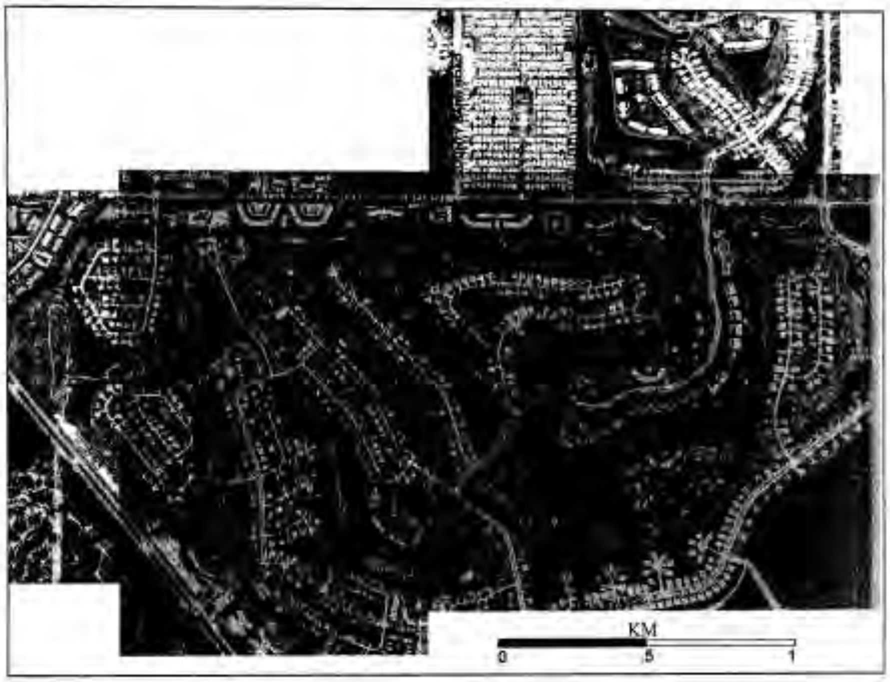

Figure 5. Configuration of Site 2, Royal Palm Country Club, and 2 neighboring 18-hole courses. (See Fig. 4 for names)

METHODS

Landscape Evaluation and Censusing

Surveys of golf course landscapes and fox squirrel populations were conducted to determine the status of fox squirrels and to identify landscape features favorable to their survival.

Sampling.-Sixty golf courses in western Lee and Collier counties were selected for landscape analysis and squirrel censusing. In selecting the courses I looked for a range of landscape types relating to:

- density of development surrounding the club boundaries, from heavily developed to undeveloped;
- type and configuration of development on the course, from undeveloped, nonresidential courses to those with dense development of houses and/or condominiums;
- character of the rough vegetation, from little and scattered, through open tree stands, to dense forest stands with heavy understory.

To obtain pre-visit information about age and landscape configuration for many of the 80+ courses in Lee and Collier counties I interviewed Tim Hires, Collier's Reserve Country Club, Naples, and Mike Mongoven, Ft. Myers and Eastwood Golf Clubs. I selected 66 courses for examination and contacted the courses through their superintendents of maintenance, individuals frequently most familiar with the landscape activities and wildlife on the courses. Superintendents proved to be excellent and often interested sources of information and influence. In most cases they remained the course contact throughout the study.

I made introductory visits to a majority of the 66 courses in August 1995-December 1995. Exceptions were made for courses flooded by heavy summer and autumn rains. Three clubs did not wish to take part in the study; from the remaining 63 courses I selected 60 courses in 48 clubs, 42 in Collier County and 18 in Lee County (Appendix B).

Each club in the study was visited 3 times for censusing fox squirrels and landscape analysis. The exceptions were those courses at which I did not see fox squirrels or sign of fox squirrels on the first visit and the superintendent and course workers had not seen fox squirrels for at least 1 year. At these courses I made no more than 2 visits for landscape analysis and squirrels censusing. Squirrel censusing took place between September 15 and May 15 each year, as squirrels were less active on the ground in the summer. Squirrel counts were conducted mornings, 0700-1030, or late afternoons, 1500-1730, when squirrels were most likely to be on the ground and visible (Jodice and Humphrey 1993). Sampling times were limited to sunny days with light or no wind and temperatures over 18 C.

I sampled for squirrels by driving around the course in reverse order, to decrease my interference with golfers. I stopped at each fairway for 10 minutes and selected 1 or 2 locations most likely to attract squirrels: open tree stands, trees with food items, and feeder areas. I searched trees and areas with open ground while listening for sounds of movement and communication. I recorded squirrel sign, nests, cone middens, and palm leaf or bark pealing. I recorded each squirrel spotting and did not attempt to determine if animals were recounted after moving to another area of the course. I counted individuals on private property adjoining the fairways, such as those using feeders. The highest count of the repeated visits was recorded as the number of squirrels seen at that course. Five categories of squirrel counts were created to allow grouping of courses by population levels. They were:

- Level 1-none present, a course at which I did not see fox squirrels and the superintendent and workers had not seen them for over a year;
- Level 2-none seen, a course at which I did not see fox squirrels but the superintendent reported sightings within the past year. This often meant traveling squirrels were on the course for a few weeks or 1 or 2 come from neighboring courses for occasional use.
- Level 3-low, the highest number of squirrels seen on the course was 1-5.
- Level 4-medium, the highest number of squirrels seen on the course was 6-10.
- Level 5-high, the highest number of squirrels seen on the course was 11 or more.

In the evaluation of habitat variation between courses I was interested in landscape features which could impact squirrel feeding, movement, nesting or predation. With these needs in mind I collected data on course configuration, place in a larger landscape, vegetation composition and structure, predators, course history and human interactions with squirrels. A field survey of questions which could be answered with a yes or no response was developed to report on this range of landscape attributes. All questions could be completed during a 3 hour tour of an 18 hole course and a 20 minute interview with a knowledgeable superintendent. All final landscape surveys were conducted between April and December 1997.

Data Analysis.-Fifty-one responses, or attributes, from the landscape surveys were used to examine landscape variation among the 60 sampled courses. Two methods of examining variation were used. Single linkage cluster analysis was used to identify aggregations of similar courses based on 51 landscape attributes (Statistical Analysis System 6.0). Two prominent clusters were selected for further examination. Chi-square (α=0.05) was used to test the hypothesis that attributes were randomly distributed between these clusters. Factor analysis was used as another method to identify factors or groups of attributes which explained variation among the courses (SPSS).

The 29 distinguishing attributes identified though cluster and factor analyses were used to create a Landscape Evaluation Index (LEI) (Bender et al. 1996, Brooks 1997, Reading et al. 1996, Thomasma et al. 1991, USFWS 1980, 1981). The Index allowed ranking of all courses and a comparison to squirrel population levels. These attributes were grouped into 3 components according to the landscape feature they described: 1) vegetation, 2) ground cover, and 3) landscape position. Attributes were weighted according to the differences in their frequency between high and low cluster courses and their ranking in factor analysis. For each course, the sum of attribute weights was expressed as a fraction of the sum of weights for an ideal course. A score of 1 indicated that a course had all of the desirable characteristics; a score of 0 indicated that it had none. The geometric mean of the 3 component scores was taken as an overall LEI (Reading et al. 1996). Courses were then ranked according to the Index and compared to patterns of squirrel sightings, as indicated by the 5 levels of population (Van Horne 1983).

Habitat Use and Demography

Radio-telemetry.–A radio-telemetry study was conducted to gather data on home range, dispersal patterns, habitat use, feeding patterns and demography of two fox squirrel populations. Two sites were selected for the study, one without residential development, containing a high number of squirrels, and another, well developed, with lower numbers of squirrels. Criteria for selection required that the sites have: 18-hole courses with similar size fairways and roughs, prominence of open pine stands, a course configuration which allowed movement around the course throughout the day, absence of 3 highly invasive exotic tree species (*Casuarina* spp., *Schinus terebinthifolius*, and *Melaleuca quinquenervia*), squirrels that were not fed by golfers and therefore not tame, and the strong support of the course superintendent and the club greens committee for the research project. The last was especially important as the clubs would provide golf carts for 12-20 months of tracking endeavors and would support the regular presence of a non-member researcher and collared fox squirrels on their courses. Permission to work on Royal Poinciana Cypress Course was granted in November 1995 and that for Royal Palm in July 1996.

Trapping took place during 4 periods: Site 1 only, December 1995-March 1996; Sites 1 and 2, July-August 1996, November 1996-February 1997, and July 1997. Because of the public nature of the trap sites and the desire to decrease stress to individuals, especially females who might be pregnant or nursing, a trap line was not used. Instead, squirrels were trapped using a focused trapping method in which 1 or more traps were set for 1 or 2 specific individuals in a small area. One-ended Tomahawk #204 squirrel traps were baited with an oily, natural peanut butter and pecans. Traps were placed on the ground under trees where squirrels were feeding or resting or within 7 meters of individuals feeding on the ground. Often the traps were covered with Spanish moss or palm leaves. The traps were baited, set and covered with moss at some distance from the trap site and rapidly dropped off from a golf cart. Squirrels were acclimated to carts and would return to the place of feeding after I moved away from the trap. I watched the traps from 30-50 m. In the season of low food supply, squirrels could frequently be baited into the traps within 10 minutes to 1 hour. This method was generally successful during the winter months, when 2 or 3 individuals might be trapped and collared in a day. In the summer and autumn months, particularly in food-rich 1996, squirrels were extremely difficult to trap.

To ensure recapture and collar removal at the end of the study in July 1997, individuals were baited with oily peanut butter and pecans for 2 weeks prior to the trapping period as they were located during normal radio-tracking. Final trapping was further aided by an apparently lower pine and cypress productivity in 1997.

Trapped squirrels were covered and moved to the cart within 1 minute. Removal of the trap cover encouraged them to move into a dark cloth and net restriction tube which was attached to the opening end of the trap. While constrained in the bag they were weighed and given an injection of Ketamine HCl (100mg/ml) in the hip. Individuals 675-800 gms were given 0.25cc, those 800-1000 gms received 0.3cc. After 4 minutes or when they showed little sign of movement, they were removed from the bag and were tagged in both ears with monel sequentially number tags (size #3, National Band and Tag, Newport, KY), measured, aged, fitted with radio-transmitters and photographed. Females with darkened nipples of any size were considered adult. Males with developed testes descended into the scrotum were considered adult. Males with no obvious scrotum development or with slight development were considered subadult. There was a clear difference in the pelage and scrotal development between subadult males who had never developed sexually and adult males undergoing seasonal fluctuations of testicle development. Subadults had shorter, fine fur and no vestige of scrotal development. No animals under 5 months of age were captured.

Squirrels were released at the site of capture after spending 3-4 hours in a 60 x 30 x 30 cm ventilated wooden wake-up box. Rapid retrieval, covering of the trap and immediate anesthetization appeared to reduce trauma; no squirrels died during trapping or collaring procedures.

From December 1995 to mid 1996, 25 gm AVM (AVM Instrument Co., Livermore, CA) radio transmitters configured as resin pods with machine belting neck bands and 6 inch back antennae were used. This model proved unsatisfactory due to repeated transmitter failure, poor service and removal by squirrels cutting the belting. In late 1996, I began using ATS (Advanced Telemetry Systems, Inc., Isanti, MN) transmitters with resin pods, very fine stainless steel chain neck bands and back antennae, total weight of 28 gms. These worked extremely well, with no radio failure or removal by the squirrels. Final recapture did show that 2 individuals had slight neck abrasions.

Collared squirrels were located a minimum of 2 times a week, except when weather, golf course conditions or course use would not allow (Mech 1983). Individuals was located once a week in 2 of 3 daily tracking periods, 0630 to 1030, 1031 to 1430, and 1431 to 1900 EST. Squirrels were frequently located more than once in a sampling period; data were collected on each siting. Open vegetation and ready access to trees allowed visual sighting following radio location. When a squirrel was in a nest or concealed by heavy vegetation and visual sighting was not possible, I was able to identify the tree and the area of the tree in which the animal was located. When an animal moved to another golf course I used triangulation (White and Garrott 1990) to determine its location and then I traveled to the course for visual sighting and collection of activity data if possible. When a squirrel disappeared from the course and could not be located at a neighboring course, I searched the surrounding area in all directions. In December 1996, I conducted an aerial search of Collier County west of highway 951 in an attempt to locate squirrels that had disappeared.

Once an individual was sighted, its location was mapped on aerial photographs. Recorded data included: time, activity (3 points at 60 sec. intervals), nature of the site and location at the site, food type if feeding on identifiable material, reproductive condition if visible, number of squirrels present within 5 m (both fox and gray), and number of collared squirrels within 5 m. Records of temperature, dew point, sky condition, and wind were recorded at the start of each session.

At least once a month throughout the course of the study I took visual counts of fox squirrels at each study site. I followed the procedure outlined for the 60 course squirrel counts and in addition recorded if each sighted squirrel was collared or uncollared. These counts were used to estimate the fox squirrel population of the 2 study sites.

Vegetation Sampling.-The tree stands on three courses, Royal Poinciana Cypress and Pines and Royal Palm, were sampled and mapped to allow comparison of habitats used by the two radio collared populations. The Pines course was included in the vegetation sampling because it bordered site 1 on 2 sides and collared male squirrels frequently used the area. The large forested stands at the Poinciana courses were sampled using a structured pattern of 20 meter diameter circular plots placed at intervals of 25 meter from center to center on a north-south line and at intervals of 30 meters from center to center in an east-west line. This arrangement was designed for the most complete yet rapid sampling of the generally north-south tending forested areas. In the front 9 of the Pines course the pattern was oriented in an east west direction as the fairways in that section ran at right angles to the rest of the club. Within each plot, all trees over 10 cm dbh were identified and measured. All palms were counted. Presence of all saplings were recorded. Understory coverage was recorded as percentage and type and the ground cover was recorded as litter if over half of the plot had a significant layer of pine or pine and cypress litter. If not noted, ground cover was dominated by grass with occasional patches of bare soil.

In the narrow or small plots of Royal Poinciana and for the entire Royal Palm course, all the trees in each discrete plot were counted. If 10 or fewer of 1 species were counted, each tree was measured. If more than 10 of 1 species was found in a stand, 10 of the trees were measured. Saplings and ground cover were recorded as in the circular plots.

The Royal Palm site contained a large region of private lands belonging to condominium complexes and private homes. All pines and cabbage palms on the condo lands were counted and all trees on private lands on the 3 streets of private housing were counted.

Seven courses known to be used by the squirrels of the 2 study sites were evaluated using the method designed for the 60 course landscape evaluation portion of the study. This provided data on tree species present, identification of dominant species, types of ground cover, proportion of the course in tree stands, density of the understory and types of ground cover. The large pine stand south of the Cypress course and the developing landscape east of the Pines course were not accessible for sampling.

Data Analysis.- In January 1996, I conducted 10 repeat counts of fox squirrels on the Cypress course to estimate the reliability of my squirrel census technique. The counts followed the standard format presented in the landscape analysis methods section. Results of the 10 counts ranged from 8-16 with a mean of 12.4 and standard error of 0.79. Calculation of 95% confidence limits for a small sample gave a range of 10.6-14.2 squirrels (Fowler and Cohen 1992). Such a range was considered reliable for the populations with higher numbers of squirrels. Reliability in smaller populations was expected to be lower.

Survival and birth rates of collared fox squirrels were calculated on 6 month intervals, as opposed to 12 months, to allow for movement of subadults out of the sample population on the Cypress course or into the adult cohort of the sample population. Only squirrels persistent in the sample population were considered survivors. Squirrels no longer persistent in the sample population included subadults who dispersed to other locations, individuals who disappeared, adults, generally males, who no longer used the study site course but were known to remain on neighboring courses, and individuals known to be dead. Survival rates for adult females, adult males, subadult males and subadult females were calculated as the proportion of the collared squirrels remaining active in the study site at the end of a 6-month period. The birth rate was taken as the number of young known to leave the nest. The survival rate for juveniles was the proportion of the summer 1996 cohort of young known to be alive at the end of 6 months, 7 of whom were part of the collared population in 1997. Most subadults, collared at around 6 months of age, moved into the adult cohort at about 12 months of age.

Estimates of population size, the number of fox squirrels using the Cypress course, were taken from 13 counts of collared and uncollared fox squirrels on the course taken in the spring and summer of 1996 and spring of 1997. In late summer and fall 1996, counts were not taken because the number of collared squirrels had declined due to collar removal and squirrel sightings were extremely low during these months of concentrated feeding in pines. Procedure for the counts followed that presented in the initial description of fox squirrel censusing. From these counts I calculated the minimum know alive (MKA), the Lincoln Index, and the Bailey unbiased population estimator for small sample sizes (Bailey 1952, Krebs 1999.).

I used the RAMAS Ecolab software (version 2.0, Applied Biomathematics) to estimate growth rates in the Cypress population. Estimates of the 6-month survival and birth rates of life stages were used to construct the stage-based population projection matrix. I used birth rates from the lowest and highest 6 month periods and an average of the 3 periods to generate a range of growth rates seen during the study.

Tracking locations were digitized using Atlas GIS software, (Strategic Mapping, Inc., Santa Clara, CA), on an overlay of air photographs (TRW-REDI Property Data, 1996) registered to 7.5 minute topographic quadrangles. Accompanying data for each point were coded and attached to point locations using Atlas GIS software.

Home range was determined using the kernel method and CALHOME software (Kie et al. 1996, White and Garrott 1990, Worton 1989, 1995). Only 1 point per sampling period was used in home range analysis (Cresswell and Smith 1992). Points were selected randomly in cases where 2 or more points were recorded during 1 sampling period. The 95% contour was used to define the home range boundary of each individual and the 50% contour as the core area (Kenward 1992, Wray et al. 1992). I calculated separate home range data for year 1 (December 1995-October 31, 1996) and year 2 (November 1, 1996-July 30, 1997) to allow for changes in the make up of the population and in the make of the collared population. I used a two-tailed t-test for paired samples (α=0.05) to compare home range sizes of Site 1 females that appeared in both year 1 and year 2. I compared home range size of adult females to adult males in both years and 2nd year subadults from sites 1 and 2 using a Mann-Whitney test (α=0.05) (Fowler and Cohen 1990). The small number of adult females and adult males at Site 2 precluded statistical comparisons using those individuals.

Habitat maps were created from aerial photographs using Atlas GIS software. All vegetation sampling plots, including condominium areas, water features, residential areas and streets, and course fairways and non-forest roughs were outlined and the area of each type was measured. I calculated basal area, density, relative basal area, and relative density of each tree species by plot. Nine categories were defined to represent the diversity of vegetation seen on all 3 courses. Vegetation categories were defined by the relative basal area (percent of total dm^2/ha.) of pine, cypress, cabbage palm, and other native and exotic species. Tree stands were then categorized by density (stems/ha.). Plots with a pine needle litter layer or a shrub layer were identified and mapped as such.

Using Atlas GIS to analyze use of the vegetation types, tracking points were overlaid on maps of vegetation classes for each course. I compared actual use of vegetation types to that predicted by the percent area of each vegetation category. Chi-square tested (α=0.05) the hypothesis that tracking points were randomly distributed among vegetation categories.

Feeding patterns were examined by analyzing the tracking data in which the food item was clearly identified. All food types taken more than 5 times in the 19 months of feeding observations were considered. Changes in monthly feeding patterns were determined by calculating the percent monthly total of each species or food type consumed each month for the 19 months of feeding records. A diversity index of species use, the inverse Simpson (Krebs 1999, MacArthur 1972, Williams 1964), was used to measure both richness and evenness of use of the 13 food types.

RESULTS

Landscape Evaluation and Censusing

Squirrel counts.-I was able to sight fox squirrels at all courses that reported regular observations by course personnel. During the squirrel counts, 5 or fewer squirrels were seen at 48 (80%) of the 60 courses. Fourteen courses (23%) were level 1, with no squirrels seen during surveys and no sightings by course staff in the past year. Nine courses (15%) were level 2, with no squirrels sighted during the surveys, but course personnel reported occasional sightings in the past year. Reported sightings on these courses were frequently traveling squirrels or an occasional visiting squirrel or 2 from a higher level neighboring course. Level 3, 1-5 sightings, was the largest category with 25 courses, 42% of the total. I sighted 6 or more squirrels on only 12 courses: 6 courses (10%) were level 4, 6-10 squirrels, and 6 were level 5, with more than 10 squirrels seen.

Course attributes.-Cluster analysis of the 60 courses with 51 attributes produced a dendrogram with a prominent cluster of 11 courses and a broader cluster of 18 courses (Fig. 6). The 11 course cluster, cluster 1, contained courses with a high occurrence of attributes favorable to fox squirrels and the 18 course cluster, cluster 2, contained courses with a higher level of landscape attributes unfavorable to fox squirrels.

Chi square tests of the 51 attributes showed that 20 attributes were non-randomly distributed between the 2 clusters. Courses in cluster 1 were characterized by: large patches of pine and cypress trees, open understories in the tree stands, large areas of pine litter, having adjoining courses, being part of a multi-course club, and having at least 50 acres of adjoining forest. Cluster 2 courses were characterized by: a high degree of isolation, few or no sizable tree stands, low numbers of pine and cypress, no obvious dominant tree species, heavy development and busy roadways around the course (Table 1).

Factor analysis produced 2 independent factors or groups of attributes explaining 27% of the variation among the courses. Factor 1 accounted for 14.6% of the variance and factor 2 for 12.3%. Factor 1 describes variation similar to that seen in cluster analysis, large stands of open forest on larger, grouped courses vs well developed, isolated, courses with more sparse tree cover and few native species. Thirteen attributes contributing to factor 1 were the same as those showing non-random distribution between clusters in the previous analysis (Table 1). Factor 2 is a comparison of "natural" courses with a heavy understory to courses with clear understory and the presence of planted exotic trees. Eight attributes contributed to the variation explained by factor 2 (Table 1).

While cluster and factor analysis were quite useful in identifying characteristics that distinguished high and low quality courses in this study, it must be noted that they do not provide a complete listing of all features which are either beneficial or harmful to squirrel survival. Attributes such as untrimmed cabbage palms, while helpful to fox squirrels were found on over half of the courses and occurred in all types of landscapes. Similarly, known predators such as domestic cats and raptors were found throughout the range of course landscapes. For this reason they did not appear as distinguishing attributes of high or low clusters. The list of distinguishing characters must not be confused with a more complete listing of characters favorable or unfavorable to fox squirrels.

Landscape Evaluation Index.-The Landscape Evaluation Index was calculated using 28 attributes, 16 in the vegetation component, 3 describing ground cover, and 10 relating to landscape position (Table 1). The 60 courses ranged from 0.0 to 0.987 on the scale of 0.0 to 1.0 (Appendix B, Fig. 7)). Seven courses were over 0.90, 18 from 0.50 to 0.751, and 35 were below 0.50. There was a gap with no courses from 0.90 to 0.752. Examination of the landscape configuration of the courses shows that the 7 courses above 0.90 are either undeveloped or have a perimeter development plan for each course or for the entire club (Fig.8). Courses with a LEI of 0.75 or lower generally have more complex development plans such as the shown in levels B and C in Figure 8. These require squirrels to cross streets or travel through or around larger forest stands with dense understory vegetation to move from one portion of the course to another.

Index values were strongly correlated with squirrel levels ($r = 0.747$, $p << 0.01$). In Figure 7 courses that adjoin high level courses, but do not themselves have an index value over 0.90, are identified as Neighbors. Three such courses have level 4 populations, though their index values would indicate a lower capacity, and 4 of the level 3 courses have higher populations than expected. Four of the level 1 courses have moderate LEI ratings, yet no squirrels. These courses are newer, developing courses at which the large forested areas have heavy, closed understory vegetation not favorable to fox squirrels.

Demographics and Habitat Use

Radio-telemetry produced 2497 tracking points and accompanying records on 29 individuals at site 1 between December 1995 and July 1997, and 254 sightings at site 2 between January and July 1997. These data were used to examine population structure, size and location of home ranges (Appendix C), nesting sites, habitat use, and feeding patterns.

Survival.- Eighteen fox squirrels were collared at site 1 in the first year, 9 males and 9 females. In the second year, 11 more individuals were added to the study, 4 females and 7 males. Adult male fox squirrels had lower average survival rates than adult females (Table 2). Three individuals were known dead or moved to a neighboring course as adults. Four individuals disappeared from the population and were not located again on the Cypress course or on neighboring courses.

Adult females had an average 6 month survival of 0.87, the highest rate at site 1. Two adult females disappeared in the fall of 1997. One had a home range between 2 aggressive females and was regularly chased by each. It is possible this female moved west into the Hole in the Wall and

Wilderness area, though she was never seen on the courses. The second female disappeared on the same day her collar was found at the base of a tree near a busy cart path.

At 0.78 the survival of subadult males was higher than adult males and subadult females (Table 2). The immediate fate of all subadult males was known. In the first year of study, 3 of the 4 remained on the course and moved into the adult cohort, and the fourth dispersed to Bear's Paw course and later disappeared. In 1997, 3 of 4 subadult males survived to the end of the study and stayed on the course. The fourth died while infected with skin fungus.

Subadult females showed the greatest change in survival rates from one season to another (Table 2). In winter/spring 1996, 3 of the 5 subadult females dispersed from the course, for a 6 month survival rate of 0.40. Two of these were found dead on other courses, 1 within the summer and the other within the year. The third dispersing female disappeared from a developed neighboring course. In winter/spring 1997, the 3 collared subadult females remained on the course in their natal home ranges though the end of the study. At that time they ranged in age from 11 to 13 months. None had reproduced though 1 was known to be the object of a mating chase.

There was no new subadult cohort, male or female, in the summer 1996. All collared subadults from the winter had dispersed or would disperse in early August, or they entered the adult cohort. Trapping difficulties in the summer 1996 meant than no subadults from winter litters could be collared.

The survival data for Royal Palm, site 2, covered a shorter period of time, only 7 months (Table 3). Four adults were collared, 2 males and 2 females. All remained alive throughout the study. Four subadults were collared, 2 male and 2 females. None remained on the course at the end of 6 months. One male disappeared shortly after collaring. Both females died: 1 following a severe infestation of skin fungus, the other after being hit by a vehicle on Augusta Boulevard. The surviving subadult male moved from the course through a series of progressively more distant feeding sites. At the end of the study he was living near a feeder on the edge of Hibiscus course along highway 41.

Reproduction.- Reproduction at site 1 varied widely between seasons and between individuals (Table 2). Winter reproduction was lower in 1995-1996 and 1996-1997 than the summer/fall of 1996, with only 4 and 3 young known to leave the nest in the 2 cooler seasons. The 6 month rate of reproduction for the first winter season was 1.00/adult female, in the second winter season it was 0.60/adult female. Winter young were born in December through February, emerging from the nest in January through April. The summer of 1996 was one of high reproduction. Five of the 6 adult females produced evident young, with 2-4 young seen emerging from each 5 nest, for a total known reproductive output of 15, a rate of 2.50/adult female for the 6 months. Warm season young were born from early July to September and emerged form the nests between August and late October. Mating chases were recorded in April though July and in October.

Neither female at site 2, Royal Palm, produced young from a nest during the course of the study. One female was obviously pregnant at the time of collaring and appeared to tend a brood nest for a few weeks. She failed to show signs of long-term nursing and no young emerged from the nest. She appeared to be tending a brood nest when her collar was removed, as did the other female in the study. The surviving subadult male in the study was the offspring of one of the collared adult females, undoubtedly born in the summer of 1996. At the time of his collaring, he and another subadult regularly accompanied her. Though reproduction was not observed in collared animals during the study, some adult females were successfully reproducing at site 2, though apparently at a lower rate than site 1.

Mortality and Disease.-Known causes of death in the collared populations of sites 1 and 2 were: automobiles (2), skin fungus infection (2), and electrocution (1). Three subadult uncollared fox squirrels at site 1 also died from vehicle accidents, 1 from a car on the entrance road and 2 from golf carts on the course. Of the 5 squirrels known to be killed by cars or carts at the study sites, only 1 remained at the site of impact. The others moved away, sometimes several meters, before they died.

Skin fungus (Dr. Sharon Taylor, person. commun.), causing heavy fur loss and blackened crusting of the skin, was apparent in both populations in 1997, affecting at least 8 collared individuals. One subadult died at each site. It affected primarily subadults, though also was seen in 2 adults. The proportion of affected individuals appeared similar in collared and uncollared squirrels. One uncollared subadult died at site 1 within a month of the collared individual. The fur loss and darkened skin was observed in squirrels at courses adjacent to the study sites prior to 1997. It was easily transmitted by contact and feeding areas appeared to be vectors, especially when squirrels fed from a concentrated food supply. At least 3 squirrels with severe fur loss and skin damage were seen sharing a feeder at CCN. The 4 collared individuals who survived the spring 1997 skin fungus infestation regained a thick, healthy coat in the late spring molt.

Information on predation is slight. A bobcat was seen killing a ground feeding, uncollared fox squirrel at site 1 in 1997 (A. Grieser, person. commun.). At least 1 female bobcat and 2 young were regularly seen in the forest areas adjacent to Poinciana on the east and west. The adult bobcat began frequenting Poinciana in daylight hours when the area immediately east of the course was being cleared for development in 1997. There is no evidence of raptor kills on the study sites, though I did find apparent raptor-killed fox squirrels at 2 other nearby courses.

Population estimates.-Estimates of population size, derived from repeat squirrel counts at the study sites, are presented in Table 4. Range of minimum number alive (MNA) at site 1 is 15-26. The Lincoln estimates range from 15.9-32.5 and the Bailey estimate for small samples is 15.6-30.5. Counts in July were understandably lower as a number of subadults had dispersed from the course

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and young of the season would not emerge from nests until early fall. At site 2, the MNA range is 3-8, the Lincoln estimates range from 8.3 to 15, and the Bailey unbiased estimates are lower at 7.5 to 11.7.

RAMAS Ecolab software (2.0, Applied Biomathematics) using the site 1 winter/spring 1997 reproductive rate of 0.23 young/adult for 6 months, lowest of the 3 periods, calculated an annual growth rate (λ) of 0.803. Use of the summer/fall 1996 reproductive rate of 1.25 young/adult gave an annual growth rate of 1.39. The average birth rate/adult for the 3 periods of study, 0.67, yielded an annual growth rate of 1.10.

Home range.-At site 1, in the first year of study, adult female home range size varied from 7.98 to 12.00 ha ($\bar{x}$=10.10 ha) (Table 5). Home ranges of the 6 adult females cover the study site (Fig. 9) from the north end to the southern border. No other adult females were observed to make exclusive use of the course during the first year of study. A light color female occasionally fed in the northeast section of the study site, though the core area of her home range was east of the study site in the Pines course. Of the 431 tracking locations recorded for the females between December 1995 and November 1996, only 10 were outside of the course boundaries, all but 2 of these 10 remained within the boundaries of the Poinciana. Females did not range into neighboring pine or cypress stands and only #06 crossed the entrance roadway on the club grounds to feed in a large ficus immediately north of the road. All adult females showed some home range overlap with other adult females, though none showed range overlap with more than 2 other adult females.

In summer/fall 1996 all females maintained a brood nest in a location within a core area outside the home ranges of all other adult females. In the first few weeks the of summer brood nest occupancy females stayed in the nest most of the day and greatly reduced the area in which they fed (Table 6). Placement of the nest within a small mixed stand often allowed them to feed without moving to the ground. A similar pattern of reduced movement and isolation was not observed during the winter brood nesting period.

Adult males at site 1, year 1, had home ranges of 42.52 ha to 118.40 ha ($\bar{x}$ = 70.84 ha) (Table 5), significantly larger than those of the adult females (Mann-Whitney U=0, $p<0.05$). The home ranges of all 4 adult males overlapped in the center of the study site (Fig 10). Other adult males were regularly seen on the course. ROPO 04 and ROPO 07 used the Cypress course almost exclusively, while ROPO 16 used all of the Cypress course and the adjoining back nine of the Pines course on the east. ROPO 17 used portions of 4 courses, the Cypress, Pines, Hole in the Wall, and the Country Club of Naples to the west. Though ROPO 17 used the open edges of large forested stands within and between courses, he was never found in the interior of these stands. He did not need to cross the roadway to move from CCN to HIW and was regularly observed moving to HIW by crossing the canal between the Cypress course and HIW by way of a natural tree bridge on the west side of fairway 2. These tree routes were frequently used by several individuals in moving between these 6 neighboring courses separated by canals.

Home ranges of the 6 collared subadults at site 1, year 1 (Table 5, Fig. 11), ranged from 10.66 ha to 49.07 ha ($\bar{x}$ = 22.16 ha). ROPO 13, a male, began making long day trips to the back nine of the Poinciana Pines course in the month prior to his dispersal. His large home range, twice as large as the mean and the next largest subadult home range, reflects these trips. The 4 subadults in the southern half of the study site show a strong overlap (Fig. 1), with all four commonly using forested areas along the 7th and 13th fairways. Three of these 4 dispersed to other courses between March and August 1996. The fourth stayed on the Cypress course until the end of the study.

ROPO 10, a subadult female, dispersed from the southern section of site 1 to Poinciana Pines at the end of March 1996 and in early April moved to the CCN (Fig. 13). Her initial movement to the front nine of the Pines course was 1.4 km with an additional 0.85 km to CCN. She also frequented a home feeder at point B and crossed Burning Tree Drive regularly. She slipped her collar in June 1996 and was seen only once again. She was not seen in subsequent searches.

ROPO 14, a subadult female, dispersed from the northeast section of site 1 in late April 1996 (Fig. 14), moving to Bear's Paw Country Club. Her dispersal distance from her site 1 to her first sighting at BP was 2.8 km. She occasionally fed on scraps put out at site A, with the remaining tracking sites at the edges of heavy forest on the northeast edge of the course. In July she was limping badly (L. Molden, person. commun.) and was found dead in dense undergrowth on July 24, 1996. At least 1 large cat regularly roamed the small area where she was found.

In mid-May 1996, ROPO 09, a subadult female, moved from the center of site 1 to the eastern end of the Quail Run Golf Course (Fig. 15), a heavily developed course with few tree stands, a dense street network and heavy traffic. By the end of June 1996, ROPO 09 had moved to the CCN where she often fed at a home feeder station used by 2 or 3 other fox squirrels, at least 2 of which had severe fur loss with accompanying thick, dark skin, probably related to a skin fungus. By August, ROPO 09 was suffering from a similar fur loss when she was tracked to the center of the HIW. She returned to site 1, Cypress course, for a brief period in September 1997. Regular contact was lost in early fall due to collar failure. She continued to use the HIW and the south end of the CCN, where she frequently crossed roadways in her daily movements. She was found dead at the side of the road at the entrance to CNN in April 1997. Her initial dispersal distance was 2.6 km and the total distance moved from the original home range to HIW was 6.0 km.

ROPO 13, a subadult male, dispersed from the southern section of site 1 to Bear's Paw Country Club in August 1996 (Fig. 16). On August 8, 1996, he moved from the south border of site 1 to Golden Gate Parkway, through 1.2 km of pine forest. The following morning he crossed the busy 4 lane roadway into BP, where he was tracked until mid August 1996. His initial 24 hour dispersal distance was 1.9 km; his total movement distance from his original home range was 3.5 km.

At site 1, year 2, the home ranges of the 5 adult females varied from 9.08 ha to 20.92 ha ($\bar{x}$=16.40) (Fig. 17). The 4 adult females collared from the previous year, showed significant increases in home range size (Table 5) (t=3.95, P=0.029, df=3) though each female continued to use approximately the same section of the course. ROPO 03 and ROPO 05 increased use of the edges of large forest stands on the eastern edge of HIW and ROPO 15 used open edges of forested roughs at Wilderness Country Club and a feeder area on private property adjoining the southeast corner of site 1. ROPO 03 expanded to the north into the previous home range of ROPO 06, who disappeared in December 1996. Core areas of ROPO 03, ROPO 05, and ROPO 15 showed increases from year 1 to year 2. ROPO 15 and ROPO 28 had high overlap, though location of core areas indicated that ROPO 28 made heaviest use of the southeast portion of the course and ROPO 15 the southwest corner of the corner.

Only ROPO 03 was tending a summer brood nest when the study ended in July 1997. The second year home range of ROPO 05, a female, had expanded to include the fall 1996 brood nest site of ROPO 03. ROPO 03 moved her 1997 summer brood nest to the north, into a tree stand formerly within the home range of ROPO 06, an adult female.

The 6 adult males of site 1, year 2, used portions of 5 courses (Figs. 18 & 19). Home range size varied from 44.06 ha to 121.00 ha ($\bar{x}$ = 90.91 ha) (Table 5), significantly larger than adult female home ranges in the second year (Mann-Whitney U=0, $p<0.05$). All of the males used at least some part of 2 or more courses and did so with little crossing of roadways. ROPO 20 used much of the Cypress course, visited the front and back sections of the Pines course and frequently moved into Hole in the Wall. ROPO 18 rarely visited the Cypress course, spending most of his time in the northern section of the Pines course and the CCN. ROPO 07 and ROPO 08 used the Cypress course and both sections of the Pines course. ROPO 08 and ROPO 20 had the smallest home ranges, each using portions of the Cypress course and the back nine of the Pines course. Males again showed strong overlap of home ranges.

Seven subadults at site 1, year 2, had home ranges of 5.88 ha to 21.47 ha ($\bar{x}$=14.93) (Figs. 20 & 21). All subadults show overlap with at least 3 other subadults. None of the subadults dispersed before the end of tracking in July 1997, though ROPO 21, a male, began to use the northeast corner of Wilderness Country Club to feed in June and July 1997.

Five of the subadults at site 1, year 2, were born to adult females ROPO 02, ROPO 03, and ROPO 05 who remained on the course in the same home range areas throughout the study. Figures 22 and 23 compare the 1997 spring/summer home ranges of the collared offspring to the 1997 home ranges of their mothers. The female offspring of ROPO 02 and ROPO 03 had home ranges entirely contained within those of their mothers, while the male offspring of ROPO 03 and ROPO 05 had home ranges that extended beyond those of their mothers. The overlap of the subadult home ranges with the core area of their mother, ROPO 05, is clear (Fig. 23).

Adult female ROPO 01 disappeared in December 1996 and offers no comparison with her 1997 home range area with those of her offspring, ROPO 21 and ROPO 24 . Nevertheless, it is clear that her 1996 offspring, male ROPO 21 and female ROPO 24, continued to use their natal home range, the core area of female ROPO 01 before her disappearance (Fig. 24). ROPO 24 expanded to the northeast in her mothers absence and ROPO 21 expanded to the south and west.

All 7 of the subadults continued to use their natal homeranges for the first year of their lives, 5 sharing with their mothers, 2 remaining after their mother disappeared.

Seven of the 8 squirrels collared at site 2 in year 2 remained to provide usable home range data. ROPA 01 and ROPA 08, adult males, had home ranges of 136.1 ha and 303.8 ha, respectively (Table 5). ROPA 01 used most of site 2, Royal Palm, while ROPA 08 used site 2 and most of the neighboring Hibiscus Country Club (Fig. 25). ROPA 08 readily moved from the east to the west end of his home range, a distance of 2.5 km, within 24 hours. Both males regularly crossed Augusta Boulevard, while their movements on either side of that busy street generally followed the fairways and appeared to minimize travel through housing. Though their home ranges overlapped, they were never seen together as males at site 1 often were.

The two adult females at site 2 had home ranges of 13.06 ha and 30.57 ha (Table 5, Fig. 26). Adult female ROPA 04 had a home range 50% larger than any at site 1. She often crossed Augusta Boulevard. Adult female ROPA 06 had a home range similar in size to those at site 1. Her home range included a regularly stocked feeder at a private residence. On rare occasions she crossed into the central pine stand within the private housing area. Though the home ranges of these 2 adult females were widely separated, no other adult females where ever observed in the area between their 2 home ranges.

Three of the 4 collared subadults at site 2 provided data on home range size, these varied from 25.77 ha to 108.50 ha ($\bar{x} = 58.34$ ha) (Table 5, Fig. 27), significantly larger than site 1 subadults for the same period (Mann-Whitney $U=0$, $p<0.05$). Male ROPA 02 was an older subadult who disappeared within a month of being collared and provides no usable home range. Female ROPA 03 used an area on both sides of Augusta Boulevard and across Forest Hills Boulevard into the Hibiscus course. Female ROPA 05 used an area on both sides of Palmetto Dunes Circle. Male ROPA 07, summer 1996 offspring of adult female ROPA 06, had an unusual home range use pattern, sequential use of small patches. He spent a few weeks to a month in a small area of a hectare or less and then moved to another area, each time moving away from his natal home range at the northwest corner of site 2. In the final week before his collar was removed he had moved to the west side of Hibiscus Country Club along U. S. 41, 1.2 km from his natal home range.

Nest Sites.-At site 1 fox squirrels made regular use of untrimmed or lightly trimmed cabbage palms, bromeliads and cypress cavities for sleeping nests. Stick nests were used on occasion. The common use of untrimmed palms and bromeliads as nests eliminated the possibility of counting nests and determining the nest to squirrel ratio. Squirrels were regularly observed carrying Spanish moss (*Tillandsia usneoides*) to nesting sites. Squirrels rarely constructed open platform nests for daytime resting but simply draped themselves along branches to rest.

Brood nests were readily observed at site 1 in summer 1996 as females seldom moved from the nests for 2 -3 weeks. Nests were located in mixed stands of pine, untrimmmed or lightly trimmed palms, and cypress (Fig. 9). Three females used cavities high in large cypress trees, 1 raised a litter of 4 from such a cavity, another a litter of 3. Two females raised young in the center of densely leafed palms, one a queen palm (*Arecastrum romanzoffianum*) and the other a cabbage palm. The remaining female used a large bromeliad high in a large pine for her nest site. The nest was located in the base of the large plant. All females used Spanish moss in constructing and maintaining nests. The queen palm nest also contained shredded queen palm leaflets and required her to spend time stripping leaflets and tearing them into strips. Winter brood nests were similar to those in the summer of 1996 and included 2 in cypress cavities, 2 bromeliad nests, and 1 palm nest.

As the study ended at site 2, both adult females appeared to be tending brood nests. One was in a rather isolated moderately trimmed cabbage palm near a canal and the other was in a stick nest in a moderate-sized pine tree. In the winter of 1997, the same female was observed using a wood duck box with her offspring from the previous summer. All 3 nested together in the box during times of heavy rain, cooler nights, or high wind.

Landscape Composition and Vegetation Mapping.- Landscape composition of sites 1 and 2 and the Poinciana Pines course is presented in Table 7. While site 2 was 2.3 times larger than site 1, the golf course and tree stands within the roughs of the 2 courses were similar in size, though not necessarily similar in species composition or structure. The obvious difference in landscape composition between the 2 sites was the presence of housing areas at site 2. Twenty-eight percent of site 2 was occupied by residential development, streets and clubhouse property, and an additional 25% was condominium land and a private pine stand within a housing area. The 2 courses which comprised Royal Poinciana Golf Club, site 1 and the adjoining Pines course, were similar to one another in general landscape composition. The smaller area of tree stands in the Pines course reflected the open nature of the back 9 of that course and the presence of 2 driving ranges within the course.

While site 1 and 2 and the Pines course each had between 30.0 and 24.8 ha of tree stands or forested area, the species composition and structure of these plots were not alike. Site 1 sampling plots contained a greater diversity of tree species than site 2 plots. (Table 8, Fig. 28,29). A mixture of native hardwoods, pine, cabbage palm, and cypress, dominated site 1. Though site 1 was high in native hardwoods, there were no class 1, pine dominant, stands. Pines were found as co-dominants with cabbage palm (11%), cypress (3%), or both (10%). Cypress was dominant in 14% of the forested area and was co-dominate with pines and/or cabbage palms in an additional 31% of the area. Palm dominant stands accounted for 8% of the area in tree stands. At site 1, 64% of the tree stands were dominated by the pines, cypress and cabbage palms. A mixture of native species, often including oaks (*Quercus virginianum, Q. laurifolia*) , maple (*Acer rubrum*), red bay (*Persea* *borbonia*) made up another 10% of the forested landscape. While native species dominated the landscape, the importance of exotic species on the Cypress course was seen in the extent of class 9 (mixed natives with exotics), which covered 26% of the forested area.

Site 2 was dominated by pine, with 68% of the plot area in class 1(pine dominant) and an additional 6% with pines as co-dominants (Table 8, Fig. 29). Cypress was a minor element of the site 2 vegetation, dominating in only 2% of the area. Classes 6 and 7 of the mixed natives were not present at site 2. Exotics were less common than at site 1, with class 9 (mixed natives with exotics) accounting for 11% of the area.

The Pines course had a high presence of exotic species, with 51% of the tree stand area in class 9, and a much lower area dominated by a mixture of pines, cypress and cabbage palms (Table 8, Fig. 30). Pine dominated stands (class 1) accounted for 12% of the forested area and pine/cabbage palm for an additional 10%. Cypress dominated 14% of the area. Classes 5, 6 and 7, mixtures of pine cypress and cabbage palm, were absent from the Pines course.

Structure of the trees stands on the 3 courses also differed from course to course (Table 9, Figs. 28-30). Site 1 had a higher density of trees than site 2, with 24.9 ha of forested area having more than 100 stems/ha and only 5.2 ha in lower density stands. Site 2 had a much more open landscape, with 17.9 ha of low density (< 100 stems/ha) and only 8.4 ha in high and medium levels. The Pines course was a mixed course, with a dense forested front 9 on the north and an open back 9 on the south.

The presence of a litter ground cover, as opposed to grass or bare soil, and the presence of a shrub layer are noted in Figures 28-30. Site 2 had 4 plots with a significant litter layer. All were in pine dominated stands, only 1 with a high tree density. Site 1 had 8 plots with heavy litter layers, 5 of these plots had high tree density and all of these stands were dominated by a mixture of native pine, cypress or cabbage palms. Four plots at the south end of site 1 had a shrub layer, with wax myrtle (*Myrica cerifera*) the most common understory species. The Pines course had 7 plots with a litter layer and 5 of these had high tree density. The more open back nine of the Pines contained 2 large plots with heavy litter layers and high to medium density of trees.

The condominium areas and private forest stand at site 2 were dominated by pines, though tree density varied widely with the number of buildings and parking lots in each plot (Fig. 29). Most condominium plots had low pine densities, with 19.8 ha in the range of 30-99 stems/ha and 5.6 ha at < 30 stems/ha. High density pine forests (>200 stems/ha) were found in 4 plots totaling 4.5 ha and 2 plots totaling 4.0 ha had moderate densities (100-200 stems/ha). The 6 undeveloped private home vacant lots bordering the course in the summer of 1997 had dense stands of pine with scattered cabbage palms. The developed lots which circled the course on all but Augusta Boulevard had a very low density of trees, with 3 or fewer trees in most lots. Pine and queen palms (*Arecastrum romanzoffianum*) were the most common species, and black olive (*Bucida buceras*), cabbage palms, oaks and bottle brush (*Callistemon rigidus*) were scattered throughout the lots of private residences.

Habitat Use.- Locations of 2138 of the 2497 tracking points of the site 1 collared population were used to examine habitat preference on the Royal Poinciana Cypress and Pines courses. The 359 points not used were located either on neighboring courses, fairways or unforested roughs. Comparison of the aggregated area of all plots in each of the 9 vegetation classes and the number of points located within the boundaries of each class shows a non-random use of forested areas (Table 10, Fig. 31). On the Cypress course, all subsets of the population showed non-random use of the forested stands. In all cases, fox squirrels had higher than expected use of class 2 plots pine/cabbage palm co-dominated stands While class 2 plots were 11% of the forested area, they accounted for

18% of the tracking locations for females and 28% for males. A preference for class 2 plots was shown in both years of the study.

Site 1 fox squirrels showed consistent underuse of cabbage palm dominated plots, cypress dominated stands and plots of mixed natives. Females showed a preference for pine/cypress dominated plots, as well as pine/cypress/cabbage palm stands and cypress/cabbage palm forested areas (Fig. 31). Males underused or showed expected use of all vegetation types other than the pine/cabbage palm plots.

On the Pines course the aggregation of all tracking points within the tree stands shows a preference for pine plots, mixed natives and natives with exotics. Both cabbage palm plots and cypress stands were underused (Fig. 32). Females used the Pines course so rarely, only 24 points in the 2 years of the study, that they were not examined separately for patterns of use. The summer subsets were similarly small and not separately analyzed. In the first year of the study, fox squirrel use of tree stands at the Pines course indicated no significant departure from expected (Table 10).

The mixture of golf course property with private and condominium property at site 2 created a more complex landscape than seen at site 1. Analysis of the 147 tracking locations within the 26.0 hectares of tree stands on the Royal Palm property showed that squirrels used the vegetation classes in proportion to their abundance on the landscape (X^2=12.22, df=6, p=0.058). Pine plots account for 68% of the forest stands and contained 65% of the analyzed tracking points. Class 9, mixed natives with exotics, and class 3, cabbage palm dominated stands, had slightly higher than expected use. The 34.9 ha of condominium property and the private pine forest inside the back 9 of the course had only 34 tracking points. Nineteen of these were in the 1.4 ha private pine forest which contained at least 3, well-stocked feeders. The 40.1 ha of residential property accounted for only 17 tracking location, 10 at feeders.

Feeding Patterns.-Feeding data from site 1 show seasonal shifts between native and non-native food sources (Table 11). Native foods, pine, cypress, and oaks, made up over 70% of the diet from August 1996 through January 1997. In March through July of 1996 and 1997, non-natives were the primary food source. February, June, and July of the 2 years showed a changing mixture of native and non-native sources.

In 1996 squirrels began to feed on new, green pine cones in late June and early July. By August cones were mature and pine became the dominant food, with squirrels feeding alone or in small groups in or around select trees for several hours at a time. This also began the season of burying cones, in grass, litter and sand traps. Squirrels were observed burying in their core areas and at the edges of their home ranges. In December and January, cypress cones increased in importance, as pines decreased. Cypress constituted 20% or more of the diet for 7 months, July 1996 through January 1997. Despite the tent caterpillar infestation of 1997, cypress were again accounting for 29% of the diet in June and July of that year. Feeding on early pine cones began in June and July 1997.

Oaks were not a regular food source in 1996 until September, when oak feeding, primarily live oak, accounted for 30% of the diet. Fox squirrels continued to feed lightly on oaks through April 1997.

In both 1996 and 1997 fox squirrels took advantage of the bright red samara of the red maples for concentrated feeding in January and February. Late winter and spring feeding on natives was scattered. In April and May of both years squirrels fed on old pine cones, most often digging them up, but occasionally removing them from the tree. Cypress remained a minor element in the diet in all winter and spring month of 1996 and 1997, except February 1996.

Fox squirrels fed on large hypogeous fungi from February through October. While they fed on both the mycelia and the fruiting bodies, the most readily observed behavior was feeding on the large fruiting bodies. The peak season for observation of fungi feeding varied slightly, June and July in 1996 and May and June 1997. Fungi feeding was concentrated in patches which had deep litter layers, generally beneath pine and cabbage palm, but also in stands of cypress and pine. Of the 111 fungi feeding observations at 53 tracking points, 86% were in litter, 9% in grass, and 5% in trees. A squirrel might carry a fruiting body up a tree, where he would hang upside down and eat. All tree sightings were in litter areas. In peak season, I recorded periods of concentrated feeding when a squirrel would eat the large caps (5-8 cm) of 4-5 fruiting bodies within 10 minutes.

In May and June 1997 squirrels fed on concentrated patches of sawfly larva (Baker 1972) buried in soil, grass or litter. They bit the tip from the cases and pulled the small caterpillars out with their teeth. During the same period they showed no interest in the tent caterpillars which rained to the ground from the infested cypress trees.

In both 1996 and 1997, March through May were periods of concentrated feeding on non-natives. In March 1996 to June of that year, over 40% of recorded feeding was on bischofia (*Bischofia javanica*), an Asian species which forms clusters of small, dark berries. Squirrels initially fed in trees and then moved to ground feeding, where they gathered in groups of 2-8 to feed on the fallen fruit. Four large bischofia trees on the Cypress course drew squirrels in mid morning and late afternoon feeding groups. In 1997, levels of bischofia feeding were lower, with peaks in February through April in the 20-30% range.

Bottlebrush trees, native to Australia, drew squirrels to feed on their spikes of scarlet flowers in March and April of both years. Silk oaks (*Grevillea robusta*), another Australian native, with their orange-fringed flowers, also attracted fox squirrels for flower feeding. In 1996 the peak feeding was late April and May, in 1997, late March and April.

Queen palm, common throughout Royal Poinciana, produce a bright orange, aromatic, 2 cm oval fruit. A squirrel feeding on the fruit makes a distinctive, loud grating sound, whether hanging from clusters of new fruits or digging up a previously buried specimen. Queen palm feeding was high in February of both years and moderate in April and July of 1996 and May of 1997. Squirrels regularly buried queen palm fruits and most of the spring 1997 records are squirrels feeding on fruit they dug up. Heavy trimming of palms in the fall and winter of 1996-97, removed most of the available fresh crop. Regrowth and new fruits did not appear until summer of 1997.

Ten large ficus trees (*Ficus spp.*) dotted the Cypress course and stands of large ficus were common at Hole in the Wall. These drew squirrels for feeding from January through August. A variety of species with staggered fruiting times produced the most concentrated feeding in May through July.

Fruit of the tallow tree (*Sapium sebiferum*) and Java plum (*Syzigium cumini*) trees were feeding sites for short seasons. Tallow tree provided feeding in January and February and Java plum in June and July. Feeding on Java plum was high in July 1997 as the study ended, as squirrels gathered in 4 stands which produced aromatic crops of fruit on the Cypress course.

The 1996 fall feeding on native species was the period with the lowest food diversity. In both years, diversity was higher in February through July. Diversity was noticeably higher in 1997, February to April and June, when a broader range of non-native species and a greater use of native species were seen in the feeding records. This difference was not only a result of changes in who was collared, but was reflected in the expanded diets of individuals collared both seasons. While 4 squirrels showed concentrated bischofia feeding in spring 1996 (8-23 observations), none of these repeated the pattern in 1997. All increased the number of species they used. Only 1 individual, subadult 27, showed concentrated bischofia feeding in spring 1997 and she regularly fed on the 2 large bischofia trees near her birth tree. Her mother, #02, fed on at least 10 species each spring.

The feeding data at site 2, covering January to July 1997, were aggregated due to low numbers (Table 12). Feeding on non-natives was dominant, as it was in the late winter and spring at site 1. Native foods included pines, larvae and mushrooms. Pine feeding, 16% of total, was primarily cones from previous seasons. Larvae of the same species as site 1 and mushrooms accounted for an additional 16% of feeding records. Cypress were a minor element of the diet and not common at site 2 or neighboring courses. Sixty-seven percent of the recorded feeding was on non-native sources, while 33% of the sightings were squirrels feeding at feeders. Ten feeders were available to fox squirrels, whether placed there for their use or for birds. Eight of the feeders were on Royal Palm property or adjoining residential property, 2 were on the west side of the neighboring Hibiscus course (Figure 25). Bottlebrush trees and queen palms provided feeding opportunities at Royal Palm, while Java plums and ficus were grouped in a small area of the Hibiscus course. Only ROPA 08 was seen begging, and that, successfully, at the public Hibiscus course.

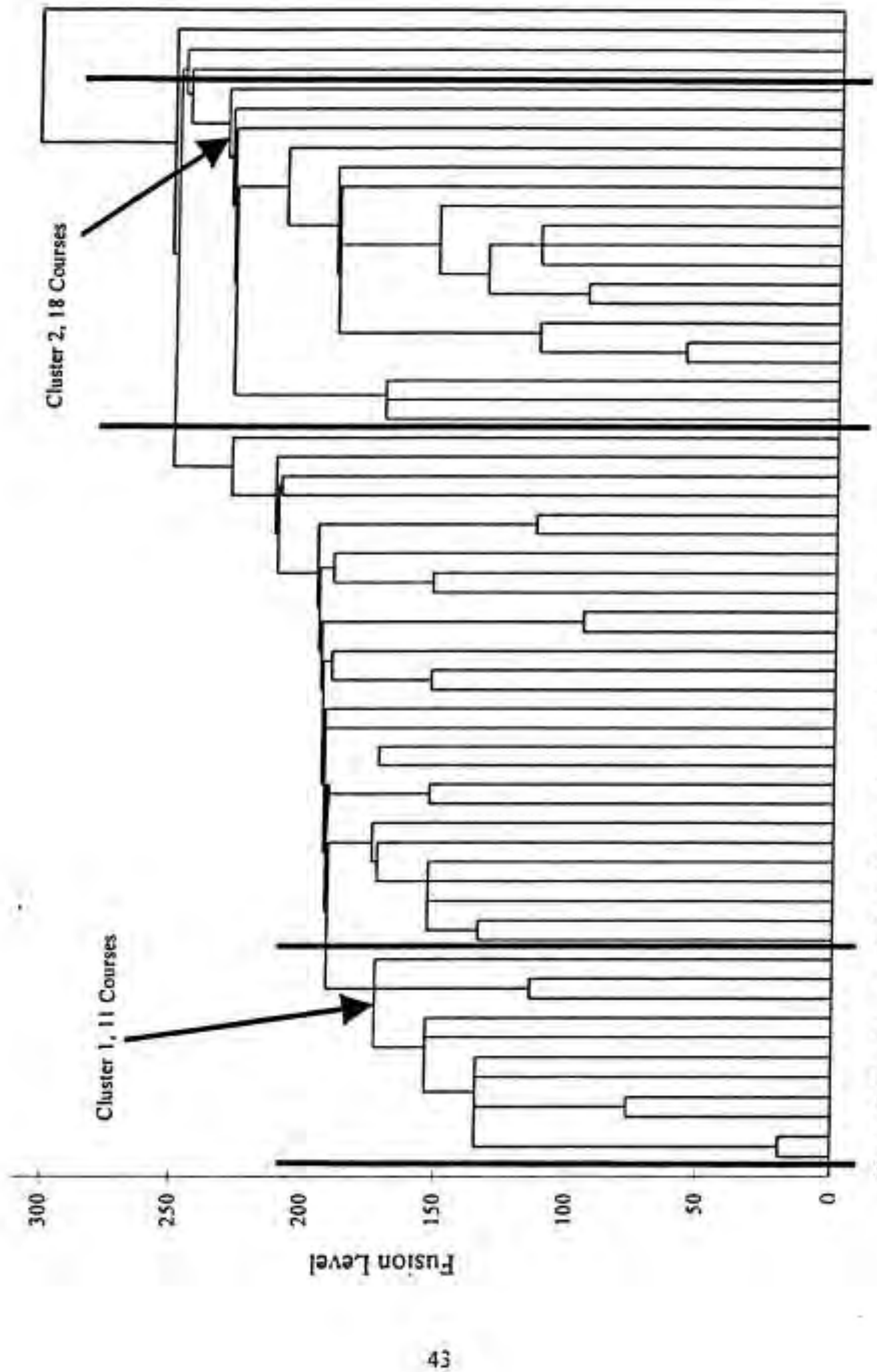

Figure 6. Dendrogram of single linkage cluster analysis of 60 golf courses using 50 attributes of vegetation, ground cover, and landscape position.

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Table 1. Distinquishing attributes as selected by cluster and factor analyses. Column 1, factors which appeared non-randomly in high and low clusters. Number is the percentage difference of occurrence between high and low clusters. Column 2, an attribute in Factor 1 or Factor 2 as determined through factor analysis. Column 3, attributes are grouped as components of the Landscape Evaluation Index. Column 4, a desired answer indicates it is an attribute favorable to fox squirrels. Index weight determined by columns 1 and 2.

1 Cluster difference %	2 Factor #	3 Index Component	4 Desired Answer	5 Index Weight	6 Attri. #	Attributes
		Vegetation-				
76.3	1	1	Y	7	11	well forested, large patches around course and often between fairways
72.7	1	1	Y	7	19	pines stands of 20 or more on most holes
81.8	1	1	Y	7	33	Pines , pines/cypress, or pines co-dominant
72.2		1	Y	5	17	over 100 large pines/ 18 holes
79.8	1	1	Y	5	18	pines occur throughout the course
61.1	1	1	Y	5	20	over 50 large cypress/ 18 holes
56.1	1	1	Y	5	21	at least 4 stands of 20+ cypress trees/18holes
74.2		1	Y	5	29	Palmetto present
	2	1	Y	3	30	4 or more exotic food trees common, ie q palm,
88.9	1	1	N	7	9	course "tight", narrow roughs,trees scattered, few or no large stands
85.4	1	1	N	7	34	no obvious dominant/s
	2	1	N	5	13	more than 3 marginally managed stands of trees/18 holes
	2	1	N	3	12	heavy forested vegetation in roughs, often cannot see more than 1 hole at a time and housing on 0-1side
	2	1	N	3	36	mixed natives majority of forest/stands
	2	1	N	3	47	Large snakes present
50.0		1	N	1	31	eucalyptus present
		Ground cover-				
85.4	1	2	Y	7	16	open understory, large areas with pine litter, open soil
	2	2	Y	3	15	managed forests have understory over 75%clear
	2	2	N	3	14	unmanaged stands show vine invasion and/ or other dense understory
		Landscape				
50.5	1	position-3	Y	5	5	club has 36 holes or more
	1	3	Y	5	40	at least 1 adjoining course has high levels of fox squirrels
65.2		3	Y	3	39	adjoining forest over 50 acres
54.0		3	Y	1	51	10-25 years old in 1997
77.8	1	3	N	7	37	Completely surrounded by housing,business or industrial development, or golf courses, or roads
68.7	1	3	N	5	3	club has only 18 holes
50.0	1	3	N	5	41	0 adjoining courses with fox squirrels
70.7		3	N	5	43	1 or more boundaries with busy 2 or 4+ lane roads
	2	3	N	3	50	less than 10 years old in 1997
38.9		3	N	1	38	0 adjoining courses

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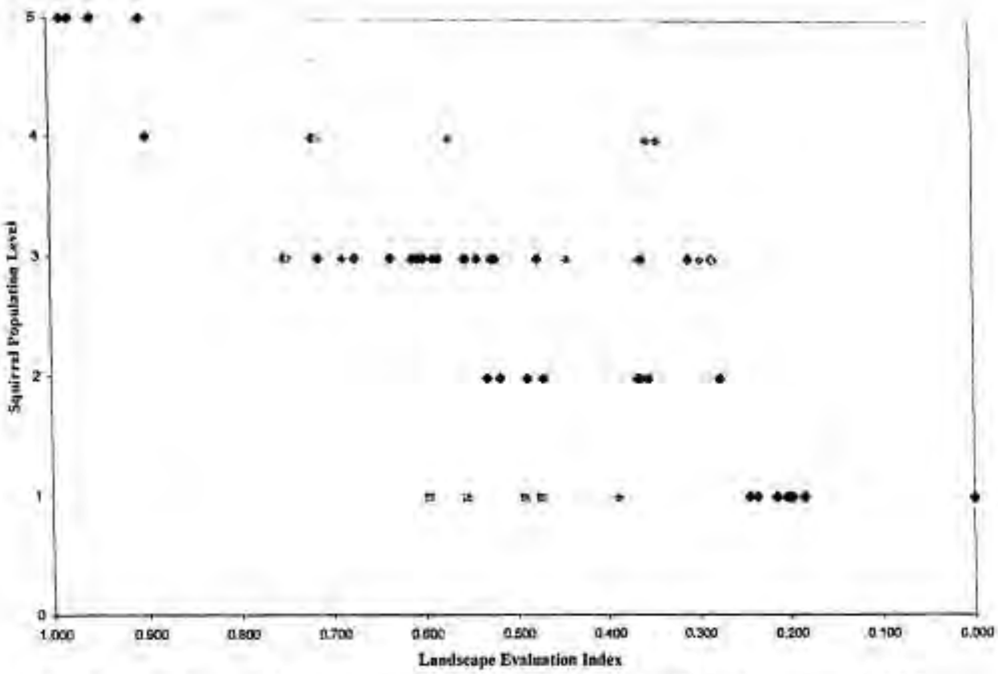

Figure 7. Comparison of Landscape Evaluation Index values to squirrel population levels. Trend line is a linear regression (r^2=0.557). Courses that adjoin the 7 courses (level 5 has 6 courses, symbols overlap) with index values of 0.90 or higher are identified with gray diamonds as Neighbors. Four courses that have large areas of native tree stands with heavy understory growth are identified by large gray squares, in level 1.

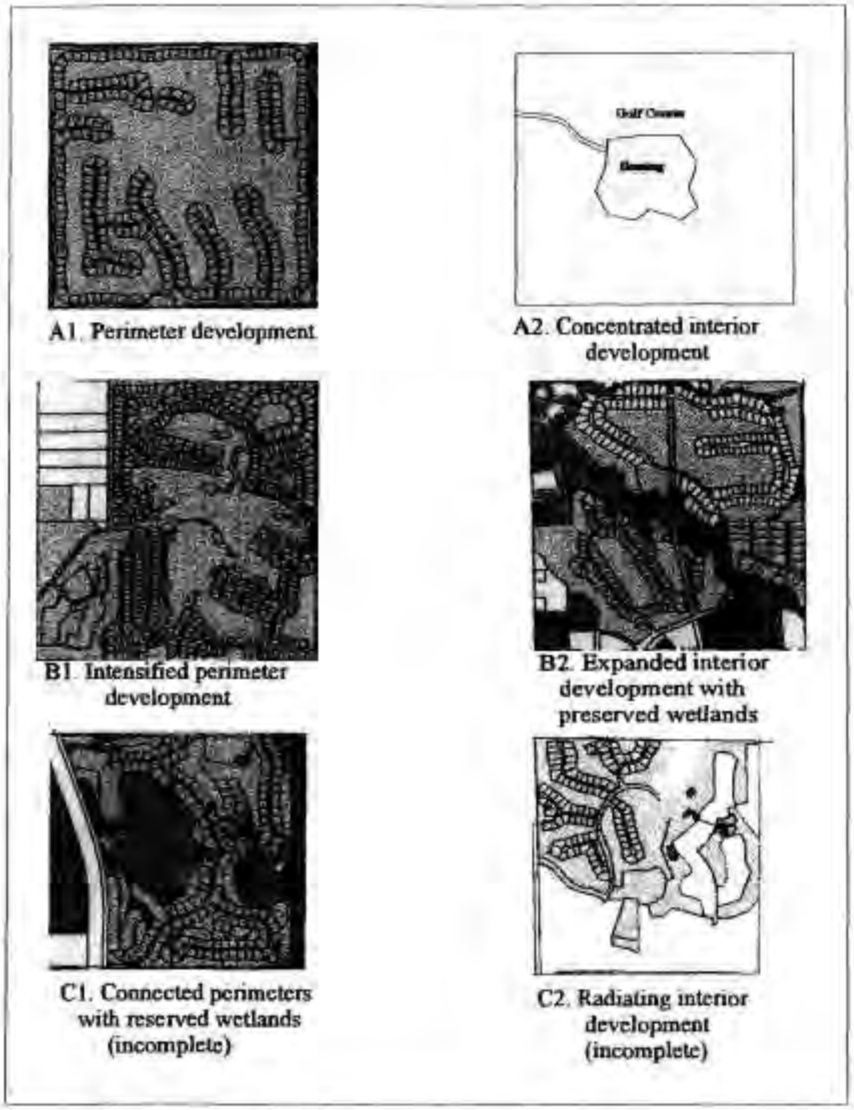

Figure 8 . Configurations of golf course development, ranging from higher quality in level A, to less desirable in levels B and C. A2 is a schematic, others are examples seen in the Collier County planning maps. Each plot is 1 section, 260 hectares. Clear tan areas are the golf courses and accompanying forest stands. Green patches are reserved wetland areas. Other colors:white, to be developed residential; brown, agricultural; pink and purple, commercial.Housing areas are the represented by subdivided lots and street patterns.

Table 2. Survival and birth rates for site 1, calculated in 6 month intervals. Survival equals persistence in the course population. Birth rates are calculated from the number of young emerging from the nest. Weighted averages for each sex and age class are the sum of persistent individuals in the 3 time periods divided by the sum of n for the 3 time periods.

SITE 1 FEMALES - *adults*	n	Known dead in population	Moved or dispersed	Disappeared	Persistent in population	Survival rate		Young from nest	Births/ adult female	Births/ adult
Jan.-June 1996	4	0	0	0	4	1.00		4	1.00	0.50
July-Dec. 1996	6	0	0	2	4	0.67		15	2.50	1.25
Jan.-June 1997	5	0	0	0	5	1.00		3	0.60	0.23
	15	0	0	2	13	**0.87**	Weighted average	22	1.47	**0.67**
subadults										
Jan.-June 1996	5	0	3	0	2	0.40		0		
July-Dec. 1996	0	0	0	0	0			0		
Jan.-June 1997	3	0	0	0	3	1.00		0		
	8	0	3	0	5	**0.63**	Weighted average	0		
MALES- *adults*										
Jan.-June 1996	4	0	1	1	2	0.50				
July-Dec. 1996	6	0	1	0	5	0.83				
Jan.-June 1997	8	1	0	3	5	0.63				
	18	1	2	4	12	**0.67**	Weighted average			
subadults										
Jan.-June 1996	4	0	0	0	4	1.00				
July-Dec. 1996	1	0	1	0	0					
Jan.-June 1997	4	1	0	0	3	0.75				
	9	1	1	0	7	**0.78**	Weighted average			

0.76	Average adult 6 month survival
0.71	Average subadult 6 month survival
0.67	Average juvenile 6 month survival

Table 3. Survival rates for site 2, Royal Palm, for January 1997- July 1997. Survival equals persistence in the course population. No births were recorded in the collared population between January and July 1997.

SITE 2 MALES-	n	Known dead	Moved/ dispersed	Disappeared	Persistent in the population		Survival/6 mo
Adult	2	0	0	0	2		1.00
Subadult	2	0	1	1	0		0.00
FEMALES						b(x)	
Adult	2	0	0	0	2	0	1.00
Subadult	2	2	0	0	0	0	0.00

Table 4. Population estimates derived from repeat censusing of sites 1 and 2.

SITE 1	Total seen	Known collars	Uncollared in sample	Collars	MNA	Lincoln Index	Bailey unbiased Index	Standard error of Bailey Index
14-Apr-96	19	16	8	11	24	27.6	26.7	4.68
28-Apr-96	7	15	3	4	18	26.3	24.0	6.00
6-May-96	18	14	5	13	19	19.4	19.0	2.52
25-May-96	10	13	6	4	19	32.5	28.6	8.62
6-Jun-96	11	13	5	6	18	23.8	22.3	5.09
1-Jul-96	9	13	3	6	16	19.5	18.6	3.60
1-Jul-96	11	13	2	9	15	15.9	15.6	1.92
1-Mar-97	14	19	5	9	24	29.6	28.5	4.96
20-Mar-97	8	18	2	6	20	24.0	23.1	3.86
29-Mar-97	19	18	7	12	25	28.5	27.7	4.38
6-Apr-97	15	17	7	8	24	31.9	30.2	6.32
21-Apr-97	16	17	7	9	24	30.2	28.9	5.59
11-Jun-97	20	16	10	10	26	32.0	30.5	6.08
Means	13.6				20.9	26.2	24.9	
SITE 2								
11-Jan-97	8	0	8	0	8			
19-Feb-97	6	5	4	2	9	15.0	11.7	4.41
8-Apr-97	3	7	1	2	8	10.5	9.3	2.33
15-May-97	4	5	2	2	7	10.0	8.3	2.64
14-Jun-97	5	5	2	3	7	8.3	7.5	1.94
Means					7.8	11.0	9.2	

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Table 5. Home range summary by site and year. Home range size equals the 95% area (ha) as calculated by CALHOME, using kernel analysis. Bold numbers are the mean of each series.

	Adult females (ha)	Subadults (ha)	Adult Males (ha)
Site 1, year 1, Dec. 1995 -Oct.31, 1996	7.98	10.66	42.52
	8.80	14.56	45.98
	10.17	15.88	76.45
	10.71	20.22	118.40
	10.92	22.56	**70.84**
	12.00	49.07	
	10.10	**22.16**	
Site 1, year 2, Nov. 1996-July 29, 1997	9.08	5.88	44.06
	13.14	10.31	48.42
	19.21	12.11	99.89
	19.66	16.62	114.10
	20.92	17.30	118.00
	16.40	20.80	121.00
		21.47	**90.91**
		14.93	
Site 2, year 2, Jan. 1997-July 29, 1997	13.06	25.77	136.10
	30.57	40.76	303.80
	21.82	108.50	**219.95**
		58.34	

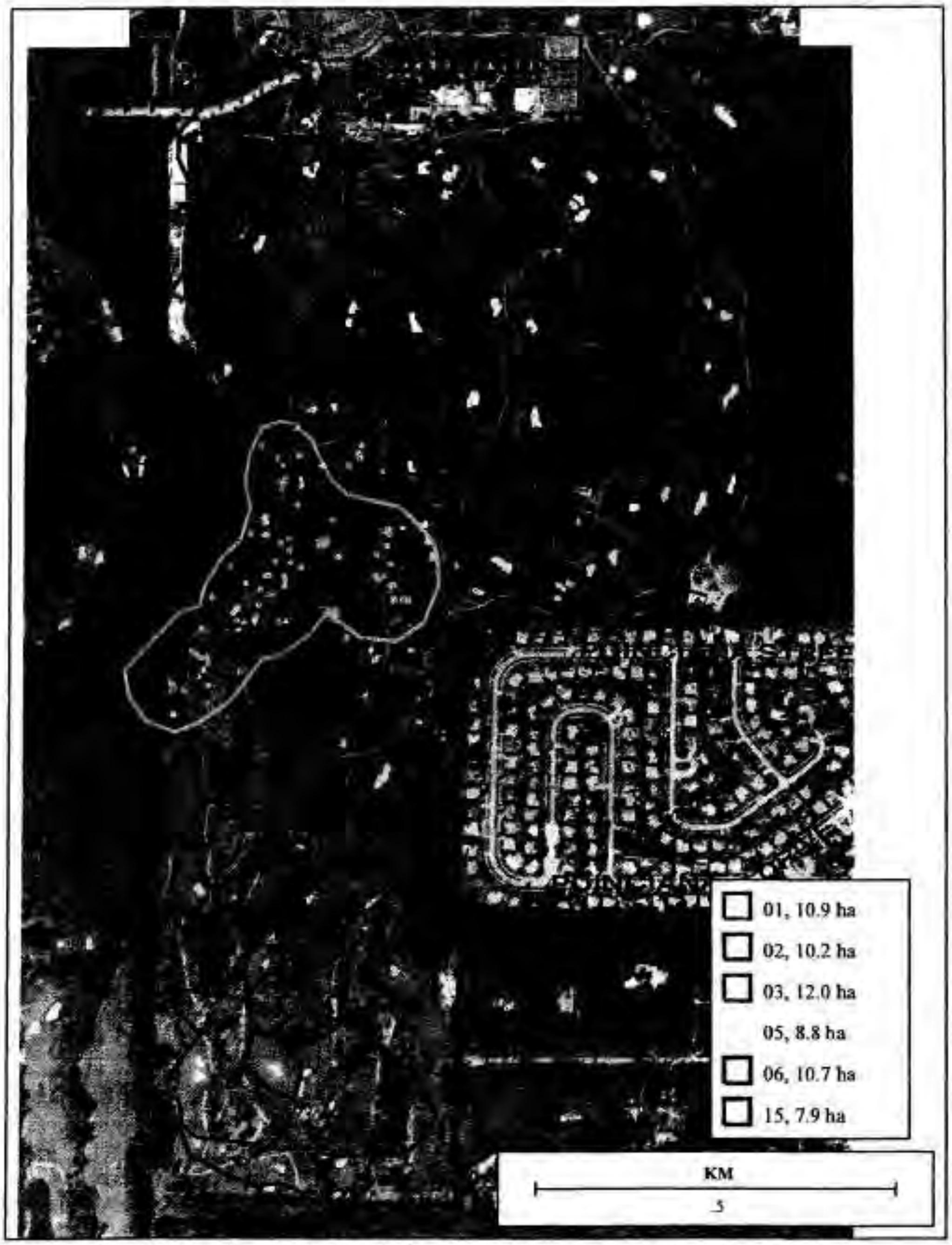

Figure 9. Adult females, site 1, year 1. Tracking locations and home range boundaries, defined by the 95% contour, kernel analysis, Calhome. The summer/fall brood nest site of each female is identified by placement of her individual number.

35

Table 6. Home range size for 3 adult females, site 1, year 1, occupying brood nests in summer/fall 1996.

	Brood nest home range, 95% contour	Brood nest core area, 50% contour	Number sightings
ROPO 02	0.77 ha	16.70 m^2	16
ROPO 03	0.30 ha	9.92 m^2	13
ROPO 06	2.12 ha	78.45 m^2	9

Figure 10. Adult males, site 1, year 1. Tracking locations and home range boundaries, defined by the 95% contour, kernel analysis, Calhome.

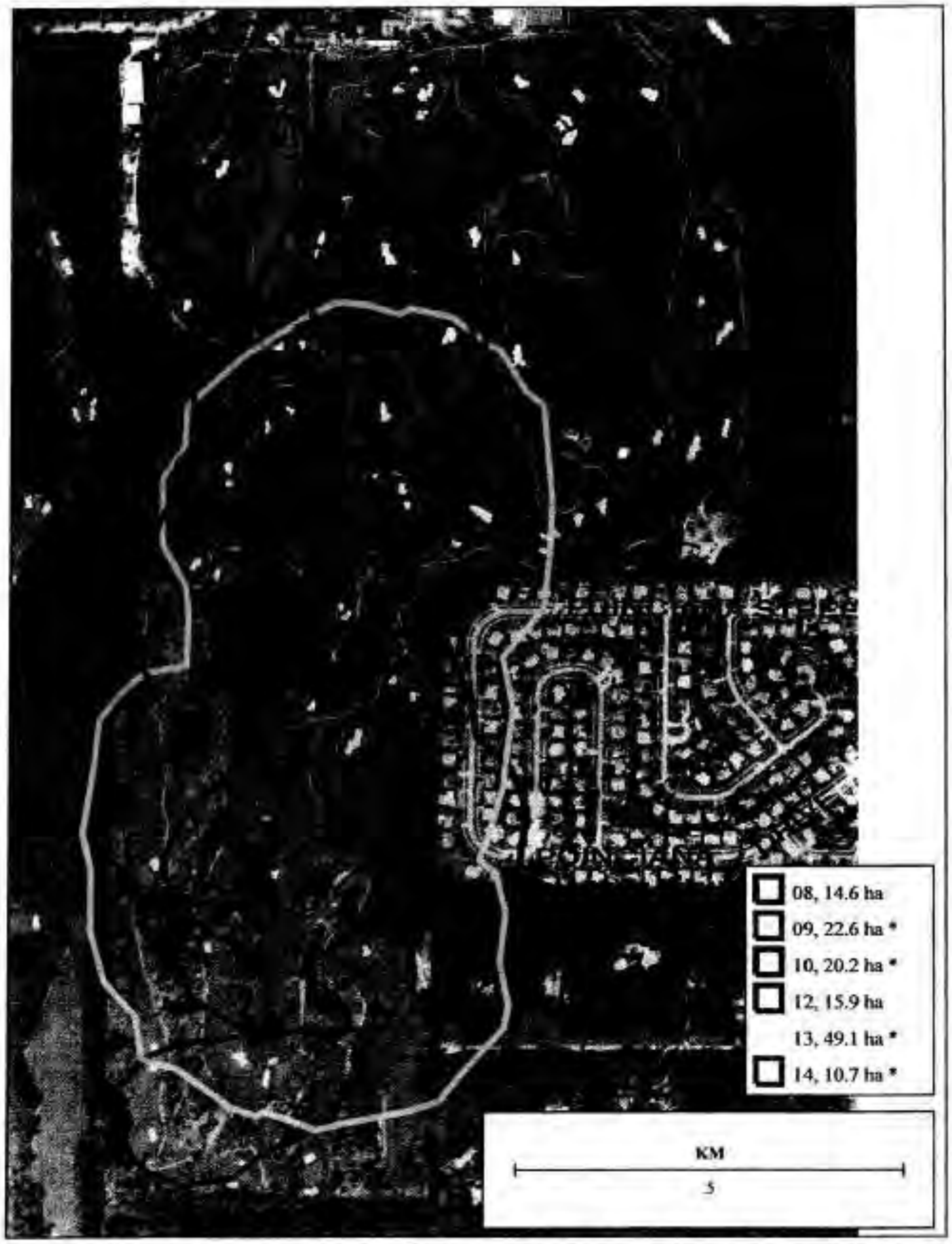

Figure 11. Subadults, male and female, site 1, year 1. Home range boundaries are defined by the 95% contour, kernel analysis, Calhome. Individuals that dispersed during the 1996 spring and summer seasons are marked (*), home ranges are those prior to dispersal.

35

Figure 12. The 4 collared subadults in the southern half of the course, site 1, year 1. Tracking locations and home range boundaries indicate use of the course. Three of 4 squirrels, 2 females, 1 male, dispersed from the course in spring and summer 1996. Only 08 remained through year 2 of the study.

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Figure 13. Dispersal movement of ROPO 10 from Site 1 to Country Club of Naples in late March, 1996. Movement from her central home range area to A was 1.4 km, and from A to B an additional 0.85 km, for a total 2 week dispersal distance of 2.2 km.

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Figure 14. Dispersal movement of ROPO 14 in April 1996 to Bear's Paw Country Club. The distance from her central home range area to the first off site location, A, was 2.8 km. She was found dead at B in late July 1996.

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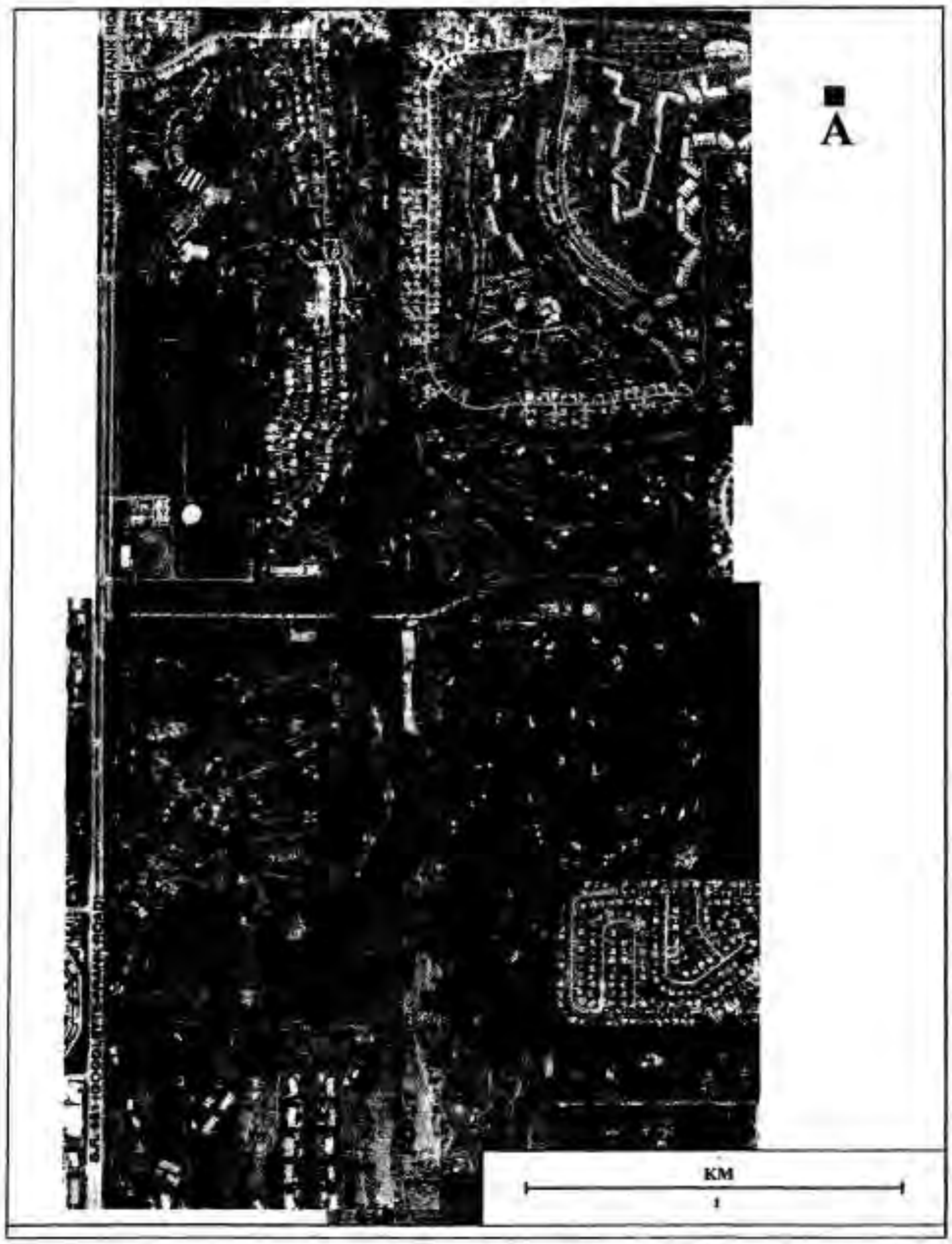

Figure 15. Dispersal movement of ROPO 09 in mid May 1996. First off-site location at A, a move of 2.3 km from previous home range on May 20, 1996. Located at B on May 27, 1996; at C, home feeding site on June 28, at D on August 23, and found dead at E, hit by vehicle, in April 1997.

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Figure 16. Dispersal of ROPO 13 from Site 1 to Bear's Paw Country Club on August 8, 1996. Points north of A are tracking locations of 13before that date. Movement from A to B, 1.2 km, took 3 hours. He crossed from B to C the following morning, for a total 24 hour dispersal distance of 1.5 km. The total distance traveled to his final sighting was 3.5 km.

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Figure 17. Adult females, site1, year 2. Tracking locations and home range boundaries, defined by the 95% contour, kernel analysis, Calhome. Numbered site is 1997 summer brood nest of female 03.

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Figure 18. Three adult males, site 1, year 2. Tracking locations and home range boundaries, defined by the 95% contour, kernel analysis, Calhome.

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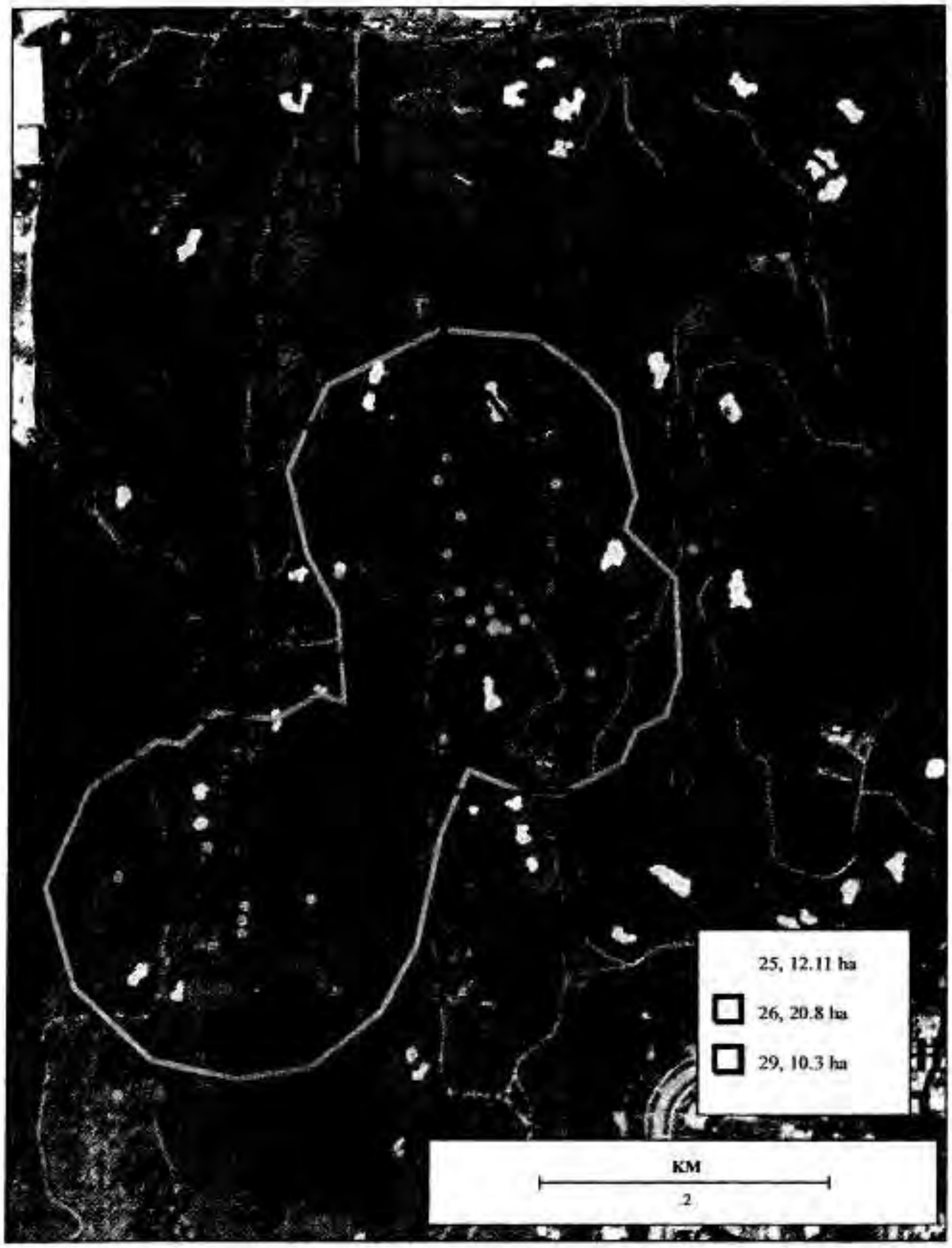

Figure 20. Three of 7 collared subadults, site 1, year 2. Tracking locations and home range boundaries as defined by the 95% contour, kernel analysis, Calhome.

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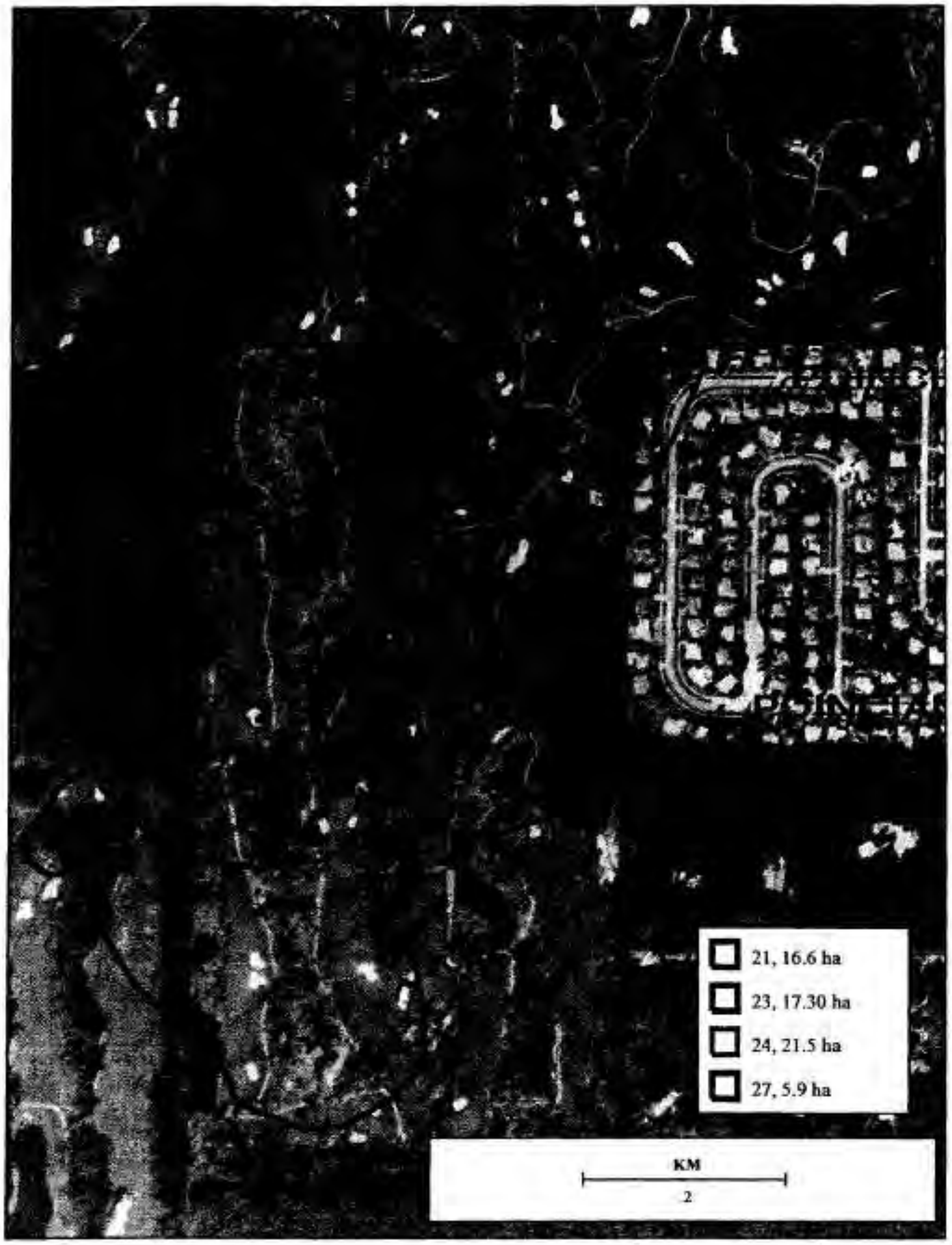

Figure 21. Four of 7 collared subadults, site 1, year 2. Tracking locations and home range boundaries as defined by the 95% contour, kernel analysis, Calhome.

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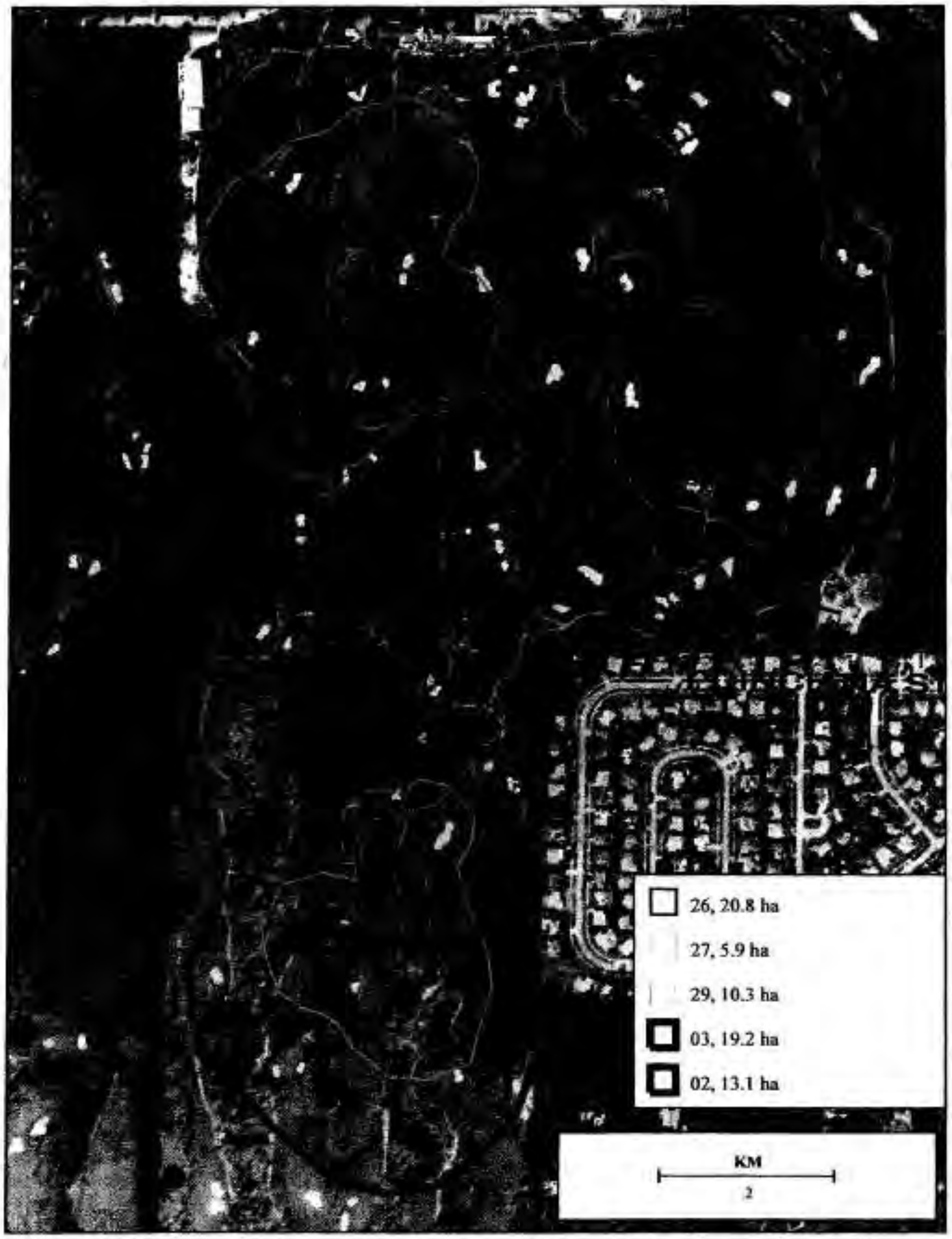

Figure 22. Site 1, year 2. Two adult females, 03 and 02, and their collared offspring from summer 1996. Thin lines are subadult offspring. Squirrels 27 and 29 are females, 26 is male.

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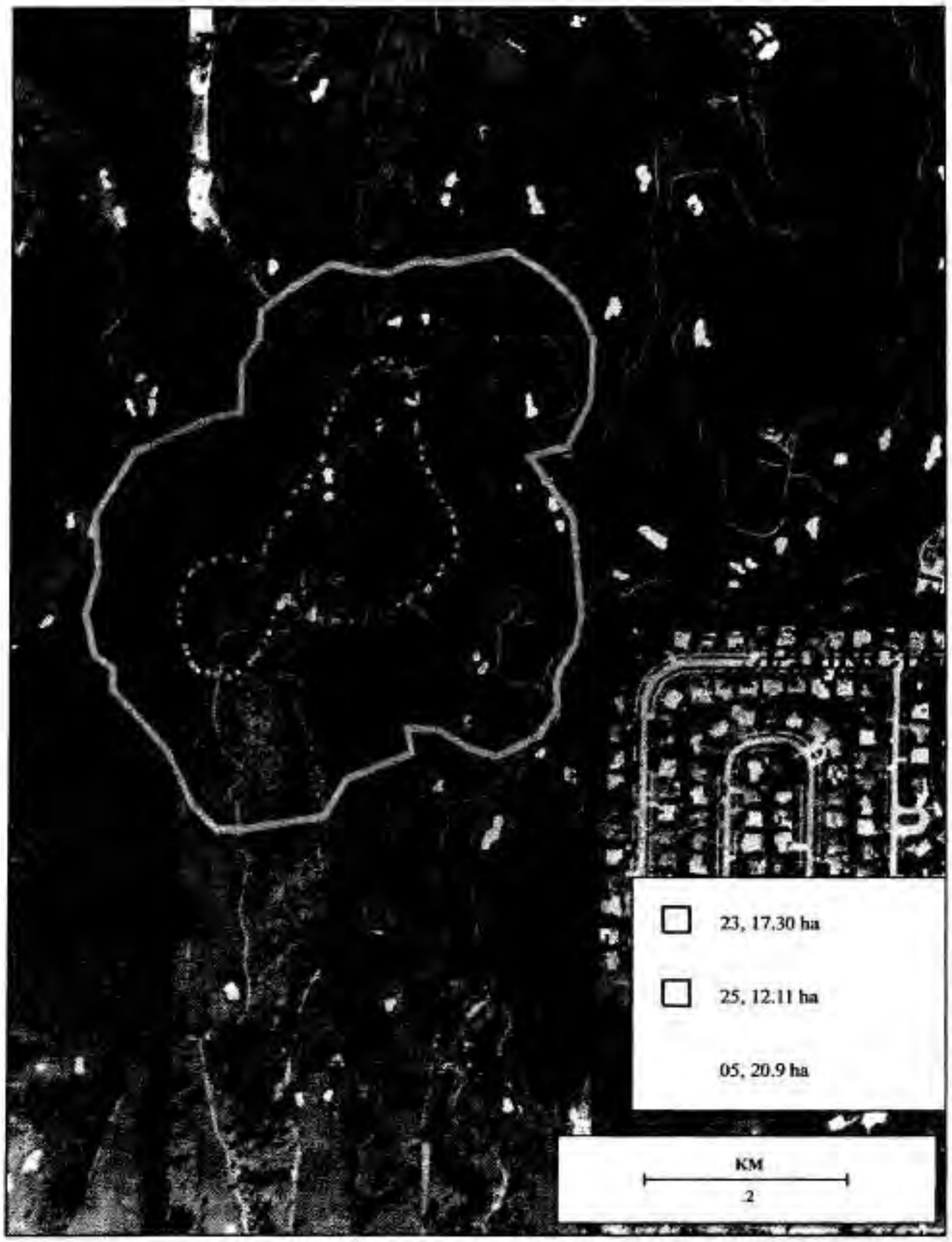

Figure 23. Site 1, year 2, adult female 05 and collared male offspring 23 and 25 from summer 1996. Yellow dots indicate the core area, 50% contour, of female 05.

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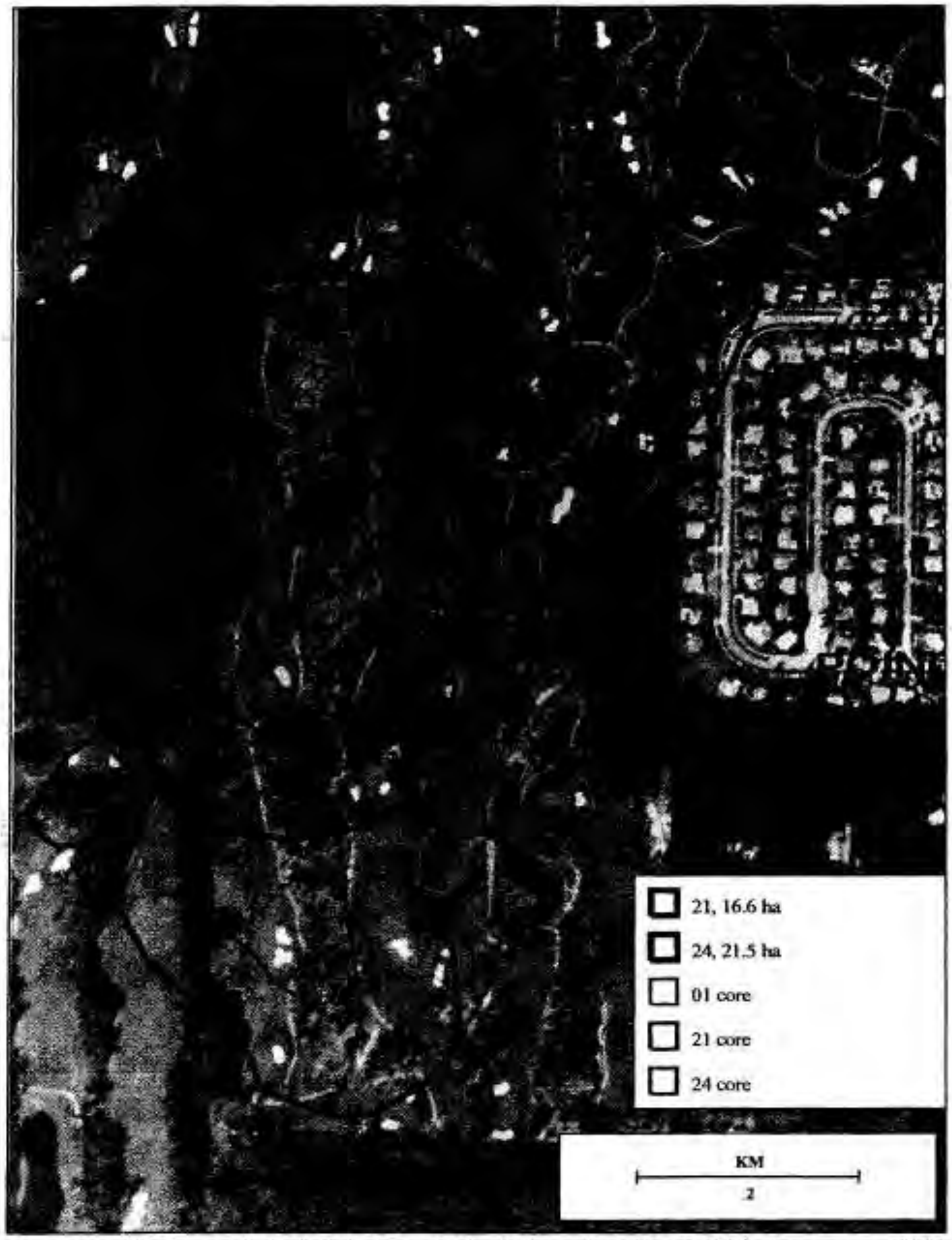

Figure 24. Site 1, year 2. Subadults 21 and 24, siblings from female 01 in the summer 1996, show overlap of home ranges and core areas. Core area of 01, who disappeared in December 1996, is show in light blue.

47

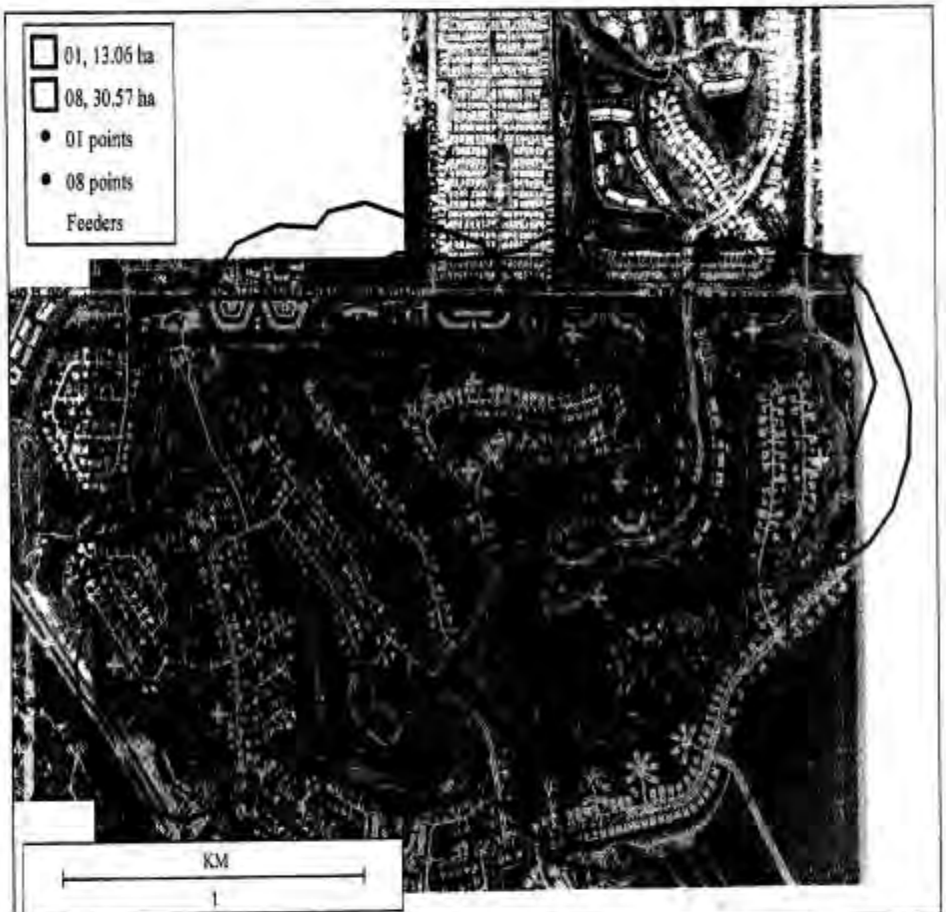

Figure 25. Adult males, site 2, 1997, Tracking locations and home range boundaries as defined by the 95% contour, kernel analysis, Calhome. Yellow crosses mark the locations of feeders.

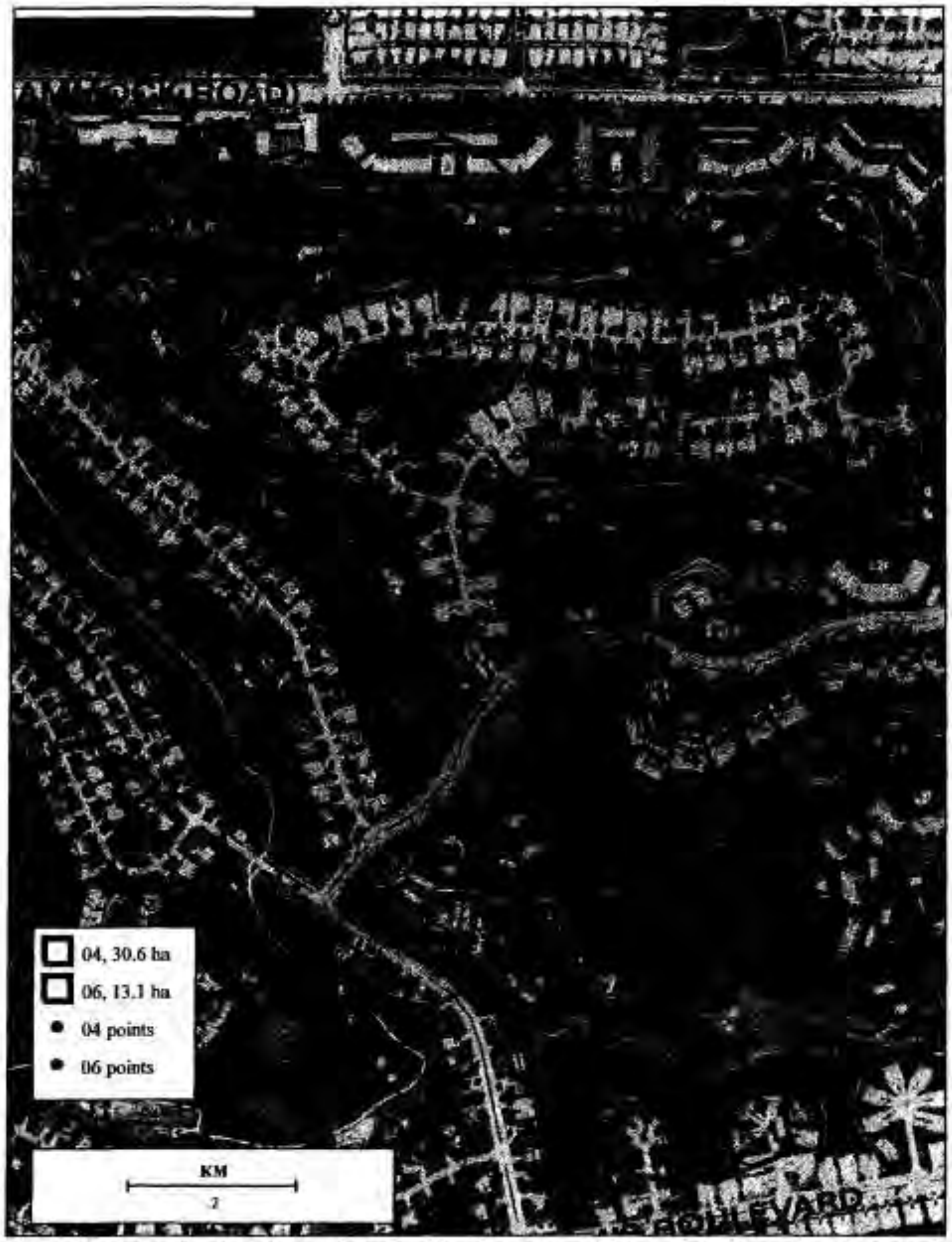

Figure 26. Adult females, site 2, 1997. Tracking locations and home range boundaries as defined by the 95% contour, kernel analysis, Calhome.

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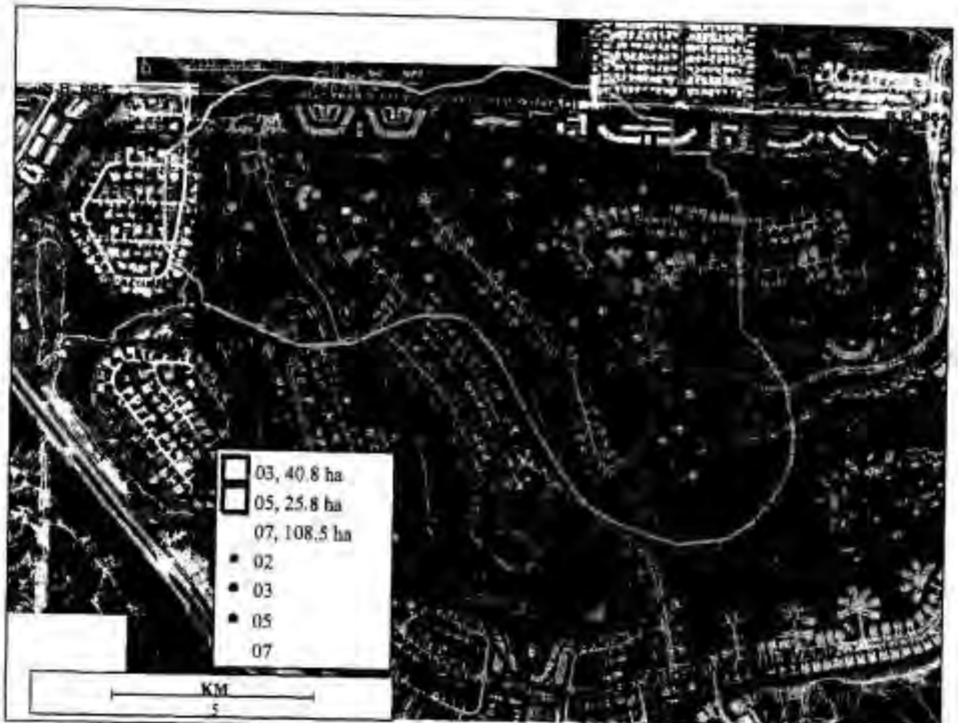

Figure 27. Subadults, site 2, 1997. Tracking location and home range boundaries as defined by the 95% contour, kernel analysis, Calhome.

Table 7. Landscape composition of site 1, site 2 and Royal Poinciana Pines course.

	Royal Poinciana Cypress Site 1		Royal Palm Site 2		Royal Poinciana Pines Course	
	Area, ha	% of total	Area, ha	% of total	Area, ha	% of total
Total size of site	61.4		141.9		62.9	
Club property in tree stands	30.0	49%	26.0	18%	24.8	39%
Condominium land in trees	0.0	0	34.9	25%	0.0	0
Residential, streets and clubhouse	0.0	0	40.1	28%	0.0	0
Lakes, canals, wetlands	5.5	9%	8.0	6%	5.3	8%
Fairways, greens, sandtraps, driving ranges, unforested roughs	25.9	42%	32.9	23%	32.8	52%

Table 8. Vegetation classification of site 1, site 2, and Royal Poinciana Pines.

	Royal Poinciana Cypress Site 1		Royal Palm Site 2		Royal Poinciana Pines Course	
Vegetation classes, by relative basal area	Area, ha	%	Area, ha	%	Area, ha	%
1-Pine, 70% or more pine	0.0	**0**	17.8	**68**	3.0	**12**
2-Pine and cabbage palm, 30% or more of each	3.2	**11**	0.9	**3**	2.4	**10**
3-Palm, 60% or more cabbage palm	2.4	**8**	1.4	**5**	2.0	**8**
4-Cypress, 60% or more cypress	4.4	**14**	0.4	**2**	3.5	**14**
5-Pine and cypress, 30% or more each of pine and cypress	0.9	**3**	0.7	**3**	0.0	**0**
6-Pine, cypress, c. palm, over 85% of the 3 combined, with each being over 20%	2.9	**10**	0.0	**0**	0.0	**0**
7-Cypress and c. palm, 30% or more of each cypress and pine	5.5	**18**	0.0	**0**	0.0	**0**
8-Mixed natives-none of the above with 20% or less exotics	2.9	**10**	2.1	**8**	1.2	**5**
9-Mixed natives with exotics-not 1-7, with more than 20% exotics	7.8	**26**	2.8	**11**	12.7	**51**

Table 9. Denisty of trees at site 1, site 2, and Royal Poinciana Pines.

	High > 200 stems/ha	Medium 100-199 stems/ha	Low <100 stems/ha
Site 1, R. P. Cypress-			
area in ha	5.4	19.5	5.2
%	**18%**	**65%**	**17%**
Site 2, Royal Palm			
area in ha	0.7	7.4	17.9
%	**3%**	**28%**	**69%**
Royal Poinciana Pines			
area in ha	7.8	9.9	7.1
%	**32%**	**40%**	**28%**

Figure 28. Tree stand characteristics at site 1, Royal Poinciana Cypress course. Nine classes are color coded. H= high density (>200 stems/ha), L=low density (<100stems/ha), all patches not marked H or L are moderate density (100-199 stems/ha). Presence of dense litter layer is indicated by an asterick (*), S= presence of a shrub layer.

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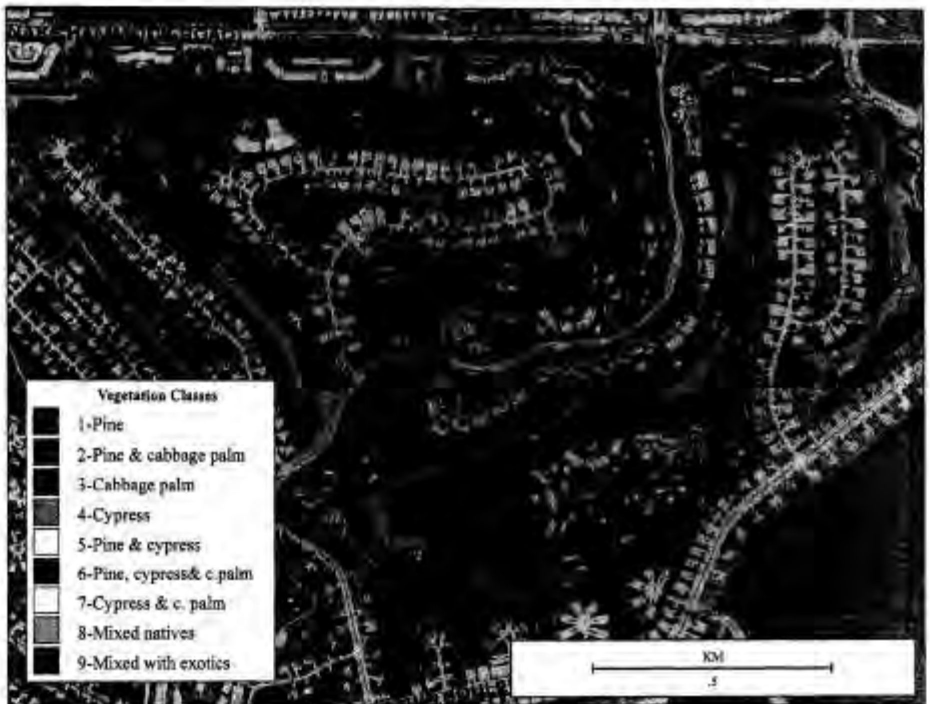

Figure 29. Tree stand characteristics at site 2, Royal Palm. Nine classes are color coded. H=high density (>200 stems/ha), L=low density (<100 stems/ha), VL=Very Low density (<30 stems/ha). All patches not marked are moderate density (100-199 stems/ha). Presence of litter layer is indicated by an asterisk (*). Areas along Augusta Boulevard that are outlined in dark green and contain letters indicating tree density are the condominium properties. The outline area in the upper left is the private pine forest.

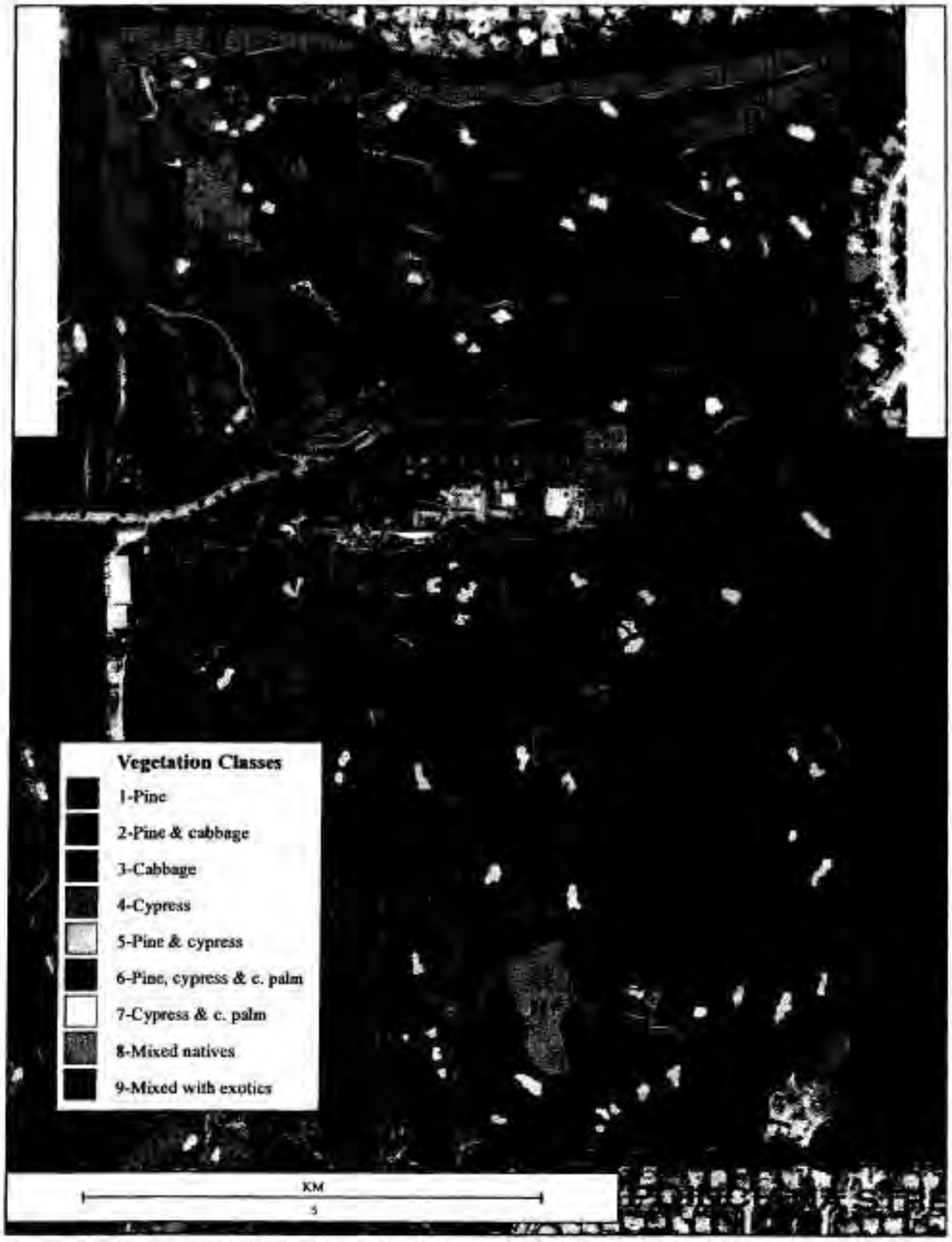

Figure 30. Tree stand characteristics for Royal Poinciana Pines course. Nine classes are color coded. H=high density (>200 stems/ha), L=low density (<100 stems/ha), all patches not marked H or L are moderate density (100-199 stems/ha). Presence of a dense litter layer is indicated by an asterick (*), S= presence of a shrub layer.

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Table 10. Habitat preference tests on tracking points at Royal Poinciana Cypress, Site 1, and the neighboring Pines course. Chi-square tests the hypothesis that points are randomly distributed among vegetation types. Area of each vegetation class predicts the number of points. Only tracking locations within the mapped plots of forested stands are included. Double asterisk indicates results are significant at the 0.01 level.

	Number of Tracking Points	X^2	df	p
Cypress				
Females, both years	1206	154.08	7	5.60E-30 **
Males, both years	768	242.76	7	9.60E-49 **
Year 1, all squirrels	1036	208.12	7	2.18E-41 **
Year 2, all squirrels	938	128.51	7	1.28E-24 **
Summer 1996	276	81.57	7	6.59E-15 **
Summer 1997	340	41.29	7	7.12E-07 **
Pines				
All points	164	20.73	5	0.0009 **
Males, both years	140	17.59	5	0.0035 **
Year 1 all squirrels	65	7.99	5	0.1570
Year 2 all squirrels	99	18.31	5	0.0026 **

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Table 11. Feeding patterns of fox squirrels on the 13 main food species eaten by the collared population of site 1. Data include all feeding records, at all locations used by the site 1 collared squirrels for 19 months, n=817. Diversity Index is the inverse Simpson measurement for richness and evenness. Cell shading :Section A, dark=≥50%, light=15-49%, white=<15%, blank cells =0; Section B, dark=≥ 50%.

Section A- Species data	Jan 96	Jan 97	Feb 96	Feb 97	Mar 96	Mar 97	Apr 96	Apr 97	May 96	May 97	Jun 96	Jun 97	Jul 96	Jul 97	Aug 96	Sept 96	Oct 96	Nov 96	Dec 96
%Natives																			
Pine	25	22	2	8		7	1	14	4	6	3	10	5	20	65	56	58	67	17
Cypress	42	37		18	4	5	2	1	6	4	16	21	21	20	23	18	19	33	52
Red maple	8	4	20	14															
Oak sp.		7		6		3		8	4							10	13		30
Mushrooms			4	3		8	2	1	2	27	21	12	26	5		8	4		
Larva										4		15							
%Non-natives																			
Q. palm	8	7	33	22	7	5	16	4	4	18	3	6	16	5		8	6		
Ficus sp.		4	20	2	6	16	4	3	17	39	11	23	21	5	4				
Tallow		19	2	5		3	1	1											
Bischofia	17		18	23	56	26	50	29	42	2	42	2	11		4				
Bottlebrush					28	22	18	21	6		3			10					
Silk oak						4	5	18	15										
Java plum											3	12		35	4				
n=	12	27	45	65	54	73	94	78	52	49	38	52	19	30	26	39	48	3	23

Section B- Summary	Jan		Feb		Mar		Apr		May		Jun		Jul		Aug	Sept	Oct	Nov	Dec
%Natives	75	70	27	49	4	23	5	24	15	41	39	58	53	45	88	92	94	100	100
%Non-natives	25	30	73	51	96	77	95	76	85	59	61	42	47	55	12	8	6	0	0
Diversity Index	3.6	4.3	4.4	6.0	2.5	6.1	3.2	5.3	4.1	3.8	3.8	6.2	5.1	4.5	2.1	2.7	2.5	1.8	2.5

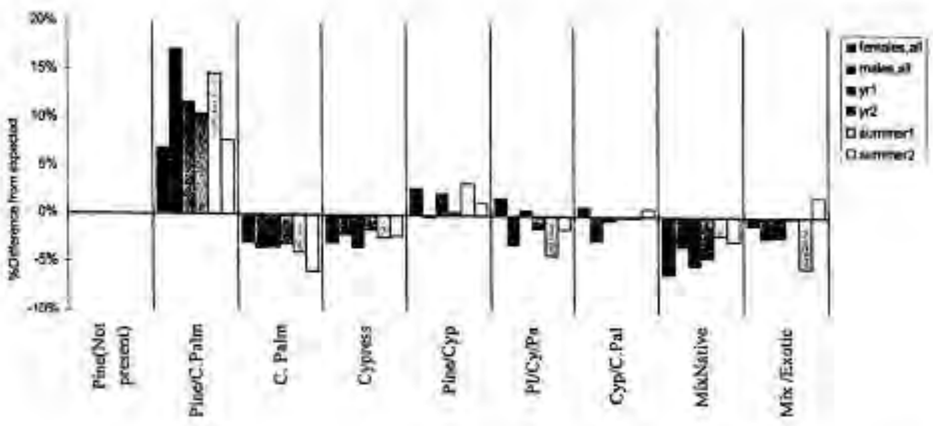

Figure 31. Difference in expected and observed use of vegetation classes at Site 1, Cypress course, by subgroups of the tracked population.The nine classes of tree stands are shown on the x axis. Positive values indicate a stronger than expected preference for a given vegetation class, negative values indicate less than expected use of a vegetation class. Table 10 presents Chi-square results for tests of random distribution among vegetation classes for each of the subgroups shown here.

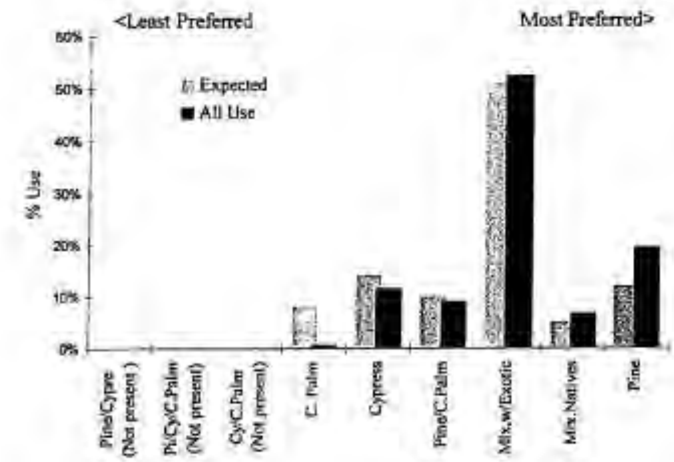

Figure 32. Habitat preferences for all fox squirrels at the Pines course, Royal Poinciana. Tracking points within the mapped vegetation plots on the Pines course are included, n=164.

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Table 12. Feeding patterns of fox squirrels at site 2. Data include all feeding records at all locations used by the site 2 collared squirrels from January 1997 through July 1997. All food items are listed. N=45.

Non-natives	Feeders	Bottlebrush	Java plum	Ficus	Silk oak	Queen palm	Begging
67%	33%	13%	9%	4%	2%	2%	2%

Natives	Pine, new & old cones	Larva	Mushrooms	Cypress
33%	16%	9%	7%	2%

DISCUSSION

The goal of this study was to gain an understanding of the present and future role of golf courses in offering suitable habitat for Big Cypress fox squirrels. In this discussion, we will first look at the characteristics of the 2 radio-collared populations in the high and low quality golf course landscapes. One was a diverse and productive landscape that provided for a stable fox squirrel population likely to withstand the pressures of immediate surrounding development. The second, less productive and more hazardous, fostered an unstable population which is not likely to persist through the next 20 years of development. We will then interpret the findings of the Landscape Evaluation Index. The two courses with collared populations will serve as reference points for the further interpretation of the broad range of golf course landscapes identified and ranked through the use of this index.

Higher Quality Golf Course Landscape

Site 1, Royal Poinciana Cypress Course, provided high quality fox squirrel habitat with few intrusions by traffic. The course rated 0.956 on the Landscape Evaluation Index, with large, moderately dense to dense tree stands of mixed natives dominated by pine, cypress and cabbage palms. Scattered exotics provided a majority of late winter and spring feeding sites. Numerous non-irrigated areas with pine litter ground cover provided centers of concentrated feeding on fungi. Mixed tree stands with large trees, bromeliads, and moderately trimmed palms provided a variety of protected nesting sites.

As would be expected, adult females had smaller home ranges than males (Kantola 1990, Weigl et al. 1989). Mean home range size for adult females was 10.10 in 1996 and 16.40 in 1997. Home range means for males were 70.84 in 1996 and 90.91 in 1997, larger than previously reported in work on southeastern fox squirrels. Kantola's work with *S. n. Shermani* in north Florida (1990) showed female home ranges averaging 16.7 ha and male home ranges averaging 42.8 ha (harmonic mean). In North Carolina, Weigl et al. (1989) found an average female home range size of 17.2 ha and an average male home range size of 26.6 ha (MCP).

Site 1 male home ranges were 7 times larger than female home ranges in year 1 and 5.5 times larger in year 2, showing a much greater difference between the sexes than reported by previous workers in the southeast (Kantola 1990, Weigl et al. 1989). The large male home ranges may be explained by the fact that many males used neighboring courses where resources were more scattered and of generally lower quality. Males with a substantial portion of their home ranges in neighboring courses had larger home ranges. The strong overlap seen in home ranges of both males and females at site 1 appears to be unusual for southeastern fox squirrels (Kantola 1990, and Weigl et al 1989). Kantola found little overlap in female home ranges, while Weigl et al. (1989) note seasonal variation with no overlap of male home ranges in times of winter scarcity.

Squirrel densities of 42.4 squirrels/km^2 (from high MNA of 26) to 49.8 squirrels/km^2 (from high Bailey estimate of 30.5) are higher than previous reports of fox squirrels in Florida. Estimates of 8.4 squirrels/km^2 and 38 squirrels/km^2 were reported by Humphrey et al. (1985) and Moore (1957). In Georgia, at the Piedmont National Wildlife Refuge, Tappe et al. (1993) found fox squirrel densities of 15.3-17.7 squirrels/km^2 in mark and recapture studies.

Fox squirrels at site 1 had 2 breeding seasons, as reported in other southeastern fox squirrel populations (Moore 1957, Weigl et al. 1989). Contrary to previous work at more northern locations (Larson 1990, Weigl et al. 1989), reproduction was higher in the summer season than the 2 winter seasons. Litter size, as young from the nest, ranged from 1 to 4 with a mean of 2.4, within the reported range of 1.6 to 3.0 (Larson 1990, Moore 1957, Weigl et al. 1989). While 4 of the 7 site 1 adult females in the study produced 2 litters in the 3 breeding seasons studied, none produced 3 litters. Weigl et al. (1989) show a strong correlation between food availability and female reproductive capacity. In the summer of 1996, 5 of 6 females produced young from the nest and raised them into the fall. The smaller home ranges in that year and the concentrated feeding patterns of spring through fall of 1996 indicate a rich food supply, probably resulting from the high rains of fall 1995.

Frequent squirrel feeding on fungi was also reported by Weigl et al. (1989) in North Carolina. Presence of mycorrhizal hypogeous fungi and associated bacteria form mutualistic relationships with a variety of tree species, including pines (Li et al. 1986, Slankis 1973).The fungi are nutritionally beneficial to fox squirrels who then disperse fungal spores as they defecate in their wide travels (Maser et al. 1978, Trappe and Maser 1977). Maintenance of the fungi-rich litter areas within site 1 preserved a food source for fox squirrels and probably provided benefit to a tree species also of primary importance to the squirrels. Weigl et al. (1989) believed the fitness of squirrels, trees and fungi benefited from this relationship and that it may be coevolutionary in nature.

High densities, high reproduction, and high overlap of home ranges suggested a food supply which is strong though obviously variable. Occupancy of site 1 by 5 or 6 adult females maintaining fairly constant home ranges throughout the 20-month study indicated the adult female density was at a maximum. Site 1 and its companion course, Pines, together had 40-50 squirrels in residence, though it must be noted that at least half of the adult males used neighboring clubs. The population appeared stable, with surplus subadults dispersing to neighboring courses.

Royal Poinciana and its buffer courses to the west provided the most productive and stable golf course site for fox squirrels within the currently developed landscape in western Collier county and the most stable in this study. Immediate and dramatic changes in the landscapes of Poinciana or the 2 neighboring courses most frequently used by males are not anticipated. On the other hand, these landscapes are managed. The composition and maintenance of trees, tree stands and ground cover are subject to change at the will of the managers. East and south of site 1, the condition of developing and undeveloped properties will change in the coming decade, with anticipated development of the large pine forest south of Poinciana and current development of the lots east of the club. Such development will affect sources and movement of squirrels in and out of Poinciana and could bring more domestic predators, especially cats, to the borders of the courses.

Lower Quality Golf Course Landscape

Site 2, Royal Palm Country Club, contained lower quality fox squirrel habitat weaving through a developed landscape with an increasing flow of vehicle traffic. The club rated 0.719 on the Landscape Evaluation Index with moderately dense to open pine-dominated tree stands on club property and neighboring condominium land. There was a lower diversity of tree species, both native and non-native, and fewer and more widely scattered pine litter areas than at site 1. In the absence of oaks and maples, and with lower numbers of large fungi feeding areas or fruiting exotics, squirrels fed heavily at feeders in the spring and summer.

The 2 adult females at site 2 had home ranges of 13.06 ha and 30.57 ha. The difference may result from the former having a regularly supplied feeder in the center of her home range and the latter having only an occasionally stocked one at the edge of her home range. The home range of the first female is similar to others in this study and to previous studies, while the home range of the second female is larger than any other in this study and the averages reported in other studies (Kantola 1990, Weigl et al. 1989). Male home ranges of 136.1 ha and 303.80 ha were larger than others in the study and larger than means reported by Kantola (1990) or Weigl et al. (1989). All adult and subadult home ranges at site 2, except the 1 adult female with a well-stocked feeder, were larger than comparable individuals in the study and larger than reported means in previous studies. Adult female home ranges did not overlap or touch as they did at site 1.

Fox squirrel densities at site 2 were extremely low, 6.3/km^2 (MNA of 9) and 8.2/km^2 (high Bailey estimate of 11.7). These are similar to the estimates of Humphrey et al.(1985), though much lower than reported by Moore (1957) or Tappe et al. (1993). They are 84% lower than the fox squirrel densities at site 1. While the 4 collared adults lived and persisted on the course through the 7 months of collaring, none of the collared subadults remained. Two of the 4 subadults were known dead, 1 disappeared early in the study, and 1 dispersed to a very low quality habitat in an adjoining course and was using a feeder near a major highway.

At Royal Palm, low population density, large home ranges, and poor subadult persistence indicate an unstable population. A small number of adults maintained themselves and reproduced in times of higher food supply, but young had a difficult time surviving to adulthood. A more open, less diverse food supply required fox squirrels to make larger movements to feed and mate, and so expose themselves to the hazards of automobile traffic and the stresses of travel and food search, all especially hard on subadults. At both sites 1 and 2 vehicle accidents were a common source of mortality of collared and uncollared squirrels. Weigl et al. (1989) found that automobile traffic was a major cause of fox squirrel mortality in their 8-year study in rural areas of the North Carolina coastal plain.

Royal Palm is a course with marginal fox squirrel habitat and more development yet to come. Completion of housing that borders the fairways will eliminate the remaining tree-covered vacant lots. Growth of adjacent developments to the east and north will increase traffic on Augusta Boulevard and connecting roadways. As with site 2, the quality of course vegetation is dependent on management. It could be improved with the addition of a variety of native trees such as cypress, oaks, and maples, with the addition of spring fruiting non-natives, and with more pine litter areas. While feeders are obviously a vital part of squirrel diet at site 1, reliance on feeders puts squirrels at the mercy of suppliers and perhaps increases the risk of exposure to contagious disease. The course adjoining Royal Palm to the west, used by adult males and at least 2 dispersing subadults in the study, had very low quality habitat and would not support fox squirrels without the resources of Royal Palm.

As we shall see in the next section of the discussion, site 1 was an unusual golf course in southwest Florida, both in its rich landscape without residential development and in its high numbers of fox squirrels. Site 2, on the other hand, was more common. It was a mix of the favorable and unfavorable landscape features. It had the levels of development and traffic seen in many courses of level 3 and 4, and though it was not isolated, the 2 neighboring courses furnished very low quality fox squirrel habitat. It was superior to most courses in the presence of relatively high quality pine stands, the open understory of all tree stands, and the occurrence of scattered pine litter areas.

Landscape Evaluation

The study revealed a wide variety of golf course habitat types and course configurations in Lee and Collier counties. Landscapes surrounding these courses, which are critical to fox squirrel movements, ranged from highly developed with heavy vehicle traffic to more rural sites surrounded by mixed agricultural and forest stands.

The ability of golf courses to support fox squirrels differed greatly. Six of the courses with an LEI of 0.90 or above had high levels of fox squirrels and make up 3 clubs, each of 36 holes (Fig. 33, Appendix B). These 3 clubs have the highest potential for supporting fox squirrels in a developed landscape. The 1 course with an LEI of 0.90 and moderate levels of fox squirrels is also part of a 36 hole course, but its companion course has an LEI of 0.71, with high traffic and more intense development in the future. This 0.90 LEI course does not have a strong potential for continued support of fox squirrel populations. The remaining 53 courses have LEI ratings of 0.75 and lower, and will not be capable of supporting fox squirrel populations through intense development of the next 2 decades.

The 6 courses with an LEI of 0.90 and above and with high levels of fox squirrels, including site 1, are characterized by:

- large contiguous areas, over 120 hectares, with no housing or automobile traffic
- residential development absent or only on the perimeter of each course or the entire club
- adjoining golf courses on at least 2 sides of the club
- undeveloped forest on at least 1 side
- lack of busy roadways around the course
- easy movement of fox squirrels from 1 course to another, often aided by large trees across canals or smaller streets
- large, open, pine-rich tree stands, with cypress, palms and a variety of native tree species
- few or no areas of forest with heavy understory growth
- high-quality nesting sites in minimally trimmed cabbage palms, bromeliads, or large trees, often pine and cypress
- spring and early summer food supplies available from diverse native species, fungi rich litter areas, non-native tree species, or artificial food sources.

Four of these 6 high level courses will have further development along the fairways and all will have increased development around their boundaries within the next 10 years. Except for site 1 and its companion Pines course, squirrels fed from feeders or begged from golfers.

The future of fox squirrels at even these 6 high level courses will depend on the maintenance of high quality tree stands through understory clearing, and planting and replacement of native trees. Changes in surrounding landscapes and food supplies offered at feeders will also affect squirrel survival. Given the lack of development at site 1 and the relative protection of the surrounding buffering courses it appeared to offer a relatively stable, high quality environment for fox squirrels, though it is certainly suburban and will eventually become more isolated. The other high level courses will undoubtedly undergo much more change with stronger potential for declining habitat.

The 7 courses with an LEI over 0.90 obviously provided habitat superior to any other courses in the study and each had a strong combination of favorable landscape attributes. The remaining 53 courses had LEI ratings of 0.76 or lower (Fig. 33, Appendix B). Each of these courses had one or more strong negative elements in their landscapes. Features of isolation, course configuration, low quality vegetation, and heavy understory, combined to decrease the ability of these courses to foster fox squirrel populations.

Course isolation within a heavily developed landscape cannot be mitigated in most cases. This is especially true if the course is small and contains few or scattered tree stands. A group of 9 older courses with low LEI ratings is circled in the lower portion of Figure 33. Each of these courses is the only course in an 18 hole club. The courses may have experienced loss of trees with long-term development. They frequently have few remaining tree stands and low levels of native tree species, especially pines. They are surrounded by residential and commercial development, though some are adjacent to similar courses. At first glance they may appear to offer fox squirrel habitat, but in fact, they provide insufficient food and nesting resources for this relatively large squirrel species.

Complex course configurations, as presented previously in Figure 8, levels B and C, are a common landscape element that create precarious habitat for fox squirrels. Unlike the higher LEI courses which have no development or only perimeter development, 39 of the 53 courses (74%) with LEI below 0.75 have intensified or connected perimeter patterns, or radiating interior development. Such development configurations divide the course and the bordering rough areas into small patches. These patches may or may not contain high quality tree stands, but these divided landscapes require squirrels to move though a maze of housing and streets in search of food, mates, and nesting sites. For animals with home ranges of 10 to 100 hectares and more, the increased fragmentation of an already fragmented landscape becomes even more precarious and stressful, as resources become more widely spread.

Development of courses with complex configurations creates a landscape which is ultimately highly unfavorable to fox squirrels. Deceptively, initial and temporary stages of development may actually improve habitat for fox squirrels. The early development may increase edges and open the forests understory, thus creating the habitat fox squirrels prefer. Eighteen of the level 3 courses (72%) are at this stage. Unfortunately, as courses age and development continues, construction removes tree stands and corridors required by fox squirrels. Vehicle traffic within and around a course increases and the habitat becomes less productive and more stressful for fox squirrels. The result, as seen at site 2, is that fox squirrel home ranges must become exceptionally large to reach scattered resources. Constant travel in a developed landscape from one feeding patch to another is stressful and hazardous. This situation is especially difficult for younger squirrels. As these small populations of widely scattered individuals become more isolated, they become more susceptible to stochastic events or dying out in years of low food production.

Low quality vegetation stands are common in golf course landscapes. Few courses have a high diversity of native species or large pine stands, few have large areas of pine litter to support growth of fungi, and few have the older, large trees which can offer ideal nesting sites. The first component of the LEI indicates the quality of the vegetation at a course. The 6 high level courses each have a rating of 0.9 and higher in this component. Of the remaining 54 courses, only 4 are above 0.80 in this component, while 30 of the courses, 50% of those in the study, have ratings below 0.6.

Heavy understory, with the dense growth of vines and shrubs in tree stands, is a landscape element that renders habitat unsuitable to fox squirrels. Eighteen courses in the study (30%) have varying amounts of heavy understory in their landscapes. For 16 of the 18 courses it is just one impediment to fox squirrel presence. Four of the 16 courses are circled in Figure 33. They continue be developed and have complex course configurations with highly fragmented habitat. Clearing of the understory in these courses will not create quality fox squirrel habitat

The four prominent elements which affect the quality of fox squirrel habitat on golf courses vary in their ability to be changed through good management. Two of these, course isolation and course configuration are critical elements affecting squirrel movements and the availability of resources. They must be addressed prior to development. The latter two, the presence of heavy understory, and the composition and density of tree stands, can be mitigated to some degree on an existing course, though they will not nullify the impacts of isolation, heavy development, and poor course configuration in the long run.

The improvement of the tree stands and ground cover should be encouraged on courses which currently have fox squirrels in residence or in the adjacent lands. While all level 3 and 4 courses are candidates for vegetation improvement, the 11 courses which have high quality courses for neighbors should be strongly encouraged to undertake habitat improvement for fox squirrels (Fig. 33). Work to increase and diversify native tree species, to create clear understory, to increase the number of moderately trimmed palms, to increase spring food sources, and to increase areas of pine litter ground cover will improve habitat.

In addition to this larger group of level 3 and 4 courses, two relatively new, non-residential courses east of I-75 warrant special attention for habitat improvement efforts. The 2 courses, each 18 holes at the time of the study, are part of clubs that will become 36 holes or larger. The courses contain large stands of pines, cypress, palms, and associated native tree species. They are surrounded by undeveloped forests, large-lot residential areas and agriculture. They are less than 3 km apart. At the time of the study both courses had heavy understory growth and the resulting low LEI ratings and low numbers of fox squirrels. Habitat improvement through understory clearing would surely increase the potential for these clubs as fox squirrel habitat. Their position in a less developed landscape and their non-residential status gives them a unique opportunity to provide habitat for Big Cypress fox squirrels.

Summary

Will golf courses provide habitat for Big Cypress fox squirrels in rapidly developing southwest Florida where human populations are expected to double by 2020? As noted earlier, even the 6 courses with high levels of squirrels do not all have a strong potential as future fox squirrel habitat. Of these 6, site 1 and its companion course at Royal Poinciana, offer the most favorable and most secure habitat for fox squirrels over the next 2 decades. The other 4, as residential courses, will continue to be developed and will have greater changes within and around their boundaries. Their potential will decline.

The remaining 54 courses will not provide good, long-term resources for fox squirrels. Certainly, all of the 23 courses in levels 1 and 2, have more than one strongly negative landscape element and most do not have the potential to support fox squirrels even with mitigation of vegetation. Most of the 31 courses at level 3 and 4 will not provide good quality habitat for the long-term due to unalterable planning and design patterns.

This study demonstrated that even in extremely high quality habitat, Big Cypress fox squirrels require large tracts of land for daily and seasonal movements and even larger ones to allow for dispersal of subadults. Few courses or groups of courses offer safe and stable habitat in large enough tracts to endure the upcoming intensity of development, especially in the western sections of Lee and Collier counties. The few that do must maintain open, diverse, pine-rich forested areas, preferably with substantial areas of pine litter ground cover. Maintenance of such a landscape is labor-intensive and expensive. Fewer than 5 of the 48 clubs examined in this study are capable of providing the habitat required to maintain golf course populations through the intensive development expected between now and 2020.

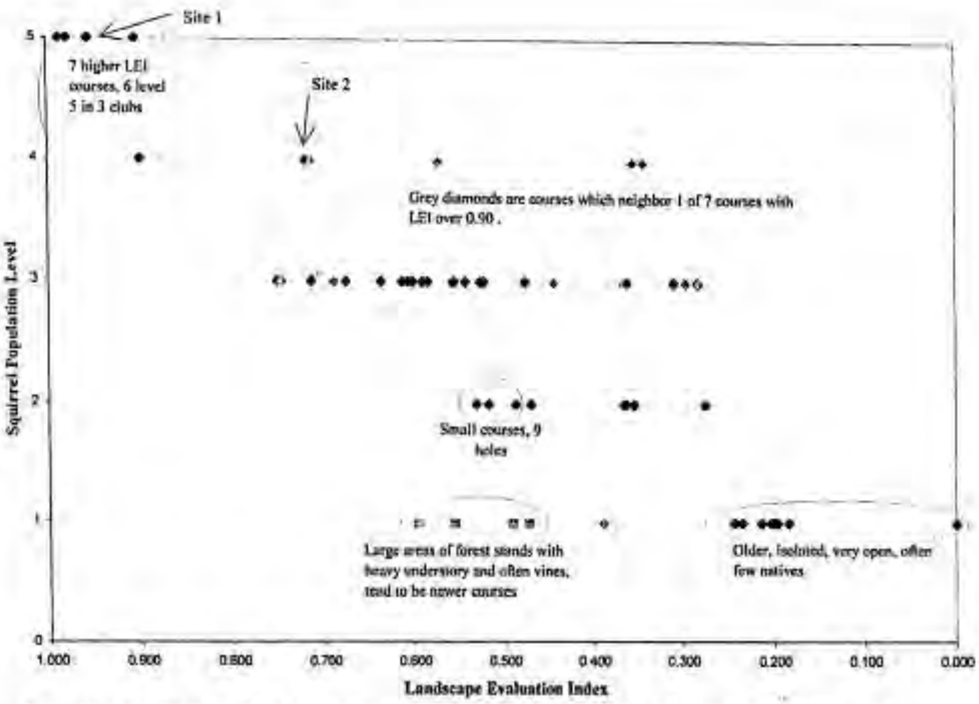

Figure 33. Landscape Evaluation Index and squirrel population levels with highlighting of course groups to accompany discussion.

MANAGEMENT RECOMMENDATIONS

Management for quality Big Cypress fox squirrel habitat must start at the landscape level. Placement and configuration of courses and the development which accompanies them is critical. Because fox squirrels use large areas, up to 150 hectares, for daily and seasonal movements, they require large contiguous areas of suitable habitat free from vehicle traffic and dense development. They must be able to move from one club to another as few single courses will provide adequate habitat. Developments should be connected by open forested corridors. Movement across 2 lane roadways can be facilitated by maintaining large over-hanging trees. Squirrels have adapted to using wooden walkways through wetlands at several southwest Florida courses. This indicates they would be able to do so to cross other obstructions, perhaps even busy roadways separating 2 courses or clusters of courses.

A course or club must be designed to contain large contiguous areas, 120 hectares per club, of green space with large, open stands of native trees. This should be accomplished by concentrating the development either around the outside edges and leaving the central area of the course as green space or by concentrating development in the center, with only 1 roadway into the developed center. This creates a large circle of green space free of vehicle traffic. Adjoining courses with this central development could provide large areas for wildlife.

In more recently developed courses, the design and planning phase has included much attention to preserving lands within the developed areas that have been designated as critical wetlands or drier pine habitat for gopher tortoises. This often appears to preserve large areas of habitat suitable for fox squirrels. In truth, the habitats do not remain suitable for many of the species they are designed to conserve, and they generally become unsuitable for fox squirrels. Areas set aside as native habitat are allowed to become clogged with invasive vines and a heavy understory of native and exotic shrubs and small trees. The resulting vine-infested forests often become barriers to wildlife movement, instead of habitat and corridors. Without proper training in management of wild habitats or the funding to carry out the required tasks of burning or hand clearing, managers cannot preserve these habitats. If such patches are to be preserved within private property, funding for maintenance and training must be provided and regular checks must be made to see that landowners comply with management plans. The management and usefulness of these areas require examination. Are they the best way to preserve wildlife habitat? Are they proving beneficial to the species they are intended to protect? If they are to be maintained, what programs are required to insure they fulfill their expected roles in the landscape?

Big Cypress fox squirrels have shown a strong dependence on pines and cypress, using them for food, nesting, and resting areas. Preservation and planting of pines and cypress should be strongly encouraged. Golf courses are currently moving away from full coverage irrigation and this will hopefully allow more native pines to persist in developed landscapes. In addition to pine and cypress, planting a diversity of native trees, including oaks, maples, cabbage palms, bays, and hollies should be encouraged. The current study showed a heavy use of spring-fruiting non-native tree species by fox squirrels. Though the planting of non-natives is against the policy of groups such as the Audubon Sanctuary Program, they do allow squirrels to obtain year-round food in a small area. Managers should create diverse stands of trees which provide a range of food sources within a small space. This forms a richer, more resilient food source and provides the diverse environment fox squirrels prefer for brood nests. Course designers and managers must have information on native plant sources, and plants must be available at competitive prices before native plantings will become common.

On completed courses, correct management of existing tree stands is crucial. Fox squirrels require open tree stands for movement and frequent ground feeding. Forested areas must have open understories, free of dense shrubs, vines and tall grasses. This can be accomplished by hand clearing or light burning. At present, it is extremely difficult to obtain burning permits for golf courses, despite the fact that ready irrigation systems provide excellent protection against uncontrolled burns. The smoke created by such a burn is undoubtedly less harmful than most of the chemicals used in hand clearing. Progress along these lines, and studies addressing the efficacy of burning golf course roughs, would help the more forward thinking managers who would like to promote burning as a management tool for larger forested stands within their courses.

Cabbage palms provide fox squirrels with high quality nesting sites, food, and sheltered resting areas. Current golf course management practices frequently involve extreme trimming of palms. This removes all the fruiting stalks and the lower leaves. What remains is barely a tree and is not habitat for the range of wildlife frequently seeking protection from sun and storms under the layered leaves and long leaf bases. Moderation in trimming is one of the easiest and least expensive management techniques benefiting fox squirrels. It should be encouraged.

The presence of pine litter ground layers in pine stands is an important management technique that promotes squirrel feeding on fungi. The fungi have been shown to be beneficial to pines and provide a needed food source in early summer months. The litter layers can readily reduce maintenance and remove the need for irrigation of grass in a stand of native trees.

If nesting sites in pines, large bromeliads, cabbage palms, and cypress are in short supply, managers may wish to supplement with nest boxes. Wood duck boxes are the proper size and should be placed at least 5 meters up the trunk of a fairly large tree. Such boxes will provide shelter in the few times of extreme cold weather and in driving rain and wind storms. They may also be used for brood nests.

Education is critical for management of fox squirrels on golf courses. Managers must be educated on methods to create and maintain favorable habitat. Members should also be educated. Squirrels are easily killed on courses by cart drivers who are speeding along and looking for golf balls instead of squirrels. Members should at least be encouraged to look out for squirrels, on the course and on the roadways into the course. Members must also be educated not to feed squirrels. If squirrels are not fed by people they will not be attracted to people or carts. They will avoid carts and not hang around cart paths at tees and greens waiting for food. They will be less likely to be killed by speeding carts or angry golfers who have just lost a muffin to a sneaky squirrel.

If course members or managers have the desire to feed fox squirrels, this should be done in an isolated area away from cart or automobile traffic. Food should be spread on the ground, not in small feeders which require squirrels to climb around on the same small area. Such high concentration and repeated rubbing of fur and feet on a feeder creates an ideal vector for contagious diseases, especially skin fungus. Food should be natural, not processed human food. Squirrels benefit from nuts, berries, and grains. Trimmed fruits from palms may also be added to the feeding site.

Both club members and fox squirrels will benefit if education programs share something of the lives of fox squirrels. Many golf course members in Florida are not familiar with our native wildlife and plants. A little education may go a long way in helping them to understand and appreciate these unique and beautiful fox squirrels and the larger natural heritage of Florida.

APPENDIX A

Common Name	Family	Species	Site 1 Cypress	Site 2 Royal Palm	Royal Poinciana Pines
Red maple	Aceraceae	*Acer rubrum*	x		x
Holly	Aquifoliaceae	*Ilex opaca*	x	x	x
Schefflera	Araliaceae	*Schefflera actinophylla*	x		x
Norfolk Island Pine	Araucariaceae	*Araucaria heterophyla*		x	x
Queen palm	Arecaceae	*Arecastrum romanzoffianum*	x	x	x
Fishtail palm	Arecaceae	*Caryota mitis*		x	
Royal palm	Arecaceae	*Roystonea spp.*	x	x	x
Cabbage palm	Arecaceae	*Sabal palmetto*	x	x	x
Jacaranda	Bignoniaceae	*Jacaranda mimosffolia*	x	x	
Trumpet Tree	Bignoniaceae	*Tabebuia argentea*		x	x
Toog Tree	Bischofiaceae	*Bischofia javanica*	x		x
Austrailian Pine	Casuarinaceae	*Casuarina cunninghamiana*		x	
Black olive	Combretaceae	*Bucida buceras*	x	x	x
Southern Red Cedar	Cupressaceae	*Juniper silicicola*			x
Tallow tree	Euphorbiaceae	*Sapium sebiferum*	x	x	x
Earleaf acacia	Fabaceae	*Acacia auriculiformis*	x	x	x
Rosewood	Fabaceae	*Dahlbergia sissoo*	x	x	x
Poincianna	Fabaceae	*Delonix regia*	x		x
Copper pod	Fabaceae	*Peltaphorum pterocarpum*	x		
Pongam	Fabaceae	*Pongamia pinnata*			x
Laurel oak	Fagaceae	*Quercus laurifolia*	x	x	x
Live oak	Fagaceae	*Quercus virginianum*	x	x	x
Red bay	Lauraceae	*Persea borbonia*	x		
Avocado	Lauraceie	*Persea americana*			x
Mahogany	Meliaceae	*Swietenia mahogani*	x	x	
Wild Tamarind	Mimosaceae	*Lysiloma latisiliquum*	x		
Fig	Moraceae	*Ficus spp.*	x		x
Eucalyptus	Myrtaceae	*Eucalyptus sp.*			x
Eugenia	Myrtaceae	*Eugenia sp.*		x	
Java plum	Myrtaceae	*Syzigium cumini*	x		x
Bottle-brush	Myrtacece	*Callistemon rigidus*	x	x	x
White Ash	Oleaceae	*Fraxinus americana*			x
Screw Pine	Pandanaceae	*Pandanus utilis*	x		x
Slash pine	Pinaceae	*Pinus elliottii var. densa*	x	x	x
Silk oak	Proteaceae	*Grevillea robusta*	x		x
Orange	Rutaceae	*Citrus sinensis*	x	x	x
Grapefruit	Rutaceae	*Citrus x paradisi*		x	x
Pond cypress	Taxodiaceae	*Taxodium ascendens*	x	x	x
Bald cypress	Taxodiaceae	*Taxodium distichum*	x		x

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APPENDIX B

Club	Course	Course #	Squirrel level	LEI
Quail Creek	Quail course	30	5	0.987
Quail Creek	Creek course	29	5	0.987
Royal Poinciana	Pines	46	5	0.979
Royal Poinciana	Cypress Course	48	5	0.956
Fiddlesticks	Long Mean	34	5	0.955
Fiddlesticks	Pipers Challenge	33	5	0.904
Imperial	Imperial East	45	4	0.900
Wyndemere	Green and White	32	3	0.751
Eagle Ridge		28	3	0.745
Royal Palm		52	4	0.719
Imperial	Imperial West	43	4	0.713
Forest	Bear	36	3	0.713
Quail West	Preserve Course	12	3	0.687
Lely Country Club	Flamingo Island	17	3	0.674
Lely Country Club	Classics Course	11	3	0.635
Forest	Bobcat	16	3	0.612
Foxfire	old 18, red	35	3	0.605
Pelican Nest	Gator &Seminole	25	3	0.600
Bonita Bay	Marsh Course	6	1	0.595
Bears Paw		41	3	0.589
Wyndemere	Gold course	31	3	0.583
Old Hickory		13	4	0.571
Name withheld		5	3	0.555
Bonita Bay	Bay Island	7	1	0.554
Countryside GC		22	3	0.554
Wildcat Run		23	3	0.541
Foxfire	new 9	3	2	0.530
Royal Wood		19	3	0.525
Glades	Palmetto	44	3	0.522
Spanish Wells	North 9, New 9	2	2	0.516
Pelican Marsh	Marsh Course	8	1	0.491
Glades	Pines	53	2	0.487
Spanish Wells	east and west 9	39	3	0.475
Vines		24	1	0.473
Olde Florida		9	2	0.470
Wilderness		42	3	0.443
Quail West	Lakes	4	1	0.388
Eastwood		40	2	0.365
Colliers Reserve		10	3	0.365
Marriott Club		15	2	0.363
Audubon CC		18	3	0.361

APPENDIX B. Continued

Club Course	Course #	Squirrel level	LEI
Hole in the Wall	58	4	0.354
Vineyards North	21	2	0.354
Embassy Woods	14	2	0.354
CC of Naples	55	4	0.343
Vineyards South	20	3	0.309
Bonita Bay Cypress C(	1	3	0.309
Quail Run	50	3	0.296
Hibiscus	56	3	0.283
Palm River	38	3	0.281
Cross Creek	27	2	0.275
Marco Shores	49	1	0.243
Myerlee	47	1	0.235
Windstar	26	1	0.214
Ft. Myers GC	60	1	0.204
Cypress Lake	54	1	0.200
Naples Beach	59	1	0.196
Moorings	57	1	0.196
Whiskey Creek	51	1	0.184
Club at Pelican Bay	37	1	0.000

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APPENDIX C

Home range data for Site 1, December 1995 through October 1996

Squirrel #	Sex	Stage at capture	Stage most of trapping season	Months tracked	Total radio-tracking locations	Radio-locations used in home range analysis	Home range size, 95% contour (ha)	Core area size, 50% contour (ha)	Time in study
15 ROPO	F	Adult	Adult	7.0	103	79	7.98	1.92	entire
5 ROPO	F	Adult	Adult	9.5	100	83	8.80	2.61	entire
2 ROPO	F	Sub	Adult	10.5	147	106	10.17	1.99	entire
6 ROPO	F	Adult	Adult	9.5	131	108	10.71	2.53	gone 96
1 ROPO	F	Sub	Adult	7.5	67	51	10.92	1.39	gone 96
3 ROPO	F	Adult	Adult	9.0	129	100	12.00	1.59	entire
7 ROPO	M	Sub+	Adult	5.5	51	37	42.52	6.41	entire
4 ROPO	M	Sub+	Adult	3.3	45	21	45.98	8.51	gone 96
16 ROPO	M	Adult	Adult	5.0	47	43	76.45	19.44	gone 96
17 ROPO	M	Adult	Adult	4.0	51	43	118.40	22.44	gone 97
14 ROPO	F	Sub	Sub	5.0	19	*15	10.66	1.00	disperse 96
8 ROPO	M	Sub	Sub	8.0	89	66	14.36	5.71	entire
12 ROPO	M	Sub	Sub	3.0	53	24	15.89	1.50	gone 97
10 ROPO	F	Sub	Sub	4.5	24	*19	20.22	1.15	disperse 96
9 ROPO	F	Sub	Sub	7.5	64	*38	22.56	3.37	disperse 96
13 ROPO	M	Sub	Sub	6.0	76	*45	49.07	4.83	disperse 96
11 ROPO	M	Adult	Adult	2.0	17	NA			entire

* Asterisk, used only points prior to dispersal

APPENDIX C continued

Home range data for site 1, November 1996 through July 1997

Squirrel #	Sex	Stage at capture/ recapture	Stage most of trapping season	Months tracked	Total radio-tracking locations	Radio-locations used in home range analysis	Home range size, 95% contour (ha)	Core area size, 50% contour (ha)	Time in study
28 ROPO	F	Adult	Adult	6.5	66	63	9.08	2.05	2nd yr
2 ROPO	F	Adult	Adult	8.0	78	70	13.14	2.10	entire
3 ROPO	F	Adult	Adult	7.5	75	61	19.21	3.96	entire
15 ROPO	F	Adult	Adult	9.0	77	67	19.66	3.30	entire
5 ROPO	F	Adult	Adult	7.5	78	63	20.92	4.12	entire
8 ROPO	M	Adult	Adult	8.5	68	62	44.06	9.50	entire
22 ROPO	M	Adult	Adult	8.0	78	69	48.42	10.62	2nd year
11 ROPO	M	Adult	Adult	5.5	55	49	99.89	12.82	entire
7 ROPO	M	Adult	Adult	7.5	71	63	114.10	16.87	entire
18 ROPO	M	Adult	Adult	7.0	52	48	118.00	15.26	2nd yr,died
20 ROPO	M	Adult	Adult	8.0	52	47	121.00	18.20	2nd year
27 ROPO	F	Sub	Sub	6.5	62	57	5.88	0.47	2nd year
29 ROPO	F	Sub	Sub	6.5	64	59	10.31	2.24	2nd year
25 ROPO	M	Sub	Sub	7.5	27	27	12.11	1.77	2nd yr,died
21 ROPO	M	Sub	Sub	8.0	74	68	16.62	4.23	2nd year
23 ROPO	M	Sub	Sub	7.5	76	65	17.30	3.65	2nd year
26 ROPO	M	Sub	Sub	7.0	64	60	20.80	3.80	2nd year
24 ROPO	F	Sub	Sub	7.5	65	60	21.47	3.41	2nd year

APPENDIX C continued

Home range data for site 2, January 1997 through July 1997

Squirrel #	Sex	Stage at capture/ recapture	Stage most of trapping season	Months tracked	Radio-locations used in home range analysis	Home range size, 95% contour (ha)	Core area size, 50% contour (ha)	Time in study
ROPA 4	F	Adult	Adult	7.0	51	30.57	1.58	entire
ROPA 6	F	Adult	Adult	6.5	49	13.06	1.87	entire
ROPA 1	M	Adult	Adult	7.0	51	136.10	29.88	entire
ROPA 8	M	Adult	Adult	6.0	31	303.80	71.38	entire
ROPA 2	M	Sub+	Sub+	0.5	NA			gone
ROPA 3	M	Sub	Sub	2.0	14	40.76	5.46	died
ROPA 5	M	Sub	Sub	2.0	11	25.77	5.07	died
ROPA 7	M	Sub	Sub	6.0	48	108.50	15.28	left course

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POPULATION ESTIMATES, HABITAT REQUIREMENTS, AND LANDSCAPE DESIGN AND MANAGEMENT FOR URBAN POPULATIONS OF THE ENDEMIC BIG CYPRESS FOX SQUIRREL (*Sciurus niger avicennia*)

By

REBECCA SELFRIDGE DITGEN

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

1999

Dedicated to my father,
who first took me outdoors and shared his love for wild things,
and in loving memory of my mother,
whose life of gentle strength and patience continues to inspire me.

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Abstract of Dissertation Presented to the Graduate School
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Requirements for the Degree of Doctor of Philosophy

POPULATION ESTIMATES, HABITAT REQUIREMENTS, AND LANDSCAPE DESIGN AND MANAGEMENT FOR URBAN POPULATIONS OF THE ENDEMIC BIG CYPRESS FOX SQUIRREL (*Sciurus niger avicennia*)

By

Rebecca Selfridge Ditgen

December 1999

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

The Big Cypress fox squirrel (*Sciurus niger avicennia*) is endemic to open forests of southwest Florida. Rare in wild lands of southwest Florida, its remains on certain golf courses in Lee and Collier counties. This study was carried out from August 1995 to December 1997 to document squirrel population levels in a variety of golf course landscapes, to determine habitat use and requirements of course populations, and to provide guidelines for favorable landscape design and management in developing areas.

Elements of vegetation composition and structure, and landscape configuration were recorded at 60 golf courses. Counts of squirrels were made at each course to determine fox squirrel population levels. A Landscape Evaluation Index, developed from

cluster and factor analyses of landscape elements, allowed ranking of the 60 courses in terms of their suitability for fox squirrels.

Radio-telemetry was used to examine home range size, habitat use, and population dynamics at 1 high quality course and 1 lower quality course. Tracking studies indicated a density of 42.4-49.8 squirrels/km^2 at Site 1 and a density of 6.3-8.2 squirrels/km^2 at Site 2. Squirrels fed heavily on pine and cypress from late summer to mid-winter, and relied on native and exotic species between March and May. At Site 2, squirrels showed a heavy reliance on feeders between January and July.

The Index identified 7 courses with high quality landscapes. All were part of 36 hole courses, contained large stands of open pine and cypress, and had large contiguous areas free of automobile traffic. The remaining courses had unfavorable landscape elements: isolation within developed landscapes, small stands of undesirable species, heavy understory vegetation, and complex development patterns. Twenty-three courses offer little opportunity for habitat improvement. Thirty courses can improve habitat for present fox squirrel residents, but do not contain the landscape features required for long-term populations.

Landscape design and placement are crucial in creating and preserving fox squirrel habitat. Courses, or groups of courses, must contain large areas free of roadways and development to allow safer movement within large home ranges. Vegetation must include large stands of pine, cypress, cabbage palms, and associated native trees with open understories.

INTRODUCTION

Framework

In the past decade, questions of ecologically sound landscape design and management have attracted the attention of an increasing diversity of scholars and practitioners. Researchers in wildlife and conservation biology, landscape architects, planners, developers, and a range of physical and biological scientists have worked to integrate a growing body of biological principles and physical science with species and community ecology to manage landscapes for diversity and sustainability (Forman 1995, Saunders et al. 1991, Soule and Kohn 1989, Turner 1989). With an understanding of the rapid rates of land conversion and a cognizance of perceived human needs, the visions of design and management reach from large-scale regional preserves (Carr et al. 1994) and statewide, single species management plans (Mech 1998, Stith et al. 1996), to smaller scale, county-wide urban parks (Mazzotti and Morgenstern 1997) and woodlot planning (Fitzgibbon 1993).

Within this larger movement toward ecological design and management, stirrings of interest have emerged in some previously untouched arenas. One of these is in the community of golf course designers and managers, where individuals have begun to search for ways to create more ecologically responsible golfing developments (Grigg 1990, Foy 1989). Golf courses, considered by opponents of development to be the antithesis of ecological diversity and sustainability, have been portrayed as destroyers of wildlands and conduits for pesticides and fertilizers (Edmundson 1987, Foy 1989, Tietge 1992). In response to such criticism and because of personal and professional interest in a more diverse environment, advocates for change are attempting to move golf courses and accompanying developments toward more ecologically sound designs, to create more "naturalistic landscapes", and thus to encourage the preservation of native plants and animals (Dodson 1990, 1994, Leuzinger 1994).

To date, much of the effort toward responsible golf course design and management has focused on badly needed reviews of turf systems and course facilities, as well as broader looks at maintenance of native vegetation in roughs (Balough and Walker 1992, European Golf Association Ecology Unit 1995, Weston 1990, 1994). Scientific research examining the benefits to wildlife of more natural and diverse golf course landscapes is just emerging. Initial research addresses the role these newer or more "naturalistic" courses may play as habitat for birds. Early work indicates they may contain more species than surrounding landscapes of agriculture or dense development (Terman 1997). Because even the most sensitively designed golf courses will save native vegetation in patches separated by manicured, exotic grass, and generally contain private homes and accompanying vehicle traffic, they cannot be expected to favor bird species easily disturbed by humans or those in need of large areas without edges (Moul and Elliott 1994, Terman 1997). Recent work in Kansas has shown that more natural courses preserving large remnants of native vegetation may create an avian habitat intermediate to dense development and wildlands (Terman 1997).

While there is a growing interest in understanding and improving golf courses as habitat for avian species, little research has been undertaken to examine their ability to support mammals or other non-avian wildlife, nor has research considered the impact of surrounding landscapes on golf course wildlife (Terman 1997). Work by Jodice and Humphrey (1992) in southwest Florida suggested that the threatened Big Cypress fox squirrels may occur at higher densities on golf courses near the coast than in preserve lands to the east (Jodice and Humphrey 1992, 1993, Maehr 1993). An investigation of golf courses as potential habitat for these relatively small, though wide-ranging mammals, offers an excellent opportunity to address the broader question of golf course landscapes as habitat for non-avian wildlife.

Problem

Fox squirrels (*Sciurus niger*) are a diurnal, arboreal species inhabiting open forests of the eastern and central United States (Hall 1981). The 4 subspecies of the southeastern states are larger and more varied in color than those to the north and west and prefer open pine forests with oaks and associated hardwoods (Kantola and Humphrey 1990, Moore 1957, Weigl et al. 1989). Of these, the Big Cypress fox squirrel (*S. n. avicennia*) is the most restricted in geographic range, found only in the southwest tip of Florida, south of the Caloosahatchee River and west of the true Everglades. Native to open stands of slash pine (*Pinus elliottii*), cypress (*Taxodium spp.*), and tropical hardwoods, these squirrels frequently feed and move on the ground. Their relatively large size and habits of ground use make them especially vulnerable to the widespread landscape changes promoted in recent decades (Humphrey and Jodice 1992, Moore 1956, Williams and Humphrey 1979).

Human activities affecting fox squirrel populations are widespread and varied in southwest Florida. Changes in fires cycles on large preserves and privately owned forests have allowed development of heavy understory vegetation not conducive to fox squirrel movement and ground feeding. Conversion of range lands to citrus groves in northern and central agricultural areas has eliminated open, parklike habitat favorable to fox squirrels (Pearlstine et al. 1997). Rapid urbanization of coastal property in Lee and Collier counties, from Naples to Ft. Myers, has created fragmented habitat with serious obstructions to squirrel movement, resulting in isolated populations amid shrinking green space (Moore 1954, Williams and Humphrey 1979, Jodice and Humphrey 1993).

Demographic trends in Lee and Collier counties, two of the fastest growing counties in Florida, clearly illustrate the forces driving land conversion in the coastal zones of both counties. The 1970 permanent population of Collier County was 38,040. Between 1980 and 1990, Collier County grew by 77% (Collier County DESD 1996). In 1995, Collier had a permanent population of 197,400 and a seasonal population of 245,000. Projections indicate it will grow to between 508,00 and 770,00 by 2020 (Collier County 1996). The 1999 population of Lee County is given as 410,000 and is expected to reach 940,800 in 2020 (Lee County DCD 1998). Most of the development in both counties will be concentrated along the coast, with Collier County expecting full development west of highway 951 by 2050 (D. Weeks, person. commun.).

While fox squirrel populations have apparently declined in preserves such as Big Cypress and Corkscrew Swamp and have vanished from dense housing developments and commercial areas, they remain on certain golf courses within and near the burgeoning developments of western Lee and Collier counties (Deborah Jansen pers. commun., Jodice

1990, Jodice and Humphrey 1992, 1993). Golf courses with remnant open pine and cypress stands preserve fragments of suitable habitat within a swirl of traffic and commerce.

In an effort to understand the ecology of these golf course fox squirrel populations, Jodice (Jodice and Humphrey 1992) undertook a study of their diet and activity patterns on 4 Naples courses in 1989-1990. His work relied on focal-animal sampling of individuals located visually rather than by radio-telemetry, undoubtedly allowing bias in a species that is often difficult to see. His work successfully highlighted questions of population levels and suitability of golf course habitats (Jodice and Humphrey 1993, Maehr 1993). It became clear that little is known about spatial needs, movements, habitat requirements, or demography of these urban populations and still less about the prevalence of these golf course populations and the landscapes that might promote their survival.

To evaluate the usefulness of golf courses as refugia for Big Cypress fox squirrels we must know more about the ecology of the species as well as the impact of landscape features and configuration on their survival. Can they feed, move, reproduce, and survive for sustained periods within the fragmented habitats found on golf courses? Are all courses suitable or just a few? And why? This study will address these questions by looking at home range size, habitat use, feeding patterns and demography of fox squirrels on golf courses and by identifying golf course landscape features favorable to their survival.

The specific goals are as follows:

1. To survey the status of golf course populations and the landscape elements of a range of golf course types in order to determine which features favor their survival. Sixty courses in western Lee and Collier counties will be considered.

2. To gather data on home range size, dispersal, habitat use, and population dynamics through the use of radio-telemetry. Two golf course populations in Collier County will be studied, one with high numbers of squirrels and one with lower numbers of squirrels.

3. To evaluate the potential of the 60 golf courses as refugia for urban populations of fox squirrels.

4. To provide recommendations for design and management of golf course landscapes to improve habitat for Big Cypress fox squirrels.

STUDY SITE

All study sites were located in the western half of Collier and Lee counties in southwest Florida (Fig. 1). The area has a humid subtropical climate with heavy influence from the surrounding warm waters and the seasonal changes in the Bermuda high (Chen and Gerber 1990). These features give rise to cool dry winters and warm, rainy summers and autumns, with extreme events such as occasional hard frosts and hurricanes playing a strong role in the composition of the vegetation community. Native vegetation of the flatwoods physiographic region in which the sites were located includes pine flatwoods, cypress domes, and mangroves. The presence of Entisols, Histosols, and Spodosols reflect a mixed terrain of high, relatively dry, sandy ridges, and low, poorly drained swamps (Brown et al. 1990).

Patterns of temperature and precipitation varied from year to year in the 3 calendar years of the study, with wide deviations from normal in summer precipitation (NOAA, 1995-97). Summer and fall of 1995 were extremely wet. Stations at Ft. Myers and Naples reported 1.7 m or more of precipitation between June 1 and October 31, more than 0.76 m above normal. Flooding and long-term standing water were common on most sites during late summer and fall 1995. In the same months of 1996 the stations received only 0.56 m of rain, a 0.36 m deficit. January 1997 to August 1997, when the tracking studies ended, had normal levels of precipitation. The winter of 1995-1996 had at least 2 cool periods, with 4 nights of 0 C , and widespread damage to the more tropical flora. The winter of

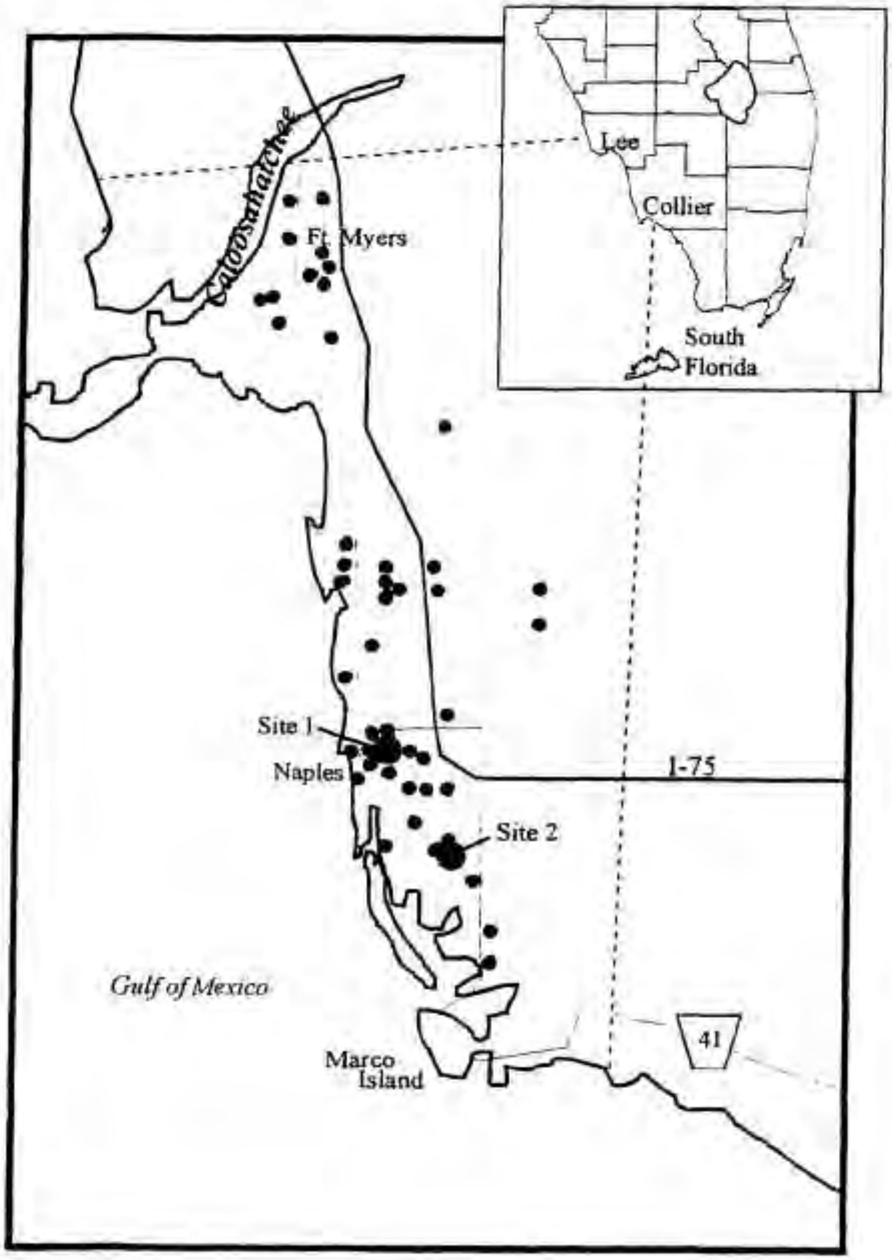

Figure 1. Location of study sites in western Lee and Collier counties. Black dots are clubs visited for landscape and squirrel surveys. Red dots are sites of the radio-telemetry studies.

1996-1997 was warmer than normal. An average January, with warm weather (19 C) and 1 light frost, was followed by 2 months of high temperatures. February averaged 22 C, 3.5 C above normal, and March 24 C, 3 C above normal.

Landscape Study

Of the 60 golf courses selected for the landscape analysis and fox squirrel censusing, 18 were in Lee County, south of the Caloosahatchee River, and 42 were in Collier County. Course landscapes ranged from undeveloped, with large tracts of native vegetation, to intensely developed courses having close-set, multiple story condominiums on both sides of the fairways. Highly developed courses usually allowed for few trees, native or exotic, in the roughs. Courses ranged in age from over 40 years to those recently opened and still under development. The oldest courses in the study, located near the Gulf Coast, commonly were isolated from other clubs and were surrounded by development. On the eastern edge of development courses tended to be newer, often grouped together, and were located within a mixture of increasing development and remnants of pine and cypress stands.

Radio-Telemetry Study

Two 18-hole golf courses in Collier County, Florida, were selected for the radio-telemetry studies (Figs. 2,3). Site 1, the 18-hole Royal Poinciana Cypress Course, was half of a 36-hole private Royal Poinciana Golf Club built in 1971 in central Naples. Royal Poinciana has no residential development within the 135 ha of the golf course grounds. Fairways are bordered by open stands of moderate-size pines (*Pinus elliotti* var. *densa*),

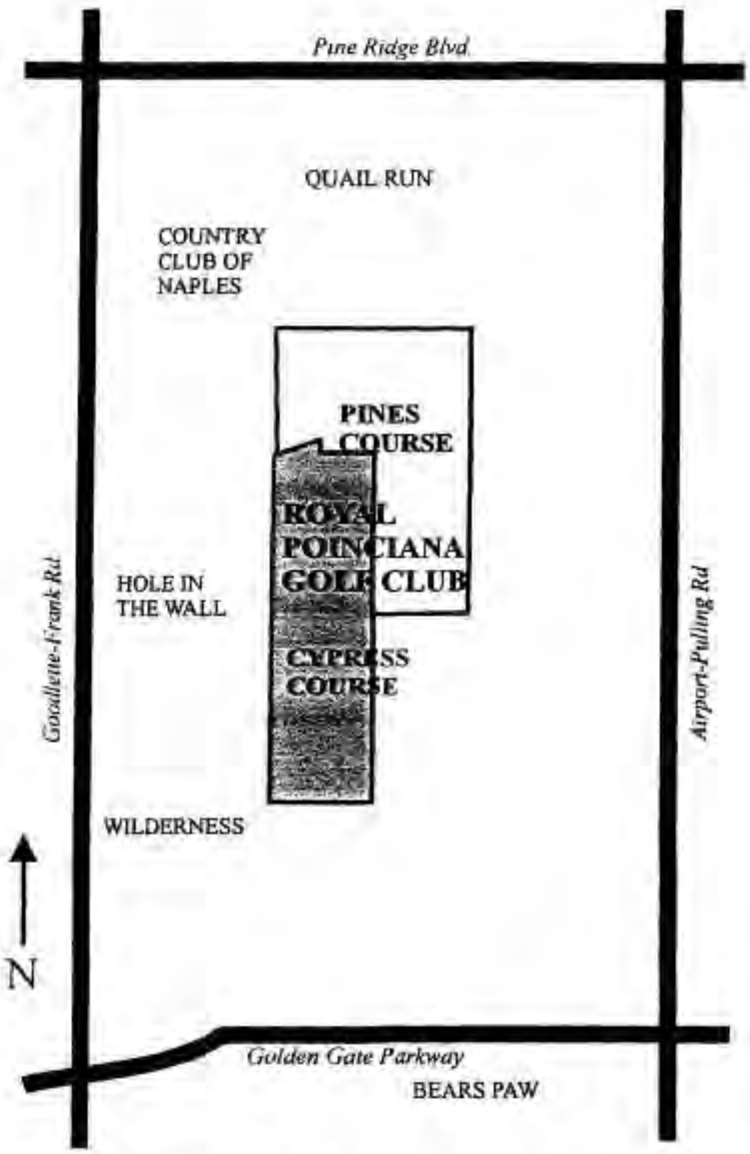

Figure 2. Site 1, location map. Identification of golf courses known to be used by fox squirrels from Site 1, Royal Poinciana Golf Club, Cypress Course. Five courses adjoin Site 1, including the Pines Course in the same club. Bear's Paw is south across Golden Gate Parkway. Stippled area is pine forest.

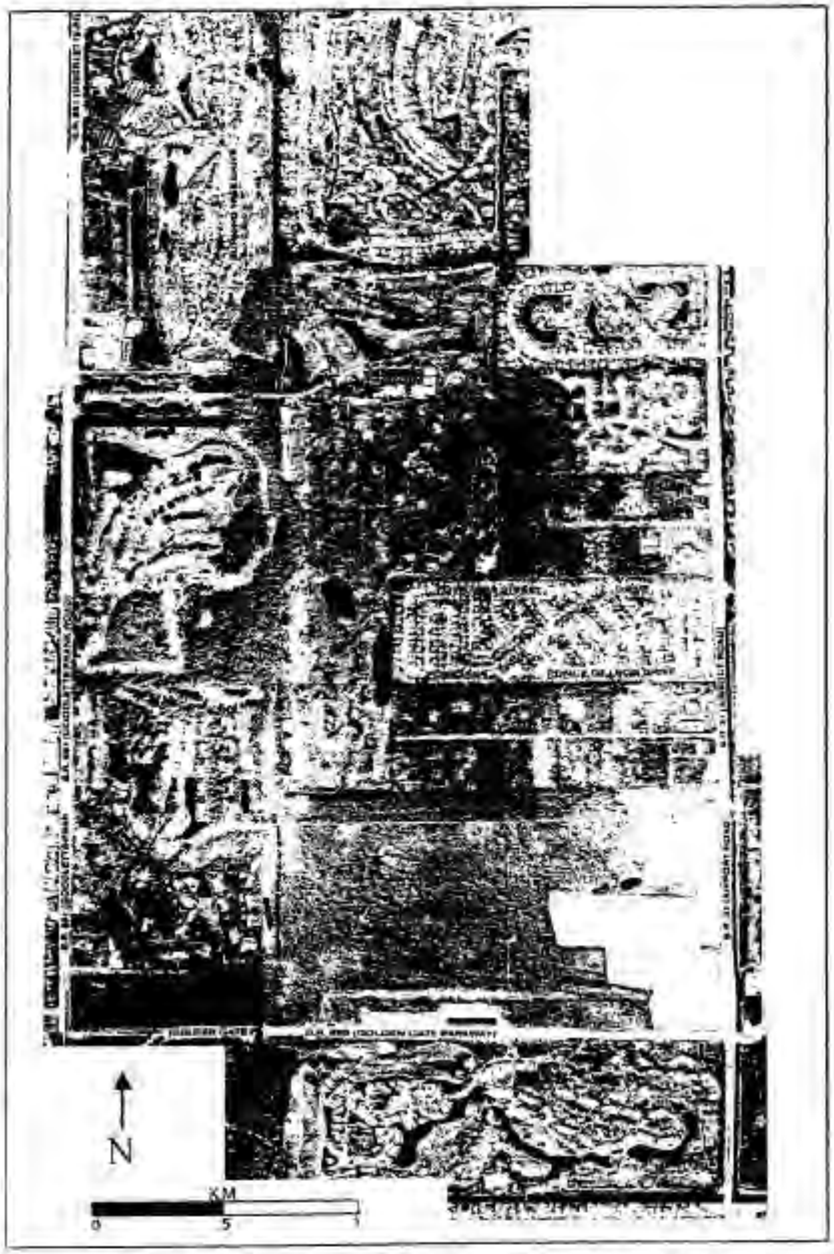

Figure 3. Site 1, aerial photograph. Configuration of Site 1 and the surrounding landscape. Royal Poinciana Cypress Course is located in the center, with 6 other 18-hole courses nearby. Names on Fig. 2.

cypress (*Taxodium ascendens* and *T. distichum*) and cabbage palms (*Sabal palmetto*), and plantings of non-native broad-leafed evergreens (Appendix A).

Automobile traffic around the Cypress Course is limited to a short segment of private entrance roadway on the north side of the Cypress Course, with no public roadways on the boundaries of the course. Three golf courses, including the 18-hole Pines Course within the same club, comprise the western, northern and part of the eastern boundaries. The south boundary is an undeveloped pine stand of 115 ha and the remaining eastern boundary is residential development of varying density. Royal Poinciana and the neighboring clubs are located within a tract of approximately 1020 ha containing 6, 18-hole golf courses, of which 3 are undeveloped, 2 moderately developed, and 1 heavily developed. The tract contains 230 ha of forested land, ranging from drier pine to swampy cypress stands. The 1020 ha tract is bordered by 4 extremely busy roadways, Goodlette-Frank, Pine Ridge, Airport-Pulling, and Golden Gate Parkway.

Known predators at the site included eagles, bobcats, great horned owls, raccoons, rat snakes, and the club house cat, which was allowed to roam the course at night.

Site 2, Royal Palm Country Club, is a developed 18-hole course near the eastern limit of intense suburban development along Highway 41 East (Figs. 4 & 5). The club, built in 1970, and the adjoining housing development cover 150 ha, of which 75 ha are private homes, condominium property and roadways. The club lies within a landscape currently undergoing rapid and dense development. All the fairways have development on both sides, either single family homes or large condominiums. When I began research at this site in 1996, 8 undeveloped, pine-covered lots remained along the fairways. In the next 12 months at least 4 of these were developed, with all of the pines being cut. The

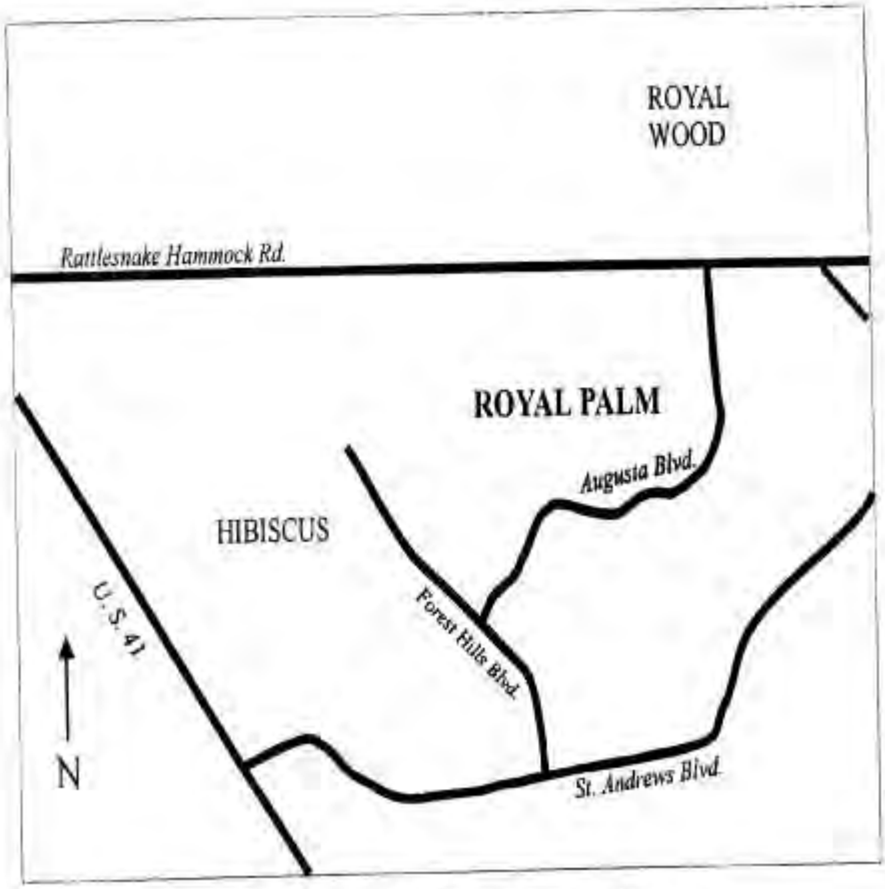

Figure 4. Site 2, location map. Royal Palm Country Club, Site 2, and 2 neighboring 18-hole courses.

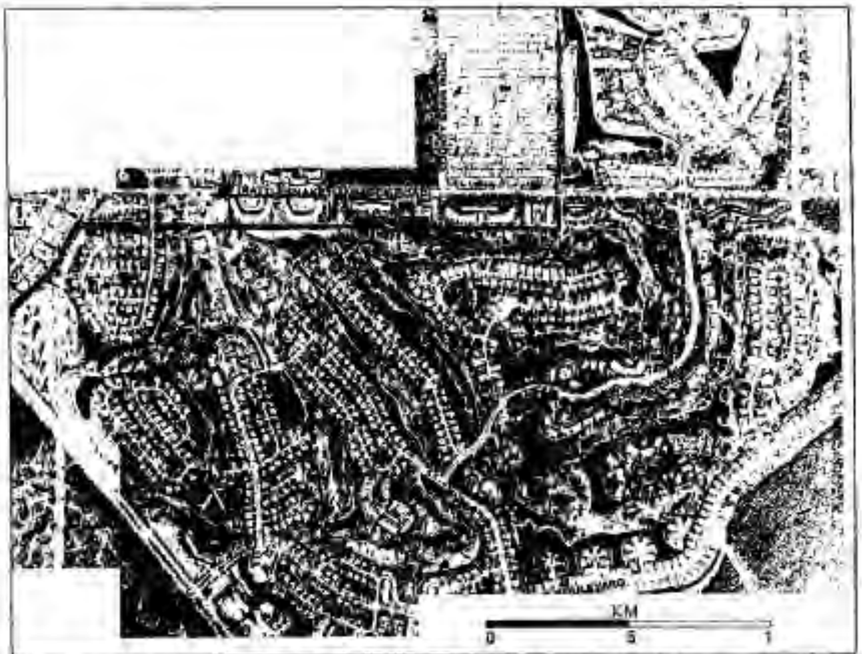

Figure 5 Site 2, aerial photograph. Royal Palm Country Club, and 2 neighboring 18-hole courses. Names on Figure 4.

dominant vegetation of the Royal Palm roughs and the surrounding condominiums is open pine stands. Non-native trees of a limited variety are scattered around the course and are common in the small lots of the surrounding private homes. Cypress trees are present but are not common and generally are small. The southwest boundary of Royal Palm adjoins the public 18-hole Hibiscus Golf Course. The Hibiscus course and surrounding dense development, together 132 ha, have few native tree species and narrow, open roughs with only small and scattered stands of trees (Appendix A). Busy 2-lane and 4-lane roadways border Royal Palm on the north, east and south, and Augusta Boulevard bisects the course from north to south. Known predators at the site included eagles, raccoons, and a domestic cat.

Activity on the courses changed with the seasons. Golf play was heavy on both courses from December until April, with Royal Palm frequently having play on every hole from 0730 until late afternoon. Royal Poinciana was generally less crowded. Summer play was light, with each course closing 1 day a week for intensive maintenance work on the course and roughs. Daily maintenance work began at 0530 or 0600 and continued until late afternoon. In winter, maintenance crews worked on the courses every day, 0630 until 1430 weekdays, and 0630 until noon on weekends. Maintenance for the removal of vegetation in the understory of tree stands included mowing, hand removal of shrubs and herbaceous plants, the addition of pine straw and the use of herbicides. Both clubs irrigated the fairways, greens and tees in the early morning and often again in the early evening.

Cone production on the study courses was noticeably higher in 1996 than 1997. In the summer and fall of 1996, following a wet 1995 summer and fall, cone production on both pine and cypress trees appeared to be high, with both species heavily laden throughout the Cypress Course. In 1997, little cone production was evident on pines and the cypress suffered an infestation of tent caterpillars in the late spring, resulting in widespread defoliation of cypress and lower early season cone production.

METHODS

Landscape Evaluation and Censusing

Surveys of golf course landscapes and fox squirrel populations were conducted to determine the status of fox squirrels and to identify landscape features favorable to their survival.

Sampling

Sixty golf courses in western Lee and Collier counties were selected for landscape analysis and squirrel censusing. In selecting the courses I looked for a range of landscape types relating to

- density of development surrounding the club boundaries, from heavily developed to undeveloped;
- type and configuration of development on the course, from undeveloped, nonresidential courses to those with dense development of houses and/or condominiums;
- character of the rough vegetation, from little and scattered, through open tree stands, to dense forest stands with heavy understory.

To obtain pre-visit information about age and landscape configuration for many of the 80+ courses in Lee and Collier counties I interviewed Tim Hires, Collier's Reserve Country Club, Naples, and Mike Mongoven, Ft. Myers and Eastwood Golf Clubs. I selected 66 courses for examination and contacted the courses through their superintendents of maintenance, individuals frequently most familiar with the landscape activities and wildlife on the courses. Superintendents proved to be excellent, and often interested, sources of information and influence.

I made introductory visits to a majority of the 66 courses in August 1995-December 1995. Exceptions were made for courses flooded by heavy summer and autumn rains. Three clubs did not wish to take part in the study; from the remaining 63 courses I selected 60 courses in 47 clubs, 42 in Collier County and 18 in Lee County (Appendix B).

Each club in the study was visited 3 times for censusing fox squirrels and landscape analysis. The exceptions were those courses at which I did not see fox squirrels or sign of fox squirrels on the first visit and the superintendent and course workers had not seen fox squirrels for at least 1 year. At these courses I made no more than 2 visits for landscape analysis and squirrels censusing. Squirrel censusing took place between September 15 and May 15 each year, as squirrels were less active on the ground in the summer. Squirrel counts were conducted mornings, 0700-1030, or late afternoons, 1500-1730, when squirrels were most likely to be on the ground and visible (Jodice and Humphrey 1993). Sampling times were limited to sunny days with light or no wind and temperatures over 18° C.

I sampled for squirrels by driving around the course in reverse order, to decrease my interference with golfers. I stopped at each fairway for 10 minutes and selected 1 or 2 locations most likely to attract squirrels: open tree stands, trees with food items, and feeder areas. I searched trees and areas with open ground while listening for sounds of movement and communication. I recorded squirrel sign, nests, cone middens, and palm leaf or bark pealing. I recorded each squirrel spotting and did not attempt to determine if animals were recounted after moving to another area of the course. I counted individuals on private property adjoining the fairways, such as those using feeders. The highest count of the repeated visits was recorded as the number of squirrels seen at that course. Five categories of squirrel counts were created to allow grouping of courses by population levels. They were

- Level 1--none present, a course at which I did not see fox squirrels and the superintendent and workers had not seen them for over a year;
- Level 2--none seen, a course at which I did not see fox squirrels but the superintendent reported sightings within the past year. This often meant traveling squirrels were on the course for a few weeks or 1 or 2 come from neighboring courses for occasional use.
- Level 3--low, the highest number of squirrels seen on the course was 1-5.
- Level 4--medium, the highest number of squirrels seen on the course was 6-10.
- Level 5--high, the highest number of squirrels seen on the course was 11 or more.

In the evaluation of habitat variation between courses I was interested in landscape features that could impact squirrel feeding, movement, nesting or predation. With these needs in mind I collected data on course configuration, place in a larger landscape, vegetation composition and structure, predators, course history and human interactions with squirrels. A field survey of questions that could be answered with a yes or no response was developed to report on this range of landscape attributes. All questions could be completed during a 3 hour tour of an 18 hole course and a 20 minute interview with a knowledgeable superintendent. All final landscape surveys were conducted between April and December 1997.

Data Analysis

Fifty-one responses, or attributes, from the landscape surveys were used to examine landscape variation among the 60 sampled courses. Two methods of examining variation were used. Single linkage cluster analysis was used to identify aggregations of similar courses based on 51 landscape attributes (Statistical Analysis System 6.0). Two prominent clusters were selected for further examination. Chi-square (α=0.05) was used to test the hypothesis that attributes were randomly distributed between these clusters. Factor analysis was used as another method to identify factors or groups of attributes that explained variation among the courses (SPSS).

The 29 distinguishing attributes identified though cluster and factor analyses were used to create a Landscape Evaluation Index (LEI) (Bender et al. 1996, Brooks 1997, Reading et al. 1996, Thomasma et al. 1991, USFWS 1980, 1981). The Index allowed ranking of all courses and a comparison to squirrel population levels. These attributes were grouped into 3 components according to the landscape feature they described: 1) vegetation, 2) ground cover, and 3) landscape position. Attributes were weighted according to the differences in their frequency between high and low cluster courses and their ranking in factor analysis. For each course, the sum of attribute weights was expressed as a fraction of the sum of weights for an ideal course. A score of 1 indicated that a course had all of the desirable characteristics; a score of 0 indicated that it had none. The geometric mean of the 3 component scores was taken as an overall LEI (Reading et al. 1996). Courses were then ranked according to the Index and compared to patterns of squirrel sightings, as indicated by the 5 levels of population (Van Horne 1983).

Habitat Use and Demography

Radio-telemetry

A radio-telemetry study was conducted to gather data on home range, dispersal patterns, habitat use, feeding patterns and demography of two fox squirrel populations.

Two sites were selected for the study, one without residential development, containing a high number of squirrels, and another, well developed, with lower numbers of squirrels. Criteria for selection required that the sites have: 18-hole courses with similar size fairways and roughs, prominence of open pine stands, a course configuration that allowed movement around the course throughout the day, absence of 3 highly invasive exotic tree species (*Casuarina* spp., *Schinus terebinthifolius*, and *Melaleuca quinquenervia*), squirrels that were not fed by golfers and therefore not tame, and the strong support of the course superintendent and the club greens committee for the research project. The last was especially important as the clubs would provide golf carts for 12-20 months of tracking endeavors and would support the regular presence of a non-member researcher and collared fox squirrels on their courses. Permission to work on Royal Poinciana Cypress Course was granted in November 1995 and that for Royal Palm in July 1996.

Trapping took place during 4 periods: Site 1 only, December 1995-March 1996; Sites 1 and 2, July-August 1996, November 1996-February 1997, and July 1997. Because of the public nature of the trap sites and the desire to decrease stress to individuals, especially females who might be pregnant or nursing, a trap line was not used. Instead, squirrels were trapped using a focused trapping method in which 1 or more traps were set for 1 or 2 specific individuals in a small area. One-ended Tomahawk #204 squirrel traps were baited with an oily, natural peanut butter and pecans. Traps were placed on the ground under trees where squirrels were feeding or resting or within 7 meters of individuals feeding on the ground. Often the traps were covered with Spanish moss or palm leaves. The traps were baited, set and covered with moss at some distance from the trap site and rapidly dropped off from a golf cart. Squirrels were acclimated to carts and would return to the place of feeding after I moved away from the trap. I watched the traps from 30-50 m. In the season of low food supply, squirrels could frequently be baited into the traps within 10 minutes to 1 hour. This method was generally successful during the winter months, when 2 or 3 individuals might be trapped and collared in a day. In the summer and autumn months, particularly in food-rich 1996, squirrels were extremely difficult to trap.

To ensure recapture and collar removal at the end of the study in July 1997, individuals were baited with oily peanut butter and pecans for 2 weeks prior to the trapping period as they were located during normal radio-tracking. Final trapping was further aided by an apparently lower pine and cypress productivity in 1997.

Trapped squirrels were covered and moved to the cart within 1 minute. Removal of the trap cover encouraged them to move into a dark cloth and net restriction tube that was attached to the opening end of the trap. While constrained in the bag they were weighed and given an injection of Ketamine HCl (100mg/ml) in the hip. Individuals 675-800 gms were given 0.25cc, those 800-1000 gms received 0.3cc. After 4 minutes or when they showed little sign of movement, they were removed from the bag and were tagged in both ears with monel sequentially number tags (size #3, National Band and Tag, Newport, KY), measured, aged, fitted with radio-transmitters and photographed. Females with darkened nipples of any size were considered adult. Males with developed testes descended into the scrotum were considered adult. Males with no obvious scrotum development or with slight development were considered subadult. There was a clear difference in the pelage and scrotal development between subadult males who had never developed sexually and adult males undergoing seasonal fluctuations of testicle development. Subadults had shorter, fine fur and no vestige of scrotal development. No animals under 5 months of age were captured.

Squirrels were released at the site of capture after spending 3-4 hours in a 60 x 30 x 30 cm ventilated wooden wake-up box. Rapid retrieval, covering of the trap and immediate anesthetization appeared to reduce trauma; no squirrels died during trapping or collaring procedures.

From December 1995 to mid 1996, 25 gm AVM (AVM Instrument Co., Livermore, CA) radio transmitters configured as resin pods with machine belting neck bands and 6 inch back antennae were used. This model proved unsatisfactory due to repeated transmitter failure, poor service and removal by squirrels cutting the belting. In late 1996, I began using ATS (Advanced Telemetry Systems, Inc., Isanti, MN) transmitters with resin pods, very fine stainless steel chain neck bands and back antennae, total weight of 28 gms. These worked extremely well, with no radio failure or removal by the squirrels. Final recapture did show that 2 individuals had slight neck abrasions.

Collared squirrels were located a minimum of 2 times a week, except when weather, golf course conditions or course use would not allow (Mech 1983). Individuals were located once a week in 2 of 3 daily tracking periods, 0630 to 1030, 1031 to 1430, and 1431 to 1900 EST. Squirrels were frequently located more than once in a sampling period; data were collected on each siting. Open vegetation and ready access to trees allowed visual sighting following radio location. When a squirrel was in a nest or concealed by heavy vegetation and visual sighting was not possible, I was able to identify the tree and the area of the tree in which the animal was located. When an animal moved to another golf course I used triangulation (White and Garrott 1990) to determine its location and then I traveled to the course for visual sighting and collection of activity data if possible. When a squirrel disappeared from the course and could not be located at a neighboring course, I searched the surrounding area in all directions. In December 1996, I conducted an aerial search of Collier County west of highway 951 in an attempt to locate squirrels that had disappeared.

Once an individual was sighted, its location was mapped on aerial photographs. Recorded data included: time, activity (3 points at 60 sec. intervals), nature of the site and location at the site, food type if feeding on identifiable material, reproductive condition if visible, number of squirrels present within 5 m (both fox and gray), and number of collared squirrels within 5 m. Records of temperature, dew point, sky condition, and wind were recorded at the start of each session.

At least once a month throughout the course of the study I took visual counts of fox squirrels at each study site. I followed the procedure outlined for the 60 course squirrel counts and in addition recorded if each sighted squirrel was collared or uncollared. These counts were used to estimate the fox squirrel population of the 2 study sites.

Vegetation Sampling

The tree stands on three courses, Royal Poinciana Cypress and Pines and Royal Palm, were sampled and mapped to allow comparison of habitats used by the two radio collared populations. The Pines course was included in the vegetation sampling because it bordered Site 1 on 2 sides and collared male squirrels frequently used the area. The large forested stands at the Poinciana courses were sampled using a structured pattern of 20 meter diameter circular plots placed at intervals of 25 meter from center to center on a north-south line and at intervals of 30 meters from center to center in an east-west line.

This arrangement was designed for the most complete yet rapid sampling of the generally north-south tending forested areas. In the front 9 of the Pines course the pattern was oriented in an east west direction as the fairways in that section ran at right angles to the rest of the club. Within each plot, all trees over 10 cm dbh were identified and measured. All palms were counted. Presence of all saplings were recorded. Understory coverage was recorded as percentage and type and the ground cover was recorded as litter if over half of the plot had a significant layer of pine or pine and cypress litter. If not noted, ground cover was dominated by grass with occasional patches of bare soil.

In the narrow or small plots of Royal Poinciana and for the entire Royal Palm course, all the trees in each discrete plot were counted. If 10 or fewer of 1 species were counted, each tree was measured. If more than 10 of 1 species was found in a stand, 10 of the trees were measured. Saplings and ground cover were recorded as in the circular plots.

The Royal Palm site contained a large region of private lands belonging to condominium complexes and private homes. All pines and cabbage palms on the condo lands were counted and all trees on private lands on the 3 streets of private housing were counted.

Seven courses known to be used by the squirrels of the 2 study sites were evaluated using the method designed for the 60 course landscape evaluation portion of the study. This provided data on tree species present, identification of dominant species, types of ground cover, proportion of the course in tree stands, density of the understory and types of ground cover. The large pine stand south of the Cypress course and the developing landscape east of the Pines course were not accessible for sampling.

Data Analysis

In January 1996, I conducted 10 repeat counts of fox squirrels on the Cypress course to estimate the reliability of my squirrel census technique. The counts followed the standard format presented in the landscape analysis methods section. Results of the 10 counts ranged from 8-16 with a mean of 12.4 and standard error of 0.79. Calculation of 95% confidence limits for a small sample gave a range of 10.6-14.2 squirrels (Fowler and Cohen 1992). Such a range was considered reliable for the populations with higher numbers of squirrels. Reliability in smaller populations was expected to be lower.

Survival and birth rates of collared fox squirrels were calculated on 6 month intervals, as opposed to 12 months, to allow for movement of subadults out of the sample population on the Cypress course or into the adult cohort of the sample population. Only squirrels persistent in the sample population were considered survivors. Squirrels no longer persistent in the sample population included subadults who dispersed to other locations, individuals who disappeared, adults, generally males, who no longer used the study site course but were known to remain on neighboring courses, and individuals known to be dead. Survival rates for adult females, adult males, subadult males and subadult females were calculated as the proportion of the collared squirrels remaining active in the study site at the end of a 6-month period. The birth rate was taken as the number of young known to leave the nest. The survival rate for juveniles was the proportion of the summer 1996 cohort of young known to be alive at the end of 6 months, 7 of whom were part of the collared population in 1997. Most subadults, collared at around 6 months of age, moved into the adult cohort at about 12 months of age.

Estimates of population size, the number of fox squirrels using the Cypress course, were taken from 13 counts of collared and uncollared fox squirrels on the course taken in the spring and summer of 1996 and spring of 1997. In late summer and fall 1996, counts were not taken because the number of collared squirrels had declined due to collar removal and squirrel sightings were extremely low during these months of concentrated feeding in pines. Procedure for the counts followed that presented in the initial description of fox squirrel censusing. From these counts I calculated the minimum know alive (MKA), the Lincoln Index, and the Bailey unbiased population estimator for small sample sizes (Bailey 1952, Krebs 1999.).

I used the RAMAS Ecolab software (version 2.0, Applied Biomathematics) to estimate growth rates in the Cypress population. Estimates of the 6-month survival and birth rates of life stages were used to construct the stage-based population projection matrix. I used birth rates from the lowest and highest 6 month periods and an average of the 3 periods to generate a range of growth rates seen during the study.

Tracking locations were digitized using Atlas GIS software (Strategic Mapping, Inc., Santa Clara, CA) on an overlay of air photographs (TRW-REDI Property Data, 1996) registered to 7.5 minute topographic quadrangles. Accompanying data for each point were coded and attached to point locations using Atlas GIS software.

Home range was determined using the kernel method and CALHOME software (Kie et al. 1996, White and Garrott 1990, Worton 1989, 1995). Only 1 point per sampling period was used in home range analysis (Cresswell and Smith 1992). Points were selected randomly in cases where 2 or more points were recorded during 1 sampling period. The 95% contour was used to define the home range boundary of each individual and the 50%

contour as the core area (Kenward 1992, Wray et al. 1992). I calculated separate home range data for year 1 (December 1995-October 31, 1996) and year 2 (November 1, 1996-July 30, 1997) to allow for changes in the make up of the collared population. I used a two-tailed t-test for paired samples (α=0.05) to compare home range sizes of Site 1 females that appeared in both year 1 and year 2. I compared home range size of adult females to adult males in both years and 2nd year subadults from Sites 1 and 2 using a Mann-Whitney test (α=0.05) (Fowler and Cohen 1990). The small number of adult females and adult males at Site 2 precluded statistical comparisons using those individuals.

Habitat maps were created from aerial photographs using Atlas GIS software. All vegetation sampling plots, including condominium areas, water features, residential areas and streets, and course fairways and non-forest roughs were outlined and the area of each type was measured. I calculated basal area, density, relative basal area, and relative density of each tree species by plot. Nine categories were defined to represent the diversity of vegetation seen on all 3 courses. Vegetation categories were defined by the relative basal area (percent of total dm^2/ha.) of pine, cypress, cabbage palm, and other native and exotic species. Tree stands were then categorized by density (stems/ha.). Plots with a pine needle litter layer or a shrub layer were identified and mapped as such.

Using Atlas GIS to analyze use of the vegetation types, tracking points were overlaid on maps of vegetation classes for each course. I compared actual use of vegetation types to that predicted by the percent area of each vegetation category. Chi-square tested (α=0.05) the hypothesis that tracking points were randomly distributed among vegetation categories.

Feeding patterns were examined by analyzing the tracking data in which the food item was clearly identified. All food types taken more than 5 times in the 19 months of feeding observations were considered. Changes in monthly feeding patterns were determined by calculating the percent monthly total of each species or food type consumed each month for the 19 months of feeding records. A diversity index of species use, the inverse Simpson (Krebs 1999, MacArthur 1972, Williams 1964), was used to measure both richness and evenness of use of the food types.

RESULTS

Landscape Evaluation and Censusing

Squirrel counts

I was able to sight fox squirrels at all courses that reported regular observations by course personnel. During the squirrel counts, 5 or fewer squirrels were seen at 48 (80%) of the 60 courses. Fourteen courses (23%) were level 1, with no squirrels seen during surveys and no sightings by course staff in the past year. Nine courses (15%) were level 2, with no squirrels sighted during the surveys, but course personnel reported occasional sightings in the previous year. Reported sightings on these courses were frequently traveling squirrels or an occasional visiting squirrel from a higher level neighboring course. Level 3, 1-5 sightings, was the largest category with 25 courses, 42% of the total. I sighted 6 or more squirrels on only 12 courses: 6 courses (10%) were level 4, 6-10 squirrels, and 6 were level 5, with more than 10 squirrels seen.

Course attributes

Cluster analysis of the 60 courses with 50 attributes produced a dendrogram with a prominent cluster of 11 courses and a broader cluster of 18 courses (Fig. 6). The 11 course cluster, cluster 1, contained courses with a high occurrence of attributes favorable to fox squirrels and the 18 course cluster, cluster 2, contained courses with a high number of landscape attributes unfavorable to fox squirrels.

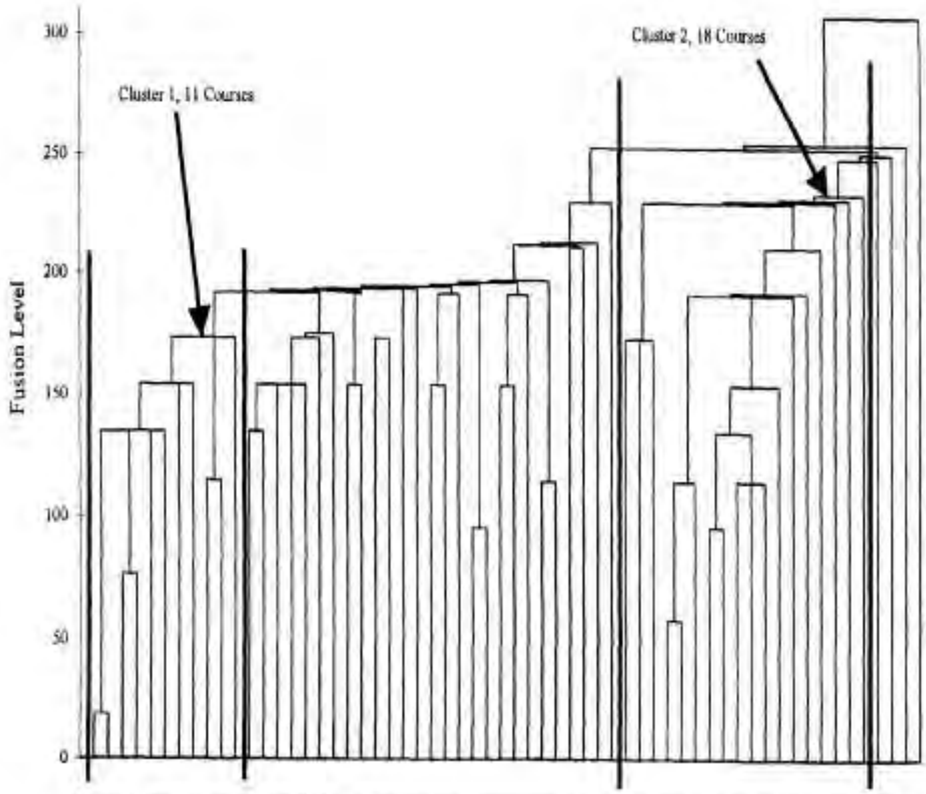

Figure 6. Dendrogram of single linkage cluster analysis. Arrangement of 60 golf courses using 50 attributes of vegetation, ground cover, and landscape position.

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Chi square tests of the 50 attributes showed that 20 attributes were non-randomly distributed between the 2 clusters. Courses in cluster 1 were characterized by: large patches of pine and cypress trees, open understories in the tree stands, large areas of pine litter, having adjoining courses, being part of a multi-course club, and having at least 50 acres of adjoining forest. Cluster 2 courses were characterized by: a high degree of isolation, few or no sizable tree stands, low numbers of pine and cypress, no obvious dominant tree species, heavy development and busy roadways around the course (Table 1).

Factor analysis produced 2 independent factors or groups of attributes explaining 27% of the variation among the courses. Factor 1 accounted for 14.6% of the variance and factor 2 for 12.3%. Factor 1 describes variation similar to that seen in cluster analysis, large stands of open forest on larger, grouped courses vs well developed, isolated, courses with more sparse tree cover and few native species. Thirteen attributes contributing to factor 1 were the same as those showing non-random distribution between clusters in the previous analysis (Table 1). Factor 2 is a comparison of "natural" courses with a heavy understory to courses with clear understory and the presence of planted exotic trees. Eight attributes contributed to the variation explained by factor 2 (Table 1).

While cluster and factor analysis were quite useful in identifying characteristics that distinguished high and low quality courses in this study, it must be noted that they do not provide a complete listing of all features that are either beneficial or harmful to squirrel survival. Attributes such as untrimmed cabbage palms, while helpful to fox squirrels were found on over half of the courses and occurred in all types of landscapes. Similarly, known predators such as domestic cats and raptors were found throughout the

Table 1. Distinguishing attributes as selected by cluster and factor analyses. Column 1, factors which appeared non-randomly in high and low clusters. Number is the percentage difference of occurrence between high and low clusters. Column 2, an attribute in Factor 1 or Factor 2 as determined through factor analysis. Column 3, attributes are grouped as components of the Landscape Evaluation Index. Column 4, a desired answer indicates it is an attribute favorable to fox squirrels. Index weight determined by columns 1 and 2.

1 Cluster difference%	2 Factor #	3 Index Component	4 Favorable to Squirrels	5 Index Weight	6 Attri. #	Attributes
76.3	1	Vegetation- 1	Y	7	11	well forested, large patches around course and often between fairways
72.7	1	1	Y	7	19	pines stands of 20 or more on most holes
81.8	1	1	Y	7	33	Pines or pines co-dominant
72.2		1	Y	5	17	over 100 large pines/ 18 holes
79.8	1	1	Y	5	18	pines occur throughout the course
61.1	1	1	Y	5	20	over 50 large cypress/ 18 holes
56.1	1	1	Y	5	21	at least 4 stands 20+ cypress trees/18hole
74.2		1	Y	5	29	Palmetto present
	2	1	Y	3	30	4 or more exotic food trees common
88.9	1	1	N	7	9	course "tight", narrow roughs,trees scattered, few or no large stands
85.4	1	1	N	7	34	no obvious dominant/s
	2	1	N	5	13	3+ marginally managed stands/18 holes
	2	1	N	3	12	heavy forest vegetation in roughs, can't see more than 1 hole housing 0-1side
	2	1	N	3	36	mixed natives majority of forest/stands
	2	1	N	3	47	Large snakes present
50.0		1	N	1	31	eucalyptus present
85.4	1	Ground cover-2	Y	7	16	open understory, large areas pine litter, open soil
	2	2	Y	3	15	managed forests, understory 75%+clear
	2	2	N	3	14	unmanaged stands show vine invasion and/ or other dense understory
50.5	1	Landscape position-3	Y	5	5	club has 36 holes or more
	1	3	Y	5	40	at least 1 adj. course has high levels F.S.
65.2		3	Y	3	39	adjoining forest over 50 acres
54.0		3	Y	1	51	10-25 years old in 1997
77.8	1	3	N	7	37	Completely surrounded by development
68.7	1	3	N	5	3	club has only 18 holes
50.0	1	3	N	5	41	0 adjoining courses with fox squirrels
70.7		3	N	5	43	1 or more boundaries with busy 2 or 4+ lane
	2	3	N	3	50	less than 10 years old in 1997
38.9		3	N	1	38	0 adjoining courses

range of course landscapes. For this reason they did not appear as distinguishing attributes of high or low clusters. The list of distinguishing characters must not be confused with a more complete listing of characters favorable or unfavorable to fox squirrels.

Landscape Evaluation Index

The Landscape Evaluation Index was calculated using 29 attributes, 16 in the vegetation component, 3 describing ground cover, and 10 relating to landscape position (Table 1). The 60 courses ranged from 0.0 to 0.987 on the scale of 0.0 to 1.0 (Appendix B, Fig. 7)). Seven courses were over 0.90, 18 from 0.50 to 0.751, and 35 were below 0.50. There was a gap with no courses from 0.90 to 0.752. Examination of the landscape configuration of the courses shows that the 7 courses above 0.90 are either undeveloped or have a perimeter development plan for each course or for the entire club (Fig.8). Courses with a LEI of 0.75 or lower generally have more complex development plans such as the shown in levels B and C in Figure 8. These require squirrels to cross streets or travel through or around larger forest stands with dense understory vegetation to move from one portion of the course to another.

Index values were strongly correlated with squirrel levels ($r = 0.747$, $p << 0.01$). Courses that adjoin high level courses, but do not themselves have an index value over 0.90, are identified as Neighbors in Figure 7. Three of these courses have level 4 populations, though their index values would indicate a lower capacity, and 4 of the level 3 courses have higher populations than expected. Four of the level 1 courses have moderate LEI ratings, yet no squirrels. These courses are newer, developing courses at which the large forested areas have heavy, closed understory vegetation not favorable to fox squirrels.

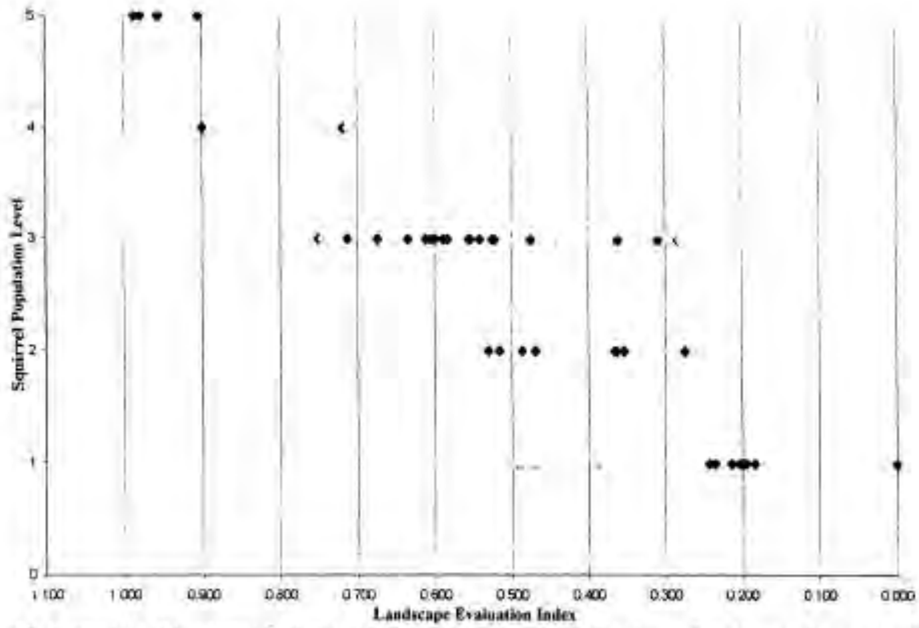

Figure 7. Comparison of Landscape Evaluation Index values to squirrel population levels. Trend line is a linear regression (r^2=0.557). Courses that adjoin the 7 courses (level 5 has 6 courses, symbols overlap) with index values of 0.90 or higher are identified with gray diamonds as Neighbors. Four courses that have large areas of native tree stands with heavy understory growth are identified by large gray squares, in level 1.

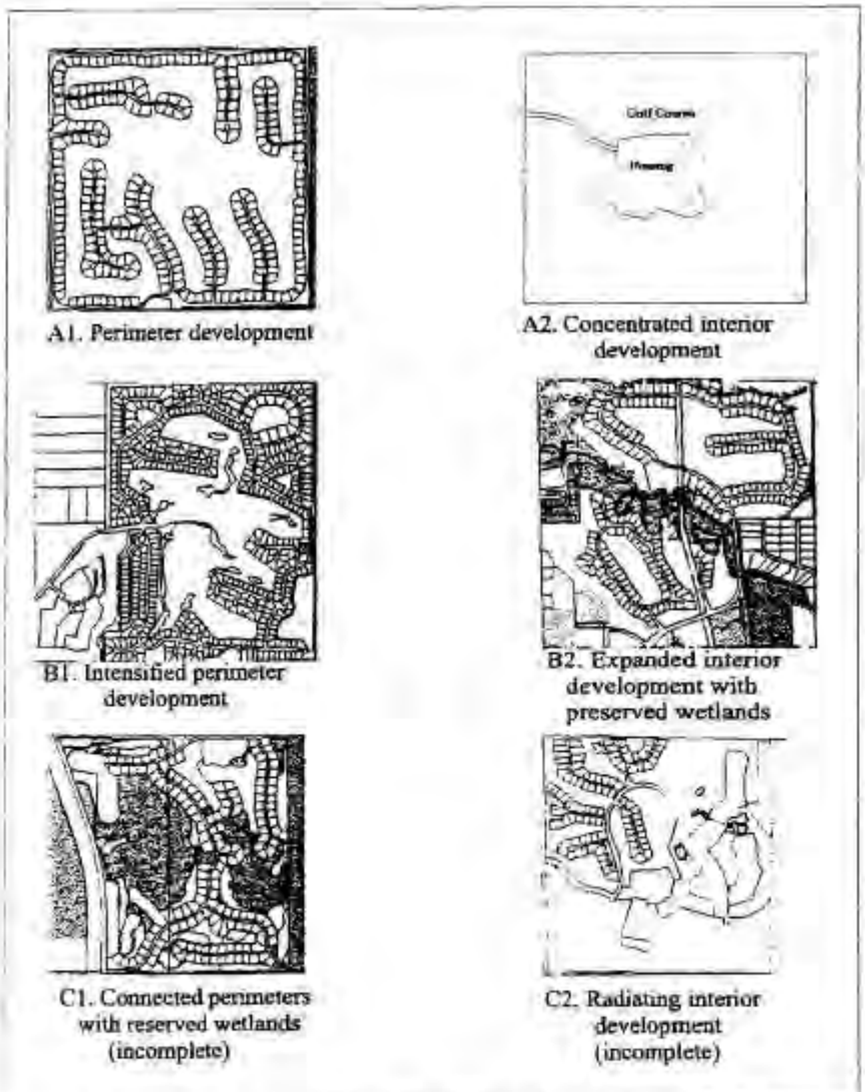

Figure 8. Development patterns. Configurations of golf course development, from higher quality in level A, less desirable in levels B and C. A2 is a schematic, others are examples seen in the Collier County planning maps. Each plot is 1 section, 260 hectares. Clear tan areas are the golf courses and accompanying forest stands. Green patches are reserved wetland areas. Other colors: white, to be developed residential; brown, agricultural; pink and purple, commercial. Housing areas are represented by subdivided lots and street patterns.

Demographics and Habitat Use

Radio-telemetry produced 2497 tracking points and accompanying records on 29 individuals at Site 1 between December 1995 and July 1997, and 254 tracking points at Site 2 between January and July 1997. These data were used to examine population structure, size and location of home ranges (Appendix C), nesting sites, habitat use, and feeding patterns.

Survival

Eighteen fox squirrels were collared at Site 1 in the first year, 9 males and 9 females. In the second year, 11 more individuals were added to the study, 4 females and 7 males. Adult male fox squirrels had lower average survival rates than adult females (Table 2). Three individuals were known dead or moved to a neighboring course as adults. Four individuals disappeared from the population and were not located again on the Cypress course or on neighboring courses.

Adult females had an average 6 month survival of 0.87, the highest rate at Site 1. Two adult females disappeared in the fall of 1997. One had a home range between 2 aggressive females and was regularly chased by each. It is possible this female moved west into the Hole in the Wall and Wilderness area, though she was never seen on the courses. The second female disappeared the same day her collar was found at the base of a tree near a busy cart path.

At 0.78, the survival of subadult males was higher than adult males and subadult females (Table 2). The immediate fate of all subadult males was known. In the first year of study, 3 of the 4 remained on the course and moved into the adult cohort, and the

Table 2. Survival and birth rates for Site 1. Rates calculated in 6 month intervals. Survival equals persistence in the course population. Birth rates are calculated from the number of young emerging from the nest. Weighted averages for each sex and age class are the sum of persistent individuals in the 3 time periods divided by the sum of n for the 3 time periods.

SITE 1 FEMALES - *adults*	n	Known dead in population	Moved or dispersed	Disappeared	Persistent in population	Survival rate		Young from nest	Births/ adult female	Births/ adult
Jan.-June 1996	4	0	0	0	4	1.00		4	1.00	0.50
July-Dec. 1996	6	0	0	2	4	0.67		15	2.50	1.25
Jan.-June 1997	5	0	0	0	5	1.00		3	0.60	0.23
	15	0	0	2	13	**0.87**	Weighted average	22	**1.47**	**0.67**
subadults										
Jan.-June 1996	5	0	3	0	2	0.40		0		
July-Dec. 1996	0	0	0	0	0			0		
Jan.-June 1997	3	0	0	0	3	1.00		0		
	8	0	3	0	5	**0.63**	Weighted average	0		
MALES - *adults*										
Jan.-June 1996	4	0	1	1	2	0.50				
July-Dec. 1996	6	0	1	0	5	0.83				
Jan.-June 1997	8	1	0	3	5	0.63				
	18	1	2	4	12	**0.67**	Weighted average			
subadults										
Jan.-June 1996	4	0	0	0	4	1.00				
July-Dec. 1996	1	0	1	0	0					
Jan.-June 1997	4	1	0	0	3	0.75				
	9	1	1	0	7	**0.78**	Weighted average			

0.76	Average adult 6 month survival
0.71	Average subadult 6 month survival
0.67	Average juvenile 6 month survival

fourth dispersed to Bear's Paw course and later disappeared. In 1997, 3 of 4 subadult males survived to the end of the study and stayed on the course. The fourth died while infected with skin fungus (Dr. Sharon Taylor, personal communication).

Subadult females showed the greatest change in survival rates from one season to another (Table 2). In winter/spring 1996, 3 of the 5 subadult females dispersed from the course, for a 6 month survival rate of 0.40. Two of these were found dead on other courses, 1 within the summer and the other within the year. The third dispersing female disappeared from a developed neighboring course. In winter/spring 1997, the 3 collared subadult females remained on the course in their natal home ranges though the end of the study. At that time they ranged in age from 11 to 13 months. None had reproduced though 1 was known to be the object of a mating chase.

Trapping difficulties in the summer 1996 meant than no subadults from winter litters could be collared. All subadults collared in the winter of 1995-1996 dispersed by August, or they entered the adult cohort.

The survival data for Royal Palm, Site 2, covered a shorter period of time, only 7 months (Table 3). Four adults were collared, 2 males and 2 females. All remained alive throughout the 7 months. Four subadults were collared, 2 male and 2 females. None remained on the course at the end of 6 months. One male disappeared shortly after collaring. Both females died: 1 following a severe infestation of skin fungus, the other after being hit by a vehicle on Augusta Boulevard. The surviving subadult male moved from the course through a series of progressively more distant feeding sites. At the end of the study he was living near a feeder on the edge of Hibiscus course along Highway 41.

Table 3. Survival rates for Site 2, Royal Palm, for January 1997- July 1997. Survival equals persistence in the course population. No births, b(x), were recorded in the collared population between January and July 1997.

SITE 2 MALES-	n	Known dead	Moved/ dispersed	Disappeared	Persistent in the population	b(x)	Survival/6 mo
Adult	2	0	0	0	2		1.00
Subadult	2	0	1	1	0		0.00
FEMALES						b(x)	
Adult	2	0	0	0	2	0	1.00
Subadult	2	2	0	0	0	0	0.00

Reproduction

Reproduction at Site 1 varied widely between seasons and between individuals (Table 2). Winter reproduction was lower in 1995-1996 and 1996-1997 than the summer/fall of 1996, with only 4 and 3 young known to leave the nest in the 2 cooler seasons. The 6 month rate of reproduction for the first winter season was 1.00/adult female, in the second winter season it was 0.60/adult female. Winter young were born in December through February, emerging from the nest in January through April. The summer of 1996 was one of high reproduction. Five of the 6 adult females produced evident young, with 2-4 young seen emerging from each of the 5 nests, for a total known reproductive output of 15, a rate of 2.50/adult female for the 6 months. Warm season young were born from early July to September and emerged form the nests between August and late October. Mating chases were recorded in April though July and in October.

Neither female at Site 2, Royal Palm, produced young from a nest during the course of the study. One female was obviously pregnant at the time of collaring and appeared to tend a brood nest for a few weeks. She failed to show signs of long-term nursing and no young emerged from the nest. She appeared to be tending a brood nest when her collar was removed, as did the other female in the study. The surviving subadult male in the study was the offspring of one of the collared adult females, undoubtedly born in the summer of 1996. At the time of his collaring, he and another subadult regularly accompanied her. Though reproduction was not observed in collared animals during the study, some adult females were successfully reproducing at Site 2, though apparently at a lower rate than Site 1.

Mortality and Disease

Known causes of death in the collared populations of Sites 1 and 2 were: automobiles (2), skin fungus infection (2), and electrocution (1). Three subadult uncollared fox squirrels at Site 1 also died from vehicle accidents, 1 from a car on the entrance road and 2 from golf carts on the course. Of the 5 squirrels known to be killed by cars or carts at the study sites, only 1 remained at the site of impact. The others moved away, sometimes several meters, before they died.

Skin fungus (Dr. Sharon Taylor, person. commun.), causing heavy fur loss and blackened crusting of the skin, was apparent in both populations in 1997, affecting at least 8 collared individuals. One subadult died at each site. It primarily affected subadults, though also was seen in 2 adults. The proportion of affected individuals appeared similar in collared and uncollared squirrels. One uncollared subadult died at Site 1 within a month of the collared individual. Fur loss and darkened skin as seen in a skin fungus infection was observed in squirrels at courses adjacent to the study sites prior to 1997. It was easily transmitted by contact and feeding areas appeared to be vectors, especially when squirrels fed from a concentrated food supply. At least 3 squirrels with severe fur loss and skin damage were seen sharing a feeder at CCN. The collared individuals who survived the spring 1997 skin fungus infestation regained a thick, healthy coat in the late spring molt.

Information on predation is slight. A bobcat was seen killing a ground feeding, uncollared fox squirrel at Site 1 in 1997 (A. Grieser, person. commun.). At least 1 female bobcat and 2 young were regularly seen in the forest areas adjacent to Poinciana on the east and west. The adult bobcat began frequenting Poinciana in daylight hours when the area immediately east of the course was being cleared for development in 1997. There is her home range was east of the study site in the Pines course. Of the 431 tracking locations recorded for the females between December 1995 and November 1996, only 10 were outside of the course boundaries, all but 2 of these 10 remained within the boundaries of the Poinciana. Females did not range into neighboring pine or cypress stands and only ROPO 6 crossed the entrance roadway on the club grounds to feed in a large ficus immediately north of the road. All adult females showed some home range overlap with other adult females, though none showed range overlap with more than 2 other adult females.

In summer/fall 1996 all females maintained a brood nest in a location within a core area outside the home ranges of all other adult females. In the first few weeks the of summer brood nest occupancy females stayed in the nest most of the day and greatly reduced the area in which they fed (Table 6). Placement of the nest within a small mixed stand often allowed them to feed without moving to the ground. A similar pattern of reduced movement and isolation was not observed during the winter brood nesting period.

Adult males at Site 1, year 1, had home ranges of 42.52 ha to 118.40 ha ($\bar{x}$ = 70.84 ha) (Table 5), significantly larger than those of the adult females (Mann-Whitney U=0, $p<0.05$). The home ranges of all 4 adult males overlapped in the center of the study site (Fig 10). Other adult males were regularly seen on the course. ROPO 04 and ROPO 07 used the Cypress course almost exclusively, while ROPO 16 used all of the Cypress course and the adjoining back nine of the Pines course on the east. ROPO 17 used portions of 4 courses, the Cypress, Pines, Hole in the Wall, and the Country Club of Naples to the west. Though ROPO 17 used the open edges of large forested stands within

Table 6. Brood nest home ranges. Home range size for 3 adult females occupying brood nests in summer/fall 1996, Site 1. Home range determined by kernel analysis, CALHOME.

	Brood nest home range, 95% contour	Brood nest core area, 50% contour	Number sightings
ROPO 02	0.8 ha	16.7 m^2	16
ROPO 03	0.3 ha	9.9 m^2	13
ROPO 06	2.1 ha	78.5 m^2	9

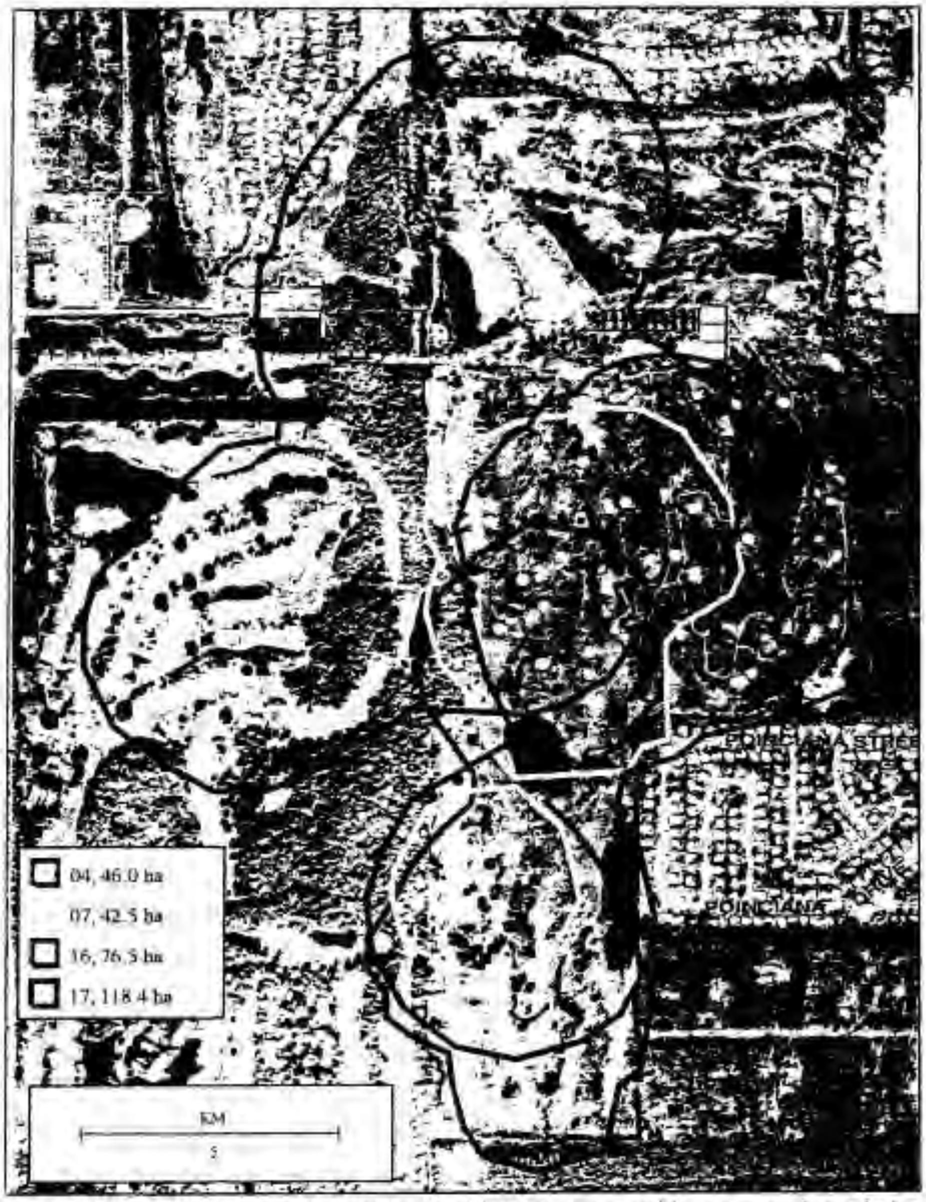

Figure 10. Adult males, Site 1, year 1. Tracking locations and home range boundaries, defined by the 95% contour, kernel analysis, CALHOME.

and between courses, he was never found in the interior of these stands. He did not need to cross the roadway to move from CCN to HIW and was regularly observed moving to HIW by crossing the canal between the Cypress course and HIW by way of a natural tree bridge on the west side of fairway 2. These tree routes were frequently used by several individuals in moving between these 6 neighboring courses separated by canals.

Home ranges of the 6 collared subadults at Site 1, year 1 (Table 5, Fig. 11), ranged from 10.66 ha to 49.07 ha ($\bar{x}$ = 22.16 ha). ROPO 13, a male, began making long day trips to the back nine of the Poinciana Pines course in the month prior to his dispersal. His large home range, twice as large as the mean and the next largest subadult home range, reflects these trips. The 4 subadults in the southern half of the study site show a strong overlap (Fig. 12), with all four commonly using forested areas along the 7th and 13th fairways. Three of these 4 dispersed to other courses between March and August 1996. The fourth stayed on the Cypress course until the end of the study.

ROPO 10, a subadult female, dispersed from the southern section of Site 1 to Poinciana Pines at the end of March 1996 and in early April moved to the CCN (Fig. 13). Her initial movement to the front nine of the Pines course was 1.4 km with an additional 0.85 km to CCN. She also frequented a home feeder at point B and crossed Burning Tree Drive regularly. She slipped her collar in June 1996 and was seen only once again, despite subsequent searches.

ROPO 14, a subadult female, dispersed from the northeast section of Site 1 in late April 1996 (Fig. 14), moving to Bear's Paw Country Club. Her dispersal distance from her Site 1 to her first sighting at BP was 2.8 km. She occasionally fed on scraps put out at Site A, with the remaining tracking sites at the edges of heavy forest on the northeast edge

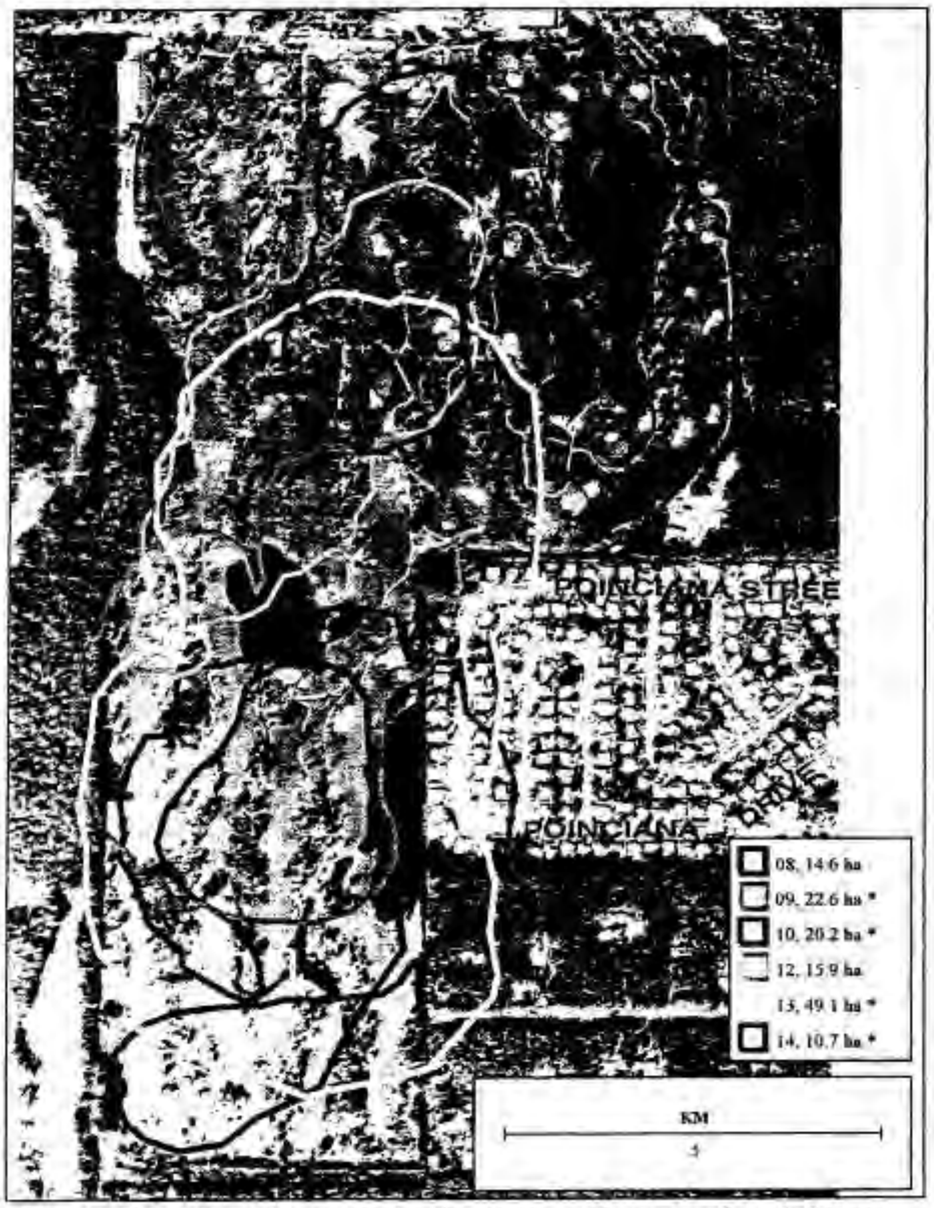

Figure 11. Subadults, male and female, Site 1, year 1. Home range boundaries are defined by the 95% contour, kernel analysis, CALHOME. Individuals that dispersed during the 1996 spring and summer seasons are marked (*), home ranges are those prior to dispersal.

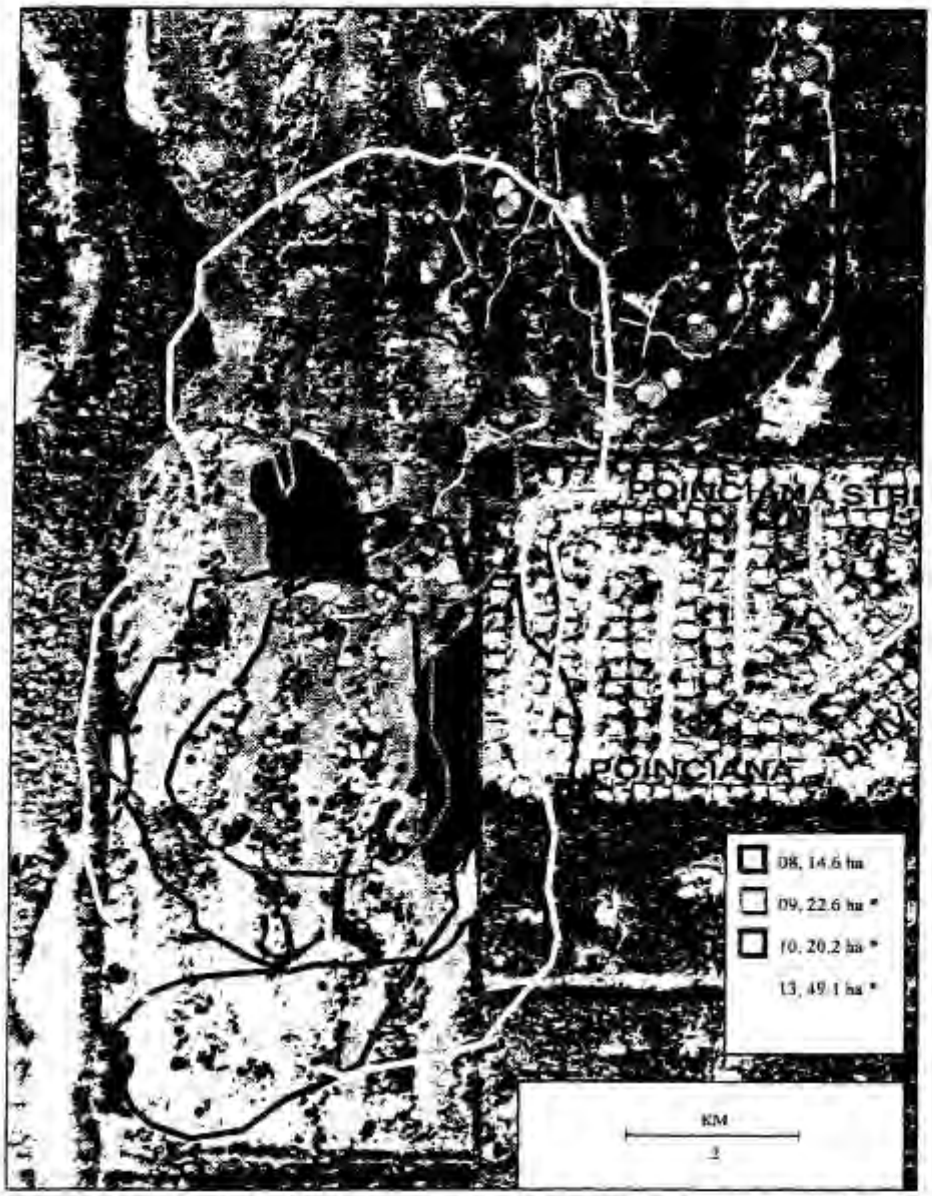

Figure 12. Four subadults, Site 1, year 1 Collared subadults in the southern half of the course. Tracking locations and home range boundaries indicate use of the course. Three of 4 squirrels, 2 females, 1 male, dispersed from the course in spring and summer 1996. Only ROPO 08 remained through year 2 of the study.

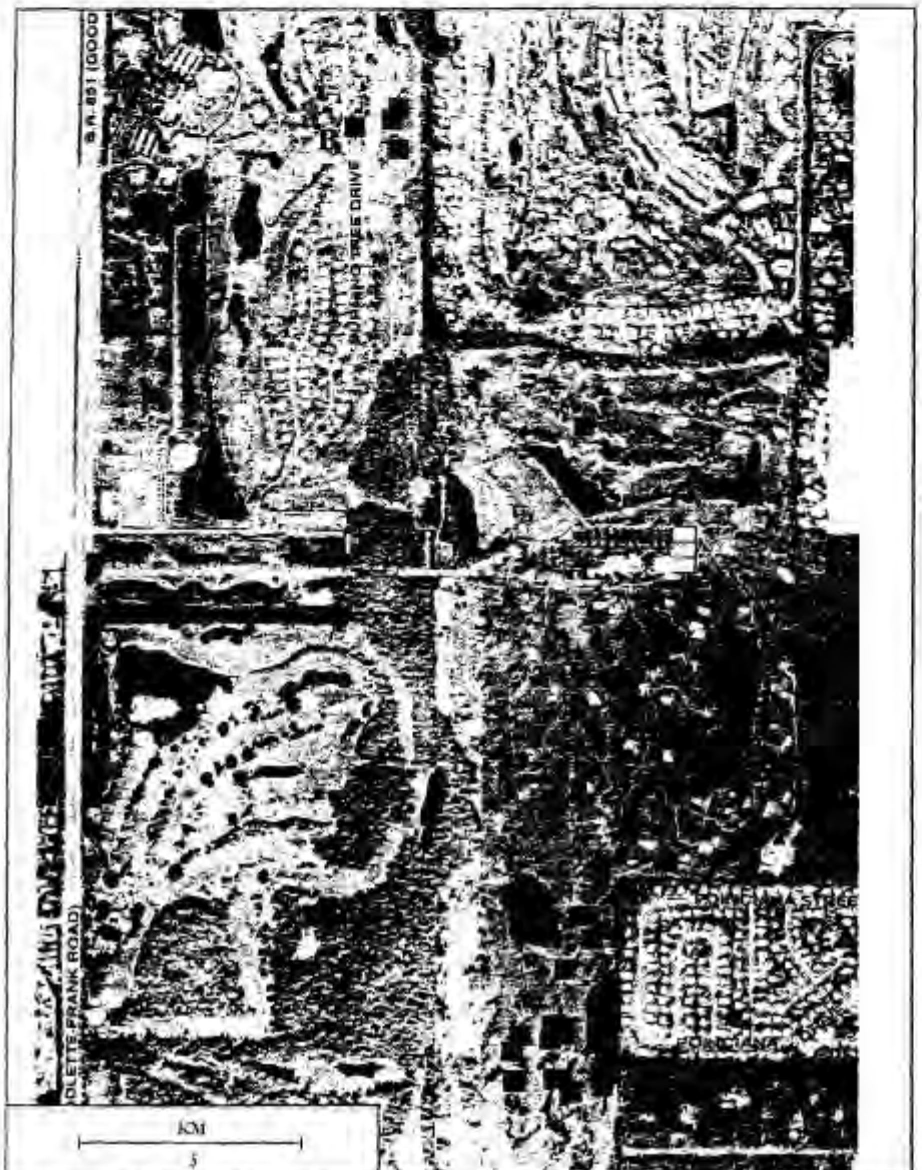

Figure 13. Dispersal movement of ROPO 10. Movement from Site 1 to Country Club of Naples in late March, 1996. Movement from her central home range area to A was 1.4 km, and from A to B an additional 0.85 km, for a total 2-week dispersal distance of 2.2 km.

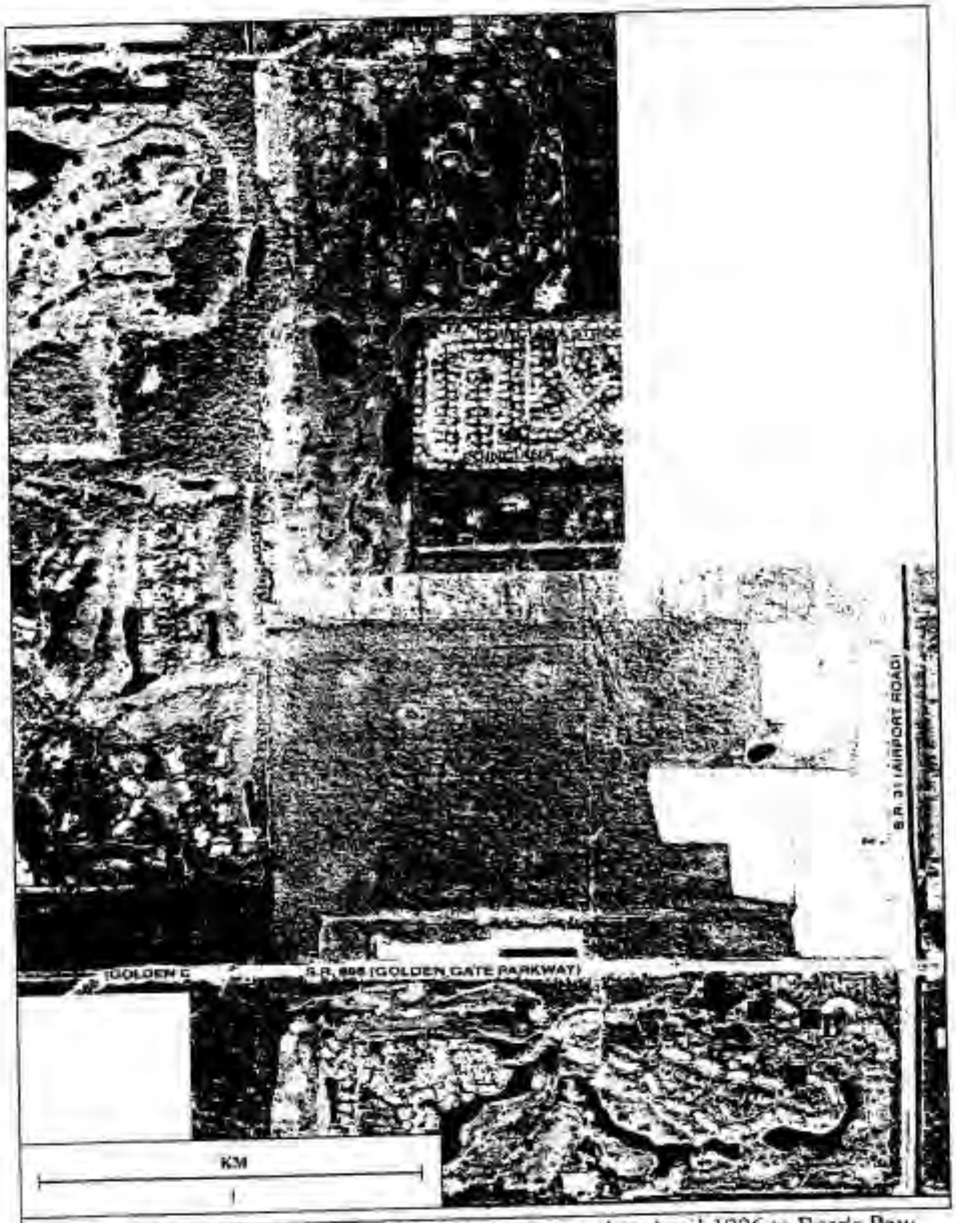

Figure 14. Dispersal movement of ROPO 14. Dispersal in April 1996 to Bear's Paw Country Club. The distance from her central home range area to the first off-site location, A, was 2.8 km. She was found dead at B in late July 1996.

of the course. In July she was limping badly (L. Molden, person. commun.) and was found dead in dense undergrowth on July 24, 1996. At least 1 large cat regularly roamed the small area where she was found.

In mid-May 1996, ROPO 09, a subadult female, moved from the center of Site 1 to the eastern end of the Quail Run Golf Course (Fig. 15), a heavily developed course with few tree stands, a dense street network and heavy traffic. By the end of June 1996, ROPO 09 had moved to the CCN where she often fed at a home feeder station used by 2 or 3 other fox squirrels, at least 2 of which had severe fur loss with accompanying thick, darkened skin, probably related to a skin fungus. By August, ROPO 09 was suffering from a similar fur loss when she was tracked to the center of the HIW. She returned to Site 1, Cypress course, for a brief period in September 1997. Regular contact was lost in early fall due to collar failure. She continued to use the HIW and the south end of the CCN, where she frequently crossed roadways in her daily movements. She was found dead at the side of the entrance road to CNN in April 1997. Her initial dispersal distance was 2.6 km and the total distance moved from the original home range to HIW was 6.0 km.

ROPO 13, a subadult male, dispersed from the southern section of Site 1 to Bear's Paw Country Club in August 1996 (Fig. 16). On August 8, 1996, he moved from the south border of Site 1 to Golden Gate Parkway, through 1.2 km of pine forest. The following morning he crossed the busy 4 lane roadway into BP, where he was tracked until mid August 1996. His initial 24 hour dispersal distance was 1.9 km; his total movement distance from his original home range was 3.5 km.

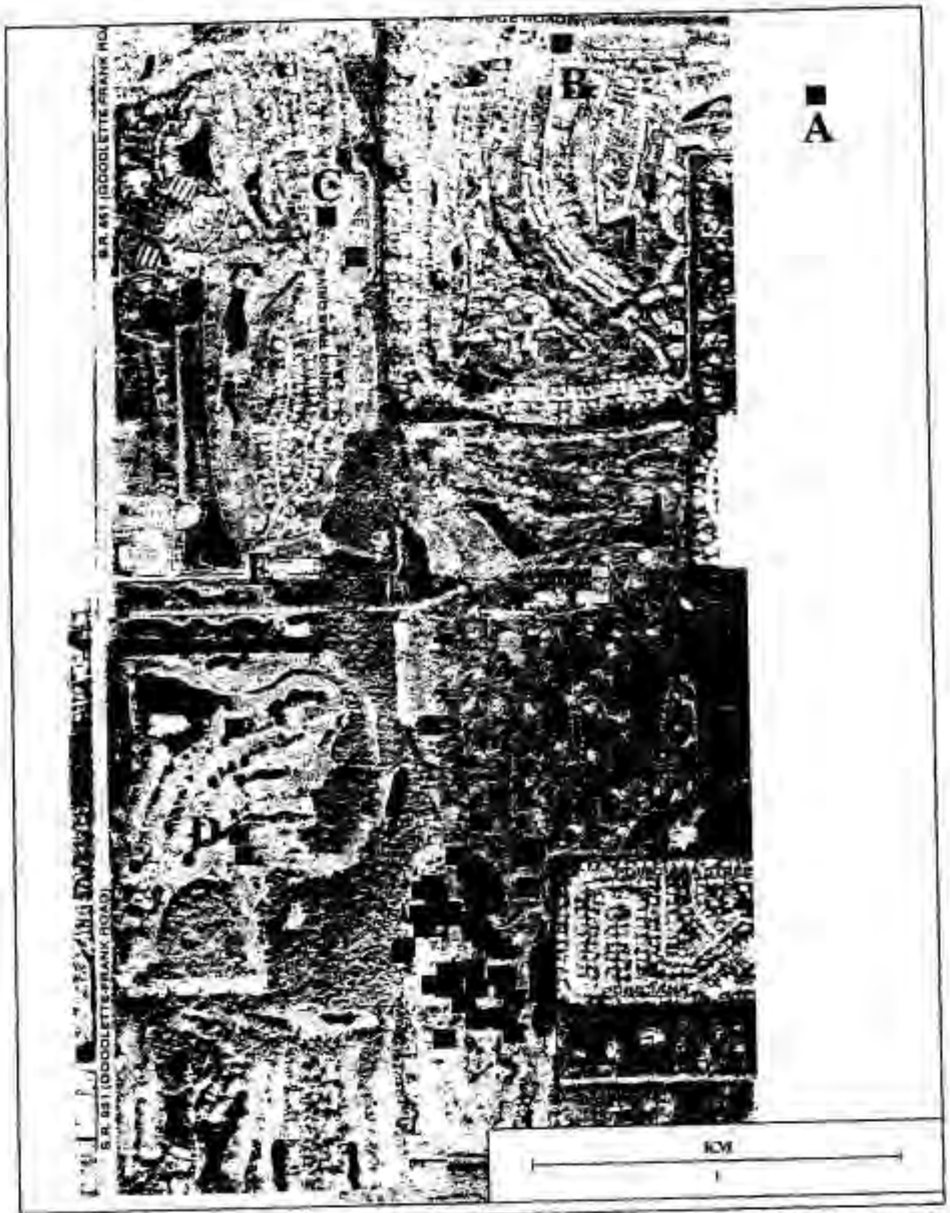

Figure 15. Dispersal movement of ROPO 09, mid May 1996. First off-site location at A, a move of 2.3 km from previous home range on May 20, 1996. Located at B on May 27, 1996, at C, home feeding site on June 28, and at D on August 23. She was found dead at E, hit by vehicle, in April 1997.

Figure 16. Dispersal of ROPO 13. Movement from Site 1 to Bear's Paw Country Club on August 8, 1996. Points north of A are tracking locations of 13 before that date. Movement from A to B, 1.2 km, took 3 hours. He crossed from B to C the following morning, for a total 24-hour dispersal distance of 1.5 km. The total distance traveled to his final sighting was 3.5 km.

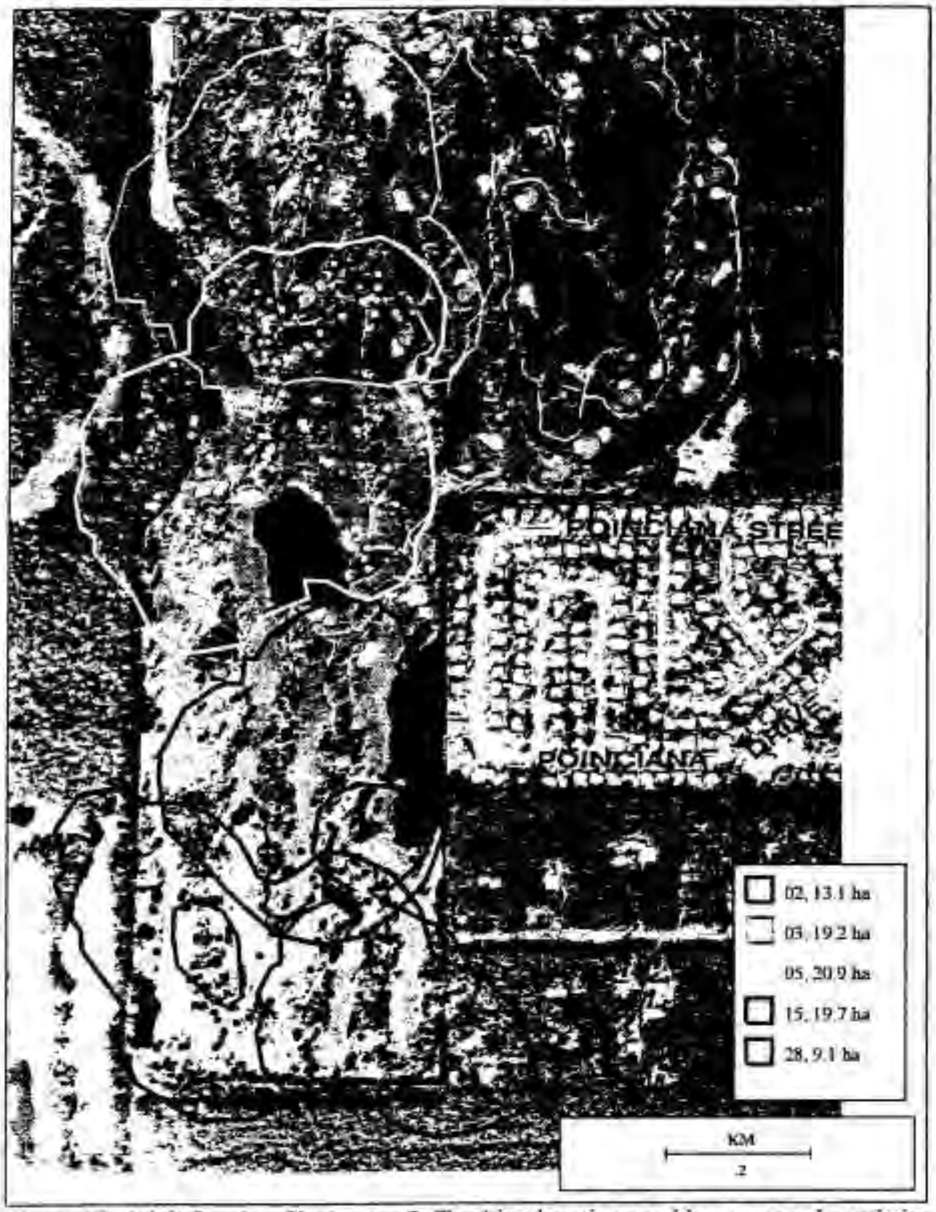

Figure 17 Adult females, Site1, year 2. Tracking locations and home range boundaries, defined by the 95% contour, kernel analysis, CALHOME. Numbered site is 1997 summer brood nest of female 03

At Site 1, year 2, the home ranges of the 5 adult females varied from 9.08 ha to 20.92 ha ($\bar{x}$=16.40) (Fig. 17). The 4 adult females collared from the previous year, showed significant increases in home range size (Table 5) (t=3.95, P=0.029, df=3) though each female continued to use approximately the same section of the course. ROPO 03 and ROPO 05 increased use of the edges of large forest stands on the eastern edge of HIW and ROPO 15 used open edges of forested roughs at Wilderness Country Club and a feeder area on private property adjoining the southeast corner of Site 1. ROPO 03 expanded to the north into the previous home range of ROPO 06, who disappeared in December 1996. Core areas of ROPO 03, ROPO 05, and ROPO 15 showed increases from year 1 to year 2. ROPO 15 and ROPO 28 had high overlap, though location of core areas indicated that ROPO 28 made heaviest use of the southeast portion of the course and ROPO 15 the southwest corner of the corner.

Only ROPO 03 was tending a summer brood nest when the study ended in July 1997. The second year home range of ROPO 05, a female, had expanded to include the fall 1996 brood nest site of ROPO 03. ROPO 03 moved her 1997 summer brood nest to the north, into a tree stand formerly within the home range of ROPO 06, an adult female.

The 6 adult males of Site 1, year 2, used portions of 5 courses (Figs. 18, 19). Home range size varied from 44.06 ha to 121.00 ha ($\bar{x}$ = 90.91 ha) (Table 5), significantly larger than adult female home ranges in the second year (Mann-Whitney U=0, p<0.05). All of the males used at least some part of 2 or more courses and did so with little crossing of roadways. ROPO 20 used much of the Cypress course, visited the front and back sections of the Pines course and frequently moved into Hole in the Wall. ROPO 18 rarely visited the Cypress course, spending most of his time in the northern

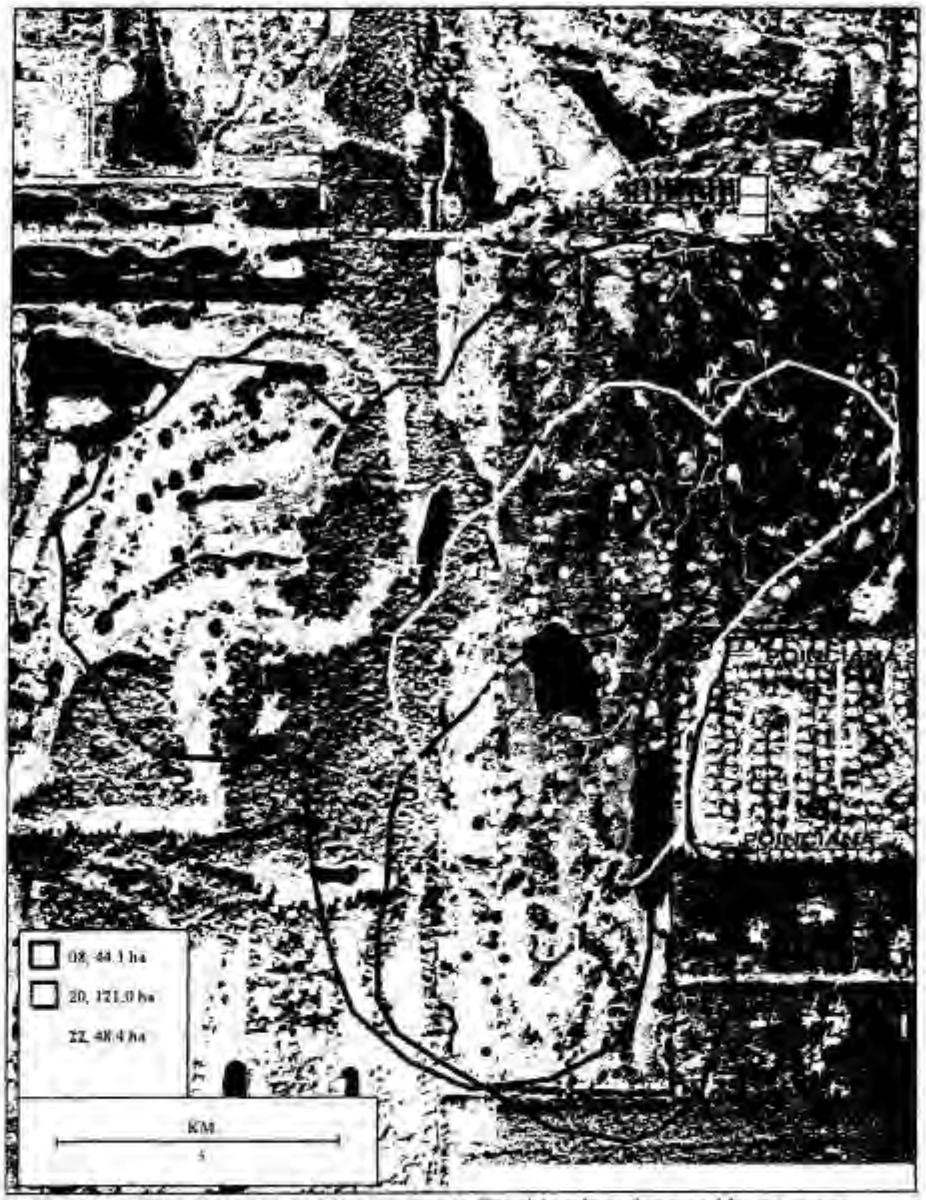

Figure 18 Three adult males, Site 1, year 2. Tracking locations and home range boundaries, defined by the 95% contour, kernel analysis, CALHOME.

Figure 19. Three adult males, Site 1, year 2. Tracking locations and home range boundaries defined by the 95% contour, kernel analysis, CALHOME.

section of the Pines course and the CCN. ROPO 07 and ROPO 08 used the Cypress course and both sections of the Pines course. ROPO 08 and ROPO 20 had the smallest home ranges, each using portions of the Cypress course and the back nine of the Pines course. Males again showed strong overlap of home ranges.

Seven subadults at Site 1, year 2, had home ranges of 5.88 ha to 21.47 ha ($\bar{x}$=14.93) (Figs. 20 & 21). All subadults show overlap with at least 3 other subadults. None of the subadults dispersed before the end of tracking in July 1997, though ROPO 21, a male, began to use the northeast corner of Wilderness Country Club to feed in June and July 1997.

Five of the subadults at Site 1, year 2, were born to adult females ROPO 02, ROPO 03, and ROPO 05 who remained on the course in the same home range areas throughout the study. Figures 22 and 23 compare the 1997 spring/summer home ranges of the collared offspring to the 1997 home ranges of their mothers. The female offspring of ROPO 02 and ROPO 03 had home ranges entirely contained within those of their mothers, while the male offspring of ROPO 03 and ROPO 05 had home ranges that extended beyond those of their mothers. The overlap of the subadult home ranges with the core area of their mother, ROPO 05, is clear (Fig. 23).

Adult female ROPO 01 disappeared in December 1996 and offers no comparison with her 1997 home range area with those of her offspring, ROPO 21 and ROPO 24. Nevertheless, it is clear that her 1996 offspring, male ROPO 21 and female ROPO 24, continued to use their natal home range, the core area of female ROPO 01 before her disappearance (Fig. 24). ROPO 24 expanded to the northeast in her mothers absence and ROPO 21 expanded to the south and west.

Figure 20. Three of 7 collared subadults, Site 1, year 2. Tracking locations and home range boundaries as defined by the 95% contour, kernel analysis, CALHOME.

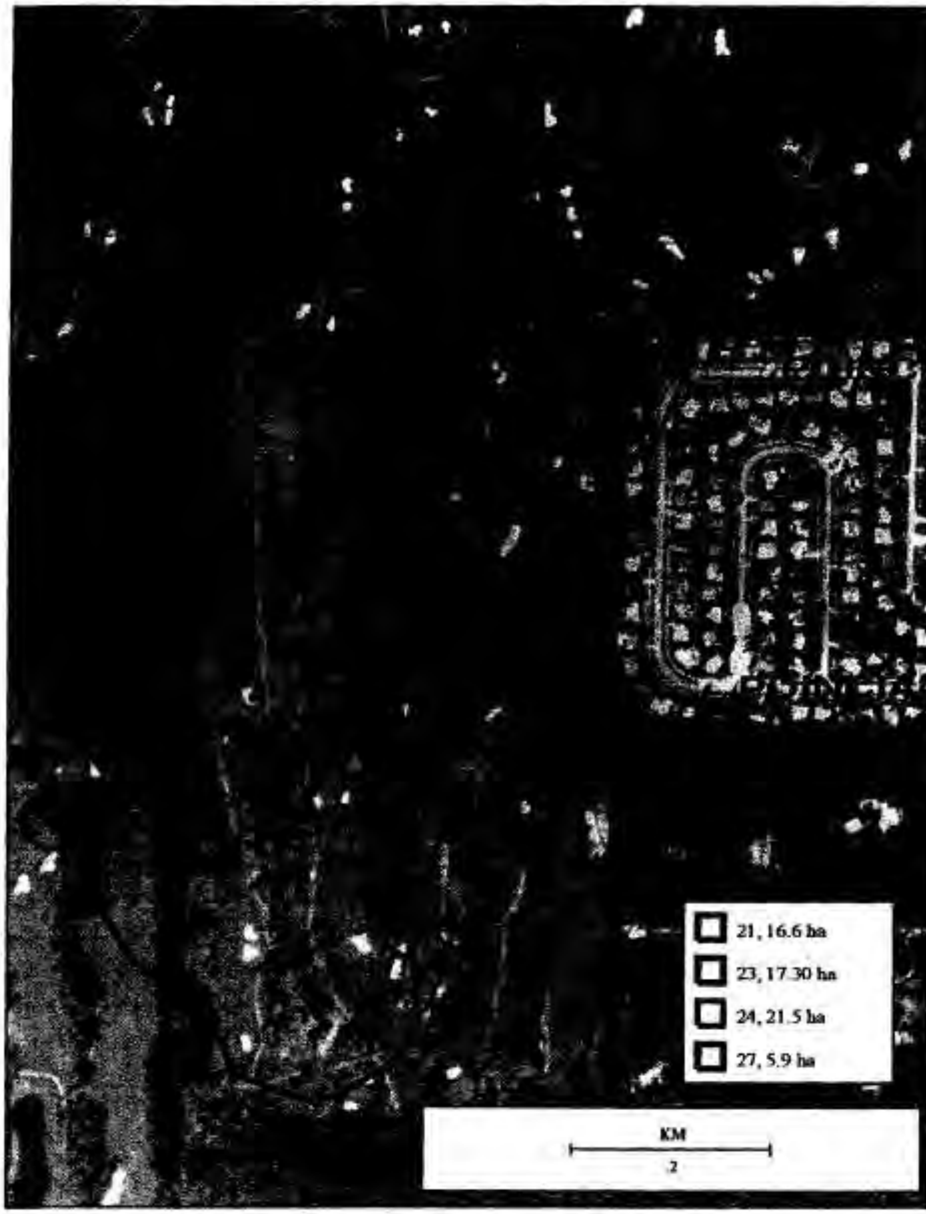

Figure 21. Four of 7 collared subadults, Site 1, year 2. Tracking locations and home range boundaries as defined by the 95% contour, kernel analysis, CALHOME.

Figure 22. Two adult females and offspring, Site 1, year 2. Females, 03 and 02, and their collared offspring from summer 1996. Thin lines are subadult offspring. Squirrels 27 and 29 are females, 26 is male.

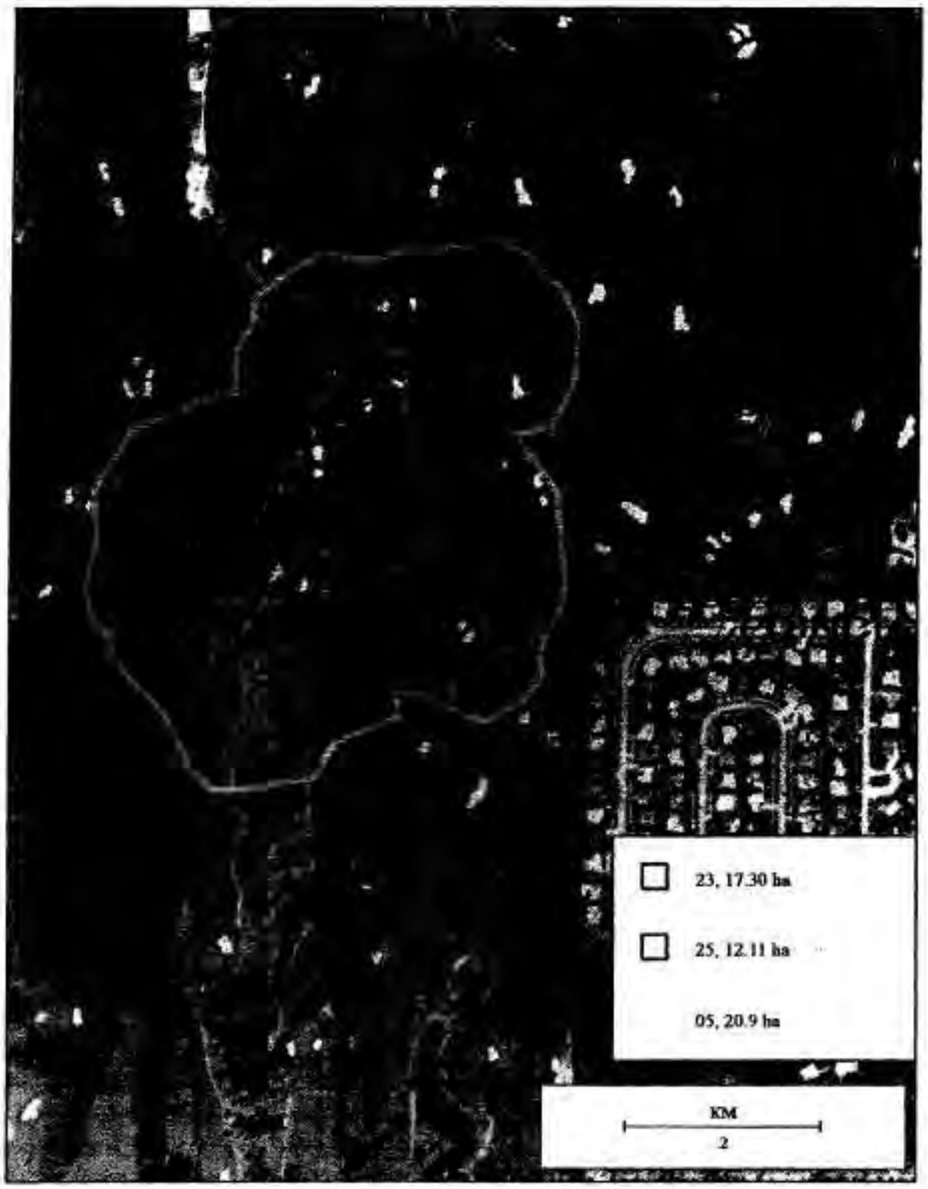

Figure 23. Home ranges of adult female and offspring, Site 1, year 2. Adult female 05 and collared male offspring 23 and 25 from summer 1996. Yellow dots indicate the core area, 50% contour, of female 05.

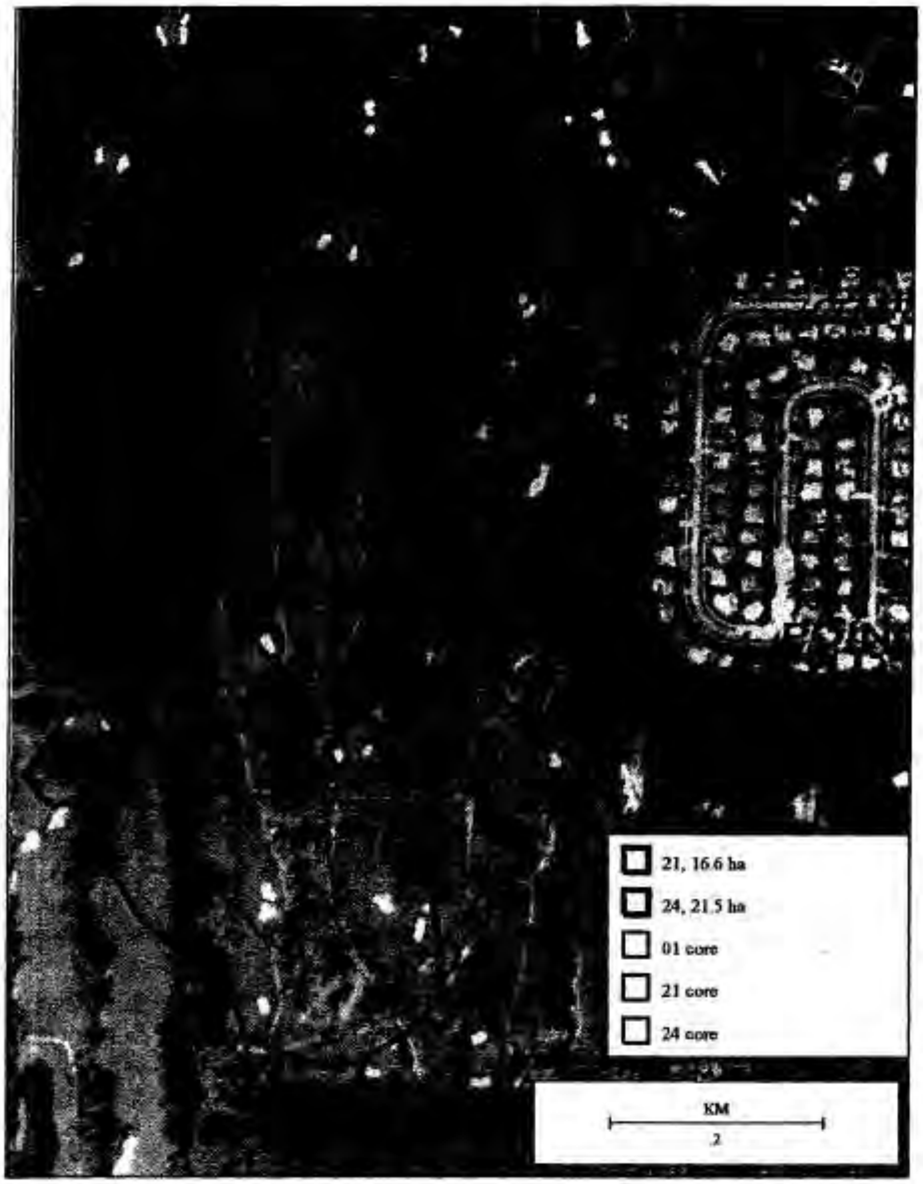

Figure 24. Home ranges of female and 2 offspring, Site 1, year 2. Subadults 21 and 24, siblings from female 01 in the summer 1996, show overlap of home ranges and core areas. Core area of 01, who disappeared in December 1996, is shown in light blue.

All 7 of the Site 1, Year 2, subadults continued to use their natal homeranges for the first year of their lives, 5 sharing with their mothers, 2 remaining after their mother disappeared.

Seven of the 8 squirrels collared at Site 2 in year 2 remained to provide usable home range data. ROPA 01 and ROPA 08, adult males, had home ranges of 136.1 ha and 303.8 ha, respectively (Table 5). ROPA 01 used most of Site 2, Royal Palm, while ROPA 08 used Site 2 and most of the neighboring Hibiscus Country Club (Fig. 25). ROPA 08 readily moved from the east to the west end of his home range, a distance of 2.5 km, within 24 hours. Both males regularly crossed Augusta Boulevard, while their movements on either side of that busy street generally followed the fairways and appeared to minimize travel through housing. Though their home ranges overlapped, they were never seen together as males at Site 1 often were.

The two adult females at Site 2 had home ranges of 13.06 ha and 30.57 ha (Table 5, Fig. 26). Adult female ROPA 04 had a home range 50% larger than any at Site 1. She often crossed Augusta Boulevard. Adult female ROPA 06 had a home range similar in size to those at Site 1. Her home range included a regularly stocked feeder at a private residence. On rare occasions she crossed into the central pine stand within the private housing area. Though the home ranges of these 2 adult females were widely separated, no other adult females where ever observed in the area between their 2 home ranges.

Three of the 4 collared subadults at Site 2 provided data on home range size, these varied from 25.77 ha to 108.50 ha ($\bar{x}$ = 58.34 ha) (Table 5, Fig. 27), significantly larger than Site 1 subadults for the same period (Mann-Whitney U=0, $p<0.05$). Male ROPA 2

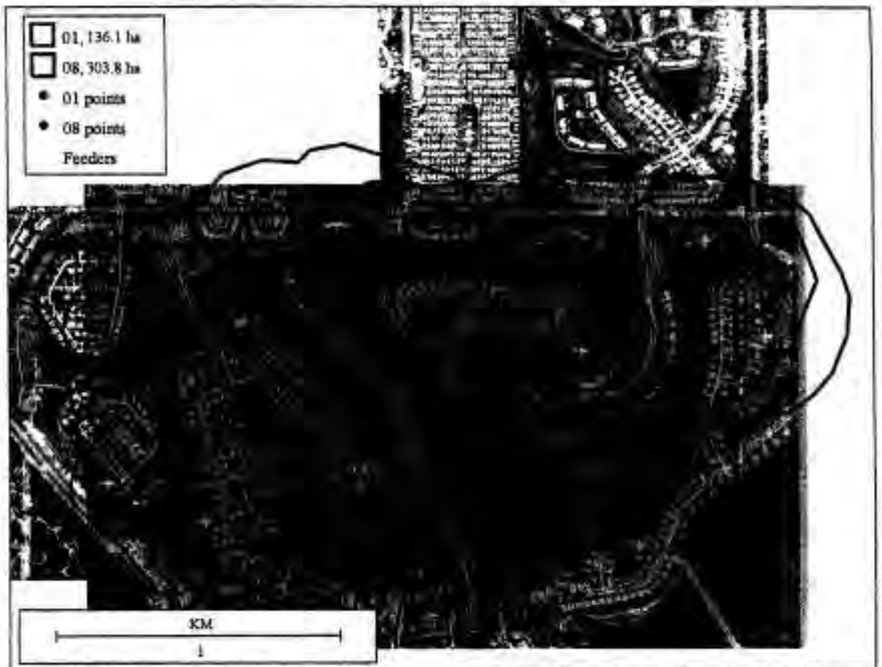

Figure 25. Adult males, Site 2, 1997. Tracking locations and home range boundaries as defined by the 95% contour, kernel analysis, CALHOME. Yellow crosses mark the locations of feeders.

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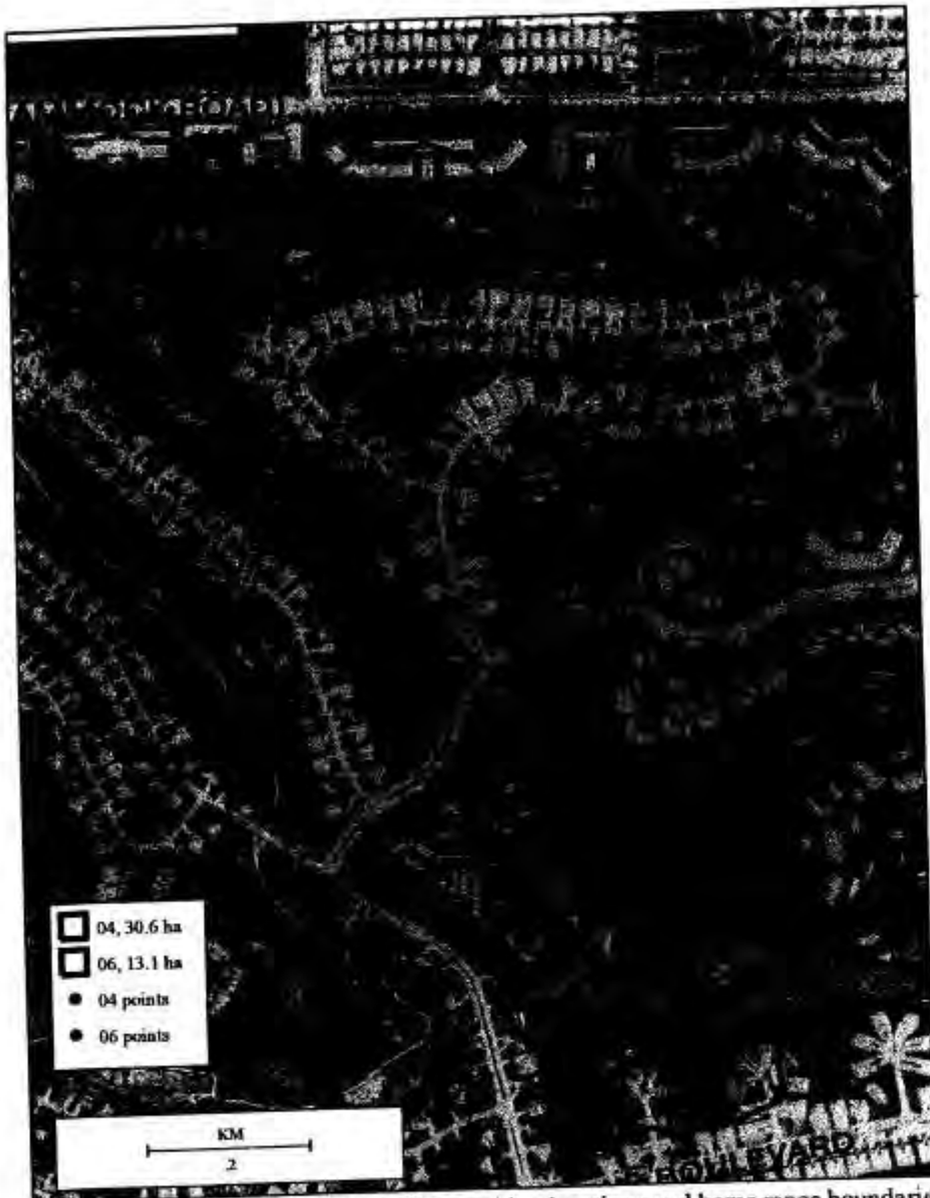

Figure 26. Adult females, Site 2, 1997. Tracking locations and home range boundaries as defined by the 95% contour, kernel analysis, CALHOME

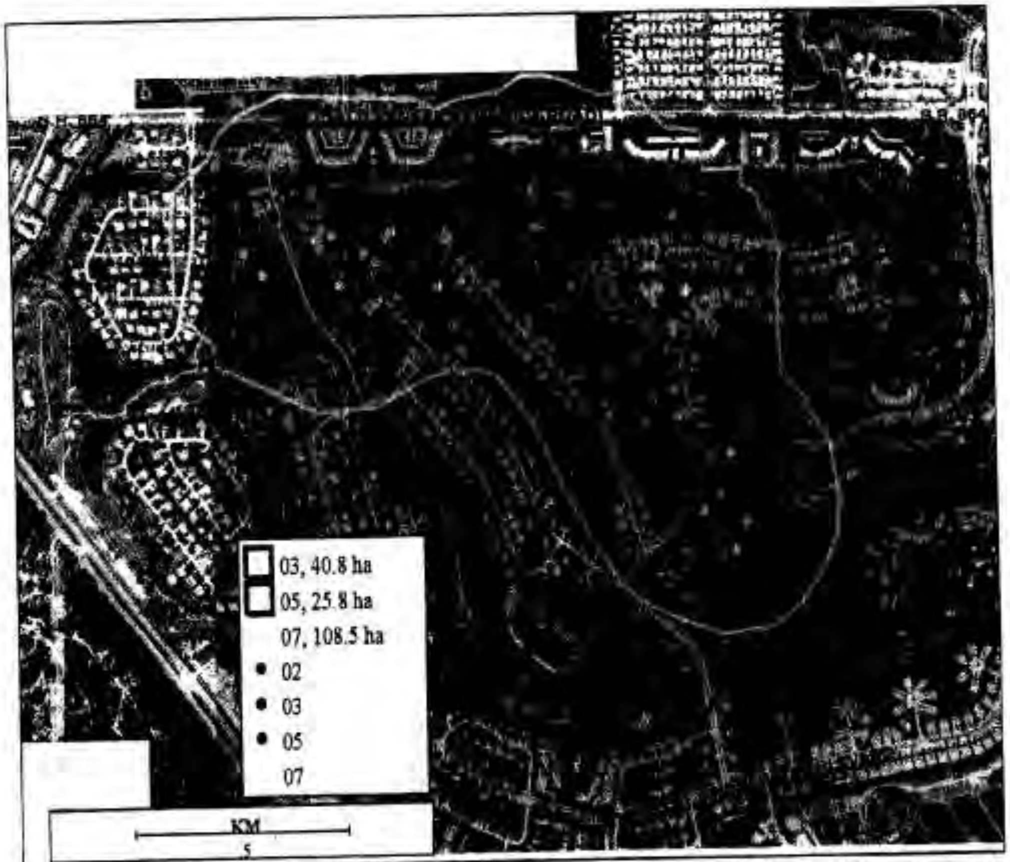

Figure 27. Subadults, Site 2, 1997. Tracking locations and home range boundaries as defined by the 95% contour, kernel analysis, CALHOME

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was an older subadult who disappeared within a month of being collared and provides no usable home range. Female ROPA 3 used an area on both sides of Augusta Boulevard and across Forest Hills Boulevard into the Hibiscus course. Female ROPA 05 used an area on both sides of Palmetto Dunes Circle. Male ROPA 07, summer 1996 offspring of adult female ROPA 06, had an unusual home range use pattern, sequential use of small patches. He spent a few weeks to a month in a small area of a hectare or less and then moved to another area, each time moving away from his natal home range at the northwest corner of Site 2. In the final week before his collar was removed he had moved to the west side of Hibiscus Country Club along U. S. 41, 1.2 km from his natal home range.

Nest Sites

At Site 1 fox squirrels made regular use of untrimmed or lightly trimmed cabbage palms, bromeliads and cypress cavities for sleeping nests. Stick nests were used on occasion. The common use of untrimmed palms and bromeliads as nests eliminated the possibility of counting nests and determining the nest to squirrel ratio. Squirrels were regularly observed carrying Spanish moss (*Tillandsia usneoides*) to nesting sites. Squirrels rarely constructed open platform nests for daytime resting but simply draped themselves along branches.

Brood nests were readily observed at Site 1 in summer 1996 as females seldom moved from the nests for 2 -3 weeks. Nests were located in mixed stands of pine, untrimmmed or lightly trimmed palms, and cypress (Fig. 9). Three females used cavities high in large cypress trees, 1 raised a litter of 4 from such a cavity, another a litter of 3. Two females raised young in the center of densely leafed palms, one a queen palm (*Arecastrum romanzoffianum*) and the other a cabbage palm. The remaining female used a large bromeliad high in a large pine for her nest site. The nest was located in the base of the large plant. All females used Spanish moss in constructing and maintaining nests. The queen palm nest also contained shredded queen palm leaflets and required her to spend time stripping leaflets and tearing them into strips. Winter brood nests were similar to those in the summer of 1996 and included 2 in cypress cavities, 2 bromeliad nests, and 1 palm nest.

As the study ended at Site 2, both adult females appeared to be tending brood nests. One was in a rather isolated moderately trimmed cabbage palm near a canal and the other was in a stick nest in a moderate-sized pine tree. In the winter of 1997, the same female was observed using a wood duck box with her offspring from the previous summer. All 3 nested together in the box during times of heavy rain, cooler nights, or high wind.

Landscape Composition and Vegetation Mapping

Landscape composition of Sites 1 and 2 and the Poinciana Pines course is presented in Table 7. While Site 2 was 2.3 times larger than Site 1, the golf course and tree stands within the roughs of the 2 courses were similar in size, though not necessarily similar in species composition or structure. The obvious difference in landscape composition between the 2 sites was the presence of housing areas at Site 2. Twenty-eight percent of Site 2 was occupied by residential development, streets and clubhouse property, and an additional 25% was condominium land and a private pine stand within a housing area. The 2 courses that comprised Royal Poinciana Golf Club, Site 1 and the adjoining Pines course, were similar to one another in general landscape composition. The smaller

Table 7. Landscape composition. Landscape cover of Site 1, Site 2, and Royal Poinciana Pines course.

	Royal Poinciana Cypress Site 1		Royal Palm Site 2		Royal Poinciana Pines Course	
	Area, ha	% of total	Area, ha	% of total	Area, ha	% of total
Total size of site	61.4		141.9		62.9	
Club property in tree stands	30.0	49%	26.0	18%	24.8	39%
Condominium land in trees	0.0	0	34.9	25%	0.0	0
Residential, streets and clubhouse	0.0	0	40.1	28%	0.0	0
Lakes, canals, wetlands	5.5	9%	8.0	6%	5.3	8%
Fairways, greens, sandtraps, driving ranges, unforested roughs	25.9	42%	32.9	23%	32.8	52%

area of tree stands in the Pines course reflected the open nature of the back 9 of that course and the presence of 2 driving ranges within the course.

While Site 1, Site 2, and the Pines course each had between 30.0 and 24.8 ha of tree stands or forested area, the species composition and structure of these plots were not alike. Site 1 sampling plots contained a greater diversity of tree species than Site 2 plots. (Table 8, Fig. 28,29). A mixture of native tree species, pine, cabbage palm, and cypress, dominated Site 1. Though Site 1 was high in native hardwoods, there were no class 1, pine dominant, stands. Pines were found as co-dominants with cabbage palm (11%), cypress (3%), or both (10%). Cypress was dominant in 14% of the forested area and was co-dominate with pines and/or cabbage palms in an additional 31% of the area. Palm dominant stands accounted for 8% of the area in tree stands. At Site 1, 64% of the tree stands were dominated by the pines, cypress and cabbage palms. A mixture of native species, often including oaks (*Quercus virginianum, Q. laurifolia*) , maple (*Acer rubrum*), red bay (*Persea borbonia*) made up another 10% of the forested landscape. While native species dominated the landscape, the importance of exotic species on the Cypress course was seen in the extent of class 9 (mixed natives with exotics), which covered 26% of the forested area.

Site 2 was dominated by pine, with 68% of the plot area in class 1(pine dominant) and an additional 6% with pines as co-dominants (Table 8, Fig. 29). Cypress was a minor element of the Site 2 vegetation, dominating in only 2% of the area. Classes 6 and 7 of the mixed natives were not present at Site 2. Exotics were less common than at Site 1, with class 9 (mixed natives with exotics) accounting for 11% of the area.

Table 8. Vegetation classification of Site 1, Site 2, and Royal Poinciana Pines.

	Royal Poinciana Cypress Site 1		Royal Palm Site 2		Royal Poinciana Pines Course	
Vegetation classes, by relative basal area	Area, ha	%	Area, ha	%	Area, ha	%
1-Pine, 70% or more pine	0.0	**0**	17.8	**68**	3.0	**12**
2-Pine and cabbage palm, 30% or more of each	3.2	**11**	0.9	**3**	2.4	**10**
3-Palm, 60% or more cabbage palm	2.4	**8**	1.4	**5**	2.0	**8**
4-Cypress, 60% or more cypress	4.4	**14**	0.4	**2**	3.5	**14**
5-Pine and cypress, 30% or more each of pine and cypress	0.9	**3**	0.7	**3**	0.0	**0**
6-Pine, cypress, c. palm, over 85% of the 3 combined, with each being over 20%	2.9	**10**	0.0	**0**	0.0	**0**
7-Cypress and c. palm, 30% or more of each cypress and pine	5.5	**18**	0.0	**0**	0.0	**0**
8-Mixed natives-none of the above with 20% or less exotics	2.9	**10**	2.1	**8**	1.2	**5**
9-Mixed natives with exotics-not 1-7, with more than 20% exotics	7.8	**26**	2.8	**11**	12.7	**51**

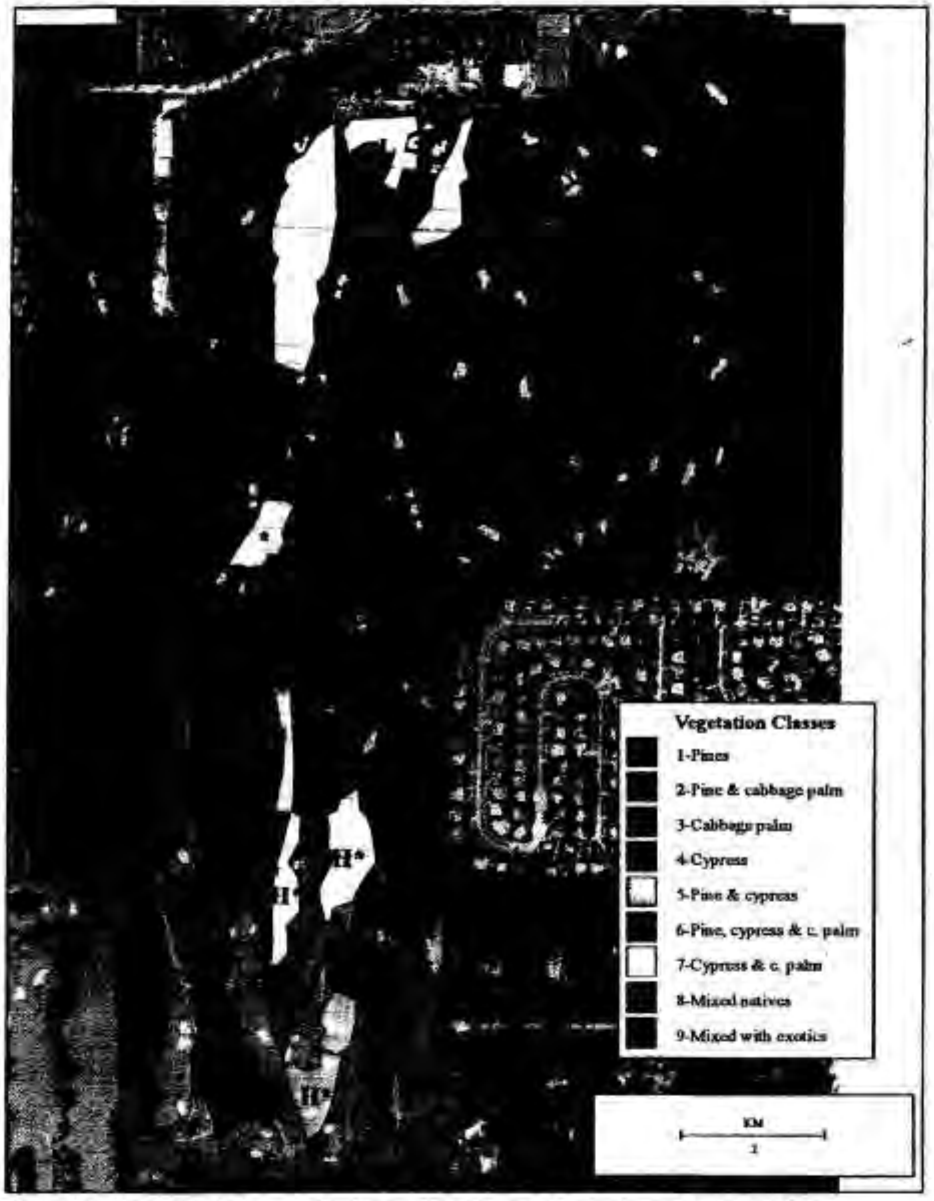

Figure 28. Tree stand characteristics at Site 1, Royal Poinciana Cypress. Nine vegetation classes are color coded. H= high density (>200 stems/ha), L=low density (<100stems/ha), all patches not marked H or L are moderate density (100-199 stems/ha). Presence of dense litter layer is indicated by an asterick (*); S= presence of a shrub layer. Light gray areas between tree stands are the fairways, tees, and greens.

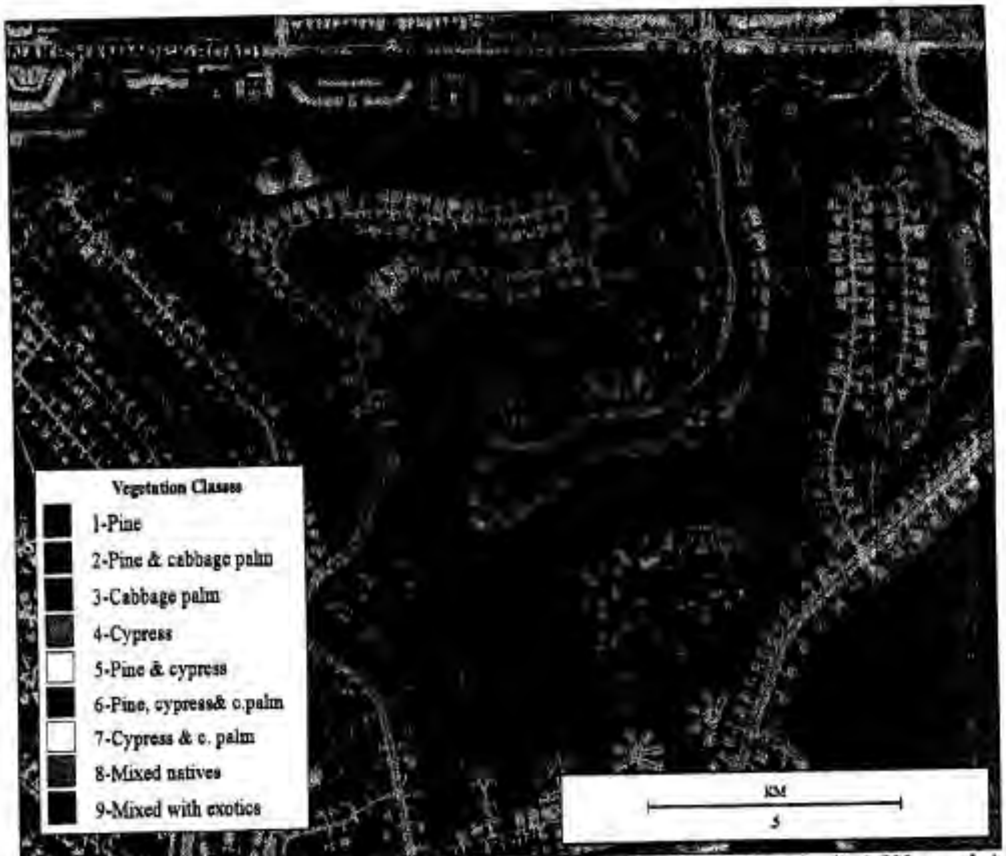

Figure 29. Tree stand characteristics at Site 2, Royal Palm. Nine classes are color coded. H=high density (>200 stems/ha), L=low density (<100 stems/ha), VL=Very Low density (<30 stems/ha). All patches not marked are moderate density (100-199 stems/ha). Presence of litter layer is indicated by an asterisk (*). Areas along Augusta Boulevard that are outlined in dark green and contain letters indicating tree density are the condominium properties. The outline area in the upper left is the private pine forest.

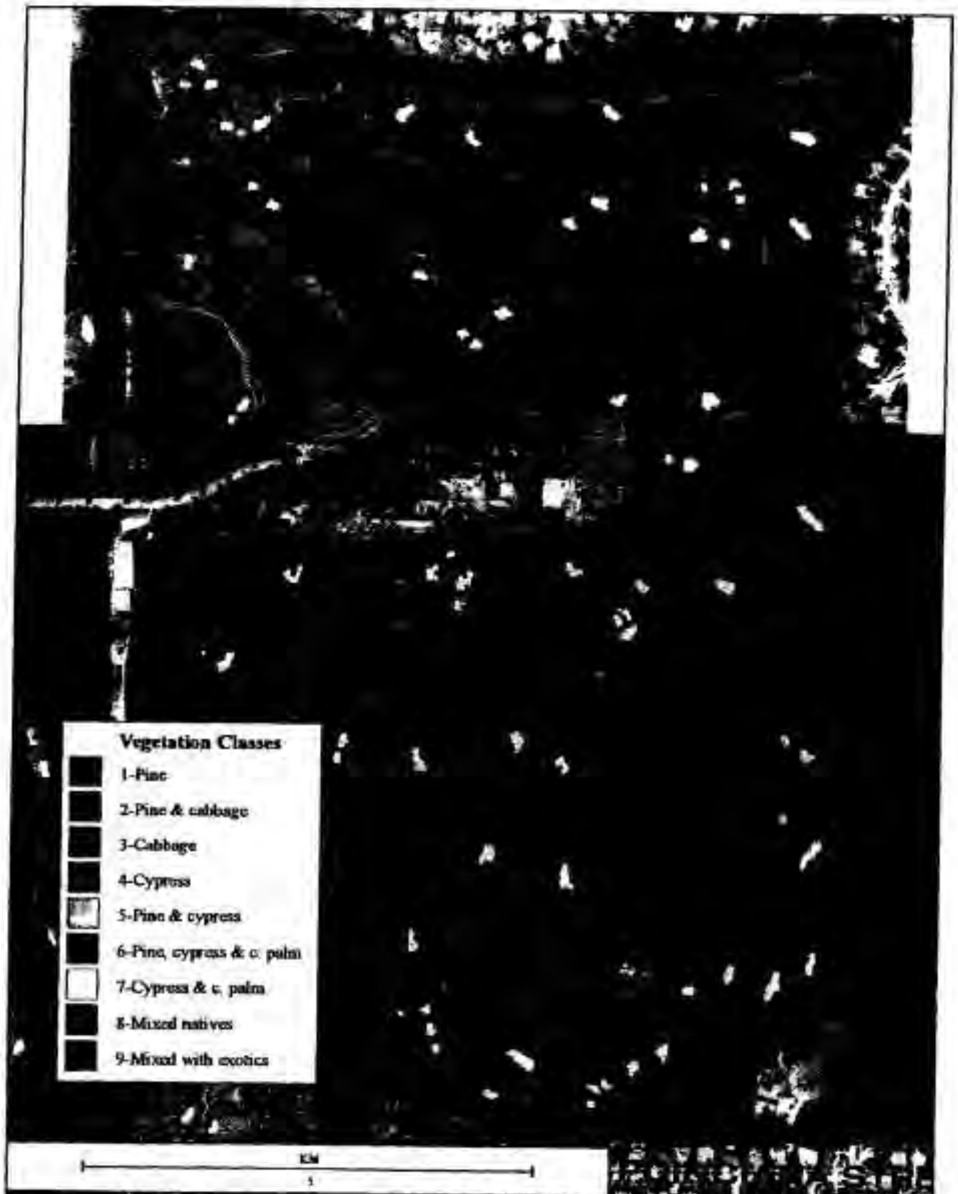

Figure 30. Tree stand characteristics for Royal Poinciana Pines course. Nine classes are color coded. H=high density (>200 stems/ha), L=low density (<100 stems/ha), all patches not marked H or L are moderate density (100-199 stems/ha). Presence of a dense litter layer is indicated by an asterisk (*); S= presence of a shrub layer. Gray areas between tree sands are fairways.

The Pines course had a high presence of exotic species, with 51% of the tree stand area in class 9, and a much lower area dominated by a mixture of pines, cypress and cabbage palms (Table 8, Fig. 30). Pine dominated stands (class 1) accounted for 12% of the forested area and pine/cabbage palm for an additional 10%. Cypress dominated 14% of the area. Classes 5, 6 and 7, mixtures of pine cypress and cabbage palm, were absent from the Pines course.

Structure of the trees stands on the 3 courses also differed from course to course (Table 9, Figs. 28-30). Site 1 had a higher density of trees than Site 2, with 24.9 ha of forested area having more than 100 stems/ha and only 5.2 ha in lower density stands. Site 2 had a much more open landscape, with 17.9 ha of low density (< 100 stems/ha) and only 8.4 ha in high and medium levels. The Pines course was a mixed course, with a dense forested front 9 on the north and an open back 9 on the south.

The presence of a litter ground cover, as opposed to grass or bare soil, and the presence of a shrub layer are noted in Figures 28-30. Site 2 had 4 plots with a significant litter layer. All were in pine dominated stands, only 1 with a high tree density. Site 1 had 8 plots with heavy litter layers, 5 of these plots had high tree density and all of these stands were dominated by a mixture of native pine, cypress or cabbage palms. Four plots at the south end of Site 1 had a shrub layer, with wax myrtle (*Myrica cerifera*) the most common understory species. The Pines course had 7 plots with a litter layer and 5 of these had high tree density. The more open back nine of the Pines contained 2 large plots with heavy litter layers and high to medium density of trees.

The condominium areas and private forest stand at Site 2 were dominated by pines, though tree density varied widely with the number of buildings and parking lots in

Table 9. Density of trees at Site 1, Site 2, and Royal Poinciana Pines.

	High > 200 stems/ha	Medium 100-199 stems/ha	Low <100 stems/ha
Site 1, R. P. Cypress-			
area in ha	5.4	19.5	5.2
%	**18%**	**65%**	**17%**
Site 2, Royal Palm			
area in ha	0.7	7.4	17.9
%	**3%**	**28%**	**69%**
Royal Poinciana Pines			
area in ha	7.8	9.9	7.1
%	**32%**	**40%**	**28%**

each plot (Fig. 29). Most condominium plots had low pine densities, with 19.8 ha in the range of 30-99 stems/ha and 5.6 ha at < 30 stems/ha. High density pine forests (>200 stems/ha) were found in 4 plots totaling 4.5 ha and 2 plots totaling 4.0 ha had moderate densities (100-200 stems/ha). The 6 undeveloped private home vacant lots bordering the course in the summer of 1997 had dense stands of pine with scattered cabbage palms. The developed lots that circled the course on all but Augusta Boulevard had a very low density of trees, with 3 or fewer trees in most lots. Pine and queen palms (*Arecastrum romanzoffianum*) were the most common species. Black olive (*Bucida buceras*), cabbage palms, oaks and bottle brush (*Callistemon rigidus*) were scattered throughout the lots of private residences.

Habitat Use

Locations of 2138 of the 2497 tracking points of the Site 1 collared population were used to examine habitat preference on the Royal Poinciana Cypress and Pines courses. The 359 points not used were located either on neighboring courses, fairways or unforested roughs. Comparison of the aggregated area of all plots in each of the 9 vegetation classes and the number of points located within the boundaries of each class shows a non-random use of forested areas (Table 10, Fig. 31). On the Cypress course, all subsets of the population showed non-random use of the forested stands. In all cases, fox squirrels had higher than expected use of class 2 plots pine/cabbage palm co-dominated stands. While class 2 plots were 11% of the forested area, they accounted for 18% of the tracking locations for females and 28% for males. A preference for class 2 plots was shown in both years of the study.

Table 10. Habitat preference tests on tracking points at Royal Poinciana Cypress and Pines courses. Chi-square tests the hypothesis that points are randomly distributed among vegetation types. Area of each vegetation class predicts the number of points. Only tracking locations within the mapped plots of forested stands are included. Double asterisk indicates results are significant at the 0.01 level.

	Number of Tracking Points	X^2	df	p
Cypress				
Females, both years	1206	154.08	7	5.60E-30 **
Males, both years	768	242.76	7	9.60E-49 **
Year 1, all squirrels	1036	208.12	7	2.18E-41 **
Year 2, all squirrels	938	128.51	7	1.28E-24 **
Summer 1996	276	81.57	7	6.59E-15 **
Summer 1997	340	41.29	7	7.12E-07 **
Pines				
All points	164	20.73	5	0.0009 **
Males, both years	140	17.59	5	0.0035 **
Year 1 all squirrels	65	7.99	5	0.1570
Year 2 all squirrels	99	18.31	5	0.0026 **

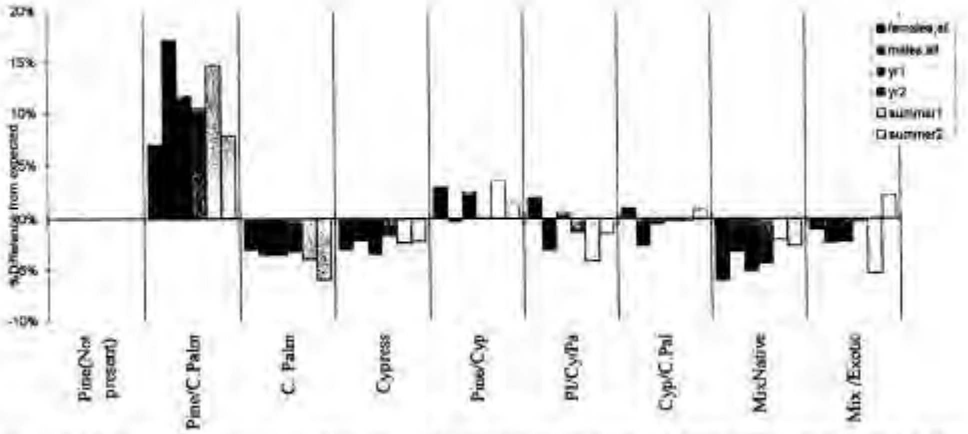

Figure 31. Difference in expected and observed use of vegetation classes at Site 1, Cypress course, by subgroups of the tracked population. The nine classes of tree stands are shown on the x axis. Positive values indicate a stronger than expected preference for a given vegetation class, negative values indicate less than expected use of a vegetation class. Table 10 presents Chi-square results for tests of random distribution among vegetation classes for each of the subgroups shown here.

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Site 1 fox squirrels showed consistent underuse of cabbage palm dominated plots, cypress dominated stands and plots of mixed natives. Females showed a preference for pine/cypress dominated plots, as well as pine/cypress/cabbage palm stands and cypress/cabbage palm forested areas (Fig. 31). Males underused or showed expected use of all vegetation types other than the pine/cabbage palm plots.

On the Pines course the aggregation of all tracking points within the tree stands shows a preference for pine plots, mixed natives and natives with exotics. Both cabbage palm plots and cypress stands were underused (Fig. 32). Females used the Pines course so rarely, only 24 points in the 2 years of the study, that they were not examined separately for patterns of use. The summer subsets were similarly small and not separately analyzed. In the first year of the study, fox squirrel use of tree stands at the Pines course indicated no significant departure from expected (Table 10).

The mixture of golf course property with private and condominium property at Site 2 created a more complex landscape than seen at Site 1. Analysis of the 147 tracking locations within the 26.0 hectares of tree stands on the Royal Palm property showed that squirrels used the vegetation classes in proportion to their abundance on the landscape (X^2=12.22, df=6, p=0.058). Pine plots account for 68% of the forest stands and contained 65% of the analyzed tracking points. Class 9, mixed natives with exotics, and class 3, cabbage palm dominated stands, had slightly higher than expected use. The 34.9 ha of condominium property and the private pine forest inside the back 9 of the course had only 34 tracking points. Nineteen of these were in the 1.4 ha private pine forest that contained at least 3, well-stocked feeders. The 40.1 ha of residential property accounted for only 17 tracking location, 10 at feeders.

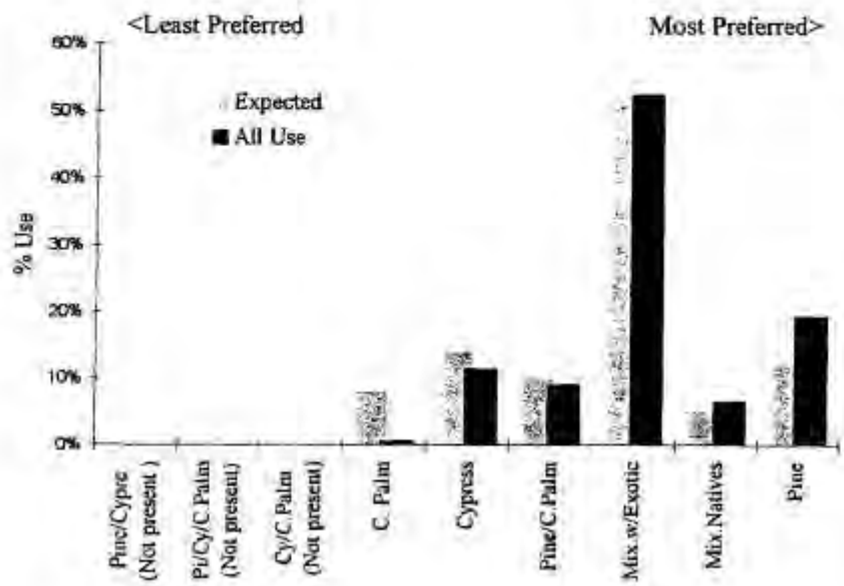

Figure 32. Habitat preferences for all fox squirrels at the Pines course, Royal Poinciana. All tracking points within the mapped vegetation plots on the Pines course are included, n=164.

Table 11. Feeding patterns of fox squirrels on the 13 main food species eaten by the collared population of Site 1. Data include all feeding records, at all locations used by the Site 1 collared squirrels for 19 months, n=817. Diversity Index is the inverse Simpson measurement for richness and evenness. Cell shading: Section A, dark=≥50%, light=15-49%, white=<15%, blank cells =0; Section B, dark=≥ 50%

Section A-Species data	Jan 96	Jan 97	Feb 96	Feb 97	Mar 96	Mar 97	Apr 96	Apr 97	May 96	May 97	Jun 96	Jun 97	Jul 96	Jul 97	Aug 96	Sept 96	Oct 96	Nov 96	Dec 96
%Natives																			
Pine	25	22	2	8		7	1	14	4	6	3	10	5	20	[illegible]	[illegible]	[illegible]	[illegible]	17
Cypress	42	37		18	4	5	2	1	6	4	16	21	21	20	23	18	19	33	[illegible]
Red maple	8	4	20	14															
Oak sp		7		6		3		8	4							10	13		30
Mushrooms			4	3		8	2	1	2	27	21	12	26	5		8	4		
Larva										4		15							
%Non-natives																			
Q. palm	8	7	33	22	7	5	16	4	4	18	3	6	16	5		8	6		
Ficus sp		4	20	2	6	16	4	3	17	39	11	23	21	5	4				
Tallow		19	2	5		3	1	1											
Bischofia	17		18	23	[illegible]	26	[illegible]	29	42	2	42	2	11		4				
Bottlebrush					28	22	18	21	6		4			10					
Silk oak						4	5	18	15										
Java plum											3	12		33	4				
n=	11	27	45	62	54	73	94	78	52	49	38	52	19	20	26	39	48	3	23

Section B-Summary	Jan		Feb		Mar		Apr		May		Jun		Jul		Aug	Sept	Oct	Nov	Dec
%Natives	75	70	27	49	4	23	5	24	15	41	39	58	53	45	88	92	94	100	100
%Non-natives	25	30	73	51	96	77	95	76	85	59	61	42	47	55	12	8	6	0	0
Diversity Index	3.6	4.3	4.4	6.0	2.5	6.1	3.2	5.3	4.1	3.8	3.8	6.2	5.1	4.5	2.1	2.7	2.5	1.8	2.5

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Feeding Patterns

Feeding data from Site 1 show seasonal shifts between native and non-native food sources (Table 11). Native foods, pine, cypress, and oaks, made up over 70% of the diet from August 1996 through January 1997. In March through July of 1996 and 1997, non-natives were the primary food source. February, June, and July of the 2 years showed a changing mixture of native and non-native sources.

In 1996 squirrels began to feed on new, green pine cones in late June and early July. By August cones were mature and pine became the dominant food, with squirrels feeding alone or in small groups in or around select trees for several hours at a time. This also began the season of burying cones, in grass, litter and sand traps. Squirrels were observed burying in their core areas and at the edges of their home ranges. In December and January, cypress cones increased in importance, as pines decreased. Cypress constituted 20% or more of the diet for 7 months, July 1996 through January 1997. Despite the tent caterpillar infestation of 1997, cypress were again accounting for 29% of the diet in June and July of that year. Feeding on early pine cones began in June and July 1997.

Oaks were not a regular food source in 1996 until September, when oak feeding, primarily live oak, accounted for 30% of the diet. Fox squirrels continued to feed lightly on oaks through April 1997.

In both 1996 and 1997 fox squirrels took advantage of the bright red samara of the red maples for concentrated feeding in January and February. Late winter and spring feeding on natives was scattered. In April and May of both years squirrels fed on old pine cones, most often digging them up, but occasionally removing them from the tree. Cypress remained a minor element in the diet in all winter and spring months of 1996 and 1997, except February 1996.

Fox squirrels fed on large hypogeous fungi from February through October. While they fed on both the mycelia and the fruiting bodies, the most readily observed behavior was the feeding on the large fruiting bodies. The peak season for observation of fungi feeding varied slightly, June and July in 1996 and May and June 1997. Fungi feeding was concentrated in patches that had deep litter layers, generally beneath pine and cabbage palm, but also in stands of cypress and pine. Of the 111 fungi feeding observations at 53 tracking points, 86% were in litter, 9% in grass, and 5% in trees. A squirrel might carry a fruiting body up a tree, where he would hang upside down and eat. In peak season, I recorded periods of concentrated feeding when a squirrel would eat the large caps (5-8 cm) of 4-5 fruiting bodies within 10 minutes.

In May and June 1997 squirrels fed on concentrated patches of Mahogany webworm larva, *Macalla thyrsialis* (John Heppner, personal communication), buried in soil, grass or litter. They bit the tip from the cases and pulled the small caterpillars out with their teeth. During the same period they showed no interest in the tent caterpillars that rained to the ground from the infested cypress trees.

In both 1996 and 1997, March through May were periods of concentrated feeding on non-natives. In March 1996 to June of that year, over 40% of recorded feeding was on bischofia (*Bischofia javanica*), an Asian species that forms clusters of small, dark berries. Squirrels initially fed in trees and then moved to ground feeding, where they gathered in groups of 2-8 to feed on the fallen fruit. Four large bischofia trees on the Cypress course drew squirrels in mid morning and late afternoon feeding groups. In 1997, levels of bischofia feeding were lower, with peaks in February through April in the 20-30% range.

Bottlebrush trees, native to Australia, drew squirrels to feed on their spikes of scarlet flowers in March and April of both years. Silk oaks (*Grevillea robusta*), another Australian native, with their orange-fringed flowers, also attracted fox squirrels for flower feeding. In 1996 the peak feeding was late April and May, in 1997, late March and April.

Queen palms, common throughout Royal Poinciana, produce a bright orange, aromatic, 2 cm oval fruit. A squirrel feeding on the fruit makes a distinctive, loud grating sound, whether hanging from clusters of new fruits or digging up a previously buried specimen, and so identification is easy. Queen palm feeding was high in February of both years and moderate in April and July of 1996 and May of 1997. Squirrels regularly buried queen palm fruits and most of the spring 1997 records are squirrels feeding on fruit they dug up. Heavy trimming of palms in the fall and winter of 1996-97, removed most of the available fresh crop. Regrowth and new fruits did not appear until summer of 1997.

Ten large ficus trees (*Ficus spp.*) dotted the Cypress course and stands of large ficus were common at Hole in the Wall. These drew squirrels for feeding from January through August. A variety of species with staggered fruiting times produced the most concentrated feeding in May through July.

Fruit of the tallow tree (*Sapium sebiferum*) and Java plum (*Syzigium cumini*) trees were feeding sites for short seasons. Tallow trees provided feeding in January and February and Java plum in June and July. Feeding on Java plum was high in July 1997 as the study ended, when squirrels gathered in 4 stands that produced aromatic crops of fruit on the Cypress course.

The 1996 fall feeding on native species was the period with the lowest food diversity. In both years, diversity was higher in February through July. Diversity was noticeably higher in 1997, February to April and June, when a broader range of non-native species and a greater use of native species were seen in the feeding records. This difference was not only a result of changes in who was collared, but was reflected in the expanded diets of individuals collared both seasons. While 4 squirrels showed concentrated bischofia feeding in spring 1996 (8-23 observations), none of these repeated the pattern in 1997. All increased the number of species they used. Only 1 individual, subadult ROPO 27, showed concentrated bischofia feeding in spring 1997 and she regularly fed on the 2 large bischofia trees near her birth tree. Her mother, ROPO 2, fed on at least 10 species each spring.

The feeding data at Site 2, covering January to July 1997, were aggregated due to low numbers (Table 12). Feeding on non-natives was dominant, as it was in the late winter and spring at Site 1. Native foods included pines, larvae and mushrooms. Pine feeding, 16% of total, was primarily cones from previous seasons. Larvae of the same species as Site 1 and mushrooms accounted for an additional 16% of feeding records. Cypress were a minor element of the diet and not common at Site 2 or neighboring courses. Sixty-seven percent of the recorded feeding was on non-native sources, while 33% of the sightings were squirrels feeding at feeders. Ten feeders were available to fox squirrels, whether placed there for their use or for birds. Eight of the feeders were on Royal Palm property or adjoining residential property, 2 were on the west side of the neighboring Hibiscus course (Figure 25). Bottlebrush trees and queen palms provided feeding opportunities at Royal

Palm, while Java plums and ficus were grouped in a small area of the Hibiscus course Only ROPA 8 was seen begging, and that, successfully, at the public Hibiscus course.

Table 12. Feeding patterns of fox squirrels at Site 2. Data include all feeding records at all locations used by the Site 2 collared squirrels from January 1997 through July 1997. All food items are listed.

N=45

Non-natives	Feeders	Bottlebrush	Java plum	Ficus	Silk oak	Queen palm	Begging
67%	33%	13%	9%	4%	2%	2%	2%

Natives	Pine, new & old cones	Larva	Mushrooms	Cypress
33%	16%	9%	7%	2%

DISCUSSION

The goal of this study was to gain an understanding of golf courses as suitable habitat for Big Cypress fox squirrels. In the following discussion I will address this goal by integrating the data on fox squirrel ecology with that on course landscapes. I will first look at the characteristics of the 2 radio-collared populations in the high and low quality golf course landscapes. Then I will interpret the findings of the Landscape Evaluation Index. The two courses with collared populations will serve as reference points for the further interpretation of the broad range of golf course landscapes identified and ranked through the use of this index. Recommendations for design and management of course landscapes will be presented in the final chapter.

Higher Quality Golf Course Landscape

Site 1, Royal Poinciana Cypress Course, provided high quality fox squirrel habitat with few intrusions by traffic. The course rated 0.956 on the Landscape Evaluation Index, with large, moderately dense to dense tree stands of mixed natives dominated by pine, cypress and cabbage palms. Scattered exotics provided a majority of late winter and spring feeding sites. Numerous non-irrigated areas with pine litter ground cover provided centers for concentrated feeding on fungi. Mixed tree stands with large trees, bromeliads, and moderately trimmed palms provided a variety of protected nesting sites.

As would be expected, adult females had smaller home ranges than males (Kantola and Humphrey 1990, Weigl et al. 1989). Mean home range size for adult females was 10.10 in 1996 and 16.40 in 1997. Home range means for adult males were 70.84 in 1996 and 90.91 in 1997, larger than previously reported in work on southeastern fox squirrels. Kantola and Humphrey's (1990) work with *S. n. Shermani* in north Florida showed female home ranges averaging 16.7 ha and male home ranges averaging 42.8 ha (harmonic mean). In North Carolina, Weigl et al. (1989) found an average female home range size for *S. n. niger* of 17.2 ha and an average male home range size of 26.6 ha (MCP).

Site 1 adult male home ranges were 7 times larger than adult female home ranges in year 1 and 5.5 times larger in year 2, showing a much greater difference between the sexes than reported by previous workers in the southeast (Kantola and Humphrey 1990, Weigl et al. 1989). Males with a substantial portion of their home ranges in neighboring courses of generally lower quality had larger home ranges. The strong overlap seen in home ranges of both males and females at Site 1 appears to be unusual for southeastern fox squirrels (Kantola and Humphrey 1990, and Weigl et al 1989). Kantola and Humphrey found little overlap in female home ranges, while Weigl et al. (1989) note seasonal variation with no overlap of male home ranges in times of winter scarcity.

Subadult home ranges for both years of the study averaged 18.3 ha, not significantly different from adult females. Male 13 increased the mean size by 2.6 ha with at least 3 long day trips into the Pines course the month before he dispersed out of the club to the south.

Though home range size for subadults remained consistent throughout the study, dispersal of subadults differed greatly between 1996 and 1997. Four of the 10 individuals, 3 females and 1 male, collared as subadults in 1995-96 dispersed from the course in the spring and summer of 1996. Three of the 4 were frequently observed being chased by adults before they left the course. In 1997, none of the 7 squirrels collared as subadults dispersed before the end of July when collars were removed. None of the subadults was observed being chased by adults in the 1997 season. All continued to have a majority of their home range within that of their mothers and all were known to be 11-13 months of age when the study ended. The sample of dispersers was too small to allow for detection of a sex bias. Unbiased dispersal would be expected if dispersal is resource driven, as it appears to be in solitary, promiscuous squirrels such as red squirrels (Anderson 1989, Larsen and Boutin 1998) and gray squirrels (Thompson 1978).

Interpretation of the differences between the 2 years is difficult. As Tappe and Guynn (1998) pointed out, little work pertaining to dispersal in fox squirrels has been reported. Much that is available is speculation. While some researchers have asserted that all fox squirrel juveniles disperse (Hansen et al. 1986, Koprowski 1991), that was not evident here. The relatively small samples of 1996 and 1997 did show that some fox squirrels do not disperse and that both males and females disperse.

One explanation for the differences in dispersal is that Big Cypress fox squirrels may not disperse before one year of age, though previous research indicates that dispersal of fox squirrels would be expected before that age. In more northern fox squirrels dispersal of spring born individuals peaks in the fall before they are a year old (Allen 1943, Baumgartner 1943). Size and sexual condition at the time of capture indicated dispersing individuals in the current study were born in summer 1995 and so dispersed just before they were one year of age. So why did their counterparts in 1996 stay at home? Perhaps in years of lower resources more tropical subspecies such as Big Cypress fox squirrels can delay dispersal and reproduction until later in the season.

Perhaps dispersal was driven by changes in resources or related changes in female reproductive cycles. Data indicate that resources were less favorable in 1997 than 1996, and there were differences in reproduction. In 1996, 4 of the 6 adult females had brood nests by the end of July. In summer 1997, only 1 of the 5 collared adult females was known to be attending a summer brood nest by the end of July. Interestingly, in spring and summer 1997, adult female ROPO 02 had a collared subadult from summer 1996 and offspring from early 1997 all using her core area, 3 generations, though none of the female offspring were reproductively active.

If we consider that dispersal is resource related (Anderson 1989, Larsen and Boutin 1998), that agonistic behavior is the highest during periods of reproductive activity (Benson 1980), and that adult females are the most aggressive in motivating offspring to disperse (Adams 1984, Larsen and Boutin 1998), it would follow that adult females would motivate male and female subadults to leave in equal numbers in years of high resources when they are in a reproductive state. In years of lower resources females may not enter a reproductive state and may not encourage their offspring to leave, especially if resources are not critically low enough to threaten their own survival. Spring/summer 1996 was a time of high enough food to allow widespread reproduction and thus instigated aggressive behavior on the part of adult females toward subadults. Spring/summer 1997 was a year of lower food supply, maybe of an intermediate level, low enough to prevent reproduction, but not low enough to create chronic food stress in adults, thereby causing them to drive away subadults. This explanation is certainly tentative. The questions raised here do illustrate the need for research on dispersal and the driving mechanisms in a variety of environments.

The dispersing subadults of 1996 did not fare well after they left Site 1. Two of the 3 dispersing females were known dead on neighboring courses within the time of the study, 1 was hit by a vehicle, the other died after an injury of an unknown origin. Neither had successfully reproduced. The remaining 2 dispersers disappeared from neighboring courses within 2 months and were not sighted during 12 months of frequent searches. Courses to the west and north of Site 1 had LEI ratings of 0.44-0.30, while the course to the south, at which ROPO 14 died, had an LEI of 0.59. All these ratings were much lower than Site 1. The area surrounding the cluster of 7 courses was dense development bordered by 2 of the busiest roadways in Collier County. Squirrels were not known outside of golf courses in the developed parts of the county. Successful dispersal away from the course cluster was highly unlikely.

Non-dispersing individuals captured as subadults at Site 1 fared better than dispersers. In the 1995-1996 cohort of collared subadults, 50% of non-dispersers, 1 female and 2 males, remained at Site 1 throughout the study. Eighty-three percent of non-dispersers remained on the course through December 1996. Two of the females successfully reproduced in summer 1996 and by the end of the study the 2 produced 7 young from the nest. One male of the 1996-96 subadult cohort was generally the lead male in mating chases by the end of the study. In 1997, 6 of the 7 collared subadults survived and remained on the course until collars were removed at the end of July. The 1 mortality was a subadult suffering from skin fungus. Two other subadults with the disease, 1 a sibling of the dead squirrel, recovered with the spring/summer molt. Though none of the individuals reproduced, 1 female was the focus of a mating chase in July.

The persistence and success of subadults that remained at Site 1 indicates it was providing a rich habitat. Dispersing subadults moved into less favorable environments. Site 1 appeared to be a source of fox squirrels for surrounding courses, which the 1996 data and the LEI ratings would indicate were acting as sinks (Pulliam 1988).

Site 1 squirrel densities of 42.4 squirrels/km^2 (from high MNA of 26) to 49.8 squirrels/km^2 (from high Bailey estimate of 30.5) were higher than previous reports of fox squirrels in Florida. Estimates of 8.4 squirrels/km^2 and 38 squirrels/km^2 were reported by Humphrey et al. (1985) in south Florida and Moore (1957) in central Florida. In Georgia, at the Piedmont National Wildlife Refuge, Tappe et al. (1993) found fox squirrel densities of 15.3-17.7 squirrels/km^2 in mark and recapture studies.

Fox squirrels at Site 1 had 2 breeding seasons, as reported in other southeastern fox squirrel populations (Moore 1957, Weigl et al. 1989). Contrary to previous work at more northern locations (Larson 1990, Weigl et al. 1989), reproduction was higher in the summer season than the 2 winter seasons. Litter size, as young from the nest, ranged from 1 to 4 with a mean of 2.4, within the reported range of 1.6 to 3.0 (Larson 1990, Moore 1957, Weigl et al. 1989). While 4 of the 7 Site 1 adult females in the study produced 2 litters in the 3 breeding seasons studied, none produced 3 litters. Weigl et al. (1989) showed a strong correlation between food availability and female reproductive capacity. In the summer of 1996, 5 of 6 females produced young from the nest and raised them into the fall. The smaller home ranges in that year and the concentrated feeding patterns of spring through fall of 1996 indicate a rich food supply, probably resulting from the high rains of fall 1995.

Frequent squirrel feeding on fungi was also reported by Weigl et al. (1989) in North Carolina. Presence of mycorrhizal hypogeous fungi and associated bacteria form mutualistic relationships with a variety of tree species, including pines (Li et al. 1986, Slankis 1973). The fungi are nutritionally beneficial to fox squirrels who then disperse fungal spores as they defecate in their wide travels (Maser et al. 1978, Trappe and Maser 1977). Maintenance of the fungi-rich litter areas within Site 1 preserved a food source for fox squirrels and probably provided benefit to a tree species also of primary importance to the squirrels. Weigl et al. (1989) believed the fitness of squirrels, trees and fungi benefited from this relationship and that it may be coevolutionary in nature.

High densities, high reproduction, and high overlap of home ranges suggested a food supply that was strong though obviously variable. Occupancy of Site 1 by 5 or 6 adult females maintaining fairly constant home ranges throughout the 20-month study indicated the adult female density was at a maximum. The course was able to retain subadults in both years. In 1996, 60% of the collared subadults remained on the course, with 50% of the non-dispersers surviving through the end of the study. In 1997, 6 of the 7 collared subadults remained alive on the course until the end of the study. Site 1 and its companion course, Pines, together had 40-50 squirrels in residence, though it must be noted that at least half of the adult males used neighboring clubs. The Site 1 population appeared stable. Surplus subadults dispersed to neighboring courses where mortality undoubtedly was higher.

Royal Poinciana and its buffer courses to the west provided the most productive and stable golf course site for fox squirrels within the currently developed landscape in western Collier county and the most stable in this study. Drastic changes in the landscapes of Poinciana or the 2 neighboring courses most frequently used by males are not anticipated in the next 5-10 years. On the other hand, these landscapes are managed. The composition and maintenance of trees, tree stands and ground cover are subject to change at the will of the managers. East and south of Site 1, the condition of neighboring properties will change in the coming decade, with anticipated development of the large pine forest south of Poinciana and current development of the lots east of the club. Such conversion will affect sources and movement of squirrels in and out of Poinciana and could bring more domestic predators, especially cats, to the borders of the courses.

Lower Quality Golf Course Landscape

Site 2, Royal Palm Country Club, just one year older than Site 1, contained lower quality fox squirrel habitat surrounded by a developed landscape and a seasonally heavy flow of vehicle traffic. The club rated 0.719 on the Landscape Evaluation Index with moderately dense to open pine-dominated tree stands on club property and neighboring condominium land. There was a lower diversity of tree species, both native and non-native, and fewer and more widely scattered pine litter areas than at Site 1. In the absence of oaks and maples, and with lower numbers of large fungi feeding areas or fruiting exotics, squirrels fed heavily at feeders in the spring and summer.

The 2 adult females at Site 2 had home ranges of 13.06 ha and 30.57 ha. The difference probably resulted from the former having a regularly supplied feeder in the center of her home range and the latter having only an occasionally stocked one at the edge of her home range. The home range of the first female was similar to those at Site 1 and to previous studies, while the home range of the second female was larger than any other female in this study and the averages reported in other studies (Kantola and Humphrey 1990, Weigl et al. 1989). Male home ranges of 136.1 ha and 303.80 ha were larger than others in the study and larger than means reported by Kantola and Humphrey (1990) or Weigl et al. (1989). All adult and subadult home ranges at Site 2, except the 1 adult female with a well-stocked feeder, were larger than comparable individuals at Site 1 and larger than reported means in previous studies. Adult female home ranges did not overlap or touch as they did at Site 1.

While the 4 collared adults lived and persisted on the course through the 7 months of tracking, none of the collared subadults remained. Two of the 4 subadults were known dead by June 1997, the third had a habit of feeding in roadways and disappeared early, and the forth dispersed to a very low quality habitat in an adjoining course and was using a feeder near a major highway. One of the subadults died from extreme emaciation while suffering a severe skin fungus, the other was killed by a car on Augusta Boulevard. Vehicle accidents at the study sites involving automobiles, course equipment and carts, were a known source of mortality for 6 collared and uncollared squirrels. Weigl et al. (1989) found that automobile traffic was a major cause of fox squirrel mortality in their 8-year study in rural areas of the North Carolina coastal plain.

Neither adult female reproduced during the study, though 1 appeared to be tending a brood nest as the study ended. Both males were observed with females at Site 2 and the 2 neighboring courses

Fox squirrel densities at Site 2 were extremely low, 6.3/km^2 (MNA of 9) and 8.2/km^2 (high Bailey estimate of 11.7). These were similar to the estimates of Humphrey et al.(1985), though much lower than reported by Moore (1957) or Tappe et al. (1993). They were 84% lower than the fox squirrel densities at Site 1.

At Royal Palm, low population density, large home ranges, and poor subadult persistence indicate an unstable population. A small number of adults maintained themselves and reproduced in times of higher food supply, but young had a difficult time surviving to adulthood. A more open, less diverse food supply required fox squirrels to make larger movements to feed and mate, and so expose themselves to the hazards of automobile traffic and the stresses of travel and food search. Such large home ranges and movement through traffic were especially difficult for subadults.

Royal Palm was a course with marginal fox squirrel habitat and more development yet to come. Completion of housing along the fairways will eliminate the remaining tree-covered vacant lots. Growth of adjacent developments to the east and north will increase traffic on Augusta Boulevard and connecting roadways. As with Site 1, the quality of course vegetation is dependent on management. It could be improved with the addition of a variety of native trees such as cypress, oaks, and maples, with added pine litter areas, and with non-native food sources such as spring-fruiting trees. While feeders were obviously a vital part of squirrel diets at Site 2, reliance on feeders puts squirrels at the mercy of suppliers and perhaps increases the risk of exposure to contagious disease. The course adjoining Royal Palm to the west, used by adult males and at least 2 dispersing subadults in the study, had very low quality habitat (LEI 0.28) and would not support fox squirrels for long without the resources of Royal Palm.

As we shall see in the next section of the discussion, Site 1 was an unusual golf course in southwest Florida, both in its rich landscape without residential development and in its high numbers of fox squirrels. Site 2, on the other hand, was more common. It was a mix of the favorable and unfavorable landscape features. It had the levels of development and traffic seen in many courses of level 3 and 4, and though it was not isolated, the 2 neighboring courses furnished very low quality fox squirrel habitat. It was superior to most courses in the presence of relatively high quality pine stands, the open understory of all tree stands, and the occurrence of scattered pine litter areas.

Landscape Evaluation

The study revealed a wide variety of golf course habitat types and course configurations in Lee and Collier counties. Landscapes surrounding these courses, which are critical to fox squirrel movements, ranged from highly developed with heavy vehicle traffic to more rural sites surrounded by mixed agricultural and forest stands.

The ability of golf courses to support fox squirrels differed greatly. Six of the courses with an LEI of 0.90 or above had high levels of fox squirrels and make up 3 clubs, each of 36 holes (Fig. 33, Appendix B). These 3 clubs had the highest potential for supporting fox squirrels in a developed landscape.

The 6 courses with an LEI of 0.90 and above and with high levels of fox squirrels, including Site 1, were characterized by:

- large contiguous areas, over 120 hectares, with no housing or automobile traffic
- residential development absent or only on the perimeter of each course or the entire club
- adjoining golf courses on at least 2 sides of the club
- undeveloped forest on at least 1 side
- lack of busy roadways around the course

- easy movement of fox squirrels from 1 course to another, often aided by large trees across canals or smaller streets
- large, open, pine-rich tree stands, with cypress, palms and a variety of native tree species
- few or no areas of forest with heavy understory growth
- high-quality nesting sites in minimally trimmed cabbage palms, bromeliads, or large trees, often pine and cypress
- spring and early summer food supplies available from diverse native species, fungi rich litter areas, non-native tree species, or artificial food sources.

Four of these 6 high level courses will have further housing development along the fairways and all will have increased development around their boundaries within the next 10 years. Except for Site 1 and its companion Pines course, squirrels fed from feeders or begged from golfers.

The future of fox squirrels at even these 6 high level courses will depend on the maintenance of high quality tree stands through understory clearing, and planting and replacement of native trees, especially pines and cypress. Changes in surrounding landscapes and food supplies offered at feeders will also affect squirrel survival. Given the lack of development at Site 1 and the relative protection of the surrounding buffering courses it appeared to offer a relatively stable, high quality environment for fox squirrels, though it is certainly suburban and will eventually become more isolated. The other high level courses will undergo much more change with stronger potential for declining habitat.

The 1 course with an LEI of 0.90 and moderate levels of fox squirrels was also part of a 36 hole course, but its companion course had an LEI of 0.71, with high traffic and more intense development in the future. This 0.90 LEI course does not have a strong potential for continued support of fox squirrel populations.

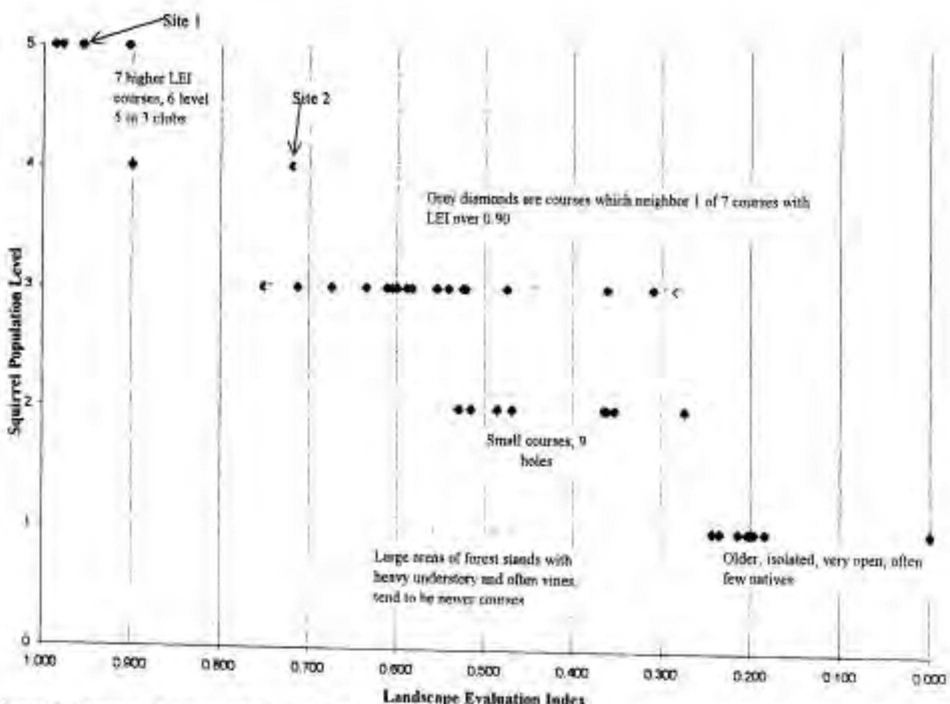

Figure 33. Landscape Evaluation Index and squirrel population levels, with highlighting of course groups to accompany discussion.

The 7 courses with an LEI over 0.90 obviously provided habitat superior to any other courses in the study and each had a strong combination of favorable landscape attributes. The remaining 53 courses had LEI ratings of 0.76 or lower (Fig. 33, Appendix B). Each of these courses had one or more strong negative elements in their landscapes. Features of isolation, course configuration, low quality vegetation, and heavy understory, combined to decrease the ability of these courses to foster fox squirrel populations.

Course isolation within a heavily developed landscape cannot be mitigated in most cases. This is especially true if the course is small and contains few or scattered tree stands. A group of 9 older courses with low LEI ratings is circled in the lower portion of Figure 33. Each of these courses was the only course in an 18 hole club. The courses may have experienced loss of trees with long-term development. They frequently had few remaining tree stands and low levels of native tree species, especially pines. They were surrounded by residential and commercial development, though some were adjacent to similar courses. At first glance they appeared to offer fox squirrel habitat, but in fact, they provided insufficient food and nesting resources for this relatively large squirrel species.

Complex course configuration, as presented previously in Figure 8, levels B and C, were a common landscape element that created precarious habitat for fox squirrels. Unlike the higher LEI courses that had no development or only perimeter development, 39 of the 53 courses (74%) with LEI below 0.75 had intensified or connected perimeter patterns, or radiating interior development. Such development configurations divided the course and the bordering rough areas into small patches. These patches may or may not have contained high quality tree stands, but these divided landscapes required squirrels to move though a maze of housing and streets in search of food, mates, and nesting sites. For animals with home ranges of 10 to 100 hectares and more, the increased and complicated fragmentation of an already fragmented landscape becomes even more precarious and stressful, as resources become more widely spread (Collinge 1998).

Development of courses with complex configurations creates a landscape that is ultimately highly unfavorable to fox squirrels. Deceptively, initial and temporary stages of development may actually improve habitat for fox squirrels. The early development may increase edges and open the forests understory, thus creating the habitat fox squirrels prefer. Eighteen of the level 3 courses (72%) are at this stage. Unfortunately, as courses age and development continues, construction removes tree stands and corridors required by fox squirrels. Vehicle traffic within and around a course increases and the habitat becomes less productive and more stressful for fox squirrels. The result, as seen at Site 2, is that fox squirrel home ranges must become exceptionally large to reach scattered resources. Constant travel in a developed landscape from one feeding patch to another is stressful and hazardous. This situation is especially difficult for younger squirrels. As these small populations of widely scattered individuals become more isolated, they become more susceptible to stochastic events or dying out in years of low food production.

Low quality vegetation stands were common in the golf course landscapes. Few courses had a high diversity of native species or large pine stands, few had large areas of pine litter to support growth of fungi, and few had the older, large trees that offer ideal nesting sites. The first component of the LEI indicates the quality of the vegetation at a course. The 6 high level courses each have a rating of 0.9 and higher in this component. Of the remaining 54 courses, only 4 are above 0.80 in this component, while 30 of the courses, 50% of those in the study, have ratings below 0.6.

Heavy understory, with the dense growth of vines and shrubs in tree stands, is a landscape element that renders habitat unsuitable to fox squirrels. It was a common and difficult problem in unmanaged set-aside areas. Eighteen courses in the study (30%) had varying amounts of heavy understory in their landscapes. For 16 of the 18 courses it was just one impediment to fox squirrel presence. Four of the 16 courses are circled in Figure 33. They will continue to be developed and have complex course configurations with highly fragmented habitat. Clearing of the understory in these courses will not create quality fox squirrel habitat.

The four prominent elements that affect the quality of fox squirrel habitat on golf courses vary in their ability to be changed through good management. Two of these, course isolation and course configuration are critical elements affecting squirrel movements and the availability of resources. They must be addressed prior to development. The latter two, the presence of heavy understory, and the composition and density of tree stands, can be mitigated to some degree on an existing course, though they will not nullify the impacts of isolation, heavy development, and poor course configuration in the long run. Mitigation of heavy understory growth in set-aside areas is especially difficult and expensive.

The improvement of the tree stands and ground cover should be encouraged on courses that currently have fox squirrels in residence or in the adjacent lands. While all level 3 and 4 courses are candidates for vegetation improvement, the 11 courses that have high quality courses for neighbors should be strongly encouraged to undertake habitat improvement for fox squirrels (Fig. 33). Work to increase and diversify native tree species, to create clear understory, to increase the number of moderately trimmed palms, to increase spring food sources, and to increase areas of pine litter ground cover will improve habitat.

In addition to this larger group of level 3 and 4 courses, two relatively new, non-residential courses east of I-75 warrant special attention for habitat improvement efforts. The 2 courses, each 18 holes at the time of the study, were part of clubs that will become 36 holes or larger. The courses contained large stands of pines, cypress, palms, and associated native tree species. They were surrounded by undeveloped forests, large-lot residential areas, and agriculture. They were less than 3 km apart. At the time of the study both courses had heavy understory growth and the resulting low LEI ratings along with low numbers of fox squirrels. Habitat improvement through understory clearing would surely increase the potential for these clubs as fox squirrel habitat. Their position in a less developed landscape and their non-residential status gives them a unique opportunity to provide habitat for Big Cypress fox squirrels.

Summary

Will golf courses provide habitat for Big Cypress fox squirrels in rapidly developing southwest Florida where human populations are expected to double by 2020? As noted earlier, even the 6 courses with high levels of squirrels do not all have a strong potential as future fox squirrel habitat. Of these 6, Site 1 and its companion course at Royal Poinciana, offer the most favorable and most secure habitat for fox squirrels over the next 2 decades. The other 4, as residential courses, will continue to be developed and will have greater changes within and around their boundaries. Their potential will decline

The remaining 54 courses will not provide good, long-term resources for fox squirrels. Certainly, all of the 23 courses in levels 1 and 2, have more than one strongly negative landscape element and most do not have the potential to support fox squirrels even with mitigation of vegetation. Most of the 31 courses at level 3 and 4 will not provide good quality habitat for the long-term due to unalterable planning and design patterns. Many of these are relatively new courses where time and development will continue to degrade the remaining tree stands and unmanaged set-aside areas.

This study demonstrated that even in extremely high quality habitat, Big Cypress fox squirrels require large tracts of land for daily and seasonal movements and even larger ones to allow for dispersal of subadults. Few courses or groups of courses offer safe and stable habitat in large enough tracts to endure the upcoming intensity of development, especially in the western sections of Lee and Collier counties. The few that do must maintain open, diverse, pine-rich forested areas, preferably with substantial areas of pine litter ground cover. Maintenance of such a landscape is labor-intensive and expensive. Fewer than 5 of the 48 clubs examined in this study are capable of providing the habitat required to maintain golf course populations through the intensive development expected between now and 2020.

MANAGEMENT RECOMMENDATIONS

Management for quality Big Cypress fox squirrel habitat must start at the landscape level. Placement and configuration of courses and the development that accompanies them is critical. Because fox squirrels use large areas, up to 150 hectares, for daily and seasonal movements, they require large contiguous areas of suitable habitat free from vehicle traffic and dense development. They must be able to move from one club to another as few single courses will provide adequate habitat. Developments should be connected by open forested corridors. Movement across 2 lane roadways can be facilitated by maintaining large over-hanging trees. Squirrels have adapted to using wooden walkways through wetlands at several southwest Florida courses. This indicates they would be able to do so to cross other obstructions, perhaps even busy roadways separating 2 courses or clusters of courses.

A course or club must be designed to contain large contiguous areas, 120 hectares per club, of green space with large, open stands of native trees. This should be accomplished by concentrating the development either around the outside edges and leaving the central area of the course as green space or by concentrating development in the center, with only 1 roadway into the developed center. This creates a large circle of green space free of vehicle traffic. Adjoining courses with this central development could provide large areas for wildlife.

In more recently developed courses, the design and planning phase has included much attention to preserving lands within the developed areas that have been designated as critical wetlands or drier pine habitat for gopher tortoises. This often appears to preserve large areas of habitat suitable for fox squirrels. In truth, the habitats do not remain suitable for many of the species they are designed to conserve, and they generally become unsuitable for fox squirrels. Areas set aside as native habitat are allowed to become clogged with invasive vines and a heavy understory of native and exotic shrubs and small trees. The resulting vine-infested forests often become barriers to wildlife movement, instead of habitat and corridors. Without proper training in management of wild habitats or the funding to carry out the required tasks of burning or hand clearing, managers cannot preserve these habitats. If such patches are to be preserved within private property, funding for maintenance and training must be provided and regular checks must be made to see that landowners comply with management plans. The management and usefulness of these areas require examination. Are they the best way to preserve wildlife habitat? Are they proving beneficial to the species they are intended to protect? If they are to be maintained, what programs are required to insure they fulfill their expected roles in the landscape?

Big Cypress fox squirrels have shown a strong dependence on pines and cypress, using them for food, nesting, and resting areas. Preservation and planting of pines and cypress should be strongly encouraged. Golf courses are currently moving away from full coverage irrigation and this will hopefully allow more native pines to persist in developed landscapes. In addition to pine and cypress, planting a diversity of native trees, including oaks, maples, cabbage palms, bays, and hollies should be encouraged. The current study showed a heavy use of spring-fruiting non-native tree species by fox squirrels. Though the planting of non-natives is against the policy of some organizations promoting more natural golf course landscapes, presence of these non-native species provides year-round food in these restricted habitats. Managers should create diverse stands of trees that provide a range of food sources within a small space. This forms a richer, more resilient food source and provides the diverse environment fox squirrels prefer for brood nests. Course designers and managers must have information on native plant sources, and plants must be available at competitive prices before native plantings will become common.

On completed courses, correct management of existing tree stands is crucial. Fox squirrels require open tree stands for movement and frequent ground feeding. Forested areas must have open understories, free of dense shrubs, vines and tall grasses. This can be accomplished by hand clearing or light burning. At present, it is extremely difficult to obtain burning permits for golf courses, despite the fact that ready irrigation systems provide excellent protection against uncontrolled burns. The smoke created by such a burn is undoubtedly less harmful than most of the chemicals used in hand clearing. Progress along these lines, and studies addressing the efficacy of burning golf course roughs, would help the more forward thinking managers who would like to promote burning as a management tool for larger forested stands within their courses.

Cabbage palms provide fox squirrels with high quality nesting sites, food, and sheltered resting areas. Current golf course management practices frequently involve extreme trimming of palms. This removes all the fruiting stalks and the lower leaves. What remains is barely a tree and is not habitat for the range of wildlife frequently seeking protection from sun and storms under the layered leaves and long leaf bases. Moderation in trimming is one of the easiest and least expensive management techniques benefiting fox squirrels. It should be encouraged.

The presence of pine litter ground layers in pine stands is an important management technique that promotes squirrel feeding on fungi. The fungi have been shown to be beneficial to pines and provide a needed food source in early summer months. The litter layers can readily reduce maintenance and remove the need for irrigation of grass in a stand of native trees.

If nesting sites in pines, large bromeliads, cabbage palms, and cypress are in short supply, managers may wish to supplement with nest boxes. Wood duck boxes are the proper size and should be placed at least 5 meters up the trunk of a fairly large tree. Such boxes will provide shelter in the few times of extreme cold weather and in driving rain and wind storms. They may also be used for brood nests.

Education is critical for management of fox squirrels on golf courses. Managers must be educated on methods to create and maintain favorable habitat. Members should also be educated. Squirrels are easily killed on courses by cart drivers who are speeding along and looking for golf balls instead of squirrels. Members should at least be encouraged to look out for squirrels, on the course and on the roadways into the course. Members must also be educated not to feed squirrels. If squirrels are not fed by people they will not be attracted to people or carts. They will avoid carts and not hang around cart paths at tees and greens waiting for food. They will be less likely to be killed by speeding carts or angry golfers who have just lost a muffin to a sneaky squirrel.

If course members or managers have the desire to feed fox squirrels, this should be done in an isolated area away from cart or automobile traffic. Food should be spread on the ground, not in small feeders that require squirrels to climb around on the same small area. Such high concentration and repeated rubbing of fur and feet on a feeder creates an ideal vector for contagious diseases, especially skin fungus. Food should be natural, not processed human food. Squirrels benefit from nuts, berries, and grains. Trimmed fruits from palms may also be added to the feeding site.

Both club members and fox squirrels will benefit if education programs share something of the lives of fox squirrels. Many golf course members in Florida are not familiar with our native wildlife and plants. A little education may go a long way in helping them to understand and appreciate these unique and beautiful fox squirrels and the larger natural heritage of Florida.

APPENDIX A
TREE SPECIES ON STUDY SITES

Common Name	Family	Species	Site 1 Cypress	Site 2 Royal Palm	Royal Poinciana Pines
Red maple	Aceraceae	*Acer rubrum*	x		x
Holly	Aquifoliaceae	*Ilex opaca*	x	x	x
Schefflera	Araliaceae	*Schefflera actinophylla*	x		x
Norfolk Island Pine	Araucariaceae	*Araucaria heterophyla*		x	x
Queen palm	Arecaceae	*Arecastrum romanzoffianum*	x	x	x
Fishtail palm	Arecaceae	*Caryota mitis*		x	
Royal palm	Arecaceae	*Roystonea spp.*	x	x	x
Cabbage palm	Arecaceae	*Sabal palmetto*	x	x	x
Jacaranda	Bignoniaceae	*Jacaranda mimosffolia*	x	x	
Trumpet Tree	Bignoniaceae	*Tabebuia argentea*		x	x
Toog Tree	Bischofiaceae	*Bischofia javanica*	x		x
Austrailian Pine	Casuarinaceae	*Casuarina cunninghamiana*		x	
Black olive	Combretaceae	*Bucida buceras*	x	x	x
Southern Red Cedar	Cupressaceae	*Juniper silicicola*			x
Tallow tree	Euphorbiaceae	*Sapium sebiferum*	x	x	x
Earleaf acacia	Fabaceae	*Acacia auriculiformis*	x	x	x
Rosewood	Fabaceae	*Dahlbergia sissoo*	x	x	x
Poincianna	Fabaceae	*Delonix regia*	x		x
Copper pod	Fabaceae	*Peltaphorum pterocarpum*	x		
Pongam	Fabaceae	*Pongamia pinnata*			x
Laurel oak	Fagaceae	*Quercus laurifolia*	x	x	x
Live oak	Fagaceae	*Quercus virginianum*	x	x	x

Red bay	Lauraceae	*Persea borbonia*	x		
Avocado	Lauraceie	*Persea americana*			x
Mahogany	Meliaceae	*Swietenia mahogani*	x	x	
Wild Tamarind	Mimosaceae	*Lysiloma latisiliquum*	x		
Fig	Moraceae	*Ficus spp.*	x		x
Eucalyptus	Myrtaceae	*Eucalyptus sp.*			x
Eugenia	Myrtaceae	*Eugenia sp.*		x	
Java plum	Myrtaceae	*Syzigium cumini*	x		x
Bottle-brush	Myrtacece	*Callistemon rigidus*	x	x	x
White Ash	Oleaceae	*Fraxinus americana*			x
Screw Pine	Pandanaceae	*Pandanus utilis*	x		x
Slash pine	Pinaceae	*Pinus elliottii var. densa*	x	x	x
Silk oak	Proteaceae	*Grevillea robusta*	x		x
Orange	Rutaceae	*Citrus sinensis*	x	x	x
Grapefruit	Rutaceae	*Citrus x paradisi*		x	x
Pond cypress	Taxodiaceae	*Taxodium ascendens*	x	x	x
Bald cypress	Taxodiaceae	*Taxodium distichum*	x		x

APPENDIX B
GOLF COURSES, SQUIRREL LEVELS, AND LEI RANKINGS

Club	Course	Course #	Squirrel level	LEI
Quail Creek	Quail course	30	5	0.987
Quail Creek	Creek course	29	5	0.987
Royal Poinciana	Pines	46	5	0.979
Royal Poinciana	Cypress Course	48	5	0.956
Fiddlesticks	Long Mean	34	5	0.955
Fiddlesticks	Pipers Challenge	33	5	0.904
Imperial	Imperial East	45	4	0.900
Wyndemere	Green and White	32	3	0.751
Eagle Ridge		28	3	0.745
Royal Palm		52	4	0.719
Imperial	Imperial West	43	4	0.713
Forest	Bear	36	3	0.713
Quail West	Preserve Course	12	3	0.687
Lely Country Club	Flamingo Island	17	3	0.674
Lely Country Club	Classics Course	11	3	0.635
Forest	Bobcat	16	3	0.612
Foxfire	old 18, red	35	3	0.605
Pelican Nest	Gator &Seminole	25	3	0.600
Bonita Bay	Marsh Course	6	1	0.595
Bears Paw		41	3	0.589
Wyndemere	Gold course	31	3	0.583
Old Hickory		13	4	0.571
Name withheld		5	3	0.555
Bonita Bay	Bay Island	7	1	0.554
Countryside GC		22	3	0.554
Wildcat Run		23	3	0.541
Foxfire	new 9	3	2	0.530
Royal Wood		19	3	0.525
Glades	Palmetto	44	3	0.522
Spanish Wells	North 9, New 9	2	2	0.516
Pelican Marsh	Marsh Course	8	1	0.491
Glades	Pines	53	2	0.487
Spanish Wells	east and west 9	39	3	0.475

Club	Course	Course #	Squirrel level	LEI
Vines		24	1	0.473
Olde Florida		9	2	0.470
Wilderness		42	3	0.443
Quail West	Lakes	4	1	0.388
Eastwood		40	2	0.365
Colliers Reserve		10	3	0.365
Marriott Club		15	2	0.363
Audubon CC		18	3	0.361
Hole in the Wall		58	4	0.354
Vineyards	North	21	2	0.354
Embassy Woods		14	2	0.354
CC of Naples		55	4	0.343
Vineyards	South	20	3	0.309
Bonita Bay	Cypress Course	1	3	0.309
Quail Run		50	3	0.296
Hibiscus		56	3	0.283
Palm River		38	3	0.281
Cross Creek		27	2	0.275
Marco Shores		49	1	0.243
Myerlee		47	1	0.235
Windstar		26	1	0.214
Ft. Myers GC		60	1	0.204
Cypress Lake		54	1	0.200
Naples Beach		59	1	0.196
Moorings		57	1	0.196
Whiskey Creek		51	1	0.184
Club at Pelican Bay		37	1	0.000

APPENDIX C
HOME RANGE DATA FOR SITES 1 AND 2

Home range data for Site 1, December 1995 through October 1996

Squirrel #	Sex	Stage at capture	Stage most of trapping season	Months tracked	Total radio-tracking locations	Radio-locations used in home range analysis	Home range size, 95% contour (ha)	Core area size, 50% contour (ha)	Time in study
15 ROPO	F	Adult	Adult	7.0	103	79	7.98	1.92	entire
5 ROPO	F	Adult	Adult	9.5	100	83	8.80	2.61	entire
2 ROPO	F	Sub	Adult	10.5	147	106	10.17	1.99	entire
6 ROPO	F	Adult	Adult	9.5	131	108	10.71	2.53	gone 96
1 ROPO	F	Sub	Adult	7.5	67	51	10.92	1.39	gone 96
3 ROPO	F	Adult	Adult	9.0	129	100	12.00	1.59	entire
7 ROPO	M	Sub+	Adult	5.5	51	37	42.52	6.41	entire
4 ROPO	M	Sub+	Adult	3.3	45	31	45.98	8.51	gone 96
16 ROPO	M	Adult	Adult	5.0	47	43	76.45	19.44	gone 96
17 ROPO	M	Adult	Adult	4.0	51	43	118.40	22.44	gone 97
14 ROPO	F	Sub	Sub	5.0	19	*15	10.66	1.00	disperse 96
8 ROPO	M	Sub	Sub	8.0	89	66	14.56	5.71	entire
12 ROPO	M	Sub	Sub	3.0	53	24	15.89	1.50	gone 97
10 ROPO	F	Sub	Sub	4.5	24	*19	20.22	1.15	disperse 96
9 ROPO	F	Sub	Sub	7.5	64	*38	22.56	3.37	disperse 96
13 ROPO	M	Sub	Sub	6.0	76	*45	49.07	4.83	disperse 96
11 ROPO	M	Adult	Adult	2.0	17	NA			entire

* Asterisk, used only points prior to dispersal

Home range data for Site 1, November 1996 through July 1997

Squirrel #	Sex	Stage at capture/ recapture	Stage most of trapping season	Months tracked	Total radio-tracking locations	Radio-locations used in home range analysis	Home range size, 95% contour (ha)	Core area size, 50% contour (ha)	Time in study
28 ROPO	F	Adult	Adult	6.5	66	63	9.08	2.05	2nd yr
2 ROPO	F	Adult	Adult	8.0	78	70	13.14	2.10	entire
3 ROPO	F	Adult	Adult	7.5	75	61	19.21	3.96	entire
15 ROPO	F	Adult	Adult	9.0	77	67	19.66	3.30	entire
5 ROPO	F	Adult	Adult	7.5	78	63	20.92	4.12	entire
8 ROPO	M	Adult	Adult	8.5	68	62	44.06	9.50	entire
22 ROPO	M	Adult	Adult	8.0	78	69	48.42	10.62	2nd year
11 ROPO	M	Adult	Adult	5.5	55	49	99.89	12.82	entire
7 ROPO	M	Adult	Adult	7.5	71	63	114.10	16.87	entire
18 ROPO	M	Adult	Adult	7.0	52	48	118.00	15.26	2nd yr,died
20 ROPO	M	Adult	Adult	8.0	52	47	121.00	18.20	2nd year
27 ROPO	F	Sub	Sub	6.5	62	57	3.88	0.47	2nd year
29 ROPO	F	Sub	Sub	6.5	64	59	10.31	2.24	2nd year
25 ROPO	M	Sub	Sub	7.5	27	27	12.11	1.77	2nd yr,died
21 ROPO	M	Sub	Sub	8.0	74	68	16.62	4.23	2nd year
23 ROPO	M	Sub	Sub	7.5	76	65	17.30	3.65	2nd year
26 ROPO	M	Sub	Sub	7.0	64	60	20.80	3.80	2nd year
24 ROPO	F	Sub	Sub	7.5	65	60	21.47	3.41	2nd year

Home range data for Site 2, January 1997 through July 1997

Squirrel #	Sex	Stage at capture/ recapture	Stage most of trapping season	Months tracked	Radio-locations used in home range analysis	Home range size, 95% contour (ha)	Core area size, 50% contour (ha)	Time in study
ROPA 4	F	Adult	Adult	7.0	51	30.57	1.58	entire
ROPA 6	F	Adult	Adult	6.5	49	13.06	1.87	entire
ROPA 1	M	Adult	Adult	7.0	51	136.10	29.88	entire
ROPA 8	M	Adult	Adult	6.0	31	303.80	71.38	entire
ROPA 2	M	Sub+	Sub+	0.5	NA			gone
ROPA 3	M	Sub	Sub	2.0	14	40.76	5.46	died
ROPA 5	M	Sub	Sub	2.0	11	25.77	5.07	died
ROPA 7	M	Sub	Sub	6.0	48	108.50	15.28	left course

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Biological Status Review for the Big Cypress fox squirrel (*Sciurus niger avicennia*)

EXECUTIVE SUMMARY

The Florida Fish and Wildlife Conservation Commission (FWC) directed staff to evaluate all species listed as Threatened or Species of Special Concern as of September 1, 2010. Public information on the status of the Big Cypress fox squirrel was sought from September 17 to November 1, 2010. The members of the biological review group (BRG) met on November 3-4, 2010. Group members were Elina Garrison (FWC lead), Bob McCleery (University of Florida), and John Kellam (National Park Service). In accordance with rule 68A-27.0012 Florida Administrative Code (F.A.C.), the BRG was charged with evaluating the biological status of the Big Cypress fox squirrel using criteria included in definitions in 68A-27.001(3), F. A. C., and following the protocols in the *Guidelines for Application of the IUCN Red List Criteria at Regional Levels (Version 3.0)* and *Guidelines for Using the IUCN Red List Categories and Criteria (Version 8.1)*. Please visit http://www.myfwc.com/WILDLIFEHABITATS/imperiledSpp_listingprocess.htm to view the listing process rule and the criteria found in the definitions.

The Big Cypress fox squirrel Biological Review Group concluded from the biological assessment that the Big Cypress fox squirrel met criteria for listing. Based on the literature review, information received from the public, and the biological review findings, FWC staff recommends retaining the species on the FWC list of threatened species.

This work was supported by a Conserve Wildlife Tag grant from the Wildlife Foundation of Florida.

BIOLOGICAL INFORMATION

Taxonomic Classification – The Big Cypress fox squirrel (*Sciurus niger avicennia*), one of 3 subspecies of the fox squirrel occurring in Florida, is defined on the basis of size (it is smaller than both *S. n. niger* and *S. n. shermani*; Moore 1956; Turner and Laerm 1993 as cited in Wooding 1997). *Sciurus n. a.* has been variously known as the Big Cypress fox squirrel, mangrove fox squirrel, Everglades fox squirrel, and south Florida fox squirrel (Hafner *et al.* 1998).

Life History – Big Cypress fox squirrels are large tree squirrels with variable dorsal fur color. Most commonly, individuals have a black head and dorsal fur with buff sides and belly, buff and black tail, and white nose and ears (Florida Natural Areas Inventory 2001). They are a primarily ground-dwelling species that inhabits stands of cypress, slash pine savanna, mangrove swamps, tropical hardwood forests, live oak woods, coastal broadleaf evergreen hammocks, and suburban habitats including golf courses, city parks, and residential areas (Hafner *et al.* 1998; Humphrey and Jodice 1992; Jansen 2008; Williams and Humprey 1979). In Big Cypress National Preserve, one of the most important habitat components is the presence of large cypress domes with good adjacent foraging habitat (Jansen 2008; Kellam and Jansen 2010). Optimum habitat for *S. n. avicennia* includes an open understory free of bushes and undergrowth (Brown 1978 as cited in Hafner *et al.* 1998).

Reproductive behaviour of *Sciurus niger* is summarized as follows for the species in general (see Koprowski 1994 for additional citations). Fox squirrels can mate at any time of the year but most breeding occurs between November and February with a peak in December and between April and July with a peak in June. On a golf course in western Collier County, more reproduction was observed in the warm summer/autumn season than in the winter/spring season because exotic foods supplemented a limited summer native diet (Ditgen and Shepherd 2007). *Sciurus niger* females go into estrus for only one day during which several males aggregrate on a female's home range and form linear dominance hierarchies. Females mate with more than one of these males. Average litter size is generally 2 or 3 offspring. Females can become sexually mature at 8 months of age, but more generally wait to reproduce until they are over a year old and then may breed for more than 12 years.

Territorial behaviour of *Sciurus niger* is also summarized as follows for the species in general (see Koprowski 1994 for additional citations). *Sciurus niger* adults, especially females, defend exclusive core areas but home ranges of individuals overlap and territoriality is not observed. Average home ranges are 0.85-17.2 ha for females and 1.54-42.8 ha for males. All juveniles disperse from their natal area but some may remain with their mother during the first winter.

Big Cypress fox squirrels translocated from Naples, Florida, to Big Cypress National Preserve exhibited inconsistent site fidelity and movements of up to 32km that could be attributed to dispersal, post-release investigative behavior, or long-distance foraging (Jodice 1993). Crude estimates of Big Cypress fox squirrel population densities have been calculated at 0.0009 squirrels/ha in typical Big Cypress Swamp habitat in Corkscrew Swamp Sanctuary and 0.0192 squirrels/ha in ranchland woodlots (Jodice and Humphrey 1993). Humphrey and Jodice (1992) stated that these densities are probably much too low, however, because they included some unoccupied habitat. Densities estimated for other squirrels in the southeastern United States are 0.05 squirrels/ha for *S. n. niger* (as summarized in Koprowski 1994) and a range of 0.04 to 0.38 squirrels/ha for *S. n. shermani* (Kantola and Humphrey 1990; Wooding 1997; Humphrey et al. 1985, Kantola 1986, and Moore 1957 as cited in Kantola 1992).

Big Cypress fox squirrels have been documented eating java plum, *Ficus* sp., fig fruit, Bischofia berries, acorns, red maple samaras, bottlebrush and silk oak flowers, insects, fungi, bromeliad buds, thistle seed, pond apple fruit, cabbage palm fruit, holly fruit, queen palm fruit, Palmetto fruit, pine seeds, slash pine cones, and cypress cones (Ditgen and Shepherd 2007; Jansen 2008; Jodice and Humphrey 1992; Kellam and Jansen 2010). Pine cones, cypress cones, and queen palm fruits are scatter hoarded (Ditgen and Shepherd 2007; Jodice and Humphrey 1992).

Nests of individuals translocated into Big Cypress National Preserve were either stick structures or were nestled among the leaves of bromeliads in co-dominant or dominant cypress trees in cypress or mixed-swamp habitat (Jodice 1993). Fox squirrels living in Big Cypress National Preserve have been found to build nests in bald cypress trees (98% of nests), cabbage palm trees, and slash pine trees (only 1 nest; Kellam and Jansen 2010). Four types of nest are built: (1) stick nests, (2) stick nests that also contain thinly stripped cypress bark, (3) bromeliad nests with stripped bark, or (4) cabbage palm nests with stripped bark.

Geographic Range and Distribution – The Big Cypress fox squirrel is the only species of fox squirrel endemic to Florida (Turner and Laerm 1993 as cited in Wooding 1997). It can be found in the southwestern tip of peninsular Florida, in Hendry and Lee Counties south of the Caloosahatchee River, Collier County, mainland northern Monroe County, and extreme western Miami-Dade County (a strip of land that is largely in Big Cypress National Preserve; Williams and Humphrey 1979; Moore 1956; see summary in FWS 2002). *Sciurus niger avicennia* occupies "the mangrove, the pinelands, and the Big Cypress west of the Everglades and south of the Caloosahatchee River" (Moore 1956).

Population Status and Trend –The status of Big Cypress fox squirrels in the core of their range in Big Cypress National Preserve and the Everglades is largely unknown because of the difficulty of studying and observing squirrels in such habitat (Jansen 2008; Jodice and Humphrey 1992; Jodice and Humphrey 1993; Maehr 1993). According to Humphrey and Jodice (1992), "since the Big Cypress National Preserve was established in 1974, preserve staff have recorded progressively fewer fox squirrels, concluding that the population is not prospering there." Furthermore, according to the IUCN Rodent Specialist Group, *S. n. avicennia* has not been seen recently in the Everglades and is currently restricted in distribution to Big Cypress Swamp and its adjacent pinelands (Brown 1978). In particular, the Big Cypress fox squirrel is no longer present at the Cape Sable coast of Everglades National Park in the vicinity of Flamingo, Monroe County (FWS 2002). Big Cypress fox squirrels have also been completely extirpated from Corkscrew Swamp Sanctuary and Everglades City (Jodice and Humphrey 1992). Isolation of Big Cypress fox squirrel populations has occurred in western Lee and Collier counties due to rapid urbanization (Ditgen and Shepherd 2007; Endries *et al*. 2009; Kellam and Jansen 2010).

In the future, the Big Cypress fox squirrel is likely to lose some habitat to urbanization, agriculture, and mining. Furthermore, although at least fifty-five percent of potential Big Cypress fox squirrel habitat exists in conservation lands and is therefore protected from development (FWS 2002, Endries *et al*. 2009), analyses by Florida's Wildlife Legacy Initiative indicate that the majority of *S. n. avicennia*'s habitat (natural pineland and pine rockland) is both poor in quality and declining (FWC 2005). Big Cypress fox squirrels are, however, fairly adaptable; they can be found in disturbed/transitional habitat such as on private ranches and in urban areas like golf courses (Ditgen and Shepherd 2007; FWC 2005; FWS 2002; Jodice and Humphrey 1992).

Quantitative Analyses – A population viability analysis was carried out on the Big Cypress fox squirrel using demographic information from the species as a whole (Root and

Barnes 2006; Endries *et al*. 2009). The baseline model estimated juvenile survivorship at 0.5, adult survivorship at 0.66, adult fecundity at 0.4125, and juvenile survivorship to adulthood at 0.25, resulting in a growth rate of 0.9725. Distance between populations was estimated at 5km. Initial abundance was estimated at 0.025 while carrying capacity was estimated at 0.18. Results revealed that small changes in the model had large impacts on population trends. Risk of extinction in the next 100 years was found to be zero for both managed habitat and all potential habitat. The risk of large declines, however, was quite large. The probability of a 95% decline in abundance in the next 100 years was about 50%. Abundance was particularly reduced when only managed habitat was considered. The model was sensitive to changes in the adult survival value and adult fecundity. Only the largest populations containing at least 200 individuals survived throughout the 100 year simulation indicating that smaller populations will not persist without dispersal into the population.

BIOLOGICAL STATUS ASSESSMENT

Threats – The biggest threat to Big Cypress fox squirrels on the periphery of their range is destruction of habitat and habitat fragmentation due to encroaching development (FWC 2005; FWC 2008; Jansen 2008; Jodice and Humphrey 1992; Koprowski 1994; Zwick and Carr 2006). Rapid urbanization has isolated Big Cypress fox squirrel populations in fragmented habitat in western Lee and Collier counties (Ditgen and Shepherd 2007). Similarly, the conversion of rangeland to citrus groves has destroyed Big Cypress fox squirrel habitat in the flatwoods region of Hendry County (Ditgen and Shepherd 2007) while fire suppression has led to the decline of Big Cypress fox squirrel numbers in seasonally inundated areas of Big Cypress Swamp and the Everglades because extensive understory growth makes forests uninhabitable (Ditgen and Shepherd 2007).

A skin fungus is known to cause mortality of Big Cypress fox squirrels in urban areas but no researchers have indicated that this fungus could be a major threat to populations as a whole (as summarized in FWS 2002). In 2010, a Big Cypress fox squirrel was found in the summer to be infected with Squirrel Poxvirus (J, Kellam, unpublished data). Squirrel Poxvirus has a 75-100% mortality rate in squirrels infected with the disease which can spread throughout a population through contact among conspecifics (NPS 2010). The US National Park Service is currently monitoring Big Cypress fox squirrels in Big Cypress National Preserve for an outbreak of Squirrel Poxvirus (NPS 2010).

Although some authors believe that illegal poaching in Big Cypress National Preserve may be having an impact on Big Cypress fox squirrel numbers (Humphrey and Jodice 1992), the US Fish and Wildlife Service states that it does not have evidence to support this claim (FWS 2002).

The US Fish and Wildlife Service reviewed the status of the Big Cypress fox squirrel in 2002 and concluded that this subspecies does not qualify for listing as an endangered or threatened species due to any of the five factors as defined in the Endangered Species Act (FWS 2002).

Sciurus niger avicennia is currently listed as Lower Risk, conservation dependent by the IUCN Rodent Specialist Group "based on the historical loss of habitat and restricted number and distribution of populations of *S. n. avicennia*, probably including Big Cypress National Preserve" (Hafner *et al*. 1998).

Recommended actions of the IUCN Rodent Specialist Group (Hafner *et al*. 1998) are:

- "Conduct studies to determine the optimum habitat requirements of *S. n. avicennia*, and survey for presence of populations in Big Cypress National Preserve
- Conduct controlled burns to open up the understory for better foraging areas for *S. n. avicennia*
- Set aside remaining occupied habitat as refuges for *S. n. avicennia* (Brown 1978)"

Statewide Population Assessment – Findings from the Biological Review Group are included in a Biological Status Review information table.

LISTING RECOMMENDATION – Staff recommends that the Big Cypress fox squirrel be listed as a Threatened species because the species met two of the criteria for listing as described in 68A-27.001(3), F. A. C.

SUMMARY OF THE INDEPENDENT REVIEW

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Biological Status Review Information Findings	
Species/taxon:	Big Cypress Fox Squirrels (*Sciurus niger avicennia*)
Date:	11/04/10
Assessors:	John Kellam, Elina Garrison, Robert McCleery
Generation length:	Generation length = 3 years, used 10 year time frame as 3 generations is < 10 years.

Criterion/Listing Measure	Data/Information	Data Type*	Criterion Met?	References
*Data Types - observed (O), estimated (E), inferred (I), suspected (S), or projected (P). Criterion met - yes (Y) or no (N).				
(A) Population Size Reduction, ANY of				
(a)1. An observed, estimated, inferred or suspected population size reduction of at least 50% over the last 10 years or 3 generations, whichever is longer, where the causes of the reduction are clearly reversible and understood and ceased[1]	There has not been a 50% decline in the past 10 years where the causes of reduction are clearly reversible or understood.	I	N	
(a)2. An observed, estimated, inferred or suspected population size reduction of at least 30% over the last 10 years or 3 generations, whichever is longer, where the reduction or its causes may not have ceased or may not be understood or may not be reversible[1]	Direct observation of reduction, no longer found at certain localities. Decline in area of occupancy and quality of habitat. Biologist from multiple state and federal agencies concur that BCFS sightings have remained extremely low in the past 10 years. The lands these biologist manage represent the core of the BCFS range. Extent of decline difficult to quantify.	I	N	Ditgen and Shepherd 2007; Endries et al. 2009; Humphrey and Jodice 1992; Jansen 2008; Jodice and Humphrey 1992; Kellam and Jansen 2010; Koprowski 1994. J. Kellam, D. Jansen and S. Bass (National Park Service), M. Owen (Florida Fish and Wildlife Commission) and E. Carlson (Corkscrew Swamp Sanctuary); personal communications.
(a)3. A population size reduction of at least 30% projected or suspected to be met within the next 10 years or 3 generations, whichever is longer (up to a maximum of 100 years) [1]	The human population growth from 2010 through 2020 for the counties (Hendry, Lee, and Collier) in which the species occurs, is projected to increase by 26.1%. We suspect BCFS population reduction will occur due to habitat loss and fragmentation, as a result of development and habitat degradation due to changes in land management practices (e.g. fire reduction); also there is a possible population reduction due to disease (i.e. squirrel poxvirus). However, it is unknown what the relationship between habitat loss and population reduction is.	I	N	Zwick and Carr 2006, John Kellam (NPS), unpublished data.

(a)4. An observed, estimated, inferred, projected or suspected population size reduction of at least 30% over any 10 year or 3 generation period, whichever is longer (up to a maximum of 100 years in the future), where the time period must include both the past and the future, and where the reduction or its causes may not have ceased or may not be understood or may not be reversible.[1]	See above A(a)3.	I	N	
[1] based on (and specifying) any of the following: (a) direct observation; (b) an index of abundance appropriate to the taxon; (c) a decline in area of occupancy, extent of occurrence and/or quality of habitat; (d) actual or potential levels of exploitation; (e) the effects of introduced taxa, hybridization, pathogens, pollutants, competitors or parasites.				
(B) Geographic Range, EITHER				
(b)1. Extent of occurrence < 20,000 km^2 (7,722 mi^2) OR	Extent of occurrence was calculated by adding up the area of all counties of occurrence. Total area came to 16,679 km^2**.**	E, I	Y	Williams and Humphrey 1979, Wooding 1997; Moore 1956, Endries et al. 2009, John Kellam, personal communication.
(b)2. Area of occupancy < 2,000 km^2 (772 mi^2)	Estimated areas of occupancy based on GIS habitat analyses range from 1,677 km^2 to 3,840 km^2. However, current research being conducted at Big Cypress National Preserve is finding that GIS based habitat models have overestimated the potential habitat and therefore the actual area of occupancy.	E, I	Y	Cox et al. 1994, FWS 2002, Endries et al. 2009, J. Kellam and D. Jansen (NPS), unpublished data.
AND at least 2 of the following:				
a. Severely fragmented or exist in ≤ 10 locations	Populations are known to be severely fragmented in western Lee and Collier Counties and in other isolated patches of habitat in urban areas. However, extent of the fragmentation is unknown.	I	N	Ditgen and Shepherd 2007; Endries et al. 2009; Kellam and Jansen (NPS), unpublished data.
b. Continuing decline, observed, inferred or projected in any of the following: (i) extent of occurrence; (ii) area of occupancy; (iii) area, extent, and/or quality of habitat; (iv) number of locations or subpopulations; (v) number of mature individuals	Decline projected in (ii), (iii), (iv), and (v). See A(a)3 and C(c)2b.	I, P	Y	FWS 2002; Jansen 2008; Jodice and Humphrey 1992; Koprowski 1994.
c. Extreme fluctuations in any of the following: (i) extent of occurrence; (ii) area of occupancy; (iii) number of locations or subpopulations; (iv) number of mature individuals	Extreme fluctuations in area of occurrence, area of occupancy and number of locations or subpopulations have occurred in the Cape Sable coast of Everglades National Park, Corkscrew Swamp Sanctuary and Big Cypress National Preserve. Extreme fluctuations in the number of mature individuals occurred in Corkscrew Swamp Sanctuary between mid-70's and mid-80's (Ed Carlson, personal communication). In addition, in the mid-1990s, BCFS in Corkscrew Swamp Sanctuary were found dead or dying, followed by a period of absence for years afterward (Ralph Arwood, personal communication).	I	Y	Jodice and Humphrey 1992; J. Kellam, E. Carlson and R. Arwood, personal communications.

(C) Population Size and Trend				
Population size estimate to number fewer than 10,000 mature individuals AND EITHER	Density estimates for BCFS range from 0.09 to 1.92 squirrels/km^2. Using Endries et al. 2009, available habitat (2,858 km^2) would result in a population size of 257 - 5,487 squirrels. Although these density estimates are believed to be low, interviews with state and federal biologists, concurred that population size of mature individuals is well below 10,000.	I	Y	Cox et al. 1994, FWS 2002; Endries et al. 2009, Jodice and Humphrey 1992, J. Kellam and D. Jansen, personal communication.
(c)1. An estimated continuing decline of at least 10% in 10 years or 3 generations, whichever is longer (up to a maximum of 100 years in the future) OR	No estimates of decline available.	I	N	
(c)2. A continuing decline, observed, projected, or inferred in numbers of mature individuals AND at least one of the following:	See additional notes and citations in B2b.	I	Y	
a. Population structure in the form of EITHER	Unknown	I	N	
(i) No subpopulation estimated to contain more than 1000 mature individuals; OR				
(ii) All mature individuals are in one subpopulation	No	I	N	
b. Extreme fluctuations in number of mature individuals	See above B(b)2c. In addition, Squirrel poxvirus has been detected recently in BCFS within Big Cypress National Preserve. This highly virulent disease (mortality rate of 75-100%) has the potential to cause significant population loss.	I	Y	J. Kellam (NPS), unpublished data.
(D) Population Very Small or Restricted, EITHER				
(d)1. Population estimated to number fewer than 1,000 mature individuals; OR	There are more than 1000 estimated mature individuals.	I	N	
(d)2. Population with a very restricted area of occupancy (typically less than 20 km^2 [8 mi^2]) or number of locations (typically 5 or fewer) such that it is prone to the effects of human activities or stochastic events within a short time period in an uncertain future	AOO is greater than 20 km^2 and number of locations is greater than 5.	I	N	
(E) Quantitative Analyses				
e1. Showing the probability of extinction in the wild is at least 10% within 100 years	PVA did not show probability of extinction of at least 10%. However, the PVA model used was based upon a habitat model that overestimated the actual AOO.	P	N	Endries et al. 2009, J. Kellam, personal communication. Also see notes on Bb2.

Initial Finding (Meets at least one of the criteria OR Does not meet any of the criteria)	Reason (which criteria are met)

Yes, meets 2 criteria	Bb ii, iii, iv, v, cii, iii, iv; C2b
Is species/taxon endemic to Florida? (Y/N)	Yes
If Yes, your initial finding is your final finding. Copy the initial finding and reason to the final finding space below. If No, complete the regional assessment sheet and copy the final finding from that sheet to the space below.	
Final Finding (Meets at least one of the criteria OR Does not meet any of the criteria)	Reason (which criteria are met)
Meets 2 criteria	Bb ii, iii, iv, v, cii, iii, iv; C2b

Appendix 1. Biological Review Group Members Biographies

Elina Garrison has a M.S. in Wildlife Ecology and Conservation from the University of Florida. She has worked as a biologist in FWC's Terrestrial Mammal Research Subsection since 2004. Ms. Garrison has experience with a variety of Florida mammals, including black bears, white-tailed deer, and fox squirrels, and she has assisted with fox squirrel risk assessments and compiling statewide range maps.

John Kellam has a BS in Biology from Humboldt State. John has been the lead biologist on a field study of Big Cypress fox squirrels in Big Cypress National Preserve since 2007. To date, 20 radio-collared individuals have been monitored 3 times per week to determine movements, habitat use, food preferences, and nest tree selection.

Robert McCleery has a Ph.D. in Wildlife Science from Texas A & M University. He currently serves as an assistant professor in the Department of Wildlife Ecology and Conservation at the University of Florida. Dr. McCleery has over 15 years experience in research and conservation of wildlife and has worked extensively on the ecology of fox squirrels, Key Largo woodrats, Keys marsh rabbits, Florida Key deer and Indiana bats.

Appendix 2. Summary of letters and emails received during the solicitation of information from the public.

There is a thriving population of fox squirrels in the pine lands, about 11- 14 miles north of US 41, off sand road. I have observed as many as 10 at one location, along with others in the area. Several color variations.

- Dick Kempton

Appendix 3. Information and comments received from the independent reviewers.