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Big Cypress Fox Squirrel (Sciurus niger avicennia) Diet, Activity and Habitat Use on a Golf Course in Southwest Florida

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ABSTRACT.—Habitat use, feeding and activity patterns of Big Cypress fox squirrels (*Sciurus niger avicennia*) were studied in southwest Florida to identify golf course features favorable to fox squirrels. The location, behavior and foods of 30 radio-located squirrels were recorded twice weekly from Dec. 1995 to Jul. 1997. Diet was >85% food from native conifers for 6 mo (Aug.–Jan.), >75% flowers and fruits of planted exotics for 3 mo (Feb.–Apr.) and a variety of foods supplemented by mushrooms and webworm larvae for 3 mo (May–Jul.). Ground feeding accounted for 69.6% of observations. Use of foods from exotic species was associated with greatest reproduction in the summer. Five categories of behavior in adults (feeding, travel, resting, nesting, social interactions) showed significant interaction between sex and time-of-day and season and time-of-day in a log-linear model. Squirrels were least active during the hottest part of the year. Squirrels concentrated their activity in tree stands of the course's roughs. Squirrels were more likely to use open areas to travel between tree stands than for other activities. Among patches of trees, stands dominated by *Pinus elliottii* and *Taxodium* sp. and by *P. elliottii* and *Sabal palmetto* were used the most. Squirrels used pure stands of *S. palmetto* and stands of mixed natives less than expected based on availability. Dense understory reduced overall stand use and ground foraging. Golf course design and management directly affect features favorable to Big Cypress fox squirrels and may determine the value of golf courses in conservation.

INTRODUCTION

Fox squirrels (*Sciurus niger*) are a diurnal species inhabiting open forests of the eastern and central United States (Hall, 1981; Koprowski, 1994). The four subspecies of the southeast are larger and more varied in color than those to the north and west and occupy open pine forests with oaks and associated hardwoods (Moore, 1957; Weigl *et al.*, 1989; Kantola and Humphrey, 1990). Of these subspecies, the Big Cypress fox squirrel (*S. n. avicennia*, BCFS) 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 (Moore, 1956). Native to open stands of slash pine (*Pinus elliottii*), cypress (*Taxodium* sp.) and tropical hardwoods, these squirrels frequently feed and move on the ground.

The BCFS's range consists of three areas that differ in physiography, habitat suitability and potential threats. First, the squirrels use elevated areas of seasonally inundated landscapes in Big Cypress Swamp and the Everglades, areas where fire suppression has

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contributed to the apparent recent decline of BCFS. Second, in the flatwoods region of Hendry County, grazing helps maintain favorable open habitat, but conversion of range lands to citrus groves has diminished BCFS habitat (Pearlstine *et al.*, 1997). Finally, in the drier flatwoods of western Lee and Collier Counties, rapid urbanization has isolated squirrel populations in habitat fragments (Moore, 1954; Williams and Humphrey, 1979; Jodice and Humphrey, 1993). Amid shrinking green space, BCFS remain on some golf courses within and near burgeoning development (Jodice, 1990; Jodice and Humphrey, 1992, 1993; Ditgen, 1999). Relatively large size and terrestrial habits make BCFS especially vulnerable to recent widespread landscape changes (Moore, 1956; Williams and Humphrey, 1979; Jodice and Humphrey, 1992).

The state of Florida has protected BCFS as a threatened species since 1979. The US Fish and Wildlife Service (Anonymous, 2002) found that federal listing was not warranted. Among the principal lines of evidence leading to the finding were that 58% of potential BCFS habitat is conservation lands and that persistence on golf courses is evidence of "opportunistic" use of available habitats. While BCFS habitat is protected in Big Cypress Swamp and the Everglades, qualitative evidence suggests that squirrel densities are very low in these areas (Jodice and Humphrey, 1993). High BCFS densities on some golf courses indicate that these areas might serve as refugia in the part of their range where they face the greatest threat (Jodice and Humphrey, 1992, 1993), but squirrels on existing golf courses might justify further development and additional loss of wild habitat (Maehr, 1993). BCFS use of golf courses deserves more careful consideration because of its controversial role in conservation and its contribution to the denial of federal protection.

We studied diet, habitat use and behavioral activity patterns on a golf course in southwest Florida to identify golf course features favorable to BCFS and to describe the ecology of a threatened subspecies that remains poorly known and difficult to study in the wild (Jodice and Humphrey, 1993).

STUDY SITE

The Royal Poinciana Golf Club 18-hole Cypress Course (26°11′46″N, 81°46′59″W) was built in western Collier County in 1971. A large portion of the course was occupied by stands of native vegetation. Fairways were bordered by open stands of moderate-size slash pines (*Pinus elliottii* var. *densa*), cypress (*Taxodium ascendens* and *T. distichum*) and cabbage palms (*Sabal palmetto*) with scattered oaks (*Quercus virginianum* and *Q. laurifolia*) and red maple (*Acer rubrum*). Plantings of non-native broad-leafed evergreens, bischofia (*Bischofia javanica*), tallow tree (*Sapium sebiferum*), Java plum (*Syzigium cumini*), bottlebrush (*Callistemon* sp.) and Royal palm (*Roystonea* sp.) were scattered throughout the course. The club had no residential development within its 135 hectares. Roads and automobile traffic were limited to a short entrance roadway. Royal Poinciana was located within a tract of approximately 1020 ha that contained 6 18-hole golf courses, of which three did not have residential development. Within the tract there were 230 ha of stands of trees and forested land, ranging from upland pine to swampy cypress. The Cypress Course was one of 6 of 60 golf courses in Lee and Collier counties that had a large numbers of squirrels (Ditgen, 1999).

METHODS

Data on habitat use, diet and behavior were collected from squirrels trapped between Dec. 1995 and Jan. 1997 and fitted with 25 g AVM (AVM Instrument Co., Livermore, CA) or 28 g ATS (Advanced Telemetry Systems, Isanti, MN) radio-transmitting collars engineered for this project (Ditgen, 1999). Study of these animals continued until Jul. 1997. We used

radio-telemetry to locate collared squirrels at least twice a week in two of three daily tracking periods (Mech, 1983): morning (0600–1030 hr), midday (1031–1430 hr) and afternoon (1431–1900 hr). After radio-location, visual sighting without disturbing the animals was possible because of the openness of the vegetation and their habituation to humans in golf carts. In addition to tracking location, at each sighting we recorded behavior, food type when identifiable, vegetation and/or substrate and position in or relative to trees.

For the analysis of seasonal influences, we divided the year into four seasons based on average monthly rainfall and temperature (NOAA, 1995–1997). From Nov. through Apr., monthly temperatures averaged 20 C and monthly rainfall less than 50 mm. These months were divided into Early Dry Season from Nov. to Jan. and Late Dry Season from Feb. through Apr. Wet season monthly temperatures averaged 27 C and monthly rainfall averaged 180 mm. Early Wet Season extended from May through Jul. and Late Wet Season from Aug. through Oct.

We recognized five categories of squirrel behavior: (1) feeding, which included eating, searching, digging, burying; (2) travel, on the ground and in trees; (3) resting, on the ground or in trees; (4) nesting, which included building, carrying nest materials, and being tracked to, but not visible in, nests; and (5) social interactions, which included mating chases, scent marking, aggression, chasing other squirrels and play. Among these categories, a squirrel was defined as active when feeding, traveling or engaging in social interactions and defined as inactive when resting or nesting. Small sample sizes prevented us from analyzing grooming and alert stances.

We assessed temporal autocorrelation among behavioral observations using occasions in which an individual was observed twice in one day. Repeated observation of the same behavior could result from autocorrelation and from the overall likelihood of observing the behavior. Elevated frequency of repeated behavior at shorter time intervals would indicate temporal autocorrelation. We compared the frequency of repeated behavior in successively longer time intervals, using a chi-squared test (Quinn and Keough, 2002). When the frequency of repeat behavior did not differ significantly from that in intervals of more than 5 h, we considered this a lack of autocorrelation and included those observations in our analysis.

Observations of adults were available in all seasons, but due to the timing of reproductive periods, the maturation of the individuals and the end of the study, observations of subadults were not available for the Late Wet Season. As a result, data for adults and subadults were analyzed separately. A goodness-of-fit maximum likelihood chi-square test identified the best log-linear model (Quinn and Keough, 2002) in Statistica 6.1®. We used odds-ratios to compare categories within the log-linear model and to summarize relationships within contingency table of frequencies (Agresti, 1996; Quinn and Keough, 2002).

Correspondence analysis was used to assess the interdependence of month and diet (Quinn and Keough, 2002). Dietary diversity was measured with the inverse of Simpson's index, which can be interpreted as an equivalent number of equally-used species (Krebs, 1999). This index has a maximum value equal to the number of species in the diet.

Arboreal habitat patches ranged from parcels of semi-natural forest to groups of trees with a groundcover of turf or pine litter. We use the generic term "tree stand" to recognize this wide range and the simple structure of many of the patches. We sampled tree stands using 20 m diameter circular quadrats placed at intervals of 25 m from center to center. Within each quadrat, all trees over 10 cm dbh were identified and the circumference of each measured. Percent coverage of the understory was estimated for shrubs, herbs and saplings that were 1–3 m tall. Area of pine litter substrate was estimated as a percentage where it was

not covered by understory vegetation. We placed tree stands into one of six habitat categories: (1) cypress-palm-pine, dominated by a mixture of cypress and cabbage palm, with <20% basal area of pine; (2) mixed natives, a mixture of native species not dominated by slash pine, cypress and cabbage palm, but containing oaks, red maple, red bay (*Persia borbonia*) and/or holly (*Ilex opaca*) and with <20% basal area of exotics; (3) mixed natives-exotics, natives as in type 2, but with >20% basal area of exotic species; (4) palm, >60% basal area of cabbage palm; (5) pine-cabbage palm, with each of those species contributing at least 30% of stand basal area; (6) pine-cypress, with each of those species contributing at least 30% of stand basal area. Understory coverage of 30–90% was classified as dense (compared to other stands where it was less than 5%). We recognized two other habitat types without woody plants: (1) open areas, which consisted of the managed paths, turf and sand traps of the playing surface; and (2) wet areas, which had standing water and sometimes a narrow littoral marsh.

We measured habitat availability on a digitized map of course vegetation in AtlasGIS 3.0® and sampled habitat use by overlaying tracking points on the vegetation map (Design I of Manly *et al.*, 2002). We calculated the Manly standardized selection index which can be interpreted as the probability a habitat type will be selected if all types were equally available or abundant (Manly *et al.*, 1972, 2002).

RESULTS

Thirty squirrels were tracked for 299 squirrel-months of tracking data. During the study, collared animals averaged 74% of mark-recapture estimates of the squirrel population on the course (Ditgen, 1999).

DIET

Food items were clearly identified in 817 observations in which 13 food species were taken more than 5 times. The first axis of variation in monthly diet was strongly correlated with food from native trees ($r = -0.98$, $df = 11$, $P < 0.001$, Fig. 1). The second axis was strongly correlated with ground feeding on mushrooms and insect larvae ($r = -0.89$, $df = 11$, $P < 0.001$). There were three distinct dietary periods. In the Late Wet and Early Dry Seasons (Aug.–Jan.) the diet was uniformly concentrated in food from native trees, which made up >85% of observations. In the Late Dry Season (Feb.–Apr.) the diet shifted rapidly as food from exotic trees made up >75% of observations. In the Early Wet Season, almost 20% of observations consisted of mushrooms and larvae and feeding in exotic trees dropped to <60% of observations. Feeding on the ground comprised 69.6% of observations throughout the year and seasonal differences were not significant ($X^2 = 11.66$, $df = 3$, $P = 0.09$). Squirrels were observed burying and digging up food items in all seasons. They buried pine and cypress cones as well as the fruits of queen palm.

In the Late Wet and Early Dry Seasons, the dietary diversity index was 2.98. Squirrels fed heavily on maturing slash pine cones and later switched to cypress cones. Slash pine (48%) and cypress (31%) comprised the majority of feeding observations. Squirrels also fed on acorns, mainly those of live oaks. The end of this period was marked by the early spring availability of red maple samaras, on which they fed during the transition from native to exotic trees.

The dietary diversity index for the Late Dry Season was 5.76. Bischofia berries were 33% of recorded feeding. Fresh and buried fruits of the queen palm (*Arecastrum romanzoffianum*) and bottlebrush flowers accounted for 14% and 15% respectively of observations. Squirrels began feeding on *Ficus* sp.

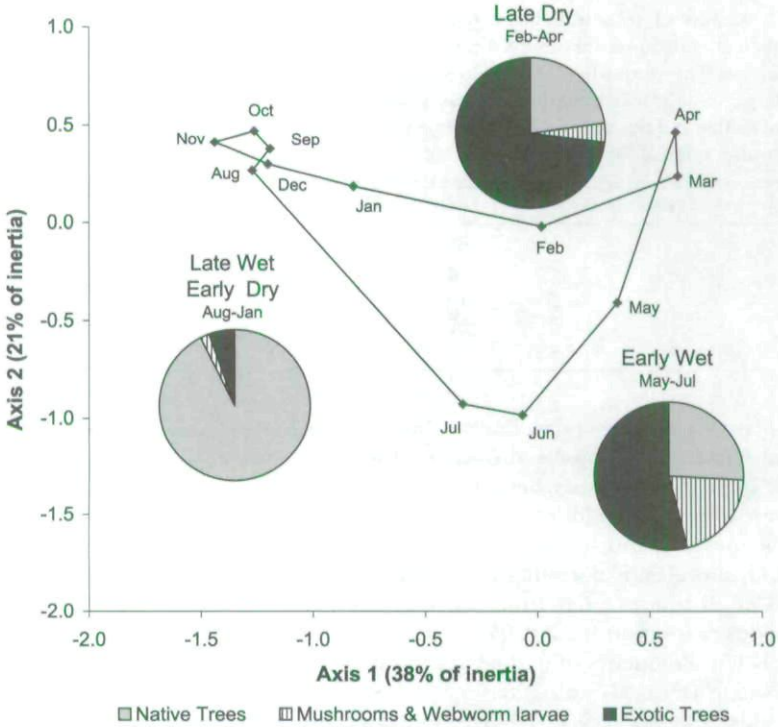

FIG. 1.—Correspondence analysis of feeding observations of Big Cypress fox squirrels on the Royal Poinciana Cypress Course in Collier County, Florida. Points summarize the diet for each month. Pie charts indicate the diet components for the three dietary periods. n = 817 observations of clearly identified food items in 13 food species taken more than five times

In the Early Wet Season, the dietary diversity index reached its maximum of 7.66, with no species accounting for more than 20% of observations. Exotic species continued to comprise the majority of the diet with *Ficus* sp. (19%), bischofia (16%), queen palm (9%) and java plum (9%) being the most frequently observed. The most characteristic food items were large hypogeous fungi. Feeding on fungi was concentrated (86% of observations) in patches with deep litter layers of pine and/or cypress needles, generally in pine/cabbage palm patches, but also in cypress/cabbage palm patches. Squirrels sometimes ate the large (5–8 cm) caps of 4–5 fruiting bodies within 10 min. Squirrels also fed on concentrated patches of Mahogany webworm larvae *Macalla thyrsisalis* buried in soil, grass or litter. They bit the tip from the casings and pulled the small caterpillars out with their teeth. During the same period squirrels showed no interest in the tent caterpillars *Malacosoma disstria* that rained to the ground from infested cypress trees.

ACTIVITY

Because repeated behavior was significantly more likely when observations were separated by less than 30 min (Table 1), only observations separated by longer intervals were analyzed. Observations separated by 30–60 min were fewer than 4% of observations.

The best log-linear model of 1611 observations of 13 female and 15 male adults (X^2 = 44.0, df = 45, P = 0.514) included two-way interactions between sex and time-of-day and

TABLE 1.—Results of tests for autocorrelation in behavioral observations of 30 Big Cypress fox squirrels when an individual was observed twice in one day on Royal Poinciana Cypress Course in Collier County, Florida. The proportion of repeated behavior is the likelihood the same behavior (feeding, travel, resting, nesting, social interaction) was observed on both occasions. X^2 for a time interval tests the hypothesis that the frequency of repeated behavior is the same for observations in that interval and the longest time interval (>5 h)

Interval between observations (min)	n	Proportion of repeated behavior	X^2	$p(X^2)$
0–30	63	0.62	4.532	0.03
30–60	74	0.42	0.004	0.94
60–180	315	0.43	0.040	0.84
180–300	87	0.49	1.309	0.25
>300	46	0.41	–	–

between season and time-of-day, but not between sex and season. Males were much more likely than females to be observed traveling (odds ratio 1.5, 95% Confidence Interval 1.2–2.1), with high travel frequencies in morning and afternoon (Fig. 2a). Most records of nesting were of females (odds ratio 11.1, 95% CI 4.5–27.7) occupying and maintaining brood nests in the morning and afternoon. Males had more social interaction (odds ratio 3.3, 95% CI 2.1–40.1), more midday resting and highest levels of feeding in the afternoon. Travel decreased at all times of day from the Early Dry Season through the Early Wet Season (Fig. 2b, odds ratios morning 3.2, 95% CI 1.7–6.3, midday 3.6, 95% CI 1.5–8.7, afternoon 3.0, 95% CI 1.0–9.5). Frequency of midday resting stayed about the same during the Dry Season (Early Dry-Late Dry odds ratio 1.8, 95% CI 0.8–4.0), but then increased in the Early Wet Season (odds ratio 2.0, 95% CI 1.2–3.4) and again in the Late Wet Season (odds ratio 2.3, 95% CI 1.2–4.4) before decreasing sharply at the start of the Early Dry Season (odds ratio 0.1, 95% CI 0.05–0.3). Nesting (odds ratio 3.7, 95% CI 2.3–5.8) and social interactions (odds ratio 1.9, 95% CI 1.2–3.1) were most common in the Late Wet Season compared to other seasons combined.

We observed one mating chase in the Late Dry Season, nine in the Early Wet Season and two in the Late Wet Season. Four young were seen leaving their natal nests in the first Dry Season, 15 in the only Wet Season and three in the second Dry Season.

In the best log-linear model of 513 observations of 17 sub-adults ($X^2 = 20.6$, df = 24, P = 0.662) the sexes displayed differences in seasonal activity patterns and daily patterns of activity. In the Late Dry and Early Wet Seasons, males were more frequently observed in social interactions (Early Wet odds ratio 2.8, 95% CI 1.6–489) and females were more frequently observed resting (odds ratio 4.0, 95% CI 1.5–10.5).

HABITAT USE

In 2333 tracking locations, squirrels concentrated their activity in tree stands around and between open and wet areas of the course (selection index = 0.83, Table 2). No squirrels were observed using wet areas and fewer than 16% of tracking points were located in the open portions of the golf course itself. Moreover, squirrels located in open areas were more than seven times more likely to be traveling than squirrels on the ground within tree stands (odds ratio 7.5, 95% CI 5.4–10.3, n = 1234).

Among arboreal habitats, the squirrels exhibited the strongest selectivity toward stands of pine/palm (selection index = 0.32, Table 2) and pine/cypress (selection index = 0.23). They used stands of cabbage palm and stands of mixed natives less than expected from availability.

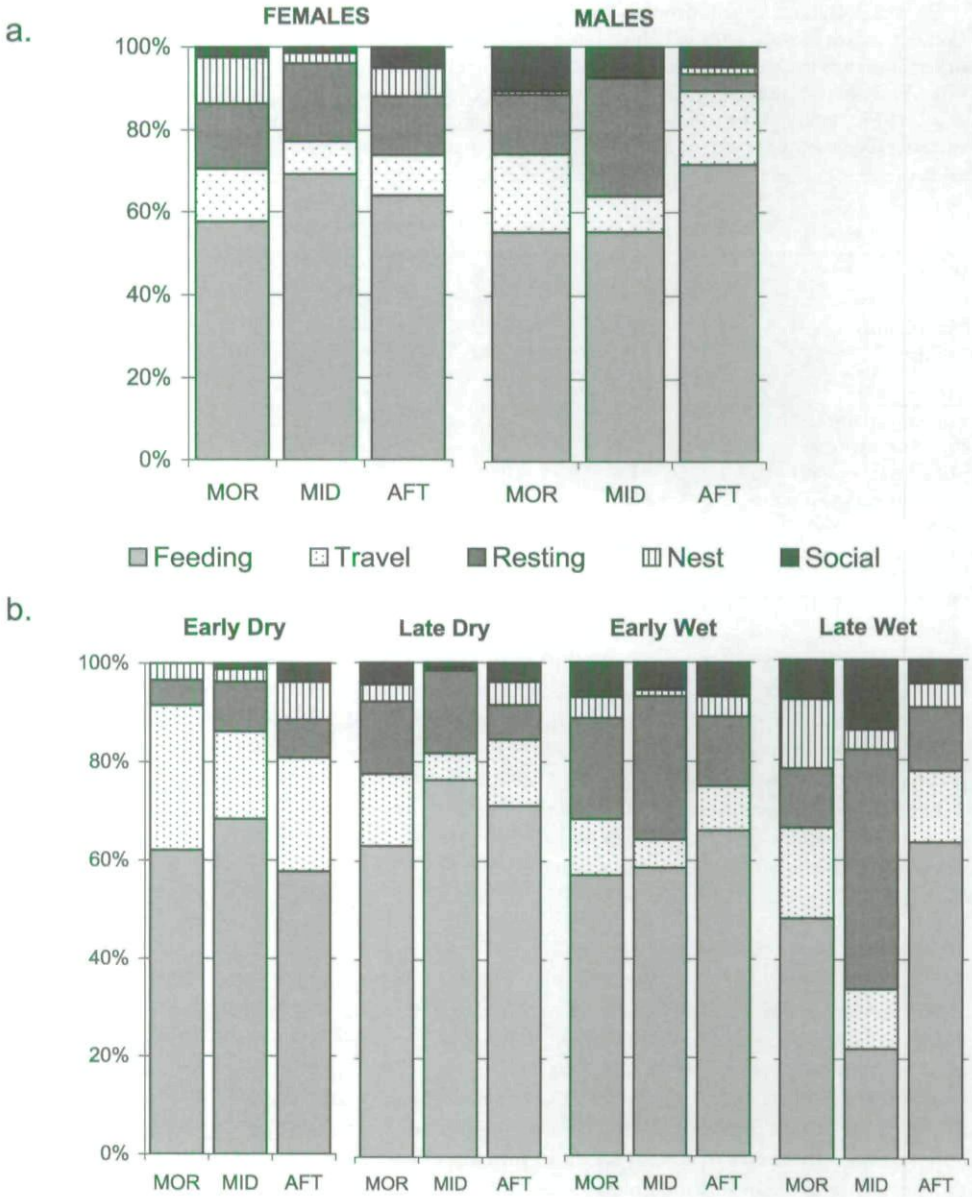

FIG. 2.—Activity patterns of 28 adult Big Cypress fox squirrels on the Royal Poinciana Cypress Course in Collier County, Florida. a. Daily activity of 13 females and 15 males. b. Daily activity of both sexes in four seasons. Early Dry Season: Nov.–Jan.; Late Dry Season: Feb.–Apr.; Early Wet Season: May–Jul.; Late Wet Season: Aug.–Oct. MOR: morning, 0630–1030; MID: midday, 1031–1430; AFT: afternoon, 1431–1900. n = 1611 observations

TABLE 2.—Habitat selection by 30 Big Cypress fox squirrels on Royal Poinciana Cypress Course in Collier County, Florida. Area of habitat was measured from aerial photos using Atlas GIS 3.0. Each usage observation was the radio-location of a collared squirrel within the patch. Standardized selection index is the probability a habitat type would be selected if all types were equally available or abundant (Manly *et al.*, 1972, 2002). Open areas consisted of the managed paths, turf and sand traps of the playing surface. Tree stands are classified according to the dominant species

Habitat type	Availability		Usage		Standardized selection index
	Area (ha)	Proportion	n	Proportion	
Wet areas	5.5	0.09	0	0.00	0.00
Open areas	25.9	0.42	359	0.15	0.17
Tree Stands	30.0	0.49	1974	0.85	0.83
Totals	61.4	1.00	2333	1.00	1.00
Tree Stands					
Pine and palm	3.2	0.11	438	0.22	0.32
Pine and cypress	0.9	0.03	89	0.05	0.23
Mixed natives with exotics	7.8	0.26	488	0.25	0.15
Pine, cypress and palm	12.8	0.43	765	0.39	0.14
Palm	2.4	0.08	91	0.05	0.09
Mixed natives	2.9	0.10	103	0.05	0.08
Totals	30.0	1.00	1974	1.00	1.00

Dense understory was most common in stands dominated by cypress. Squirrels used cypress stands with open understory (standardized selection index = 0.61) much more than those with dense understory (standardized selection index = 0.39). Individuals using cypress stands with dense understory were much less likely to be on the ground than individuals in cypress stands with open understory (odds ratio 0.07, 95% CI 0.02–0.20, n = 383).

Eleven brood nests were located on the course: five in cavities in cypress trees, three in large bromeliads in pine trees, two in cabbage palms and one in a queen palm. All of these were located in cypress-pine-palm stands.

DISCUSSION

DIET

Southeastern fox squirrels depend on mast from native oak and pine trees when it is available (Kantola and Humphrey, 1990; Loeb and Moncrief, 1993). On the North Carolina coastal plain, squirrels harvested acorns during the major autumn masting season (Weigl *et al.*, 1989). A summer dearth, during which they often consumed hypogeous fungi, preceded the start of a new cycle as conifer cones began to ripen. Similarly in this study, BCFS concentrated on the cones of native slash pine and cypress for 6 mo and consumed fungi in the period before these foods became available.

Big Cypress fox squirrels extended availability of some seasonal foods by scatter-hoarding. We observed BCFS burying and retrieving cones of pine and cypress and fruits of queen palm. Some studies in the southeast specifically report a lack of observations of caching by wild fox squirrels (Weigl *et al.*, 1989 for *Sciurus niger niger* and Moore, 1957 for *S. n. shermani*), but caching by captive *S. n. shermani* (Moore, 1957) and wild *S. n. avicennia* (Moore, 1954) has also been reported. Scatter hoarding is widely reported for *S. niger* in other areas (Cahalane, 1942; Stapanian and Smith, 1978, 1984; Whitaker and Hamilton, 1998; Steele and Koprowski, 2003).

There are several differences between the foods taken by BCFS in this study and those reported for fox squirrels in other southeastern studies (Moore, 1957; Weigl *et al.*, 1989; Kantola and Humphrey, 1990). First, mast from native hardwood species such as oaks made a much smaller contribution to the diet. Second, BCFS fed heavily on non-native fruits and flowers when other fox squirrels are reported to experience a summer dearth of foods. These exotic foods dominated their diet from Feb. through Jul. Third, insect larvae were a common food during the part of the year when BCFS also frequently ate fungi.

Quite different dietary patterns were reported for BCFS on the same golf course (Jodice and Humphrey, 1992). In that study most observations were reported only as "ground feeding" without identification of the food. Consequently, the results did not show the shift from native to non-native foods that we observed. The "ground feeding" category also obscured the frequency of mushroom and webworm larvae in the Early Wet Season. Significantly, cabbage palms were not trimmed and feeding time in cabbage palm was greater than that in either pine or cypress. Five years later during this study, fruiting structures were trimmed from palms and BCFS were denied a common native food.

Previous research suggested that food probably limits fox squirrel population size (Weigl *et al.*, 1989). Koprowski (1990) found juvenile mortality and low body weights were associated with a low supply of favored foods. In earlier fox squirrel research in the southeast (Moore, 1957; Weigl *et al.*, 1989; Loeb and Moncrief, 1993), more young were produced in the winter/spring breeding season than in the summer/autumn season. In contrast, we observed more reproduction in the warm summer/autumn season, when exotic foods supplemented a limited summer native diet. Upon leaving the nest the young fed on the plentiful pine and cypress crops available in the Late Wet season and the Early Dry season. These observations are consistent with the argument (Koprowski, 1990; Weigl *et al.*, 1989) that food shortage limits summer reproduction. The abundance of native slash pine and cypress and of exotic foods may contribute to the high population density we observed. Such food sources may be necessary when small populations are confined to habitat islands within a developed landscape.

ACTIVITY PATTERNS

As in previous studies (Weigl *et al.*, 1989; Loeb and Moncrief, 1993; Koprowski and Corse, 2005), BCFS activity reflects local changes in the physical environment, food availability and reproduction. BCFS were least active during the Late Wet Season, when they exhibited a morning-and-afternoon pattern that may have thermoregulatory benefits (Weigl *et al.*, 1989). Squirrels were most active in the Late Dry Season, with a unimodal peak in activity (Fig. 2).

In North Carolina, activity levels peaked as pine and oak mast became available after a summer of food scarcity (Weigl *et al.*, 1989). Because plantings of exotic species supplemented native summer foods, the shift in food availability and activity was not as sharp in this study. The transition to a diet dominated by pine and cypress in the Late Wet Season occurred during the extended period of heat stress and morning-and-afternoon activity of squirrels. When temperatures lowered and rains stopped, squirrels traveled more, feeding on native foods throughout the day (Fig. 2).

The seasonal activity patterns reported for BCFS without radio-collars on this same course (Jodice and Humphrey, 1992) may have been affected by a detectability bias that favored observation of squirrels in the open. Uncollared squirrels were less likely to be detected feeding in the dense foliage of exotic trees in the Late Dry Season or resting and nesting high in pines and cypress in the Wet Season.

Males exhibited more social interactions than females. Adult males were aggressive toward transient males and subadult males were frequently observed in non-aggressive interactions with sibling males. Increased social interaction during the Early Wet Season occurred because adults of both sexes chased maturing subadult males.

HABITAT USE

BCFS used primarily the tree stands of the golf course (Table 2). Although they sometimes buried cones and dug for webworm larvae on fairways and greens, they were much more likely to be seen traveling across open areas. This suggests that the course of play itself acts like a matrix through which move moved to reach tree stands.

BCFS show selectivity in their use of habitat patches (Table 2), which probably reflects foraging optimization (Steele and Weigl, 1992) among other constraints. Slash pine, cypress and cabbage palm provided food and nesting opportunities; native hardwoods and hammock species were used much less. Because trimming of palms reduced or eliminated feeding opportunities, squirrels used pure palm stands much less than expected. The avoidance of heavy understory vegetation is expected for a species that frequently moves and feeds on the ground (Weigl *et al.*, 1989; Loeb and Moncrief, 1993; Steele and Koprowski, 2003). Perkins and Conner (2004) did not find sexual or seasonal effects in habitat selection, but did find strong preferences in location of home ranges. The selective habitat use in this study area also reflects the fact that surrounding developed areas constrained squirrel movement and choices of home range and habitat.

INTEGRATION OF CONSERVATION AND MANAGEMENT

While there is a movement to create golf courses favorable to wildlife (Harker *et al.*, 1993; Terman, 1997; Gillihan, 1999; Dodson, 2000, 2005), this "naturalization" of golf courses often focuses on the inclusion of areas of low maintenance native vegetation. Such a generic approach may encourage generalist "suburban-adaptable" species, but it is a poor alternative to wild lands for species of conservation concern (LeClerc and Cristol, 2005). Species may suffer lower fecundity (Smith *et al.*, 2005), lower reproductive success and greater emigration rates (Dale, 2004) when their habitat is within the matrix of a golf course. Golf courses may contribute to conservation of target species (Rodewald *et al.*, 2005), but this is a complex endeavor, sometimes requiring intensive management.

BCFS habitat requirements must be incorporated into course design and maintenance for golf clubs to serve as refugia in southwest Florida. Where clubs are green islands within a developed landscape, isolation intensifies needs and magnifies management consequences. A population of BCFS depends on food from mature stands of slash pine, cypress and untrimmed cabbage palm. If such stands are extensive, they help to buffer the population against supra-annual masting cycles. Historically, fire maintained the open understory needed by this ground-feeding species. Absent natural fire or human maintenance, understory quickly becomes dense, overgrown and unsuitable for BCFS. Planting of tall bunch grasses or shrubs has the same negative impact. Natural or artificial areas of deep pine litter are needed to foster the growth of fungi. In an environmental-design movement that promotes use of native species, the planting of exotic trees may be controversial. In this study, foods from exotic trees may have contributed to higher wet season reproduction than is typical of fox squirrels. All of these requirements are feasible for motivated planners, managers and club members. Even in such high quality habitat, BCFS may require large tracts of land for daily and seasonal movements. This study demonstrates that a golf course can support a population of BCFS. Whether golf courses can contribute to BCFS conservation may depend on how courses are designed and managed.

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