Big Cypress fox squirrel (*Sciurus niger avicennia*) ecology and habitat use in a cypress dome swamp-pine forest mosaic

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Forested wetlands are in decline, as are many species that are obligate residents. Big Cypress fox squirrels (BCFS; *Sciurus niger avicennia*) are a threatened endemic to wet pine and cypress forests in southwestern Florida. The region is characterized by development resulting in habitat loss, habitat fragmentation, and hydrological change that influence the quality of these wet forests. Through radiotelemetry and field observations, we examined the ecology and habitat use of BCFS in a natural cypress dome-pine forest mosaic. BCFS selected cypress domes for food and nests throughout the year. Cypress dome habitats were the only habitat type to be used more than available; however, the availability of nearby pine forest was also important. Home ranges were large relative to other tree squirrels, with male home ranges exceeding female ranges. Males overlapped more females than males, while sharing similar food preferences and use patterns with females, suggesting that the sexual dimorphism in home range size is related to mate searching. Roads and oil extraction pads were used less frequently than expected and were incorporated into home ranges less than randomly generated features. The importance of cypress domes within the wet forests and grasslands of Big Cypress National Preserve demonstrates the value of maintaining this delicate mosaic.

Key words: cypress dome swamp, Florida, forested wetlands, oil development, pine forest, *Sciurus niger avicennia*, space use, threatened

Wetland loss worldwide due to conversion to agriculture, human residence, and salinization continues to be a major environmental concern (Hassan et al. 2005). Global loss rates for wetlands are estimated at 6% from 1993 to 2007 (Prigent et al. 2012). In North America, less than 50% of wetlands remain from the period of European colonization < 300 years ago (Dahl 2000). More than 95% of recent losses have occurred in forested and freshwater wetlands (Dahl 2000, 2011). The rapid loss of these habitats in addition to future loss rates related to climate change suggest the considerable value of such sites that are known to harbor exceptional diversity (Hassan et al. 2005).

Tree squirrels (Sciuridae: Sciurini and Tamiasciurini) are common inhabitants of forested habitats (Gurnell 1987; Thorington et al. 2012) and can serve as indicators of forest condition (Koprowski and Nandini 2008; Zugmeyer and Koprowski 2009). However, outside of temperate and boreal forests, tree squirrels are little studied (Koprowski and Nandini 2008). The Big Cypress fox squirrel (BCFS; *Sciurus niger avicennia*) is a subspecies of the wide-ranging eastern fox squirrel (*S. niger*) found in southwestern Florida and is isolated from other subspecies (Howell 1919; Moore 1956; Williams and Humphrey 1979; Eisenberg et al. 2011).

Big Cypress fox squirrels were once a game species in Florida (Duever et al. 1986). However, from the mid-1950s through the early 1970s, populations declined noticeably throughout their range which led the Florida Fish and Wildlife Conservation Commission (FWC) to ban BCFS hunting in 1973 and declare the subspecies "Threatened" (Duever et al. 1986; Humphrey and Jodice 1992). Historic and recent declines in BCFS populations have been attributed to habitat fragmentation, and loss, as well as habitat modification from fire exclusion, changes in hydrological conditions, hunting, poaching, wildlife diseases, predation, road mortality, and hurricanes (Brown 1978; Duever

et al. 1986; Humphrey and Jodice 1992; Ditgen et al. 2007; Kellam 2010).

Due to the scarcity of BCFS in natural habitats and difficulties in capturing the species (Weigl et al. 1989; Jodice 1990; Eisenberg-Munim et al. 2007), past studies were conducted on urban golf courses (Jodice and Humphrey 1992; Ditgen et al. 2007) or on urban BCFS that were radiocollared and translocated to Big Cypress National Preserve (BICY—Jodice 1993; Dusek et al. 1998). A lack of information on BCFS demographic parameters and trends in natural habitats, and a growing list of threats to the species, led to a petition being filed in 1998 with the United States Fish and Wildlife Service (USFWS) to list the BCFS as a federally protected species and designate critical habitat (USFWS 2002). The petition was denied, in part, due to a lack of data on BCFS ecology, and the large area of potential BCFS habitat found on state and federal conservation lands (USFWS 2002; Ditgen et al. 2007). In 2007, we initiated a 4-year study of BCFS within the Raccoon Point region of BICY to begin filling these information gaps. Herein, we report our findings on home range, movements, habitat use, nest use, and diet of BCFS in their natural habitats.

Materials and Methods

Study area.—Big Cypress National Preserve, covering 295,245 ha of southwestern Florida, represents the core range of the BCFS (Williams and Humphrey 1979; Humphrey and Jodice 1992). Raccoon Point (UTM 507148/2874313) contains the largest remaining unlogged stands of South Florida slash pine (*Pinus elliottii* var. *densa*; hereafter, pine—Patterson and Robertson 1981). A long-term fire ecology study in Raccoon Point (Snyder and Belles 2000) used prescribed fire to treat burn units that resulted in pine forests having the open canopies and low understories preferred by BCFS (Duever et al. 1986; Humphrey and Jodice 1992; Koprowski 1994a; Eisenberg et al. 2011). The fire-maintained pine forest exists within a codominant mosaic of unlogged pond cypress (*Taxodium distichum* var. *imbricarium*; hereafter, cypress) dome swamps (Gunderson and Loope 1982; Duever et al. 1986; Ewel 1990). All survey, trapping, radiocollaring, and monitoring efforts took place within a 2,500-ha area of Raccoon Point characterized by cypress dome-pine forest habitat, dirt roads, and oil exploration pads.

For habitat analyses, the 100% minimum convex polygon (MCP—Mohr 1947) of all telemetry locations for male and female BCFS buffered by 150 m was used to delineate the 923-ha study area boundary. Vegetation classification maps created by the University of Georgia (UGA—Madden et al. 1999; Welch et al. 1999) identified 14 habitat types in the study area that were reclassified into 7 generalized habitat types based on Gunderson and Loope (1982), Duever et al. (1986), and Burch (2011), to conform with standardized BICY habitat definitions: (1) Pine forest (394.9 ha), (2) Cypress dome (294.0 ha), (3) Cypress prairie (127.0 ha), (4) Pine forest with cypress associates (69.9 ha), (5) Hardwood hammock (12.3 ha), (6) Marsh (7.3 ha), and (7) Disturbed (17.6 ha). The dirt roads and oil exploration pads that comprise the Disturbed category are typically

raised 0.5–1.5 m above water level with rocks added to the margins to minimize erosion. Due to the dominance of pine forest and cypress dome habitats and distinct habitat boundaries (e.g., semicircular-shaped cypress domes) distinguishable on aerial photos and via ground truthing, we believed that our refined classifications relative to BCFS habitat use are robust.

Big Cypress National Preserve has a tropical savannah climate characterized by spring droughts, heavy summer rains, and mild, dry winters (Hela 1952), with an annual average rainfall of 1,360 mm (Duever et al. 1986). We defined the wet season as 1 May–31 October, and the dry season as 1 November–30 April. The mean annual temperature for BICY is 23°C, with a mean low of 14°C in January and a mean high of 28°C in August (Duever et al. 1986).

Presence surveys.—Prior to each trapping effort, we conducted ground searches for BCFS presence indicators. As our trapping results confirmed, the best indicator of BCFS presence was the location of fresh cypress bark nests with adjacent fresh partially consumed BCFS food items (e.g., cypress and pine seed cones). Fresh-stripped cypress bark, which is typically a bright orange/red color when fresh, oxidizes to a dull reddish brown/grey color when exposed to the elements for > 1 month.

Capture and handling.—Box traps (61 × 18 × 18 cm) constructed of 1.3 × 2.5-cm wire mesh (Model No. 605; Tomahawk Live Trap Co., Hazelhurst, Wisconsin) were baited with a dried corncob and peanut butter. Depending on hydrologic conditions within cypress dome nest areas, baited traps (1–2) were either placed on the ground ≤ 2 m from a nest tree (dry) or on 200 × 90-cm freestanding trapping platforms attached to the base of nest trees (wet). In addition, ground-based traps were placed at 10–20-m intervals along adjacent pine forest edges containing partially consumed pine cones. Traps were wired open and prebaited for 3–7 days, then armed at dawn and checked every 2 h until closing at dusk for 2–5 days.

Captured BCFS were transferred to a cloth handling cone (Koprowski 2002) to determine sex and age class, reproductive condition, and body mass. Adult and subadult BCFS ≥ 490 g were fitted with Holohil RI-2D radiocollars (Holohil Systems Ltd., Carp, Ontario, Canada) weighing ≤ 2.4% of body mass. All methods were in accordance with American Society of Mammalogists (ASM) guidelines (Sikes et al. 2011) and a State of Florida-FWC special purpose permit.

Radiotelemetry and home range estimation.—Radiocollared BCFS were located once per day and averaged 2.2 monitoring efforts per week. Although attempts were made to evenly distribute BCFS monitoring efforts (n = 2,061) among 4 time periods, 27.4% occurred from 0700 to 1000 h, 46.2% from 1001 to 1300 h, 18.4% from 1301 to 1600 h, 6.1% from 1601 to 1900 h, and 1.8% prior to and after these periods, due to afternoon/evening thunderstorm activity during the wet season and logistical constraints.

Digital R-1000 Telemetry Receivers (Communications Specialists, Inc., Orange, California) and RA-2AK antennas (Telonics, Inc., Mesa, Arizona) were used to locate animals by homing (White and Garrott 1990). Location data were recorded using handheld Garmin GPSmap 76CS GPS units (< 10 m accuracy typical; Garmin International, Inc., Olathe, Kansas—Wing

2008). For each observation, we recorded the following data: BCFS location, date, time, habitat type, nest tree location/species/diameter at breast height (DBH), nest substrate, and foraging (i.e., direct observation or evidence of fresh BCFS food item use ≤ 10 m from a BCFS or occupied tree).

We used ArcView 3.3 (ESRI 2002) and Animal Movement Analyst Extension (AMAE—Hooge and Eichenlaub 2000) software to calculate 95% MCP (Mohr 1947) and 50% and 95% fixed-kernel density estimator (KDE—Worton 1989; Seaman and Powell 1996) home range areas. We measured and reported MCP estimates to allow comparisons with previous studies. We used the 5% harmonic mean outlier removal setting for calculating 95% MCP estimates. To minimize smoothing (Worton 1989; Seaman and Powell 1996), we used least squares cross validation to estimate 95% KDE (termed "range") and 50% KDE (termed "core") home range estimates. Individuals with ≥ 46 telemetry locations were used for 95% MCP and KDE analysis. For seasonal analyses, individuals with ≥ 20 locations/season were used. We had sufficient telemetry data to compare home range sizes for 17 individuals (10 females and 7 males) in the wet season and 11 individuals (7 females and 4 males) in the dry season. For comparisons between seasons (wet and dry), we used linear mixed models (lmm) with home range size (core or range) as the response variable, sex and season as explanatory variables, and animal ID as a random factor to account for repeated observations of the same individual in both seasons (package nlme, function lme—R Core Development Team 2013). For comparisons of male and female differences across seasons, we used linear models (lm) with home range size (core or range) as the response and sex as the explanatory variable.

Home range overlap.—We used Ranges 8 v. 2.7 (Kenward et al. 2008) to calculate home range overlaps within 3 dyads: males overlapping females, males overlapping males, and females overlapping females, and by season (wet and dry). We examined overlaps for individuals that were contemporaneously radiocollared in the study and had sufficient telemetry data within a given year (2007–2009). We also examined overlaps for all individuals that could potentially overlap across all years (2007–2011) within and across seasons to account for the fact that animals were captured and radiocollared, entered into or left the study area at different times. Thus, the absence of an animal in a given year of the study did not necessarily mean it was absent from the study area (most individuals were known to be in the study for ≈1 year). We first calculated 95% fixed-kernel home ranges for all animals across and by seasons in Ranges 8 (a prerequisite for overlap analysis), then used the 2D range overlap function to calculate the percentage of a given animal's home range that overlapped with other animals' home ranges. Therefore, we calculated all overlaps across all years and all seasons, overlaps within years (2007–2009), and within and across seasons for a given year and compared mean percent overlaps among the 3 dyads. We used Kruskal–Wallis rank sum tests (kruskal.test in R) to compare percent overlap values by season, then by overlap dyad type for individuals that actually and potentially overlapped.

Spatial distribution of used locations.—We used the Multi-Distance Spatial Cluster Analysis tool in ArcGIS to assess the degree of spatial clustering of BCFS nests and telemetry locations over a range of distances within the study area compared to a random spatial distribution. This tool is based on Ripley's *K* function and summarizes clustering over a range of distances where the observed spatial distribution of locations is compared to a random distribution within a specified distance. We specified 20 distance bands, increasing in width by 45-m increments, and 100 permutations for defining the limits of 95% confidence envelopes whereby for each permutation within each distance band, the spatial data are randomized and the *k* values that deviated the most above and below the expected *k* value are used to define the upper and lower confidence envelope. For distance bands where the observed number of neighboring features is greater than expected and falls above the upper 95% confidence envelope, the observed distribution is considered statistically more clustered than expected due to random chance.

Selection of vegetation community types.—We examined BCFS selection of vegetation community types at 3 hierarchical levels: 1st order—the selection of the physical range occupied by all animals in the study, 2nd order—the selection of individual home ranges within the study area, and 3rd order—the selection of resources within an animal's individual home range (Johnson 1980).

For this analysis, we used the classified vegetation map with 7 redefined vegetation community types described previously. To quantify 1st-order selection, we compared the percentage of all telemetry fixes and all nest site locations falling within each vegetation community type (used) to the percentage of each vegetation community type within the study area polygon (available). To quantify 2nd-order selection, we compared the percentage of each vegetation community type within individual home range kernels (used) to the percentage of each vegetation community type within the study area boundary polygon (available). To quantify 3rd-order selection, we compared the percentage of telemetry fixes for each habitat type within each individual home range (used) to the percentage of each vegetation community type within each individual home range (available). We used the Spatial Join tool in ArcGIS to quantify vegetation community type at telemetry and nest site locations and the Tabulate Intersection tool to quantify the percentage of each vegetation community type within home ranges and the study area. We investigated habitat selection in 2 ways. First, we examined use versus availability at each order of selection to determine what vegetation community types were selected. We then used ComposAnalysis 6.2plus (Smith 2005) to conduct compositional analysis comparing proportional habitat use and rank order of selection (Aebischer et al. 1993) by BCFS for each of the 7 vegetation community types at all 3 orders of selection. For 3rd-order selection, we removed the cypress prairie and marsh vegetation community types from analysis due to their scarcity within BCFS home ranges. For each level of analysis, ComposAnalysis 6.2 calculates the log-ratio transformation of the proportion of used and available habitat types and simultaneously compares the pairwise differences in used and available log ratios across all habitat types to assess random habitat use (see Aebischer et al. 1993 for further details). We specified that ComposAnalysis

6.2 run 999 permutations of the data, which allowed α = 0.05 for statistical tests. We report Wilks' lambda values calculated for the observed data along with a chi-square statistic. Wilks' lambda values are the ratio of matrix determinants derived from the observed raw and mean-corrected sums of squares of cross products of log-ratio differences.

Interaction with man-made features.—To determine whether man-made features (roads, oil pads) within the study area were avoided by BCFS, we compared home range overlap on roads and oilpads to that for randomly located lines and rectangles within the study area. To generate random linear features, we created a 25 random-points shapefile in ArcGIS then added 2 new fields to the shapefile attribute table: "bearing" (random integers between 1 and 360) and "distance" (random integers between 200 and 2,000), based on the range of road segment lengths within the BCFS study area. We used the Bearing Distance to Line tool to create lines originating from the random X and Y coordinates, whose direction and magnitude were determined by the random bearing and distance fields. To generate random rectangles, we created a 25 random-points shapefile then used the Repeating Shapes ArcGIS plug-in (Jenness 2012) to generate a regular array of 70 × 190-m (the average dimension of rectangular oilpads within the study area) rectangles within the study area boundary, specifying a 50% offset and randomized offset direction of 76.4 degrees. We selected only rectangles intersecting this new set of random points for analysis. We used the Tabulate Intersection tool in ArcGIS to extract the length of road or random line (km) and areal extent of oilpads or random rectangles (ha) overlapped by each BCFS home range.

We tested for the effects of season, sex, linear overlap type (road or random line), and rectangular overlap type (oilpad or rectangle) on the length of the linear feature or the area of the rectangle that was overlapped and the proportion of each individual's home range that overlapped a rectangular feature. We used lmm with animal ID as a random factor to account for repeated observations of the same individual in both seasons (package nlme, function lme—R Core Development Team 2013). For summary statistics, we report means (± 1 *SD*).

RESULTS

Capture and handling.—From 10 April 2007 to 26 April 2011, we captured 24 individuals (28 total captures) during 704 trap days (3.4 captures/100 trap days). Thirteen captures occurred during the wet season (1 May–31 October) and 15 occurred during the dry season (1 November–30 April). Ten males (8 adults and 2 subadults) and 10 females (9 adults and 1 subadult) were radiocollared. Body mass for adult males ($n = 10$) was 713.0±65.4 g, for adult females ($n = 10$), 733.6±50.3 g, for subadult males ($n = 2$), 492.5±3.5 g, and for subadult females ($n = 1$), 527.0 g; and 1 subadult was not handled and released (estimated < 490 g body mass). Three distinct pelage color phases were captured (Fig. 1).

Radiotelemetry and home range estimation.—From 13 May 2007 to 20 April 2011, 51.2% of our telemetry locations ($n = 2,061$) were of males, and 48.8% were of females. Mean number of telemetry locations per individual was 105.6±105.3 locations for males and 100.5±55.4 locations for females. Of the total telemetry locations, BCFS were visually observed in 41.8%, concealed in a nest in 33.8%, and 24.4% were telemetry fixes only.

Season had little effect on mean core (50% KDE) or range (95% KDE) sizes (core: $F_{1,10} = 2.13$, $P = 0.17$; range: $F_{1,10} = 2.56$,

Fig. 1.—Color phases of Big Cypress fox squirrels captured from 2007 to 2011 within the Raccoon Point area of Big Cypress National Preserve, Florida. A) Orange phase BCFS ($n = 17$); B) Black phase BCFS ($n = 6$); C) Tan phase BCFS ($n = 1$). Photos copyright Ralph Arwood. BCFS = Big Cypress fox squirrels.

$P = 0.14$). Home range size was most influenced by sex (core: $F_{1,15} = 8.46$, $P = 0.01$; range: $F_{1,15} = 12.38$, $P = 0.003$), with male home ranges larger than females in each case, especially during the wet season (Table 1). For home ranges calculated across seasons, mean male ranges were 65.2 ha larger than that of females, and mean male cores were 7.7 ha larger than for females. Across seasons, male 95% MCP areas were larger than females in each case (Table 1).

Home range overlap.—For individual BCFS confirmed to overlap in time and space (Fig. 2), the mean percentage of an individual's home range overlapped by another animal's home range did not differ between seasons (Kruskal–Wallis $\chi^2 = 1.26$, $d.f. = 1$, $P = 0.26$) or among dyads (Kruskal–Wallis $\chi^2 = 1.76$, $d.f. = 2$, $P = 0.41$). For individual BCFS that potentially overlapped spatially, the mean percentage of an individual's home range overlapped by another animal's home range did not differ between seasons (Kruskal–Wallis $\chi^2 = 0.01$, $d.f. = 1$, $P = 0.92$) but did differ among dyads (Kruskal–Wallis $\chi^2 = 10.68$, $d.f. = 2$, $P = 0.005$). Males potentially overlapped a larger percentage of female home ranges compared to other dyads (males overlapping females: 51.78% ± 26.22; males overlapping males: 23.15% ± 8.19; females overlapping females: 14.54% ± 12.42; Fig. 2).

Movements.—Maximum distance between any 2 telemetry locations for individuals was 2320.1 m for males and 991.4 m for females. Maximum distance BCFS moved ≤ 24h was 1180.1 m for males and 555.7 m for females. Mean distance BCFS moved ≤ 24h was 237.8±221.5 m for males ($n = 219$) and 138.7±128.2 m for females ($n = 209$).

Selection of vegetation community types.—Big Cypress fox squirrel telemetry locations and nest site locations were spatially clumped together. The number of neighboring telemetry fixes within each distance band was higher than

Table 1.—Big Cypress fox squirrel home range (95% MCP, 50% fixed kernel, 95% fixed kernel) in hectares by season and sex from 2007 to 2011 in the Raccoon Point area of Big Cypress National Preserve, Florida. Mean MCP and fixed kernels (core, range) are listed ± *SD*, with minimum and maximum observations in parentheses. MCP = minimum convex polygon.

Season	n	Core	Range
Male			
Wet	7	17.78 ± 18.50 (3.10–46.05)	95.03 ± 80.22 (33.63–253.45)
Dry	4	7.79 ± 7.84 (1.22–18.97)	60.51 ± 42.84 (15.23–113.46)
All	7	8.91 ± 10.48 (2.03–32.13)	75.60 ± 62.99 (25.59–204.11)
		95% MCP	
All	7	91.34 ± 51.93 (28.13–189.52)	
Female			
Wet	10	1.32 ± 0.79 (0.58–3.31)	11.16 ± 3.85 (5.14–16.73)
Dry	7	1.43 ± 1.87 (0.34–5.35)	10.79 ± 11.84 (2.18–29.61)
All	10	1.25 ± 1.13 (0.45–3.94)	10.37 ± 6.17 (3.07–21.76)
		95% MCP	
All	10	16.43 ± 5.77 (7.77–26.14)	

expected and therefore more clumped than a random distribution, with the observed number of neighboring telemetry fixes falling above the 95% confidence envelope for the expected number of neighbors at all distance bands. The number of neighboring nest site locations was higher than expected and more clumped than a random distribution within distance bands < 450 m, with the observed number of neighboring nest sites falling above the 95% confidence envelope for the expected number of neighbors. At distance bands > 450 m, the number of neighboring nest site locations was similar to a random distribution and not significantly higher than expected.

At all orders of selection, the cypress dome vegetation community type was used at proportions exceeding its availability on the landscape, whereas all other vegetation types were used at proportions lower than their availability (Fig. 3). Available vegetation types within the study area included 42.8% pine forest, 31.9% cypress domes, 13.8% cypress prairie, 7.6% pine with cypress associates, 2% disturbed, 1.3% hardwood hammock, and 0.8% marsh, yet, 79.8% of the vegetation types BCFS used were cypress domes (Fig. 3). The ranking of selection for vegetation community types is as follows (from highest to lowest): 1st-order selection = cypress dome, pine forest, hardwood hammock, disturbed, marsh, pine with cypress associates, and cypress prairie (1st-order Wilks' lambda: $\lambda = 0.02$, $\chi^2 = 81.30$, $d.f. = 6$, $P < 0.001$); 2nd-order selection = cypress dome, pine forest, disturbed, pine with cypress associates, hardwood hammock, marsh, and cypress prairie (2nd-order Wilks' lambda: $\lambda = 0.09$, $\chi^2 = 41.62$, $d.f. = 6$, $P < 0.001$); 3rd-order selection = cypress dome, hardwood hammock, pine forest, disturbed, and pine with cypress associates (3rd-order Wilks' lambda: $\lambda = 0.07$, $\chi^2 = 45.54$, $d.f. = 4$, $P < 0.001$).

Interactions with man-made features.—Home range overlap with linear features was influenced by overlap type ($F_{1,36} = 4.73$, $P = 0.04$) and sex and season ($F_{1,36} = 12.21$, $P = 0.001$). Roads were overlapped 0.2 km less than random lines ($t_{36} = -2.17$, $P = 0.04$), male home ranges overlapped 0.63 km more linear features compared to females ($t_{15} = 1.64$, $P = 0.12$), and female home ranges overlapped roads less in the wet season (0.12±0.13 km wet versus 0.16±0.24 km dry), whereas males overlapped roads more in the wet season (1.29±1.22 km wet versus 0.91±0.77 km dry; Table 2). Male and female home ranges intersected roads less than randomly generated lines ($t_{16} = -2.20$, $P = 0.04$), suggesting that BCFS exhibit some road avoidance throughout the year (Table 2; Fig. 4). Home range overlap with rectangular features was strongly influenced by overlap type ($F_{1,37} = 10.85$, $P = 0.002$), sex ($F_{1,15} = 9.35$, $P = 0.009$), but not season ($F_{1,37} = 0.80$, $P = 0.37$). Male and female home ranges overlapped on average 1.12 ha more random rectangles compared to oilpads ($t_{37} = 3.29$, $P = 0.002$), suggesting that BCFS strongly avoid oilpads throughout the year (Table 2; Fig. 4).

Nest use.—Six nest types were documented among 403 nests: (1) Stick-cypress bark ($n = 215$), (2) Cardinal airplant (*Tillandsia fasciculata*, bromeliad)-cypress bark ($n = 180$), (3) Cabbage palm (*Sabal palmetto*)-cypress bark and palm frond
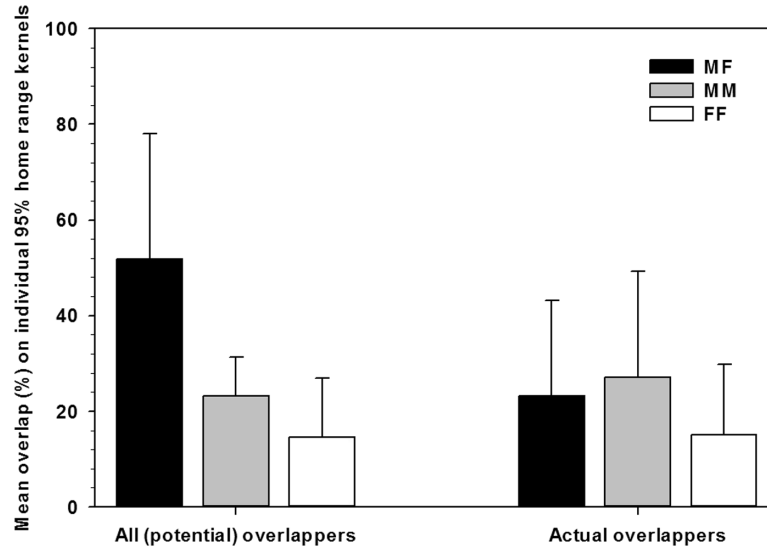
Fig. 2.—Mean (± *SD*) percent overlap of individual Big Cypress fox squirrel 95% home range kernels by dyad (MF = males overlapping females, MM = males overlapping males, FF = females overlapping females) within the Raccoon Point area of Big Cypress National Preserve, Florida. Overlaps are summarized for animals that actually overlapped in time and space from 2007 to 2011 (i.e., telemetry data were collected contemporaneously) and animals that potentially overlapped spatially (i.e., home ranges were calculated across years and seasons and overlaps calculated among all home ranges independent of year and season). Means were calculated from overlapping kernels only.
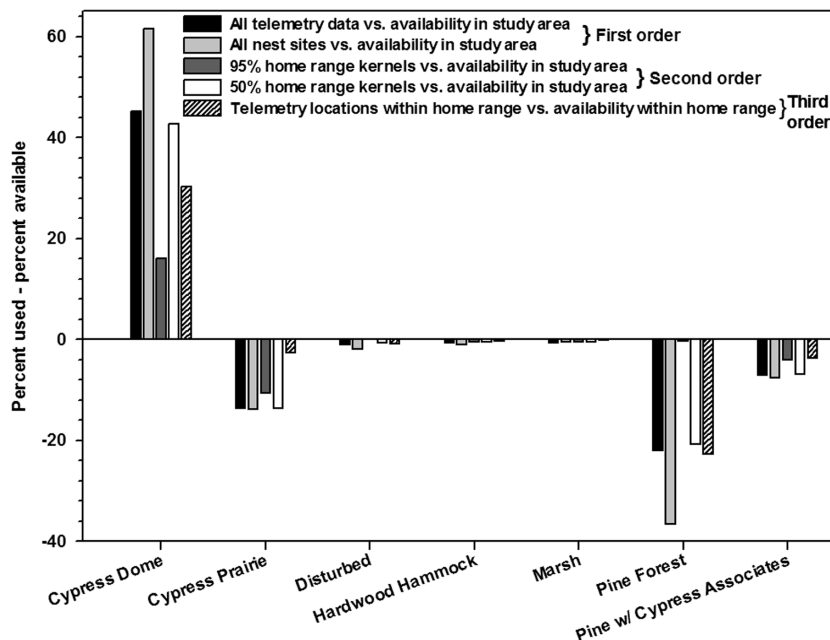

Fig. 3.—Comparison of use versus availability for 7 vegetation types used by Big Cypress fox squirrels from 2007 to 2011, in the Raccoon Point area of Big Cypress National Preserve, Florida. Bars represent the mean percentage of each vegetation community type used minus the mean percentage of vegetation community type available at 3 orders of selection.

fibers (*n* = 4), (4) Cypress tree defect (splintered trunk)-cypress bark (*n* = 2), (5) Stick-Spanish moss (*T. usneoides*, *n* = 1), and (6) Bromeliad-Spanish moss (*n* = 1). No tree cavity or leaf drey nests were found. Measured cypress bark nests that had fallen to the ground averaged 31.0 cm in diameter. Estimated stick-cypress bark (or Spanish moss) nest sizes ranged from ≈30 to 100 cm in diameter. Estimated bromeliad-cypress bark nest sizes (and all other nonstick platform nests) ranged from ≈25 to 50 cm in diameter. Nests were typically located in the upper

third of the canopy and ≥ 8 m in height. The species and mean DBH of nest trees were: (1) Cypress (*n* = 398) is 30.6 ± 10.8 cm DBH, (2) Cabbage palm (*n* = 4) is 27.5 ± 4.8 cm DBH, and (3) Pine (*n* = 1) is 23.6 cm DBH. Among the BCFS nests found, 97.5% were located in cypress domes, 1.7% were in pine forests with cypress associates, and 0.7% were in pine forests. BCFS nests were generally located in close proximity to each other: 58.1% were < 20 m apart, 27.1% were < 10 m apart, and 11.4% were < 5 m apart. BCFS exhibited diurnal behavior and

Table 2.—Summary of Big Cypress fox squirrel home range kernels (50% core, 95% range) overlapping man-made features related to oil extraction infrastructure (roads, oilpads) and randomly generated features (random lines, random rectangles) from 2007 to 2011 in the Raccoon Point area of Big Cypress National Preserve, Florida. Overlaps are broken down by season (wet, dry) and sex.

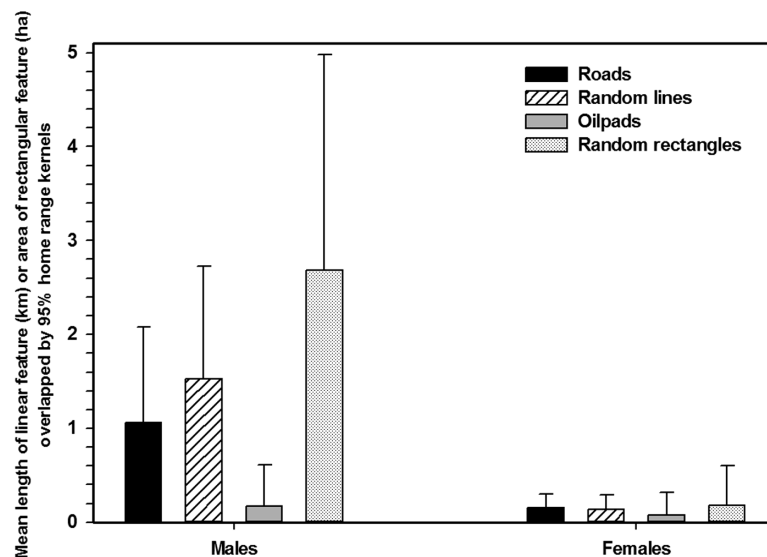|	n	Kernel probability contour (%)	Kernels intersecting road	Kernels intersecting random linear feature	Road overlappers % of total	Random line overlappers % of total	Kernels intersecting oil pad	Kernels intersecting random rectangular feature	Oil pad overlappers % of total	Random rectangle overlappers % of total
Male home ranges (all)	7	50 (core)	3	4	42.86	57.14	0	2	0.00	28.57
	7	95 (range)	7	7	100.00	100.00	1	7	14.29	100.00
Female home ranges (all)	10	50 (core)	2	2	20.00	20.00	0	1	0.00	10.00
	10	95 (range)	8	7	80.00	70.00	1	4	10.00	40.00
Male home ranges (wet)	7	50 (core)	5	3	71.43	42.86	0	3	0.00	42.86
	7	95 (range)	7	7	100.00	100.00	2	7	28.57	100.00
Female home ranges (wet)	10	50 (core)	2	2	20.00	20.00	1	1	10.00	10.00
	10	95 (range)	7	8	70.00	80.00	1	4	10.00	40.00
Male home ranges (dry)	4	50 (core)	2	3	50.00	75.00	0	1	0.00	25.00
	4	95 (range)	4	4	100.00	100.00	1	4	25.00	100.00
Female home ranges (dry)	7	50 (core)	0	0	0.00	0.00	0	1	0.00	10.00
	7	95 (range)	4	5	40.00	50.00	1	2	10.00	20.00

Fig. 4.—Mean (± *SD*) length (km) of linear features (roads, random lines) and area (ha) of rectangular features (oilpads, random rectangles) overlapped by Big Cypress fox squirrel male and female 95% home range kernels from 2007 to 2011, within the Raccoon Point area of Big Cypress National Preserve, Florida.

were typically found occupying nests within ≈1 h of sunset and beginning their daily activities ≈1–2 h after sunrise.

Use of food items.—We recorded 702 foraging observations involving 12 unique foods: (1) Cypress seed cones ($n = 460$), (2) Pine seed cones ($n = 130$), (3) Bromeliad floral buds/meristematic stem tissue ($n = 84$), (4) Pond apple (*Annona glabra*) fruit ($n = 13$), (5) Cabbage palm fruit ($n = 5$), (6) Cocoplum (*Chrysobalanus icaco*) berries ($n = 2$), (7) Eastern lubber grasshopper (*Romalea guttata*, $n = 2$), (8) Purple thistle (*Cirsium horridulum*) flowers/seeds ($n = 2$), (9) Saw palmetto (*Serenoa*

repens) berries ($n = 1$), (10) Wax myrtle (*Myrica cerifera*) berries ($n = 1$), (11) Fungi spp. ($n = 1$), and (12) Hog plum (*Ximenia americana*) fruit ($n = 1$; Fig. 5). Gender was not a significant factor in seasonal BCFS food preference and use patterns.

DISCUSSION

Cypress domes appear to be critical to the ecology of BCFS at all levels of habitat selection (Johnson 1980). Cypress domes were
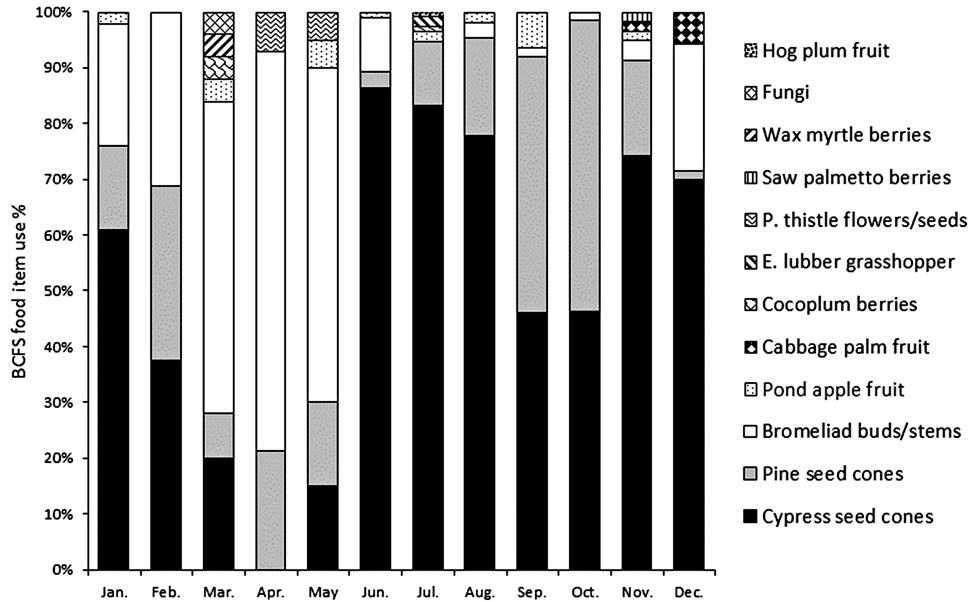
Fig. 5.—Total male (*n* = 10) and female (*n* = 10) Big Cypress fox squirrel food item use (*n* = 702) percentage per month within the Raccoon Point area of Big Cypress National Preserve, Florida, from 2007 to 2011.

the only habitat type that was used more than expected (79.8% of use although only 31.9% of the landscape). Additionally, cypress and cypress-associated bromeliads dominated nest sites, nesting materials, and food sources, consistent with previous anecdotal information on the species (Jodice 1990, 1993). Cypress domes provide a dense canopy that enables ease of travel during the wet and dry seasons (compared with more open wetlands and pine forests—Weigl et al. 1989) and may serve as windbreaks during hurricanes or other high wind events (Oberbauer et al. 1996). The dense overstory and relatively cool/deep waters of cypress dome interiors also present thermoregulatory benefits during warm summer months when females are nursing young (Ditgen 1999; Ditgen et al. 2007). Survey and monitoring efforts revealed that BCFS construct the majority of their nests in discrete cypress domes that meet pine forest edges.

Although BCFS are clearly tied to cypress domes, the intervening upland pine matrix provides year-round sources of energy-rich foods (e.g., pine seeds) and nest trees (pine and cabbage palm) and thus appears to be of substantial importance to species persistence, as it is for many fox squirrel subspecies in the southeastern United States (Weigl et al. 1989; Kantola and Humphrey 1990). Pine forests treated with prescribed fire within the study area (Snyder and Belles 2000) have the open canopies and low/sparse understories that BCFS prefer (Duever et al. 1986; Humphrey and Jodice 1992; Koprowski 1994a; Eisenberg et al. 2011). Long hydroperiods within cypress domes also create open understory and sparse groundcover conditions by hindering the growth of mesophytic species (Duever et al. 1986; Ewel 1990). Eastern gray squirrels (*Sciurus carolinensis*), a potential BCFS competitor in more upland habitats (Brown 1997), occupy forests with dense understories (Nixon et al. 1978; Brown and Batzli 1984; Koprowski 1994a, 1994b). Open fire-maintained pine forests punctuated by cypress domes

with natural long hydroperiods appear to provide the habitat conditions that BCFS favor.

Habitat used by BCFS during the daytime appears to be related to the availability of seasonal food items. Primary BCFS food sources were pine and cypress seed cones and bromeliad tissues. Pine seed cones were used year-round, with peak use from September to October. Cypress seed cones use by BCFS peaked from June to August, when the most common food, pine cones, are not yet widely available; thus they provide an important seasonal food source during a critical period of resource depletion for fox squirrels (Koprowski 1991). The dominant use of bromeliad buds and meristematic stem tissue and the increased use of berries, fruit, flowers, and fungi from March to May coincide with peak cardinal airplant flowering (Nehrling 1944; Heppner and Frank 1998) and reduced availability of pine and cypress seed cones (Bonner 1974; Gunderson 1977; Lohrey and Kossuth 1990).

Home ranges of BCFS are extremely large and exhibit considerable male-biased sexual dimorphism in size. Male BCFS home range size was 76.6% greater than the conspecific Sherman's fox squirrel (*S. n. shermani*—Kantola and Humphrey 1990) and exceeded mean male 95% MCP and 95% KDE home range sizes for all subspecies of eastern fox squirrels in natural habitats; female BCFS home range size was 37.7% smaller than that of female Sherman's fox squirrels and comparable to females of other conspecifics (Edwards 1986; Powers 1993; Koprowski 1994a; Connor 2000; Prince 2013). The size of male BCFS home ranges dwarfs those of most Holarctic tree squirrels except for those that occupy open conifer forests in the southeastern (Koprowski 1994a) and western United States (Koprowski 1998; Edelman and Koprowski 2006). The relatively large home range areas of male BCFS are likely a result of dispersal (Koprowski 1994a; Ditgen 1999) and long-distance mating-related movements between widely spaced nest areas

occupied by females at low densities (Williams and Humphrey 1979; Jodice 1990, 1993; Eisenberg et al. 2011). On average, female BCFS had 1.3-ha nonoverlapping core areas centered within the boundary of discrete cypress dome nest areas that were often separated by > 500 m of pine forest habitat. The majority of male movements ≥ 500 m occurred from May to August during the breeding period (Jodice and Humphrey 1992; Ditgen 1999; Ditgen et al. 2007). Additionally, males shared similar food preferences and use patterns with females, and their ranges overlapped those females more than those of other males. Despite a lack of sexual dimorphism in body size, male tree squirrels of most species, including BCFS (Ditgen 1999), have larger home range sizes than females and move greater distances (Weigl et al. 1989; Kantola and Humphrey 1990; Koprowski 1998, 2007). The availability of food resources is expected to strongly influence space use by females (Ostfeld 1985), whereas the availability of females is the primary determinant of space use by males (Ims 1987; Clutton-Brock 1989; Koprowski 1998, 2007).

The large home ranges traversed by BCFS result in increased road crossings and interactions with oilpads, especially among males. Roads can decrease connectivity for some species but also may serve as travel routes for others (Adams and Geis 1983; Hellgren et al. 1991; Fahrig and Rytwinski 2009). Although BCFS incorporate roads into their home ranges, we show a tendency for avoidance of this habitat element, especially in males whose home ranges overlapped a smaller linear extent of roads compared to randomly generated lines within and across seasons. Similarly, the less frequent use of oilpads compared to randomly generated sites of similar size and shape by both sexes across seasons suggests the potential for strong avoidance. Oilpads are generally devoid of significant vegetation and lack canopy cover (Baynard et al. 2014; Garman and McBeth 2014), and oil/gas operations can create chronic loud noise conditions (Barber et al. 2010); however, the reason for the apparent avoidance remains unclear.

The BCFS is an FWC-Florida State–listed Threatened species and meets the International Union for Conservation of Nature (IUCN) Red List criteria for a Threatened species (FWC 2011). Although our study has provided new information on BCFS ecology within cypress dome swamp-pine forest mosaic habitats, the ecology and status of the BCFS in other natural habitats (e.g., mangrove swamps and coastal broadleaf evergreen hammocks—Howell 1919; Moore 1956; Williams and Humphrey 1979) are unknown. The rapid decline of forested wetlands (Dahl 2000, 2011) and the threats of changing hydrology due to development and increased salinization with rising sea levels (Ross et al. 1994; Williams et al. 1999) highlight the importance of filling such knowledge gaps. Projected human population growth in southwestern Florida (Zwick and Carr 2006) indicates that habitat degradation, fragmentation, and loss will remain the greatest threats to the BCFS (Williams and Humphrey 1979; Humphrey and Jodice 1992; Eisenberg et al. 2011). The long-term survival of the BCFS will depend upon habitat management practices on both private and public lands, where the use of prescribed fire, the control of invasive nonnative plants/animals, and the maintenance of natural hydrologic conditions will be necessary to retain the habitat characteristics favored by BCFS.

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