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Nest tree and site selection of an introduced population of red-bellied squirrels (*Sciurus aureogaster*)

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Nests play a crucial role in the life history of tree squirrels, and can be a critical component of their biology that enables them to be a successful invasive species. Red-bellied squirrels (*Sciurus aureogaster*) were introduced to Elliott Key, Florida, in the late 1930s, and spread to nearby islands. Red-bellied squirrels were believed extirpated by Hurricane Andrew in 1992, but were rediscovered on Elliott Key in 2005. In 2006 and 2007, we surveyed for squirrel nests and measured vegetation to evaluate forest characteristics associated with nest-site selection by squirrels, and compared these data to measurements collected at random locations. Squirrels placed nests in large trees with more canopy linkages in mixed-hardwood forest, and the nest trees were in areas with large trees, high tree density and canopy cover, and lower recent hurricane damage. Red-bellied squirrels selected characteristics of nest trees and forest structure in similar ways to individuals in their native range, and to other species of tree squirrels in general. Results from our research allowed land managers to assess possible management actions and provided important information for them to develop an effective management strategy. Park officials are currently working toward complete eradication of the introduced population of red-bellied squirrels from the Florida Keys. We suggest that behaviors of individuals in native ranges may elucidate patterns for individuals introduced to novel environments; however, we also caution that care must be taken in further extrapolation. Our findings emphasize the importance of understanding ecology of introduced species for effective management.

Key words: Biscayne National Park, Elliott Key, Florida, habitat selection, invasive species, Mexican gray squirrel, nesting behavior, species eradication, *Swietenia mahagoni*, tree squirrel

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Nests serve numerous functions: protection from weather and predators, a place to rest, access to food, and sites for reproduction (Goodall 1962; Holway 1991; Fruth and Hohmann 1993; Steele and Koprowski 2001; Benson et al. 2008). Regardless of function, nests require suitable materials for construction and an appropriate site for placement. Individuals use cues to select a site for nest construction (Hamerstrom et al. 1973; Snyder and Linhart 1994; Edelman and Koprowski 2005). Understanding the environmental cues associated with nest-site selection is critical for management and conservation of native species and also for the detection of invasive species that use nests.

Tree squirrels are small mammals that play an important ecological role in many different ecosystems (Gurnell 1987; Steele and Koprowski 2001; Thorington et al. 2012), and use leaf and stick (dreys), cavity, and ground nests (Gurnell 1987). We focus on dreys, which tree squirrels use for all of the aforementioned functions. Different species of squirrels may use similar forest structure cues to determine suitable nesting locations within habitat. Tree squirrels tend to build nests in larger trees located in areas with dense stands of trees and a high percentage of canopy cover in comparison with areas randomly selected in the forest (Halloran and Bekoff 1994; Merrick et al. 2007; Cudworth and Koprowski 2011). Such forest structure may serve to increase the functionality of nests, including provision of escape routes from predators, access to forage, thermal retention, and reduced exposure to weather extremes (Farentinos 1972; Edelman and Koprowski 2005).

The red-bellied squirrel (*Sciurus aureogaster*), also referred to as the Mexican gray squirrel, is a tree squirrel that occurs in a variety of forest types in Mexico and Guatemala (Musser 1968), and selects areas to build nests in ways similar to other tree squirrels. In an oak–pine forest in Michoacán, Mexico, red-bellied squirrels build leaf nests close to the trunks of the largest and tallest trees (Ramos-Lara and Cervantes 2007). Additionally, squirrels select 3 species of oaks (*Quercus* spp.) disproportionate to their abundance as sites for nest construction (Ramos-Lara and Cervantes 2007).

Red-bellied squirrels were introduced to Elliott Key, Florida, in 1938 by an island resident who brought 4 squirrels from eastern Mexico and released them onto the island (Brown and McGuire 1969, 1975). This introduction provided an opportunity to assess important cues used for nest tree and site selection in a novel environment. The island lacked native tree squirrels and the introduced squirrels spread across the island and occupied the length of the island by the 1950s (Schwartz 1952). Individuals dispersed naturally from the island possibly by swimming (an individual was captured swimming south from Elliott Key by a Park Service employee in the 1970s) or by floating on marine debris and established populations on Sands Key and Adams Key were recorded by the 1970s (Layne 1997). A 40-year-old study on Elliott Key suggested that squirrels might favor West Indies mahogany (*Swietenia mahagoni*) and avoid Florida poisonwood trees (*Metopium toxiferum*), the most common tree in their study area; however, statistical analyses were not conducted and this was the only information related to nest-site selection reported (Brown and McGuire 1975).

Since Brown and McGuire (1975), 2 large-scale forest disturbances have occurred: hurricanes, including Hurricane Andrew in 1992, a powerful storm that passed directly over the island (Ogden 1992), and more recent hurricanes in 2005, have impacted vegetation on the island; and an introduced plant removal program was implemented in the mid-1980s, which focused on a number of introduced plant species that squirrels historically exploited for food and nesting resources. Despite these events, squirrels continue to occupy Elliott Key (Koprowski et al. 2005), and have colonized other nearby islands (Palmer et al., in press). We sought to document forest and tree characteristics used by squirrels on Elliott Key to understand patterns of habitat use and nest-site selection, and to determine whether selection criteria differ from those of red-bellied squirrels in native habitat and other tree squirrel species. Mahogany trees are a native species, so have not been subject to eradication by the introduced plant removal program. They are both common and resilient in areas prone to disturbance such as the Florida Keys (Francis 2000; Duryea et al. 2007), so we expect mahogany to have roughly the same abundance as previously observed. Therefore, we predict squirrels will continue to use mahogany most often as nest sites. Tree squirrels generally appear to build nests in larger trees located in areas with dense stands of trees and a high percentage of canopy cover in comparison to randomly selected areas in the same forest (Edelman and Koprowski 2005; Merrick et al. 2007; Ramos-Lara and Cervantes 2007; Cudworth and Koprowski 2011). We chose to measure many of the same parameters that are most often measured in habitat-use studies on other tree squirrels (Smith and Mannan 1994; Ramos-Lara and Cervantes 2007; Cudworth and Koprowski 2011) to allow us to compare this introduced population of red-bellied squirrels to other tree squirrels. We predict that red-bellied squirrels in this novel environment will follow patterns seen in other tree squirrels.

MATERIALS AND METHODS

Study area.—We conducted our study on Elliott Key, Miami-Dade County, Florida, an island 24 km south of Miami, Florida (25°26′35.16″N, 80°11′49.92″W) that is 11 km long and 0.6 km wide (670 ha). We delineated 5 distinct vegetation communities: mixed-hardwood forest, mangrove forest, buttonwood scrub, scrubland, and an area maintained as open parkland for visitor use. The mixed-hardwood forest dominated the interior of the island; pigeon plum (*Coccoloba diversifolia*), Florida poisonwood (*Metopium toxiferum*), leadwood (*Krugiodendron ferreum*), gumbo limbo (*Bursera simaruba*), blolly (*Guapira discolor*), false tamarind (*Lysiloma latisiliquum*), and West Indies mahogany (*S. mahagoni*) were the most common trees. Nonnative Brazilian pepper (*Schinus terebinthifolius*), sapodilla (*Manilkara zapota*), coconut palm (*Coco nucifera*), and Australian pine (*Casuarina equisetifolia*), historically found in the mixed-hardwood forest and all important food sources for red-bellied squirrels (Brown and McGuire 1973, 1975), were eradicated in the past 20 years by the National Park Service (United States National Park Service 2010). Mangrove (black mangrove [*Avicennia germinans*] and white mangrove [*Laguncularia racemosa*]) forest dominated the margins of the island. The buttonwood scrub was dominated by buttonwood (*Conocarpus erectus*) and was a transitional forest between the mangrove and mixed-hardwood forest. Scrubland was dominated by low-growing tangles of vines and shrubs including nickerbean (*Caesalpinia bonduc* and *C. major*) and cat's claw vine (*Macfadyena unguis-cati*) with a few thatch palms (*Thrinax* spp.). The National Park Service maintained visitor facilities at Elliott Key harbor, including a dock, campground, and visitor center; the area had manicured turf with very little native vegetation present.

Northern raccoons (*Procyon lotor*) and marsh rabbits (*Sylvilagus palustris*) were the only native mammals encountered on the island, and we recorded no sign of bobcats (*Lynx rufus*) or white-tailed deer (*Odocoileus virginianus*), which were both previously documented on the island (see Brown and McGuire 1975). Nonnative populations of house mice (*Mus musculus*) and black rats (*Rattus rattus*) occupy areas in and around human-made structures on the island, and rats were encountered occasionally in the forest. Virginia opossum (*Didelphis virginiana*) is not known from Elliott Key; however, the carcass of 1 individual was found in the mangrove forest on the west side of the island and may have drifted from the mainland.

Initial leaf nest survey.—Tree squirrels use cavities in tree trunks, dreys located in branches or forks, or ground nests (Gurnell 1987). Red-bellied squirrels constructed dreys on Elliott Key, but no cavity or ground nests were documented. In January 2006, we surveyed the entire island for dreys constructed by red-bellied squirrels by walking parallel transects spaced 60 m apart and perpendicular to a trail that runs the length of Elliott Key from north to south. Prior to surveys, we determined that visibility permitted a surveyor to see leaf nests from $\leq$ 30 m, thus we were confident that nearly 100% of the nests were detected between transects spaced 60 m apart. We resurveyed 10% of transects, and no new nests were detected by a 2nd independent observer. Nest trees were marked with forestry flagging and nest locations were recorded with a handheld global positioning system.

Nest characteristics.—We measured the height and aspect of the drey within the nest tree. The nest aspect was the direction of the nest recorded in degrees from the trunk of the tree to the nest. We categorized the nest structural support as main trunk, side branches, or crown (leaves and branches associated with the canopy of the tree). We determined nest occupancy as occupied, possibly occupied, or not occupied based on the structural integrity and condition of the nesting materials.

Nest tree characteristics.—We recorded the species, total height, lowest major branch height, length of canopy, diameter at breast height (DBH), and condition (live or dead) of the nest tree. The distance, species, and DBH of the closest tree to the nest tree also were recorded. We counted the number of canopy linkages as the number of surrounding trees whose branches were within 0.5 m of the focal tree. Fifty random locations were generated in ArcView 3.3 (Environmental Systems Research Institute 2002), the tree closest to the random point was selected as the random focal tree when each location was visited, and the same data were collected for random trees for comparison to nest trees to determine what characteristics of the focal tree were most important to squirrels when selecting a tree in which to build a nest.

Nest-site characteristics.—We collected data on vegetation characteristics within 10-m circular plots (0.03 ha) centered on the nest tree, and refer to plots as "sites" throughout the remainder of the paper (Smith and Mannan 1994; Edelman and Koprowski 2005). The same data were collected at random sites centered on the 50 random trees for comparison to nest sites to determine variables important in differentiating nest sites from random sites.

Species, DBH, condition (live or dead), and proximity to focal tree ($\leq$ 5 m or $>$ 5 m) were recorded for all trees (DBH $\geq$ 7 cm, the smallest tree with a nest) within each site. Densiometer readings were taken at 0 m, 5 m, and 10 m in all 4 cardinal directions around the focal tree. Shannon–Weiner diversity index, total basal area (m^2/ha), number of live and dead trees per hectare, and canopy cover at 0 m, 5 m, 10 m, and total for the site were calculated from data collected within each site.

We classified the amount of recent hurricane damage sustained by vegetation in each site and ranked the damage on a scale from 0 to 4: 0) no damage; 1) leaves removed from canopy, all branches remain intact; 2) branches and twigs broken, tree trunk tops broken; 3) major branches broken off of trees, some trees downed or trunks broken; and 4) total destruction, majority of trees uprooted or trunks broken.

We employed 2 methods to quantify the amount of low-growing woody vegetation (DBH $\leq$ 7 cm) within each site. A modified Robel pole method was used with a 2-m Robel pole marked at 20-dm increments and held upright against the focal tree, and the number of sections covered by vegetation from 10 m away in a random direction was recorded (Robel et al. 1970). A visual obstruction measurement (%) was calculated from the number of sections of the pole covered by vegetation. We recorded the number of woody stems (DBH $<$ 7 cm) in a 2 × 10-m plot randomly placed within each site, and calculated stem density (stems/ha).

Our research protocol was approved by The University of Arizona Institutional Animal Care and Use Committee (IACUC protocol 7022) and in accordance with guidelines of the American Society of Mammalogists (Sikes et al. 2011).

Data analysis.—We analyzed nest aspect as circular data with a Rayleigh's uniformity test in Oriana version 4.01 (Kovach 2011) to determine if nests were uniformly distributed around the tree trunk. We analyzed all other characteristics with JMP 10 (SAS Institute Inc. 2012). We examined the distribution of all variables prior to analyses and transformed any variable that lacked a normal distribution to meet assumptions of normality for statistical analyses (Ramsey and Schafer 2002). Count variables (number of canopy linkages, number of shrub stems, number of live trees, number of dead trees, and number of trees within 5 m of focal tree) were all cube-root transformed, variables expressed as proportions (canopy cover, visual obstruction, and proportion canopy) were arcsine transformed, and the natural logarithm of DBH (cm) of focal tree and basal area (m^2/ha) of sites were calculated prior to analyses. We report transformed parameter estimates (± *SE*) from statistical analyses, but report untransformed means (± *SE*).

We used a Pearson's chi-square goodness-of-fit test to determine if squirrels used any tree species as a nest tree disproportionate to tree species availability in the forest. We used information collected on frequency of each tree species at random sites to calculate tree species availability. We used a 1-way analysis of variance (ANOVA) to determine if tree height varied among the most common tree species (mahogany, pigeon plum, and poisonwood). Characteristics of nest trees and random trees were compared individually with 2-tailed *t*-tests (with a Bonferroni-corrected α-value $\leq$ 0.006). Characteristics of forest structure at nest sites and random sites also were compared individually with 2-tailed *t*-tests (with a Bonferroni-corrected α-value $\leq$ 0.004).

We chose a model selection approach based on information-theoretic methods (Burnham and Anderson 2002) to assess characteristics of focal trees and sites that are most important to red-bellied squirrels because nest tree and nest-site selection for red-bellied squirrels has been explored in Mexico (Ramos-Lara

Table 1.—Percentage of tree species used as nest trees (observed) by red-bellied squirrels (*Sciurus aureogaster*) and available (expected) in random habitat plots on Elliott Key, Florida, 2006–2007.

Scientific name	Common name	Observed (%)	Expected (%)
Amyris elemifera	Torchwood	0	0.4
Bourreria ovata	Bahama strongbark	3	1.5
Bursera simaruba	Gumbo limbo	0.6	6.7
Coccoloba diversifolia	Pigeon plum	2.4	24.4
Coccoloba uvifera	Sea grape	0	0.3
Colubrina elliptica	Soldierwood	0	0.1
Conocarpus erectus	Buttonwood	4.9	3.5
Drypetes diversifolia	Milkbark	1.2	3.5
Exothea paniculata	Inkwood	0	0.2
Ficus aurea	Strangler fig	0	3.5
Guapira discolor	Blolly	3.7	6.3
Krugiodendron ferreum	Leadwood	3.7	6.8
Leucaena leucocephala	Leadtree	0	0.4
Lysiloma latisiliquum	False tamarind	9.8	4.9
Metopium toxiferum	Florida poisonwood	6.7	24.5
Piscidia piscipula	Jamaican dogwood	0	0.4
Pithecellobium unguis-cati	Catclaw	0	0.1
Sapindus saponaria	Soapberry	0	0.1
Sideroxylon foetidissimum	Mastic	1.2	2.6
Simarouba glauca	Paradise tree	0	0.3
Swietenia mahagoni	West Indies mahogany	61.6	9
Thrinax radiata	Florida thatch palm	0	0.2
Ximenia americana	Hog plum	0	0.3
Zanthoxylum fagara	Wild lime	1.2	0

and Cervantes 2007), to a very limited extent on Elliott Key (Brown and McGuire 1975), and more extensively in other species of tree squirrels (Halloran and Bekoff 1994; Edelman and Koprowski 2005; Merrick et al. 2007; Cudworth and Koprowski 2011). We built a set of 9 logistic regression models as candidate models to determine characteristics of focal trees most important to squirrels, and another set of 9 logistic regression models as candidate models to determine characteristics of sites most important to squirrels. We used Akaike's information criterion (AIC) to rank models and evaluate support for competing models. Variables were only included in the models if correlation among variables was low ($r < 0.70$) to reduce any influence of multicollinearity; in instances of high correlation coefficients, variables that accounted for the most variation (higher F-value in logistic regression) were chosen for inclusion. Number of live trees per hectare was highly correlated ($r = 0.967$) with basal area (m^2/ha) and was not included in the models. Canopy cover measurements taken at 0, 5, and 10 m were highly correlated ($r = 0.705$, $r = 0.796$, and $r = 0.725$, respectively) with total canopy cover and also were not included in the models.

RESULTS

Initial leaf nest survey.—We documented 115 nests on Elliott Key during the initial survey and an additional 87 newly constructed nests that squirrels constructed during the course of our study, for a total of 202 nests. From the 202 nests recorded, we randomly selected 164 nest trees to measure, and of these, we measured vegetation characteristics within circular plots at 118 randomly selected nest trees. Measures also were collected for 50 random locations for comparison.

Nests were found only within the mixed-hardwood forest. We observed no squirrel sign in the scrubland and areas maintained for visitors, indicating these areas did not constitute squirrel habitat and that this is possibly due to the paucity of trees in these 2 types of areas. We never documented nests in the mangrove or buttonwood forest types during surveys; however, squirrels foraged and collected nesting materials in these areas (Palmer et al. 2007).

Nest characteristics.—Squirrels built nests at a mean height of 7.6 m ± 0.24 SE ($n = 164$). Nests were not uniformly distributed around the tree trunk ($Z = 16.18$, $n = 169$, $P < 0.0001$), with a mean nest aspect of 6.56° ± 9.82°. Nests were not randomly placed on supporting structures of the nest tree ($\chi^2_1 = 24.20$, $n = 161$, $P < 0.0001$), with most nests observed in the tree crown (52%), with the remaining nests supported by major side branches (25%) or the main trunk (23%). Most nests were in good condition and were likely occupied when 1st documented (58%, $n = 96$), whereas the remaining nests were either in mild disrepair and possibly occupied (25%, $n = 41$) or in disrepair and likely not occupied (17%, $n = 29$).

Nest tree characteristics.—Nests were located only in live trees (100%, $n = 164$). Four tree species were used more often than expected as nest locations ($\chi^2_3 = 662.70$, $n = 164$, $P < 0.0001$; Table 1). West Indies mahogany was selected nearly 7 times more often than expected, and accounted for more than 60% of the nest trees; false tamarind was used 2 times more than expected, and accounted for almost 10% of the nest trees. Florida poisonwood and pigeon plum were selected about 25% and 10% as often as expected, respectively (Table 1). Mean height did not differ between mahogany (9.17 ± 0.4 m), pigeon plum (7.94 ± 0.6 m), or poisonwood (8.90 ± 0.5 m; ANOVA: $F_{2,37} = 1.43$, $P = 0.25$). Nest trees were taller with an overall greater length of canopy and more canopy linkages to other nearby trees than random trees when analyzed with univariate methods (Table 2).

Tree height, DBH of focal tree, live canopy length, and number of canopy linkages were characteristics of focal trees included in the top-performing candidate model, as well as an interaction term between the DBH and the height of the focal tree (Table 3). Nest trees averaged 1 m taller ($\beta = 0.31 \pm 0.12$, $\chi^2 = 6.58$, $P = 0.01$) and averaged 1.5 times more canopy linkages ($\beta = 0.53 \pm 0.13$, $\chi^2 = 15.82$, $P < 0.0001$) than random focal trees (Table 2). Although DBH of focal tree and live crown length did not have strong explanatory value within the model, the interaction between DBH of focal tree and tree height was significant ($\beta = -0.02 \pm 0.01$, $\chi^2 = 5.23$, $P = 0.02$; Table 2).

Nest-site characteristics.—Univariate analyses revealed that nest sites had higher canopy cover at all 3 distances (0, 5, and 10 m) and total canopy cover compared to random sites (Table 2). Hurricane damage was lower at nest sites compared to random sites (Table 2). Nest sites had more live trees compared to random sites ($P = 0.004$; Table 2). Nest sites had higher

Table 2.—Univariate (t-statistics with degrees of freedom and P-values) comparisons of focal tree and site characteristics ($\bar{X} \pm SE$) at nest and random locations for red-bellied squirrels (*Sciurus aureogaster*) on Elliott Key, Florida, 2006–2007. Significance ($P < 0.006$ for focal tree characteristics or $P < 0.004$ for site characteristics) is indicated by an asterisk (*). DBH = diameter at breast height (cm).

	Nest (n = 164)	Random (n = 50)	t_{212}	P-value
Focal tree characteristic				
DBH (cm)	21.1 ± 0.8	17.9 ± 1.0	1.52	0.129
Tree height (m)	9.99 ± 0.2	8.95 ± 0.2	3.31	0.001*
Height to 1st major branch (m)	3.71 ± 0.1	3.55 ± 0.2	0.74	0.459
Live crown length (m)	5.59 ± 0.09	4.97 ± 0.1	3.05	0.003*
Proportion live crown	0.57 ± 0.01	0.56 ± 0.02	0.53	0.595
No. canopy linkages	3.6 ± 0.1	2.4 ± 0.2	4.87	< 0.001*
Distance to near tree (m)	1.4 ± 0.07	1.3 ± 0.1	0.23	0.818
DBH of near tree (cm)	13.2 ± 0.5	14.2 ± 1.6	0.10	0.924
	Nest (n = 118)	Random (n = 50)	t_{166}	P-value
Site characteristics				
Canopy cover 0 m (%)	93.2 ± 0.5	88.5 ± 1.2	4.36	< 0.001*
Canopy cover 5 m (%)	91.2 ± 0.6	85.4 ± 1.6	4.01	< 0.001*
Canopy cover 10 m (%)	90.5 ± 0.6	85.5 ± 1.5	3.51	0.001*
Canopy cover total (%)	91.6 ± 0.4	86.4 ± 1.1	5.00	< 0.001*
Visual obstruction (%)	78.1 ± 1.9	82.2 ± 2.2	−0.88	0.379
Shrub stems (no./ha)	19,364.4 ± 608.6	20,340.0 ± 1,315.3	−0.18	0.859
Live trees (no./ha)	1,450.3 ± 36.6	1,240.0 ± 78.2	3.63	0.001*
Dead trees (no./ha)	116.1 ± 8.4	119.3 ± 13.9	−0.12	0.905
Hurricane class (range 0–4)	2.2 ± 0.04	2.6 ± 0.07	−4.29	< 0.001*
Basal area (m^2/ha)	1,038.3 ± 46.4	840.0 ± 85.4	3.54	0.001*
Shannon–Wiener diversity	1.6 ± 0.03	1.8 ± 0.04	−1.58	0.116
No. trees within 5 m of focal tree	12.4 ± 0.4	9.4 ± 0.6	4.56	< 0.001*

basal area and number of trees within 5 m of the focal tree than random sites (Table 2).

Total canopy cover, hurricane class, and number of trees within 5 m of the focal tree were characteristics of sites included in the 2 top-performing candidate models (Table 3). When we consider the simplest top model, nest sites had 5% more closure of canopy on average ($\beta = 5.18 \pm 1.61$, $\chi^2 = 10.28$, $P = 0.0013$), 3 more trees on average within 5 m of the focal tree ($\beta = 1.3 \pm 0.44$, $\chi^2 = 8.90$, $P = 0.0028$), and slightly lower hurricane damage from recent storm activity ($\beta = -1.17 \pm 0.38$, $\chi^2 = 9.23$, $P = 0.0024$; Table 2) than random sites.

Discussion

Red-bellied squirrels continue to select West Indies mahogany trees to build nests more often than expected (61.6% in this study versus 63.9%—Brown and McGuire 1975). Why squirrels select mahogany so often remains unknown; however, mahogany consistently has one of the highest survival rates during hurricanes of any tree species in the region (Francis 2000; Duryea et al. 2007), and the antimicrobial properties of the sap make it resistant to decay (Majid et al. 2004). Florida poisonwood appears to be avoided as a nest tree (Brown and McGuire 1975), and tree chemistry may influence this behavior. Poisonwood contains urushiol in the sap, the same toxic-irritant oil that is found in poison ivy, and the sap is exuded from numerous places on the bark of the tree (Gross and Baer 1975; Lampe 1986). Urushiol may act as an irritant for squirrels and may discourage nest building in this tree species, or the tree simply may not possess the physical characteristics necessary to function as a nest tree. Chemical composition of some tree species affected other *Sciurus* species when selecting nest trees (Snyder and Linhart 1994). The reason for underuse of pigeon plum and overuse of false tamarind remains unknown, but protection from hurricanes seems to be an important factor influencing nest-site selection by squirrels. Perhaps the characteristics (defoliation, wood characteristics, crown characteristics, and root systems) that influence survivorship during storms could explain the difference in use of these 2 species as nest trees by squirrels (Duryea et al. 2007). Despite impacts to vegetation sustained from Hurricane Andrew, other recent storm systems, and the introduced plant removal program, red-bellied squirrels appear to use trees species as nest trees in similar proportions as previously documented (Brown and McGuire 1975).

Red-bellied squirrels on Elliott Key appear to have similar criteria for selecting nest locations to individuals in native range. Nest trees are larger and taller than random trees, a pattern similar to nest trees selected by red-bellied squirrels in their native range (Ramos-Laura and Cervantes 2007). In Michoacán, Mexico, red-bellied squirrels selected areas with a high density of trees surrounding the nest tree (Ramos-Laura and Cervantes 2007), and our comparison of number of trees within 5 m of the focal tree confirms that squirrels on Elliott Key also appear to select areas with higher tree density immediately surrounding the nest tree than randomly available in the forest. Nest trees also had more canopy linkages than random trees on Elliott Key, which also suggests individuals

Table 3.—Model selection statistics and performance measure for models using logistic regression to explain differences between focal tree and site characteristics at nest and random locations for red-bellied squirrels (*Sciurus aureogaster*) on Elliott Key, Florida, 2006–2007. K = number of parameters, AIC = Akaike's information criterion values, ΔAIC = AIC relative to the most-parsimonious model, w_i = AIC model weight.

Model	K	AIC	ΔAIC	w_i	R^2
Focal tree models[a]					
DBH, height, DBH × height, crown, linkages	5	199.34	0.00	0.716	0.19
height, crown, linkages	3	201.72	2.38	0.218	0.17
height, height × linkages, linkages	3	204.63	5.29	0.051	0.16
crown, linkages	2	207.00	7.66	0.016	0.14
linkages	1	214.79	15.45	0.000	0.09
height, crown, p. crown, height × crown, crown × p. crown	5	223.57	24.23	0.000	0.09
height, crown, height × crown	3	224.85	25.51	0.000	0.07
height	1	225.13	25.79	0.000	0.05
DBH, height, DBH × height, 1st branch, height × 1st branch	5	225.97	26.63	0.000	0.08
null	0	234.70	35.36	0.000	0.00
Site models[b]					
cover, hurricane, no. in 5 m, cover × hurricane, cover × no. in 5 m	5	168.81	0.00	0.417	0.24
cover, hurricane, no. in 5 m	3	168.98	0.18	0.381	0.21
cover, hurricane, basal area, no. in 5 m	4	170.48	1.67	0.189	0.22
cover, hurricane, cover × hurricane	3	174.98	6.18	0.019	0.19
basal area, hurricane, no. in 5 m, basal area × no. in 5 m	4	180.72	11.47	0.001	0.17
cover	1	185.25	16.45	0.000	0.11
basal area, no. shrubs, diversity, hurricane	4	187.6	18.79	0.000	0.13
no. dead trees, hurricane, no. dead trees × hurricane	3	195.75	26.94	0.000	0.08
no. shrubs, VO, no. live trees, no. shrubs × VO	4	201.61	33.26	0.000	0.06
null	0	206.59	37.26	0.000	0.00

[a] DBH = diameter at breast height of focal tree (cm), height = height of focal tree (m), crown = length of live crown (m), linkages = number of canopy linkages, p. crown = proportion live crown, 1st branch = height to 1st major branch on focal tree (m).

[b] cover = canopy cover total (%), hurricane = hurricane class (range 0–4), no. in 5 m = number of trees within 5 m of focal tree, basal area = basal area (m^2/ha), no. shrubs = number of shrub stems per hectare, diversity = Shannon–Weiner diversity, no. dead trees = number of dead trees per hectare, VO = visual obstruction (%), no. live trees = number of live trees per hectare.

select areas with high tree density. Squirrels are using similar cues to those used by individuals in native range when selecting for nest sites.

Furthermore, introduced red-bellied squirrels also select similar forest and nest tree structure as other tree squirrels (Edelman and Koprowski 2005; Merrick et al. 2007; Cudworth and Koprowski 2011). Red-bellied squirrels build nests in the upper 25% of the nest tree, similar to Abert's squirrels (*Sciurus aberti*—Edelman and Koprowski 2005) and Arizona gray squirrels (*S. arizonensis*—Cudworth and Koprowski 2011). These characteristics may provide a strong, stable support for a nest, adequate protection from predators and weather, and direct access to a maximal amount of food resources.

One difference exhibited by red-bellied squirrels on Elliott Key compared to other tree squirrels was the aspect of the nest. Tree squirrels in the Northern Hemisphere often build their nests on the south and east sides of trees, presumably to take advantage of solar energy to warm and dry the nest (Farentinos 1972; Edelman and Koprowski 2005). Nests were predominately built on the north side of trees on Elliott Key, and although some of the nests were measured immediately following the 2005 hurricane season, new nests were built by squirrels constantly. We feel confident this pattern is expressed by squirrels, and not a result from hurricanes destroying nests with other aspects. Squirrels possibly build nests on the north side of the tree to avoid daily wind desiccation and damage from frequent strong storms. Prevailing winds are from the southeast in summer; however, winds can vary in direction depending on time of year (Lee and Williams 1999). Strong tropical weather systems typically move in from the east and south (Blake et al. 2011).

Other studies have reported slope, slope aspect, and number of logs as characteristics important to squirrels (Edelman and Koprowski 2005; Merrick et al. 2007; Ramos-Lara and Cervantes 2007; Cudworth and Koprowski 2011); however, we did not measure these characteristics because Elliott Key is a flat coral key with maximum elevation of 1.5 m, and virtually no logs were present in the forest due to high rates of decay in the tropical climate.

Red-bellied squirrels have spread beyond the confines of Elliott Key (Layne 1997; Palmer et al., in press), and have the potential to negatively impact native species (Palmer et al. 2007, in press). With this information, management strategies to minimize impacts of red-bellied squirrels on native species and eliminate the threat of red-bellied squirrels spreading farther have been considered (Pernas and Clark 2011). A plan to remove *S. aureogaster* from Elliott Key and other surrounding islands has been implemented based on our research, with eradication efforts focused on nest sites (Pernas and Clark 2011). Nests are a reliable sign of squirrel presence, serve as nocturnal refuges for squirrels, and our research indicates that squirrels select particular forest and nest tree characteristics to place nests which narrows the scope of the removal project to certain areas of the islands. The management team has focused efforts to locate nests during daylight hours in mixed-hardwood forest and remove nests and subsequently remove squirrels at night (Pernas and Clark 2011). Forty-nine squirrels have been removed to date, and the project goal is full eradication by 2013.

The ability to construct nests is a key biological characteristic that enables tree squirrels to be successful in introduced populations (Palmer et al. 2007; Wood et al. 2007); understanding nest-building behavior is critical for management of these populations. We demonstrate a similar pattern of selection by squirrels within native and novel habitats; however, we caution that the range of conditions that can be exploited by a species must still be examined. Many introduced populations pose serious threats to native species, and cost millions of dollars each year in order to minimize impacts (Long 2003; Pimentel et al. 2004). Understanding ecology and behavior of introduced species is a crucial step in the evaluation of realized and potential impacts that the species can have on native species. Such knowledge allows land managers to judge potential plans to monitor, control, or eradicate introduced populations to preserve native species populations.

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