ECOLOGICAL ASSESSMENT OF RED-BELLIED SQUIRRELS (*SCIURUS AUREOGASTER*) INTRODUCED TO ELLIOTT KEY, FLORIDA

by

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A Thesis Submitted to the Faculty of the

SCHOOL OF NATURAL RESOURCES AND THE ENVIRONMENT

In Partial Fulfillment of the Requirements
For the Degree of

MASTERS OF SCIENCE
WITH A MAJOR IN WILDLIFE AND FISHERIES SCIENCE

In the Graduate College

THE UNIVERSITY OF ARIZONA

2012

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___________________________________ 13 December 2012

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ACKNOWLEDEGMENTS

I would first like to thank my advisor and mentor, Dr. John L. Koprowski for his endless support, guidance, and most of all, patience throughout my graduate career. My committee, Dr. Courtney Conway and Dr. Bill Matter for the scientific dialogues and advice over the years. My family and friends for their love and support! Tony Pernas of the National Park Service for securing the funding for the project and supporting the project from start to finish in every way. Shelby Moneysmith, Richard Curry, Jim Chadwick, Vicente Martinez, Sergio Martinez, Max Tritt, Chris Tillman, Todd Kellison, Elsa Alvear, Jason Marsh, Miranda Marsh, and George West of Biscayne National Park for all of the help while working on Elliott Key. Matt Patterson and Shasha at the South Florida and Caribbean Network for assistance with mapping and GIS. Zach Koprowski, Nate Gwinn, Kate Pasch, Brett Pasch, Claire Zugmeyer, Seafha Blount, Pedro M. Chavarria, and Rebecca Lechalk for their assistance in the field. Bill and Pam Dooley for their companionship on Elliott Key. Melissa Merrick for all of the help with stats and GIS. The Kopow lab: Rosa Jessen, Tim Jessen, Melissa Merrick, Karen Munroe, Nate Gwinn, Kate Pasch, Brett Pasch, Claire Zugmeyer, Seafha Blount, Nichole Cudworth, Nicolás Ramos-Lara, Erin Posthumus, Vicki Greer, Shari Ketcham, Hsiang Ling Chen, Sandy Doumas, Debbie Buecher, David Wood, and Mags Rheude. The faculty and staff of the School of Natural Resources and the Environment, Department of Ecology and Evolutionary Biology, and Department of Molecular and Cellular Biology.

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ABSTRACT

Introduced species present one of the greatest threats to biodiversity of native species, and knowledge of introduced species ecology is imperative for the development of management plans to ensure conservation of native species populations. We sought to determine the distribution and nesting behavior of an introduced population of red-bellied squirrels (*Sciurus aureogaster*) on islands of the Florida Keys currently managed as part of Biscayne National Park, and document potential for the species to impact native flora and fauna. Squirrels were difficult to observe in the dense vegetation of the subtropical forest, so we relied on their leaf nests, which were highly visible in the canopy of trees, to determine current presence and distribution on the Park's islands. We found nests throughout the mixed-hardwood forests of Elliott Key and Sands Key, and also documented a single, old nest on Old Rhodes Key, the first ever documentation of the species that far south in the Upper Keys.

Nests were located in tall trees with more canopy linkages than random focal trees, and nests were placed in the upper canopy on the north side of the nest tree more often than expected by chance. Squirrels selected West Indies mahogany (*Swietenia mahagoni*) to place nests more often than available in the forest. Squirrels used areas with greater tree density and canopy cover, but lower recent hurricane damage and fewer woody shrub stems, than areas available at random in the forest. Squirrels built nests only in mixed-hardwood forest. Overall, this introduced species exhibited nest site selection behavior similar to other tree squirrels, and appears capable of continued spread despite the initial site of introduction on an oceanic island. Knowledge obtained from

this research is being used by managers and applied to an eradication program to remove this invasive species from Biscayne National Park.

CHAPTER 1: INTRODUCTION

Introduced species pose one of the greatest threats to biodiversity of native species, and do so through a number of ecological processes that include: predation, competition, spread of disease, and changes in ecosystem structure and function (Lever 1985, Simberloff 1997, Tompkins et al. 2003). Endangered species and oceanic island communities are especially vulnerable to the potentially detrimental impacts of non-native species (Courchamp et al. 2003). Of introduced vertebrates, mammals pose one of the greatest threats to novel terrestrial ecosystems (Lever 1985). Tree squirrels are excellent models for the ecological and economic threats that mammals can pose when introduced. Introduced populations of tree squirrels have impacted native species through competition (Bryce et al. 2001, Gurnell et al. 2004), spread of disease (Rushton et al. 2000, McInnes et al. 2006), and predation (Tilmant 1980, Dagnall et al. 1998, Edelman and Koprowski 2005, Mountford 2006); and have significant economic impacts for humans (Hori et al. 2006, Signorile and Evans 2007).

Tree squirrels possess a number of biological characteristics that facilitate successful invasions. Tree squirrels are able to establish viable populations from a very small number of propagules (Brown and McGuire 1975, Long 2003, Wood et al. 2007). Most tree squirrels reproduce twice a year with a mean litter size between 2 and 4 individuals (Heaney 1984, Koprowski 1994a,b). Tree squirrels are long lived with ecological longevity that reaches 15 years (Koprowski 1994a,b), allowing populations to grow rapidly and spread quickly. Tree squirrels are capable of dispersing great distances, with squirrels known to cross waterways (Layne 1997), agricultural areas, and urban areas (Jameson and Peeters 1988). Tree squirrels are capable of using a wide variety of plant and animal material for food (Steele and Koprowski 2001, Thorington et al. 2012). Tree squirrels construct nests for protection against weather and predators (Koprowski 1994a,b, Steele and Koprowski 2001), and many species of tree squirrel have the ability to acclimate to human-impacted environments (Jameson and Peeters 1988, Geluso 2004, Jessen et al. 2010).

In 1938, 4 red-bellied squirrels (*Sciurus aureogaster*) were introduced to Elliott Key, Florida by J. Arthur Pancoast (Brown 1969, Brown and McGuire 1975, Brown 1997, Layne 1997). The National Park Service began administering Elliott Key and the surrounding islands in 1968, which later became part of Biscayne National Park. A growing concern over the impact the introduced squirrel had on native species led to our project. We sought to determine the current status, distribution, and ecology, specifically related to the possible impacts *S. aureogaster* could have on native species on Elliott Key in Biscayne National Park, and in south Florida should red-bellied squirrels spread.

CHAPTER 2: PRESENT STUDY

The methods, results, and conclusions of this study are presented in the papers appended to this thesis. The following is a summary of the most important findings in this document.

We first offer a review of tree squirrel introductions worldwide to document and better understand the current distribution and impacts of introduced tree squirrel populations. We discuss aspects of tree squirrel biology that predispose this taxon to be successful invaders of novel environments, and summarize management strategies to combat negative impacts to native flora and fauna. Additionally we present monitoring techniques for introduced tree squirrels that are effective tools to assure management actions are successful. We highlight our own research on red-bellied squirrels *(Sciurus aureogaster*) in Biscayne National Park, Florida, and document potential impacts that this introduced species has on native species. Red-bellied squirrels were observed feeding on phloem of trees and collecting plant material for nest construction, both of which could be threatening long term survival of trees. Squirrels consumed seeds of numerous plant species which may limit reproductive success for some plant species. All of these potential impacts are of special concern for the persistence of Sargent's palm (*Pseudophoenix sargentii*, Florida Endangered Species) because very few mature palms capable of reproduction exist on Elliott Key, so any impact the squirrel has on palm survivorship and reproduction could be detrimental to such a small population. The potential impacts of predation on Florida tree snail (*Liguus fasciatus*; Florida Species of Special Concern) by red-bellied squirrels, and the potential for competition with white-crowned pigeon (*Patagioenas leucocephala*; Florida Threatened Species) for food were also of great concern to the National Park Service. The threat of spread from the initial introduction site on Elliott Key was found to be the chief concern, as continued spread would possibly put the introduced squirrel in direct competition with several rodent species of conservation concern in the Florida Keys and south Florida. This chapter was published as part of *Managing Vertebrate Invasive Species: Proceedings of an International Symposium* (Palmer et al. 2007).

We analyzed nest-site selection by squirrels on Elliott Key at multiple scales to determine the most influential factors. At the finest scale, squirrels placed nests in the upper 25% of the tree supported by the tree's crown with nests located on the north side more often than expected. Nest tree species were not selected at random, with West Indies mahogany (*Swietenia mahagoni*) selected over 60% of the time despite only composing 9% percent of trees available. Nest trees tended to be larger and have more canopy linkages than randomly available at random trees. At the broadest scales, squirrels selected mixed-hardwood forest exclusively in which to construct nests in areas with greater canopy cover and basal area, more trees close to the nest tree, and less hurricane damage than random sites. Red-bellied squirrels appear to have specific selection criterion at all scales, which informs managers where to concentrate management and monitoring efforts. This chapter is formatted for submission to the *Journal of Mammalogy*.

Finally, we document red-bellied squirrel distribution within the island archipelago of Biscayne National Park, finding sign of squirrels on Sands and Old Rhodes Key, but failing to document presence on Adam's Key. We analyzed nest distribution on Elliott Key and determined nests have a clumped distribution within the mixed-hardwood forest. Distribution information for red-bellied squirrels within Biscayne National Park proved valuable to managers as they implemented an eradication campaign to remove all red-bellied squirrels from the Park. This chapter is formatted for submission to *Mammalia*.

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APPENDIX A: TREE SQUIRRELS AS INVASIVE SPECIES: CONSERVATION AND MANAGEMENT IMPLICATIONS*

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*This chapter was published as part of *Managing Vertebrate Invasive Species: Proceedings of an International Symposium (2007)*

ABSTRACT

The impact of invasive species on native biodiversity is increasing worldwide. Mammalian invaders are formidable ecological and economic threats, and tree squirrels are models of such challenges. We review the worldwide distribution of tree squirrel introductions and detail their nearly universal success. The biological characteristics of tree squirrels that enable success as invasive species are: high reproductive potential, high vagility, diverse food habits, ability to construct nests, and plasticity in human-impacted landscapes. We document costs and benefits of tree squirrel introductions, and discuss existing management strategies planned for some species. We focus on an introduced population of Mexican red-bellied squirrels (*Sciurus aureogaster*) found in Biscayne National Park, Florida, USA. Originally introduced to Elliot Key in 1938, the population expanded until Hurricane Andrew in 1992. The population was thought to be extirpated, but recent sightings initiated a project to assess status and distribution within the Park. A field study has provided valuable information on potential and realized impacts that the squirrel population has on the native ecosystem that includes several species of conservation concern. Management strategies for Mexican red-bellied squirrels are informed by research to develop

prudent and effective means to meet the challenges that result from control measures to deal with this exotic species.

Key Words: *Sciurus*, *Tamiasciurus*, *Callosciurus*, *Funambulus*, exotic, Florida

INTRODUCTION

Introductions of mammals outside of their native range have been commonplace often with significant negative impacts (Long 2003). Nine species of tree squirrel have been successfully introduced outside their native range, with nearly 100 individual cases of introduction (Long 2003). Here we include all species of the family Sciuridae that maintain an arboreal lifestyle, and do not limit our discussion strictly to the tribe Sciurini (Wilson and Reeder 1993). Tree squirrels have been introduced mostly for the aesthetic novelty and pleasure they bring (Aprile and Chicco 1999), but also to increase hunting and trapping opportunities (Davis and Brown 1988, Long 2003). We first review the major introductions of tree squirrels (Table 1), and then discuss the biology of tree squirrels that make them successful in novel environments. Finally, we discuss management and monitoring techniques for introduced populations of tree squirrels.

SPECIES ACCOUNTS

Eastern Gray Squirrel (*Sciurus carolinensis*)

The native range of the eastern gray squirrel includes the eastern United States from the Gulf Coast to southern Canada (Hall 1981, Koprowski 1994a, Long 2003). *S. carolinensis* has been the subject of the most numerous and widest geographic range of tree squirrel introductions (Long 2003). The species has been introduced beyond its native range to numerous localities within the United States and Canada (Koprowski 1994a, Long 2003). Introduced populations of *S. carolinensis* can be found in the Canadian provinces of southern

British Columbia, southern Quebec, southern New Brunswick, Saskatchewan, and Nova Scotia (Banfield 1974, Peterson 1966). Numerous introduced populations can be found in urban areas of California within city parks and other wooded areas (Jameson and Peeters 1988). Introduced populations also occur in Lewiston and Moscow, Idaho (Larrison and Johnson 1981). Records of introduced individuals were collected beginning in the mid 1960's in Montana (Hoffman et al. 1969). Multiple introductions have taken place in North Dakota, and all have been successful in establishing breeding populations (Hibbard 1956). Approximately 20 squirrels were transplanted from Pennsylvania to Marion County, but the population has remained restricted to urban areas within the county while also being introduced to Sweet Home, Oregon (Verts and Carraway 1998). Although native to eastern Texas, *S. carolinensis* has been introduced into the western side of the state (Schmidly 2004). *S. carolinensis* has also been introduced to Fort Lewis, Seattle, and other urban areas in Washington State (Flyger and Gates 1982) where their range overlaps that of the state threatened western gray squirrel (*Sciurus griseus*: Bayrakci et al. 2001, Ryan and Carey 1995, Washington Department of Wildlife 1993). Wisconsin also received multiple introductions of this species (Long 2003). Two populations were established in northern Baja California, Mexico (Huey 1964); however, the fate of these populations remains unclear (Koprowski et al. 2006).

S. carolinensis has been introduced outside of North America to the British Isles, Italy, South Africa, Hawaii, and Australia (Koprowski 1994a, Long 2003). However, the Hawaiian population now appears extirpated (Kramer 1971), and the Australian populations in Melbourne and Ballarat have gone extinct (Lever 1985, Long 2003, Seebeck 1995). Introduced to Cape Town, South Africa, the species has spread to inhabit the Cape Peninsula including the Cape of Good Hope Nature Reserve (Haagner 1920, Lever 1985, Macdonald et al. 1988). Introductions as early as the 1820's allowed the species to establish on the British Isles, however multiple introductions occurring in the early 1900's allowed the squirrel to become a nuisance animal as it spread to much of the former range of the native Eurasian red squirrel (*S. vulgaris*: Lever 1985). *S. carolinensis* has been introduced to Italy on four separate occasions, with three populations being established (Bertolino and Genovesi 2005, Long 2003).

Numerous negative impacts have been reported from areas of introduction including damage to trees and agriculture (Mountford 1997, Mountford 2006, Rayden and Savill 2004), competition with native squirrels (Bayrakci et al. 2001, Gurnell et al. 2004b, Macdonald 1988, Washington Department of Wildlife 1993, Wauters et al. 2000), and transmission of disease to native species (McInnes 2006, Rushton et al. 2000). Gardens and orchards in South Africa were reported as damaged by introduced squirrels (Haagner 1920). *S. carolinensis* damages orchard, garden, and farm crops in the British Isles and is an ecological pest taking native bird's eggs and nestlings (Lever 1985). *S. carolinensis* also debarks trees and can severely affect the forest structure (Mountford 1997, Mountford 2006, Rayden and Savill 2004), however, impacts in some areas can be minimal (Signorile and Evans 2007). Interspecific competition with native sciurids has occurred in many areas where *S. carolinensis* was introduced. Eastern gray squirrels now occur in areas of Washington occupied by the state threatened western gray squirrel (Bayrakci et al. 2001, Washington Department of Wildlife 1993), where the invasive squirrel is better able to acclimate to human development (Ingles 1947, Ryan and Carey 1995). *S. carolinensis* is more commonly observed in line transect studies in Fort Lewis than native western gray squirrels (Ryan and

Carey 1995). *S. carolinensis* negatively impacts native Eurasian red squirrel populations in the British Isles and Italy through competitive exclusion for space and food resources (Bryce et al. 2001, Gurnell et al. 2004b, Wauters et al. 2000) and spreading a poxvirus to which *S. vulgaris* is highly susceptible, but which does not affect *S. carolinensis* (McInnes 2006, Rushton et al. 2000).

Abert's Squirrel (*Sciurus aberti*)

The Abert's squirrel is native to the pine forests of Arizona, Colorado, New Mexico, Utah, and Wyoming in the United States as well as occurring in Sonora and Chihuahua into southern Durango in Mexico (Wilson and Reeder 1993). *S. aberti* was transplanted outside its native range beginning in the early 1900's by several state game agencies to increase hunting opportunities, with most of these transplants occurring in the state of Arizona (Davis and Brown 1988). Beginning in the 1940's, Arizona Game and Fish Department released individuals from northern Arizona into many of the "sky island" mountain ranges in southeastern Arizona (Davis and Brown 1988). The only population to receive much scientific attention is located in the Pinaleño Mountains of southeastern Arizona, which is home to the endangered endemic Mount Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*: Edelman and Koprowski 2005, Edelman and Koprowski 2006, Hutton et al. 2003, Rushton et al. 2006, USFWS 1993).

Abert's squirrels and Mount Graham red squirrels feed on many of the same foods and seek similar trees for nest sites (Edelman and Koprowski 2005, Edelman and Koprowski 2006, Hutton et al. 2003). *S. aberti* raid red squirrel middens and are chased by the territorial red squirrel (Hutton et al. 2003). All of these factors are of conservation concern for the Mount Graham red squirrel, as modeling reveals that the continued presence of the Abert's squirrel could severely impact the viability and persistence of the population of this endangered subspecies of red squirrel (Rushton et al. 2006). Abert's squirrels are known to reduce cone crops and pine tree growth by clipping branch tips for food (Allred et al. 1994, Allred and Gaud 1994).

Eastern Fox Squirrel (*Sciurus niger*)

The eastern fox squirrel (*Sciurus niger*) is native to the eastern and central United States and southern Canada (Koprowski 1994b, Hall 1981), and has been introduced in the western United States and Canada (Long 2003). *S. niger* is now found in numerous locations throughout Idaho, occurring in urban and agricultural areas, and have expanded their range since initial introduction in the state and neighboring Washington (Koprowski 1994b, Larrison and Johnson 1981, Marshall 1941, Wright and Weber 1979). The squirrel is also found in Asotin County and the Seattle area of Washington (Flahaut 1941, Yocom 1950). This species is currently found in 8 counties in Oregon, but is primarily restricted to urban areas and nut tree orchards (Flyger and Gates 1982, Verts and Carraway 1998). *S. niger* can now be found in many urban areas and woodlands in the Central Valley and Coastal Range of California due to numerous introductions (Jameson and Peeters 1988). Although the species occurs naturally in Colorado, many populations are present because of introductions in the early 1900's (Fitzgerald et al. 1994). Fox squirrels are also expanding their range naturally in Colorado; following riparian corridors, invading urbanized areas, and inhabiting areas newly cultivated with deciduous trees (Fitzgerald et al. 1994, Geluso 2004). Fox squirrels are present in Hondo, Roswell, and Carlsbad, New Mexico and western Texas presumably because of introductions (Frey and Campbell 1997), however the date and source of the introductions is unknown (Findley 1987). The eastern fox squirrel was also introduced to Pelee Island on Lake Erie in Ontario, Canada (Peterson 1966).

Fox squirrels are able to invade riparian areas, oak woodlands, and areas with increased edge, tolerate low tree density (Fitzgerald et al. 1994, Verts and Carraway 1998, Wolf and Roest 1971). Fox squirrels will readily consume a variety of agricultural products including many fruits and nuts (Flyger and Gates 1982, Koprowski 1994b, Wolfe and Roest 1971), and will nest in introduced *Eucalyptus globulus* and the attics of homes (Koprowski 1994b, Verts and Carraway 1998, Wolf and Roest 1971). The impact of *S. niger* on the native western gray and Douglas squirrels (*T. douglasii*) on the western U.S. coast is attributed to competition for resources, and is a growing conservation concern (Ingles 1947, Robinson 1954). Abert's squirrels in the Black Forest of Colorado have experienced a population decline attributed to competition with introduced fox squirrels (Fitzgerald et al. 1994).

Eurasian Red Squirrel (*Sciurus vulgaris*)

The Eurasian red squirrel occurs naturally from the Iberian Peninsula and Great Britain east to Kamchatka Peninsula in Russia and Japan, and occurs as far south as the Mediterranean and Black seas, and parts of Mongolia and China (Wilson and Reeder 1993).

S. vulgaris has been successfully introduced to a few areas just outside of its native range in Europe and Asia, including Russia and many independent republics of the former U.S.S.R., as well as Germany (Long 2003). Re-introduction projects have been implemented to re-establish populations in parts of Great Britain (Long 2003). The squirrel is known to strip the bark from conifers, damaging the trees and impacting plantations (Long 2003).

Pallas's Squirrel (*Callosciurus erythraeus*)

Pallas's squirrel is native to Southeast Asia (Wilson and Reeder 1993), and has been introduced to Argentina west of Buenos Aires, France, and Japan (Aprile and Chicco 1999, Gurnell and Wauters 1999, Long 2003). Pallas's squirrel damages trees utilized for agriculture, silviculture, and horticulture in both Argentina and Japan (Guichon et al. 2005). Squirrels have been observed eating eggs of native and domestic birds, and destroying irrigation systems for tree plantations and poultry farms in Argentina (Guichon et al. 2005, Setoguchi 1990, Tamura and Ohara 2005). Dispersal and subsequent spread of the species appears facilitated by anthropogenic environments (Guichon et al. 2005, Miyamoto et al. 2004), and squirrels are also spread in Argentina by people who find them attractive (Guichon et al. 2005). Continued spread in Japan is of conservation concern as the species will likely encounter *Sciurus lis*, a declining tree squirrel native to Japan (Miyamoto et al. 2004). The density of the introduced population in France is now higher than the native *S. vulgaris* (Gurnell and Wauters 1999).

Finalayson's Squirrel (*Callosciurus finlaysoni*)

Finalayson's squirrel is native to Southeast Asia including Burma, Cambodia, Laos, and Vietnam (Wilson and Reeder 1993). Two pairs of squirrels were introduced to an urban park in Acqui Terme, Italy in 1981 (Bertolino et al. 1999). The species persists at the park with an estimated population between 40-50 squirrels (Bertolino et al. 2004). The squirrels have been observed consuming many parts of native plants, and are known to strip bark (Bertolino et al. 1999, Bertolino et al. 2004).

Northern Palm Squirrel (*Funambulus pennantii*)

The northern palm squirrel is native to portions of the Middle East and India (Wilson and Reeder 1993), and was introduced to the Australian cities of Perth, Western Australia and Sydney, New South Wales (Long 2003). The population in Sydney has since been extirpated (Long 2003). The squirrel is known to eat citrus and stone fruits, and also chew on electrical wiring in and around the city of Perth (Long 2003).

American red squirrel (*Tamiasciurus hudsonicus*)

The American red squirrel is native to boreal forests of Canada and the northern United States as well as occupying the Cascade, Rocky, and Appalachian mountains (Steele 1998). *T. hudsonicus* was introduced to many islands associated with Alaska and Canada including Newfoundland, Vancouver Island, the Queen Charlotte Islands, Kodiak Island, Afognak Islands, and the Alexander Archipelago (Long 2003, Payne 1976). Negative impacts from this species have not been reported, and the populations have limited ability to disperse from most islands (Long 2003).

Mexican Red-bellied Squirrel (*Sciurus aureogaster*)

The Mexican red-bellied squirrel is native to Mexico and northern Guatemala (Wilson and Reeder 2003), and was introduced to Elliott Key, Florida, in 1938 by a resident of that island (Brown and McGuire 1969, Layne 1997, Long 2003). Squirrels became common on the island, and were reported on nearby Sands Key and Adams Key, likely a result of natural dispersal from individuals swimming (Brown and McGuire 1969, Layne 1997). One individual was captured while swimming across Caesar's Creek in the direction of Old Rhodes Key to the south of Elliott Key (Layne 1997). The population was considered extirpated by Hurricane Andrew in 1992 (Layne 1997), however Koprowski et al. (2005) confirmed the squirrel's persistence on Elliott Key.

Mexican red-bellied squirrels relied heavily upon introduced plant species for food including the coconut palm (*Cocos nucifera*), Australian pine (*Casuarina equisetifolia*), and sapodilla (*Manilkara zapota*) as well as papaya (*Carica papaya*) to a lesser extent (Brown and McGuire 1973, Brown and McGuire 1975). However, beginning in the early 1990's, the National Park Service implemented a plan to eradicate non-native plants from all of the islands in Biscayne National Park. The removal of these plants eliminated major food sources for the squirrel, forcing *S. aureogaster* to rely exclusively on native plants. We documented the squirrels consuming numerous native seeds including mahogany pods (*Swietenia mahagoni*), tamarind pods (*Lysiloma latisiliquum*), blackbead (*Pithecellobium unguis-cati*), and Florida poisonwood berries (*Metopium toxiferum*). The squirrels also clipped numerous branches when seeds were unavailable and consumed the phloem of plants, especially from wild mastic trees (*Masitchodendron foetidissimum*). Tilmant (1980) found squirrels using thatch palm leaves (*Thrinax* spp.) in lining their nests, where as Brown and McGuire (1975) noted that the majority of nest material came from the nest tree itself. All of these factors demonstrate a negative impact on native plants from the exotic squirrel on Elliott Key.

We were also concerned with the impact of Mexican red-bellied squirrels on native fauna. The white-crowned pigeon (*Columba leucocephala*) occurs in Biscayne National Park, and is listed as threatened by the Florida Fish and Wildlife Conservation Commission (FFWCC). *C. leucocephala* relies on many of the same food resources as the introduced squirrel such as Florida poisonwood and pigeon plum (*Coccoloba diversifolia*) berries (Bancroft and Bowman 1994, FFWCC 2004). Also occurring within Biscayne National Park is the Florida tree snail (*Liguus faciatus*), a state species of special concern (FFWCC 2004). This snail may serve as a food resource for *S. aureogaster* occasionally. Although this population of *S. aureogaster* was not observed raiding bird nests, other *Sciurus* species take bird's eggs and nestlings as food (Koprowski 1994a). The squirrel's ability to disperse to other islands is also of great concern as *S. aureogaster* will encounter more opportunities to impact native flora and fauna as well as agriculture. Two native tree squirrels occur in Florida, and dispersing Mexican red-bellied squirrels would be an unwelcome source of competition for these species. *S. aureogaster* would encounter *S. carolinensis* upon reaching Key Largo (~8.5 km straight line distance from Elliott Key) or the mainland (~12.5 km straight line distance from Elliot Key: Brown 1997). The Big Cypress fox squirrel (*Sciurus niger avicennia*) is the nearest population of eastern fox squirrels to Elliott Key at approximately 84 km (Brown 1997, Hall 1981), and is listed as threatened in Florida (FFWCC 2004). Resource requirements of the threatened fox squirrel and the red-bellied squirrel would likely overlap greatly (Brown and McGuire 1975, Brown 1997).

The National Park Service has implemented a plan to eradicate Mexican red-bellied squirrels from Biscayne National Park as the species poses a threat to native species and agriculture. Squirrel nests will be marked with reflective flagging, and trained personnel will return to each nest at night when squirrels are likely occupying the nest, and discharge non-toxic shot from a shotgun into the nest. Nesting material will be completely removed from the nest tree, and the squirrel carcasses collected for further study. Nest boxes will be erected as both a monitoring tool and an additional way to capture individual squirrels that reside in the nest boxes.

REASONS FOR SUCCESS OF INTRODUCED SQUIRREL POPULATIONS

Tree squirrels are able to establish viable populations from a very small number of propagules (Aprile and Chicco 1999, Brown and McGuire 1975, Long 2003). Success rates of introductions appear to be extraordinarily high, even from small (< 20 individuals) starting populations (Wood et al. 2007). Most tree squirrels reproduce twice a year with a mean litter size between 2 and 4 individuals (Heaney 1984, Koprowski 1994a, Koprowski 1994b), so populations can experience rapid growth after initial introduction to novel environments. Tree squirrels are long lived, with individuals living between 5 and 15 years (Koprowski 1994a, Koprowski 1994b). The ability to disperse is important to the spread of an invasive species, and tree squirrels are capable of dispersing great distances, with squirrels known to cross waterways (Layne 1997), and agricultural and urban areas (Jameson and Peeters 1988). Tree squirrels are capable of using a wide variety of plant and animal material for food, and possess strong jaw muscles enable them to open most seeds and nuts, which are excellent sources of fats and proteins (Steele and Koprowski 2001). Nests are constructed for protection against the elements, and can either be a stick and leaf nest (drey) or cavity in a tree (Koprowski 1994a, Koprowski 1994b). Many species of tree squirrel have the ability to acclimate to human-impacted environments (Geluso 2004, Jameson and Peeters 1988).

MANAGEMENT

In some cases, introduced populations of tree squirrels pose such a great threat to conservation and economic interests to warrant control or eradication. In Great Britain, *S. carolinensis* has been subject to a wide range of control and eradication tactics including trapping, shooting, and poisoning (Dagnall et al. 1998). A grass-roots movement by farmers and woodland owners initiated the first concerted effort to reduce the introduced squirrel population, with hundreds of "Grey Squirrel Hunting Clubs" springing up to exterminate an estimated 100,000 squirrels by 1947 (Sheail 1999). The British government offered free cartridges to participating clubs in support of the eradication effort, and promoted an "anti-grey squirrel" campaign over BBC radio (Sheail 1999). In 1952, the government decided to offer bounties on squirrel tails, a program that lasted until 1957, and resulted in 1,000,000 squirrels being turned in (Sheail 1999). The bounty program was ended because the squirrel population had not been reduced to a manageable level, with some suggesting that the problem had even grown worse despite the effort (Sheail 1999), however, whether the removal of so many individuals slowed population expansion is not known. Government support returned in the form of the Squirrel (Warfarin) Order of 1973, which initiated a poisoning program that was deemed most effective for squirrel control (Dagnall et al. 1998, Sheail 1999). Increasing pressure from animal rights groups against poisoning of squirrels despite the squirrel's invasive nature has given rise to new ideas on controlling *S. carolinensis* in Great Britain (Dagnall et al. 1998). Managing forests in a way that will reduce squirrel numbers, and current research into sterilization techniques that will involve a vaccine induced immuno-contraceptive for squirrels have been recent focuses of research for grappling with the *S. carolinensis* problem (Dagnall et al. 1998). Eastern gray squirrels were the focus of an eradication attempt in Italy that was initially successful but halted because of objection from animal rights groups (Bertolino and Genovesi 2003).

MONITORING

The continual monitoring of introduced squirrel populations will be important in understanding impacts that introduced species have on native species and to detect range expansions. Numerous monitoring techniques facilitate these goals. Nest boxes attract squirrels seeking temporary refuge and also to build nests for long term use (Brown and McGuire 1975), and are an important method to determining success of an eradication effort or to monitor range expansion as squirrels colonize new areas. Hair tubes or snares collect hairs from individual squirrels which is helpful to determine presence or absence in areas that are in danger of being colonized by a spreading population (Gurnell et al. 2004a). Transect surveys through forested areas in or near sites of introduction can determine squirrel density and distribution (Brown and McGuire 1975, Koprowski et al. 2005, Koprowski et al. 2006).

Conclusions

Understanding the impacts created by invasive tree squirrel populations is important for the conservation and continuation of native species, especially native tree squirrels. Invasive tree squirrels can affect the environments in a multitude of ways, and documentation of these impacts is important to enable justification of control and eradication programs. Assessment of current distributions and knowledge of ecology of an introduced population is crucial in predicting the path of spread and planning ways to possibly slow or eliminate population expansion. The continued growth in global interest in invasive species and the rapid anthropogenic spread of tree squirrels make these species excellent model systems for the study of impacts. Furthermore, the nearly cosmopolitan distribution, questionable conservation status, and poor knowledge of native tree squirrel species (Koprowski and Rajamani 2007) make studies of the tree squirrels imperative.

Acknowledgements

We wish to thank the National Park Service for funding our research, and Biscayne National Park employees including Richard Curry, Shelby Moneysmith, Todd Kellison, Elsa Alvear, Jim Chadwick, Sergio Martinez, Vicente Martinez, Jason and Miranda Marsh, and Max Tritt for their support. Seafha Blount, Nate Gwinn, Zach Koprowski, Rebecca Lechalk, Kate Leonard, Bret Pasch, and Claire Zugmeyer for their hard work in the field. Vicki Greer, Karen Munroe, Nichole Cudworth, and David Kahrs for additional assistance on this project.

Fairchild Botanical Gardens, The Florida and Caribbean Parks Office, and The University of Arizona.

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Tables

Table 1. Date and locations of tree squirrel (Family Sciuridae) introductions worldwide.

Species Name	Date	State/Province/Region	Country	Reference
Sciurus aberti	1940's, 1970's	Arizona	U.S.A.	Davis and Brown 1988
Sciurus aberti	1929,40,55,69	New Mexico	U.S.A.	Davis and Brown 1988
Sciurus aberti	1898-1908	Utah	U.S.A.	Davis and Brown 1988
Sciurus aureogaster	1938	Florida	U.S.A.	Brown and McGuire 1969
Sciurus carolinensis	circa 1900,37	Victoria, Melbourne	Australia	Seebeck 1995
Sciurus carolinensis	1914	numerous sites	Canada	Banfield 1974
Sciurus carolinensis	1876-1929	numerous sites	U. K.	Long 2003
Sciurus carolinensis	1913		Ireland	Long 2003
Sciurus carolinensis	1948,66,94	numerous sites	Italy	Bertolino and Genovesi 2003
Sciurus carolinensis	1958	Baja Norte	Mexico	Huey 1964
Sciurus carolinensis	1890's	Cape Town	S. Africa	Macdonald et al. 1988
Sciurus carolinensis	circa 1850's	California	U.S.A.	Jameson and Peeters 1988
Sciurus carolinensis	1943	Hawaii	U.S.A.	Kramer 1971
Sciurus carolinensis	not reported	Idaho	U.S.A.	Larrison and Johnson 1981
Sciurus carolinensis	1919	Oregon	U.S.A.	Verts and Carraway 1998
Sciurus carolinensis	1958,66,68	Montana	U.S.A.	Hoffman et al. 1969
Sciurus carolinensis	1904-1952	North Dakota	U.S.A.	Hibbard 1956
Sciurus carolinensis	not reported	Texas	U.S.A.	Schmidly 2004
Sciurus carolinensis	1934,49,66,68	Wisconsin	U.S.A.	Long 2003
Sciurus carolinensis	circa 1920	Washington	U.S.A.	Flahaut 1941
Sciurus niger	1890	Ontario	Canada	Peterson 1966
Sciurus niger	early 1900's	California	U.S.A.	Jameson and Peeters 1988
Sciurus niger	early 1900's	Colorado	U.S.A.	Fitzgerald et al. 1994
Sciurus niger	not reported	Idaho	U.S.A.	Larrison and Johnson 1981

Sciurus niger	not reported	Montana	U.S.A.	Hoffman et al. 1969
Sciurus niger	prior to 1958	New Mexico	U.S.A.	Frey and Campbell 1997
Sciurus niger	1935,38,41,53,54	North Dakota	U.S.A.	Hibbard 1956
Sciurus niger	not reported	Oregon	U.S.A.	Verts and Carraway 1998
Sciurus niger	not reported	Texas	U.S.A.	Frey and Campbell 1997
Sciurus niger	1915	Washington	U.S.A.	Yocum 1950
Sciurus vulgaris	not reported		Germany	Long 2003
Sciurus vulgaris	not reported	Caucasus	Crimea	Long 2003
Sciurus vulgaris	not reported		Kazakhstan	Long 2003
Sciurus vulgaris	not reported		Kyrgyzstan	Long 2003
Callosciurus erythraeus	1970	Buenos Aires	Argentina	Aprile and Chicco 1999
Callosciurus erythraeus	1970's	Cap d'Antibes	France	Gurnell and Wauters 1999
Callosciurus erythraeus	1935,54		Japan	Steoguchi 1990
Callosciurus finlaysoni	1981		Italy	Bertonlino et al. 1999
Funambulus pennantii	1898	numerous sites	Australia	Long 2003
Tamiasciurus hudsonicus	1963,64	numerous sites	Canada	Payne 1976
Tamiasciurus hudsonicus	1920's	Alaska	U.S.A.	Long 2003

APPENDIX B: CHARACTERISTICS OF NEST SITES, NEST TREES, AND NESTS OF AN INTRODUCED POPULATION OF RED-BELLIED SQUIRRELS (*SCIURUS AUREOGASTER*)*

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ABSTRACT

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 successful invasive species. Red-bellied squirrels were introduced to Elliott Key, Florida in the late 1930's, and spread to nearby islands. Red-bellied squirrels were believed extirpated by Hurricane Andrew in 1992, but red-bellied squirrels were rediscovered on Elliott Key in 2005. In 2006 and 2007, we surveyed for squirrel nests and measured vegetation to evaluate selection of forest characteristics by squirrels when placing nests. Squirrels selected large nest trees with more canopy linkages in areas with large trees, high tree density and canopy cover, and lower recent hurricane damage. Squirrels continued to select nest sites, nest trees, and nest placement for nests in ways similar to individuals on Elliott Key prior to forest altering events including recent storms and management program to removed introduced plants. Red-bellied squirrels also selected for characteristics similar to individuals in their native range, and to tree squirrels in general. We suggest behaviors of individuals in native ranges may elucidate patterns for individuals introduced to novel environments, and emphasize the importance of understanding ecology of introduced species for effective management.

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

INTRODUCTION

Nests serve numerous functions: protection from weather and predators, a place to rest, access to food, and sites for reproduction (Benson et al. 2008; Fruth and Hohmann 1993; Goodall 1962; Holway 1991; Steele and Koprowski 2001). 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 (Edelman and Koprowski 2005; Hamerstrom et a. 1973; Snyder and Linhart 1994). Understanding the environmental cues necessary to incite nest building behavior is critical for management and conservation of 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 areas with larger and denser trees and a high percentage of canopy cover when compared to areas randomly selected in the forest (Cudworth and Koprowski 2011; Edelman and Koprowski 2005; Halloran and Bekoff 1994; Merrick et al. 2007; Ramos-Lara and Cervantes 2007). Such forest structure may serve to increase the functionality of nests, including provision of escape routes, maximize thermal retention, and reduced exposure to weather extremes (Edelman and Koprowski 2005; Farentinos 1972).

Red-bellied squirrels (*Sciurus aureogaster*) are a tree squirrel that occurs in a variety of forest types in Mexico and Guatemala (Musser 1968). This species is known build leaf nests close to the trunks of the largest and tallest trees in an oak-pine forest in Michoacán, Mexico (Ramos-Lara and Cervantes 2007). Squirrels selected 3 species of oaks (*Quercus* spp.) disproportionate to their abundance for nest construction (Ramos-Lara and Cervantes 2007).

Red-bellied squirrels were introduced to Elliott Key, Florida in 1938 (Brown and McGuire 1969), which provides an opportunity to assess the most important cues used for nest tree and site selection in a novel environment. The island lacked native tree squirrels, and the newly introduced species were observed throughout the island (Schwartz 1952). Individuals began dispersing from the island and populations established on Sands and Adams Key (Layne 1997). A 40 year-old study on Elliott Key suggested that squirrels might favor West Indies mahogany (*Swientenia mahagoni*) and avoid Florida poisonwood trees (*Metopium toxiferum*), however statistical analyses were not conducted (Brown and McGuire 1975).

Since the study of Brown and McGuire (1975), 2 large-scale forest disturbances have occurred: 1) hurricanes, including Hurricane Andrew in 1992, a powerful storm that passed directly over the island (Ogden 1992), and other more recent hurricanes in 2005 have impacted vegetation on the island; and 2) an introduced plant removal program was implemented in the mid-1980's, which focused on a number of introduced plant species that squirrels historically exploited for food and nesting resources. Despite these events, squirrels occupy Elliott Key (Koprowski et al. 2005), and colonized other nearby islands (Palmer 2012). We sought to document forest and tree characteristics used by squirrels post-disturbance 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.

METHODS

Study area.—We conducted our study on Elliott Key, Dade County, Florida, an island 24 km south of Miami, Florida 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 Indian mahogany (*Sweitentia mahagoni*) were the most common trees. Non-native 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. Mangrove (black mangrove, *Avicennia germinans*; 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 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.

Common raccoons (*Procyon lotor*) and marsh rabbits (*Sylvilagus palustris*) were the only native mammals encountered on the island, and we recorded no sign or sightings of bobcats (*Lynx rufus*) or white-tailed deer (*Odocoileus virginianus*) (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 one individual was found in the mangrove forest on the west side of the island and may have drifted to the island.

Initial leaf nest survey.—Tree squirrels use cavities in tree trunks, bolus leaf and stick nests ("dreys") located in branches or forks, or ground nests (Gurnell 1987). Red-bellied squirrels constructed dreys on Elliott Key, and 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 the Elliott Key from north to south. Prior to surveys, we determined that visibility permitted a surveyor to see a leaf nest from <30 m, thus we were confident that nearly 100% of the nests were detected between transects spaced 60 m apart. Nest trees were marked with forestry flagging and nest locations were recorded with a handheld global positioning system (GPS).

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 (m), lowest major branch height (m), length of canopy (m), diameter at breast height (DBH: cm), and condition (live or dead) of the nest tree. The distance (m), species, and DBH (cm) of the closest tree to the nest tree were also 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), a random tree was selected 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 (Edelman and Koprowski 2005, Smith and Mannan 1994). The same data were collected at random sites centered on the 50 random trees (from above) 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 (≤ 5 m, > 5 m) were recorded for all trees (DBH ≥ 7 cm, the smallest tree with a nest) within the circular plot. Canopy cover was measured by densiometer readings at 0, 5, 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/ha, and canopy cover at 0 m, 5 m, 10 m, and total for the site were calculated from data collected within each circular plot.

We classified the amount of recent hurricane damage sustained by vegetation in each plot and ranked the damage on a scale from 0-4: 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; 4) total destruction, majority of trees uprooted or trunks broken.

We employed two methods to quantify the amount of low-growing woody vegetation (DBH ≤ 7cm) within the circular plot. 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 m X 10 m plot randomly placed within the circular plot, 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 ASM guidelines (Sikes et al. 2011).

Data Analysis.—We analyzed nest aspect as circular data with a Rayleigh's Uniformity Test in Oriana v. 4.01 (Kovach Computing Services, Pentraeth, Isle of Anglesey, Wales, United Kingdom) to determine if nests were uniformly distributed around the tree trunk. We analyzed all other characteristics with JMP 10 (SAS Institute, Inc., Cary, North Carolina, USA). Variables were transformed 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), but report untransformed means (± SE).

We used a Pearson's chi-squared 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 an one-way ANOVA to determine if tree height varied among the most common tree species (mahogany, pigeon plum, and Florida poisonwood). Characteristics of nest trees and random trees were compared individually with 2-tailed *t*-tests (with a Bonferroni corrected α-value). Characteristics of forest structure at nest sites and random sites were also compared individually with 2-tailed *t*-tests (with a Bonferroni corrected α-value).

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 and Cervantes 2007), to some extent on Elliott Key (Brown and McGuire 1975), and in other species of tree squirrels (Cudworth and Koprowski 2011; Edelman and Koprowski 2005; Halloran and Bekoff 1994; Merrick et al. 2007). 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 (Table 3). 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/ha was highly correlated ($r = 0.967$) with basal area (m^2/ha) and was discarded for inclusion 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 were also discarded.

RESULTS

Initial leaf nest survey.—We documented 115 nests on Elliott Key during the initial survey and 202 nests by the end of the study. 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 were also collected for 50 random locations for comparison.

Nests were found only within the mixed-hardwood forest. We determined that scrubland and areas maintained for visitors did not constitute squirrel habitat due to paucity of trees and lack of squirrel sign. 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 7.6m ± 0.24 (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 (χ^2 = 24.20, n = 161, P < 0.0001), with most nests observed in the nest 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 first 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 (χ^2 = 662.70, n = 164, P < 0.0001; Table 1). West Indian mahogany was selected nearly 7 times more often than expected, and accounted for over 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 one quarter and one tenth as often as expected, respectively (Table 1). Mean height did not differ between mahogany (9.17 m ± 0.4), pigeon plum (7.94 ± 0.6) or poisonwood (8.9 ± 0.5; 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 nests 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 modestly more live trees compared to random sites ($P = 0.004$: Table 2). Nest sites had higher 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 top 2 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 than random sites ($\beta = -1.17 \pm 0.38$, $\chi^2 = 9.23$, $P = 0.0024$; Table 2).

Discussion

Red-bellied squirrels continue to select West Indies mahogany trees to build nests more often than expected (61.6% in this study vs. 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 (Duryea et al. 2007; Francis 2000), 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 allergen inducing 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). 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 in the forest in ways similar to those previously documented (Brown and McGuire 1975).

Red-bellied squirrels on Elliott Key appear to have similar criteria for selecting nest locations as in their 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 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. arizonae*: 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, possibly to avoid daily wind desiccation and damage from frequent strong storms. Prevailing winds are from the southeast in summer, however, 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 selected by squirrels (Cudworth and Koprowski 2011; Edelman and Koprowski 2005; Merrick et al. 2007; Ramos-Lara and Cervantes 2007); 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 2012), and have the potential to negatively impact native species (Palmer 2012). With this information, management strategies to minimize impact of red-bellied squirrels on native species and eliminate the threat of red-bellied squirrels spreading farther have been carefully considered (Pernas and Clark 2011). A plan to remove *S. aureogaster* from Elliott Key and other surrounding islands has been implemented with 49 individuals removed to date.

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 found evidence that the selection criteria of red-bellied squirrels introduced to a different foreign ecosystem remained similar to selection in their native ranges. This appears to be a pattern expressed in other introduced populations of tree squirrels (Edelman and Koprowski 2005; Hori et al. 2006; Setoguchi 1991), suggesting knowledge of behavior in native ranges could provide important insight into current introduced population distributions, and possibly provide predictive power for species spread and natural range expansion of populations in the future.

Many introduced populations pose serious threats to native species, and cost millions of dollars each year in order to minimize impacts (Long 2003; Pimental 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.

ACKNOWLEDGEMENTS

We wish to thank the Florida/Caribbean Exotic Plant Management Team for funding the project. We thank Richard Curry, Shelby Moneysmith, Max Tritt, Jim Chadwick, Sergio Martinez, Vicente Martinez, Todd Kellison and the rest of the staff of Biscayne National Park for their support of this project. Special thanks to Zach Koprowski, Nate Gwinn, Kate Pasch, Brett Pasch, Claire Zugmeyer, Seafha Blount, Pedro M. Chavarria, and Rebecca Lechalk for their assistance in the field.

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TABLES AND FIGURES

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

Scientific name	Common Name	Observed (%)	Expected (%)
Amyris elemifera	Torchwood	0.0	0.4
Bourreria ovata	Bahama strongbark	3.0	1.5
Bursera simaruba	Gumbo limbo	0.6	6.7
Coccoloba diversifolia	Pigeon plum	2.4	24.4
Coccoloba uvifera	Sea grape	0.0	0.3
Colubrina elliptica	Soldierwood	0.0	0.1
Conocarpus erectus	Buttonwood	4.9	3.5
Drypetes diversifolia	Milkbark	1.2	3.5
Exothea paniculata	Inkwood	0.0	0.2
Ficus aurea	Strangler fig	0.0	3.5
Guapira discolor	Blolly	3.7	6.3
Krugiodendron ferreum	Leadwood	3.7	6.8
Leucaena leucocephala	Leadtree	0.0	0.4
Lysiloma latisiliquum	False tamarind	9.8	4.9
Metopium toxiferum	Florida poisonwood	6.7	24.5
Piscidia piscipula	Jamaican dogwood	0.0	0.4
Pithecellobium unguis-cati	Catclaw	0.0	0.1
Sapindus saponaria	Soapberry	0.0	0.1
Sideroxylon foetidissimum	Mastic	1.2	2.6
Simarouba glauca	Paradise tree	0.0	0.3
Swietenia mahagoni	West Indies mahogany	61.6	9.0
Thrinax radiata	Florida thatch palm	0.0	0.2
Ximenia americana	Hog plum	0.0	0.3
Zanthoxylum fagara	Wild lime	1.2	0

TABLE 2. Comparison of focal tree and site characteristics ($\bar{x}$ ± SE) at nest and random locations for red-bellied squirrels (*Sciurus aureogaster*) on Elliott Key, FL, USA 2006-2007.

Focal Tree Characteristic	**Nest (*n* = 164)**	**Random (*n* = 50)**
DBH (cm)	21.1 ± 0.8	17.9 ± 1.0
Tree height (m)[a]	9.99 ± 0.2	8.95 ± 0.2
Height to 1st major branch (m)	3.71 ± 0.1	3.55 ± 0.2
Live crown length (m)[a]	5.59 ± 0.09	4.97 ± 0.1
Proportion live crown	0.57 ± 0.01	0.56 ± 0.02
No. of canopy linkages[a]	3.6 ± 0.1	2.4 ± 0.2
Distance to near tree (m)	1.4 ± 0.07	1.3 ± 0.1
DBH of near tree (cm)	13.2 ± 0.5	14.2 ± 1.6
Site Characteristic	**Nest (*n* = 118)**	**Random (*n* = 50)**
Canopy cover 0 m (%)[b]	93.2 ± 0.5	88.5 ± 1.2
Canopy cover 5 m (%)[b]	91.2 ± 0.6	85.4 ± 1.6
Canopy cover 10 m (%)[b]	90.5 ± 0.6	85.5 ± 1.5
Canopy cover total (%)[b]	91.6 ± 0.4	86.4 ± 1.1
Visual obstruction (%)	78.1 ± 1.9	82.2 ± 2.2
Shrub stems (no./ha)	19364.4 ± 608.6	20340.0 ± 1315.3
Live trees (no./ha)[b]	1450.3 ± 36.6	1240.0 ± 78.2
Dead trees (no./ha)	116.1 ± 8.4	119.3 ± 13.9
Hurricane class (range 0-4)[b]	2.2 ± 0.04	2.6 ± 0.07
Basal area (m^2/ha)[b]	1038.3 ± 46.4	840.0 ± 85.4
Shannon-Wiener Diversity	1.6 ± 0.03	1.8 ± 0.04
No. of trees within 5m of focal tree[b]	12.4 ± 0.4	9.4 ± 0.6

[a] Indicates variables are different at $\alpha \leq 0.008$ (Bonferroni adjusted value for focal tree characteristic analysis) in 2-tailed *t*-test.

[b] Indicates variables are different at $\alpha \leq 0.0038$ (Bonferroni adjusted value for site characteristic analysis) in 2-tailed *t*-test.

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, FL, USA 2006-2007.

Focal Tree Models					
Model[a]	***K***[b]	**AIC**[c]	**ΔAIC**[d]	w_i[e]	R^2
DBH, height, DBH x 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 x 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 x crown, crown x p. crown	5	223.57	24.23	0.000	0.09
height, crown, height x crown	3	224.85	25.51	0.000	0.07
height	1	225.13	25.79	0.000	0.05
DBH, height, DBH x height, 1st branch, height x 1st branch	5	225.97	26.63	0.000	0.08
Site Models					
Model[f]	***K***[b]	**AIC**[c]	**ΔAIC**[d]	w_i[e]	R^2
cover, hurricane, # in 5 m, cover x hurricane, cover x # in 5 m	5	168.81	0.00	0.417	0.24
cover, hurricane, # in 5 m	3	168.98	0.18	0.381	0.21
cover, hurricane, basal area, # in 5 m	4	170.48	1.67	0.189	0.22
cover, hurricane, cover x hurricane	3	174.98	6.18	0.019	0.19
basal area, hurricane, # in 5 m, basal area x # in 5 m	4	180.72	11.47	0.001	0.17
cover	1	185.25	16.45	0.000	0.11
basal area, # shrubs, diversity, hurricane	4	187.60	18.79	0.000	0.13
# dead trees, hurricane, # dead trees x hurricane	3	195.75	26.94	0.000	0.08
# shrubs, VO, # live trees, # shrubs x VO	4	201.61	33.26	0.000	0.06

[a] DBH = Diameter at Breast Height of focal tree (cm), height = height of focal tree (m), crown = length of live crown (m), linkages = # of canopy linkages, p. crown = proportion live crown, 1st branch = height to first major branch on focal tree (m).
[b] *K* = number of parameters.
[c] AIC = Akaike's Information Criterion values.
[d] ΔAIC = AIC relative to the most parsimonious model.
[e] w_i = AIC model weight.
[f] cover = canopy cover total (%), hurricane = hurricane class (range 0-4), # in 5 m = number of trees within 5 m of focal tree, basal area = basal area (m^2/ha), # live trees = live trees (no./ha), # shrubs = shrub stems (no./ha), diversity = Shannon/Weiner diversity, # dead trees = dead trees (no./ha), VO = visual obstruction (%).

APPENDIX C: DISTRIBUTION AND SPREAD OF AN INTRODUCED INSULAR POPULATION OF RED-BELLIED SQUIRRELS (*SCIURUS AUREOGASTER*), FLORIDA, USA*

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ABSTRACT

Introduced populations of species pose one of the greatest threats to the persistence of native species. Documentation of distribution, range expansion, and habitat use of introduced populations are key components of developing effective management strategies for control and eradication of invasive species. In 2006 and 2007, we surveyed 4 islands in Biscayne National Park for nests to evaluate presence of red-bellied squirrels (*Sciurus aureogaster*) and the distribution and index of dispersion of their nests in the Florida Keys archipelago within the Atlantic Ocean. Red-bellied squirrels were initially introduced to Elliott Key, Florida, USA in 1938. We documented evidence of squirrels on 2 additional islands, Sands Key and Old Rhodes Key, which adds to concern of spread of this introduced squirrel to areas with endangered endemic insular mammals. Squirrel nests were documented only in mixed-hardwood forest, and nests had a clumped distribution within this forest type. Range expansion was a chief concern to the National Park Service, as continued spread could result in squirrels exiting the Park, and prompted management action. Understanding nest site selection and

distribution was critical for developing an eradication strategy for the introduced population of red-bellied squirrels from south Florida.

Key words: colonization, habitat selection, invasive species, index of dispersion, species eradication

INTRODUCTION

Biological invasions are considered one of the greatest threats to biological diversity of native species (Vitousek et al. 1997). Introduced species can lead to diminished native populations through competition, predation, and disease transmission (Lockwood et al. 2007). An estimated 50,000 plant and animal species have been introduced into the United States (Pimentel 2004), and of those, an estimated 4,300 have become established (Corn et al. 1999). Introduced species threaten 49% of federally protected species in the United States (Wilcove et al. 1998), a percentage that will likely continue to increase with the combined effects of habitat loss and global climate change.

Biological invasions have four stages: transport, establishment, spread, and impact (Lockwood et al. 2007). A number of factors influence the success of introduced species in each of these stages (Williamson 1996). The spread, or dispersive stage, determines the spatial extent of the potential ecological impacts (Lockwood et al. 2007). The ability for long-distance dispersal is a major influence on the spread of invasive species (Shigesada and Kawasaki 1997). Finally, dispersal abilities and the resistance of potential barriers vary among taxa (Williamson 1996).

Mammals have been widely introduced around the world (Lever 1985, Long 2003). Historically, the barrier created by aquatic environments often results in oceanic islands that are depauperate of mammals (Williamson and Fitter 1996). As such, introduced mammals can have profound and complex impacts on native flora and fauna, especially in insular ecosystems (Courchamp et al. 2003).

Four red-bellied squirrels (*Sciurus aureogaster*) were introduced to Elliott Key, Dade County, Florida from Mexico in 1938 (Brown and McGuire 1969). The island is part of the Florida Keys, an archipelago of coral islands in the Atlantic Ocean. Elliott Key was home to the native marsh rabbit (*Sylvilagus palustris*) and common raccoon (*Procyon lotor*), but no squirrel species was native to the island. Elliott Key, the surrounding islands, and Biscayne Bay were incorporated into 700 km^2 Biscayne National Park in 1980. Red-bellied squirrels of both the red-bellied gray and melanistic morphs flourished on Elliott Key with few predators and achieved an estimated density of 2.47 squirrels/ha in the mixed-hardwood forest on the island by 1972 (Brown and McGuire 1975). Individuals dispersed naturally and spread to nearby Adams Key and Sands Key separated by salt water, where additional populations were established (Layne 1997). A squirrel was also captured by Biscayne National Park employees as the animal swam from Elliott Key towards Old Rhodes Key, which lies < 500 m to the south across Caesar Creek, a marine passage between islands (Layne 1997). However, the introduced squirrel was believed to be extirpated from Biscayne National Park in 1992 when the tidal surge from Hurricane Andrew submerged the islands under >3 m of saltwater (Ogden 1992, Davis et al. 1993, Layne 1997). Subsequent surveys of the island documented squirrels on Elliott Key, indicating that the species had survived the storm (Koprowski et al. 2005). We initiated an island-wide survey on Elliott Key to determine the distribution of the species on the island, and surveyed 3 adjacent islands within

Biscayne National Park to determine the extent of the dispersive stage and to assess if squirrels had spread beyond Elliott Key.

METHODS

Red-bellied squirrels construct dreys (spherical leaf and stick nests) in trees; dreys are visible from the ground, are excellent indicators of tree squirrel presence (Don 1985), and were the primary means by which we documented presence of this introduced species. The squirrel nests are unique in design and shape, so could not be confused with nests of other animal species. We walked parallel transects spaced 60 m apart through forested areas of the island chain, we used forestry flagging to mark nest trees, and a handheld global positioning system (GPS) to record nest locations. Prior to surveys, we determined that visibility permitted a surveyor to see a leaf nest from <30 m, thus we were confident that nearly 100% of the nests were detected between transects spaced 60 m apart.

Elliott Key was the main study site from January-July 2006 and subsequent visits in January and March of 2007. Elliott Key had 3 main forest types: mixed-hardwood, mangrove, and buttonwood forest. The mixed-hardwood forest covered most of the island interior with pigeon plum (*Coccoloba diversifolia*), Florida poisonwood (*Metopium toxiferum*), false tamarind (*Lysiloma latisiliquum*), leadwood (*Krugiodendron ferreum*), gumbo limbo (*Bursera simaruba*), blolly (*Guapira discolor*), and West Indian mahogany (*Swietenia mahagoni*) as the most common trees. Island margins were dominated by mangrove forest (black mangrove, *Avicennia germinans* and white mangrove, *Laguncularia racemosa*). The buttonwood forest was composed of one species, the buttonwood (*Conocarpus erectus*) tree, and this forest type served as a transitional forest between the mangrove and mixed-hardwood forest.

In addition to Elliott Key, we surveyed Sands Key and Adams Key, 2 islands that squirrels occupied prior to Hurricane Andrew, but on which the current status of the squirrels was unknown. We also surveyed Old Rhodes Key and chose to do so for 3 reasons: 1) at least 1 squirrel attempted to swim to the island in the past 2) the island appeared to have adequate habitat to support a sustainable squirrel population based on recent vegetation cover imagery viewed in GIS 3) a squirrel population on Old Rhodes Key could act as a source for individuals to disperse to nearby Key Largo and exit Biscayne National Park. Other islands within Biscayne National Park did not appear to have adequate habitat to support red-bellied squirrels, so were not surveyed.

Initial nest surveys on Elliott Key revealed that nests appeared to have a clumped distribution within the forest. In order to test this hypothesis, we generated 115 random points on Elliott Key and overlaid both a 50 m X 50 m grid (0.25-ha cells) and a 100 m X 100 m grid (1.0-ha cells). We created the grids using the Create Vector Grid tool within Hawth's Analysis Tools for ArcGIS (Beyer, H. L. 2004. Hawth's Analysis Tools for ArcGIS. Available at http://www.spatialecology.com/htools), and selected only grid cells that were completely contained in or intersected with the island perimeter. We used Count Points in Polygons tool within Hawth's Analysis Tools for ArcGIS to summarize the number of squirrel nests and number of random points within each cell at both grid scales. We calculated the index of dispersion (D = variance in the number of points per grid cell / mean number of points per cell) at both grid scales (Shelby 1965). If the calculated value D for squirrel nests is > 1, the distribution of squirrel nests is clumped, and if D is ≤ 1, the distribution of squirrel nests is non-clumped. The random points generated in ArcGIS had a non-clumped distribution based on our calculation of the index of dispersion (Table 1), so the random points could serve as an appropriate comparison to the distribution of squirrel nests.

RESULTS

We documented red-bellied squirrel nests throughout the mixed-hardwood forest on Elliott Key, 115 nests during the initial survey, but documented no nests in any other forest type (Figure 1). Mixed-hardwood forest covered ~90% or 603 ha of Elliott Key.

We surveyed Adam's Key (Figure 1), located < 200 m to the southwest of Elliott Key monthly from January to July of 2006, and squirrel sign was never detected. The island likely could no longer support a self-sustaining population of squirrels because little remained of the mixed-hardwood forest after damage from Hurricane Andrew.

On 25 March 2007, we traversed the mixed-hardwood hammock forest on Old Rhodes Key (Figure 1) in search of squirrel sign. We documented one drey, however the nest was in disrepair and not currently occupied. We also found fruit from introduced sapodilla trees (*Manilkara zapota*) that exhibited the characteristic incisor marks that indicate feeding by squirrels.

On 26 March 2007, we surveyed Sands Key, which lies < 500 m to the north of Elliott Key, and documented 7 dreys; 2 exhibited signs of current occupation, whereas 4 were in disrepair, and likely unoccupied. Black guard hairs typical of the melanistic squirrels common to Elliott Key (Brown and McGuire 1975) were found in the cup of 1 nest, and red hairs likely from the abdomen of a squirrel with the typical gray and red coat coloration were found in 2 nests. This suggests that multiple squirrels were present on the island, including both the melanistic and red-bellied gray morphs. Clipped branches from false mastic trees (*Sideroxylon foetidissimum*) were found on the forest floor, and the branches had been gnawed consistent with phloem feeding as seen in other *Sciurus* species (Allred and Gaud 1994).

Nest locations had a clumped distribution when compared to random points both at the 50 m X 50 m grid scale (0.25-ha) and the 100 m X 100 m grid scale (1.0 ha; Table 1). However, the clumped association was stronger at the 100 m X 100 m level than at the 50 m X 50 m level.

DISCUSSION

The higher index of dispersion at the 1.0-ha scale compared to the 0.25-ha scale may be explained by the home range size of this species on Elliott Key. Male and female squirrels on Elliott Key are known to have a mean home range size of 2.3 ha and 0.9 ha, respectively based on estimations generated through a live-trapping grid method (Brown and McGuire 1975), and individuals have been observed to use multiple nests within their home range. The 100 m X 100 m grid scale roughly represents the home range of an individual, whereas the 50 m X 50 m grid scale likely represents the core range of an individual. Thus, the smaller grid may be too fine a scale and a single clump of nests of an individual squirrel may be divided into multiple, smaller clumps, reducing the index of dispersion; whereas the 100 m X 100 m grid scale leaves groups of nests from one individual together.

The ability of red-bellied squirrels to survive a catastrophic natural disturbance and continue to proliferate is of great management concern for the National Park Service. This introduced species has demonstrated the ability to overcome marine barriers in this island ecosystem (Layne 1997, Palmer 2012). Red-bellied squirrels do not appear to have an established breeding population on Old Rhodes Key at present, but a population on this island could serve as a source for individuals dispersing to Key Largo, the largest and closest island to the south of Old Rhodes Key. Spread to Key Largo would bring squirrels into contact with the federally endangered Key Largo woodrats (*Neotoma floridana smalli*) and Key Largo cotton mice (*Peromyscus gossypinus allapaticola*: USFWS 1984). Red-bellied squirrels would likely compete with woodrats and cotton mice for food, nesting materials, and potentially tree cavities for nesting sites (Barbour and Humphrey 1982, Humprey 1992, USFWS 1999, McCleery et al. 2006a,b). Although we did not document red-bellied squirrels nesting in cavities, previous studies found individuals to nest in cavities and also to use nest boxes (Brown and McGuire 1975). This is not surprising since other *Sciurus* species are known to nest in cavities (Gurnell 1987).

Continued spread of red-bellied squirrels could also lead to range overlap with native tree squirrels, the eastern gray squirrel (*S. carolinensis*) and the state threatened Big Cypress fox squirrel (*S. niger avicennia*: FFWCC 2004), on the mainland (Brown 1997). Red-bellied squirrels would likely compete with native tree squirrel species for food and nesting sites, and could engage in agonistic behaviors with native individuals. Introduced populations of *S. carolinensis* have severe negative impacts on the native Eurasian red squirrel (*S. vulgaris*) in England and Italy (Bryce et al. 2001, Gurnell et al. 2004). The endangered Mount Graham red squirrel (*T. hudsonicus grahamensis*) faces many factors threatening the species with extinction including an introduced population of Abert's squirrel (*S. aberti*; Edelman and Koprowski 2009). Native western gray squirrels (*S. griseus*) suffer from habitat loss and also compete for food and space with introduced eastern gray squirrels and eastern fox squirrels in California, Oregon, and Washington (Linders and Stinson 2007). These native tree squirrels that struggle to survive the invasion of a nonnative squirrels warn of the potential danger that red-bellied squirrels pose if they continue to spread.

A management plan was implemented by the National Park Service's Florida/Caribbean Exotic Plant Management Team based in part on the results of this research (Palmer et al. 2007, Pernas and Clark 2011). The Team removed 1,410 nests from 1,360 different trees on the affected islands in Biscayne National Park. Thirty-three squirrels (15 males and 18 females) have been removed from Elliott and Sands Key (Pernas and Clark 2011). Eradication and monitoring efforts will continue until the population has been completely removed from Biscayne National Park. Our results demonstrate the need to combine an effective program to monitor the squirrel population with eradication efforts.

Introduced mammalian populations on island ecosystems have decimated native species populations worldwide, and recent removal efforts have sought to eliminate the threats that these introduced species pose, often with immediate positive results (Courchamp et al. 2003). Tree squirrels possess biological characteristics that make the group of species very successful invaders of novel areas (Palmer et al. 2007). A better understanding of the distribution of introduced species, monitoring spread, and their impact on native species are all management priorities in future conservation efforts.

ACKNOWLEDGEMENTS

We wish to thank the Florida/Caribbean Exotic Plant Management Team for funding the project. We thank Richard Curry, Shelby Moneysmith, Todd Kellison, Max Tritt, Jim Chadwick, Sergio Martinez, and Vicente Martinez of the National Park Service for their support of this project and survey effort. Special thanks to Zach Koprowski, Nate Gwinn, Kate Pasch, Brett Pasch, Claire Zugmeyer, Seafha Blount, Pedro M. Chavarria, and Rebecca Lechalk for their assistance in the field. We thank Melissa Merrick for her assistance with GIS, map design, and statistical analyses. Funding and support from the Florida/Caribbean Exotic Plant Management Team and the University of Arizona was greatly appreciated.

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TABLES AND FIGURES

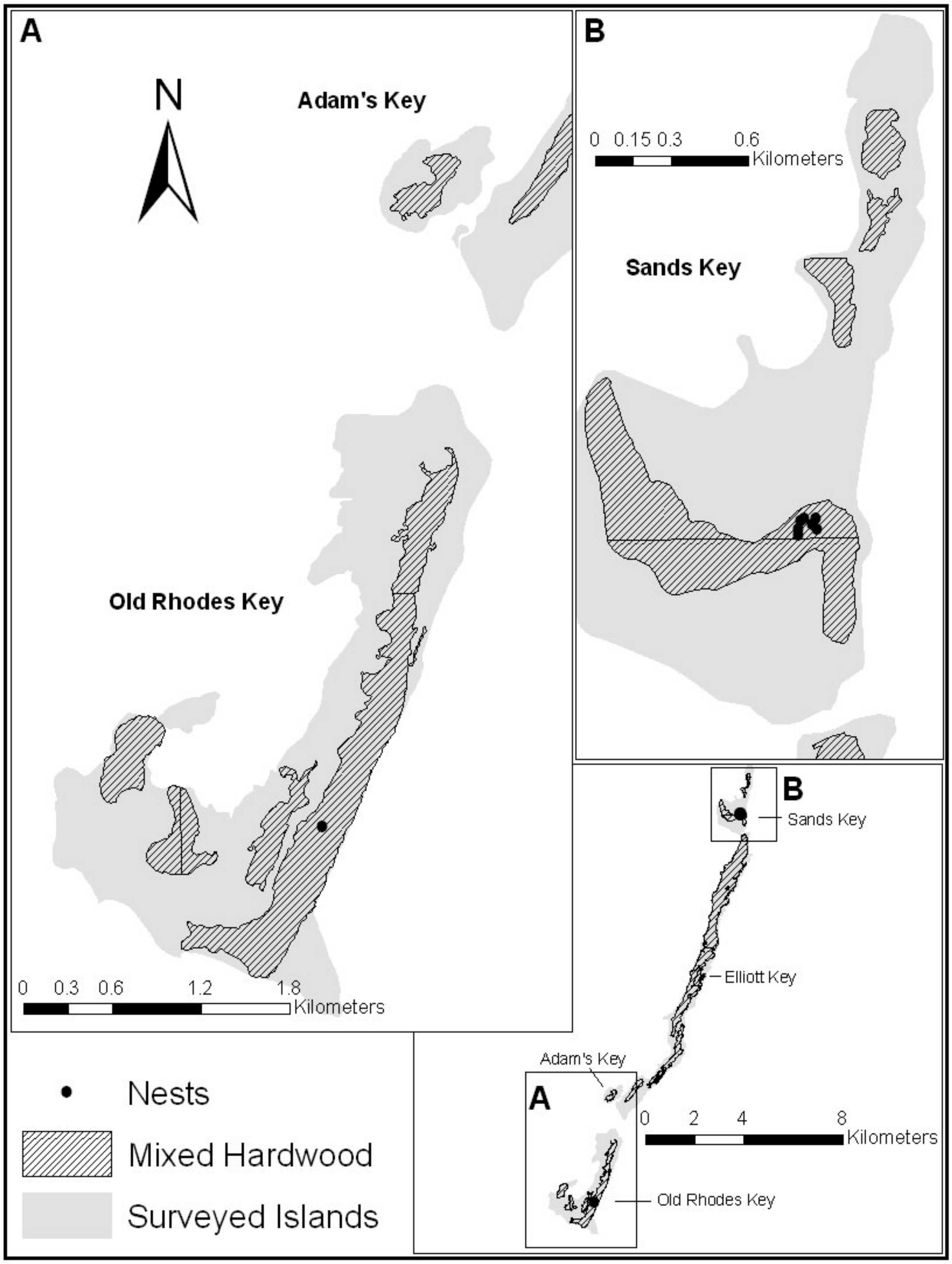

FIGURE 1. Lower right represents island strand within Biscayne National Park including all 4 islands surveyed for the presence of red-bellied squirrels. Left side (A) shows distribution of potential squirrel habitat on Adam's and Old Rhodes Keys, and nest site found on Old Rhodes Key. Upper right (B) shows potential habitat and nest locations on Sands Key.

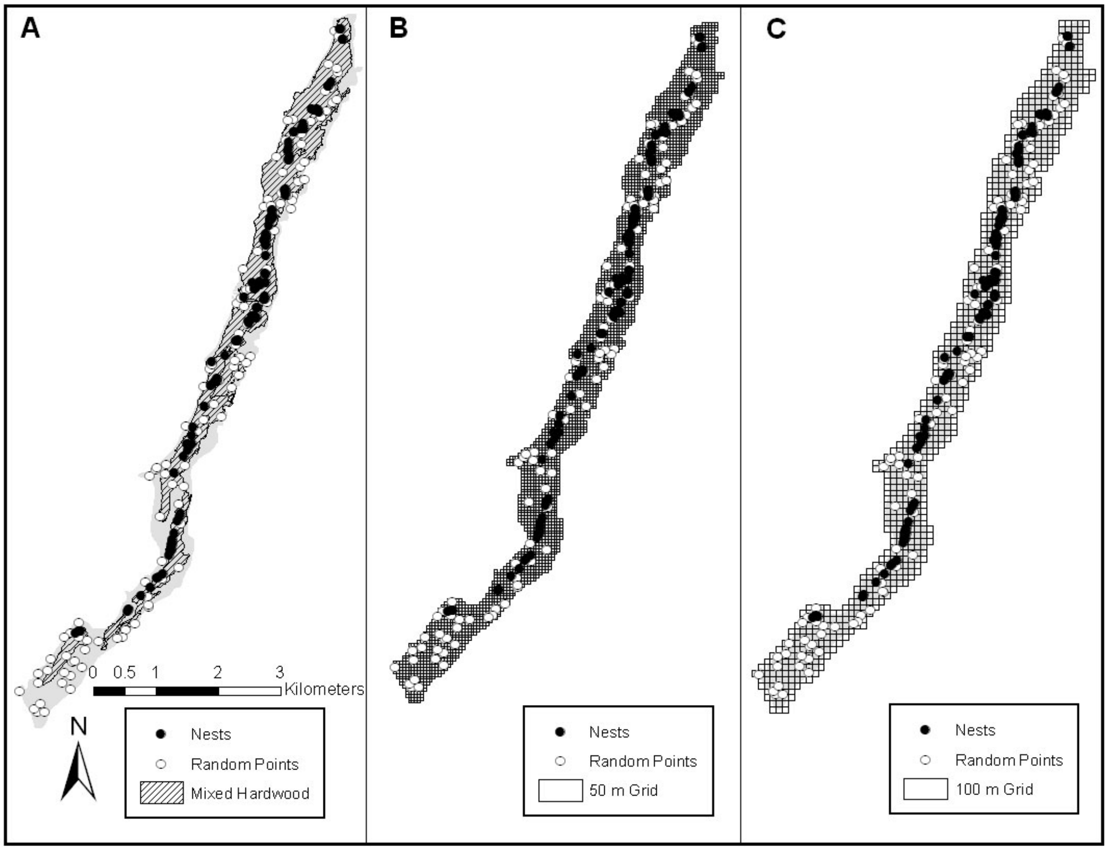

FIGURE 2. Potential red-bellied squirrel habitat on Elliott Key, Florida, USA, and includes locations of nests and random points (A). Center (B) depicts (A) with the overlay of a 50m X 50m grid system, and the right (C) is the overlay of a 100m X 100m grid on (A).

TABLE 1. Index of dispersion calculations for red-bellied squirrel nests and random points for both a 50 m x 50 m grid and a 100 m x 100 m grid on Elliot Key, Florida, USA.

	50 m X 50 m Grid		100 m X 100 m Grid	
	Nest Points	**Random Points**	**Nest Points**	**Random Points**
Sum	108	115	110	115
Mean	0.034	0.036	0.123	0.129
Variance	0.048	0.035	0.296	0.123
Index of Dispersion (D)	1.411	0.972	2.407	0.96