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Distribution and spread of an introduced insular population of red-bellied squirrels (*Sciurus aureogaster*) in Florida

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 the control and eradication of invasive species. In 2006 and 2007, we surveyed four islands in Biscayne National Park for nests to evaluate the 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 in 1938. We documented evidence of squirrels on two additional islands, Sands Key and Old Rhodes Key, which adds to concerns 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.

Keywords: colonization; habitat selection; index of dispersion; invasive species; species eradication.

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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, hybridization and disease transmission (Mooney and Cleland 2001, Lockwood et al. 2007) and impact ecosystems (Manchester and Bullock 2000, Moore et al. 2012). An estimated 50,000 plant and animal species have been introduced into the United States (Pimentel et al. 2004), and, of those, an estimated 4300 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), and the ability to overcome barriers to enter subsequent stages (Richardson et al. 2000, Blackburn et al. 2012). The ability of a species to overcome barriers to dispersal and achieve long-distance dispersal has a major influence on the spread of invasive species and determines the spatial extent of the potential ecological and economical impacts (Shigesada and Kawasaki 1997, Richardson et al. 2000, Lockwood et al. 2007, Blackburn et al. 2011). 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).

Red-bellied squirrels (*Sciurus aureogaster*; Cuvier 1829), also known as Mexican gray squirrels, are native to Mexico and Guatemala and can be found from

tropical forests in lowlands to conifer forests in highlands (Koprowski et al. in press). Four red-bellied squirrels, three with the common red-bellied gray color pattern and one with a melanistic color pattern (Koprowski et al. in press), were introduced to Elliott Key, Dade County, Florida by a resident who imported the squirrels from eastern Mexico in 1938 (Brown and McGuire 1969, 1975). Elliott Key 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*; Bachman 1837) and raccoon (*Procyon lotor*; Linnaeus 1758), but no squirrels were native to the island, and supported few predators capable of capturing and eating squirrels (Brown and McGuire 1975). Elliott Key, the surrounding islands and Biscayne Bay were incorporated into the 700 km^2 Biscayne National Park in 1980. Red-bellied squirrels of both the red-bellied gray and melanistic morphs flourished on Elliott Key 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 across saltwater barriers, likely by swimming or possibly floating on marine debris, and additional populations were established on nearby Adams Key and Sands Key by the 1970s (Layne 1997). A squirrel was also captured by Biscayne National Park employees as the animal swam from Elliott Key toward Old Rhodes Key, which lies <500 m to the south across Caesar Creek, a marine passage between islands (Layne 1997). The islands, and especially the forest interior of the islands, are rarely visited by humans. No records document any human-mediated translocations to nearby islands, and although possible, natural dispersal is suspected over human-mediated translocations that resulted in population spread. 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 >6 m of saltwater (Ogden 1992, Davis et al. 1993, Layne 1997). Subsequent surveys of Elliott Key documented squirrels on the island and indicated that the species had survived the storm (Koprowski et al. 2005); however, the current distribution on Elliott Key and the full extent of the current range of red-bellied squirrels within Biscayne National Park remained unknown. We initiated an island-wide survey on Elliott Key to determine the distribution of the species on the island and surveyed three adjacent islands within Biscayne National Park to determine the extent of the dispersive stage and to assess if squirrels had spread beyond Elliott Key.

Materials and 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 they 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 to July 2006 and subsequent visits in January and March of 2007. Elliott Key had three main forest types: mixed-hardwood, mangrove and buttonwood. Mixed-hardwood forest covered most of the island interior with pigeon plum (*Coccoloba diversifolia*; Jacquin 1760), Florida poisonwood (*Metopium toxiferum*; Krug and Urban 1896), false tamarind (*Lysiloma latisiliquum*; Bentham 1875), leadwood (*Krugiodendron ferreum*; Urban 1902), gumbo limbo (*Bursera simaruba*; Sargent 1890), blolly (*Guapira discolor*; Little 1968) and West Indian mahogany (*Swietenia mahagoni*; Jacquin 1760) as the most common trees. Island margins were dominated by mangrove forest (black mangrove, *Avicennia germinans*; Linnaeus 1759 and white mangrove, *Laguncularia racemosa*; Gaertner 1807). The buttonwood forest was composed of one species, the buttonwood (*Conocarpus erectus*; Linnaeus 1753) tree, and this forest type served as a transitional forest between the mangrove and mixed-hardwood forests.

In addition to Elliott Key, we surveyed Sands Key and Adams Key, two 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; we chose to do so for 3 reasons: 1) at least one 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 geographic information systems (GIS); and 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 they were not surveyed.

Initial nest surveys on Elliott Key revealed that nests appeared to have a clumped distribution within the

forest. To test this hypothesis, we generated 115 random points on Elliott Key and overlaid both a 50 m×50 m grid (0.25-ha cells) and a 100 m×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 forests cover ~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 by Hurricane Andrew.

On March 25, 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*; Royen 1953) that exhibited the characteristic incisor marks that indicate feeding by squirrels.

On March 26, 2007, we surveyed Sands Key, which lies <500 m to the north of Elliott Key, and documented seven dreys; two exhibited signs of current occupation, whereas four 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 one nest, and red hairs likely from the abdomen of a squirrel with the typical gray and red coat coloration were found in two 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*; Jacquin 1760) were found on the forest floor, and the branches had been gnawed in a manner consistent with phloem feeding as seen in other *Sciurus* species (Allred and Gaud 1994).

Nest locations had a clumped distribution (Figure 2) when compared to random points both at the 50 m×50 m grid scale (0.25 ha) and the 100 m×100 m grid scale (1.0 ha; Table 1). However, the clumped association was stronger at the 100 m×100 m level than at the 50 m×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) that often underestimates home range size, and individuals have been observed to use multiple nests within their home range. The 100 m×100 m

Table 1 Index of dispersion calculations for red-bellied squirrel (*Sciurus aureogaster*) nests and random points for both a 50 m×50 m grid and a 100 m×100 m grid on Elliott Key, Florida.

	50 m×50 m grid		100 m×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

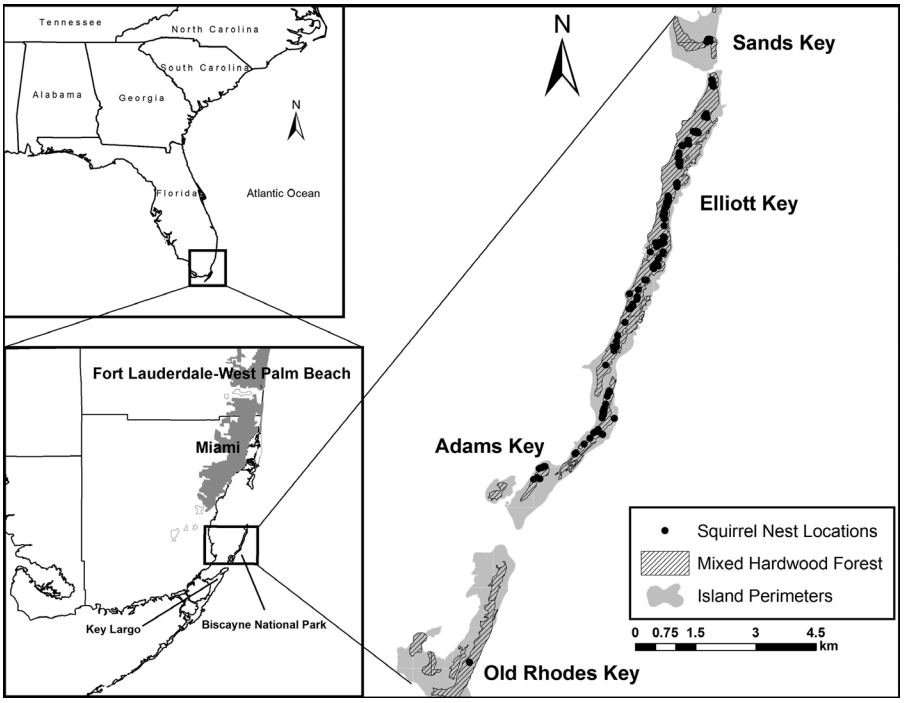

Figure 1 The southeastern United States (upper left), south Florida and the Florida Keys (lower left) and the island strand within Biscayne National Park, including all four islands (right) surveyed for the presence of red-bellied squirrels (*Sciurus aureogaster*). Potential habitat is delineated by gray shading, and nest locations are marked by black circles on each island.

grid scale roughly represents the home range of an individual, whereas the 50 m×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×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 and establish additional populations that 1) increases the potential for greater ecological and economic impact and 2) potentially reduces the likelihood of natural events (weather, disease, etc.) from eradicating the introduced squirrel. 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 woodrat (*Neotoma floridana smalli*; Sherman 1955) and Key Largo cotton mouse (*Peromyscus gossypinus allapaticola*; Le Conte 1850: 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, Humphrey 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 as other *Sciurus* species are known to nest in cavities (Gurnell 1987).

The continued spread of red-bellied squirrels could also lead to range overlap with native tree squirrels, the eastern gray squirrel (*Sciurus carolinensis*; Gmelin 1788) and the state threatened Big Cypress fox squirrel (*S. niger avicennia*; Linnaeus 1758: 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 had severe negative impacts on the native Eurasian red squirrel (*S. vulgaris*; Linnaeus 1758) in England and Italy (Bryce et al. 2001, Gurnell et al. 2004). The endangered Mount Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*; Erxleben 1777) faces many factors threatening the species with extinction, including an introduced population of Abert's squirrel (*S. aberti*;

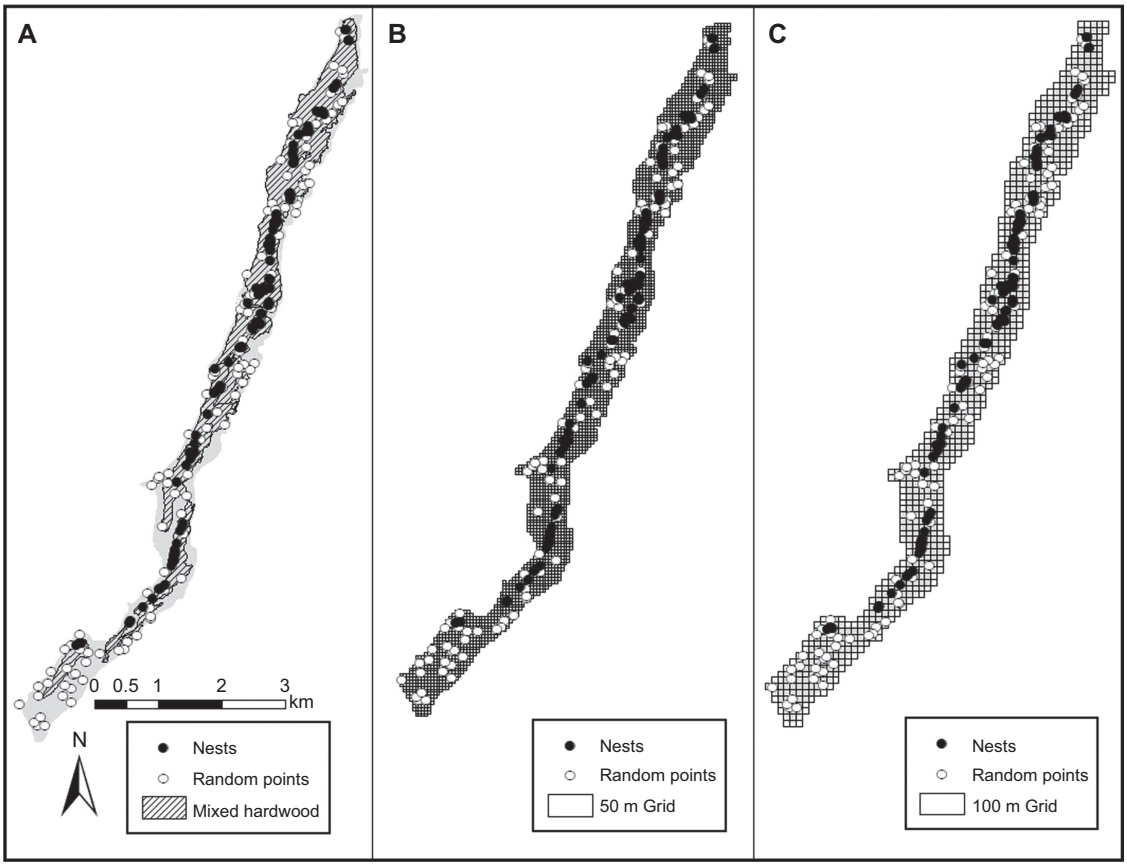

Figure 2 Potential red-bellied squirrel (*Sciurus aureogaster*) habitat on Elliott Key, Florida, including locations of nests and random points (A). Center (B) depicts (A) with the overlay of a 50 m×50 m grid system, and the right (C) is the overlay of a 100 m×100 m grid on (A).

Woodhouse 1853: Edelman and Koprowski 2009). Native western gray squirrels (*S. griseus*; Ord 1818) 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 non-native 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, in press, Pernas and Clark 2011). From March 2006 to July 2012, the team removed 1650 nests on the affected islands in Biscayne National Park. Forty-nine squirrels (22 males and 27 females) have been removed from Elliott and Sands Key. 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, Wood et al. 2007). A better understanding of the distribution of introduced species and monitoring their spread and impact on native species are all management priorities in future conservation efforts.

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