

University of Nebraska - Lincoln

DigitalCommons@University of Nebraska - Lincoln

---

Managing Vertebrate Invasive Species

USDA National Wildlife Research Center  
Symposia

---

August 2007

## TREE SQUIRRELS AS INVASIVE SPECIES: CONSERVATION AND MANAGEMENT IMPLICATIONS

Geoffrey H. Palmer

*School of Natural Resources, The University of Arizona, Tucson, Arizona, USA*

John Koprowski

*School of Natural Resources, The University of Arizona, Tucson, Arizona, USA*

Tony Pernas

*Florida/Caribbean Exotic Plant Management Team, The National Park Service, Miami, Florida, USA*

Follow this and additional works at: <https://digitalcommons.unl.edu/nwrcinvasive>



Part of the [Environmental Indicators and Impact Assessment Commons](#)

---

Palmer, Geoffrey H.; Koprowski, John; and Pernas, Tony, "TREE SQUIRRELS AS INVASIVE SPECIES: CONSERVATION AND MANAGEMENT IMPLICATIONS" (2007). *Managing Vertebrate Invasive Species*. 36. <https://digitalcommons.unl.edu/nwrcinvasive/36>

This Article is brought to you for free and open access by the USDA National Wildlife Research Center Symposia at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in Managing Vertebrate Invasive Species by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.

# TREE SQUIRRELS AS INVASIVE SPECIES: CONSERVATION AND MANAGEMENT IMPLICATIONS

GEOFFREY H. PALMER AND JOHN L. KOPROWSKI, School of Natural Resources, The University of Arizona, Tucson, Arizona, USA

TONY PERNAS, Florida/Caribbean Exotic Plant Management Team, The National Park Service, Miami, Florida, USA

**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, United States. Originally introduced to Elliot Key in 1938, the population expanded until Hurricane Andrew in 1992. Thought to be extirpated, 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 can be formed after research to develop prudent and effective means to meet the challenges that result from control measures to deal with this exotic species.

**Key Words:** *Callosciurus*, exotic, Florida, *Funambulus*, invasive species, *Sciurus*, *Tamiasciurus*.

Managing Vertebrate Invasive Species: Proceedings of an International Symposium (G. W. Witmer, W. C. Pitt, K. A. Fagerstone, Eds). USDA/APHIS/WS, National Wildlife Research Center, Fort Collins, CO. 2007.

---

## 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 invasives. 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 (US) 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 in eastern Canada and the US to 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 exotic

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

Species Name	Date	State/Province/Region	Country	Reference	
<i>Sciurus aberti</i>	1940s, 1970s	Arizona	US	Davis and Brown 1988	
	1929,40,55,69	New Mexico	US	Davis and Brown 1988	
	1898-1908	Utah	US	Davis and Brown 1988	
<i>Sciurus aureogaster</i>	1938	Florida	US	Brown and McGuire 1969	
<i>Sciurus carolinensis</i>	circa 1900,37	Victoria, Melbourne	Australia	Seebeck 1995	
	1914	numerous sites	Canada	Banfield 1974	
	1876-1929	numerous sites	U.K.	Long 2003	
	1913		Ireland	Long 2003	
	1948,66,94	numerous sites	Italy	Bertolino and Genovesi 2003	
	1958	Baja Norte	Mexico	Huey 1964	
	1890s	Cape Town	S. Africa	Macdonald et al. 1988	
	circa 1850's	California	US	Jameson and Peeters 1988	
	1943	Hawaii	US	Kramer 1971	
	not reported	Idaho	US	Larrison and Johnson 1981	
	1919	Oregon	US	Verts and Carraway 1998	
	1958,66,68	Montana	US	Hoffman et al. 1969	
	1904-1952	North Dakota	US	Hibbard 1956	
	not reported	Texas	US	Schmidly 2004	
	1934,49,66,68	Wisconsin	US	Long 2003	
	circa 1920	Washington	US	Flahaut 1941	
	<i>Sciurus niger</i>	1890	Ontario	Canada	Peterson 1966
		early 1900s	California	US	Jameson and Peeters 1988
		early 1900s	Colorado	US	Fitzgerald et al. 1994
		not reported	Idaho	US	Larrison and Johnson 1981
not reported		Montana	US	Hoffman et al. 1969	
prior to 1958		New Mexico	US	Frey and Cambell 1997	
1935,38,41,53,54		North Dakota	US	Hibbard 1956	
not reported		Oregon	US	Verts and Carraway 1998	
not reported		Texas	US	Frey and Cambell 1997	
1915		Washington	US	Yocum 1950	
<i>Sciurus vulgaris</i>		not reported		Germany	Long 2003
		not reported	Caucasus	Crimea	Long 2003
		not reported		Kazakhstan	Long 2003
	not reported		Kyrgyzstan	Long 2003	
<i>Callosciurus erythraeus</i>	1970	Buenos Aires	Argentina	Aprile and Chicco 1999	
	1970s	Cap d'Antibes	France	Gurnell and Wauters 1999	
	1935,54		Japan	Setoguchi 1990	
<i>Callosciurus finlaysoni</i>	1981		Itlay	Bertolino et al. 1999	
<i>Funambulus pennantii</i>	1898	numerous sites	Australia	Long 2003	
<i>Tamiasciurus hudsonicus</i>	1963,64	numerous sites	Canada	Payne 1976	
	1920s	Alaska	US	Long 2003	

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 1960s 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, Oregon, 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 (Flyger and Gates 1982) where their range overlaps that of the state threatened western gray squirrel (*Sciurus griseus*,

Washington Department of Wildlife 1993, Ryan and Carey 1995, Bayrakci et al. 2001). 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, Seebeck 1995, Long 2003). 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 1820s allowed the species to establish on the British Isles, however multiple introductions occurring in the early 1900s allowed the squirrel to become a nuisance animal as it spread to occupy much of the former range of the native Eurasian red squirrel (*Sciurus vulgaris*, Lever 1985). *S. carolinensis* has been introduced to Italy on four separate occasions, with three populations being established (Long 2003, Bertolino and Genovesi 2005).

Numerous negative impacts have been reported from areas of introduction including damage to trees and agriculture (Mountford 1997, Rayden and Savill 2004, Mountford 2006), competition with native squirrels (Macdonald 1988, Washington Department of Wildlife 1993, Wauters et al. 2000, Bayrakci et al. 2001, Gurnell et al. 2004b), and transmission of disease to native species (Rushton et al. 2000, McInnes 2006). 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, Rayden and Savill 2004, Mountford 2006), however, impacts in some areas are 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 (Washington Department of Wildlife 1993, Bayrakci et al. 2001), 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 the native Eurasian red squirrel populations in the British Isles and Italy through competitive exclusion for space and food resources (Wauters et al. 2000, Bryce et al 2001, Gurnell et al. 2004b) and spreading a poxvirus to which *S. vulgaris* is highly susceptible, but which does not effect *S. carolinensis* (Rushton et al. 2000, McInnes 2006).

### **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 US as well as occurring in Sonora and Chihuahua into southern Durango in Mexico (Wilson and Reeder 1993). *Sciurus aberti* was transplanted outside its native range beginning in the early 1900s by different 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 1940s, 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 Pinaleno Mountains of southeastern Arizona, which is home to the endangered endemic Mount Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*, United States Fish and Wildlife Service 1993, Hutton et al. 2003, Edelman and Koprowski 2005, Edelman and Koprowski 2006, Rushton et al 2006).

Abert's squirrels and Mount Graham red squirrels feed on many of the same foods and seek similar trees for nest sites (Hutton et al. 2003, Edelman and Koprowski 2005, Edelman and Koprowski 2006). *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 US and southern Canada (Hall 1981, Koprowski 1994b), and has been introduced in the western US 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 (Marshall 1941, Wright and Weber 1979, Larrison and Johnson 1981, Koprowski 1994b). The squirrel is also found in Asotin County and the Seattle area of Washington (Flahaut 1941, Yocom 1950). This species is currently found in eight 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 1900s (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 (Wolf and Roest 1971, Fitzgerald et al. 1994, Verts and Carraway 1998). Fox squirrels will readily consume a variety of agricultural products including many fruits and nuts (Wolfe and Roest 1971, Flyger and Gates 1982, Koprowski 1994b), and will nest in introduced *Eucalyptus globulus* and the attics of private homes (Wolf and Roest 1971, Koprowski 1994b, Verts and Carraway 1998). The impact of *S. niger* on the native western gray and Douglas squirrels (*Tamiasciurus douglasii*) on the western US coast is attributed to competition for resources, and is a growing conservation concern (Ingles 1947, Robinson and McTaggart-Cowan 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, while occurring as far south as the Mediterranean and Black Seas, parts of Mongolia and China (Wilson and Reeder 1993).

*S. vulgaris* has been successfully introduced to a few areas just outside of 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, which can damage 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 native as well as domestic bird eggs, and they destroy irrigation systems used to provide water for tree plantations and poultry farms in Argentina (Setoguchi 1990, Guichon et al. 2005, 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 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 US 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 (Payne 1976, Long 2003). Negative impacts from this species have not been reported, and the populations have limited ability to disperse as a result of the insular introductions (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 sources including the coconut palm (*Cocos nucifera*), Australian pine (*Casuarina equisetifolia*), and sapodilla (*Manilkara zapota*) as well as consuming papaya (*Carica papaya*) to a lesser extent (Brown

and McGuire 1973, Brown and McGuire 1975). However, beginning in the early 1990s, 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 latisiliqua*), 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 the plant, especially from wild mastic trees (*Masichodendron foetidissimum*). Tilmant (1980) found squirrels utilizing thatch palm leaves (*Thrinax* spp.) in lining their nests, while 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, 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 (Florida Fish and Wildlife Conservation Commission 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 items (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 floral 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 Elliott 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 (Hall 1981, Brown 1997). This is of particular concern as this subspecies is listed as threatened by the State of Florida, and resource needs of the threatened fox squirrel and the red-bellied squirrel would overlap greatly (Brown and McGuire 1975, Brown 1997, Florida Fish and Wildlife Conservation Commission 2004).

The National Park Service has implemented a plan to eradicate this species from Biscayne National Park as the species poses a threat to native species and agriculture. Squirrel nests will be marked with reflective forestry 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 came to reside in the nest boxes.

## REASONS FOR SUCCESS

Tree squirrels are able to establish viable populations from a very small number of propagules (Brown and McGuire 1975, Aprile and Chicco 1999, 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), 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 adapt to human-impacted environments (Jameson and Peeters 1988, Geluso 2004,).

## 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 squirrel numbers, 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 their 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 right's 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). Manipulation of the physical environment, namely 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 invasives have in their new location 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).

## CONCLUSION

Understanding the impacts created by invasive tree squirrel populations is important for the conservation and continuation of native species, especially native tree squirrels. As discussed herein, 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 an invasive population's ecology 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 In Press) make studies of the tree squirrels imperative.

## ACKNOWLEDGMENTS

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. We also thank 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 provided additional assistance on this project. We also acknowledge the Fairchild Botanical Gardens, The Florida and Caribbean Parks Office, and The University of Arizona.

## LITERATURE CITED

- ALLRED, W. S., AND W. S. GAUD. 1994. Effects of Abert squirrel herbivory on foliage and nitrogen losses in ponderosa pine. *Southwestern Naturalist* 39:350-353.
- ALLRED, W. S., W. S. GAUD, AND J. S. STATES. 1994. Effects of herbivory by Abert's squirrels (*Sciurus aberti*) on cone crops of ponderosa pine. *Journal of Mammalogy* 75:700-703.
- APRILE, G., AND D. CHICCO. 1999. Nueva especie exotica de mamifero en la Argentina: la ardilla la de vientre rojo (*Callosciurus erythraeus*). *Mastozoologia Neotropical* 6:7-14.
- BANCROFT, G. T., AND R. BOWMAN. 1994. Temporal patterns in diet of nestling white-crowned pigeons: implications for conservation of frugivorous columbids. *Auk* 111:844-852.
- BANFIELD, A. W. F. 1974. The mammals of Canada. University of Toronto Press, Toronto, Canada.
- BAYRAKCI, R., A. B. CAREY, AND T. M. WILSON. 2001. Current status of the western gray squirrel population in the Puget Trough, Washington. *Northwest Science* 75:333-341.
- BERTOLINO, S., I. CURRADO, AND P. J. MAZZOGLIO. 1999. Finlayson's (variable) squirrel *Callosciurus finlaysoni* in Italy. *Mammalia* 63:522-525.
- BERTOLINO, S., AND P. GENOVESI. 2003. Spread and attempted eradication of the grey squirrel (*Sciurus carolinensis*) in Italy, and consequences for the red squirrel (*Sciurus vulgaris*) in Eurasia. *Biological Conservation* 109:351-358.
- BERTOLINO, S., P. J. MAZZOGLIO, M. VAIANA, AND I. CURRADO. 2004. Activity budget and foraging behavior of introduced *Callosciurus finlaysoni* (Rodentia, Sciuridae) in Italy. *Journal of Mammalogy* 85:254-259.
- BERTOLINO, S., AND P. GENOVESI. 2005. The application of the European strategy on invasive alien species: an example with introduced squirrels. *Hystrix: Italian Journal of Mammalogy* 16:59-69.
- BROWN, L.N., AND R.J. MCGUIRE. 1969. Status of the red-bellied squirrel (*Sciurus aureogaster*) in the Florida Keys. *American Midland Naturalist* 82:629-630.
- BROWN, L. N. 1997. *Mammals of Florida*. Windward Publishing Company, Minneapolis, USA.
- BROWN, L. N. AND R. J. MCGUIRE. 1973. Coconut feeding behavior of the red-bellied squirrel on Elliot Key, Dade County, Florida. *American Midland Naturalist* 89:498.

- BROWN, L. N., AND R. J. MCGUIRE. 1975. Field ecology of the exotic Mexican red-bellied squirrel in Florida. *Journal of Mammalogy* 56:405-419.
- BRYCE, J. M., J. R. SPEAKMAN, P. J. JOHNSON, AND D. W. MACDONALD. 2001. Competition between Eurasian red and Eastern grey squirrels: the energetic differences of body mass. *Proceedings of the Royal Society of London* 268:1731-1736.
- DAGNALL, J., J. GURNELL, AND H. PEPPER. 1998. Bark-stripping damage by gray squirrels in state forests of the United Kingdom: a review. Pages 249-261 in M. A. Steele, J. F. Merritt, and D. A. Zegers, editors. *Ecology and evolutionary biology of tree squirrels*. Special Publication, Virginia Museum of Natural History, Martinsville, USA.
- DAVIS, R., AND D. E. BROWN. 1988. Documentation of the transplanting of Abert's squirrels. *Southwestern Naturalist* 32:490-492.
- EDELMAN, A. J., AND J. L. KOPROWSKI. 2005. Diet and tree use of Abert's squirrels (*Sciurus aberti*) in a mixed-conifer forest. *The Southwestern Naturalist* 50:461-465.
- EDELMAN, A. J., AND J. L. KOPROWSKI. 2006. Characteristics of Abert's squirrel (*Sciurus aberti*) cavity nests. *The Southwestern Naturalist* 51:64-70.
- FINDLEY, J. S. 1987. *The natural history of New Mexican mammals*. University of New Mexico, Albuquerque, USA.
- FITZGERALD, J. P., C. A. MEANEY, AND D. M. ARMSTRONG. 1994. *Mammals of Colorado*. University Press of Colorado, Boulder, USA.
- FLAHAUT, M. R. 1941. Exotic squirrels in the Seattle area. *The Murrelet* 22:63-64.
- FLORIDA FISH AND WILDLIFE CONSERVATION COMMISSION. 2004. *Florida's endangered species, threatened species, and species of special concern*. Florida Fish and Wildlife Conservation Commission, Tallahassee, USA.
- FLYGER, V., AND J. E. GATES. 1982. Fox and gray squirrels. Pages 209-229 in J. A. Chapman and G. A. Feldhamer, editors. *Wild mammals of North America*. Johns Hopkins University, Baltimore, USA.
- FREY, J. K., AND M. L. CAMPBELL. 1997. Introduced populations of fox squirrel (*Sciurus niger*) in the Trans-Pecos and Llano Estacado regions of New Mexico and Texas. *Southwestern Naturalist* 42:356-358.
- GELUSO, K. 2004. Westward expansion of the eastern fox squirrel (*Sciurus niger*) in northeastern New Mexico and southeastern Colorado. *Southwestern Naturalist* 49:111-116.
- GUICHON, M. L., M. BELLO, AND L. FASOLA. 2005. Expansion poblacional de una especie introducida en la Argentina: la ardilla de vientre rojo *Callosciurus erythraeus*. *Mastozoologia Neotropical* 12:189-197.
- GURNELL, J., AND L. WAUTERS. 1999. *Callosciurus erythraeus* (Pallas, 1779). Pages 182-183 in A. J. Mitchell-Jones, editor. *The atlas of European mammals*. Academic Press, London, United Kingdom.
- GURNELL, J., P. W. W. LURZ, M. D. F. SHIRLEY, S. CARTMEL, P. J. GARSON, L. MAGRIS, AND J. STEELE. 2004a. Monitoring red squirrels *Sciurus vulgaris* and grey squirrels *Sciurus carolinensis* in Britain. *Mammal Review* 34:51-74.
- GURNELL, J., L. A. WAUTERS, P. W. W. LURZ, AND G. TOSI. 2004b. Alien species and interspecific competition: effects of eastern grey squirrels on red squirrel population dynamics. *Journal of Animal Ecology* 73:26-35.
- HAAGNER, A. 1920. *South African mammals*. H. F. & G. Witherby, London, United Kingdom.
- HALL, E. R.. 1981. *The mammals of North America*. Volume 2. The Ronald Press Company, New York, USA.
- HEANEY, L. R. 1984. Climatic influences on life-history tactics and behavior of North American tree squirrels. Pages 43-78 in J. O. Murie and G. R. Michener, editors. *The biology of ground-dwelling squirrels: annual cycles, behavioral ecology, and sociality*. University of Nebraska, Lincoln, USA.
- HIBBARD, A. H. 1956. Range and spread of the gray and fox squirrels in North Dakota. *Journal of Mammalogy* 37:525-531.
- HOFFMAN, R. S., P. L. WRIGHT, AND F. E. NEWBY. 1969. The distribution of some mammals in Montana. I. Mammals other than bats. *Journal of Mammalogy* 50:579-604.
- HUEY, L. M. 1964. The mammals of Baja California, Mexico. *Transactions of the San Diego Society of Natural History* 13:85-168.
- HUTTON, K. A., J. L. KOPROWSKI, V. L. GREER, M. I. ALANEN, C. A. SCHAUFFERT, AND P. J. YOUNG. 2003. Use of mixed-conifer and spruce-fir forests by an introduced population of Abert's squirrels. *The Southwestern Naturalist* 48:257-260.
- INGLES, L. G. 1947. Ecology and life history of the California gray squirrel. *California Fish and Game* 33:139-158.
- JAMESON JR., E. W., AND H. J. PEETERS. 1988. *Mammals of California*. University of California, Berkeley, USA.
- KOPROWSKI, J. L. 1994a. *Sciurus carolinensis*. *Mammalian Species* 480:1-9.
- KOPROWSKI, J. L. 1994b. *Sciurus niger*. *Mammalian Species* 479:1-9.
- KOPROWSKI, J. L., G. T. KELLISON, AND S. L. MONEYSMITH. 2005. Status of red-bellied squirrels (*Sciurus aureogaster*) introduced to Elliott Key, Florida. *Florida Field Naturalist* 33:128-129.
- KOPROWSKI, J. L., N. RAMOS, B. S. PASCH, AND C. A. ZUGMEYER. 2006. Observations on the ecology of the endemic Mearns's squirrel (*Tamiasciurus mearnsi*). *The Southwestern Naturalist* 51:426-430.

- KOPROWSKI, J. L., AND N. RAJAMANI. In Press. Global hotspots, centers of diversity, and conservation of the tree and flying squirrels. *Current Science* 92.
- KRAMER, R. J. 1971. Hawaiian land mammals. Charles E. Tuttle Co., Rutland, USA.
- LARRISON, E. J., AND D. R. JOHNSON. 1981. Mammals of Idaho. The University Press of Idaho, Moscow, USA.
- LAYNE, J. 1997. Nonindigenous mammals. Pages 157-186 in D. Simberloff, D. Schmitz, and T. Brown, editors. Strangers in paradise: impact and management of nonindigenous species in Florida. Island Press, Washington, D.C., USA.
- LEVER, C. 1985. Naturalized mammals of the world. Longman, London, United Kingdom.
- LONG, J. L. 2003. Introduced mammals of the world. CABI Publishing, Wallingford, United Kingdom.
- MACDONALD, I. A. W., D. M. GRABER, S. DEBENEDETTI, R. H. GROVES, AND E. R. FUENTES. 1988. Introduced species in nature reserves in Mediterranean-type climatic regions of the world. *Biological Conservation* 44:37-66.
- MARSHALL, W. H. 1941. The fox squirrel in Idaho. *The Journal of Mammalogy* 22:86-87.
- MCINNES, C. J., A. R. WOOD, K. THOMAS, A. W. SAINSBURY, J. GURNELL, F. J. DEIN, AND P. F. NETTLETON. 2006. Genomic characterization of a novel poxvirus contributing to the decline of the red squirrel (*Sciurus vulgaris*) in the UK. *Journal of General Virology* 87:2115-2125.
- MIYAMOTO, A., N. TAMURA, K. SUGIMURA, AND F. YAMADA. 2004. Predicting habitat distribution of the alien formosan squirrel using logistic regression model. *Global Environmental Research* 8:13-21.
- MOUNTFORD, E. P. 1997. A decade of grey squirrel bark stripping damage to beech in Lady Park Wood, UK. *Forestry* 70:17-29.
- MOUNTFORD, E. P. 2006. Long-term patterns and impacts of grey squirrel debarking in Lady Park Wood young-growth stands (UK). *Forest Ecology and Management* 232:100-113.
- PAYNE, N. F. 1976. Red squirrel introduction to Newfoundland. *The Canadian Field-Naturalist* 90:60-64.
- PETERSON, R. L. 1966. The mammals of eastern Canada. Oxford University Press, Toronto, Canada.
- RAYDEN, T. J., AND P. S. SAVILL. 2004. Damage to beech woodlands in the Chilterns by the grey squirrel. *Forestry* 77:249-253.
- ROBINSON, D. J., AND I. MCTAGGART-COWAN. 1954. An introduced population of the grey squirrel (*Sciurus carolinensis* Gmelin) in British Columbia. *Canadian Journal of Zoology* 32:261-282.
- RUSHTON, S. P., P. W. W. LURZ, J. GURNELL, AND R. FULLER. 2000. Modelling the spatial dynamics of parapoxvirus disease in red and grey squirrels: a possible cause of the decline in the red squirrel in the UK? *Journal of Applied Ecology* 37:997-1012.
- RUSHTON, S. P., D. J. A. WOOD, P. W. W. LURZ, AND J. L. KOPROWSKI. 2006. Modelling the population dynamics of the Mt. Graham red squirrel: can we predict its future in a changing environment with multiple threats? *Biological Conservation* 131:121-131.
- RYAN, L. A., AND A. B. CAREY. 1995. Distribution and habitat of the western gray squirrel (*Sciurus griseus*) on Ft. Lewis, Washington. *Northwest Science* 69:204-216.
- SEEBECK, J. H. 1995. Eastern grey squirrel. Page 234 in P. W. Menkhorst, editor. *Mammals of Victoria*. Oxford University Press, Melbourne, Australia.
- SETOGUCHI, M. 1990. Food habits of red-bellied tree squirrels on a small island in Japan. *Journal of Mammalogy* 71:570-578.
- SHEAIL, J. 1999. The grey squirrel (*Sciurus carolinensis*)-a UK historical perspective on a vertebrate pest species. *Journal of Environmental Management* 55:145-156.
- SCHMIDLY, D. J. 2004. The mammals of Texas. University of Texas, Austin, Texas, USA.
- SIGNORILE, A. L., AND J. EVANS. 2007. Damage caused by the American grey squirrel (*Sciurus carolinensis*) to agricultural crops, poplar plantations and semi-natural woodland in Piedmont, Italy. *Forestry* 80:89-98.
- STEELE, M. A. 1998. *Tamiasciurus hudsonicus*. *Mammalian Species* 586:1-9.
- STEELE, M. A., AND J. L. KOPROWSKI. 2001. North American tree squirrels. Smithsonian Institution, Washington D.C., USA.
- TAMURA, N., AND S. OHARA. 2005. Chemical components of hardwood barks stripped by the alien squirrel *Callosciurus erythraeus* in Japan. *Journal of Forestry Research* 10:429-433.
- TILMANT, J. T. 1980. Investigations of rodent damage to the thatch palms *Thrinax morrisii* and *Thrinax radiata* on Elliot Key, Biscayne National Park, Florida. South Florida Research Center, Everglades National Park, USA.
- UNITED STATES FISH AND WILDLIFE SERVICE. 1993. Mount Graham red squirrel recovery plan. United States Fish and Wildlife Service, Albuquerque, USA.
- VERTS, B. J. AND L. N. CARRAWAY. 1998. Land mammals of Oregon. University of California, Berkeley, USA.
- WASHINGTON DEPARTMENT OF WILDLIFE. 1993. Status of the western gray squirrel (*Sciurus griseus*) in Washington. Final status report. Olympia, Washington, USA.
- WAUTERS, L. A., P. W. W. LURZ, AND J. GURNELL. 2000. The effects of interspecific competition by grey squirrels (*Sciurus carolinensis*) in the space use and population dynamics of red squirrels (*S. vulgaris*) in conifer plantations. *Ecological Research* 15:271-284.

- WILSON, D. E., AND D. M. REEDER. 1993. Mammal species of the world. Smithsonian Institution, New York, USA.
- WOLFE, T. F., AND A. I. ROEST. 1971. The fox squirrel (*Sciurus niger*) in Ventura County. California Fish and Game 57:219-220.
- WOOD, D. J. A., J. L. KOPROWSKI, P. W. W. LURZ. 2007. Tree squirrel introduction: a theoretical approach with population viability analysis. Journal of Mammalogy 88:1271-1279.
- WRIGHT, G. M. AND J. W. WEBER. 1979. Range extensions of the fox squirrel in southeastern Washington and into adjacent Idaho. The Murrelet 60:73-75.
- YOCOM, C. F. 1950. Fox squirrels in Asotin County, Washington. The Murrelet 31:34.