The aggressive invasion of exotic reptiles in Florida with a focus on prominent species: A review

Richard ENGEMAN1*, Elliott JACOBSON2, Michael L. AVERY3, Walter E. MESHAKA, Jr.4

1 USDA/APHIS/Wildlife Services/National Wildlife Research Ctr, 4101 LaPorte Ave., Fort Collins, CO 80521-2154, USA
2 College of Veterinary Medicine University of Florida, Gainesville, FL 32610, USA
3 USDA/APHIS/Wildlife Services/National Wildlife Research Ctr, 2820 East University Ave., Gainesville, FL 32641, USA
4 The State Museum of Pennsylvania, 300 North Street, Harrisburg, Pennsylvania 17120, USA

Abstract Florida, along with Hawaii, has among the two worst invasive species problems in the USA, and the state is especially susceptible to establishment by alien reptiles. Besides the large numbers of established non-native reptile species in Florida, many of these species present novel difficulties for management, or have other characteristics making effective management extremely challenging. Moreover, initiation of management action requires more than recognition by experts that a potentially harmful species has become established. It also requires the political will along with concomitant resources and appropriate personnel to develop effective methods and apply them. We review the situation in Florida, including assessment of risk for establishment, and we use a subset of prominent species to illustrate in more detail the array of invasive reptile species circumstances in Florida, including routes of introduction, impacts, and potential and implemented management actions. These examples not only highlight the severity of the invasive reptile problems in the state, but they also show the diversity in resolve and response towards them and the motivating factors [Current Zoology 57 (5): 599–612, 2011].

Keywords Argentine black and white tegus, Biophysical ecology, Burmese pythons, Control, Green and spiny-tailed iguanas, Invasive species, Nile monitors, Northern curlytail lizards

1 Introduction: Overview, How They Get to Florida, and Why They Thrive

When considering the numbers and proportion of species that are invasive, Florida’s reptile fauna is in dysfunction. Exotic snakes, lizards, turtles, and crocodilians are all breeding in Florida (e.g., Meshaka et al., 2004a). Waves of exotic lizards have swept across much of the state, only to be joined or supplanted by subsequent lizard species (e.g., Bartlett and Bartlett, 1999; Meshaka et al., 2004a). The largest snakes in Florida are constrictors from other continents, and the five largest lizard species breeding in Florida are from Africa, South America, and Central America. Many exotic arrivals to Florida do not appear in the public consciousness. For example, the mainstream public is typically unaware that the number of non-native lizard species breeding in Florida now exceeds the number of native species, with over three times as many non-native lizard species as native breeding in south Florida (Hardin, 2007). Many of the non-native lizard species can eat various life stages of other lizards and also compete for food or space (Meshaka et al., 2004a). Nonetheless, problems with several large reptile species in recent years have received public/media attention, a factor sometimes serving to catalyze action. To date, large constrictor snakes have received the vast majority of the attention, although a variety of other species occasionally have been highlighted in the media.

Florida’s subtropical climate in the south, its major ports of entry for many wildlife species to the U.S. (both legal and illegal), its thriving captive wildlife industry, and its location in an area of destructive hurricanes that can release captive animals make the state especially susceptible to the introduction and establishment of a wide range of species (e.g. Corn et al., 2002; Hardin, 2007). Moreover, Florida is isolated from land with similar climates, resulting in the state’s vertebrates typically originating in the southeast U.S. at the southern extremes of their range. Invaders to Florida there-
fore find relatively fewer native species to contend with than in most tropical/subtropical locations (Hardin, 2007). Not surprisingly, Florida, along with Hawaii, is one of the two states with the most severe invasive species problems in the United States (U.S. Congress, 1993; Corn et al., 2002). Notably, Florida has more introduced animals than any other region of the U.S. and also ranks high in this respect globally, with breeding populations of new species regularly identified (SFWMD, 2008). Given Florida's climate, it is no coincidence that a large proportion of Florida's invasive vertebrate species are reptiles. Establishment of non-native herpetofauna has been documented in Florida for over 135 years (Cope, 1875; Meshaka et al., 2004a), and the rate at which invasive herpetofauna species have accumulated has been accelerating in the last half century (Meshaka et al., 2004a).

The negative impacts inflicted by exotic species on native species and ecosystems may only be exceeded by human-caused habitat destruction (Parker et al., 1999; Wilcove et al., 1998). Exotic species have played a role in the listing of 42% of the species protected by the U.S. Endangered Species Act (Stein and Flack, 1996). South Florida, in particular, provides an ideal medium in which invasive species, the “pathogens of globalization” (Bright, 1999), can incubate. In fact, quantitative indicators for assessing non-native species situations are analogous to epidemiological descriptors of disease status in a population (Meyerson et al., 2008).

The impacts from many introductions are unknown or not readily perceived by the public, while others are immediately apparent or have their negative potential revealed over time. Even highly prolific invasive species may fester unnoticed for a considerable time before exhibiting an explosive expansion of their range (Shigesada and Kawasaki, 1997). Management of non-indigenous species requires more than the recognition of a potential problem, it also requires a governmental/public motivation to address the problem. Invasive species often present novel control situations for managers, requiring the acquisition of biological knowledge focusing on potential vulnerabilities, and the development and testing of control technologies and strategies (see, for example, Engeman and Vice, 2001). This is especially true for reptiles where relatively few broad programs have been applied around the world to develop and implement control methods for reptiles, with the most notable being for brown treesnakes Boiga irregularis on Guam (Engeman and Vice, 2001).

The situation in Florida is best understood first by examining factors for assessing risk of establishment and spread of invasive reptiles, and then through some prominent examples of invasive reptiles in Florida. Overall, the examples not only demonstrate the breadth of the invasive reptile problems in the state, but they also show the diversity in resolve and response among the many species and the motivating factors.

2 Assessing Risk of Establishment and/or Range Expansion

The zoogeography of reptiles is substantially influenced by environmental factors, with ambient temperature critically affecting their distribution. Reptiles regulate their body temperature both physiologically and behaviorally, with the critical thermal maximum and critical thermal minimum setting the temperature limits for their survival. Possibly, the minimum activity temperature is of greater importance in reptile distribution than their maximal thermal tolerance (Jacobson and Whitford, 1970). The preferred optimum temperature ranges and thermal limits have not been defined for most reptiles. Therefore, climate matching is a commonly applied technique for estimating the geographical limits and risk potential of an invading species based on where they are found in their native geographic ranges. However, there is a lack of specific protocols to insure the selection of variables applied in a climate matching analysis will produce an accurate reflection of where the invading species might expand its range.

Recent examples have shown the importance of using daily extreme high and low temperatures from native ranges, rather than only mean monthly temperatures, when assessing the thermal tolerances of invasive species in their introduced ranges (Avery et al., 2010a). Moreover, when developing climate data from native ranges, it is essential to first have an accurate assessment of the native range with actual record locations, rather than loosely connected boundary lines within which record locations are broadly found. Otherwise, it is impossible to associate with certainty a weather station to an area in which the species is found. It is essential to avoid the trap of strictly considering species record locations and meteorological stations based on two-dimensional map distances without also considering intervening three dimensional altitudinal topographies, as this could greatly bias the climate data for the native range (e.g., Barker and Barker, 2010).

Climate modeling is a fairly simple concept whereby a species’ potential to spread to an exotic location is extrapolated from characteristics of its native range.
Bomford et al. (2009) suggested that climate modeling can be a valuable tool for assessing the risk of establishment of alien herpetofauna, and many researchers have been exploring and evaluating attributes for assessing establishment risk (Bomford et al., 2009; Hayes and Barry, 2008; Stohlgren and Schnase, 2006). As with all statistics and modeling, the data upon which a model is generated and the analytical methods used to produce the results determine the accuracy of inferences. Thus, details such as the most appropriate native climate data to use in projections of introduced species ranges and the associated analytical methodology can radically alter predictions.

Since temperature has such a major effect on their distribution, a climate matching model was used to estimate the geographical limits and invasive risk potential of nine large constrictor snakes in the United States (Rodda et al., 2009; Reed and Rodda, 2009). In these reports, the Burmese python (Python molurus bivittatus, and recently classified as Python bivittatus) was lumped together with its close relative, the Indian python Python molurus molurus, as Python molurus in an attempt to define the areas in the United States climatically suitable for colonization by Burmese pythons (despite the Indian python being treated separately under CITES [www.cites.org, accessed 12 January 2011] and others considering them to be separate species [see Jacobs et al., 2009 for a formal definition of the Burmese python as a distinct species]). The modeling results projected a potential range encompassing much of the southern third of the U.S. (Reed and Rodda, 2009). In a subsequent report, ecological niche models contradicted these findings and indicated the only suitable habitat for Burmese pythons in the United States is limited to extreme southern Florida and extreme southern Texas (Pyron et al., 2008). These radically different results demonstrate well that predictions of invasive potential of the Burmese python are highly influenced by the data sources and modeling factors.

The unusual prolonged cold front in southern Florida during January 2010 provided valuable empirical information concerning thermal tolerances of Burmese pythons and possibly also served as a model for other reptiles with similar thermal ecology and behavioral adaptations. In January 2010, the ambient temperature at Homestead Air Force Base (east of Everglades National Park) reached $\leq 0^\circ$C for 3 hours, with 7 days with minimum temperatures $\leq 5^\circ$C, and 6 days with maximum temperatures $\leq 16^\circ$C. Following the cold temperature period, 9 of 10 radio-telemetered Burmese pythons in the Everglades National Park were found dead or near dead (Mazzotti et al., 2010), suggesting a large portion of the wild population succumbed to the cold. In contrast, during the previous winter (2008–2009) there were no days of freezing temperatures and 6 days with daily minimum temperatures $\leq 5^\circ$C and only 2 days with maximum temperatures $\leq 16^\circ$C. No unusual mortality was reported. However, when mean temperatures for these months were calculated, January 2009 and January 2010 had mean monthly temperatures of 17°C and 15°C respectively. Significantly in 2010, the coldest day overall (January 10) was followed by freezing temperatures on January 11. The high temperature for January 10 was 8°C and the low was 1°C. On January 11, the high temperature was 16°C and the low was -1°C. Preceding the freeze, from January 2 to January 9, low temperatures ranged from 4°C to 9°C. This week of above freezing cold temperatures more than likely “primed” Burmese pythons for the freezing temperature on January 11, since dead pythons were encountered following that date. Such extreme daily temperature changes rather than, or in addition to, monthly mean temperatures need to be factored into climate-matching models used to define areas at risk of invasion, not only by Burmese pythons, but also other non-native reptiles as well.

3 Burmese Pythons

The Burmese python has quickly become the highest profile reptile of the many invasive reptiles in Florida. Due to its large adult size that may exceed 5 m and the range of food items at risk to be eaten, it has received considerable media attention. Graphic photos in 2005 in print and electronic media showed the carcass of a 1.8-m alligator protruding from the belly of a 4-m Burmese python. Subsequently, a highly publicized, and controversial, report hypothesizing that the snake could invade much of the southern third of the U.S. (Reed and Rodda, 2009; Rodda et al., 2009; Barker and Barker, 2008a, b) added fuel to the imagined fears of the public.

The species has been breeding in the wild in south Florida for over a quarter-century (Meshaka et al., 2000). Its invasion pathway in south Florida has been largely

1 Reed RN, Rodda GH, 2009. Giant constrictors: Biological and management profiles and an establishment risk assessment for nine large species of pythons, anacondas, and the boa constrictor. USGS Open File Report 2009–1202.
attributed to (illegal) pet releases, although the highly destructive Hurricane Andrew in 1992 may also have released many from captive breeding and holding facilities (Snow et al., 2007a; Bilger, 2009). The ecological impacts from this large invasive predator are yet to be fully understood, but Burmese pythons in south Florida are already known to consume a wide variety of native wildlife, including endangered species (Greene et al., 2007; Snow et al., 2007b). Placement of their depredations in an economic context has identified economic and policy benefits for addressing the problem (Smith et al., 2007).

While the numbers and range of Burmese python observed in south Florida have expanded in recent years, the extent of its potential range in the US has been the subject of considerable controversy (Snow et al., 2007a; Barker and Barker, 2008a,b; Pyron et al., 2008; Rodda et al., 2009). The previously highlighted climate matching approach using the combined information from within and near the native ranges of the Burmese python and the closely related Indian python produced potential range projections north to Washington, DC and west to California (Rodda et al., 2009). However, ecological niche models using biological and ecological factors for the Burmese python native range resulted in a much narrower calculated range, with only extreme south Texas added to its current introduced range (Pyron et al., 2008). These radically divergent projections on the potential range of the Burmese python led to spirited discussion, but empirical information detailing the fate of Burmese pythons during the aforementioned recent cold spell in Florida during the winter of 2009–2010 agree with the predictions of the more conservative model (Pyron et al., 2008), and indicated the snakes would not likely spread beyond extreme south Florida (Avery et al., 2010a; Mazzotti et al., 2010). Avery et al. (2010a) presented evidence that, even with refugia and heat sources, adult Burmese pythons did not demonstrate behavioral or physiological abilities to survive cold weather events in the central Florida peninsula, 400 km north of their currently known introduced range. Mazzotti et al. (2010) found 9 of 10 of their wild and free-ranging adult pythons equipped with radio transmitters in Everglades National Park at the southern tip of the Florida peninsula died subsequent to the cold spell in January 2010. A third study (Dorcas et al., 2011) was published on the results of an experiment aimed at testing whether Burmese pythons could survive in the more temperate climates predicted by Rodda et al. (2009). In that study, 10 wild-caught male pythons from Everglades National Park were released in June 2009 into a near-natural enclosure in Aiken County, South Carolina. The same cold front that severely impacted the Florida pythons also passed through South Carolina at the same time. However, temperatures in South Carolina are cooler than in Florida and 8 of the 10 pythons had already died in unseasonably cool temperatures prior to the arrival of the severe cold front in January 2010, and the final two of the pythons were found dead after the cold front (Dorcas et al., 2011). These results are expectedly congruent with those of Avery et al. (2010a) and Mazzotti et al. (2010) considering the colder temperatures found north of Florida in South Carolina, and those results also are supportive of the Pyron et al. (2008) conservative predictions for US establishment of Burmese pythons in only the extreme southern tips of Florida and Texas.

The above observations (Avery et al., 2010a; Mazzotti et al., 2010) were also congruent with those of Barker (2008) on tropical constrictors, including Burmese pythons, not displaying a survival instinct for avoiding lethally cold temperatures. The Burmese python is a tropical and subtropical species and does not appear to recognize potentially lethal cold, with the snakes’ urge to explore or bask rather than shelter placing them at risk. Barker (2008) hypothesized that descendants from tropical populations of constrictors where freezing weather is unknown may not have the ability to recognize the need to shelter from fatally cold temperatures, as such behavior is unnecessary in their native ranges where such cold extremes are unknown.

The origins of Burmese pythons in the pet trade, and hence the Florida invasive population, came from a subset of the native range, primarily Thailand near Bangkok (initially) and subsequently Viet Nam near Ho Chi Minh City after 1994 (Barker and Barker, 2008b,c). When the Indian python was listed as an endangered species, exports from India and Sri Lanka closed, with Thailand essentially becoming the only Southeast Asian country exporting native Burmese pythons. Trade with Vietnam was banned at this time. Thailand was probably the source of 95% of all Burmese pythons imported into the USA through 1985, with small numbers entering from Thailand through 1989 (Barker and Barker, 2008a). According to a major Burmese python importer, from the late 1960s until 1985 the Burmese pythons were collected for export in the general vicinity of Bangkok at elevations not exceeding 100 m (Barker and Barker, 2008a,b). Imports of Burmese pythons to the US declined from the late 1980s through the early 1990s (Barker and Barker, 2008a). Beginning in 1994, Bur-
Burmese pythons were imported from Vietnam, mostly from captive breeding farms near Ho Chi Minh City (Barker and Barker, 2008a).

Recent genetic results showed little differentiation among Burmese pythons captured in south Florida (Collins et al., 2008). The animals examined were genetically distinct from Vietnamese specimens, suggesting the predominant genetic origins of the Florida pythons were likely among those from the lowland Bangkok, Thailand area, a circumstance also within the realm of a possible release by Hurricane Andrew in 1992, although genetic comparisons to Thai pythons were not conducted. It should be noted that the destruction following Hurricane Andrew is believed responsible for the escape and introduction of at least one other invasive species from captivity, the sacred ibis Threskiornis aethiopicus (Gawlik and Calle, 2010; Herring et al., 2006). As with many exotic species, the founding population sources are probably multiple and may never be definitively known. Nevertheless, a potentially significant consequence of the low genetic variability within the south Florida population may be reduced behavioral and ecological flexibility, with a resultant inability to adapt to significant changes in climatic conditions.

Even though it appears unlikely Burmese pythons will spread very far north from where they are currently found, the issue remains how best to manage and/or reduce numbers where they are currently found. Controlling Burmese pythons in everglades habitats of wet sawgrass prairies with interspersed hardwood hammocks will be challenging. The snake appears vulnerable to approaches that take advantage of its reproductive behaviors. Telemetry trials have already demonstrated on a small scale that female snakes during breeding season can be used as lures to locate males, and telemetered males can be used to locate females (Harvey et al., 2008). Because it takes three to five years for Burmese pythons to reach sexual maturity, even if all breeding adults could be removed each year, control methods based on reproductive behaviors would require a multi-year endeavor to capture animals as they reach sexual maturity.

A set of control tools and strategies were successfully developed for another destructive invasive snake, the brown treesnake on Guam (Engeman and Vice, 2001). While the Burmese python is a significantly different species than the brown treesnake, the same conceptual approaches for developing an integrated pest management program can be applied, and to a degree are being developed. Acetaminophen was found to be toxic to brown treesnakes and is being used for their control in Guam (Savarie et al., 2001). Subsequent tests also found acetaminophen to be toxic to Burmese pythons (Mauldin and Savarie, 2010), and preference tests for bait matrices found that juvenile pythons preferred natural prey items (Avery et al., 2010b; Savarie, National Wildlife Research Center unpublished data). In Florida, bait placement would need to be specific to Burmese pythons to avoid harming non-target species. The unique combination of the python’s size, dietary potential, and movement ability could be used to make bait delivery specific to the pythons. Multi-capture traps and trap-drift fence combinations are being designed and tested for capturing pythons (Avery et al., 2010b; Hart et al., 2010). Much development of tools and methods would be needed to produce a highly efficient control program for Burmese pythons. Nevertheless, enough knowledge is probably available currently to initiate control should resources become available. It is through experience gained from application of control that development of new and more effective methods and strategies would accelerate (Engeman and Vice, 2001).

4 Nile Monitor Lizards

Also notable among Florida’s invasive reptiles are problems from a very large (up to 2.3 m), varanid lizard, the Nile monitor Varanus niloticus, which over the last 15+ years has become firmly established in the Cape Coral area (Lee County) after first being reported in 1990 (Enge et al., 2004). It also now appears established in the Homestead Air Reserve Base area (Miami-Dade County), and has been observed in at least five other Florida counties (Florida Fish and Wildlife Conservation Commission 2010, USDA/Wildlife Services unpublished data). Nile monitors have been commonly sold in the U.S. pet trade (Bayless, 1991; Faust, 2001), despite having a disposition and an adult body size that makes them ill-suited as a pet (Bennett, 1995). Its range around Cape Coral is expanding into neighboring wild-lands, and it also is found on nearby Pine Island, and possibly Sanibel Island as well, where it would be a threat to endangered sea turtles and shore birds (Enge et
al., 2004; Campbell, 2005). These more newly colonized habitats, however, would be more challenging to implement effective control than in the Cape Coral community.

The Nile monitor can rapidly outgrow many, if not most, potential predators (Meshaka, 2006), and this large-bodied carnivore is capable of eating a wide variety of vertebrate prey, potentially impacting a number of threatened and endangered species in the process (Meshaka, 2006). For example, the Florida burrowing owl *Athene cunicularia floridana*, a Florida Species of Special Concern, has already been observed as a prey item (Hardin, 2007). The Nile monitor is a prolific species capable of reaching high densities (Western, 1974). Based on its native range, this lizard could expand its range and pose severe threats to native fauna throughout Florida, and possibly beyond (Enge et al., 2004).

Accumulation of useful information for the management of the species has begun (Campbell, 2005), and this also would be a novel species to subject to control activities. Considerable development of methods and technologies would be needed for the implementation of a practical, broad-based control or eradication program, and as for the Burmese python, development of control methods would share many characteristics of the brown treesnake model (Engeman and Vice, 2001). To that end, basic information on diet, baits, and trapping technology exists for the Nile monitor (Campbell, 2005). Considerable testing and refinement of additional baits, attractants, and capture methods applicable to large-scale removal are needed. Again, as for the Burmese python, trials built on the successful development of acetalaminophen as a toxicant for brown tree snakes (Savarie et al., 2001) showed this human medicant to also be an effective toxicant for Nile monitors (Mauldin and Savarie, 2010). Bait matrix preference trials like those for the Burmese python have also been conducted for Nile monitors, but unlike the Burmese python results, multiple commercially available bait matrices were identified as promising for development for toxicant delivery (Savarie, National Wildlife Research Center unpublished data). This ready acceptance of a variety of bait matrices, both fresh and aged, is not surprising since they are known to consume a varied carnivorous diet in nature (e.g., Campbell, 2005; Enge et al., 2004; Meshaka, 2006).

Despite a reasonably high profile and media attention, funding has not yet materialized for general development of the needed control technologies, nor for initiating a general control or eradication effort. Without prompt action, the likelihood for successful eradication or containment diminishes as the species colonizes places more physically and logistically difficult to carry out management actions. It remains to be seen if denial of “de” Nile monitor will take place in time.

5 Green Iguanas and Black Spiny-tailed Iguanas

Several species of exotic iguanine lizards are established in southern Florida (Meshaka et al., 2004a), with the green iguana *Iguana iguana* and the black spiny-tailed iguana *Ctenosaura similis* being prominent in terms of human-wildlife conflicts. The green iguana has a much larger geographic range in Florida than the black spiny-tailed iguana, but it is the population of the latter species on Gasparilla Island that is subjected to an intensive control program. We review the ecology and impacts of the two species, and the basis for the control program.

Green iguanas The green iguana is a successful colonizing species in Florida as measured both by its geographic range and its ubiquity (e.g., Meshaka et al., 2004a,b). It is a seemingly omnipresent exotic lizard in southern Florida (Townsend et al., 2003; Meshaka et al., 2004a,b), expanding its geographic range there (Meshaka et al., 2004a; Meshaka et al., 2007) (although a cold spell such as the one that impacted the pythons would probably result in a green iguana range contraction), and is capable of reaching extreme population densities (up to 626.6 iguanas/km²) even in managed natural areas (Smith et al., 2006a; 2007d). Biotic potential, limiting factors, and colonization patterns of the green iguana in Florida have only recently been investigated (Meshaka et al., 2004a,b; Smith et al., 2006a; 2007a,b,c,d), and are not well understood. With few exceptions, the ecological impacts of the green iguana in Florida are likewise poorly understood. With respect to the biotic environment, it also could potentially negatively impact the Florida burrowing owl through its use of their burrows (McKie et al., 2005). The green iguana

---

1Florida Fish and Wildlife Conservation Commission, 2010. http://www.myfwc.com/wildlifehabitats/nonnative_nilemonitor.htm
2Campbell TS, 2005. Eradication of introduced carnivorous lizards from the Cape Coral area. Final Report to the Charlotte Harbor National Estuary Program, Fort Meyers, FL. Florida Fish and Wildlife Conservation Commission, 2010. http://www.myfwc.com/wildlifehabitats/nonnative_nilemonitor.htm
3Smith HT, Engeman RM, Meshaka WE Jr, Sementelli AJ, Busch GH et al., 2007a. Green iguana burrows undermining the Intracoastal Waterway seawall in H.T. Birch State Park, Broward County, Florida. Unpublished report. Hobe Sound, FL: Florida Dept. Environmental Protection, Florida Park Service.
consumes the fruits of invasive plants, and defecates the scarified seeds, thereby acting as potential dispersal agents. Green iguanas will prey on tree snails, possibly suggesting potential negative impacts for the rare species (Townsend et al., 2005; Ferriter et al., 2009). Regarding the abiotic environment, Engeman et al. (2005a) discussed airplane collision hazards with invasive green iguanas basking on airport runways in Puerto Rico and expressed similar concerns regarding the Homestead Air Reserve Base Airport and other airports in south Florida. Dense populations of green iguanas have become such an intrusive problem (Mesnaka et al., 2004a; Smith et al., 2006a; 2007a, c, d) that policies and practices require reconsideration (Sementelli et al., 2008a).

A suite of biological traits are associated with successful colonization (Drake et al., 1989), and several of them are evident in the green iguana in southern Florida; close association with humans (Brown, 1989), open niche space (Brown, 1989), and high fecundity (Baker, 1965). Two additional traits associated with successful colonization are also evident. First, achievement of sexual maturity within just over two years suggests conformation to the colonizing trait of short generation times (Ehrlich, 1989) and in the higher range of other successful colonizing amphibians and reptiles in Florida (e.g., Meshaka, 2001; Meshaka and Layne, 2005; Meshaka et al., 2006a,b). Second, the matter of predator-free space (Pimm, 1989), also comes into play, but with caveats, as there have been examples where predation has held green iguana populations below their full potential densities (Meshaka et al., 2007).

This animal, unlike many invasive exotic species, is sometimes seen as non-threatening, and is sometimes even nurtured in urban areas (Meshaka et al, 2004a). Green iguanas prefer riparian habitats where they burrow extensively on slopes, including canal banks, levees, and road and bridge embankments (Ferriter et al., 2009). Specifically, the green iguana population has increased dramatically in recent years along canals and levees in and around the “Greater Everglades,” along with growing numbers of burrows that can at the very least “present a maintenance liability to surface water infrastructure” (Ferriter et al., 2009; Smith et al., 2007a), and considering animal burrows can threaten the integrity of levees, this also presents a potential danger to residents. Currently, areas affected by burrowing include the C-7, C-11, and C-1 west canals, leading to both instability and bank erosion, with burrows ranging between 0.3 and 2.4 meters deep with a diameter of 10–20 centimeters (Ferriter et al., 2009), while Sementelli et al. (2008b) demonstrated high densities of burrows in a canal bank over 25% of which were 14–18 cm in diameter. Despite the myriad of conflicts with human interests, green iguanas are not subjected to systematic, organized management efforts in Florida.

**Black spiny-tailed iguanas (ctenosaurs)** The black spiny-tailed iguana is native from southern Mexico through Central America. Also commonly called ctenosaurs, these large lizards became established on Gasparilla Island on Florida’s west coast with an introduction of as few as three individuals around 30–35 years ago (Krysko et al., 2003). They now occur throughout this 11-km barrier island in both Lee and Charlotte counties, and also at several other locations in Florida (Krysko et al., 2003). The population on Gasparilla Island is particularly noteworthy, not only because of the ubiquity and density achieved by black spiny-tailed iguanas, but because this is the only example in Florida of an exotic lizard species whose control was initiated at the behest of affected residents. These iguanas have tremendous reproductive potential, with a single clutch containing 12–88 eggs (mean = 43; Wiewandt, 1982). The black spiny-tailed iguana population saturated the terrestrial habitats on the island in high numbers, including all residential and commercial areas. The boundary line between two counties runs across Gasparilla Island, and the iguanas had become such a nuisance to property owners through damage to landscape plants and homes (especially attics) that residents of both counties voted to self-tax so as to secure funds for control programs of this lizard. As with those of the green iguana, black spiny-tailed iguana burrows could undermine public works and private structures (Sementelli et al., 2008a,b).

Black spiny-tailed iguanas conflict with a variety of ecological interests in addition to the economic interests on the island. Although Gasparilla Island is largely developed, it also is the location for Gasparilla Island State Park, 49 ha of mostly natural area on the southern end of the island (FDEP, 2002). Also despite the development, Gasparilla Island’s beaches are home or potential nesting site for a variety of species that are federally or state-listed as threatened, endangered or of concern (FDEP, 2002). The endemic listed species on Gasparilla Island for which this species may pose a threat include eggs and young of nesting shorebirds, beach mice, hatchling sea turtles and gopher tortoises *Gopherus polyphemus* (Krysko et al., 2003). Remains of a juvenile gopher tortoise were removed from the stomach of a large male (Avery et al., 2009), and individuals may occupy gopher tortoise burrows in sufficient numbers to...
exclude the tortoises (Engeman et al., 2009b). This lizard species may also pose an attack threat to snakes on the island, as noted in an encounter between a black spiny-tailed iguana and a basking southern black racer Coluber constrictor priapus (Engeman et al., 2009c). Such agonistic behavior, which resulted in the death of the racer, could likewise place at risk some size classes of eastern indigo snakes Drymarchon corais couperi, a threatened species (Moler, 1992). Further environmental impacts include facilitating the spread of invasive plant species. Black spiny-tailed iguanas eat fruit and disperse seeds of Brazilian pepper Schinus terebinthifolius, the most problematic invasive plant on Gasparilla Island (FDEP, 2002; Jackson and Jackson, 2007). Thus, populations of both invasive species are enhanced (Jackson and Jackson, 2007). Invasive plant control is time consuming and costly, and the black spiny-tailed iguana serves to increase the problem and raise potential remediation costs.

Active iguana removal was implemented on Gasparilla Island to reduce, and possibly eradicate, their populations. The U.S. Department of Agriculture's Wildlife Services, the Federal agency with responsibility for managing conflicts with wildlife (U.S. Department of Agriculture/Animal and Plant Health Inspection Service et al., 1997), currently carries out the control in both counties. Since 2008 they have removed over 10,000 lizards, with impacts to the overall population still under investigation. Their multi-faceted control approach includes iguana removal by a variety of methods such as various capture devices and placements, as well as shooting. Research is being conducted to develop and evaluate control methods (including toxicant screening tests) as well as population indexing methods. In contrast to the results for Burmese pythons and Nile monitors, laboratory trials testing toxicants on black spiny-tailed iguanas found acetaminophen to not be sufficiently toxic to be useful as a control tool. However, zinc phosphate was found to be highly toxic (Avery et al., accepted, this issue). Trials are proceeding to identify suitable bait delivery methods that are target-specific, safe, and effective.

The species is endemic to the islands of the Little Bahama Bank, with other subspecies found in the Great Bahama Bank, Cayman Islands, and Cuba (Schwartz and Thomas, 1975; Schwartz and Henderson, 1991). A small colony was established in Palm Beach County through the intentional release of 20 pairs in the 1940s and has spread widely (Duellman and Schwartz, 1958). Prior to 1968, the Florida range for this population expanded north and south along the Atlantic coast at an average rate of 0.98 km/yr, but from 1968 to 2002 it expanded at a much greater average rate of 2.4 km/yr (Smith et al., 2004; Smith and Engeman, 2004), and is continuing to expand. Moreover, northern curlytail lizards are also found in disparate parts of south Florida through human-mediated dispersal (e.g., Meshaka et al., 2005).

The primary concern with this species (rapid) range expansion is its depredations on other (small-bodied) lizards (Meshaka et al., 2005). Saurophagy is a component of the northern curlytail’s ecology (e.g., Smith and Engeman, 2004; Dean et al., 2005), and the widely-distributed, also exotic, brown anole Anolis sagrei is a known prey species that could provide expanding populations with a nutritious prey base and a simultaneous reduction in competitors (Meshaka et al., 2005). The northern curlytail is aggressive towards animals that approximate its size class and was even observed to attack a juvenile northern mockingbird Mimus polyglottos (Smith and Engeman, 2007), the adults of which prey on northern curlytails (Smith et al., 2006b). This potential displacer/replacer for the brown anole likely will put the native lizard fauna with which the northern curlytail exists at risk, including state-listed species (Meshaka et al., 2005). The negative impacts would be especially critical in human-disturbed habitat where the northern curlytail lizard is expanding its range and native lizards might already be marginalized.

Although the northern curlytail is unlikely to receive much attention outside herpetological circles, it was described in one newspaper article as “the T-rex of ground critters” (Fleshler, 2006). Nevertheless, the northern curlytail lizard, like many of Florida's small-to-medium sized invasive lizards, is unlikely to be targeted for control or eradication. Its ubiquity within its extended range, small body size, and the difficulty in isolating it for control in the presence of native lizard species would make control or eradication difficult, prohibitively expensive, and without the high profile that would engender public support.

6 Fleshler D, 2006, The T-rex of ground critters. South Florida Sun-Sentinel, May 1, 2006, 1A–2A.
7 Argentine Black and White Tegu

Relatively new to the scene of established exotic reptiles in Florida is the Argentine black and white tegu *Tupinambis merianae*, a large omnivorous lizard native to southeastern Brazil, Uruguay, eastern Paraguay and northern Argentina (Luxmoore et al., 1988). The seven tegu species are members of the Teiidae, or whiptail family, and are the largest lizards in the New World, with the Argentine black and white tegu one of the two largest species, weighing up to 8 kg (Lopes and Abe, 1999).

Argentine black and white tegus were reported in 2006 from Hillsborough and neighboring Polk counties in west-central Florida (Hardin, 2007), and individuals have been collected in the Homestead area. The likely origin of the lizards forming this population was imported animals from Paraguay during 2000–2002 (Enge et al., 2006), and based on anecdotal reports, these lizards may have been introduced into the wild by a reptile dealer in response to declining market prices (Hardin, 2007). Credible reports at that time indicated the species already occurred in an area over 100 km² in size.

All age classes, adults, juveniles, and hatchlings have been observed in the area, particularly in the vicinity of the Balm-Boyette Scrub Nature Preserve (Enge et al., 2006; B. Kaiser, pers. Comm.). The Argentine black and white tegu is a fecund species, laying annual clutches of 20–45 eggs (Enge et al., 2006). This species has been observed using gopher tortoise burrows, and tortoise eggs and hatchlings are likely prey items. Some trapping attempts have taken place in the Balm-Boyette Scrub Nature Preserve using various designs of capture devices. While some adult and juvenile tegus have been captured (Enge et al., 2006; B. Kaiser, pers. Comm.), effective trapping has been challenging (B. Kaiser, pers. Comm.). The omnivorous diet and burrow usage suggest the Argentine black and white tegu may present the combined spectrum of threats to the environment as from both Nile monitors and iguanas. Like the iguanas, it could act as a seed disperser (Enge et al., 2006). It also could threaten through predation a similar suite of native animals, including listed species, as the Nile monitor, and its burrow usage could exclude gopher tortoises and burrowing owls from their burrows, in addition to the predation threat. Development of effective control tools could help contain its range and create the possibility of localized eradications. To date, dedicated resources have not been available for control, nor for the development of control tools.

8 Discussion

The invasive exotic herpetofaunal species situation in Florida is severe, and the breadth of invasive exotic reptiles in Florida that arguably merit eradication, or at least control, is extensive. A variety of steps have been taken to reduce the number of introductions, with some apparent success (Hardin, 2007). As is often stated, prevention is the most efficient and economical means to do away with invasive species (e.g., NISC, 2001). However, even if no new exotic reptiles become established in Florida, there is an abundance of established exotic reptiles that merit management action.

The invasive reptiles in Florida represent novel species to be considered for eradication or control. In Florida, the Gambian giant pouched rat *Cricetomyia gambiana*, black-tailed jackrabbit *Lepus californicus*, black-tailed prairie dog *Cynomys ludovicianus*, and sacred ibis are examples of how invasive vertebrate species can be identified as suitable for an eradication effort (including likelihood of success), and the necessary incentive and resources to directly design and implement a practical eradication program obtained (e.g., Engeman et al., 2006, 2007a,b). Although not characterized as an eradication effort, the black spiny-tailed iguanas on Gasparilla Island represent the first intensive control situation for an invasive reptile in Florida, and a number of agencies and organizations are conducting some degree of research into methods development for controlling Burmese pythons.

Strong value exists in examining the life history of an invasive species within the context of understanding why it is or is not successful, and what its vulnerabilities might be. Such information provides predictive power concerning its colonization in other kinds of habitats or regions and also puts to the test the sorts of biological characteristics associated with successful colonizing species. Indeed, understanding its biology in nature can provide the sorts of useful tools necessary in understanding how it might be controlled. Such an approach was taken in the study of the Cuban treefrog *Osteopilus septentrionalis* in Florida (Meshaka, 2001). The identification of vulnerabilities that might be exploited for control is underscored by others who specify the importance of results that directly assist in the removal of the species (e.g., Donlan et al., 2003; Simberloff, 2003; Campbell, 2007; Engeman et al., 2009a). To that end, Donlen et al. (2003) concluded that research directly facilitating eradication tools and projects should be of high priority. Consequently, developing the information...
and technologies from which control strategies can be developed and implemented should be considered an ideal and essential component in the research of invasive species, with priority given to the most aggressive colonizers.

Among the potential control methods already discussed here, the use of toxicants merits some additional comment. Finding a toxic compound and an acceptable bait matrix (or matrices) are only the first two steps in developing a practical and effective baiting strategy. The critical final step is to develop a mechanism and placement strategy that would deliver the bait specifically to the target species and prevent take by native non-target species. In Florida there are a number of species of concern inhabiting Florida, such as the eastern indigo snake, that would have to be prevented from accessing or consuming such baits intended for pythons. Probably the two non-target species most likely to consume the baits identified for the array of species discussed here would be raccoons *Procyon lotor* and American alligators *Alligator mississippiensis*. Raccoons are ubiquitous in Florida, often at high densities (Smith and Engeman, 2002), and if not prevented from accessing baits could cause sufficient bait loss to render a baiting program inefficient or ineffective. Exclusion of alligators should be straight-forward as they would be limited vertically and by their habitat constraints. The importance and approaches for using delivery methods that avoid non-target species has been well-discussed in Mauldin and Savarie (2010).

Many of the problematic invasive reptiles in Florida are predators. Predation not only threatens rare species (Hecht and Nickerson, 1999), but the deleterious impacts of predation are compounded by habitat loss (Reynolds and Tapper, 1996). Predators also increase the risk of catastrophic extinction of prey populations (Schoener et al., 2001). The amount of habitat lost to development in Florida and the state's proclivity for catastrophic hurricanes heighten the impacts to endangered species. Since alien predators tend to be more dangerous than native predators to prey populations (Salo et al., 2007), the impacts from invasive predators, whether small like northern curlytail lizards or large like Burmese pythons, could have significant impacts on Florida's native species, especially the rare species.

For a number of well-established reptile species in Florida, such as the green iguana, there probably is no practical means to eradicate them from the state. That does not mean on a localized scale they cannot be intensively controlled, managed, excluded, or eradicated in situations of greatest priority, especially islands. We cannot say for certain the prospects for complete eradication for any of the species discussed here are likely to happen. However, a rapid response to a newly recognized establishment of a reptile species may be identified as feasible, practical, and valuable to eradicate before they become too deeply entrenched across a broad range. Such has been the case with the Northern African python *Python sebae*, which established a small population in Miami-Dade County and was the subject of an intensive search effort by the Exotic Animal Strike Team of the Everglades Cooperative Invasive Species Management Area (Giardina et al., 2010; Reed et al., 2010), with surveillance through subsequent searches ongoing.

Parkes and Murphy (2003) delineated some “obligate rules” for successful eradication: 1) all individuals of the target species must be at risk of being killed, 2) target species must be removed at a rate greater than the rate they replace their losses, and 3) the risk of immigration must be (near) zero. However, to achieve such an end, suitable control methods must be available, probably developed in the case of reptiles, and then applied in a systematic and sustained integrated pest management program (Engeman and Vice, 2001). The third component speaks to having practical policies and procedures in place that greatly deter the intentional or accidental release of exotic species into the wild, which has been described by Hardin (2007) for Florida. The case of the black-tailed jackrabbit demonstrates that, even with many political gyrations, a population of a species with a restricted range can be eradicated without an excessive outlay of resources (Engeman, 2007a). To leave such a situation unaddressed is like leaving a slow-burning fuse lit to an ecological bomb (Engeman et al., 2009a).

**Acknowledgements** We would especially like to thank Scott Hardin for his comments, which have improved this paper.

**References**

Avery ML, Eisenmann JD, Keacher KL, Savarie PJ, 2011. Acetaminophen and zinc phosphide for lethal management of invasive lizards. Current Zoology 57: 625–629.

Avery ML, Engeman RM, Keacher KL, Humphrey JS, Bruce WE et al., 2010a. Cold weather and the potential range of invasive Burmese pythons. Biological Invasions 12: 3649–3652.

Avery ML, Humphrey J, Duffiney A, Mathies, TC, Mauldin R et al., 2010b. USDA/Wildlife Services: Developing tools and strategies Burmese python control. In: Reddy KR, Best GR ed. Abstracts, GEER 2010 – Greater Everglades Ecological Res-
toration Conference. Naples, FL: USGS, US Army Corps of Engineers, National Park Service, US Fish and Wildlife Service, University of Florida, 10.

Avery ML, Tillman EA, Krysko KL. 2009. *Gopherus polyphemus* (Gopher Tortoise), *Ctenosaura similis* (Gray’s Spiny-tailed Iguana) predation. Herpetological Review 40: 435.

Baker HG. 1965. Characteristics and modes of origin of weeds. In: Baker HG, Stebbins CL ed. *The Genetics of Colonizing Species*. NY: Academic Press, 147–169.

Barker DG. 2008. Will they come in out of the cold? Observations of large constrictors in cool and cold conditions. Bulletin of the Chicago Herpetological Society 43: 93–97.

Barker DG, Barker TM. 2008a. Comments on a flawed herpetological paper and an improper and damaging news release from a government agency. Bulletin of the Chicago Herpetological Society 43: 45–47.

Barker DG, Barker TM. 2008b. Review: An ecological risk assessment of nonnative boa and pythons as potentially invasive species in the United States by Robert N. Reed 2005. Risk Analysis 25(3): 753–766. Bulletin of the Chicago Herpetological Society 43: 63–67.

Barker DG, Barker TM. 2008c. The distribution of the Burmese python *Python molurus bivittatus*. Bulletin of the Chicago Herpetological Society 43: 33–38.

Barker DG, Barker TM. 2010. A critique of the analysis used to predict the climate space of the Burmese python in the United States by Rodda et al. 2008, 2009, and Reed and Rodda 2009. Bulletin of the Chicago Herpetological Society 45: 97–106.

Bartlett RD, Bartlett PP. 1999. A Field Guide to Florida Reptiles and Amphibians., Houston, Texas: Gulf Publishing Co.

Bayless MK. 1991. A trip from Africa. Vara News 1: 5–8.

Bennett D. 1995. A Little Book of Monitor Lizards. Glossop, UK: Viper Press.

Bilger B. 2009. Swamp things. The New Yorker April 20: 80–89

Bomford M, Kraus F, Barry S, Lawrence E. 2009. Predicting establishment success for alien reptiles and amphibians: A role for climate matching. Biol. Invasions 11: 713–724

Bright C. 1999. Invasive species: Pathogens of globalization. Foreign Policy 116: 50–64.

Brown JH. 1989. Patterns, modes, and extents of invasions by vertebrates. In: Drake JA, Mooney HA, di Castri F, Groves RH, Kruger FJ et al ed. *Biological Invasions: A Global Perspective*. New York: John Wiley and Sons Limited, 85–110.

Campbell TS. 2007. The role of early detection and rapid response in thwarting amphibian and reptile introductions in Florida. In: Witmer G, Pitt W, Fagerstone K ed. Managing Vertebrate Invasive Species: Proceedings of an International Symposium. Fort Collins, CO: USDA/APHIS/WS, National Wildlife Research Center, 146–156.

Cope ED. 1875. Check-list of North American batrachia and reptiles. Bulletin U.S. National Museum 1: 1–104.

Corn ML, Buck EH, Rawson J, Segarra A, Fischer E. 2002. Invasive Non-Native Species: Background and Issues for Congress. Washington, DC: Congressional Research Service and The Library of Congress.

Dean CL, Engeman RM, Smith HT, Mshaka WE Jr., 2005. *Leiocephalus carinatus armouri* (northern curly-tailed lizard) Cannibalism. SSAR Herpetological Review 36: 451.

Donlan CJ, Tershy BR, Campbell K, Cruz F. 2003. Research for requiems: The need for more collaborative action in eradication of invasive species. Conservation Biology 17: 1850–1851.

Dorcas ME, Willson JD, Gibbons JW. 2011. Can invasive *Burmes pythons* inhabit temperate regions of the southeastern United States? Biological Invasions 13: 793–802.

Drake JA, Mooney HA, di Castri F, Groves RH, Kruger FJ et al., 1989. Biological Invasions: A Global Perspective, New York: John Wiley and Sons Limited.

Duellman, WE, Schwartz A, 1958. Amphibians and reptiles of southern Florida. Bulletin Florida State Museum 3: 181–342.

Ehrlich PR. 1989. Attributes of invaders and the invading processes: Vertebrates. In: Drake JA, Mooney HA, di Castri F, Groves RH, Kruger FJ et al. ed. Biological Invasions: A Global Perspective. New York: John Wiley and Sons Limited 315–328.

Enge KM, Kaiser BW, Dickerson RB. 2006. Another large exotic lizard in Florida, the Argentine black and white tegu. In: Proceedings of the 28th Annual Gopher Tortoise Council Meeting. Valdosta, Georgia: Gopher Tortoise Council.

Enge KM, Krysko KL, Hankins KR, Campbell TS, King FW, 2004. Status of the Nile monitor *Varanus niloticus* in southwestern Florida. Southeastern Naturalist 3: 571–582.

Engeman RM, Constantine BU, Bunting, J., 2007a. The political, economical and management history of a successful exotic eradication: The case of black-tailed jackrabbits in Florida. In: Witmer G, Pitt W, Fagerstone K ed. Managing Vertebrate Invasive Species: Proceedings of an International Symposium. Fort Collins, CO: USDA/APHIS/WS, National Wildlife Research Center, 476–478.

Engeman RM, Constantine BU, Hardin S, Smith HT, Mshaka WE Jr. 2009a. “Species pollution” in Florida: A cross-section of invasive vertebrate issues and management responses. In: Wilcox CP, Turpin RB ed. Invasive Species: Detection, Impact and Control. Hauppauge, NY: Nova Science Publishers, 179–197.

Engeman RM, Kennedy M, Constantine BU, Christie ML, Hall PT, 2009b. *Ctenosaura similis* (black spinytail iguana), *Gopherus polyphemus* (gopher tortoise) concurrent burrow use. Herpetological Review 40: 84.

Engeman RM, Kennedy M, Constantine BU, Christie ML, Hall PT, 2009c. *Ctenosaura similis* (black spinytail iguana), *Coluber constrictor priapus* (southern black racer) nonpredatory killing. Herpetological Review 40: 84–85.

Engeman RM, Smith HT, Constantine BU, 2005a. Invasive green iguanas as airstrike hazards at San Juan International Airport, Puerto Rico. Journal of Aviation-Aerospace Education and Research 14: 45–50.

Engeman RM, Sweet EM, Smith HT, 2005b. *Iguana iguana* (Green Iguana) predation. Herpetological Review 36: 320.

Engeman RM, Vice DS. 2001. Objectives and integrated approaches for the control of brown tree snakes. Integrated Pest Management Reviews 6: 59–76.

Engeman RM, Woolard JW, Perry ND, Witmer G, Hardin S et al., 2006. Rapid assessment for a new invasive species threat: The case of the Gambian giant pouched rat in Florida. Wildlife Research 33: 439–448.

Engeman RM, Woolard JW, Witmer G, Constantine BU, Hardin S et al., 2007b. The path to eradication of the Gambian giant pouched rat in Florida. In: Witmer G, Pitt W, Fagerstone K ed.
Managing Vertebrate Invasive Species: Proceedings of an International Symposium. Fort Collins, CO: USDA/APHIS/WS, National Wildlife Research Center, 305–311.

Faust RJ, 2001. Nile monitors: Everything about History, Care, Nutrition, Handling, and Behavior. Hauppauge, NY: Barron’s Educational Series.

FDEP (Florida Department of Environmental Protection), 2002. Gasparilla Island State Park Management Plan. Tallahassee, FL: Florida Department of Environmental Protection.

Ferriter A, Thayer D, Bodie M, Doren B, 2009. South Florida Environmental Report Ch. 9: The Status of Nonindigenous Species in the South Florida Environment. West Palm Beach, FL: South Florida Water Management District.

Gawlik DE, Leonardo C, 2010. Anthropogenic resource utilization in the diet of the sacred ibis Threskiornis aethiopicus, a non-native wading bird in Southeastern Florida, USA. In: Reddy KR, Best GR ed. Abstracts, GEER 2010 – Greater Everglades Ecological Restoration Conference. Naples, FL: USGS, US Army Corps of Engineers, National Park Service, US Fish and Wildlife Service, University of Florida, p62.

Greene DU, Potts JM, Duquesnel JG, Snow RW, 2007. Geographic distribution: Python molurus bivittatus (Burmese python). Herpetological Review 38: 355.

Giardina DJ, Pernas A, Snow S, 2010. Everglades CISMA rapid response to Python sebae in Miami Dade County. In: Reddy KR, Best GR ed. Abstracts, GEER 2010 – Greater Everglades Ecological Restoration Conference. Naples, FL: USGS, US Army Corps of Engineers, National Park Service, US Fish and Wildlife Service, University of Florida, 123.

Hardin S, 2007. Managing non-native wildlife in Florida: State perspective, policy and practice. In: Wittmer G, Pitt W, Fagerstone K ed. Managing Vertebrate Invasive Species: Proceedings of an International Symposium. Fort Collins, CO: USDA/APHIS/WS, National Wildlife Research Center, 43–52.

Hart KM, Reed RN, Mazzotti FJ, Cherckiss MS, Snow S et al., 2010. A field trial of trap effectiveness for invasive Burmese pythons Python molurus bivittatus in South Florida In: Reddy KR, Best GR ed. Abstracts, GEER 2010 – Greater Everglades Ecological Restoration Conference. Naples, FL: USGS, US Army Corps of Engineers, National Park Service, US Fish and Wildlife Service, University of Florida, 135.

Harvey RG, Brien ML, Cherckiss MS, Dorcas M, Rochford M et al., 2008. Burmese Pythons in South Florida, Scientific Supplement to the Florida Field Naturalist 19: 16–17.

Hayes KR, Barry SC, 2008. Are there any consistent predictors of invasion success? Biological Invasions 10: 483–506.

Hecht A, Nickerson PR, 1999. The need for predator management in conservation of some vulnerable species. Endangered Species Update 16: 114–118.

Herring G, Call EM, Johnston MD, 2008. A non-indigenous wading bird breeding in the Florida Everglades: The sacred ibis. Florida Field Naturalist 34: 4–8.

Jackson JA, Jackson BJS, 2007. An apparent mutualistic association between invasive exotics: Brazilian pepper Schinus terebinthifolius and black spiny-tailed iguanas Ctenosaura similis. Natural Areas Journal 27: 254–257.

Jacobs HJ, Auliya M, Böhme W, 2009. Zur taxonomie des dunklen tigerpythons, Python molurus bivittatus Kuhl, 1820, speziell der population von Sulawesi. Sauria 31: 5–16

Jacobson ER, Whitford WG, 1970. The effects of acclimation on physiological responses to temperature in the snakes Thamnophis proximus and Natrix rhombifera. Comparative Biochemical Physiology 43: 439–449.

Krysko KL, King FW, Enge KM, Reppas AT, 2003. Distribution of the introduced black spiny-tailed iguana Ctenosaura similis on the southwestern coast of Florida. Florida Scientist 66: 74–79.

Lopes HR, Abe AS, 1999. Biologia reprodutivo e comportamento do teiu, Tupinambis merianae, em cativeiro (Reptilia, Teiidae). In: Fang TG, Montenegro OL, Bodmer RE ed. Manejo y Conservación de Fauna Silvestre en América Latina. La Paz, Bolivia: Instituto de Ecología, 259–272.

Luxmore R, Groombridge B, Broads S, 1988. Significant Trade in Wildlife: A Review of Selected Species in CITES Appendix II. Volume 2: Reptiles and Invertebrates. Cambridge, U.K: IUCN Conservation Monitoring Centre.

Mauldin RE, Savarie PJ, 2010. Acetaminophen as an oral toxicant for Nile monitor lizards Varanus niloticus and Burmese pythons Python molurus bivittatus. Wildlife Research 37: 215–222.

Mazzotti FJ, Cherckiss MS, Hart KM, Snow RW, Rochford MR et al., 2010. Cold-induced mortality of invasive Burmese pythons in south Florida 13: 143–151.

Mickie AC, Hammond JE, Smith HT, Meshaka WE, 2005. Invasive green iguana interactions in a burrowing owl colony in Florida. Florida Field Naturalist 33: 125–127.

Meshaka WE Jr, 2006. An update on the list of Florida’s exotic amphibians and reptile species. Journal of Kansas Herpetology 19: 16–17.

Meshaka WE Jr, 2001. The Cuban treefrog in Florida: Life History of A Successful Colonizing Species. Gainesville, FL: University Press of Florida.

Meshaka WE Jr, Bartlet R, Smith HT, 2004b. Colonization success by green iguanas in Florida. Iguana 11(3): 154–161.

Meshaka WE Jr, DeVan J, Marshall SD, 2006a. An island of cane toads Bufo marinus in an ocean of xeric uplands in south-central Florida. Florida Scientist 69: 169–176.

Meshaka WE Jr, Layne JN, 2005. Habitat relationships and seasonal activity of the greenhouse frog Eleutherodactylus planirostris in southern Florida. Florida Scientist 68: 35–43.

Meshaka WE Jr, Loftus WF, Steiner T, 2000. The herpetofauna of Everglades National Park. Florida Scientist 63: 84–103.

Meshaka WE Jr, Smith HT, Dean CL, 2006b. Gonadal cycle and growth of a West Indian lizard, the northern curlytail lizard Leiocephalus carinatus armouri in south Florida. Herpetological Conservation and Biology 1: 109–115.

Meshaka WE Jr, Engeman RM, Dean CL, Moore JA et al., 2005. The geographically contiguous and expanding range of the northern curlytail lizard Leiocephalus carinatus armouri in Florida. Southeastern Naturalist 4: 521–526.

Meshaka WE Jr, Smith HT, Golden E, Moore JA, Fitchett S et al., 2007. Green Iguanas Iguana iguana: The unintended consequence of sound wildlife management practices in a South...
Florida state park. Herpetological Conservation and Biology 2: 149–156.

Meyerson LA, Engeman RM, O’Malley R, 2008. Tracking non-native vertebrate species: Indicator design for the United States. Wildlife Research 35: 235–241.

Moler PE, 1992. Rare and Endangered Biota of Florida. Vol III, Amphibians and Reptiles. Gainesville, FL: University Press of Florida.

NISC (National Invasive Species Council), 2001. Meeting the Invasive Species Challenge: National Invasive Species Management Plan. Washington, DC: National Invasive Species Council.

Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M et al., 1999. Impact: Toward a framework for understanding the ecological effects of invaders. Biological Invasions 1: 3–19.

Parkes J, Murphy E, 2003. Management of introduced mammals in New Zealand. New Zealand Journal of Zoology 30: 335–359.

Pimm SL, 1989. Theories of predicting success and impact of introduced species. In: Drake JA, Mooney HA, di Castri F, Groves RH, Kruger FJ et al. ed. Biological Invasions: A Global Perspective. New York: John Willey and Sons Limited, 351–367.

Pyron RA, Burbrink FT, Guiher TJ, 2008. Claims of potential expansion throughout the U.S. by invasive python species are contradicted by ecological niche models. PLoS ONE 3: e2931.

Reed RN, Krysko KL, Romagosa C, Giardina D, Snow RW et al., 2010. The Northern African python Python sebae in South Florida. In: Reddy KR, Best GR ed. Abstracts, GEER 2010 – Greater Everglades Ecological Restoration Conference. Naples, FL: USGS, US Army Corps of Engineers, National Park Service, US Fish and Wildlife Service, University of Florida, 254.

Reynolds JC, Tapper SC, 1996. Control of mammalian predators in game management and conservation. Mammal Review 26: 127–156.

Rodda GH, Jarnevich CS, Reed RN, 2009. What parts of the US mainland are climatically suitable for invasive alien pythons spreading from Everglades National Park? Biological Invasion 11: 241–252.

Salo P, Korpimäki E, Banks PB, Nordström M, Dickman CR, 2007. Alien predators are more dangerous than native predators to prey populations. Proceedings of the Royal Society London B 274: 1237–1243.

Savarie PJ, Shivik JA., White GC, Hurley JL, Clark L, 2001. Use of acetaminophen for large-scale control of brown tree snakes. Journal of Wildlife Management 65: 356–365.

Schoener TW, Spilier DA, Losoa JB, 2001. Predators increase the risk of catastrophic extinction of prey populations. Nature 412: 183–186.

Schwartz A, Henderson RW, 1991. Amphibians and Reptiles of the West Indies: Descriptions, Distributions and Natural History. Gainesville, FL: University of Florida Press.

Schwartz A, Thomas R, 1975. A checklist of West Indian Amphibians and Reptiles. Carnegie Museum of Natural History, special Publication 1: 127–129.

Sementelli AJ, Smith H, Meshaka WE Jr, Alexander D, 2008b. Iguana iguana (green iguana): Colony burrow density in Florida. Journal of Kansas Herpetology 25: 11.

Sementelli A, Smith HT, Meshaka WE Jr, Engeman RM, 2008a. Just green iguanas? The associated costs and policy implications of exotic invasive wildlife in South Florida. Public Works Management and Policy 12: 599–606.

SFWMD (South Florida Water Management District), 2008. Executive Summary 2008 South Florida Environmental Report. West Palm Beach, FL: South Florida Water Management District.

Shigesada N, Kawasaki K, 1997. Biological Invasions: Theory and Practice. Oxford, UK: Oxford University Press.

Simberloff D, 2003. How much information on population biology is needed to manage introduced species? Conservation Biology 17: 83–92.

Smith HT, Engeman RM, 2002. An extraordinary raccoon Procyon lotor density at an urban park in Florida. Canadian Field-Naturalist 116: 636–639.

Smith HT, Engeman RM, 2004. A review of the colonization dynamics of the northern curly-tailed lizard Leiocephalus carinatus armouri in Florida. Florida Field Naturalist 32: 107–113.

Smith HT, Engeman RM, 2007. Leiocephalus carinatus armouri (northern curlytail lizard): Attack of northern mockingbird; assertion displays. SSAR Herpetological Review 38: 457.

Smith HT, Engeman RM, Meshaka WE Jr, 2006b. Leiocephalus carinatus armouri (northern curlytail lizard) predation. SSAR Herpetological Review 37: 224.

Smith HT, Golden E, Meshaka WE Jr, 2007b. Population density estimates for a green iguana (Iguana iguana) colony in a Florida state park. Journal of Kansas Herpetology 21: 19–20.

Smith HT, Meshaka WE Jr, Busch GH, 2007c. Jurassic park battles in paradise: Alien green iguanas collide with native mammalian predators and other interesting findings in Florida, USA: A brief update. IUCN Invasive Species Specialist Group “Aliens” Newsletter 13–15.

Smith HT, Meshaka WE Jr, Busch GH, Cowan EM, 2007d. Gray fox predation of nests as a potential limiting factor in the colonization success of the green iguana in Southern Florida. Journal of Kansas Herpetology 22: 14–16.

Smith HT, Meshaka WE Jr, Engeman RM, Crossett SM, Foley ME et al., 2006a. Raccoon predation as a limiting factor in the success of the green iguana in Southern Florida. Journal of Kansas Herpetology 20: 7–8.

Smith HT, Sementelli A, Meshaka WE Jr, Engeman RM, 2007e. Reptilian pathogens of the Florida Everglades: The associated costs of Burmese pythons. Endangered Species Update 24: 63–71.

Smith MM, Smith HT, Engeman RM, 2004. Extensive contiguous north-south range expansion of the original population of an invasive lizard in Florida. International Biodeterioration and Biodegradation 54: 261–264.

Snow RW, Brien ML, Cherkiss MS, Wilkins L, Mazzotti FJ, 2007a. Dietary habits of the Burmese python Python molurus bivittatus in Everglades National Park, FL. Herpetological Bulletin 101: 5–7.

Snow RW, Krysko KL, Enge KM, Oberhofer L, Walker-Bradley A et al., 2007b. Introduced populations of Boa constrictor (Boidae) and Python molurus bivittatus (Pythonidae) in southern Florida. In: Henderson RW, Powell R ed. The Biology of Boas and Pythons. Eagle Mountain, UT: Eagle Mountain Publishing 416–438.
Stein BA, Flack RS, 1996. America's Least Wanted: Alien Species Invasions of U.S. Ecosystems. Arlington, VA: The Nature Conservancy.

Stohlgren TJ, Schnase JL, 2006. Risk analysis for biological hazards: What we need to know about invasive species. Risk Anal. 26: 163–173

Townsend JH, Krysko KL, Enge KM, 2003. Introduced iguanas in Southern Florida: More than 35 years of establishment and range expansion. Iguana 10: 111–118.

Townsend JH, Slapcinsky J, Krysko KL, Donan EM, Golden EA, 2005, Predation of a tree snail Drymaeus multilineatus (Gastropoda: Bulimulidae) by Iguana iguana (Reptilia: Iguanidae) on Key Biscayne, FL. Southeastern Naturalist 4: 361–364.

U.S. Congress, 1993. Harmful Non-indigenous Species in the United States. Washington DC: Office of Technology Assessment, OTA-F-565, Government Printing Office.

U.S. Department of Agriculture/Animal and Plant Health Inspection Service, U.S. Department of Agriculture/Forest Service and Department of Interior/Bureau of Land Management, 1997. Animal Damage Control Program Final Environmental Impact Statement (Revised). Washington DC: USDA/Animal and Plant Health Inspection Service.

Western D, 1974. The distribution density and biomass density of lizards in a semi-arid environment of northern Kenya. East African Wildlife Journal 12: 49–62.

Wiewandt TA, 1982. Evolution of nesting patterns in iguanine lizards. In: Burghardt GM, Rand AS ed. Iguanas of the World. Park Ridge, NJ: Noyes Publications, 119–141.

Wilcove DS, Rothstein D, Dubow J, Phillips A, Losos E, 1998. Assessing the relative importance of habitat destruction, alien species, pollution, over-exploitation, and disease. BioScience 48: 607–616.