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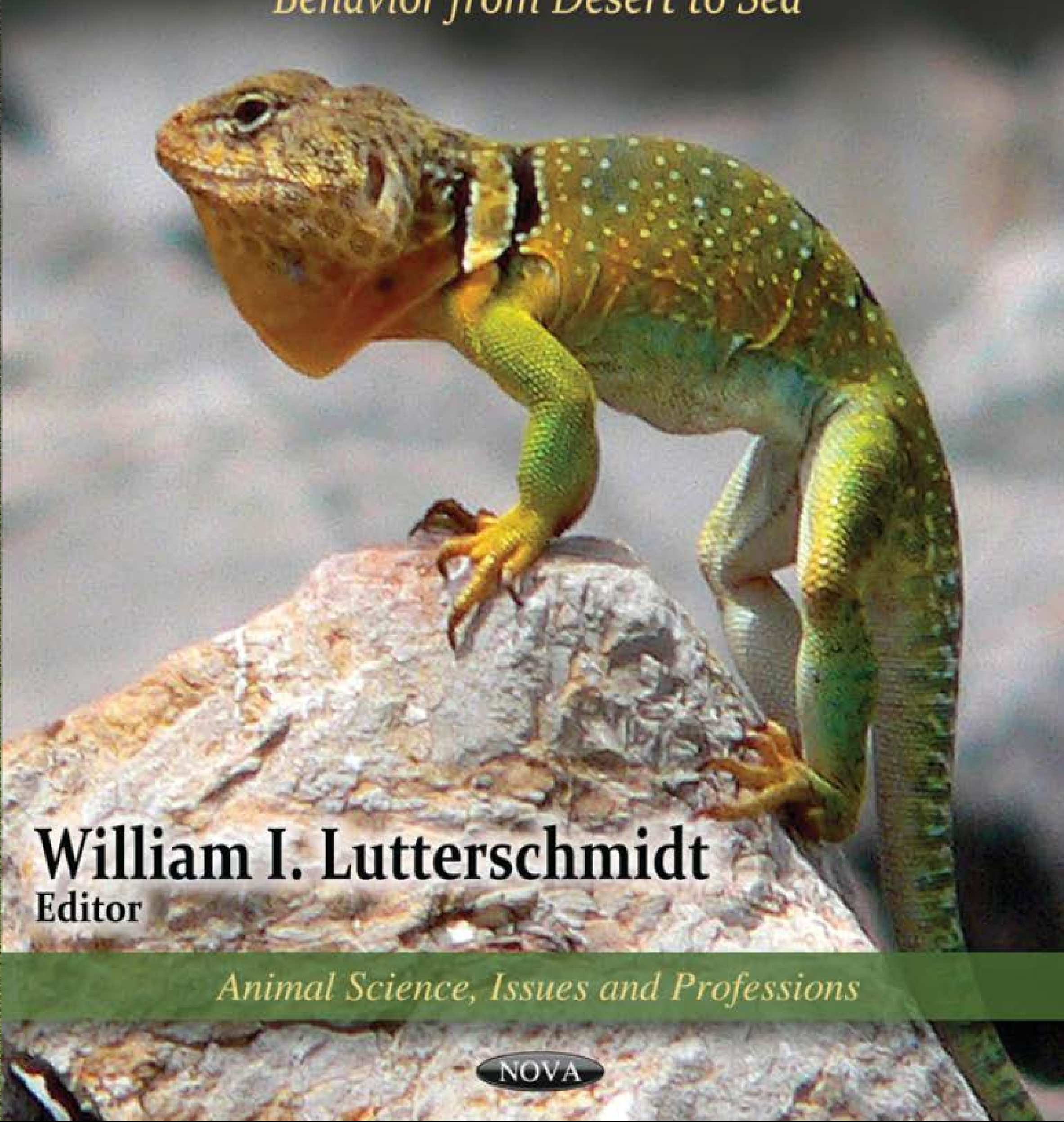

William I. Lutterschmidt
Editor

Animal Science, Issues and Professions

NOVA

ANIMAL SCIENCE, ISSUES AND PROFESSIONS

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INVESTIGATIONS OF ECOLOGY, PHYSIOLOGY, AND BEHAVIOR FROM DESERT TO SEA

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Chapter 19

HIDDEN GIANTS: PROBLEMS ASSOCIATED WITH STUDYING SECRETIVE INVASIVE PYTHONS

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ABSTRACT

The Burmese python (*Python molurus bivittatus*) is native to southern Asia and is one of the largest snakes in the world. Burmese pythons are now established firmly as an invasive species over a large portion of southern Florida. Since recognition as a reproducing population in 2000, the number of pythons found and their geographic range has expanded considerably. Pythons already appear to have caused severe declines in several species of once common mammals (e.g., raccoons, opossums, rabbits, bobcats) but the overall impacts they will have on South Florida ecosystems remain unknown. The cryptic behavior of pythons poses substantial challenges to studying their biology and developing effective management approaches. In this chapter, we review much of the research conducted on pythons, highlight the main findings of that research, and describe a study we conducted to evaluate python behavior and detectability. We show that detectability of pythons is extremely low (1% or lower) and we discuss the implications of such a low detectability for future research and management of this potentially devastating invasive species.

Keywords: Snakes, *Python molurus bivitattus,* invasive species, conservation biology, Florida, Everglades, detectability, ecological impact, population control

INTRODUCTION

The Burmese python (*Python molurus bivittatus*) is one of the largest snakes in the world and a long-time mainstay of the exotic reptile trade. The exact maximum size of Burmese pythons is unknown, but they certainly attain lengths greater than 20 feet (6 m) and may, on extremely rare occasions, exceed 25 feet (7.6 m) in total length (Reed and Rodda 2009). Burmese pythons are massive, strong constrictors, capable of killing and eating relatively large mammals, such as deer. Their color pattern is comprised of a series of dark brown, irregular black-bordered blotches on a lighter background of tan, gray, gold, or yellow, giving them excellent camouflage (Figure 1a).

The Burmese python is a subspecies of the Indian python (*P. molurus*) which is native to much of southern Asia including India, Nepal, Bangladesh, Thailand, Cambodia, and Vietnam (Reed and Rodda 2009). Burmese pythons are not found on Borneo, but they do occur on the islands of Java, Sumbawa, and in western Sulawesi. Details of the geographic range are not well known, and it is likely that human activities and development have eliminated the species from much of its historic range (Dorcas and Willson 2011). Some researchers recognize the Burmese python as a distinct species from the Indian python, but because details of their biology where the ranges of the forms overlap are lacking, most scientists continue to recognize them as a single species. Burmese pythons are found in a wide range of habitats and climates, from lowland rainforests of Vietnam to the foothills of the Himalayas (possibly as high as 8,000 feet [2483 m]) in Nepal. They are often found in or near water and may hibernate in mammal burrows in northern areas of their range (Dorcas and Willson 2011).

Like most reptiles, pythons require relatively little food compared with similarly-sized birds and mammals, and many of their behaviors and physical attributes are directly related to this low-energy approach to living. Because they are ectothermic, pythons do not require food to fuel metabolic heat production (Pough 1980). Pythons can go for more than a year without food, but can grow to over 10 feet (3 m) within two years if well-fed (Dorcas and Willson 2011). Pythons are considered ambush hunters that often remain submerged at the edge of water with only their nostrils above the surface, waiting for an unwary mammal or bird, their primary prey, to come too close. In their native range, pythons have been known to consume several species of deer, monkeys, wild boar, and antelope (Reed and Rodda 2009). They have even been reported feeding on leopards (Begbie 1907).

Burmese pythons typically lay about 40-50 eggs, but may lay more than 100. After laying, the female python coils around her eggs to protect them and will often contract her body muscles about once every two seconds, a process known as shivering thermogenesis, which raises the temperature of the clutch. Given sufficient food, a female python can produce a clutch of eggs every year, but every 2-3 years may be more common in the wild (Willson et al. 2011). Although native to southern Asia, Burmese pythons are one of many species of non-native reptile that have been introduced and are now thriving in southern Florida.

South Florida and the Everglades

The ecosystems found in southern Florida and the Everglades, in particular, represent one of America's most important ecological areas. The Everglades is a huge, shallow watershed flowing slowly from Lake Okeechobee through huge expanses of grass through mangroves and into Florida Bay (Figure 1c; Lodge 2010). The climate of South Florida is subtropical with relatively high, stable temperatures. The climate is also among the wettest in the country with the highest precipitation between April and October. The Everglades is composed mostly of shallow freshwater marshes vegetated with sawgrass and other wetland grasses interspersed with stands of cypress trees and hardwood hammocks that form "islands" (Figure 1b and c). Further south, the vast grasslands give way to dense mangrove forests along the shores of Florida Bay and the Gulf of Mexico. South Florida is one of the most important areas in the United States for wildlife including manatees, American crocodiles, Florida Panthers, and many unique species of birds. The vast marshes of the Everglades are important feeding and breeding habitats for huge numbers of wading birds. South Florida is also an extremely popular tourist destination, resulting in rampant development, especially along the eastern border of the Everglades.

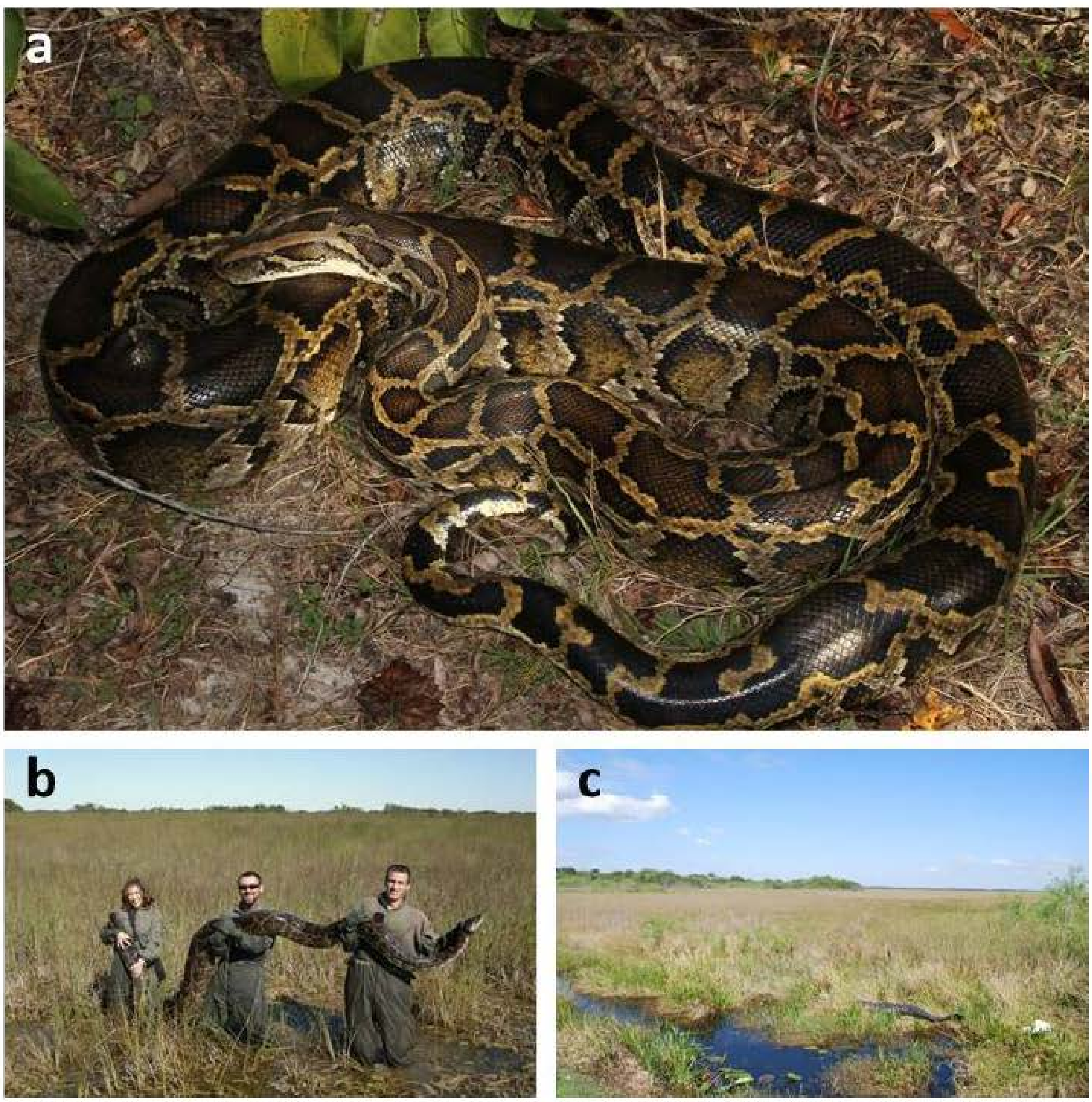

Figure 1. (a) The Burmese python (*Python molurus bivittatus*) is one of the (b) largest snakes in the world as illustrated in this photograph taken by Mike Rochford. As a popular pet it has been introduced from its native range in southern Asia to the (c) Everglades and surrounding regions in South Florida.

Invasive Species

Introduced plants and animals represent an enormous threat to native species worldwide. In the United States alone, the management and effects of invasive species cost more than $100 billion each year (Pimentel et al. 2005). Some introduced species may have little impact on native ecosystems and most scientists consider species to be "invasive" if they have measurable impacts on the ecosystems into which they have been introduced or cause economic damage. Nearly half of all imperiled native species in the United States are threatened by invasive species.

Invasive species can cause many problems for the ecosystems in which they are introduced. Some invasive species can outcompete native species for food or other resources. Invasive plants, and some invasive animals, can alter the physical structure of the environment; for example, invasive grasses in the western United States have greatly altered the soil in many places (Bradley et al. 2006). Some invasive species, such as Cane Toads (*Rhinella marina*) are toxic and have caused population declines in native and naïve predators (Shine 2010). Finally, invasive animals can prey on native species. For example, introduced rats and mongooses have devastated the fauna of many islands by preying on native species that evolved without predators (Clout and Williams 2009).

Pythons as an Invasive Species

Burmese pythons have been popular in the exotic pet trade for decades, being imported and bred in captivity by the thousands. They are beautiful, easy to care for, and generally very docile in captivity, making them a favorite pet snake for many people (de Vosjoli 2005). Often, people acquire them when they are small but when the snakes grow large, they become unmanageable. Thus, in addition to occasional escapes from captivity, many pythons are released into the wild when owners no longer want them. In the mid-1990's, Burmese pythons began to periodically be found in the southern parts of Everglades National Park (ENP) but it was not until the year 2000 that they were recognized as an established, reproducing population (Meshaka et al. 2000). Since 2000, pythons have increased dramatically, both in numbers and in geographic range (Figure 2). We are only beginning to understand the ecology of pythons in South Florida, factors that have allowed their success, or the impacts they may have on native ecosystems.

Although researchers or python hunters can often find pythons by driving roads at night or visually searching during the daytime, it has become clear that pythons spend much of their lives hidden and in habitats where they are not visible to humans. This ability to remain out-of-sight likely contributes greatly to the success of pythons as an invasive species and also poses many challenges for researchers trying to understand python ecology or how to control their populations. Unfortunately, no studies have quantified detection probability of free-ranging pythons or determined the effect that low detectability may have on our ability to understand where they occur, their density or population size, and the impacts they might have on native species.

Our objective in this chapter is to describe some of the main questions related to invasive pythons in South Florida and how they are being, or might be, addressed. Specifically, we will briefly discuss issues related to python spatial ecology, risk assessment, impacts, density estimation, and control. We will highlight how our understanding of all of these factors is impaired by low detectability and present and discuss data from a study designed to determine the detectability of pythons using a semi-natural field enclosure.

Figure 2. Approximate distribution of invasive Burmese pythons in South Florida over time. Map reprinted with permission from Dorcas and Willson (2011).

Research Methods

Methods Used To Study Invasive Pythons in Florida

A variety of techniques are used by scientists to study pythons (Dorcas and Willson 2009). Since pythons were recognized as established, a large, collaborative team of scientists from numerous institutions and agencies have attempted to remove and examine every individual found. Data on location, date, and time of day are recorded for each snake captured which allows for evaluation of daily and seasonal activity patterns and tracking the spread of the population over time (Snow et al. 2007a). Each python is euthanized after capture, and various measurements are taken, including length, mass, and sex. Most pythons are dissected to assess reproductive condition and to examine their gut for prey (Snow et al. 2007b; Dove et al. 2011). Often only hair or feathers remain in the gut, but careful examination of these by trained personnel can usually allow for exact identification of the prey species consumed. Examination of data over time may shed light on demographic patterns of the invasive python population (i.e., changes in size, sex ratio, growth, etc.).

Since 2005, a group of scientists has also been studying the activity patterns, movements, and habitat use of pythons using radiotelemetry (Mazzotti et al. 2011). Using this method, snakes are surgically implanted (Reinert and Cundall 1982) with a small radiotransmitter, released at the site of capture, and tracked using a directional antenna and receiver for periods of months to up to several years. Each time a snake is relocated, data on its location are taken and when possible, behavior, condition, and visibility are recorded. Additionally, each python is implanted with a micro-datalogger that records the internal body temperature of the animal. Comparing body temperature data with environmental temperatures allows scientists to better understand the thermoregulatory patterns, activity, and microhabitat use of pythons (Dorcas and Willson 2009).

One of the most important questions about pythons in Florida is the size of the current introduced population and how their density varies across the landscape and over time. Unfortunately, this question has proven difficult to address for several reasons. Determination of density for any snake species is difficult because of their cryptic behavior (Dorcas and Willson 2009). For most animals, density can be estimated using mark-recapture studies in which animals are captured, marked, and released. After a period of time, the population is resampled and the number of marked individuals captured can be compared to the number of unmarked individuals to estimate population size. Such an approach is impractical for pythons for two reasons. First, because removal of pythons is a major goal, every python captured is euthanized and not returned to the wild. Secondly, even if mark-recapture was attempted, the effort needed to recapture enough pythons over a large enough area to allow estimation of density would likely be extremely high (see below).

To study the impacts pythons are having on native wildlife, we conducted mammal surveys from automobiles at night using roads as transects. Specifically, we surveyed areas in the southern part of ENP where pythons have been established the longest, in areas where pythons have been discovered only more recently, and in two areas of similar habitat where pythons have not yet been detected. By comparing our results from different areas and with a similar survey conducted in ENP in 1996, before pythons became common, we were able to assess shifts in abundance of several mammal species (e.g., raccoons, opossums, rabbits, foxes, and bobcats) in relation to the spread of pythons in the region (Dorcas et al. 2012).

One major unknown about pythons is the potential risk they pose to areas outside of their current range in South Florida. Various models have been developed to estimate the extent of suitable climate for pythons in the United States (Rodda et al. 2011). Although climate models can be quite complex, the basic way that they work is that researchers super-impose climate variables from the native range of pythons onto the United States to identify areas of "climate match." Actual tests of the ability of pythons to survive in outdoor enclosures outside of southern Florida have been conducted. We conducted one of these tests in a semi-natural enclosure at the Savannah River Ecology Laboratory in South Carolina during 2009-2010. Ten adult male pythons were released into the enclosure and their body temperatures, activity, and survival were monitored (Dorcas et al. 2011).

Various methods have been proposed, tested and used to try to find and eradicate pythons. Dogs specifically trained to locate pythons have been tested (Romagosa et al. 2011), various traps have been developed and used in certain situations (Reed et al. 2011), and even drones with infra-red cameras have been proposed. In 2013, the "Python Challenge" was sanctioned by the Florida Fish and Wildlife Conservation Commission and 1600 python hunters were allowed to search for pythons over a month-long period, capture and kill them, and submit them for potential awards (longest and most pythons captured). All of the methods used to study pythons described above are limited by the cryptic nature of pythons and their overall low detectability.

Using Semi-natural Enclosures to Understand Python Detection

We used a previously constructed semi-natural outdoor enclosure (Lee and Mills 2000) at the Savannah River Ecology Laboratory on the Savannah River Site, Aiken County, South Carolina, to examine python behavior, habitat use and detectability (Figure 3). The snake-proof enclosure measured 31 x 25 m and was surrounded by a 2.5-m high, smooth-walled fence set 0.5 m deep in concrete. A 12 m x 10 m pond in the center of the enclosure varied in depth between a shallow end (ca. 0.5 m deep) and a deep end (ca. 2 m deep). One corner of the shallow end of the pond contained emergent aquatic vegetation. Numerous trees (mostly *Pinus* sp.) were present in the enclosure. We also constructed several brush piles and 4 artificial refugia consisting of a 1.0 x 0.5 x 0.5 m plastic chamber (ActionPacker; Rubbermaid, Fairlawn, OH, USA) buried approximately 1 m underground and accessed via a corrugated plastic pipe (1.5 m long x 0.15 m diameter). Although the enclosure contained a variety of habitat types, most of the terrestrial and aquatic habitats were open enough to allow easy access and good visibility (i.e., there were limited areas with thick vegetation or brush). See Dorcas et al. (2011) for details of the enclosure and study design.

Figure 3. Semi-natural outdoor enclosure in South Carolina used to investigate Burmese python behavior, habitat use, and detectability. The enclosure measured 31 x 25 m and contained a variety of terrestrial, aquatic, arboreal, and subterranean habitats. Note that although numerous habitats were available, most areas allowed good visibility.

We released ten wild-captured male pythons from ENP (2 - 3.5 m total length) into the enclosure in late June 2009 and monitored them through late December 2009. We surgically implanted a radio-transmitter (model AI-2; Holohil Ltd., Carp, Ontario) into the body cavity of each snake (Rienert and Cundall 1982) and relocated each snake via radio-telemetry during daylight hours at least three times per week beginning on 1 July. Upon relocation, we recorded the air temperature, location, behavior, habitat use, and visibility of each snake. For the purposes of this study we defined the habitat used by each snake as either aquatic (Water; majority of the snake's body in or under the water), terrestrial (Land; the majority of the snake's body on the surface of the ground, out of the water, or under cover on the ground), subterranean (Burrow; the majority of the snake's body in one of the four artificial burrows), or arboreal (Tree; the majority of the snake's body off the ground in or on vegetation). We scored each snake's visibility from 0 – 100% based on how much of the snake's body was visible without manipulating the habitat. In all cases, we attempted to avoid disturbing the snake or altering its normal behavior (e.g., when snakes were not visible, we generally did not disturb the habitat to confirm their presence).

We evaluated seasonal changes in habitat use of pythons by compiling the proportion of relocations that occurred in each habitat type (water, land, tree, burrow) in each month. We evaluated the influence of habitat type on snake detectability by compiling the proportion of relocations in each habitat type where the snake was not visible, 1-50% visible, or >50% visible by an observer without manipulating the habitat. We evaluated the effects of environmental conditions on snake behavior and visibility by examining how frequently snakes were visible at different air temperatures (5°C increments). For this analysis, we excluded snakes that were located in trees because snakes using arboreal habitats were always visible, regardless of environmental conditions.

Between 17 July and 26 August 2009, a Davidson College undergraduate student (Rick Bauer) coordinated a series of controlled searches of the python enclosure in which we recruited various observers to evaluate python detectability without the aid of radio telemetry. In total, we tested 19 different observers, primarily from the pool of researchers and employees at the Savannah River Ecology Laboratory. The observers varied considerably in terms of their experience with snakes or pythons, from those who had seldom seen snakes in the field to seasoned herpetologists with extensive experience finding snakes, including pythons, in the wild. However, none of the observers had prior knowledge of any of the python's locations or frequent patterns of habitat use within the enclosure. Each observer was shown a live example of captive Burmese python and then allowed to search the enclosure for 30 min without guidance. Observers were allowed to gently move vegetation or gently probe for snakes with a snake hook, but were not permitted to grossly alter the habitat (e.g., rip apart brush piles or dig up borrows). We recorded ambient temperature at the time of each survey and scored each observer from 0 to 4 in terms of their experience searching for snakes in the field. Following the 30-min survey, we recorded any snakes that were detected by the observer and relocated all snakes via radio telemetry to confirm their potential visibility during the survey.

Results and Discussion

General Results of Python Research

Since the year 2000, when Burmese pythons were recognized as established (Meshaka et al. 2000), the number of pythons found in South Florida has increased dramatically. More than 2000 pythons have been removed from South Florida since 2005. Although the amount of effort expended searching for pythons has varied and is not well documented, it is clear that there is a large population of Burmese pythons in Florida and that their geographic range has expanded considerably (Figure 2). Pythons of all age classes have been found, with the average size being 7-10 feet (2.1-3 m) in total length. Hatchling pythons (typically 1.5-2 feet [0.45-0.6 m]) are found less frequently than adults, likely as a result of their small size and presumably, more secretive habits. The largest males found are approximately 12 feet (3.5-4 m) in total length and the largest female pythons are 16-17.5 feet (4.8-5.3 m). The two largest pythons found were both found in 2012 and both measured over 17.5 feet (5.3 m) in total length. Female pythons in Florida produce an average of 45 eggs per clutch, but clutches up to 87 eggs have been recorded (Dorcas and Willson 2011). Females likely reproduce every other year and probably reach maturity at 4 years of age (Willson et al. 2011).

Examination of the gut contents of captured pythons has revealed that pythons will prey on nearly any bird or mammal in southern Florida. Additionally, there are several instances of pythons preying on alligators, even relatively large ones. Mammals consumed by pythons include various species of rodents, muskrats, rabbits, raccoons, opossum, bobcats, and white-tailed deer (Snow et al. 2007b). Endangered Key Largo Woodrats have been recorded as prey and it is conceivable that pythons could even prey on endangered Florida Panthers. Numerous species of birds also have been documented as prey of pythons in Florida (Dove et al. 2011). Birds associated with aquatic habitats are by far the most commonly preyed upon and include the limpkin and many species of herons, egrets, rails, coots, grebes, and ducks. Passerine birds are eaten less frequently, but meadowlarks, wrens, and blackbirds have all been reported from the guts of pythons. Several incidences of pythons feeding on domestic animals (house cats, poodles, roosters, ducks, and geese) have also been reported (Dorcas and Willson 2011). The fact that pythons will eat nearly any bird, mammal, or crocodilian species they encounter likely increases their success as an invasive species (Reed and Rodda 2009).

Spatial ecology research using radiotelemetry has shown that like most snakes, male pythons move considerably further than do females during a typical year (Harvey et al. 2009). This difference in movement patterns is likely a result of males spending more time in search of females during the spring breeding season. When radiotelemetry studies began, six pythons were relocated up to 30 km from their initial capture locations. These pythons, over the span of just a few months, moved in relatively straight paths back to the areas where they were captured (Harvey et al. 2009). Exactly how pythons can navigate such long distances through areas that they have not yet encountered is unknown, but certainly warrants further investigation. The ability to navigate may allow pythons to explore new areas in search of resources (e.g., prey) with less risk because they have the ability to return to their home area.

One of the main issues that has plagued efforts to understand python ecology, assess their impacts on native species, and control their populations is a lack of an estimate of python population size or density. In fact, without knowledge of density, it is impossible to design effective control initiatives or assess if the number of snakes removed so far has had any effect on the invasive population. Unfortunately, estimates of snake densities are notoriously difficult to obtain in most circumstances. Some efforts to extrapolate rough densities from their native range indicate that ENP alone could support a population of at least 30,000 pythons and possibly as many as 300,000 (Snow et al. 2007a). When one considers that pythons are now found in vast areas outside ENP, it is certainly possible that the invasive python population approaches or well exceeds hundreds of thousands of animals. Of course, the density of pythons likely varies considerably over time and space. The reality is, traditional density estimation methods do not work for pythons and new, innovative methods for estimating populations will be required to answer this important question.

Although we know what types of prey pythons eat in South Florida (see above), until recently, we knew little about the potential impact that pythons are having on populations of native wildlife. The results of our mammal surveys in ENP and elsewhere in South Florida showed severe declines in mammals that matched both the temporal and spatial pattern of python proliferation in the region (Dorcas et al. 2012; Figure 4). Frequency of observations in ENP declined by 99.3% for raccoons, 98.9% for opossums, and 87% for bobcats since pythons were recognized as established (Figure 4a). No foxes or rabbits were observed during recent surveys in ENP, although they were found before pythons proliferated. Mammal sighting rates in areas where pythons have more recently been documented (i.e., outside ENP) were reduced, but not to the extent found in ENP, whereas mammal populations outside the current range of pythons remained high (Figure 4b).

We know from experience that invasive snakes can devastate native ecosystems. The brown treesnake (*Boiga irregularis*), which was introduced to the Pacific island of Guam in the 1950's, has driven most of the native forest birds and bats to extinction in the wild (Rodda et al. 1997). The loss of these species has drastically altered Guam's ecosystems. Years of efforts to eradicate treesnakes have been unsuccessful. Yet efforts are still underway to at least suppress their numbers and to ensure that they are not accidentally transported to other islands, such as Hawaii. It appears that pythons already have severely impacted mammal populations in South Florida. The impacts pythons are having on populations of other animals which they are known to prey upon (e.g., birds) are unknown, as are the indirect impacts such predation might have on natural ecosystems.

The risk invasive pythons pose to the remainder of the United States (i.e., outside of South Florida) has been an area of hot debate for several years (Rodda et al. 2009, Pyron et al. 2008; Rodda et al. 2011). Most climate matching studies suggest all of Florida and large portions of the coastal southeastern United States contain suitable climate for pythons (Rodda et al. 2009; van Wilgen et al 2009; Rodda et al. 2011). Already, pythons have expanded their geographic range to well north of ENP and southward into the Florida Keys. Several questions remain unanswered that could shed light on the ability of pythons to survive outside of South Florida. For example, although Burmese pythons are found in a wide variety of climates in Asia, we still do not know if the pythons now residing in South Florida originated from tropical rainforests, from more temperate climates, or both. If all pythons in Florida originated from tropical rainforests, then their ability to spread to more temperate areas may be limited. Additionally, we know little about the ability of pythons to evolve behaviors or physiological capabilities that may enable them to better survive temperate climates. An unusually severe winter in 2009-2010 apparently killed many pythons (and many native animals) in South Florida, as well as the ten individuals maintained in an outdoor enclosure in

South Carolina. Despite this unusual cold spell, many snakes in South Florida survived, presumably by seeking refugia underground. If behavioral traits that mediate the decision to seek refuge during cool weather are heritable, then cold winters may select for individuals that are more cold tolerant over time, facilitating the spread of pythons into temperate areas (Dorcas and Willson 2011).

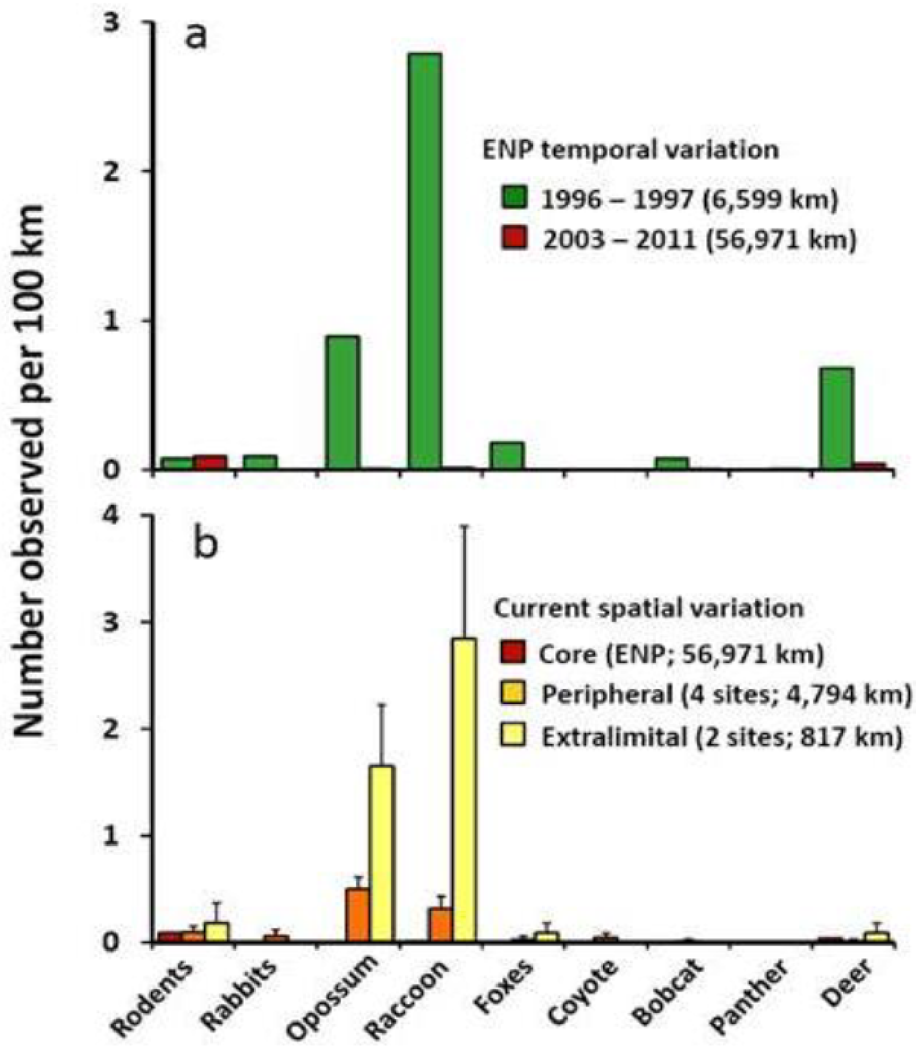

Figure 4. Variation in mammal abundances in South Florida in relation to Burmese python invasion. (a) Temporal variation in mammal encounter rates in Everglades National Park, as reflected in distance-corrected road survey counts before (1996 – 1997) and after (2003 – 2011) pythons became common in the region. (b) Current spatial variation in mammal encounter rates in core (ENP), peripheral, and extralimital regions of python range in Florida. Pythons have been recorded for over a decade in the core region, only more recently in peripheral locations, and not at all in extralimital locations. Figure adapted from Dorcas et al. (2012).

Although several methods to control python populations have been proposed or tested, none currently shows any promise for eradicating or even suppressing python populations across their range in South Florida. Use of dogs to detect pythons may be effective under certain circumstances (e.g., a python is seen in a neighborhood and needs to be found), but dogs can only be used in areas that are easily accessible to humans and the pythons' range in Florida now encompasses vast areas that are extremely difficult to access or search. Likewise, traps may work in some areas for particular purposes, but are impractical for use over large areas (Dorcas and Willson 2011). The "Python Challenge," conducted for a month during early 2013 and sponsored by the Florida Fish and Wildlife Conservation Commission, resulted in only 68 pythons being captured, despite the efforts of over 1600 registered python hunters. In Guam, dead mice implanted with acetaminophen, which is toxic to snakes, are being used to poison brown treesnakes and are even being deployed via aircraft (R. Reed pers. comm). Although a similar approach might seem appealing for pythons in Florida, the number of native animals detrimentally affected by such an approach could be devastating.

Detection of Pythons in a Semi-natural Outdoor Enclosure

Our enclosure study in South Carolina provided important information on python behavior and detectability. In Florida, invasive Burmese pythons are most frequently captured and removed when encountered, rather than observed. Likewise, because of the inaccessibility and challenging habitat of the Everglades, snakes monitored in the wild using radiotelemetry are seldom closely observed and little is known about the behavior or detectability of free-ranging pythons (Dorcas and Willson 2011). Our semi-natural enclosure allowed for detailed analysis of python behavior as well as an opportunity to conduct controlled detection surveys of pythons that were known to be present within a confined area.

The ten pythons maintained in South Carolina exhibited seasonal shifts in habitat use and visibility. During July, August, and September, pythons were most frequently located in the water (>50% of locations; Figure 5), where they were almost never visible (Figure 6A). In August, September, and October, several snakes occasionally spent extended periods of time in arboreal habitats (Figure 5), including high up in pine trees. Snakes located in trees were always highly visible, once relocated via radiotelemetry (Figure 6A). In October, November, and December, pythons exhibited a steady reduction in use of aquatic habitats, with concomitant increases in use of terrestrial habitats and burrows (Figure 5; Dorcas et al. 2011). Snakes located on land were visible more frequently than those in the water or in burrows (Figure 6A), but were still only visible approximately 40% of the time. Moreover, in many cases, 'visibility' of snakes in terrestrial habitats was limited to small patches of the body that could barely be seen though vegetation or other cover. By December, most snakes were located in burrows, where they were rarely visible. The progressive seasonal shift from aquatic, to terrestrial, to subterranean habitats led to a pattern of highest visibility in relatively cool weather (5-20°C; Figure 6B), but even within this window snakes were not visible at all in >75% of relocations. When temperatures were >25°C or <5°C, snakes were never fully visible. Overall, pythons were not at all visible during 501 of 628 (80%) total relocations.

Our series of controlled python searches confirmed the difficulty of detecting these snakes. In fact, of the 190 possible opportunities for python detection (19 observers x 10 snakes), snakes were only detected on two occasions (Table 1). Thus, even with 30 min of searching within the confines of a 31 x 25 m area, individual detection probability of pythons was approximately 1%. The two snakes that were detected were found by relatively experienced observers (scored 3 and 4), but it should be noted that several very experienced herpetologists did not detect a single snake, including those that were visible when relocated via radio telemetry. Despite the fact that pythons in arboreal habitats were highly visible (Figure 6A), observers failed to detect five pythons located in pine trees in August (Table 1). The fact that these highly visible snakes were missed in surveys may reflect a perception that pythons prefer terrestrial or aquatic habitats and thus inadequate search of arboreal habitats during surveys.

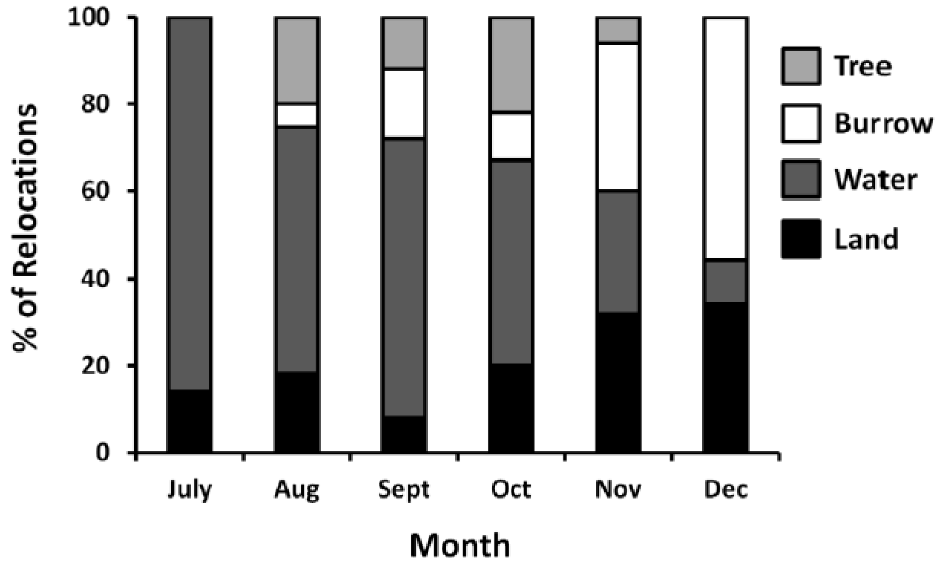

Figure 5. Seasonal habitat use of Burmese pythons maintained in a semi-natural outdoor enclosure in South Carolina from July to December 2009.

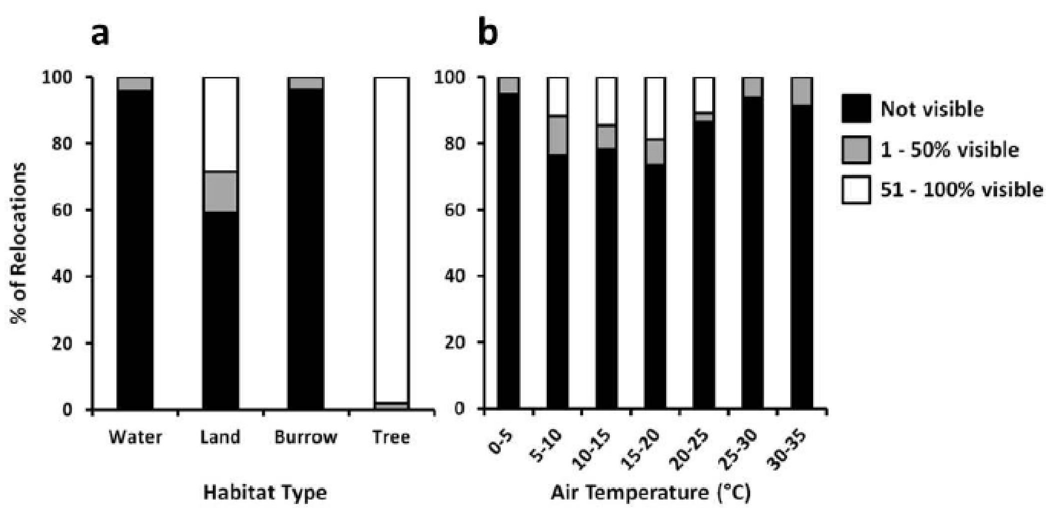

Figure 6. Visibility of Burmese pythons maintained in a semi-natural outdoor enclosure in South Carolina and monitored by radio telemetry. All snakes were relocated approximately three times per week and were considered visible if any part of their body could be observed without altering the habitat. (a) Python visibility in relation to habitat use. (b) Python visibility in relation to air temperature, excluding locations in trees, when snakes were always visible.

Implications of Low Detection for Python Research and Control

Snakes are notoriously secretive and low detectability has been a major impediment to our understanding of snake ecology and conservation (Dorcas and Willson 2009; Willson et al. 2011). In the context of an invasive snake species that appears to be having substantial impacts on native wildlife (Dorcas et al. 2012), low detectability of pythons presents numerous challenges.

Although several authors have discussed the implications of low detectability for python management (Dorcas and Willson 2011, Willson et al. 2011, Reed and Rodda 2009), our studies in South Carolina suggest that python detection probability may be even lower than was previously suspected. When located via radio telemetry, pythons in the enclosure were only visible 20% of the time, and in many cases 'visibility' was limited to a snout protruding above the water, or a few scales visible deep within a brush pile. Without the aid of telemetry, detectability dropped to 1%, even within the confines of a small enclosure and habitats that afforded good visibility. Detection probability of free-ranging pythons in Florida is undoubtedly even lower than our estimates from the enclosure. Although accurate density estimates for wild pythons are lacking, they are certainly orders of magnitude lower than the density of snakes within our enclosure (129/ha). For example, density estimates for pythons within their native range vary from as few as 0.05/ha (Burmese pythons in India; Bhupathy and Vijayan 1989) to as many as 0.75/ha (Rock pythons in Africa; Starin and Burghardt 1992). In addition to having a dramatically inflated python density, the enclosure used in our study also provided good visibility and access to most habitats. Many areas of South Florida are largely inaccessible and contain heavily vegetated or aquatic habitats that afford poor visibility. Thus, it is reasonable to assume that detection probably of wild pythons in Florida is well below 1% much of the time.

The exceptionally low detection probabilities that we documented for pythons suggests that suppressing or eradicating populations of this species will be extremely difficult, even in very limited areas. For example, with a detection probability of 1%, one hundred 30-min surveys would be needed to detect all of the 10 pythons maintained within our small enclosure. Considering that pythons in Florida likely now inhabit a geographic area greater >8000 km^2, the effort needed to eradicate this species would be astronomical. Despite the overall low detectability of pythons, our results demonstrate that pythons are most visible under specific conditions. We found that pythons were most visible in cool weather when using terrestrial habitats and while in trees. These observations correspond well with observations from Florida suggesting that pythons are found most frequently during visual surveys after cool nights when they may bask in conspicuous locations, such as canal banks (Dorcas and Willson 2011; Mazzotti et al. 2011). However, our data also suggest that even under ideal conditions, <25% of pythons were visible, even when located via radio telemetry. The one clear exception to the overall low detectability of pythons in our study was the relatively frequent use of arboreal habitats in the late summer that rendered pythons highly visible. Much of the Everglades lacks extensive tree cover and relatively few wild pythons have been captured in trees. Thus, we are unable to determine whether arboreal habitat use was an artifact of the enclosure or whether wild pythons also use arboreal habitats but are being overlooked by those searching for pythons. Our controlled searches suggest that even experienced herpetologists may fail to consider arboreal habitats when searching for pythons, perhaps biasing our perceptions of habitat use by this species.

Table 1. Detection of pythons in controlled 30 min searches of a 30 x 25 m semi-natural enclosure in South Carolina containing 10 male pythons. Observer skill level was ranked from 0 to 4, based on their prior experience collecting snakes in the field. Python habitat use indicates the habitats being used by the 10 pythons on each survey date and how many were visible when located with radio-telemetry. Note that only two pythons were detected by observers in a total of 19 surveys with 190 possible detection opportunities

Survey Date	Time	Air Temp (°C)	Observer Skill Level (0-4)	Python Habitat Use: Water	Land	Tree	Burrow	# visible	Pythons Detected: # seen	Habitat
7/17/2009	1540	33	3	8	2	0	0	0	1	land
7/20/2009	1002	23	0	9	1	0	0	0	0	
7/20/2009	1132	26	4	9	1	0	0	0	0	
7/20/2009	1212	27	0	9	1	0	0	0	0	
7/21/2009	1104	28	2	8	1	0	1	0	0	
7/22/2009	1455	30	1	10	0	0	0	0	0	
7/23/2009	1007	29	0	10	0	0	0	0	0	
7/23/2009	1106	30	0	10	0	0	0	0	0	
7/23/2009	1342	32	2	10	0	0	0	0	0	
7/27/2009	1653	29	0	8	2	0	0	0	0	
7/27/2009	1718	30	4	8	2	0	0	0	0	
7/29/2009	1443	24	0	8	1	0	1	0	0	
7/29/2009	1510	28	4	8	1	0	1	0	0	
7/29/2009	1555	27	4	8	1	0	1	0	0	
7/29/2009	1619	29	0	8	1	0	1	0	0	
7/30/2009	1100	34	4	9	1	0	0	0	0	
8/04/2009	0930	29	1	10	0	1	0	2	0	
8/04/2009	1000	32	4	10	0	1	0	2	1	water
8/26/2009	1340	33	4	8	1	3	1	3	0	

Our results also have strong implications for assessing python density. First, our results support the contention that the size of the invasive population is very large, despite the fact that snakes are sometimes difficult to find. Since the mid 2000's, 100-400 pythons have been removed annually from ENP and surrounding areas (Willson et al. 2011). Using a 1% detection probability as a benchmark, this suggests that 10,000 to 40,000 pythons may have been present, but undetected, in the areas that were searched each year. Considering that the vast majority of these captures come from the very limited areas of the Everglades that are accessible by road or canal, the total number of snakes present in the region is undoubtedly much larger than that. Second, low individual detection probability reduces our ability to accurately estimate population size or density. Mark-recapture studies are the most commonly used method for estimating density of secretive wildlife. Our data suggest that detectability of this species is so low that an extraordinarily high number of individuals would need to be marked and released and a massive amount of effort would be needed to recapture a sufficient number of individuals to generate a meaningful population estimate. Results of our research also suggest that targeting specific environmental conditions or habitats might increase capture probability to some degree. Conceivably, the efficacy of visual surveys could further improved though techniques such as detector dogs (Dorcas and Willson 2011; Romagosa et al. 2011), but it is likely that even these improvements will not increase detection probability to the point where mark-recapture is viable as a method for estimating population size. More likely, researchers will need to develop novel approaches to density estimation that do not rely on recapturing individuals. Finally, observer bias likely has a strong confounding influence on abundance estimators that rely on visual detection in the field (Rodda 1993). Although python detection rates in our surveys were too low to provide any insight into observer bias, the potential for variability among observers in their ability to locate pythons is evident in the recent "python challenge" sponsored by the Florida Fish and Wildlife Conservation Commission. More than 25% of the 68 pythons collected during this event were captured by one of the 1,600 registered hunters.

Finally, the extremely low detectability of pythons poses a major challenge to assessing the progress of the invasion and detecting newly invaded areas in time to respond appropriately. Assuming that detection of free-ranging pythons is well below the 1% estimate from our detection surveys, the effort needed to detect pythons in areas where density is very low would be enormous. Even greater effort would be needed to conclude with confidence that pythons were indeed absent from areas where they were not detected (i.e., to statistically guard against false negatives). For example, Durso et al. (2011) recently demonstrated that 1890 trap-nights of unsuccessful aquatic trapping would be needed to be 95% confident of species absence for an aquatic snake species with a 5% probability of detection in 30 trap-nights of effort. The issue of detecting pythons in newly invaded areas is further complicated by that fact that in many snakes, juveniles are the life stage that is most likely to disperse into new habitats (e.g., Waldron et al. 2013). Although we only tested adult snakes in our enclosure studies, it is reasonable to assume that detection of juveniles would be substantially lower than adults (Willson et al. 2011). Thus, our chances of being able to accurately assess invasion status of areas at the periphery of the python's range are very low. As with other aspects of python research and management, developing novel methods for sampling pythons and generating accurate and precise estimates of python detection probability in natural habitats will be critical for curbing the spread of this species and preventing establishment of additional populations in other areas.

Conclusion

It is easy to understand why pythons have been so successful in Florida. The subtropical climate and abundance of water in South Florida provide ideal habitat for pythons and the many canals and other water bodies may facilitate their movements (Dorcas and Willson 2011). The impressive reproductive potential, generalist diet, and rapid growth of Burmese pythons has likely also contributed greatly to their success and rapid spread (Reed et al. 2012). Additionally, because Burmese pythons are ectothermic, their overall food requirements are far lower than those of similar-sized endothermic predators. When food is plentiful they can devote substantial amounts of energy to growth and reproduction, and when food is scarce they can survive for very long periods without a meal (Pough 1980).

Although we know more about Burmese pythons in Florida than we do in their native range, what we know is still limited substantially by the low detectability of pythons in the wild. Our study showed that detection rates for pythons within a small enclosure are approximately 1%, but are likely much lower in the wild. Low detection probability poses significant challenges for scientists trying to study these snakes and are particularly problematic for studies attempting to determine the density of pythons or if they are established in new areas. Such low detection rates for a species found over a vast geographic area which is largely inaccessible also poses unique and potentially insurmountable problems for any efforts to control their populations. Thus, new and innovative approaches to studying and management of this cryptic, but potentially devastating, invasive species are sorely needed.

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REFERENCES

Begbie, A. 1907. The food of pythons. *Journal of the Bombay Natural History Society* 17:1021.

Bhupathy, S and VS Vijayan. 1989. Status, distribution and general ecology of the Indian Python, *Python molurus molurus* Linn. in Keoladeo National Park, Bharatpur, Rajasthan. *Journal of the Bombay Natural History Society* 86:381-387.

Bradley, BA, RA Houghton, JF Mustard, and SP Hamburg. 2006. Invasive grass reduces aboveground carbon stocks in shrublands of the Western US. *Global Change Biology* 12:1815-1822.

Clout, MN and PA Williams. 2009. *Invasive Species Management: A Handbook of Principles and Techniques*. Oxford University Press, Oxford. 336 Pp.

de Vosjoli, P. 2005. *Burmese Pythons: Plus Reticulated Pythons and Related Species*. Irvine, California, Advanced Vivarium Systems, Irvine. 79 Pp.

Dorcas, ME and JD Willson. 2009. Innovative methods for studies of snake ecology and conservation, Pp. 5-37 *In* SJ Mullin and RA Seigel (Eds.), *Snakes: Ecology and Conservation*. Cornell University Press, Ithaca. 365 Pp.

Dorcas, ME and JD Willson. 2011. *Invasive pythons in the United States: ecology of an introduced predator*. University of Georgia Press, Athens. 156 Pp.

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

Dorcas, ME, JD Willson, RN Reed, RW Snow, MR Rochford, MA Miller, WE Mehsaka, Jr, PT Andreadis, FJ Mazzotti, CM Romagosa, and KM Hart. 2012. Severe mammal declines coincide with proliferation of invasive Burmese pythons in Everglades National Park. *Proceedings of the National Academy of Sciences* 109:2418-2422.

Dove, CJ, RW Snow, MR Rochford, and FJ Mazzotti. 2011. Birds consumed by the invasive Burmese python (*Python molurus bivittatus*) in Everglades National Park, Florida, USA. *The Wilson Journal of Ornithology* 123:126-131.

Durso, AM, JD Willson, CT Winne. 2011. Needles in haystacks: estimating detection probability and occupancy of rare and cryptic snakes. *Biological Conservation* 144:1508-1515.

Harvey, RG, ML Brien, MS Cherkiss, ME Dorcas, M Rochford, RW Snow, and FJ Mazzotti. 2008. Burmese pythons in South Florida: Scientific support for invasive species management. *University of Florida Extension - http://edis.ifas.ufl.edu/uw286*.

Lee, JR and MS Mills. 2000. Design and construction of an outdoor enclosure for the study of snake thermal ecology. *Herpetological Review* 31:24-26.

Lodge, TE. 2010. The everglades handbook: understanding the ecosystem. 3rd edition. CRC Press, Boca Raton. 392 Pp.

Mazzotti, FJ, MS Cherkiss, KM Hart, RW Snow, MR Rochford, ME Dorcas, and R N Reed. 2011. Cold-induced mortality of invasive Burmese pythons in south Florida. *Biological Invasions* 13:143-151.

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

Pimentel, D, R. Zuniga R, and D Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics* 52:273-288.

Pough, FH. 1980. The advantages of ectothermy for tetrapods. *American Naturalist* 115:92-112.

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

Reed, RN, KM Hart, GH Rodda, FJ Mazzotti, RW Snow, M Cherkiss, R Rozar, and S Goetz. 2011. A field test of attractant traps for invasive Burmese pythons (*Python molurus bivittatus*) in southern Florida. *Wildlife Research* 38:114-121.

Reed, RN and GH Rodda. 2009. Giant constrictors: biological and management profiles and an establishment risk assessment for nine large species of pythons, anacondas, and the boa constrictor. *US Geological Survey Open-File Report* 1202. 302 Pp.

Reed, RN, JD Willson, GH Rodda, and ME Dorcas. 2012. Ecological correlates of invasion impact for Burmese pythons in Florida. *Integrative Zoology* 7:254-270.

Reinert, HK and D Cundall. 1982. An improved surgical implantation method for radio-tracking snakes. *Copeia* 1982:702-705.

Rodda, GH, TH Fritts, and D Chiszar. 1997. The disappearance of Guam's wildlife. *BioScience* 47:565-574.

Rodda, GH. 1993. Where's Waldo (and the snakes)? *Herpetological Review* 24:44-45.

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

Rodda, GH, CS Jarnevich, and RN Reed. 2011. Challenges in identifying sites climatically matched to the native ranges of animal invaders. *PLoS ONE* 6:e14670.

Romagosa, CR, TD Steury, MA Miller, C Guyer, B Rogers, TC Angle, RL Gillette. 2011. Assessment of Detection Dogs as a Potential Tool for Python Detection Efforts. *Final Report submitted to the National Park Service and South Florida Water Management District.* 33 Pp.

Shine, R. 2010. The ecological impact of invasive cane toads (*Bufo marinus*) in Australia. *Quarterly Review of Biology* 85:253-91.

Snow, RW, KL Krysko, KM Enge, L Oberhofer, A Warren-Bradley, and L Wilkins. 2007a. Introduced populations of *Boa constrictor* (Boidae) and *Python molurus bivittatus* (Pythonidae) in southern Florida, Pp 416-438. *In* RW Henderson and R Powell (Eds.), *Biology of the Boas and Pythons*. Eagle Mountain Publishing, Eagle Mountain. Pp. 438.

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

Starin, ED, and GM Burghardt. 1992. African rock pythons (*Python sebae*) in the Gambia: observations on natural history and interactions with primates. *The Snake* 24:50-62.

Van Wilgen, NJ, N Roura-Pascual, and DM Richardson. 2009. A quantitative climate-match score for risk-assessment screening of reptile and amphibian introductions. *Environmental Management* 44:590-607.

Waldron, JL, SH Bennett, SM Welch, ME, Dorcas, JD Lanham, and W Kalinowsky. 2006. Habitat specificity and home-range size as attributes of species vulnerability to extinction: a case study using sympatric rattlesnakes. *Animal Conservation* 9:414-420.

Willson JD, ME Dorcas, and RW Snow. 2011. Identifying plausible scenarios for the establishment of invasive Burmese pythons (*Python molurus*) in southern Florida. *Biological Invasions* 13:1493-1504.

Willson JD, BD Todd, and CT Winne. 2011. Ecological and methodological factors affecting detectability and population estimation in elusive species. *Journal of Wildlife Management* 75:36-45.