Biol Invasions (2011) 13:1493–1504
DOI 10.1007/s10530-010-9908-3

ORIGINAL PAPER

Identifying plausible scenarios for the establishment of invasive Burmese pythons (*Python molurus*) in Southern Florida

John D. Willson · Michael E. Dorcas · Raymond W. Snow

Received: 26 March 2010 / Accepted: 8 November 2010 / Published online: 21 November 2010

Abstract Successful invasions of secretive alien species often go unrecognized until spread has exceeded the point where control or eradication is feasible. In such situations, understanding factors that contributed to establishment can be critical to preventing subsequent introductions of previously-successful invaders or ecologically similar species. The Burmese python (*Python molurus bivittatus*), a native to Southeast Asia, is abundant in the pet trade and is now well-established in southern Florida. Although there can be little argument that the ultimate source of Florida pythons was the pet industry, there has been limited consideration of biological support for scenarios that may have lead to their establishment. In this study we use information on python capture rates and biologically-derived population growth models to evaluate the plausibility of various scenarios for python establishment. Our results indicate that scenarios involving relatively recent establishment (post-1990) require large numbers (100–1,000) of founders or unrealistically high juvenile survivorship. Intentional simultaneous release of large numbers of pythons is unlikely and accidental release of large numbers of founders is inconsistent with the spatial and temporal pattern of pythons captures in the region. We conclude that the most parsimonious scenario for establishment of pythons in Florida involves the release of a relatively small number of founders prior to 1985. Our results demonstrate that for pythons and other species with low inherent detection probabilities, early action during incipient phases of an invasion is critical and understanding likely introduction scenarios is important for preventing similar situations from occurring elsewhere or with other species.

Keywords Everglades National Park · Introduction · Invasive species · Population growth · *Python molurus bivittatus* · Reptiles · Snakes

Introduction

Invasive species are widely recognized as one of the greatest threats to global biodiversity (Pimentel et al. 2000; Park 2004). Often, once an alien species becomes firmly established over a large geographic

---

J. D. Willson
Savannah River Ecology Laboratory, PO Drawer E,
Aiken, SC 29809, USA

M. E. Dorcas
Department of Biology, Davidson College, Davidson,
NC 28035-7118, USA

R. W. Snow
Everglades National Park, 4001 State Road 9336,
Homestead, FL 33034, USA

J. D. Willson (✉)
Department of Fisheries and Wildlife Sciences, Virginia
Polytechnic Institute and State University, 100 Cheatham
Hall, Blacksburg, VA 24061, USA
e-mail: willsonj@vt.edu

area, eradication is functionally impossible and even large scale suppression is infeasible or prohibitively expensive. Such situations can arise from inaction during incipient phases of invasion or insufficient detection, such that presence of the invader is not appreciated until establishment is well under way. In the latter case, which is highly probable for species that exhibit inherently low detectability, understanding factors that contributed to introduction and establishment can be critical to prevent subsequent introductions of previously-successful invaders or ecologically similar species (Kraus 2009).

Among terrestrial vertebrates, snakes are among the most difficult to detect (Dorcas and Willson 2009) and their adaptability, low energetic requirements, and popularity as pets have contributed to establishment of several species outside of their native range (Martinez-Morales and Cuaron 1999; Rodda et al. 1999; Meshaka et al. 2004; Quick et al. 2005; Snow et al. 2007; Reed and Rodda 2009). An understanding of factors that have contributed to successful invasions by snakes may be one of the most powerful tools for preventing establishment of additional populations and species (Kraus 2009). For example, knowledge that introduction of the brown treesnake (*Boiga irregularis*) to the island of Guam likely occurred in approximately 1950 via stowaway in cargo (Savidge 1991), has prompted an extensive effort to minimize stowaway of snakes in cargo currently leaving the island and detection of snakes at ports in locations where threat of invasion is perceived to be high (e.g., Hawaii and other Pacific islands; Campbell et al. 1999). These efforts have been successful in detecting snakes in cargo shipments and have thus far prevented additional spread of this potentially destructive invader (Engeman and Vice 2002).

The Burmese python (*Python molurus bivittatus*), a native to Southeast Asia, is abundant in the pet trade and is now firmly-established in southern Florida, including Everglades National Park (ENP; Snow et al. 2007). Burmese pythons are very large (up to at least 5.5 m in length), long-lived, behavioral and habitat generalists that exhibit high fecundity, producing clutches of 8–107 eggs (Reed and Rodda 2009). In Florida, Burmese pythons have consumed American alligators (*Alligator mississippiensis*) and a wide variety of avian and mammalian prey including wading birds, bobcat (*Lynx rufus*), and white-tailed deer (*Odocoileus virginianus*), prompting concern that they may negatively impact populations of native wildlife including several endangered or “at risk” species (Snow et al. 2007; Rochford et al. 2010; Reed and Rodda 2009). Python densities in ENP are unknown, but were estimated conservatively at greater than 30,000 individuals in 2007 based on a density estimate of this species in India (Snow et al. 2007). Python sightings in ENP have increased exponentially since the early 1990s and the range of pythons appears to be expanding both into the Florida Keys and northward through the peninsula (Snow et al. 2007; R.W. Snow, unpublished data). A recent study indicating that climate suitable for Burmese pythons exists throughout much of the southern United States (Rodda et al. 2009) has sparked controversy over the potential for python range expansion. The explosion of Florida python populations has garnered extensive and often sensationalistic media attention. In the course of this media coverage, several scenarios for python introduction have been proposed, generally with little or no support or scientific evaluation. One particularly well-publicized idea is that the Florida python population originated from snakes released as a result of devastation caused by Hurricane Andrew in August of 1992. Although the exact circumstances that lead to introduction and establishment of Burmese pythons in Florida will never be proven, careful consideration of biological support for various introduction scenarios can provide information that is valuable for preventing additional introductions of Burmese pythons in other parts of the United States or establishment of similar species in the region.

In this study we evaluate the plausibility of various scenarios for the introduction and establishment of a reproductive population of invasive Burmese pythons in southern Florida. Specifically, we use models based on python capture rates and a life-history-based population growth model to identify a set of plausible candidate scenarios for python introduction. We then evaluate candidate models in light of spatial and temporal patterns of python captures to identify the most plausible scenarios for python introduction and establishment.

Methods

We used two modeling approaches to evaluate the plausibility of scenarios (time of introduction and characteristics of the founder population) that could have lead to the introduction and establishment of Burmese pythons in southern Florida. First, we developed a model that used the relationship between python capture rates over time and population size to evaluate likely time lines for population establishment. Next, we developed a demographic age-structured population model to estimate rates of python population growth under various introduction scenarios.

Capture rate model

Our first modeling approach was based on the assumption that python encounter rates since introduction were positively related to population size. Assuming that detection was substantially less than one (i.e., that for every python found, numerous others were present, but undetected), pythons must have been present within ENP before snakes began to be regularly encountered (i.e., mid 1990s). Thus, we used python encounter rate data from 1995 to 2008 to predict the date of python introduction in southern Florida. Specifically, we fit an exponential curve to the python capture data and, assuming a direct relationship between python capture rate and population size, standardized that curve for 2008 python population sizes varying across an order of magnitude (10,000 or 100,000 individuals). We then extrapolated those curves back in time to identify a likely range of years for establishment of a breeding population.

In the early 2000s, it became clear that pythons were established in ENP, prompting increased public attention and scientific investigation. Thus, since 2004, sampling effort for snakes has increased substantially (R. W. Snow, pers. comm.). This increased effort has likely led to an increase in the probability that any individual python in ENP would be captured in recent years (i.e., violating our assumption of a consistent relationship between encounter rates and population size). Likewise, the expansion of the python population into areas that are more frequented by humans has probably further inflated python detection probabilities in recent years; a python living on the outskirts of Miami or along Tamiami Trail (US Hwy 41) undoubtedly has a greater chance of being captured or reported than a python living in the inaccessible interior of ENP. We attempted to account for this bias by conducting an additional analysis that incorporated a twofold increase in detection probability from 2004 to 2008. However, it is likely that even a twofold increase in detection probability is not sufficient to account for the increase in search effort and accessibility in recent years and our empirical estimate of population growth rate may still be an overestimate.

Demographic population growth model

We developed various scenarios for the introduction and establishment of invasive Burmese pythons in southern Florida based on population growth rates. These included scenarios where the founder population was comprised of either hatchling snakes or reproductively mature adults. We considered founder population sizes (equal sex ratio) ranging from 2 (e.g., 1 male and 1 female) to 1,000 individuals. Inoculation methods were either a single introduction or chronic introduction over many years.

We used a demographic population model to examine the possible rate of Burmese python population growth given what is known about the natural history and demography of the introduced population within ENP. Our goal in this modeling exercise was to estimate the rate at which the south Florida python population has grown since introduction under several introduction scenarios (e.g., number and demography of founders). With this goal in mind, we made several simplifying assumptions in this model, all erring on the side of faster population growths than likely occurred. Specifically, we assumed:

1. no density-dependent negative feedback (i.e., the population always experiences exponential growth with no competition for food or other resources).
2. no mate limitation (i.e., all females find mates when mature, even at very low densities).
3. no survivorship penalty at introduction (i.e., newly-introduced individuals do not experience elevated mortality as they acclimate to the wild).
4. no reproductive penalty at introduction (i.e., adult females are assumed to be gravid at introduction and have no trouble finding mates thereafter).

Based on data from ENP, pythons certainly breed seasonally and females may be capable of maturing during their third year of life and breeding for the first time at age three (see below). Thus, we modeled Burmese python population growth using a simple age-based (three age classes) discrete-time (1-year time step) population model with no density-dependence. The iterative equation for the model can be expressed as a pre-breeding census in matrix form as:

$$\begin{bmatrix} Y1 \\ Y2 \\ A \end{bmatrix}_{t+1} = \begin{bmatrix} 0 & 0 & f_A S_{Y1} \\ S_{Y2} & 0 & 0 \\ 0 & S_{Y3} & S_A \end{bmatrix} \times \begin{bmatrix} Y1 \\ Y2 \\ A \end{bmatrix}_t$$

where $Y1 - Y2$ are immature age classes (age 12 months, and age 24 months), A represents the mature age class (age 36 months and older), f_A is the yearly fecundity of mature females, and S parameters are annual survivorships that link transition from one age class to the next. As with most population models of this sort, our model only considered the female portion of the population. However, when presenting model results we assumed a 50:50 sex ratio (supported by clutches taken from ENP Burmese pythons–R.W. Snow, unpublished data) and multiplied all population numbers by two when calculating total population sizes.

Because animal populations are comprised of discrete individuals, we rounded any fractional population sizes to integer values at the end of each time step. Likewise, because we were not interested in examining extinction risk (i.e., we know that pythons did not go extinct) we rounded fractional population sizes less than one up to one for all age classes each time step.

Parameterization

Relatively few parameters are necessary to model population growth using our model. Specifically, the following data are needed (all data pertain only to females): age at maturity, clutch size, frequency of reproduction, and survivorship of females within the three age classes. Female Burmese pythons reportedly reach maturity at 260 cm total length (Reed and Rodda 2009) and the smallest gravid female collected from the Florida population was 235 cm snout-vent length (SVL). Although female pythons have the potential to grow extremely rapidly in captivity, free ranging pythons in Florida grow more slowly. It is frequently possible to discern juvenile growth by examining temporal (seasonal) patterns in sizes of captured juveniles (e.g., Willson and Dorcas 2004; Todd et al. 2008). Using this approach (Fig. 1), it is clear that female pythons reach approximately 100–150 cm SVL by the time they are 1 yr old. Thereafter, due in part to a lack of young pythons captured during cooler months, it becomes more difficult to differentiate cohorts. However, it is likely that some female pythons top 200 cm SVL by age two and reach mature size during their third year of life (Fig. 1). Although we suspect that many females may not reproduce for the first time until age four, here we assume that females reach mature size (>230 cm SVL) between 24 and 36 months of age and produce their first litter at age 3.

Very large female pythons are capable of producing large clutches (80–107 eggs; Reed and Rodda 2009; Rochford et al. 2009). However, data suggest that most clutches in the Florida python population are smaller. As of 2009, based on 27 clutches of wild-caught Florida pythons, the mean clutch size was 39.3 eggs per female. Likewise, although well-fed captive female pythons often reproduce annually, free-ranging female pythons likely take some time to recover from the energetic demands of producing and brooding eggs (Reed and Rodda 2009). Non-gravid mature-sized females are often encountered during the season when females are gravid (March–June; Fig. 1; R.W. Snow, unpublished data) and no mature females monitored via radio telemetry have reproduced in successive years, suggesting that reproduction by female pythons in Florida is biennial for most individuals. Thus, factoring in a 50:50 sex ratio,

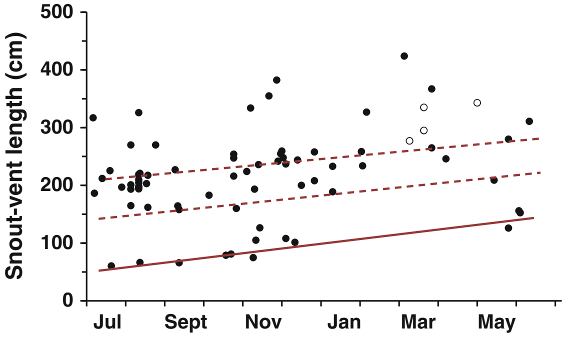


Fig. 1 Seasonal size distribution of female *Python molurus* captured in southern Florida. *Open circles* represent gravid females. Inferred first year growth is indicated by the *solid line*. *Dotted lines* represent likely growth trajectories for second- and third-year snakes. Although we suspect that many females may not reproduce for the first time until age four, our models assume that females reach mature size (>230 cm SVL) between 24 and 36 months of age and produce their first litter at age three

biennial reproduction, and an average clutch size of 40 eggs, we use a value of 10 female offspring produced per year per mature female python.

Survivorship of Florida pythons is unknown, but is generally assumed to be high. We set adult female survivorship at 0.9. Functionally, this means that >50% of females that reach maturity live to be 10 years old, >20% live to be 20 years old, and a few (<10%) live to be >25 years old. This rate is similar to, or higher than, adult survivorship rates calculated for other large snake species (e.g., Australian water pythons, *Liasis fuscus*, Madsen et al. 2006). Survivorship of immature python age classes is even less well-known. For most of our simulations, we used a value of 0.3 for first-year snakes and a linear increase in survivorship between year 1 and the adult survivorship rate of 0.9 (0.5 for second year-snakes and 0.7 for third year snakes). However, because of the uncertainty associated with this parameter, we conducted a sensitivity analysis investigating the influence of varying juvenile survivorship on our results and discuss the potential importance of this parameter to our conclusions.

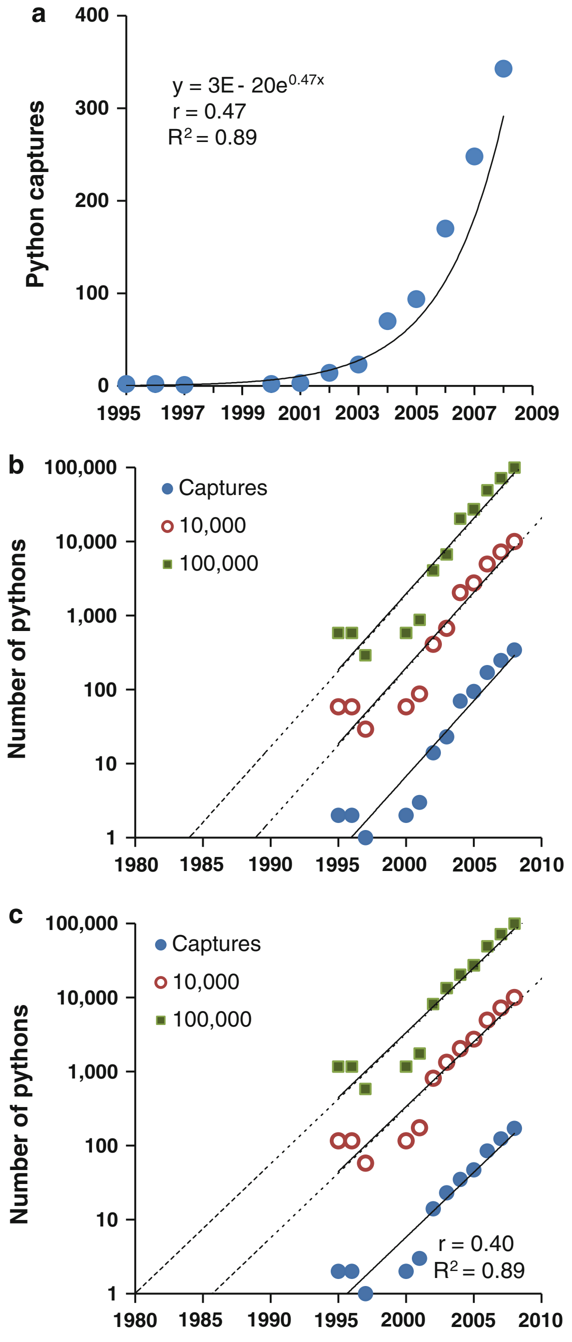
Simulations

We conducted a set of model simulations to investigate python population growth under several introduction scenarios (e.g., number and demography of founders). Specifically, we simulated three plausible introduction scenarios: 1) a scenario representing a single introduction of 2–1,000 hatchling pythons, 2) a scenario representing a single introduction of 2–1,000 adult (mature) pythons, and 3) a scenario representing chronic introduction of 2–10 adult pythons per year. In each of these simulations we compare the timeline of population growth and assess likely dates of introduction based on current perceived python population size in southern Florida. Because the current size of the python population in south Florida has not been determined, we considered a wide range of current population sizes; specifically, we considered an introduction scenario plausible if it led to a 2008 python population size of 10,000–100,000 individuals. Finally, we examined the sensitivity of our model to juvenile survivorship by generating population growth curves under scenarios where juvenile survivorship varied from 0.2 to 0.8. In this simulation we allowed a linear increase in survivorship between year 1 and the adult survivorship rate of 0.9.

Results

Python captures within southern Florida have increased dramatically since 1995 when they began to be encountered on a regular basis (Fig. 2a). This pattern of increasing capture rates is explained well using an exponential model ($R^2 = 0.89$) with a rapid exponential population growth rate ($r = 0.47$). Note that the last 5 years (2004–2008) actually fall above the curve, likely reflecting an increase in python detectability during recent years due to increasing sampling effort and spread of the python population into more inhabited areas. Assuming a consistent relationship between python encounters and population size, it is possible to estimate date of establishment (i.e., when population size <10 individuals) under different current population size scenarios–this is essentially identical to evaluating differing rates of python detectability. Assuming a 2008 population size of 10,000 animals, establishment occurred between 1988 and 1993 (Fig. 2b). Assuming a 2008 population size of 100,000 animals, establishment occurred between 1983 and 1988. If we incorporate a twofold increase in python detectability from 2004 to 2008, due to increasing sampling effort and spread of the python population into more inhabited areas, population growth rate is reduced ($r = 0.40$). Consequently, predicted establishment dates are pushed back to between 1984 and 1991 for a 2008 population equal to 10,000 animals and between 1980 and 1985 for a 2008 population of 100,000 animals (Fig. 2c).

The first set of scenarios we evaluated using the population growth model assumed a single introduction of hatchling (<1 year old) snakes (Fig. 3). Following introduction of two hatchling snakes (i.e., 1 male and 1 female), it would take 26 years for the population to exceed 10,000 animals and 33 years for the population to exceed 100,000 animals. Starting with a founder population of 100 hatchling snakes, it would take 21 years for the population to exceed 10,000 animals and 28 years for the population to exceed 100,000 animals. Beginning with 1,000 hatchling snakes, it would take 14 years to exceed 10,000 animals and 22 years to exceed 100,000 animals.



◀**Fig. 2** Timelines of python population growth derived from fitting exponential growth curves to python abundance based on capture numbers. **a** Yearly python captures in southern Florida from 1995 to 2008. **b** Python population growth over time estimated by standardizing relative abundance based on captures to 2008 python population sizes of 10,000 or 100,000 individuals. *Dotted lines* represent population size trajectories extrapolated to dates before pythons were reported. **c** Same data as **(b)**, but assuming a 100% increase in python detectability (due to increased search effort and python expanding into areas inhabited by humans) from 2004 to 2008 (i.e., that python abundance was under-estimated by a factor of two in 1995–2003, compared to 2004–2009

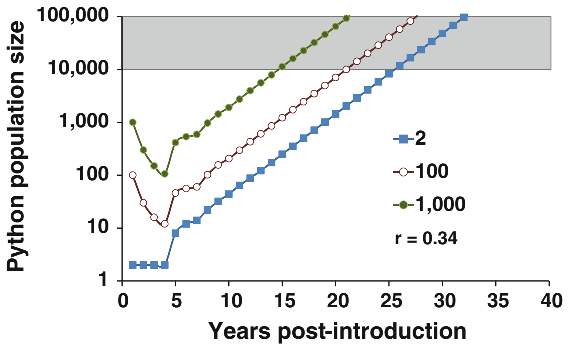


Fig. 3 Burmese python population growth under a scenario of a single introduction of hatchling pythons. Lines represent increasing numbers of first year snakes introduced. Survivorship is set at 0.3 for first year pythons, 0.5 for second year, 0.7 for third year, and 0.9 thereafter. *Shaded region* represents 2008 population sizes of 10,000–100,000 pythons, the criteria by which we judge the plausibility of introduction scenarios (combinations of initial conditions and time since introduction). Note log scale on *Y*-axis, such that *straight lines* indicate exponential population growth; '*r*' indicates the estimated rate of exponential population growth

Overall, a one-time introduction of adult pythons resulted in a faster rate of population growth (Fig. 4). Considering a single introduction of two (i.e., one male and one female) mature pythons, it would take 22 years to exceed 10,000 animals and 30 years to exceed a population size of 100,000 animals. If 10 adult pythons were introduced, it would take 19 years to exceed a population size of 10,000 animals and 26 years to exceed 100,000 individuals. If 100 adult pythons were introduced, it would take 12 years to exceed a population size of 10,000 and 19 years to exceed 100,000 animals. If 1,000 adult pythons were introduced, the population size would exceed 10,000 in 6 years and 100,000 in 12 years.

Considering scenarios of chronic introduction of small numbers of adult pythons, increasing the yearly number of snakes introduced results in small to moderate increases in population growth (Fig. 5). These differences, however, resulted primarily from inflating the numbers of founders in the first few years following introduction and introducing additional individuals only resulted in very minor increases in population growth rate ($r = 0.34$–0.36).

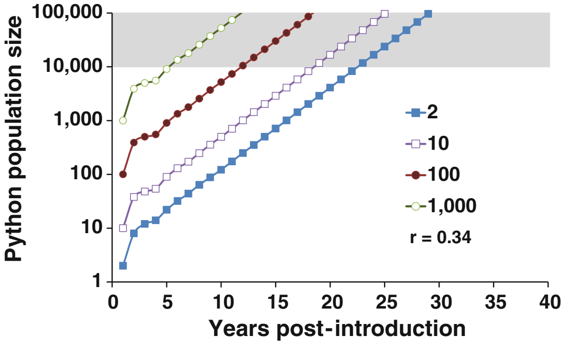


Fig. 4 Burmese python population growth under a scenario of a single introduction of adult pythons. *Lines* represent increasing numbers of adults introduced. Survivorship is set at 0.3 for first year pythons, 0.5 for second year, 0.7 for third year, and 0.9 thereafter. *Shaded region* represents 2008 population sizes of 10,000–100,000 pythons, the criteria by which we judge the plausibility of introduction scenarios (combinations of initial conditions and time since introduction). Note log scale on *Y*-axis, such that *straight lines* indicate exponential population growth; '*r*' indicates the estimated rate of exponential population growth

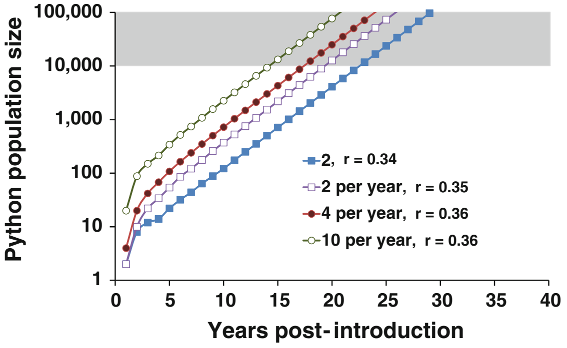


Fig. 5 Burmese python population under a scenario of chronic introduction of adult pythons. *Lines* represent increasing numbers of adults introduced. Survivorship is set at 0.3 for first year pythons, 0.5 for second year, 0.7 for third year, and 0.9 thereafter. *Shaded region* represents 2,008 population sizes of 10,000–100,000 pythons, the criteria by which we judge the plausibility of introduction scenarios (combinations of initial conditions and time since introduction). Note log scale on *Y*-axis, such that *straight lines* indicate exponential population growth; '*r*' indicates the estimated rate of exponential population growth

Introduction of 2 adult snakes per year shortened the time required to reach any population size above 100 animals by approximately 3 years compared to a one-time introduction of 2 adult snakes. Thus, chronic introduction of 2 snakes per year resulted in a population of 10,000 animals within 20 years and 100,000 within 26 years. Chronic introduction of 4 snakes per year resulted in 10,000 animals within 18 years and 100,000 animals within 24 years. Chronic introduction of 10 snakes per year resulted in a population of 10,000 animals within 15 years and 100,000 animals by 21 years.

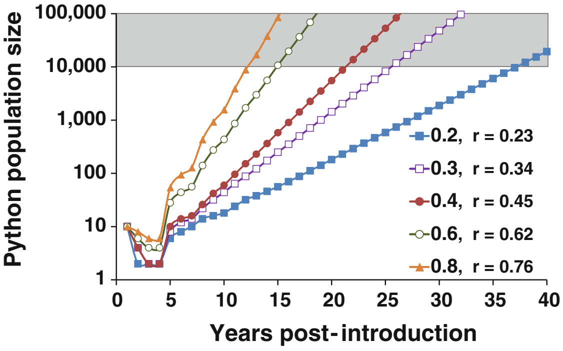


Fig. 6 Effect of juvenile survivorship on Burmese python population growth. All simulations begin with a founder population of 10 hatchling pythons. Survivorship values represent first year survivorship with a linear increase in survivorship up to 0.9 after age three. *Shaded region* represents 2008 population sizes of 10,000–100,000 pythons, the criteria by which we judge the plausibility of introduction scenarios (combinations of initial conditions and time since introduction). Note log scale on *Y*-axis, such that *straight lines* indicate exponential population growth; '*r*' indicates the estimated rate of exponential population growth

Overall, our model was sensitive to variation in juvenile survivorship (Fig. 6). Increasing juvenile annual survivorship from 0.2 to 0.8 dramatically increased population growth rate ($r = 0.23$ vs. $r = 0.76$) and shortened the number of years required to reach a population size of 10,000 animals by 32 years (48 years for 0.2; 16 years for 0.8). However, reaching population sizes greater than 10,000 animals within 20 years of introduction requires juvenile annual survivorship of approximately 0.5 or greater. Given the likely increase in python detection probability in recent years, a juvenile survivorship of approximately 0.35 yields a population growth rate that most closely approximates the empirical estimate of population growth generated from the capture rate model corrected for increase in detectability (Fig. 2c).

Discussion

Burmese pythons have been encountered with increasing regularity in southern Florida since 1994 and it is now clear that a large reproducing and expanding population exists in the region. Escalating public concern about this situation, fueled by media attention, has prompted numerous speculations about scenarios that lead to establishment of pythons in Florida. However, to date, there has been limited consideration of biological support for various proposed introduction scenarios (but see Snow et al. 2007). Here, we use information on python capture rates and biologically-derived population growth models to evaluate the plausibility of various scenarios for python establishment. Although there can be little argument that the ultimate source of Florida pythons was the exotic pet industry, understanding likely introduction scenarios is important for preventing similar situations from occurring elsewhere or with other species and, potentially, for establishing responsibility.

Based on our two modeling exercises and 2008 python population sizes ranging from 10,000 to 100,000 individuals, we consider the following to be biologically-plausible, albeit unlikely in some cases, scenarios for the introduction and establishment of the reproducing Burmese python population in southern Florida:

1. A one-time introduction of a small number of young pythons before 1980.
2. A one-time introduction of a relatively large number of young pythons (100–1,000) between 1980 and 1993.
3. A one-time introduction of a small number of adult pythons in the 1980s.
4. A one-time introduction of a large number of adult pythons after 1990.
5. Chronic introduction of small numbers of adult pythons beginning in the 1980s.
6. Recent (post-1990) introduction of a small number of juvenile pythons with subsequent very high survivorship (probably $> 50\%$ in year 1 and higher thereafter).

Below, we discuss spatial, temporal, and demographic patterns of python captures in southern Florida and evaluate our list of biologically-plausible scenarios in light of those patterns.

Spatial, temporal, and demographic patterns of Burmese python captures

Snow et al. (2007) summarized spatial, temporal, and demographic patterns of python captures in southern Florida during the years when it first became evident that pythons had established a breeding population in the region. Pythons first began to be regularly encountered within Everglades National Park in 1994 and small numbers of snakes were found in most years through 2001 (Meshaka 2000; Meshaka et al. 2004; Snow et al. 2007). Between 1994 and 2001, the majority of python encounters occurred in the saline glades and mangrove swamps in the southwestern portion of ENP on the main park road from Flamingo to West Lake. The first evidence of reproduction (i.e., capture of four hatchlings and one juvenile python) in ENP was near West Lake. This region of ENP is at least 30 km from the nearest substantial agricultural or urban areas. As of 2009, although pythons are found throughout ENP and its environs, pythons are still most frequently encountered in the saline glades and mangroves in the southern parts of ENP.

Evaluating introduction scenarios

Biologically plausible scenarios involving relatively recent (i.e., post 1985) introduction and establishment of pythons in southern Florida (Scenarios 2 and 4) require relatively large founder populations (i.e., >100 individuals). Although there are many reptile breeders and importers in South Florida, we consider it unlikely that such a large number of adult pythons would be accidentally or intentionally released because few individuals own such large numbers of adult snakes and the monetary value of these animals as breeders would be substantial. Natural disasters, such as Hurricane Andrew in 1992, could provide a mechanism for the accidental release of snakes, especially in light of large numbers of juvenile pythons frequently held by breeders and importers prior to sale and distribution. However, the spatial and demographic patterns of python captures are not consistent with such scenarios. The nexus of python encounters in the region, and the location where wild reproduction was first confirmed, is the mangrove forests and saline glades of the southern portion of ENP, located at least 30 km from the nearest reptile breeder/importers (Snow et al. 2007). Thus, in order for the python population in southern Florida to have originated from destruction of breeder/importer facilities, large numbers of pythons would have had to move over 30 km, forming the core of the invasive population, with few snakes becoming established in the intervening habitat (where pythons have since become common). Due to inaccessibility of the habitats within ENP, the majority of python captures occur along paved roads and along canal banks (Snow et al. 2007). Despite the presence of several heavily-traveled paved roads north and east of ENP (e.g., US Hwy 1 and Krome Ave.), in areas where breeder/importer facilities may have been located, most of the python captures before the year 2000 occurred along the main park road, well within ENP (Snow et al. 2007). Pythons were first encountered on US Hwy 1 and Krome Ave. around the year 2004, and are now commonly found in those areas (Snow et al. 2007; R.W. Snow, unpublished data). Thus, scenarios involving more recent introductions require increasing numbers of snakes to move this considerable distance (hundreds if introduction occurred in the 1980s to over 1,000 in the early 1990s). Therefore, we conclude that scenarios involving relatively recent introduction of large numbers of adult or juvenile pythons (Scenarios 2 and 4) are unlikely.

Biologically, achieving current population sizes from relatively recent introduction of a small number of pythons is only possible if both juvenile and adult survivorship are very high (Scenario 6). Although adult python survivorship is likely high, pythons are not invulnerable to predators, human persecution, and other sources of mortality (Snow et al. 2007; R.W. Snow, unpublished data). Sources of adult python mortality include predation by American alligators and likely Florida panthers, deliberate removal by humans, vehicular mortality, including mowers and agricultural equipment, and death or injury during wildfires or prescribed burns. In fact, at least 5 of 16 adult ENP pythons that have been monitored via radio telemetry died natural deaths (i.e., not due to complications with surgery or telemetry) while being monitored (R.W. Snow, unpublished data). Moreover, our model is relatively insensitive to increases in survivorship above 0.90; considering a scenario of two adult founders, even increasing adult survivorship to 0.98 only increased population growth rate from 0.35 to 0.41, and decreased to time needed to reach a population size of 10,000 by 2 years. Although juvenile pythons have not been monitored via radio-telemetry, and no estimates of juvenile survivorship for large constrictors have been published, it is almost certain that they exhibit lower survivorship than adults (Pike et al. 2008). Survivorship estimates for snakes are scarce, but adult North American large colubrid snakes (*Nerodia*, *Elaphe*, *Heterodon*, *Coluber*, *Pituophis*), which are similar in size to first-year pythons and likely are exposed to a similar range of predators, have annual survivorship rates ranging from 35 to 80% (Parker and Plummer 1987; Pike et al. 2008). Adult Australian water pythons (*Liasis fuscus*), similar in size to second-year *P. molurus*, exhibit 60 to 90% annual survivorship, depending on prey availability (Madsen et al. 2006). Perhaps the most ecologically relevant comparison to pythons is not a snake, but the American alligator (*Alligator mississippiensis*). Alligators inhabit similar habitats to Florida pythons, have similarly high fecundity, and are probably vulnerable to a similar range of predators as juveniles and adults. Although adult alligators exhibit very high (approaching 100%) survivorship, survival of juveniles is low (Woodward et al. 1987; Woodward and Murray 1993). In one Florida lake, only 41% of young alligators survive to age one and 8% survive to two years of age (Woodward et al. 1987). Similar survivorship patterns have been documented in other crocodilian species (Smith and Webb 1985). Thus, although survivorship of young pythons may be higher than that of the young of other snake species, it is unlikely that it is as high as 50% during the first year of life. This is particularly true considering that, in our model, first-year survivorship incorporates any losses starting from the time that clutch size is assessed (ovulation to laying); thus including loss to infertile ova, inviable embryos, nest destruction, and death due to complications during hatching. Although studies are badly needed to evaluate ecology and survivorship of juvenile pythons, the implausibility of extremely high juvenile survivorship argues strongly against recent (post-1990) introduction of small numbers of pythons as the source of the established population in southern Florida.

Chronic introduction of small numbers of adult pythons (Scenario 5) is a biologically plausible scenario for the establishment of a breeding population of snakes in the southern Florida. Such a scenario could result from the intentional, periodic release over time of unwanted pets. Based on past and continuing sporadic discoveries of obviously newly released or escaped pet pythons both throughout

Florida and elsewhere (Meshaka et al. 2004; Kraus 2009), it is clear that chronic low-level introduction of pythons is occurring in many areas. Propagule pressure is known to be one of the primary factors that promote successful invasions of alien species (Lockwood et al. 2007; Hayes and Barry 2008) and multiple introductions may benefit invasive species by ameliorating genetic bottlenecks imposed by small founder population size (Dlugosch and Parker 2008). Chronic long-term introductions may well have been required for successful initial establishment of Burmese pythons in ENP, but our results suggest that supplementing the invasive population with small numbers of additional introductions does relatively little to speed subsequent population growth. Moreover, if chronic introduction played an important role in fueling initial population growth we would expect a broad spatial pattern of initial captures that would likely include some of the aberrant color morphs (e.g., albino, green, granite etc.) that have been common in the pet trade for at least two decades. The localized distribution of initial python captures and the fact that none of the pythons captured within ENP exhibited aberrant coloration is consistent with origination of the population in South Florida from a limited number of "normal" patterned founders. Thus, although long-term chronic introduction of unwanted pet pythons may have been important in promoting initial python population establishment, it is unlikely to have played a major role in population growth trajectory after that time. Future research on the genetics of the Florida Burmese python population will be useful for evaluating the size of the founder population and the role that chronic introduction may have played in promoting establishment and early population expansion.

The final biologically plausible scenarios for the establishment of Burmese pythons in southern Florida involve introduction of small numbers of adult or juvenile pythons more than 20 years ago (Scenarios 1 and 3). Based on estimated population growth rates, successful establishment of less than 100 juvenile pythons prior to 1980 or a few (<10) adult pythons prior to 1985 could give rise to current python population sizes. This timeline fits well with establishment dates estimated based on python encounter rates (Fig. 2), especially when considering the likely increase in python sampling effort (leading to increased python detection rates) since 2004. Moreover, given the extremely low individual detectability of these snakes, it is quite probable that small numbers of pythons were established within ENP well before regular python encounters began in the early 1990s. For this reason, we consider the most plausible scenario for establishment of pythons in the region to have been a one-time release of a relatively small number of adult or juvenile pet pythons in the mangrove regions of ENP near Flamingo prior to 1985. That population grew slowly during the first decade following establishment (Figs. 2, 3) and, following the expectation of exponential population growth generally exhibited by unregulated populations, expanded rapidly in the 1990s. This scenario is entirely consistent with the spatial and demographic patterns of python captures (Snow et al. 2007). Moreover, although python-specific search efforts were not initiated within ENP until the late 1990s, isolated sightings occurred much earlier. Meshaka et al. (2000) noted that "*Python molurus bivittatus* has been reported from the saline glades and mangroves since the 1980s" and "park personnel have observed large pythons, some of which were identified as *Python molurus bivittatus*, since the 1980s." Thus, it seems likely that wild pythons existed within the southern mangroves of ENP well before their establishment was confirmed or publicized.

Conclusions

We used two modeling approaches to evaluate support for various scenarios for the establishment of invasive Burmese pythons in southern Florida. Our models erred on the side of overestimating population growth rate by assuming no density-dependent negative feedback as a result of competition for food or other limiting resources and by having females first reproduce at age three. Additionally, we assumed that snakes did not incur any penalties to reproduction or survival at low densities or while newly-introduced and acclimating to the wild. Our results indicate that scenarios involving relatively recent establishment (post-1990) require large numbers of founders or unrealistically high juvenile survivorship. Intentional release of large numbers (100–1,000) of pythons is unlikely given the high value of these snakes and lack of motivation for a large scale release. Moreover, accidental release (e.g., resulting from hurricanes or other natural disasters) of large numbers of founders from reptile breeder/importer facilities in southern Florida is inconsistent with the spatial and temporal pattern of pythons captures in the region (Snow et al. 2007). We conclude that the most parsimonious scenarios for establishment of pythons in the region involve the release of a relatively small number of founders in the southern portion of the Everglades prior to 1985.

It is noteworthy that although the most biologically plausible scenarios for python establishment suggest that introduction occurred prior to 1985, pythons were not encountered regularly in the region until the mid-1990s and not in large numbers until post-2003 (Fig. 2; Snow et al. 2007). This fact serves as a testament to the secretive behavior and low activity of the species and the inaccessibility of much of the habitat in the Everglades, which together result in extremely low individual detection probability for pythons and prevented widespread recognition of the presence of this species in southern Florida until well after establishment. Our results demonstrate that for pythons and other species with low inherent detection probability (including most snakes; Dorcas and Willson 2009), early action during incipient phases of an invasion is critical (Kraus 2009). Once it becomes clear that populations are established, population sizes may be too large or geographically widespread to feasibly eradicate or control (Reed and Rodda 2009). Alternatively, proactive measures that prevent initial introductions may be more effective than reactive control or eradication measures once successful establishment (reproduction) is detected. Our results provide a first step in modeling invasive python population dynamics in southern Florida and similar approaches may be useful for evaluating the success of control measures and optimizing allocation of resources available for study or control of this invasive species. Finally, our analyses highlight the importance of juvenile survivorship in dictating population dynamics of highly fecund species such as pythons. Understanding the ecology and survivorship of hatchling and juvenile pythons should be a focus of future research.

Acknowledgments We thank numerous people who collected python abundance and life-history data in Florida, without which these modeling exercises would not have been possible. Of particular note for their involvement in field collection and data collection for pythons are Matt Brien, Michael Cherkiss, Justin Davis, Anthony Flanagan, Wellington Guzman, Kristen Hart, Bobby Hill, Toren Hill, Frank Mazzotti, Kenneth Rice, Michael Rochford, LeRoy Rodgers, Theresa Walters, and Alex Wolf. Discussions with Kenneth Krysko, Robert Reed, and Paul Andreadis were useful in evaluating the spatial and temporal patterns of python captures. Kristen Hart, Shannon Pittman, Steven Price, Robert Reed, J. W. Gibbons, and one anonymous reviewer provided comments that helped to improve the manuscript. Partial funding for this study was provided by USGS, Davidson College Biology Department, and by National Science Foundation grant (DEB-0,347,326) to M.E. Dorcas. This material is based upon work supported by the Department of Energy under Award Number DE-FC-09-075R22506.

References

Campbell EW III, Rodda GH, Fritts TH, Bruggers RL (1999) An integrated management plan for the Brown Treesnake (*Boiga irregularis*) on Pacific islands. In: Rodda GH, Sawai Y, Chiszar D, Tanaka H (eds) Problem Snake Management: the Habu and the Brown Treesnake. Cornell University Press, Ithaca, New York, pp 423–435

Dlugosch KM, Parker IM (2008) Founding events in species invasions: genetic variation, adaptive evolution, and the role of multiple introductions. Mol Ecol 17:431–449

Dorcas ME, Willson JD (2009) Innovative methods for studies of snake ecology and conservation. In: Mullin SJ, Seigel RA (eds) Snakes: applied ecology and conservation. Cornell University Press, Ithaca, New York, pp 5–37

Engeman RM, Vice DS (2002) Objectives and integrated approaches for the control of Brown Tree Snakes. Integr Pest Manage Rev 6:59–76

Hayes KR, Barry SC (2008) Are there consistent predictors of invasion success? Biol Invasions 10:483–506

Kraus F (2009) Alien reptiles and amphibians: a scientific compendium and analysis. Springer, New York

Lockwood JL, Hoopes MF, Marchetti MP (2007) Invasion Ecology. Blackwell, Oxford

Madsen T, Ujvari B, Shine R, Olsson M (2006) Rain, rats and pythons: climate-driven population dynamics of predators and prey in tropical Australia. Austral Ecol 31:30–37

Martinez-Morales MA, Cuaron AD (1999) *Boa constrictor*, an introduced predator threatening the endemic fauna on Cozumel Island, Mexico. Biodivers Conserv 8: 957–963

Meshaka WE Jr, Loftus WF, Steiner T (2000) The herpetofauna of Everglades National Park. Fla Sci 63:84–103

Meshaka WE Jr, Butterfield BP, Hauge JB (2004) The exotic amphibians and reptiles of Florida. Krieger Co., Malabar, Florida

Park K (2004) Assessment and management of invasive alien predators. Ecol Soc 9:12

Parker WS, Plummer MV (1987) Population ecology. In: Seigel RA, Collins JT, Novak SS (eds) Snakes: ecology and evolutionary biology. The Blackburn Press, Caldwell, New Jersey, pp 253–301

Pike DA, Pizzatto L, Pike BA, Shine R (2008) Estimating survival rates of uncatchable animals: the myth of high juvenile mortality in reptiles. Ecology 89:607–611

Pimentel D, Zuniga R, Morrison D (2000) Environmental and economic costs of nonindigenous species in the United States. Bioscience 50:53–65

Quick JS, Reinert HK, de Cuba ER, Odum RA (2005) Recent occurrence and dietary habits of *Boa constrictor* on Aruba, Dutch West Indies. J Herpetol 39:304–307

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. U.S. Geological Survey Open-File Report 2009–1202

Rochford M, Brien ML, Carrigan J, Snow RW, Mazzotti FJ (2009) *Python molurus bivittatus* (Burmese Python) Clutch Size. Herpetol Rev 40:442

Rochford M, Krysko KL, Nifong J, Wilkins L, Snow RW, Cherkiss MS (2010) *Python molurus bivittatus* (Burmese Python). Diet Herpetol Rev 41:97

Rodda GH, Fritts TH, McCoid MJ, Campbell EW III (1999) An overview of the biology of the Brown Treesnake (*Boiga irregularis*), a costly pest on Pacific islands. In: Rodda GH, Sawai Y, Chiszar D, Tanaka H (eds) Problem Snake Management: the Habu and the Brown Treesnake. Cornell University Press, Ithaca, New York, pp 44–80

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? Biol Invasions 11:241–252

Savidge JA (1991) Population characteristics of the introduced brown tree snake (*Boiga irregularis*) on Guam. Biotropica 23:294–300

Smith AMA, Webb GJW (1985) *Crocodylus johnstoni* in the McKinlay river area, N.T. VII. A population simulation model. Aust Wildl Res 12:541–554

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

Todd BD, Willson JD, Winne CT, Semlitsch RD, Gibbons JW (2008) Ecology of the Southeastern crowned snake (*Tantilla coronata*). Copeia 2008:388–394

Willson JD, Dorcas ME (2004) Aspects of the ecology of small fossorial snakes in the western Piedmont of North Carolina. Southeast Nat 3:1–12

Woodward DE, Murray JD (1993) On the effect of temperature-dependent sex determination on sex ratio and survivorship in crocodilians. P Roy Soc B 252:149–155

Woodward AR, Hines TC, Abercrombie CL, Nichols JD (1987) Survival of young American alligators on a Florida lake. J Wildl Manage 51:931–937