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ORIGINAL ARTICLE

Ecological correlates of invasion impact for Burmese pythons in Florida

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Abstract

An invasive population of Burmese pythons (*Python molurus bivittatus*) is established across several thousand square kilometers of southern Florida and appears to have caused precipitous population declines among several species of native mammals. Why has this giant snake had such great success as an invasive species when many established reptiles have failed to spread? We scored the Burmese python for each of 15 literature-based attributes relative to predefined comparison groups from a diverse range of taxa and provide a review of the natural history and ecology of Burmese pythons relevant to each attribute. We focused on attributes linked to spread and magnitude of impacts rather than establishment success. Our results suggest that attributes related to body size and generalism appeared to be particularly applicable to the Burmese python's success in Florida. The attributes with the highest scores were: high reproductive potential, low vulnerability to predation, large adult body size, large offspring size and high dietary breadth. However, attributes of ectotherms in general and pythons in particular (including predatory mode, energetic efficiency and social interactions) might have also contributed to invasion success. Although establishment risk assessments are an important initial step in prevention of new establishments, evaluating species in terms of their potential for spreading widely and negatively impacting ecosystems might become part of the means by which resource managers prioritize control efforts in environments with large numbers of introduced species.

Key words: body size, Burmese python, Florida, invasive species, *Python molurus*

INTRODUCTION

Faced with a rising tide of invasive species, natural resource managers and policy-makers are increasingly interested in improving the ability to predict which introduced species are most likely to become invasive. Such knowledge is vital to production of risk assessment protocols and other screening tools designed to stem the flow of potentially harmful invaders, whether they are introduced intentionally (e.g. horticulture and pest control) or unintentionally (e.g. ballast-water contaminants and cargo stowaways). The most successful invaders exhibit characteristics that allow them to surmount 3 primary challenges (Williamson 1996). First, they must be able to enter and survive in transportation pathways by which they are moved (intentionally or unintentionally) to areas outside their native range. Sec-

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ond, they must be able to establish in the extralimital locale, by successfully reproducing and increasing their abundance sufficiently to ensure population viability. Finally, of the populations that become locally established, some must be able to spread beyond their origin (typically in anthropogenic environments) and achieve high enough population density to negatively impact ecosystems.

Several authors (e.g. Kolar & Lodge 2001; Cassey *et al.* 2005; Jeschke & Strayer 2005, 2006; Hayes & Barry 2008) have reviewed correlates of invasion success across broad taxonomic groups. Although propagule pressure (a measure of the number of individuals of a species arriving in an extralimital location [Duncan 2011] and similarity between native and introduced climates) (Bomford *et al.* 2009) has emerged as important predictors of establishment success in many reviews, failure of most attributes to generalize in predictive ability across taxonomic groups is the rule rather than the exception (Kolar & Lodge 2001; Williamson 2006; Hayes & Barry 2008). Indeed, Williamson (2006; p. 1566) concludes that, "Looking for universal attributes and causes of invasions is not profitable." Moreover, propagule pressure and climate matching principally influence probability of establishment rather than the rate or extent of subsequent spread and magnitude of ecological or economic impacts; resource managers are chiefly concerned with the latter 2 stages.

Because few predictors of invasiveness are equally applicable across taxonomic groups, taxon-specific analyses (e.g. Cassey *et al.* 2004; Forsyth *et al.* 2004; Kraus 2009) might allow more refined predictions of which traits promote invasiveness for any given group. However, research devoted to elucidating these traits has been generally focused on the factors affecting establishment probability rather than the attributes associated with spread and ecological impact. This is largely because, for some taxa (especially birds), both the number of introductions and the number of established populations resulting from these introductions are well-documented and high enough to allow statistical analysis of success/failure trends. However, although the number of introduced populations that subsequently spread and exert negative impacts is necessarily smaller than the number of established populations, improving our understanding of the correlates of spread and impacts might be a higher-priority need for those attempting to screen imports or prioritize control across large numbers of incoming species and established populations. Progress in satisfying this priority depends on incrementally increasing the knowledge base for these steps in the invasion process for a variety of taxa so as to increase the sample size available for analysis. Our goal in this contribution is to gain a richer understanding of the factors that have contributed to the rate of spread and magnitude of ecological impacts for the Burmese python (*Python molurus bivittatus* Kuhl, 1820) in Florida. We extract published correlates of invasion success from the literature and review available information for Burmese pythons vis-à-vis each of these correlates. Second, we score Burmese pythons for each of these attributes as compared to several defined comparison groups.

A native of southern Asia, the Burmese python is one of the largest snakes in the world, with reliable records of free-ranging individuals in excess of 5 m in length (Pope 1961; Murphy & Henderson 1997; Bellosa *et al.* 2007). Burmese pythons are popular in captivity, and over 300 000 individuals were imported into the USA between 1979 and 2009 (Reed & Rodda 2009). A population of Burmese pythons originating with the live animal trade is now established over several thousand square kilometers of southern Florida, including most of Everglades National Park and Big Cypress National Preserve (Snow *et al.* 2007a). Despite the fact that at least 90% of python-occupied habitat in the Everglades is largely inaccessible to humans, between 2000 and late 2011, over 1800 Burmese pythons were removed from these ecosystems and documented by officials (Everglades National Park 2012), implying the existence of a dense population. Multiple lines of evidence suggest that this snake is an especially successful invasive species, including an apparently dense population, the generally excellent body condition of captured individuals and a rapid and near-complete spread through a variety of non-urban habitats across southern Florida. Moreover, Burmese pythons appear to have significant negative impacts on Everglades ecosystems; the pythons consume a wide variety of native species in Florida, including multiple species of conservation concern (Snow *et al.* 2007b; Dove *et al.* 2011), and have been implicated in the precipitous declines of multiple species of native mammals (Dorcas *et al.* 2012).

Many species of exotic reptiles have been introduced to Florida, and dozens of species are established (Meshaka *et al.* 2004; Krysko *et al.* 2011; Meshaka 2011). However, only a few of the established species (e.g. brown anole [*Anolis sagrei* Dumeril & Bibron, 1837] and Indo-Pacific gecko [*Hemidactylus garnotii* Dumeril & Bibron, 1836] have expanded across a large area or invaded non-urban habitats. Aside from the tiny Brah-

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miny blindsnake (*Ramphotyphlops braminus* Daudin, 1803), the Burmese python is the only exotic snake to have successfully colonized a large (>1000 km^2) area of the USA. The spread of most of the exotic reptiles that are established in multiple sites in Florida appears to have been aided by human transport or multiple releases (Krysko *et al.* 2011). In contrast, historical records and population modeling exercises suggest that the Burmese python spread unassisted from a single founding population (Snow *et al.* 2007a; Willson *et al.* 2011).

Taxonomists differ as to whether the Burmese python is a full species (*P. bivittatus*) or a subspecies of the Indian python (*P. molurus bivittatus*; see e.g. de Rooij 1917; McDiarmid *et al.* 1999; Jacobs *et al.* 2009). The choice hinges on whether the adjacent gene pools have been evolutionarily isolated from each other, but genetic characterization of the potentially distinct populations has not been conducted. In lieu of definitive information, insight could be gained from the prevalence of hybrids, which should be rare in comparison to parental lineages if the gene pools are isolated. However, the traits by which the forms are distinguished are either smoothly continuous (degree of anterior darkening of the arrowhead marking on the top of the head) or strictly binary (presence/absence of subocular scale). Thus, hybrids, if they exist, cannot be readily recognized morphologically. Moreover, expression of the decisive morphological trait (i.e. presence of a subocular scale) might depend on incubation temperature (Vinegar 1974), such that subocular scale presence is an inconclusive reflection of genome. The relevance of this taxonomic discussion to the present paper is that much of the available literature on python ecology in the native range fails to distinguish between Burmese and Indian forms, and our reliance on the literature required us to follow suit. As far as is known, the 2 forms do not differ appreciably in the traits we consider in this paper.

MATERIALS AND METHODS

Extracting and scoring literature-based correlates of invasion success

We compiled a list of plausible correlates and predictors of invasion success from the literature, drawing from both general (e.g. Lodge 1993; Kolar & Lodge 2002; Stohlgren & Schnase 2006; Hayes & Barry 2008) and herpetofauna-specific reviews (Bomford *et al.* 2005; Bomford 2008; Rodda & Tyrrell 2008; Bomford *et al.* 2009; Kraus 2009). One challenge associated with reliance on this literature is that only recently have authors made the necessary strong distinction between factors affecting establishment success and those associated with ecological/economic impacts (Rodda & Tyrrell 2008; Chapple *et al.* 2011; Hui *et al.* 2011). Thus, we drew from a pool that might have conflated these stages into an overall assessment of 'invasion' success. The traits and predictors (hereafter referred to as 'attributes') typically fall into 2 categories: characteristics of invasive species and characteristics of vulnerable habitats. From the literature review we extracted a subset of organismal attributes that met the following criteria: (i) the attribute has been considered in the literature to be valid or useful for terrestrial vertebrates; (ii) the attribute promotes spread and/or increases the likelihood of an introduced animal having negative impacts on the ecosystem into which it is introduced; and (iii) the attribute is a proximate ecological, morphological, demographic or physiological feature of the organism, rather than a product of, or proxy for, such proximal traits (see below) or a predictor of habitat vulnerability. We justify these decision rules as follows.

Traits considered valid or useful for terrestrial vertebrates

Many attributes have been considered in reviews of predictors of invasiveness, but we did not consider traits that are specific to plants, fish and invertebrates. For example, attributes might be specific to plants (e.g. floristic zone, flowering time, leaf/seed characters or germination rates; Rejmánek & Richardson 1996; Hayes & Barry 2008; Milbau & Stout 2008; Dawson *et al.* 2011) or fish (e.g. dissolved oxygen tolerance and larval size; Kolar & Lodge 2002), but less obviously germane to an invasive terrestrial reptile.

Traits that promote spread and/or negative impacts

As discussed above, species that have negative ecological or economic consequences must first have been transported to an extralimital locale, released and become established (i.e. population viability assured). To avoid conflating these processes, we did not consider attributes of pythons that might have contributed to their original release in Florida (e.g. Reed 2005; Fujisaki *et al.* 2009), which are generally associated with human activities or behaviors, such as patterns of international trade or probability of escape or release from captivity. To the degree that our focus included spread, we were interested in the natural factors that facilitate spread (species and habitat attributes), rather than human-mediated spread caused by multiple releases.

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Traits that are proximate rather than a proxy for proximate traits

The literature is replete with traits correlated with an introduced organism's propensity for spreading widely and exerting negative impacts on the environment. Our contribution diverges from other reviews of this type in that we are specifically concerned with proximate ecological, physiological or morphological attributes of individuals and populations rather than the emergent results of these attributes. The geographic area occupied by a species in its native range, for example, is often considered to correlate positively with an organism's propensity to spread once introduced elsewhere, because a large native distribution implies the ability to cope with widely varying abiotic and biotic conditions (Ehrlich 1989; Gaston 1990; Kolar & Lodge 2002). A species' native distributional limits are determined by many factors, including physiological constraints, interactions with predators, prey and competitors, geographical barriers, and biogeographic history. A given species might be limited by climate at one edge of the range, by competition with a congener at another edge of the range and by the ocean along coastal portions of its range. Such distributions are, therefore, the products of interacting variables, only some of which are attributes exhibited by individuals.

Similarly, climate matching is the process of characterizing the climate experienced by a species in its native range to predict where it might be able to invade elsewhere in the world. This correlational process is widely used as a tool for screening whether species might be able to establish and/or spread widely in a particular region (Bomford *et al.* 2009). For animals generally (Hayes & Barry 2008) and for reptiles in particular (Bomford *et al.* 2009), climate matching has been found to be among the best statistical predictors of establishment success. Climate tolerance appears to be a necessary condition for establishment, but its contribution to spread or economic/ecological impacts is less clear, in part because the conventional correlational approach to climate matching relies on proxies (geographic localities) to infer climate tolerance. Climate matching for the Burmese python has received considerable attention in the literature (Pyron *et al.* 2008; Reed & Rodda 2009, 2011; Rodda *et al.* 2009; van Wilgen *et al.* 2009), and all credible peer-reviewed climate-matching analyses for the Burmese python agree that, at a minimum, peninsular Florida exhibits a climate similar to areas occupied by the species in its native range. Thus, for the south Florida area under consideration, the Burmese python exhibits the climate tolerance necessary for establishment, but whether this degree of climate tolerance contributes to spread and impacts within south Florida is not readily evaluated with the data at hand.

Defining groups for comparison with Burmese pythons

Deriving attributes from the literature and then scoring Burmese pythons in isolation for these attributes could result in bias, because traits are difficult to assess without reference to a baseline. For example, if considered in isolation we might give a very high score to Burmese pythons for a given attribute without explicitly acknowledging that such a trait is common to all reptiles rather than unique to Burmese pythons. An explicit frame of reference promotes objective scoring. Furthermore, we are most interested in a species' invasiveness compared to the alternatives (either no invasion, as referenced by resident native species, or alternate invaders, represented by different non-native species). Therefore, we scored Burmese pythons with respect to 2 comparison groups of taxa native to the Everglades and 3 comparison groups of potential invaders (non-native):

A. *American alligators.* American alligators (*Alligator mississippiensis* Daudin, 1802) provide an instructive native reference point for comparison with Burmese pythons, because both are large ectothermic predators that attain high densities in Everglades ecosystems.

B. *Snakes native to the Everglades ecosystem.* This comparison allows us to assess the ecological novelty and perhaps the competitive abilities of Burmese pythons, as they spread through a habitat already containing a diverse community of native snakes. As with the groups below, we compared pythons with a typical member of the Everglades snake community, in this case basing our assessment of species presence/absence on Ernst & Ernst (2003) and Gibbons & Dorcas (2005).

C. *Other boas and pythons.* How do Burmese pythons compare with their close relatives, none of which are native to southern Florida (based on the species listed in Appendix 1 of Henderson & Powell 2007)?

D. *Non-boid squamates (not native to southern Florida).* To what extent are Burmese pythons markedly different from other squamates (lizards and snakes)?

E. *Endothermic terrestrial vertebrates (not native to southern Florida).* How do Burmese pythons diverge from terrestrial birds and mammals?

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For the 15 attributes we considered, each author independently scored (1–5 scale) the Burmese python relative to each comparison group. Thus, a score of 3 indicated that the scorer considered Burmese pythons to be generally similar to the comparison group for the attribute under consideration, whereas a score of 1 indicated the scorer considered Burmese pythons to exhibit much 'less' of the trait relative to the comparison group. For comparison groups consisting of multiple species, scorers independently estimated the magnitude of the attribute for a typical member of the group, reaching their own definition of 'typical.' Each author also independently assigned a measure of their confidence in each attribute × comparison group score on a scale of 1 to 5 (defined in the legend to Table 1). All scoring was performed independently, and each author was blind to coauthors' scores during the scoring process.

Attributes considered in comparative evaluation

After filtering the pool of available organismal traits thought to promote successful invasion through our 3 decision rules, we were left with 15 attributes to be assessed. For each trait, we offer a definition and then provide pertinent information for the Burmese python.

Large adult body size

Definition: the approximate mean body mass of mature members of the larger sex of the taxon under consideration. This attribute is sometimes defined in the literature as large size in relation to relatives (Ehrlich 1989).

Adult Burmese pythons are giants among snakes. Captives can achieve enormous proportions (8.2 m and >175 kg; Bellosa *et al.* 2007), but free-ranging individuals exceeding 6 m are probably now extremely rare in either native or introduced ranges. Several females in Florida have exceeded 5 m and 60 kg (S. Snow, pers. comm.). However, based on records from 41 females over 235 cm snout–vent length from southern Florida (R.W. Snow, pers. comm.; this is the average length at maturation as identified by Willson *et al.* 2011), we estimate mean body mass of mature female Burmese pythons to be 19.76 kg (range 7.87–60.85 kg for this sample).

High reproductive potential

Definition: the expected mean number of offspring produced by an adult female over her lifetime.

With a maximal known clutch size of 107 eggs, maximal fecundity of Burmese python ranks second among all egg-laying snakes (Ernst & Zug 1996; Reed & Rodda 2009). Thus far, the known maximal number of oviductal eggs from Florida is 85, although the mean is lower (Brien *et al.* 2007; Krysko *et al.* 2008). Available evidence suggests that the typical adult female in Florida breeds every other year (Willson *et al.* 2011). Because the longevity of free-ranging pythons in Florida is poorly understood, and to avoid duplication of attributes (we separately consider longevity below), we used annual fecundity (clutch size divided by reproductive frequency) as a correlate of lifetime reproductive output. We assumed an average clutch size of 40 eggs and biennial reproduction (Willson *et al.* 2011) to arrive at a figure of 20 offspring per female per year.

Large offspring size

Definition: mean mass of neonates at birth or hatching.

Large hatchlings are susceptible to a narrower range of predators and are able to consume prey from a wider distribution of body sizes. The mean body size of 24 hatchling Burmese pythons from Everglades National Park was 116 g (range 49–126 g) and 60 cm total length (range 45–67 cm; Hart *et al.* 2012).

High maximum longevity

Definition: maximum estimated lifespan of free-ranging individuals of the taxon under consideration.

The longevity of free-ranging Burmese pythons is almost completely unknown, but captives have approached or exceeded 30 years of age (Bowler 1977). A lifespan that can be measured in decades increases the odds that a reproductive female Burmese python will find mates and reproduce multiple times, and that at least some of her hatchlings will be produced during years with above-average prey availability.

Low age at maturity

Definition: for female offspring, the mean number of months from birth/hatching to becoming reproductively capable.

In captivity, Burmese pythons typically mature between 2 and 3 years of age, although overfed animals can attain maturity even earlier (Frye & Mader 1985; Ross & Marzec 1990; Walls 1998). Females in Florida appear capable of maturing in their third year at approximately 30 months of age (Willson *et al.* 2011).

High degree of parental care

Definition: the degree and duration of parental care of offspring exhibited by the parents.

Parental care might serve to increase survivorship of early life stages, primarily by reducing the odds of pre-

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Table 1 Results of attribute scoring exercise

Attribute		Alligators	Native snakes	Boas and pythons	Squamates	Endotherms	Row mean scores
Large adult body size	Score (range)	2.25 (2–3)	5 (5)	4.5 (4–5)	5 (5)	4.75 (4–5)	4.3
	Confidence (range)	4.75 (4–5)	4.75 (4–5)	4.75 (4–5)	4.75 (4–5)	4 (3–5)	4.6
High reproductive potential	Score (range)	3.5 (2–5)	4.75 (4–5)	4 (4)	5 (5)	4.75 (4–5)	4.4
	Confidence (range)	3.5 (3–4)	4 (3–5)	3.75 (2–5)	4.25 (4–5)	3.75 (3–5)	3.85
Large offspring size	Score (range)	3.75 (3–4)	4.75 (4–5)	4.25 (4–5)	5 (5)	3.75 (3–5)	4.3
	Confidence (range)	4.25 (3–5)	4 (4–5)	4.5 (4–5)	4.75 (4–5)	3.25 (2–5)	4.3
High maximum longevity	Score (range)	2.25 (2–3)	4 (4)	3.5 (3–4)	4.5 (4–5)	5 (5)	3.85
	Confidence (range)	3.25 (2–4)	3.25 (2–4)	3 (1–4)	3.75 (3–5)	4 (4)	3.45
Low age at maturity	Score (range)	4.5 (4–5)	2.75 (2–3)	3 (3)	2 (1–3)	2 (2)	2.85
	Confidence (range)	3.75 (3–4)	3 (1–4)	3 (1–4)	3 (2–4)	2.75 (2–3)	3.1
High degree of parental care	Score (range)	2 (2)	4.75 (4–5)	4.25 (4–5)	5 (5)	1.75 (1–2)	3.55
	Confidence (range)	4 (3–5)	4.75 (4–5)	4.25 (4–5)	4.75 (4–5)	3.75 (2–5)	4.3
Short generation time	Score (range)	4.25 (4–5)	2.75 (2–3)	3 (3)	2 (1–3)	2.25 (2–3)	2.85
	Confidence (range)	4 (4)	2.75 (1–4)	2.5 (1–4)	3.25 (2–4)	2.75 (2–3)	3.05
High dietary breadth	Score (range)	3.75 (3–5)	4.25 (4–5)	3.75 (3–4)	4.5 (4–5)	4.25 (4–5)	4.1
	Confidence (range)	3.75 (2–5)	4 (3–5)	3 (2–4)	3.5 (2–5)	3.25 (3–4)	3.5
High vagility	Score (range)	3.25 (3–4)	4.25 (4–5)	3.5 (3–4)	5 (5)	3 (2–4)	3.8
	Confidence (range)	2.25 (2–3)	3 (2–4)	2 (1–3)	3.25 (3–4)	2.25 (2–3)	2.55
High habitat breadth	Score (range)	4.25 (4–5)	3.75 (3–5)	4 (4)	4 (4–5)	4 (3–5)	4
	Confidence (range)	3.75 (2–5)	3.5 (3–4)	3 (2–4)	3 (2–4)	2.75 (2–4)	3.2
High tolerance of disturbed habitat	Score (range)	2.25 (2–3)	3.25 (3–4)	3.25 (3–4)	3.25 (3–4)	3.25 (3–4)	3.05
	Confidence (range)	2 (1–3)	2.75 (1–4)	2.25 (1–3)	2.25 (1–3)	2 (2)	2.25
Strong association with humans	Score (range)	2.75 (2–3)	3 (3)	3 (3)	3 (2–4)	3 (2–4)	2.95
	Confidence (range)	2.75 (2–4)	3 (2–4)	2.25 (1–4)	2.25 (1–3)	1.5 (1–2)	2.35
High gregariousness	Score (range)	2.5 (2–4)	3.25 (3–4)	3 (3)	3.25 (3–4)	1.75 (1–2)	2.75
	Confidence (range)	3.25 (2–4)	3.25 (2–4)	3 (1–4)	2.75 (1–4)	3 (2–4)	3.05
High phenotypic plasticity	Score (range)	3.75 (3–4)	3.25 (3–4)	3.25 (3–4)	3.5 (3–4)	3.75 (2–5)	3.5
	Confidence (range)	2.25 (1–4)	2 (1–4)	2.5 (1–4)	2.5 (1–4)	2 (1–4)	2.25
Low vulnerability to predation	Score (range)	3 (3)	5 (5)	4 (4)	5 (5)	4.75 (4–5)	4.35
	Confidence (range)	2.5 (1–4)	4.25 (4–5)	3.5 (3–4)	4.75 (4–5)	3.75 (3–4)	3.75
Column mean scores		3.2	3.92	3.62	4	3.47	3.64
Column mean confidence		3.33	3.53	3.15	3.52	2.98	3.3

Each attribute (first column) is represented by 2 rows; the first is the mean of the authors' 4 scores for the Burmese python vis-à-vis each of the 5 comparison groups, and the second is the mean confidence in the score for the cell immediately above it. All scores are accompanied by their ranges in parentheses. Scores were assigned on a scale of 1 to 5; for example, a score of 3 indicated that the scorer considered Burmese pythons to be generally similar to the comparison group for the attribute under consideration and a score of 1 indicated the scorer considered Burmese pythons to exhibit much 'less' of the trait relative to the comparison group. For comparison groups including multiple species, scorers independently estimated the magnitude of the attribute for a typical member of the group. Each author also independently assigned a measure of their confidence in each attribute × comparison group score on a scale of 1 to 5, with numeric scores defined as follows: 1 = very uncertain; 2 = reasonably uncertain; 3 = moderately certain; 4 = reasonably certain; and 5 = very certain. The last column and bottom row, respectively, present row and column mean scores.

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dation or desiccation of eggs or juveniles. Like most pythons but unlike most other snakes, female Burmese pythons exhibit extended maternal care of eggs. After oviposition, the female remains coiled around the eggs until they hatch (Valenciennes 1841; Wall 1921; Snow *et al.* 2010). Parental care ceases once hatchlings leave the nest. Among a few species of high-latitude or high-elevation pythons, including Burmese pythons, females engage in shivering thermogenesis to raise embryonic temperatures during cool periods (Hutchison *et al.* 1966; Vinegar *et al.* 1970; Snow *et al.* 2010). When compared to snake species exhibiting no parental care, nest attendance and thermogenesis by Burmese pythons undoubtedly increase embryo survival by discouraging potential nest predators and maintaining optimal temperatures for development.

Short generation time

Definition: the average time, in number of months, from independence of a female to the time at which that female's offspring are completely independent.

For Burmese pythons, we estimated generation time at 37 months, beginning with 30 months for a female to achieve reproductive condition and adding 5 months of follicular development and post-ovulatory development of ova as well as 2 months of egg incubation. Although generation time is, therefore, only marginally longer than is age at maturity for Burmese pythons, we opted to consider this attribute independently because this might not be true of some of the comparison groups.

High dietary breadth

Definition: the taxonomic scope and size range of prey consumed by predators in each taxon (thus excluding herbivorous members of comparison groups). Dietary generalization allows a predator to survive in most sites, and to persist even if a few important prey species become locally or seasonally unavailable.

In Asia, Burmese and Indian pythons are known to consume a wide range of prey, primarily birds and mammals (Begbie 1907; Wall 1921; Reed & Rodda 2009). However, the diet of the Burmese python has been most systematically characterized in their introduced range in Florida, where over 40 species of vertebrate prey have been recorded (Snow *et al.* 2007b; Hart *et al.* 2010; Dove *et al.* 2011). Body sizes of prey taken in Florida range from small (e.g. house wren [*Troglodytes aedon* Vieillot, 1809], <15 g) to large (e.g. white-tailed deer, [*Odocoileus virginianus* (Zimmermann, 1780)], >30 kg) endothermic prey, as well as American alligators up to 2 m in total length (Snow *et al.* 2007b; Hart *et al.* 2010; Dove *et al.* 2011).

High vagility

Definition: the maximal known dispersal, migratory and other movement-related capacities of the taxon.

Heavy-bodied and cryptically patterned Burmese pythons are generally considered ambush foragers that lie in wait for endothermic prey. Although ambushing might be the dominant foraging mode among Burmese pythons, they are not exclusively sedentary. In Florida, Burmese pythons that were translocated from their home ranges to a spot more accessible to researchers stayed in the new location for several months, before returning to near their original capture locations (Harvey *et al.* 2008). These movements were notable for the distances covered (up to 78 km), the speed at which pythons moved (sometimes >1.5 km/day), and the apparent ability of individuals to navigate. Clearly, Burmese pythons are capable of engaging in long-distance directed movements when motivated to do so.

High habitat breadth

Definition: the diversity of major habitat types occupied by the taxon in its native or introduced range.

As would be expected of a snake that ranges from China to Indonesia and Sri Lanka to northern India, Burmese pythons inhabit a wide range of habitat types. In contrast to other species of giant constrictors with distributions centered on aseasonal tropical forests (e.g. reticulated pythons [*P. reticulatus* Schneider, 1801]), Burmese pythons inhabit higher latitudes and experience more seasonality in rainfall and temperature. While some assume this snake to be obligately semi-aquatic, this characterization is not supported by the population on Kinmen Island, China (24.45°N, 118.38°E). Many radiotelemetered Burmese pythons on this island are not associated with water for entire activity seasons (S-M. Lin, pers. comm.). Taken as a whole, the Burmese python's apparent generalism in habitat preferences rivals its generalism in diet.

High tolerance of disturbed habitat

Definition: the degree to which members of the taxon tolerate habitat disturbed by human activities (e.g. urbanization, agriculture and forestry) or natural events (e.g. hurricanes, floods and wildfire).

The degree to which pythons tolerate disturbed habitat is not well understood, and some of the literature is contradictory on the subject. For example, Whitaker (1978) states that Indian pythons require relatively undisturbed habitat, whereas Whitaker (1993) implies that marginal forest and scrub forest adjacent to human habitations are favored by pythons. Regardless, there ap-

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pears to be general consensus that python populations have declined precipitously in areas of the native range that are densely populated by humans (Groombridge & Luxmoore 1991). In such areas, the benefits of living in a human-disturbed system (i.e. higher numbers of rats and other human-commensal prey) are likely more than countered by intentional or unintentional killing of snakes by humans or vehicles.

Arguably, the entire Everglades ecosystem has been disturbed to some degree by a century of water management activities by humans (Lodge 2010), but most areas currently occupied by pythons exhibit low levels of ongoing major habitat alteration (Snow *et al.* 2007a). The great majority of pythons captured in Florida are recovered from roads or levees alongside canals, both of which are anthropogenic intrusions into natural habitats. Roads and levees provide access into natural habitats for human observers rather than being preferred python habitat. However, Burmese pythons can be present at moderately high densities in agricultural fields adjacent to less-disturbed habitats in southern Florida (Reed *et al.* 2011), suggesting that pythons can tolerate some level of habitat disturbance.

Strong association with humans

Definition: a measure of the taxon's capacity for, or preference for, proximity to humans. Because we considered this attribute in the context of spread and ecological impacts rather than establishment, we evaluated taxa in terms of population persistence rather than individual survival.

Many introduced reptiles have strong associations with humans and often fail to spread beyond human-occupied habitats (Meshaka *et al.* 2004; Rodda & Tyrrell 2008; Kraus 2009; Meshaka 2011); most of these are small insectivorous lizards that can reach high densities in specialized microhabitats, such as the walls of buildings (geckos) or ornamental vegetation (anoles). As a top predator that consumes a range of vertebrates, Burmese pythons are less likely to achieve high densities in these specialized microhabitats.

In its native range, a Burmese python consumed a monkey (*Macaca nemestrina* Linnaeus, 1766) beside a sidewalk in a heavily-used portion of a Thai national park while being observed by a crowd of humans (Khamcha & Sukumal 2009), but such events are notable primarily for their rarity in the literature rather than suggesting that pythons are associated with humans. Most Burmese pythons encountered in urban/suburban areas in Florida are associated with dispersal corridors (especially canals) from more pristine habitats or are along the urban/wildland interface.

High gregariousness

Definition: the tendency for individuals to group together for extended periods. This attribute can be important when a given resource is limiting in the environment and can be competitively sequestered by large groups of conspecifics. Gregariousness can facilitate spread of an invader (e.g. via splitting of large groups into several smaller groups, each containing enough individuals to ensure availability of mates during dispersal of the group).

Burmese pythons are not known to be gregarious. Breeding aggregations of several males in association with a reproductive female have been observed in Florida (Dorcas & Willson 2011; R. W. Snow, personal communication), but these occur only during the breeding season and are not indicative of long-term associations. Similarly, formation of social hierarchies and combat among male Burmese pythons has been observed in captivity (Barker *et al.* 1979), but we are unaware of any similar observations in the field and these would not be expected to lead to long-term associations.

High phenotypic plasticity

Definition: the ability to rapidly adapt to, for example, new locations and changes in resource availability. Plasticity can take the form of adaptability of individual behaviors or rapid population-level changes.

We know little regarding the ability of Burmese pythons to adapt rapidly to changes in their environment. A study conducted by Dorcas *et al.* (2011) in which 10 male pythons from Everglades National Park were relocated to a semi-natural enclosure in South Carolina showed that the snakes appeared to adjust well to the semi-natural environment, to use all available habitats and to exhibit normal behaviors. However, all 10 pythons died during unusually long and intense cold periods in December and January, indicating that these individuals might not have possessed the behavioral plasticity required to survive translocation to a substantially cooler climate.

Phenotypic plasticity might also be reflected in individuals' abilities to cope with shifts in prey availability. Rapid change in body size as a response to food availability is common among snake populations, and is most easily observed by comparing mainland and insular snakes. Dwarfism and gigantism are commonplace among insular snakes (Boback 2003). These body size differences are often solely phenotypic (Tanaka 2011),

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but such phenotypic differences can become genetically canalized (Aubret & Shine 2007; Boback & Carpenter 2007). A dwarfed subspecies of the Burmese python from Sulawesi, Indonesia has been proposed (Jacobs *et al.* 2009), although the extent to which dwarfism in this form is phenotypic or genetic has not been examined. We considered the ability to rapidly adapt to variation in prey availability to be a prominent component of phenotypic plasticity for snakes in general and, by extension, for the Burmese python in particular.

Low vulnerability to predation

Definition: the likelihood that a typical individual of the taxon will be killed by a predator during its lifetime.

Hatchling Burmese pythons are probably vulnerable to a range of native predators in Florida, but quickly grow to a size that renders them invulnerable to all but a few predators (e.g. large American alligators, Florida panthers [*Puma concolor coryi* (Bangs, 1899)] and humans). Predation on adult pythons by these large-bodied native predators is probably balanced by intra-guild predation by pythons, especially on alligators (Reed & Rodda 2009).

RESULTS AND DISCUSSION

Attribute scoring exercise

The results of the scoring exercise are presented in Table 1. Considering all 75 comparison group × attribute cells, attribute scores of Burmese pythons generally exceeded those of comparison groups (52 cells scoring higher than, 14 cells below, and 9 cells equaling the comparison group). When averaged across comparison groups, the attributes of Burmese pythons garnering the highest scores (>4; higher or much higher in magnitude as compared to the comparison group) were: high reproductive potential (4.40), low vulnerability to predation (4.35), large adult body size (4.30), large offspring size (4.30) and high dietary breadth (4.10). The lowest scores for Burmese pythons were associated with: high gregariousness (2.75), short generation time (2.85), low age at maturity (2.85) and strong association with humans (2.95). The 4 authors were unanimous in scoring 21 of 75 cells in the attribute × comparison group table.

Relative to comparison groups, mean scores of pythons were somewhat variable, ranging from a high of 4.00 for other squamates to a low of 3.20 for American alligators. For all but 2 attributes (low age at maturity and short generation time), Burmese pythons were scored as equal to or exceeding the magnitude of attributes of both native Everglades snakes and non-boid squamates. More strikingly, Burmese pythons were judged equal to (4 attributes) or exceeding (11 attributes) the magnitude of attributes of other species of boas and pythons.

Certainty of attribute scores

As compared to the comparison groups (row means in Table 1), we were most confident that Burmese pythons exhibit larger adult body size (4.60), larger offspring size (4.30), higher degree of parental care (4.30) and higher reproductive potential (3.85), and we were least confident of scores for high phenotypic plasticity (2.25), high tolerance of disturbed habitat (2.25), strong association with humans (2.35) and high vagility (2.55). Among comparison groups (column means), scores for Burmese pythons as compared to native snakes (3.53) and non-boid squamates (3.52) had the highest mean certainties, whereas endotherms (2.98) had the lowest. We were unanimous in assigning certainty scores to only 3 of the 75 comparison group × attribute cells in Table 1, whereas for 21 cells the range of our scores was broad (1–4 or 2–5). Some of the latter is explained by the tendency of authors to be somewhat consistent in scoring certainty; the mean certainty scores of the 4 authors across all group × attribute cells were 3.8, 3.35, 3.29 and 2.77; interestingly, certainties were negatively correlated ($r = -0.96$) with age of the scoring author.

Our confidence in scoring attributes largely reflected the state of scientific knowledge of the ecology of vertebrates. We were fairly certain of our scores for attributes linked to body size and reproductive output, because such traits are among the first to be quantified when organisms are subjected to scientific study. We were also confident of our scores for parental care, partially stemming from knowledge of the degree of parental care from captive studies of a large number of reptile taxa (which comprised 4 of our 5 comparison groups). In contrast, we had much lower confidence in our scores for a number of behavioral attributes because quantification of these attributes would require intensive autecological research. A complete understanding of vagility, phenotypic plasticity and associations with humans or disturbed habitat (the 4 attributes for which our confidence was lowest) for even a single species requires a significant effort, and we are as yet unable to quantify these traits for Burmese pythons even after several years of field research in Florida.

Most of our comparison groups were composites of multiple species, and authors were asked to score Bur-

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mese pythons as compared to a typical member of each composite group. Varying perceptions of what constitutes 'typical' might have been a secondary contributor to our confidence in scoring attributes (as well as producing a source of variation in attribute scores for some comparison groups). Variability and/or uncertainty in settling on typical members of comparison groups, in turn, might have led to variation among authors in assigning certainties to each attribute score. For future analyses, agreeing *a priori* on a precise definition of 'typical' might alleviate some of this secondary source of variability in confidence.

The 4 attributes receiving the highest scores (reproductive potential, vulnerability to predation, adult body size and offspring size) are associated with body size. To a larger degree among reptiles than among birds and mammals, body size is positively correlated with high fecundity (clutch or litter size) (Shine 2005), and Burmese pythons are giant ectotherms with concomitantly large clutches. Trade-offs between offspring size and offspring number are an important paradigm in life history theory (e.g. Smith & Fretwell 1974; Qu *et al.* 2011), and based on this paradigm we might expect a negative correlation between clutch size and hatchling size in Burmese pythons. Although it is true that hatchlings are very small as compared to large adults, hatchling Burmese pythons are much larger than hatchlings/neonates of all native Everglades snakes, most other boas and pythons, and non-boid squamates. Indeed, Burmese python hatchlings are larger than the adults of many Everglades snake species. Indigo snakes (*Drymarchon corais* Boie, 1827) attain the longest lengths of any snake native to the Everglades, but average <50 g at hatching (Ernst & Ernst 2003), less than the smallest recorded size of hatchling Burmese pythons. Compared to ectotherms, endotherms tend to have fewer offspring that are larger relative to parental body size (Blueweiss *et al.* 1978), but the offspring of a 'typical' 35–100 g bird or mammal (see previous paragraph) are still much smaller than a hatchling python. Therefore, Burmese pythons, and indeed most of the giant constrictor snakes (Reed & Rodda 2009), subvert the offspring size/number paradigm and received high scores for size-related attributes in our assessment because both adults and hatchlings are very large relative to comparison groups rather than because hatchlings are large relative to adult pythons.

Reviews of the invasion biology literature typically conclude that larger body sizes are advantageous to invaders (e.g. Ehrlich 1989; Rodda & Tyrrell 2008), and we used this directionality (larger = more damaging) for body size in our scoring. However, some authors (e.g. Meshaka *et at.* 2004; Meshaka 2011) have considered small body size to be a better predictor of establishment success for reptiles, and the majority of the 50 or so species of exotic reptiles established in Florida are small-bodied lizards (Krysko *et al.* 2011). These lizards are generally insectivorous and tolerant of disturbed or urbanized habitat, but only a few species have managed to spread beyond the urban fringe to less-disturbed habitats. Among squamate reptiles, therefore, small body size (along with tolerance of disturbance and associations with humans) might be a better predictor of the likelihood of establishment than it is of the likelihood of spreading widely and impacting natural ecosystems.

Although the literature-based attributes evaluated above include those most typically associated with invasion success, several other attributes associated with pythons might have contributed substantially to their post-establishment success as an invasive species in Florida. We identified 3 potentially important python attributes that might not have been adequately captured by the literature-based list of invasive characters.

Predatory mode and comparisons with native predators

Foraging mode and dietary breadth have likely played a key role in the ability of pythons to attain high densities and to expand their range in south Florida. Pythons are apparently capable of engaging in both active and ambush foraging. Because ambush foragers tend to feed and move infrequently and remain motionless and hidden for extended periods, there are remarkably few observations of prey being ingested by wild Burmese pythons. Whereas pythons have been observed consuming a handful of birds and alligators in southern Florida, we are unaware of any observations of pythons consuming mammals, despite their prevalence in python diets (approximately 70% of known diet records). Multiple nestling cotton rats (*Sigmodon hispidus* Say & Ord, 1825) were found in 1 Florida python (R. W. Snow, pers. comm.), and a python consumed a nesting guineafowl and her eggs (Dove *et al.* 2012), suggesting that active foraging does occur. In addition, in their native range, pythons might seek out sleeping birds at night in large bird colonies (Daniel 2002). The ability to use either ambush or active foraging modes likely allows pythons to adapt readily to variation in prey type and prey location, and in seasonal variation in prey abundances.

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A large-bodied predator that can switch between ambush and active foraging and that forages in both aquatic and terrestrial microhabitats represents an evolutionarily novel threat to native prey species in Florida. From a chemosensory perspective, potential mammalian prey, such as white-tailed deer [*Odocoileus virginianus* (Zimmermann, 1780)], bobcats [*Lynx rufus* (Schreber, 1777)] or raccoons (*Procyon lotor* Linnaeus, 1758) might not recognize snake scent as an indicator of potential predatory threat, because most individuals of these species are too large to be susceptible to predation by native snakes. Other native species might be threatened by the ability of pythons to forage in multiple habitats. Predation by pythons appears to have resulted in major declines in a range of mammals in the Everglades National Park, including species that differ in preferred habitat (Dorcas *et al.* 2012).

Burmese pythons are not the only large-bodied predator in Floridian ecosystems, and it is logical to ask whether pythons are merely acting as ecological equivalents for alligators or the rare Florida panther. In terms of prey composition, the answer appears to be mostly negative. Adult alligators in the Everglades subsist primarily on snakes, aquatic salamanders and snails, along with a smaller proportion of fish and even smaller proportions of birds and mammals, while juvenile alligators largely consume invertebrates and fish (Barr 1997). Panthers in Big Cypress National Preserve on the northern boundary of Everglades National Park eat a variety of mammals and the occasional wild turkey (*Meleagris gallopavo* Linnaeus 1758) or alligator. However, their diet is dominated by feral hogs (*Sus scrofa* Linnaeus 1758), white-tailed deer, raccoons and nine-banded armadillo (*Dasypus novemcinctus* Linnaeus 1758), which together represent >93% of the estimated biomass intake of Florida panthers (Maehr *et al.* 1990). Therefore, pythons are much more likely to prey on birds and small/medium mammals than are alligators, and pythons consume a much wider variety of prey than do Florida panthers; these 3 species exhibit low overlap in prey species composition.

Energetic efficiency

Reptiles generally exhibit low-energy lifestyles when compared to endotherms, and their low per-capita energetic requirements allow reptiles to persist at higher densities than their endothermic counterparts at any given level of available prey resources (Pough 1980). Infrequently feeding ectotherms, and pythons in particular, also possess a suite of adaptations related to their habit of eating infrequently that allow them to lower their energy use when not processing food. During periods between meals, metabolic rate is low and the digestive tract and other organs are downregulated, becoming smaller and less active (Secor & Diamond 1998). Immediately after a large meal, however, the metabolic rate increases (as much as 40-fold) and internal organs associated with digestion and assimilation greatly increase in size within 48 h (Secor & Ott 2007; Secor 2008; Andersen *et al.* 2011), allowing rapid and efficient processing of even very large prey items before putrefaction.

Physiological traits common to reptiles (e.g. low-energy lifestyle and high rates of assimilation) and traits that are more specialized among infrequently-feeding snakes (e.g. remarkable ability to regulate gastrointestinal and cardiovascular performance) manifest themselves in the ecology of Burmese pythons in multiple ways. Rates of converting ingested energy to somatic and reproductive tissues tend to be very high among reptiles, sometimes exceeding 80% of prey mass, and the typically low metabolic rates of reptiles combine with high conversion efficiency to facilitate high levels of energy storage (Pough 1980) for future growth and reproduction. Heavy-bodied pythons in particular can amass large amounts of body fat, often exceeding 5 kg in pythons from Florida. Because pythons can go without feeding for many months or even more than a year at a time, they are pre-adapted for capitalizing on intermittent pulses of prey, such as rodent irruptions, breeding bird aggregations and migratory bird peaks, situations that are typical of seasonally flooding wetlands, such as the Everglades. The ability to survive long periods of aphagia is by no means limited to pythons, and species from divergent families of snakes persist at high densities on very small islands that are unable to support mammalian predators because prey are only seasonally available or are present at low densities (Bonnet *et al.* 2002; Shine *et al.* 2002; Reed *et al.* 2007). However, such abilities are amplified in Burmese pythons as a result of their large body size, physiological adaptations and dietary generalism, as pythons can either become aphagic in response to reductions of prey or switch to alternative prey species of a wide range of prey sizes. Combined with the high densities at which pythons can occur because of their low per-capita energetic requirements, such abilities might have resulted in localized extirpations of some prey species (e.g. Dorcas *et al.* 2012).

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Social interactions and population density

Although territoriality was not considered directly in the list of invasion-related traits we gleaned from the literature, python social structure might be an important contributor to their success as an invader and their impacts on native ecosystems. As another large-bodied ectothermic predator in the Everglades ecosystem, American alligators provide an instructive contrast to the social system of pythons. Alligators are highly territorial, and large males maintain and control access to aquatic refugia during the dry season in southern Florida (Kushlan & Hunt 1979). Cannibalism is common, and annually accounted for 6–7% of juveniles in a perennial lake in Florida (Delany *et al.* 2011). In Louisiana wetlands, cannibalism accounted for approximately 64% of total annual death among immature alligators older than 10 months of age (Rootes & Chabreck 1993). Cannibalism of juveniles might be even higher in the Everglades as a result of the high concentration of alligators in seasonally drying wetlands. Conversely, male snakes generally exhibit defense of a resource (typically a receptive female) rather than defense of an area (Duvall *et al.* 1993; Rivas & Burghardt 2005), such that social interactions are unlikely to depress python densities. Thus, whereas intraspecific interactions such as territoriality and cannibalism are important regulators of alligator population density, python populations in the Everglades are more likely regulated by prey availability or predation.

CONCLUSIONS

Our scoring exercise suggested that Burmese pythons exhibit many of the traits associated with species that spread widely and impact ecosystems. Chief among these were attributes related to large body size and a high degree of generalism in diet and habitat tolerance. Although scores varied among attributes, Burmese pythons were considered equal to or higher than any of the comparison groups when attribute scores were averaged by group, and, for 11 of 15 attributes, Burmese pythons were scored equal to or higher than the mean attribute scores across comparison groups. However, Burmese pythons received scores of 4 (much higher than the comparison group) or more for only for 1 comparison group (non-boid squamates averaged across attributes) and 6 attributes (averaged across comparison groups). Adding taxon-specific attributes, such as novel predatory mode and energetic efficiency, appears to bolster the body of evidence suggesting that Burmese pythons exhibit a suite of characters that predispose them to spread and negatively impact ecosystems during the invasion process.

When attempting to identify attributes that promote spread and/or impacts for the purposes of refining risk assessments, taxon-specific analyses might be more precise than attempting to generalize across all taxa. Conversely, narrowing the taxonomic pool of species chosen for comparison to the species being assessed might require a cumbersome number of risk assessments, each attempting to assess risk for a small number of species in comparison to a small defined outgroup. In our case, comparing Burmese pythons with the global pool of squamate reptiles maximized the difference in average scores, perhaps suggesting that comparisons at this relatively broad taxonomic level might be an efficient means of assessing risk.

Our ranking exercise suggested that Burmese pythons might be somewhat atypical of boas and pythons in terms of their likelihood to spread as invasive species and impact native ecosystems. Burmese pythons ranked equal to, or higher than, a 'typical' boa or python species for every invasion-related trait we considered, and scored particularly high in traits related to size and degree of parental care. These traits, combined with their popularity in the pet trade (Reed 2005) and a large global climate match compared to the other giant constrictors (Reed & Rodda 2009, 2011), likely make Burmese pythons a higher risk for introductions elsewhere.

How is this exercise for Burmese pythons applicable to other species and to the practice of conducting risk assessments in general? Recall that we restricted our investigation to attributes likely to increase rate of spread or magnitude of ecological impacts. In contrast, many risk assessment protocols focus on the likelihood of establishment. The establishment risk assessment models used by the government of Australia for reptiles and amphibians (Bomford 2008), for example, relies on climate-matching, a species' history of establishment elsewhere and whether other members of the species' genus or family are extralimitally established. History of establishment and membership in broader taxonomic groups (the genus *Python*, the family Pythonidae) would not have been informative if an assessor had screened Burmese pythons before they became established in Florida, because no other invasive populations of pythons were known prior to 2010 (Reed *et al.* 2010, 2011). That would have left climate matching, which remains a nascent scientific endeavor and which in the case of Burmese pythons has not been without controversy (Rod-

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da *et al.* 2011), as the only relevant variable. Moreover, many species become established locally but fail to spread or impact native ecosystems, and establishment risk ratings might not adequately consider the likelihood or magnitude of these latter invasion stages. For example, when the Australian scheme was applied to reptiles introduced to Florida (Bomford *et al.* 2009), several small lizards (e.g. *Mabuya* (= *Eutropis*) *multifasciata* Kuhl, 1820 and *Hemidactylus turcicus* Linneaus, 1758) received 'Extreme' risk rankings, while *P. molurus* received the lower ranking of 'Serious.'

Our intent in the previous paragraph is not to belittle establishment risk assessments, which are a vital part of the toolkit for evaluating risks posed by potential invaders. In some situations, however, the type of risk assessment desired by resource managers might not coincide with a typical establishment risk assessment. Krysko *et al.* (2011) tallied 56 species of established amphibians and reptiles in Florida alone, with another 81 species introduced but not known to be established. Faced with a wide range of actual or incipient established species and dwindling budgets, resource managers are likely to desire screening tools that allow them to identify which species are most likely to spread and have negative impacts. For the Burmese python, compiling a list of literature-based attributes and evaluating them in light of what is known of python ecology offered useful insight on correlates of invasion impact, but this process required compiling ecological information from widely disparate sources as well as taxon-specific expertise during the scoring exercise.

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