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An Ecological Risk Assessment of Nonnative Boas and Pythons as Potentially Invasive Species in the United States

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The growing international trade in live wildlife has the potential to result in continuing establishment of nonnative animal populations in the United States. Snakes may pose particularly high risks as potentially invasive species, as exemplified by the decimation of Guam's vertebrate fauna by the accidentally introduced brown tree snake. Herein, ecological and commercial predictors of the likelihood of establishment of invasive populations were used to model risk associated with legal commercial imports of 23 species of boas, pythons, and relatives into the United States during the period 1989–2000. Data on ecological variables were collected from multiple sources, while data on commercial variables were collated from import records maintained by the U.S. Fish and Wildlife Service. Results of the risk-assessment models indicate that species including boa constrictors (*Boa constrictor*), ball pythons (*Python regius*), and reticulated pythons (*P. reticulatus*) may pose particularly high risks as potentially invasive species. Recommendations for reducing risk of establishment of invasive populations of snakes and/or pathogens include temporary quarantine of imports to increase detection rates of nonnative pathogens, increasing research attention to reptile pathogens, reducing the risk that nonnative snakes will reach certain areas with high numbers of federally listed species (such as the Florida Keys), and attempting to better educate individuals purchasing reptiles.

KEY WORDS: Boidae; commercialization; ecology; Pythonidae; snake

1. INTRODUCTION

Invasive species have attracted increased attention in the United States, largely due to invasions by a few species that have resulted in major ecological and/or economic damage.(1) Snakes have become known as potentially harmful invasive species largely due to the effects of the introduced brown tree snake (*Boiga irregularis*) in the Mariana Islands. Within 50 years of its introduction to the formerly snake-free island of Guam, *B. irregularis* had played a role in the loss of 10 of 13 native bird species, 6 of 12 native lizard species, and 2 of 3 bat species.(2) Other snake species may pose similar risks as potential invasives in some U.S. ecosystems, but generally the degree of risk associated with the domestic and international trade in live snakes has remained largely unanalyzed.

This article models the risk associated with boas, pythons, and relatives as potential invasive species in the continental United States. Members of the family Boidae are found in both the New and Old World, but are primarily distributed in neotropical regions and a few Pacific archipelagos. The New World boids are represented by large-bodied snakes such as the boa constrictor (*Boa*) and anaconda (*Eunectes*), as well as a number of smaller, largely arboreal, taxa (*Corallus*, *Epicrates*, etc.). The Pacific boids include a few species in the genus *Candoia*. Pythons, in contrast, are not found in the New World, and are distributed from Australia (*Morelia*, *Liasis*, *Antaresia*) through the Papuan (*Apodora*, *Leiopython*, *Liasis*, *Bothrochilus*) and Southeast Asian (*Python*) regions,

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and extending through most of Africa (*Python*). Many of these species are docile captives and readily consume prekilled prey items. A number of species are extremely attractive, often with bold patterns, pleasing colors, or a high degree of iridescence. The combination of a calm demeanor in captivity, large size, and attractive patterns has greatly increased their demand in the U.S. pet trade. From an ecological standpoint, these species are deserving of priority for risk assessment because they are medium- to large-bodied predators capable of reaching high densities in suitable habitat. Some species (including *Eunectes murinus, Python molurus, P. reticulatus,* and *P. sebae*) may exceed 7m in length and over 100 kg in weight; these species consume a wide size range of prey during various stages of ontogeny.[3] Live specimens of multiple species are imported into the United States in numbers exceeding 3,000 per year for the retail pet trade, and an unknown number of snakes subsequently escape or are released. The great majority of these released animals do not successfully found invasive populations. However, populations of some species may already be established in south Florida, although detailed data on population size and reproduction are lacking.[4,5] Furthermore, although human fatalities caused by giant snakes are rare, the largest species are capable of killing and occasionally ingesting humans (and their companion animals), adding a significant sociopolitical impetus for risk assessment.[6]

A number of additional ecological factors may predispose boid and pythonid snakes as potential invasive species. Many species are characterized by large clutch or litter sizes (boas are live-bearing, while pythons are oviparous), including clutch sizes exceeding 90 eggs in large pythons,[7] and litter sizes of over 80 young in green anacondas.[3] Wild-caught gravid females of some species (e.g., the ball python *Python regius*) are imported in large numbers for the U.S. pet trade, increasing the chances of reproduction occurring in escaped or released individuals.[8] In addition to the high fecundity of the large-bodied species, many of the oviparous pythons and relatives brood their eggs, and are able to increase egg temperatures by shivering thermiogenesis. This may allow feral populations to establish in areas where cool ambient temperatures would normally preclude embryonic development. Although sperm storage in these species has not been well studied, females of other snake species have been shown to store sperm for multiple years, and a single female may thus be capable of founding feral populations even if she has not recently mated.[9] Furthermore, parthenogenesis has been recently reported in a python,[10] whereby a single virgin female may be capable of successful reproduction. Some boas and pythons exhibit fast growth and early maturation,[11] resulting in juveniles rapidly outgrowing the capacity of many predators to ingest them. The cryptic coloration and highly secretive behavior of these snakes can result in thriving populations of large snakes even in urbanized regions.[12]

While large-bodied constrictors are usually thought of as being entirely tropical, this is not true of some species. Those species with temperate-zone distributions in their native habitats may pose the most risk in the United States, which has a comparatively small amount of tropical and subtropical habitat available to invasive snakes. The most obvious example of such a temperate-zone taxon is the carpet python (*Morelia spilota*) of Australia. The geographic distribution of this python spans tropical, temperate, and desert regions in Australia, including areas where winter temperatures routinely drop below freezing.[13] Although temperate-zone species like *M. spilota* are imported into the United States in relatively low numbers, they may pose a higher risk of feral population establishment than tropical species.

Just as climate in a snake's native range may be an important predictor of the risk of invasion, habitat specialization may predispose certain species to risk of establishment in U.S. habitats. As an example, the highly aquatic water python (*Liasis fuscus*) has been the subject of detailed ecological studies in the northern territory of Australia.[14,15] These snakes prey on locally dense dusky rats, and snake biomass may exceed 1,000 kg per square kilometer of floodplain (T. Madsen, personal communication). A snake with these types of habitat requirements could feasibly become established in the extensive swamps and marshes of the southeastern United States, and could attain population sizes capable of significantly impacting native species. The green anaconda (*Eunectes murinus*) is a similar species in terms of habitat use, but is imported in greater numbers and attains much larger body sizes.

Many tropical snakes carry high parasite loads, and invasive species may introduce foreign parasites or other pathogens into U.S. habitats. Endo- and ectoparasites known from these snakes include ticks, hemogregarines, and ascarid nematodes.[16–18] Human activities (including the pet trade) may have spread chytrid fungi beyond their native range, thus contributing to documented global declines of amphibians (which are highly susceptible to chytrid fungi, especially when already under stress[19]). The trade in boas and pythons may spread foreign pathogens to U.S. populations of squamate reptiles, and thus the risks associated with pathogens must be incorporated in any risk assessment of these snakes as invasive species.

2. METHODS

2.1. Selecting Species for Analysis

The higher taxonomy of snakes is in constant flux, and the bulk of phylogenetic relationships remain unresolved. However, many of the basal macrostomatan lineages tend to group together in phylogenetic analyses. These include members of the "families" Boidae, Pythonidae, Tropidophiidae, and Loxocemidae. I used a generic and specific taxonomy of pythonids[20] that has been widely adopted in the live animal trade and academic community. Lower taxonomy of boids has been largely stable in recent years, and I follow standard usages for *Boa*, *Corallus*, *Epicrates*, *Eunectes*, and *Candoia*. The common names of most imported snakes have not been standardized (as has been attempted for the species of the United States[21]).

Herein I analyze risk only for those species that have been legally imported into the United States during the period 1989–2000, as risk of invasion should be positively correlated with whether a species is entering the country (data after 2000 were not available at time of analysis). I selected only species with >100 total individuals imported during this 12-year period; this criterion resulted in a pool of 23 species in subsequent risk analyses (Table I). Because I wished to concentrate on terrestrially and/or arboreally active taxa, I do not address fossorial erycine snakes within the family Boidae, such as *Eryx* and *Charina*. I compiled life history and ecological data from a variety of primary and secondary sources.[3,22–32] I also spoke to snake breeders and reviewed numerous herpetocultural websites for supplemental data.

Many ecological variables could influence the likelihood that a species will establish invasive populations. Unfortunately, very few natural populations of boas and pythons have been rigorously studied. Therefore, it is not possible to conduct meta-analyses using published data for most variables that could be of interest. Reproductive frequency would be of particular interest, as high clutch or litter sizes in some species might be offset by less-than-annual reproduction. Similarly, age at maturity or the minimal body sizes at which males and females reproduce would allow inferences on how rapidly populations could be expected to expand after initial population foundation. These data, however, are not available for most natural populations. It is tempting to use reproductive data from the herpetocultural industry, but captive snakes fed regularly and maintained at optimal temperatures are not likely to exhibit reproductive traits similar to free-ranging individuals.

Table I. Common and Scientific Names of Snake Species Included in Risk-Assessment Analyses, with the Total Number of Live Individuals Imported During the Period 1989 Through 2000

Scientific Name	Common Name	Number Imported
Apodora papuana	Papuan python	146
Boa constrictor	Boa constrictor	115,131
Candoia aspera	Viper boa	812
Candoia bibroni	Solomon Islands tree boa	369
Candoia carinata	Pacific boa	4,815
Corallus caninus	Emerald tree boa	3,330
Corallus hortulanus	Common tree boa	6,542
Epicrates cenchria	Rainbow boa	1,391
Epicrates gracilis	Haitian vine boa	238
Epicrates striatus	Hispaniola and Bahama boa	177
Eunectes murinus	Green anaconda	1,418
Eunectes notaeus	Yellow anaconda	790
Leiopython albertisii	White-lipped python	1,551
Liasis mackloti	Freckled python	552
Morelia amethistina	Amethistine python	873
Morelia boeleni	Black python	173
Morelia spilota	Carpet python	309
Morelia viridis	Green tree python	493
Python curtus	Blood python	11,135
Python molurus	Burmese/Indian python	12,466
Python regius	Ball/Royal python	366,808
Python reticulatus	Reticulated python	27,992
Python sebae	African rock python	8,245

Note: Species were included if >100 individuals were imported during this time; see text for details.

In the absence of adequate data for the majority of species, therefore, I used body size and fecundity as factors in my analyses, as follows.

2.1.1. Body Size

I used the maximal total length of each species. Defining the "average" body lengths of species with indeterminate growth is problematic, so I used maximal length; this has been shown to be tightly correlated with mean adult length.[33,34]

2.1.2. Fecundity

The highest known reproductive output (number of eggs for oviparous taxa, number of live young for viviparous taxa) was used as an indicator of relative fecundity. Because reproductive frequency of free-ranging boas and pythons is poorly known for most populations, I assumed this frequency to be equal among species for modeling purposes.

2.1.3. Climatic Profiles of Native Ranges

As stated previously, most boas, pythons, and relatives are found in tropical or subtropical climates. Few species are found at high altitudes or latitudes, although there are prominent exceptions, such as *Morelia boeleni* occurring at >2,000 m elevation in Papua New Guinea.[26] Because most of these snakes are unaccustomed to temperate climates, it is unlikely that populations could be successfully established in much of the United States. Indeed, most anecdotal reports of free-ranging exotic boas and pythons in the United States have originated in southern Florida, which generally experiences a subtropical climate. However, those species that experience cool climates in their native ranges may be predisposed to successful establishment in larger portions of the United States. As an example, while few exotic reptiles have become established in temperate areas of the United States, a prominent exception is the European wall lizard (*Podarcis muralis*), which hails from temperate European climates. This species has become established in at least two regions of the United States with frigid winter conditions.[35,36] Snakes from cool climates may be capable of similar cold tolerance.

Distributional information on most tropical snake species is spotty at best. Published range maps are available for some species (e.g., Australian taxa[23] and southern Africa[37]), but distributions are available only as textual descriptions for many others (e.g., Papua New Guinea[26]). Because of this data deficiency, I could not utilize empirical climatalogical profiles across the geographic ranges of each species. Therefore, I estimated these profiles using available data on latitude and elevation, with the goal of estimating the coolest temperatures at which each species is likely to be capable of persistence and reproduction. I estimated temperature profiles of the native geographic ranges of snakes as follows:[38] (a) for temperatures of locations below 20° latitude, Temperature (°F) = 80 − (0.0026 × [Elevation in feet]); and (b) for regions between 20° and 60° latitude, temperatures can be estimated as: Temperature (°F) = (−0.988 × [Latitude in degrees] + 96.8) − (0.0026 × [Elevation in feet]). I used data collected for each species on maximal latitude and elevation of native geographic ranges to calculate the coolest mean temperature likely to be experienced by a species.

2.2. Summary of Import Data, 1989–2000

I analyzed the trade in snakes imported to the United States using data taken from the Law Enforcement Management Information System (LEMIS), which is maintained by the U.S. Fish and Wildlife Service. This database contains import and export declarations detailing the numbers, species composition, and monetary value of shipments, and comprises the only detailed record of the legal domestic reptile trade. For the purposes of this report, I extracted all import records of the 23 species of interest from 1989 through 2000.

2.3. Modeling Risk of Establishment in the United States

I estimated the risk of establishment of each snake species of interest using a quantitative model incorporating variables from the known legal trade and ecological profiles of the species.

The model is based on the following predictions:

A. **Wild-caught imports present a greater risk as invasive species**: This assumption is based on three observations. First, wild-caught individuals tend to have higher parasite loads than do captive-bred individuals, posing the risk of introducing exotic pathogens to the United States. Second, wild-caught snakes tend to be less predictable in terms of temperament and are often very defensive, perhaps increasing the chance that owners will release "problem" snakes into U.S. habitats. Third, wild-caught snakes are often less expensive than captive-bred snakes (see Prediction B).

B. **Species commanding high prices in the pet trade present a lower risk as invasive species**: Relatively inexpensive snakes are more attractive to beginning herpetoculturists, children, and other inexperienced owners. Snake owners without a significant financial stake in the animal are more likely to keep it in substandard housing (facilitating escape by the snake) or to release it when it grows too big or becomes aggressive.[39] Conversely, those investing hundreds of dollars in species like the black python (*Morelia boeleni*) are likely to invest in quality caging and advanced techniques so as to protect their investment.

C. **Species that are imported in high numbers present a greater risk as invasive species**: Increased numbers of individuals entering the United States correspond to an increased number of opportunities for snakes to escape or be released.[39] Similarly, high individual numbers may equate to a greater probability of heterosexual encounters and resultant reproductive success in U.S. habitats. Considering the large number of offspring that can be produced by some of the snakes in question, a single mating event could found a population.

D. **Species of larger body sizes present a greater risk as invasive species**: Of all the predictions listed here, this statement is perhaps the most debatable, but I defend it as follows. First, there are no native snake species with very large body sizes in the United States, such that invasive boas and pythons could encounter an unexploited niche after establishment. Second, as gape-limited predators, snakes are capable of swallowing larger diameter prey items as they grow, such that large species have a greater potential prey size distribution and can thus exploit a variety of prey in novel habitats. Lastly, the largest snake species rapidly reach daunting proportions and can represent a physical threat to their owners. This can result in apprehensive snake owners releasing their suddenly unpredictable large snake, such that the large species might be more likely to be intentionally released and to establish feral populations.

E. **Species of higher fecundities present a greater risk as invasive species**: The rationale behind this statement is similar to that given for the number of individuals entering the country, above. All else being equal, the offspring of a single gravid female from a species with high fecundity should have a better chance of finding siblings after maturity for reproductive purposes, thus more firmly establishing the incipient introduced population.

F. **Species with a greater range of climatic tolerances present a greater risk as invasive species**: Specifically, species capable of persisting in cool climates could potentially become established in larger areas in the United States. Most current reports of free-ranging exotic snakes in the United States originate in south Florida, which experiences a subtropical climate. Species capable of persisting in colder climates may pose increased risk as invasive species in more northerly latitudes.

2.3.1. Modeling Risk from Commercial Trade

Following the predictions above, I used the following equation to estimate risks associated with importation of each species of boa or python:

$$T = \%WC \times (Imports/Value),$$

where: T = relative risk associated with the international trade in live snakes; $\%WC$ = percentage of each species declared to be wild-caught in USFWS import declarations; *Imports* = mean number of individuals imported annually; and *Value* = average declared value (in U.S. dollars) per imported individual. For the latter variable, I used neither mean nor median as an indicator of central tendency. Median prices tended to fall below mean prices, largely because the mean is skewed by outlying values and a few individuals of each species often had very high declared values (these could have been rare color morphs or possibly keystroke errors in the LEMIS database). I therefore used the midpoint of mean and median as a measure of central tendency.

After speaking to breeders and importers at reptile shows and examining animals available via commercial herpetocultural businesses, I had grave doubts about the reliability of the declared source of imported animals listed in the LEMIS database. There were many improbable declarations, such as hundreds of "captive-bred" Pacific Island boas (*Candoia*) and yellow anacondas (*Eunectes notaeus*) imported despite an absence of popular knowledge of large-scale commercial breeding operations in the countries of origin. Similarly, I did not consider "ranched" or "farmed" designations to be particularly reliable or indicative of decreased risk. In western African countries, for example, gravid female royal pythons (*P. regius*) are captured and held until they oviposit, after which the females are (usually) released and the eggs incubated. However, this does not necessarily reduce the number of pathogens associated with these imports, as ticks have been observed to move into clutches of eggs to await hatching of neonates;[40] these ticks may carry a number of pathogens (see below). For the purposes of this report, I thus concluded that the declared source (captive-bred, wild-caught, etc.) of shipments entering the United States was undependable; as a conservative measure for the purposes of this report I thus set the proportion of wild-caught individuals at 1.0 for all species.

2.3.2. *Modeling Risk from Ecological Variables*

Following the predictions above, I used the following equation to estimate risks associated with body size, fecundity, and climatic profiles associated with each species: $E = Fecund + TL - Temp$, where: E = relative risk associated with these ecological variables; *Fecund* = fecundity (measured as maximal known number of offspring in a single reproductive bout); TL = maximal total length of the larger sex; and *Temp* = minimum temperature for persistence, calculated equations given above.

2.3.3. *Modeling Risk Using a Synthetic Index*

Combining variables associated with trade and ecology (listed above), I derived the following equation to model overall relative risk of establishment of each species: $R = T + E$.

2.3.4. *Data Treatment*

Data used in the models were on widely varying scales, such that some variables would greatly bias results if used without any type of transformation or standardization. I therefore standardized each variable on a scale of 0 to 1.0, and added 1.0 to each standardized value to eliminate values of 0. This ensures that each variable has equal weight in the risk analysis model.

3. RESULTS AND DISCUSSION

3.1. Summary of Commercial Trade

During the years 1989 through 2000, LEMIS records indicate that approximately 6,067 shipments containing live nonerycine boas, pythons, and relatives entered the United States, representing 404,177 individuals, 17 genera, and 40 species. The number of individuals imported varied widely among species; numerically, the most important species in the import trade include *Python regius* (366,808 individuals), *Boa constrictor* (115,131 individuals), *Python reticulatus* (27,992 individuals), *Python molurus* (12,466 individuals), *Python curtus* (11,135 individuals), and *Python*

Table II. Values for Variables Used in Risk-Assessment Models

Species	Maximum Total Body Length (m)	Maximum Clutch/Litter Size	Maximum Elevation (m)	Maximum Latitude	Temperature (°C)	Mean # Snakes Imported/Year	Average $ Value
Epicrates striatus	2.4	51	400	24	8.50	15	3.38
Epicrates gracilis	1.3	10	400	19	11.25	20	19.50
Corallus hortulanus	2.1	12	1000	26	12.42	545	19.50
Candoia carinata	1	80	1525	11	13.15	401	19.75
Python regius	1.8	15	400	11	13.40	30,567	21.00
Candoia aspera	1.2	20	1000	10	13.45	68	28.00
Candoia bibroni	1.95	20	700	12	16.99	31	33.00
Python sebae	6.75	94	1400	33	17.19	687	41.50
Boa constrictor	4.2	60	1000	33	17.80	9,594	53.50
Morelia amethistina	6	19	1600	18	17.94	73	66.00
Epicrates cenchria	2	20	1400	29	19.08	116	71.00
Eunectes murinus	8.1	82	200	25	19.08	118	74.00
Python curtus	3.1	32	500	6	19.44	928	76.25
Leiopython albertisii	3	15	1600	11	20.93	129	84.00
Liasis mackloti	2.25	20	250	9	21.33	46	91.50
Python reticulatus	8.4	103	800	26	21.93	2,332	97.00
Eunectes notaeus	4.3	30	250	31	21.93	66	102.00
Corallus caninus	1.85	18	1000	16	23.35	245	111.50
Morelia spilota	4	43	1750	35	24.30	26	117.50
Python molurus	7.1	107	1500	30	24.77	1036	118.50
Apodora papuana	4.27	35	400	10	24.77	12	238.50
Morelia viridis	1.5	17	2000	13	24.77	41	283.50
Morelia boeleni	2.7	25	2800	10	25.48	14	784.00

Note: See text for additional description of variables. Average $ value is the midpoint of mean and median values in U.S. dollars.

sebae (8,245 individuals) (Tables I and II). Over 1,000 individuals of each of six additional species and from 100 to 999 individuals of 11 species were imported during this period. The total value of imported boas and relatives was declared as $10,837,840, and the unweighted average value per individual was $19.09. However, 3,868 shipments had no declared value, including many shipments of valuable taxa such as *Sanzinia*, *Acrantophis*, *Aspidites*, and *Python timoriensis*. Correcting these records by inserting the average value per individual would significantly increase the total value of the trade. There were numerous suspect entries in the LEMIS data, such that calculation of mean values per individual may be biased by extreme values.

3.2. Risk-Assessment Results

3.2.1. *Trade Variables*

Given the huge volume of royal or ball pythons (*P. regius*) imported into the United States, it is hardly surprising that the model for trade variables predicted the highest risk associated with this species (Tables III and IV). This is a small-bodied python, and as such is often purchased as a "beginner" snake by hobbyists in the United States. They are imported for a median price of $10 per individual and usually retail for $40–$75. Captive-bred individuals, on the other hand, may retail for two or three times this price, a discrepancy that fuels the "captive-reared" import trade. Ball pythons are "ranched" in west African countries including Benin, Togo, and Ghana; the annual harvest has been estimated as being largely sustainable so long as snakes are taken largely from agricultural areas where they occur in moderately high densities.[40] This indicates that despite their relatively low clutch sizes (maximum of 13), the large numbers of imported *P. regius* are unlikely to decrease in the near future due to any visible economic reason. *Python regius* has been termed an invasive species even in its native range, as it has successfully adapted to farmland in Ghana, where it is estimated to average

Table III. Results of Models Designed to Assess Risk Associated with Establishment of Nonnative Boas, Pythons, and Relatives in the United States

Species	Trade	Ecology	Synthetic
Apodora papuana	0.769	0.340	1.109
Boa constrictor	1.234	2.594	3.829
Candoia aspera	0.971	0.948	1.919
Candoia bibroni	0.964	0.740	1.704
Candoia carinata	0.992	1.148	2.140
Corallus caninus	0.885	0.407	1.292
Corallus hortulanus	0.997	0.669	1.666
Epicrates cenchria	0.923	0.361	1.285
Epicrates gracilis	0.980	1.094	2.074
Epicrates striatus	1.000	0.081	1.081
Eunectes murinus	0.920	1.942	2.862
Eunectes notaeus	0.889	1.082	1.971
Leiopython albertisii	0.910	0.272	1.182
Liasis mackloti	0.900	1.746	2.645
Morelia amethistina	0.928	0.882	1.809
Morelia boeleni	0.500	0.581	1.081
Morelia spilota	0.873	2.483	3.356
Morelia viridis	0.737	1.102	1.839
Python curtus	0.942	0.702	1.644
Python molurus	0.901	2.399	3.299
Python regius	1.956	0.630	2.586
Python reticulatus	1.702	1.678	3.380
Python sebae	0.974	0.200	1.174

Note: Higher numbers are indicative of species that pose a greater risk as invasives. See text for derivation of model equations. "Trade," "Ecology," and "Synthetic" columns refer to results from the various model equations; all variables were standardized prior to entry in the models.

Table IV. Relative Rankings of 23 Species of Boas and Pythons Based on Risk-Assessment Models

Trade	Ecology	Synthetic
Morelia boeleni	*Epicrates striatus*	*Morelia boeleni*
Morelia viridis	*Python sebae*	*Epicrates striatus*
Apodora papuana	*Leiopython albertisii*	*Apodora papuana*
Morelia spilota	*Apodora papuana*	*Python sebae*
Corallus caninus	*Epicrates cenchria*	*Leiopython albertisii*
Eunectes notaeus	*Corallus caninus*	*Epicrates cenchria*
Liasis mackloti	*Morelia boeleni*	*Corallus caninus*
Python molurus	*Python regius*	*Python curtus*
Leiopython albertisii	*Corallus hortulanus*	*Corallus hortulanus*
Eunectes murinus	*Python curtus*	*Candoia bibroni*
Epicrates cenchria	*Candoia bibroni*	*Morelia amethistina*
Morelia amethistina	*Morelia amethistina*	*Morelia viridis*
Python curtus	*Candoia aspera*	*Candoia aspera*
Candoia bibroni	*Eunectes notaeus*	*Eunectes notaeus*
Candoia aspera	*Epicrates gracilis*	*Epicrates gracilis*
Python sebae	*Morelia viridis*	*Candoia carinata*
Epicrates gracilis	*Candoia carinata*	*Python regius*
Candoia carinata	*Python reticulatus*	*Liasis mackloti*
Corallus hortulanus	*Liasis mackloti*	*Eunectes murinus*
Epicrates striatus	*Eunectes murinus*	*Python molurus*
Boa constrictor	*Python molurus*	*Morelia spilota*
Python reticulatus	*Morelia spilota*	*Python reticulatus*
Python regius	*Boa constrictor*	*Boa constrictor*

Note: Species are ranked from LOW (top of table) estimated risk to HIGH (bottom of table) estimated risk. For example, *M. boeleni* is ranked lowest in terms of risk associated with trade and the synthetic model, and is ranked seventh from the bottom in terms of ecological risks. Each column represents the results of a different model equation, as presented in the text.

2.34 individuals per hectare.[38] Densities are thought to be even higher in these habitats than in predisturbance habitats. There is no obvious reason to suspect that the species would not be similarly successful in much of Florida, portions of Texas and California, and other warm locales with adequate rainfall.

Several other species are also of concern due to variables associated with trade, most notable of which are the enormous reticulated python (*P. reticulatus*) and the boa constrictor (*Boa constrictor*). These species have large geographic ranges in (respectively) Southeast Asia and the neotropics. Once again, the high availability of these species means that declared values are low and that imported animals can usually be sold for prices below their typical production cost for domestic breeders. At the other end of the spectrum are a number of fairly expensive snakes, which are imported in low numbers. These species are largely from Southeast Asia, and more specifically from New Guinea. The species representing the lowest risk as an invasive species is the black python (*M. boeleni*), which is endemic to New Guinea. This snake is expensive because it is completely protected in Papua New Guinea, but is exported from the Indonesian side of the island, where it has a small distribution.

3.2.2. Ecological Variables

When variables such as body size, clutch size, and temperature are considered in risk assessments, a few of the largest snake species cluster together in the top third of the ecological risk spectrum (Tables III and IV). Because body size and clutch size tend to be correlated in snakes, these two variables may have elevated the relative importance of several members of the genus *Python* and the green anaconda (*Eunectes murinus*). At the top of the list is *B. constrictor*, followed by *M. spilota*. The former is a live-bearing species that is widely distributed in the New World, with a distribution spanning 66° of latitude and the ability to persist in a variety of habitats.[41] Live-bearing in squamate reptiles (including snakes) has evolved multiple times in response to cool climates, as gravid females are able to more precisely regulate the temperature of developing embryos.[42] If established, boa constrictors are thus one of the species most likely to be able to colonize regions in the United States that experience fairly cool winters. This species is also extremely plastic in terms of body size and diet, as evidenced by multiple independently evolved dwarfed populations on offshore islands in the Caribbean;[43] this plasticity would perhaps allow the species to adapt to a range of habitat conditions and prey availabilities in the United States. To bolster these suppositions, note that a number of free-ranging boa constrictors have been found in Florida, including a large gravid female (K. Krysko, personal communication), and it is likely that the species will soon establish invasive populations, if this has not already occurred.

In the second position for ecological risk is *Morelia spilota*, a medium-sized (to 4 m) species that is widely distributed in Australia and part of New Guinea. The species is capable of surviving at moderately high latitudes and temperate ecosystems, as evidenced by populations of diamond pythons (*M. s. spilota*) as far south as the State of Victoria, Australia.[13,44] Unlike *B. constrictor*, *M. spilota* is oviparous. However, as with a number of python species, female *M. spilota* are capable of warming eggs by shivering thermiogenesis, and appear to select nest sites that buffer the eggs from cool temperatures in temperate zones.[44]

Most of the snakes associated with high risk based on ecological variables are readily bred in captivity and commonly available in the pet trade for moderately low prices (an exception is *E. murinus*, which is bred less frequently). Even so, wild-caught individuals of these species can be purchased for a pittance from collectors by exporters in developing countries. The combination of low purchase prices and the ability to ship large numbers of animals at once allows exporters to reap significant profits (these are unknown for most species, but profit margins are estimated at ~25% for *P. regius*[40]). These snakes are then usually sold to naïve buyers in the United States who are excited by the thought of purchasing an imposing pet at a moderate price, but who rarely consider the logistics and expense of caring for these pets once they reach adult sizes.

3.2.3. Synthetic Model

Incorporation of both trade and ecological variables produced few surprises as regards the species associated with the highest risk as potentially invasive species. The high rankings of *B. constrictor* in terms of both trade and ecology propelled it to the top position in the synthetic analysis. As discussed above, this species is imported in large numbers, attains a fairly large body size, is viviparous, and appears capable of adapting to a variety of habitats; these factors appear to predispose *B. constrictor* to being a very effective invader. Although this is the most commonly bred viviparous boid in captivity, most of the captive-bred specimens tend to be attractive (and thus expensive) morphs such as the "red-tailed" boas. Wild-caught individuals tend to be much less expensive, and most purchasers of these snakes are not aware of the source of the animals, thus perpetuating the import trade.

By dint of its high import volume, low individual price, huge body size, and high fecundity, the reticulated python (*P. reticulatus*) occupied the second-highest position in the risk rankings (Tables III and IV). After years of disfavor among herpetoculturalists due to its perceived aggressive demeanor, this snake has made a comeback in the domestic market, due to availability of new color morphs and a new perception that captive individuals can be adequately tamed. Captive breeding of the species has increased and captive-bred juveniles are readily available, but once again the availability of captive-bred offspring only spurs the purchase of cheaper wild-caught snakes by naïve consumers. The commercial skin trade in Indonesian *P. reticulatus* exceeds 500,000 skins per year,[45] which is much higher than the ~2,300 live individuals entering the United States each year via the pet trade. However, these populations are able to persist in the face of exploitation, probably due to rapid growth rates, early maturation, and high fecundity.[11,18] Reticulated pythons appear to thrive even in areas with high human populations, as rats are available as prey; this is likely to be true of *P. molurus* and *P. sebae* as well. Thus, the control of large-bodied, invasive snakes may be difficult once populations are established in U.S. habitats.

The Burmese python (*P. molurus*) is a close relative of *P. reticulatus*, and is likely to be somewhat similar in terms of its natural history and risk of establishing invasive populations. This snake is ranked fourth in terms of synthetic risk, and is the only large-bodied boa or python that is known to have established a reproductive population in the United States. A large number of individuals (at least 68 since the mid 1990s) have been captured in the Everglades region of Florida, and the presence of these snakes has received considerable attention from the popular press.[46,47] Without a significant increase in funding to understand the habits of this species in south Florida, it will be difficult to produce an effective management plan for containing or eradicating the current population.

3.3. Consequences of Establishment

3.3.1. Implications for Conservation of Species Listed Under the Endangered Species Act

At the level of the federal government in the United States, priority for conservation-related funding is largely focused on species that are listed as threatened or endangered under the auspices of the Endangered Species Act (ESA) of 1973. Characteristics of some listed species may predispose them to being adversely impacted by establishment of nonnative snakes. Of particular concern are listed species that may be potential prey items for introduced snakes, or listed species that might experience direct competition for resources from introduced snakes. I therefore compared geographic distributions of species listed as threatened or endangered in the United States with the areas most likely to be colonized by invasive boas and pythons. This examination only considered ESA-listed vertebrate species in the continental United States. While the State of Hawaii has numerous listed species (especially birds), which could conceivably be threatened by the establishment of nonnative snakes, Hawaii already prohibits importation and ownership of snakes, and the risk of establishment should be reduced by adequate enforcement of existing laws.[48]

Discussions of which species are most likely to be impacted by establishment of invasive snakes are, of course, speculative. However, a number of ESA-listed mammals in Florida could be negatively impacted by the introduction of large-bodied boas and pythons (Table V). The mammalian fauna of the Florida Keys may be especially vulnerable to introduced snakes (Table V). In fact, the presence of small (e.g., *Oryzomys*), medium (e.g., *Sylvilagus*), and large (e.g., *Odocoileus*) listed mammals in the Florida Keys imply that a large species of snake (e.g., *P. reticulatus* or *P. molurus*) could conceivably prey on federally listed mammals from hatching through maturity. Potential risk to these species is increased by the observations that: (a) well over 500,000 reptiles are imported annually through Miami, Florida;[49] and (b) the northernmost Florida Keys are a scant 100 km from Miami, and are closer still to known established populations of *P. molurus*. Additionally, the introduction of novel pathogens associated with boas and pythons may represent a potential threat to indigo snakes (*Drymarchon couperi*). Because indigo snakes are wide-ranging active foragers, they tend to have large individual home ranges. Thus, an indigo snake may have increased opportunities to encounter exotic species and their pathogens, and, after infection, may have increased opportunities to transmit the pathogen to conspecifics.

3.3.2. Pathogens Associated with Imported Snakes

Nonnative snakes may harbor similarly nonnative pathogens and parasites, against which native species in the United States have few defenses. These pathogens may be zoonotic (capable of transmission from animal to human), or may pose a threat only to nonhuman species. In the latter case, pathogens may either be relatively host-specific (i.e., a parasite that only affects snakes and thus could be transmitted only from nonnative to native snake species) or general (i.e., a pathogen capable of transmission to a broad range of nonhuman taxa). In some cases, the exotic parasites present on exotic reptiles may themselves carry exotic pathogens (see below for a discussion of the relationship between heartwater disease and tortoises in the pet trade).

Exotic reptiles may represent zoonotic threats to humans, although this problem is still poorly documented for many zoonoses. The best-documented zoonosis related to reptiles is salmonellosis, which affects an estimated 93,000 U.S. citizens each year.[49] At least 38 potentially zoonotic strains of *Salmonella* have been isolated from apparently healthy reptiles.[50] A number of other potential zoonotic pathogens have also been isolated from reptiles, including *Clostridium*, *Escherichia*, *Mycobacterium*, and *Staphylococcus*. Serious bacterial and viral zoonoses have been associated with live reptiles in the pet trade, including Q fever and western equine encephalitis. Parasite-mediated diseases such as Lyme disease, tularemia, Siberian tick typhus, and tick-borne relapsing fever are associated with external parasites (especially ticks) found on some reptiles.[50,51] Many of the natural geographic boundaries that prevent introduction of these diseases to the United States may be negated by transglobal shipments of live reptiles for the pet trade.

Reptile-related pathogens and parasites that are not known to be zoonotic, or which are extremely rarely zoonotic, may still be of considerable concern as pathogens of native species. A wide variety of bacterial, fungal, and viral pathogens are known from boas and pythons, as are a plethora of external and internal parasites.[52]

Of particular concern when considering boas and pythons is inclusion body disease (IBD), which has been known from captive snakes for over two decades.[53] This disease is uniformly fatal and appears to be associated with a retrovirus. Retroviruses mutate readily and produce new strains capable of infecting novel hosts. An anthropocentric example is the human immunodeficiency virus, a mutant strain of which apparently succeeded in being transmitted from wild primates to humans, resulting in the current acquired immune deficiency syndrome epidemic. IBD may present a serious threat to the native snake fauna of the United States. The retrovirus is likely to be pathogenic for native boid snakes (*Charina*) in the western United States, and mutant strains could conceivably infect more distantly related snakes. Mutations of this sort may have already occurred, as evidenced by the observation of an IBD-like disease in captive pitvipers.[54] The likelihood of this happening is increased by the common herpetocultural practice of keeping multiple species of snakes in close proximity, increasing the odds of each species being exposed to novel pathogens. Native species may escape or be released, allowing infection of natural populations. Furthermore, incoming shipments of imported snakes often contain multiple species, further increasing the risk of cross-species pathogen transfer. Although IBD has been referred to as "the most important health problem of captive snakes in the world today," it has received little research attention.[55]

Despite a slowly increasing volume of knowledge of the medical aspects of herpetoculture, overall knowledge remains spotty. Many pet owners are unwilling to spend large amounts of money on veterinary care for reptiles and thus many diseases go untreated and previously unknown reptile pathogens are never even presented for veterinary care. Given the typically high levels of host specificity of reptile pathogens, it is certain that many genera and species of pathogens remain unknown to science. Still more troubling is the fact that health screens of imported reptiles are perfunctory, if they are performed at all. Only those animals in obvious distress may be quarantined or sent back to the country of origin, and this occurs only if inspectors have been trained to recognize such distress. Thus, pathogens with mild effects on imported animals or those that require extended periods to become symptomatic are rarely detected.

The recent ban on importation and interstate transportation of three species of African tortoises (*Geochelone pardalis*, *Geochelone sulcata*, and *Kinixys belliana*) illustrates the depth of ignorance of the potential consequences of exotic pathogens from introduced reptiles. These tortoises were found to

Table V. Vertebrates Native to the United States and Listed as Threatened or Endangered Under the U.S. Endangered Species Act that are Most Likely to be Impacted by Establishment of Feral Populations of Boas or Pythons

Common Name	Latin Name	Geographic Location
A. Listed Species Likely to Experience Predation by Introduced Boas and Pythons:		
Lower Keys marsh rabbit	*Sylvilagus palustris hefneri*	Florida Keys
Silver rice rat	*Oryzomys palustris natator*	Florida Keys
Florida salt marsh vole	*Microtus pennsylvanicus dukecampbelli*	Gulf Coast of Florida
Key Largo woodrat	*Neotoma floridana smalli*	Florida Keys
Key deer	*Odocoileus virginianus clavium*	Florida Keys
Florida scrub jay	*Aphelocoma coerulescens coerulescens*	Central Florida
Everglade snail kite	*Rosthrhamus sociabilis plumbeus*	South Florida
Light-footed clapper rail	*Rallus longirostris levipes*	Southern California
Cape Sable seaside sparrow	*Ammodramus maritimus mirabilis*	South Florida
Florida grasshopper sparrow	*Ammodramus savannarum floridanus*	South Florida
B. Listed Species Likely to Experience Competition or Exposure to Pathogens from Boas, Pythons, and Relatives:		
Eastern indigo snake	*Drymarchon corais couperi*	Southeast United States

Note: This list was compiled by comparing geographic ranges of ESA-listed species with areas most likely to be colonized by invasive snakes.

carry species of ticks (tropical bont tick (*Amblyomma variegatum*), the African tortoise tick (*Amblyomma marmoreum*), and ticks of the species *Amblyomma sparsum*)) known to carry heartwater disease in their native African distributions. Heartwater disease is an acute infectious disease of ruminants, which could conceivably decimate livestock in the United States. The disease was estimated to potentially produce 60% or greater mortality rate in livestock and a 90% or greater mortality rate in white-tailed deer, indicating the problem is severe for both domestic and wild species. The rule banning importation of these tortoises (except for those individuals certified to be tick free by a USDA veterinarian) was put in place in order to allow the establishment of effective treatment and biosecurity protocols for tortoises and other reptiles. However, these protocols have been designed solely to control ticks on incoming animals, thus representing a *post hoc* solution to a problem. *A priori* methods to control as-yet-undiscovered pathogens appear to be a low priority, and funds have not been made readily available to researchers to screen other reptiles for pathogens potentially disastrous to native species in the United States.

Lastly, I call attention to a completely different potential consequence of pathogens associated with the establishment of exotic snakes in the United States. Across a wide variety of vertebrate and invertebrate taxa, individuals of introduced species tend to have decreased parasite loads as compared to individuals of that species in its native geographic range.[56] The number of parasite species in introduced populations averages half that of native populations, and fewer individuals tend to be infected in introduced populations. This is likely due to founder effects associated with introductions; because relatively few individuals typically found an introduced population, descendants of these founders will only be parasitized by the species found in the original few founders. Thus, the establishment of nonnative snakes may have two different impacts on native species. First, as mentioned above, novel pathogens may be transmitted to naïve native species, with unknown effects. Second, invasive snakes may have relatively low individual parasite loads and thus have a competitive advantage over native species. Among reptiles, analyses have only been conducted for the mourning gecko (*Lepidodactylus lugubris*), and similar studies have not been conducted on the vast majority of imported reptiles.[56]

4. CONCLUSION AND RECOMMENDATIONS

A major problem with this type of risk analysis is that it is essentially an untestable hypothesis. The only sure way to determine which species would make the best invaders is to release multiple founder populations of each species into U.S. habitats and observe the results. This is obviously the fool's choice, and so we are left with models that incorporate some amount of ambiguity and arbitrariness. The models and results presented herein may be viewed as a first step toward the development of risk assessments for snakes as invasive species. Based on the results of the preceding analyses, I recommend the following:

1. Efforts should be made to increase the attractiveness of captive-bred snakes to potential purchasers of pet snakes. Captive-bred specimens are generally healthier and harbor fewer nonnative pathogens, thus reducing one of the major risks associated with escaped or released pets.
2. Imported snakes should be subject to increased quarantine before sale in the domestic retail market. At the very least, snakes should be fumigated with a safe pesticide to eliminate external parasites. Imported reptiles conceivably present major risks to the environment and economy in the United States; it is high time to be proactive rather than reactive in preventing as-yet-unknown pathogens from reaching our shores.
3. Incoming shipments of boas and pythons should be certified clean of external parasites (as has been mandated for certain species of African tortoises), and should conceivably receive prophylactic treatment for internal pathogens. Costs of increased quarantine will pass from the importer to the consumer, and will thus increase the costs of wild-caught specimens. Reducing the price disparity between captive-bred and wild-caught snakes should increase demand for the former at the expense of the latter.
4. The Florida Keys appears to be especially vulnerable to introduced boas and pythons, with potential impacts on a variety of ESA-listed vertebrates. The subtropical conditions in the Keys would allow establishment of many species, and nearby Miami is a major arrival point for international animal shipments, further increasing risks. Given the historical role of animal dealers in accidentally and intentionally releasing nonnative herpetofauna to South Florida,[5] state and federal agencies should formulate more effective policies designed to reduce the odds of accidental releases and to increase penalties for intentional release. As a preventive measure, it may also behoove local governmental bodies to ban or strictly control the possession of pet snakes in the Florida Keys.
5. The identification of pathogens associated with imported reptiles must receive higher funding priority. An ounce of prevention is worth a pound of cure as regards invasive species, yet the astounding level of ignorance of the taxonomic variety and prevalence of pathogens in incoming shipments appears to be attracting little attention from regulatory agencies.
6. Educational efforts aimed at reducing intentional releases of nonnative snakes should be increased, perhaps via offering funds to state agencies. Many large snakes are released by well-meaning owners after reaching adult size, and threats of prosecution are unlikely to stem this practice. An excellent template is provided by the "Please don't turn it loose!" pamphlet produced by the Arizona Game and Fish Department and Partners for Amphibian and Reptile Conservation (http://www.gf.state.az.us/pdfs/i_e/please_dont_turn_it_loose.pdf). This pamphlet educates citizens on the problems associated with release of pets in clear language, without being shrill or overly negative.

Aldo Leopold reminded us that the first rule of wise tinkering is keeping all the pieces, and this phrase has been used as a justification for preserving ecological communities and larger ecosystems.[57] However, neither does the wise tinker add pieces willy-nilly to an existing mechanism, as occurs when species are introduced. Alarming numbers of nonnative boas and pythons are entering the United States annually, and the popularity of reptiles as pets appears to be still gaining in strength. The trend for potentially deleterious species to be imported with little regulatory oversight demands increased attention from natural resource agencies.

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