

Giant Constrictors: Biological and Management Profiles and an Establishment Risk Assessment for Nine Large Species of Pythons, Anacondas, and the Boa Constrictor



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Giant Constrictors: Biological and Management Profiles and an Establishment Risk Assessment for Nine Large Species of Pythons, Anacondas, and the Boa Constrictor

By Robert N. Reed and Gordon H. Rodda

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**U.S. Department of the Interior
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Frontispiece: Clockwise from upper left: Southern African Python, *Python natalensis*, in
South Africa (courtesy of G. Alexander); A clutch of hatchling Burmese Pythons (*Python
molurus bivittatus*) in Florida (courtesy of S. Snow); A brooding female Burmese Python lifted
from her eggs in Florida (courtesy of S. Snow); Green Anaconda, *Eunectes murinus*, in Brazil
(courtesy of L. Dirksen); DeSchauensee's Anaconda, *Eunectes deschauenseei* (courtesy of
L. Dirksen); Boa Constrictor, *Boa constrictor*, on Aruba Island, West Indies (courtesy of R.
Reed); Reticulated Python, *Broghammerus reticulatus*, on Sulawesi Island, Indonesia
(courtesy of B. Lardner).



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Chapter One—Introduction and Synopsis of Conclusions

In this report, we compile summaries of the biology of nine very large constrictor species and consider what effects these species might have on the ecology, economy, and domestic tranquility of the United States were such snakes to become established. Representatives of each group have been discovered in the wild in Florida, though evidence of reproduction is presently available for only three species, the Burmese Python (*Python molurus bivittatus*), the Northern African Python (*Python sebae*), and the Boa Constrictor (*Boa constrictor*). The occurrence of these three large constrictors in the wild in the same area of Florida may be a coincidence, but southern Florida has a climate that may be suitable for all of the giant constrictors and much of the commercial trade in giant constrictors passes through southern Florida. Thus the probability of exotic species establishment is greater in south Florida, though not limited to it. For each of the nine giant constrictor species under consideration, we review their climate tolerances and the areas of the country at risk (see section 10.2 in each of the species accounts: chapters Four–Nine). However, because we have established populations in south Florida, our geographic focus will always include Florida.

The selection of giant constrictor species was based on concern over the size of the potential invaders combined with their prevalence in international trade. We include the four largest species of snake, as well as similar and closely related species, and the Boa Constrictor. The four largest snakes are the true “giants,” with maximum lengths well exceeding six meters: Northern African Python (*Python sebae*), Indian Python (*Python molurus*¹), Reticulated Python (*Broghammerus reticulatus*), and Green Anaconda (*Eunectes murinus*). Although *Morelia amethestina*, the Scrub Python, and some Austropapuan relatives, which we did not include, often exceed the length of our shortest species, the Boa Constrictor, we selected the species not only for their size, but also for the likelihood of establishment. The boa is very large, much more commonly owned, and is already established in Florida; thus it is a species of special concern. The Scrub Python is less frequently encountered in the trade, and is not yet known to be a problem in the United States.

In addition to the four true giants and the Boa Constrictor, we included four species that are so similar in appearance to one of the giants that they might be confused with them, and which are in some cases not distinguished in the international live animal trade. For example, the Beni Anaconda (*Eunectes beniensis*) is a recently described and poorly known anaconda closely related to the giant Green Anaconda. Because these species are visually similar and the range of the Beni Anaconda is within the range of the Green Anaconda, we review the former species in the same chapter as the latter. Similarly, there are now two species in the yellow anaconda group: the Yellow Anaconda

¹ We treat the Burmese Python as a subspecies (*Python molurus bivittatus*) of the Indian Python (*Python molurus*). See chapter Four for taxonomic details.

(*Eunectes notaeus*), which has appeared in the wilds of Florida, and a rare and similar closely related species, DeSchaunsee's Anaconda (*Eunectes deschauenseei*). Finally, the Southern African Python, *Python natalensis*, is the sister species of the Northern African Python, but the two are not distinguished in international trade. These two species are easily distinguished by technical characters such as head scalation, but many people do not recognize the distinction. Thus we treat all nine of these large constrictors in this risk assessment; the Boa Constrictor, the four true giants, and their four look-alikes.

Although the size threshold on our characterization of a snake as a "giant" was arbitrary, the heightened focus on large constrictors has two firm foundations. First, only the largest nonvenomous snakes constitute a safety hazard for humans. Citizens have a legitimate expectation that their government will be protective of their personal safety. Second, there are no native American snakes of comparable size; thus establishment of a giant exotic snake would force native wildlife to survive in the presence of a novel-size snake predator. The history of extinctions is rife with examples of the ecological damage caused by the introduction of novel predators. Blackburn and others (2004) found that the only strong explicator of extinctions of island birds was the number of introduced predators. Novelty is less readily quantified, but most ecologists are convinced that introduced predators do significantly more damage if their predatory method includes a novel tactic for which the prey species has not evolved a defense (Rodda and others, 1997). A classic example is the doomed birds of Guam, which were unfamiliar with snakes and had not evolved any defense against a nocturnal arboreal snake predator such as the Brown Treesnake (*Boiga irregularis*, Savidge, 1987). The issue is not limited to islands, however; Allen (2006) found that novelty of body size was the best statistical predictor of which bird species have successfully invaded southern Florida.

Although giant constrictors constitute an exceptional threat to the integrity of native ecosystems, they also constitute an important element of the large and growing trade in living reptiles. We can testify to these snakes' attraction personally, as we both have kept pet giant constrictors. We can attest to these snakes' beauty, companionability, and educational value. The love of nature is often originally fostered in one's own arms, where close contact with living things engenders a connection not otherwise possible. And size does impress. Thus the social value of protecting native ecosystems must be weighed against the social value of fostering positive attitudes about the protection of nature through giant constrictor ownership. Economic benefits are also associated with importation and trade in giant constrictors; we tabulate importation, but do not quantify the economic benefits of the trade. A risk assessment quantifies as much as possible the ecological factors associated with the introduction of a species; decision-makers must account for the societal values from all viewpoints of any potential regulatory action. We will not do so in this risk assessment.

This document addresses primarily the biological impacts associated with potential colonization of the United States by any of the nine giant constrictors, and it tabulates the biological information germane to potential economic and social impacts. What it does not do is consider or assess the diverse regulatory actions that might be taken to mitigate or prevent colonization by these animals. Regulatory action could occur at the Federal level (for example, prohibit importation or interstate transfer of reptiles), or at the State level (for example, statutory or regulated restrictions on the behavior of

private owners). Each of these steps would have specific effects on the potential for establishment in the wild and on the operation of the pet trade, and the merits of each possibility could be weighed in a *regulatory evaluation*. However, such an evaluation is beyond the scope of this risk assessment. We contrast only the projected biological (and related) impacts of establishment against the conditions that would prevail in the absence of colonization by these species.

Risk assessment, by its very nature, entails uncertainty. “A risk assessment model cannot absolutely determine whether or not an introduced exotic species will establish and if it does what impact it will have” (Aquatic Nuisance Species Task Force, 1996; Bomford, 2008). We have tried to draw attention to the greatest sources of uncertainty, but all elements of a risk assessment embody some uncertainty. The ANSTF (Aquatic Nuisance Species Task Force, 1996) protocol that we follow in this document highlighted three primary sources of uncertainty:

1. uncertainty of the process–(methodology)
2. uncertainty of the assessor–(human error)
3. uncertainty about the organism–(biological and environmental unknowns).

As is explained more fully in the following chapter on methods, the biological and environmental unknowns associated with giant constrictors are numerous and profound. However, the problem is not unique to giant constrictors. The ANSTF (1996) pointed out, “...it is the biological uncertainty more than anything else that initiated the need for developing a nonindigenous risk process. Common sense dictates that the caliber of a risk assessment is related to the quality of data available about the organism and the ecosystem that will be invaded. Those organisms for which copious amounts of high quality research have been conducted are the most easily assessed.” The basic natural history of the giant constrictors is largely unknown; our risk assessment reflects this uncertainty.

In the next chapter, we explain the methods used for the risk assessment. The subsequent chapter (Three) summarizes what is known about snake eradication. Snake eradication has not been attempted with giant constrictors to the best of our knowledge. Thus our review considers the available data for other species, based primarily on experience with the Brown Treesnake in Guam and the Habu in Japan (Rodda and others, 1999d). Eradication methods are an important consideration for a risk assessment, as the risks of establishment are less worrisome if impacts can be easily eliminated or prevented by eradicating the invader. The tool-by-tool review in chapter Three provides the background material needed to put the risks in a realistic management context.

The species accounts (chapters Four–Nine) include both a summary of each species’ relevant biology and a summary of the relevant risks and management factors that apply to each species uniquely. Management attributes that are the same for all species of giant constrictor are described in chapter Three.

The formal risk assessment is the last chapter (Ten), in which we follow the format originated by the Aquatic Nuisance Species Task Force (ANSTF, 1996). Reflecting a consensus of the field, the task force concluded that the overall *probability* of establishment is a product of the risk of the organism being in a certain pathway (such as the pet trade) multiplied by the risk of the organism surviving in that pathway multiplied by the risk of that organism escaping from the pathway and colonizing the

wild multiplied by the risk of the colony spreading. The task force also concluded that the *consequences* of establishment include the sum of economic, ecological, and social/political costs. The species-specific cost and risk components are tallied within each species account and brought together in chapter Ten.

A word on terminology—a variety of terms has been used to describe an organism that is not native to the place in which it is found: exotic, introduced, invasive, nonindigenous, non-native, colonists. In this report we make no distinction among these terms. A colonization is the original population of a non-native species, perhaps a single female and her offspring. A colonization is usually considered “established” when there is physical evidence that the species’ entire life cycle can be completed in its new environment. In practical terms this means population recruitment, usually the discovery of wild-born hatchlings or neonates. However, most individual snakes go undetected by humans, and hatchlings are especially hard to detect. Thus many populations recruit successfully prior to the time when establishment has been seen by scientists and therefore documented. Though often unobserved until much later in time, “establishment” is a milestone of primary importance to the assessment of risk.

At some point, an expanding population exceeds the size at which it can still be considered a colony. A colony generally refers to a population that is compact enough that it could be eradicated with decisive and effective control measures. However, the areal capabilities of eradication tools are poorly known and improving daily; thus there is no preordained acreage beyond which a colonization is too widespread to be eradicated. Nonetheless, eradication is the final defense that could completely reverse an invasion, and thus expansion of an invading population beyond the eradication size limit is the final milestone for invasion risk.

Synopsis of Conclusions

In this risk assessment, we estimate the ecological risks associated with colonization of the United States by the world’s four largest snake species: Green Anaconda, Indian or Burmese Python, Northern African Python, and Reticulated Python (*Eunectes murinus*, *Python molurus*, *Python sebae*, and *Broghammerus reticulatus*, respectively), the Boa Constrictor (*Boa constrictor*), and four look-alikes (Southern African Python, *Python natalensis*; Yellow Anaconda, *Eunectes notaeus*; DeSchauensee’s Anaconda, *Eunectes deschauenseei*; and Beni Anaconda, *Eunectes beniensis*). At present, the only probable pathway by which these species would become established in the United States is the pet trade. Importation for the pet trade entails a risk of establishment of these animals as exotic or invasive species, but it hardly guarantees that establishment. Federal regulators have the task of appraising the importation risks and balancing those risks against economic, social, and ecological benefits associated with the importation. This risk assessment quantifies only the ecological risks, recognizing that ecosystem processes are complex and only poorly understood. We outline the types of economic impacts that may be experienced, but we leave quantification of economic costs to economists. There is great uncertainty about all aspects of this risk assessment, but we have tried very hard to bring the best available information to bear. Scientific sources are referenced in chapters Two–Ten, and omitted from this synopsis.

One element of uncertainty is the degree to which a colonization of one of these snakes could be eliminated if appropriate financial resources were available to support an eradication attempt. We have some indication from the management response to the establishment in south Florida of the Burmese Python, but we can also draw on additional insight from eradication attempts against the Brown Treesnake in Guam, the Habu in Japan, the Boa Constrictor on Cozumel Island in Mexico, and other snake management efforts worldwide. None of these management programs have progressed to the point of attempting eradication on any area nearly the size of the Burmese Python population in Florida, and no eradication effort has been successful on a scale larger than a few hectares. Chapter Three reviews the management toolbox in some detail—covering especially traps, active search, and toxicants—and concludes that future advances in technology may greatly expand the scope of snake eradication, but extant technology would not appear to be capable of eradicating any of the giant constrictors from south Florida unless the colonization were caught very early, perhaps around the present range of the Boa Constrictor population now in Miami (several hundred hectares or less). There is great uncertainty about this management prognosis because: (1) the availability of financial resources is unknown, (2) future improvements in eradication technology are uncertain, and (3) the known tools have not been adequately tested against any species of giant constrictor.

The giant constrictors differ in a number of ways important to management or control efforts. For example, the anacondas are found almost exclusively in water, complicating their control in wetlands such as the Everglades, but limiting their spread in dry upland areas. At the other extreme is the Boa Constrictor, a species that may use water but is found primarily in terrestrial environments, including arboreal habitat. The pythons appear to be completely at home in aquatic and terrestrial environments, rendering it problematic to curtail their spread.

Another important difference among the giant constrictors is their size and temperament. Although the largest individuals of all of the species covered in this work are probably capable of killing an adult human, most seem disinclined to do so. Unprovoked attacks on humans are largely limited to Reticulated Pythons, and only the larger Burmese/Indian and Northern/Southern African pythons have killed adult humans.

One very important difference among the species is the degree to which they naturally inhabit areas that freeze. The Indian or Burmese Python is exceptional in its ability to tolerate cold weather through hibernation; most of the other species are likely limited to areas where below-freezing weather is short-term and can be avoided by submergence in shallow burrows or water.

The giant constrictors differ in the degree to which they are presently in the pet trade. In the last thirty years, over 1 million of these snakes have been imported into the United States, of which about 60 percent were Boa Constrictors (based on CITES records: Appendix). Other important imports are Indian Pythons (~300,000), Reticulated Pythons (~150,000), Northern/Southern African pythons (~33,000), and Green Anacondas (~13,000). The least traded species among those documented is the Yellow Anaconda, which has been imported in small numbers (<2000), but this species has still turned up at several localities in or near Big Cypress National Preserve, Florida. These totals are documented imports, to which must be added an unknown number of imports not ascribed to any particular python species, and sales of domestically produced giant

constrictors. Domestic production is undocumented, but believed to be greatest for Reticulated and Burmese Pythons. For Burmese Pythons in particular, the domestic production is judged to be as large as or larger than importation.

This list of differences among the species is less striking than are the ecological commonalities among them. All of the species we consider are evolutionarily closely related, in two recognizable clades: boids (the anacondas and boa: live-bearing) and pythonids (the pythons: egg laying). They are of similar size, the larger species reaching a maximum of nearly 10 m in total length, though few individuals exceed 6 m. Most species occur in a very wide range of habitats, though the Reticulated Python is largely limited to tropical forest, and two species of anacondas are found in a restricted range of tropical wetland habitats. All are capable of climbing trees, especially when young, and all will seek out water to avoid harassment or predators. All can be active at night or during the day, though they seem to prefer warm weather. All well-studied species are known to live within urban areas, at least under some conditions. Most significantly, they all hunt by a similar strategy of restful alertness concealed near localities (waterholes, rodent burrows) where a prey animal is likely to transit. This sit and wait predatory style is probably responsible for their ecological success, and the extreme difficulty humans have in finding them. Detection probabilities for the Burmese Python in the Everglades are on the order of 1 in 1,000 per day, meaning that only a tiny fraction of the population can be found on demand. Sit and wait predators may also be very difficult to trap, as they encounter traps only during their infrequent moves between hiding places.

All of the species under consideration are fecund, with the Reticulated Python having the second largest number of young of any snake (maximum 124), and the other pythons are close behind. All of the species under consideration can probably move large distances over short time periods when so inclined. These two factors combine to make it hard to limit the spread of their colonies. All of the species under consideration grow relatively quickly; the fastest snake-growth records are all held by one or another of the giant pythons. The giant pythons mature at a relatively young age, with some able to breed in their second year and most capable of breeding by age 3–5, at least in captivity (maturation ages are generally unknown in the wild). Despite their quick maturation and large clutch sizes, the giant constrictors are capable of a long life, with captive longevities reported in excess of 30 years.

Introduced predators are considered to be a greater threat as invaders if they are generalist feeders, because no matter where they escape or are released they may find suitable food. The giant constrictors are generalist predators on terrestrial vertebrates, although the anacondas also regularly consume aquatic vertebrates. Generalist predators are more likely to cause the extinction of vulnerable native prey because they continue to thrive on alternate prey as they drive the vulnerable prey species to extinction. Specialist predators rarely thrive when their preferred prey become rare.

All of the giant constrictors would have few predators on themselves in the United States because they are so large. Large alligators and panthers would be capable of eating the occasional giant constrictor, but large constrictors will likely eat alligators and panthers. It is unclear whether any native predator would enjoy a net benefit.

There are a variety of reptile ticks that appear capable of transferring among any of the giant constrictors; as examples of many potential pathogens of medical or

veterinary importance, snake ticks originating in Africa may carry heartwater disease (potentially fatal to cattle) and ticks from Asia can convey capillariasis, a disease of human health significance.

There are few data on which to estimate the likely population density of giant constrictor populations, though the densities of Burmese Pythons near Everglades National Park suggest that they can reach very high densities where rodents are abundant.

The list of traits shared by the giant constrictors includes many of the traits that either increase the severity of their probable ecological impacts or exacerbate the challenge of controlling or eradicating them:

- large size
- habitat generalist
- arboreal when young
- tolerant of urbanization
- sit and wait predator
- low detectability
- high fecundity
- long-distance disperser
- rapid growth
- early maturation
- generalist predator
- host for diseases of economic and human health significance
- high-population density

Thus in comparison to potential invaders lacking these traits, this group of snakes constitutes a particularly high risk.

Using the rating system proposed by the Aquatic Nuisance Species Task Force (1996), the components of risk include four elements of probability of establishment and three elements of consequences of establishment. For the giant constrictors under consideration, we judge the risk of establishment to range from medium (Reticulated Python, DeSchauensee's Anaconda, Green Anaconda, and Beni Anaconda) to high (Indian or Burmese Python, Northern African Python, Southern African Python, Boa Constrictor, and Yellow Anaconda), with the understanding that three of the species (Southern African Python, DeSchauensee's Anaconda, and Beni Anaconda) warrant their rank primarily because they are actually or potentially sold in commerce labeled as if they were a similar and closely related species (Northern African Python, Yellow Anaconda, and Green Anaconda, respectively). If they were to be unequivocally distinguished from their look-alikes, and if the current low volume of trade in these species were to continue, they might constitute an absolutely smaller risk.

For the giant constrictors under consideration, we judge the consequences of establishment to range from low (DeSchauensee's Anaconda and Beni Anaconda) to medium (Reticulated Python, Yellow Anaconda, and Green Anaconda) to high (Indian or Burmese Python, Northern African Python, Southern African Python, and Boa Constrictor). The overall organism risk potential, which is the sum of both probability of establishment and consequences of establishment, was found to range from medium (Reticulated Python, Green Anaconda, DeSchauensee's Anaconda, and Beni Anaconda) to high (Indian or Burmese Python, Northern African Python, Southern African Python, Boa Constrictor, Yellow Anaconda).

Certainties were highly variable within each of the seven elements of the risk assessment, varying from very uncertain to very certain; see the tables in chapter Ten for certainty ratings associated with each element. In general, the highest certainties were associated with those species unequivocally established in Florida (Burmese Python and Boa Constrictor) because of enhanced ecological information on these species from studies in both their native range and in Florida.

Chapter Two—Materials and Methods

Introduction

The core of this work—the biological profiles—are a work of traditional library scholarship, gleaning relevant data from the peer-reviewed literature and talking to experts active in each taxon (augmented by unpublished data from relevant sources and by our own experiences with these species in the field and in captivity). We started with keyword searches of relevant bibliographic databases, added relevant references from our personal bibliographic records, and traced all relevant citation threads from primary and secondary sources to the original publications. The latter approach was the most time consuming, and it provided the most useful sources. We translated key original sources if published in a European language, and contracted translation of a small number of essential references in Asian languages. We relied on secondary sources only to the extent that no better record was available, or if the secondary source credibly paraphrased or translated a difficult-to-obtain primary reference. We generally did not attempt to verify distributional records, and in most cases relied on recent comprehensive distributional publications. In a few cases, we challenged certain key localities by pursuing the original records or asking curators to verify specimen identifications, but for most distributional details we relied on credible literature compendia.

In addition to secondary sources, we compiled the following number of primary sources: Indian Python, 210; Reticulated Python, 205; Northern African Python, 71; Southern African Python, 76; Boa Constrictor, 183; Green Anaconda, 67; Beni Anaconda, 2; Yellow Anaconda, 30; and DeSchauensee's Anaconda, 16. As is suggested by these counts, DeSchauensee's and Beni Anacondas are poorly known; it is at least in part for this reason that we have combined those accounts with better known related taxa. However, "better known" is a relative term, and it is noteworthy that none of the giant constrictors are well known. Despite the giant constrictors' persistent intense public interest and renown, only a few of these species have been the subject of modern ecological field studies. For example, credible dietary analyses have been published for only a few species, and using data from only a few localities. We are unable to characterize the body size, breeding season, or diet of any giant constrictor species throughout its range. Furthermore, available studies have focused on divergent ecological topics, complicating any attempt at direct comparisons of traits across species. As examples, the interaction between ecology and reproduction is best known from free-ranging Green Anacondas, whereas harvested Yellow Anacondas have yielded excellent data on size at maturity and various other reproductive parameters, and radiotelemetry of Southern African Pythons has revealed interactions between ecology and thermal biology. No single species has received across-the-board ecological study, and the ecology of some species is almost completely unknown.

Knowledge of the biology of these giant constrictors may be scanty, but knowledge of appropriate management tools for these species is almost nonexistent.

Thus for the management profiles we relied to varying degrees on inference from the management of other snake species, primarily the Brown Treesnake in Guam and the Habu in the Ryukyu Islands (Rodda and others, 1999d). Management experience with these snakes has identified natural history attributes that confine and steer management in particular directions (see especially the Epilogue in Rodda and others, 1999d). For example, the degree of arboreality of each snake species is a good predictor of the challenges associated with snake barrier construction and the extent to which the species' presence will be associated with electrical system power outages. We have used such guidance to infer likely management issues that are conveyed in the management profiles of each species account. Necessarily such inferences contain an element of uncertainty, which is reflected in the species account narratives and explicitly stated in the uncertainty ratings contained in the last chapter. Although some elements of management differ by species, the giant constrictors share many natural history attributes, and the management factors that are shared among all species are conveyed in chapter Three, the synopsis of eradication tools.

Length Measurements

The lengths of snakes are often given in terms of the snake's full length (including the tail, as the tail may be hard to distinguish without having the animal in hand). In this work, we use the abbreviation TL to designate the full or total length. However, scientists often prefer to measure snout-vent length (SVL), which can be measured somewhat more accurately and is less vulnerable to variation due to loss of the tail tip from predators, desiccation, and so forth. Neither measurement is very precise in snakes, because snakes are so elastic, and the giant constrictors are especially prone to measurement error if measured alive, as their muscles routinely overpower those of the measurer. Freshly killed material has a relatively consistent length, as long as the specimen has not been appreciably cut or dislocated during the killing process. Alas, many historical specimens of giant constrictors died a violent death and were distorted prior to measurement. Moreover, there are almost no precise measurements in the literature providing both SVL and TL (or equivalently, providing tail-length measurements, which vary slightly with sex); thus converting from one measurement to another is somewhat speculative.

In this work we provide TL measurements, estimated from the following table (Table 2.1), which was compiled from all of the available literature sources (see Bioprofiles). When the source data are measurements of total length in either feet/inches or SI (metric) units, we express the lengths in either mm or m without further annotation. If the source data are SVL measurements, we give the SVL value in parentheses.

Table 2.1. Estimated body proportions for the nine giant constrictors considered in this work, by sex (M or F) or of mixed-sex samples. These values used to convert SVL measurements to the TL values reported in the text.

Species	Tail (% of TL)			SVL/TL			TL/SVL		
	M	F	Mixed	M	F	Mixed	M	F	Mixed
Indian Python	0.12	0.10	0.11	0.88	0.90	0.89	1.14	1.11	1.12
Reticulated Python	0.15	0.12	0.135	0.85	0.88	0.865	1.18	1.14	1.16
Northern African Python	0.12	0.11	0.115	0.88	0.89	0.885	1.14	1.12	1.13
Southern African Python	0.12	0.11	0.115	0.88	0.89	0.885	1.14	1.12	1.13
Boa Constrictor	0.14	0.10	0.12	0.86	0.90	0.88	1.16	1.11	1.14
Yellow Anaconda	0.14	0.13	0.135	0.86	0.87	0.865	1.16	1.15	1.16
DeSchauensee's Anaconda	0.14	0.13	0.135	0.86	0.87	0.865	1.16	1.15	1.16
Green Anaconda	0.14	0.13	0.135	0.86	0.87	0.865	1.16	1.15	1.16
Beni Anaconda	0.14	0.13	0.135	0.86	0.87	0.865	1.16	1.15	1.16

Climate Space

“Weather” characterizes atmospheric conditions at a single point in time; “climate” characterizes seasonally average conditions, which are identified over time, typically 30 years (World Climate, 2007). Characteristic climate parameters are average rainfall or temperature at a particular time of year; typical weather values are whether it is now sunny. Climate space describes the long-term (greater than one generation) climatic conditions under which a population is known to persist, and is not equivalent to the weather that an *individual* can tolerate. Individual or physiological tolerance can be both greater and less than the climate space that supports a population. Individual tolerance depends on acclimatization, which may occur gradually. At the wrong season, or with the “wrong” recent experience, a snake may not be able to tolerate weather conditions (for example, cold) that it could tolerate at other times of year, or when primed by gradually cooling temperatures. Similarly, a snake in a burrow or hibernaculum can tolerate atmospheric conditions that include weather that it could never survive if subjected to directly. Exposed rattlesnakes cannot survive freezing weather, but populations of rattlesnakes often live in climates that freeze! Similarly, desert tortoises will die from midday heat if placed above ground on a Mojave Desert summer day, but they are protected by their behavior of remaining in burrows during these conditions.

Conversely, a snake that is placed on the surface of the ground at 5°C will probably survive (it is physiologically capable of surviving 5°C), but such a snake is so cold that it would probably be incapable of protecting itself from a predator (it is not

ecologically viable); thus physiological tolerance is a misleading guide to ecological success. Our “climate space” is a bivariate (rainfall and temperature) characterization of the climates of occupied habitats and is not to be confused with individual physiological tolerance.

Although it is widely recognized that climates are important and vary among the native ranges occupied by giant constrictors, there appears to be no standard method for characterizing climate space. Perhaps this is because climate has traditionally been viewed as fixed in relation to geographic space. We now know that the climate is presently changing at an evolutionarily unprecedented rate, and therefore it seems appropriate to explicitly record the climate conditions under which the constrictors now occur (and which presumably reflect geologically recent history and the snakes’ recent evolution).

We used published sources to infer each species’ native range (these distributions are summarized in each Species Account, section 3.1). We used exact specimen locations whenever available, and more general regional information when unavoidable, paying particular attention to records from high elevations and high latitudes. As we were focused on the climatic extremes tolerated by the species, we compiled primarily those locality records within 3 lat/long degrees of the periphery of the species’ range (spot checking of more interior localities indicated that inclusion of interior localities failed to appreciably expand the observed climate envelopes).

We used two approaches to extract climate profiles from each species’ distributional records. Where suitable climate records were obtainable from weather stations (Indian Python and Reticulated Python), we used those empirical records (see Rodda and others, 2009). On the other hand, there are many places in the world where weather station data are sparse or unreliable. For those localities we used modeled climate from Hijmans and others (2005). For the two Asian pythons, “presence” localities were matched to the geographically closest choice from among the 85,000 weather stations reported in the World Climate (2007) data set, paying particular attention to ensure an elevation match (where known). When possible, we used individual weather stations that reported both mean monthly rainfall and mean monthly temperature, but in a few cases combined records from nearby stations to obtain both climate data types. The World Climate stations are grouped into lat/long cells of 1 degree; we matched these to locality records in the same cell whenever possible, but for a few important localities could find matching weather records only for an adjacent cell (only stations with similar elevations were considered). We were able to obtain a few useful climate records for locations hosting Indian Pythons in Nepal from Schleich and Kästle (2002). To analyze rainfall on a logarithmic scale and include weather stations that reported zero rainfall during particular months, we coded zero rainfall means as 0.01 mm/mo (this value is slightly lower than the minimum possible from a weather station recording a typical 30-year climate record).

To facilitate comparisons between different species, we plotted the occupied climate space for each species on graphs with identical scaling and fixed reference lines (Fig. 2.1). To make it easier to comprehend the values associated with the reference lines, we identified familiar American cities that had seasonal climates that approximated the intersections of the reference lines (Fig. 2.1). Thus the warm wet nexus is most closely approximated by Hilo, Hawaii in summer; the warm dry nexus by Yuma, Ariz., in

late summer; the cool dry nexus by El Paso, Tex. in winter; and the cool wet nexus by Sitka, Alaska in fall. By comparing each species' climate space to the positions of the reference lines, it should be straightforward to assess their relative association with cool, warm, wet, and dry conditions respectively.

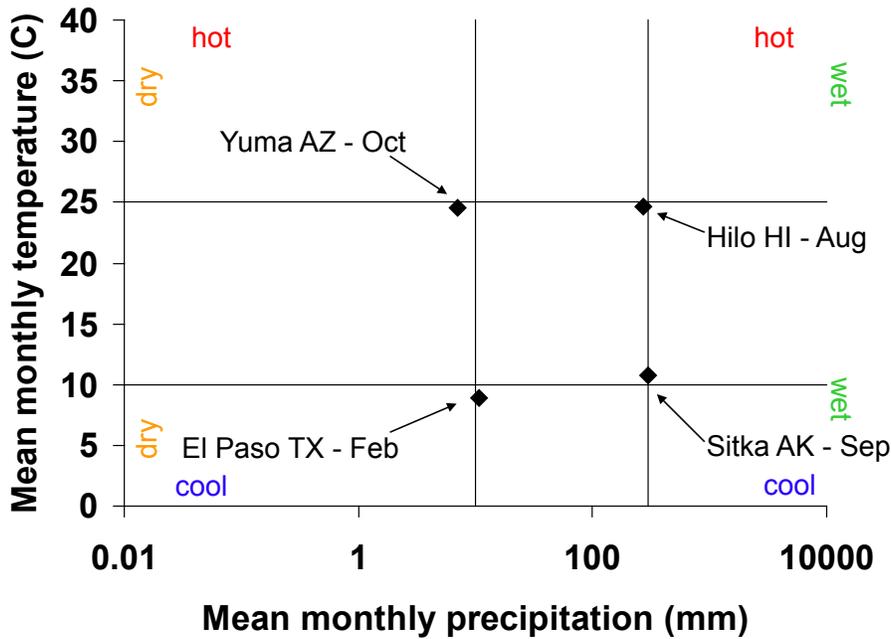


Figure 2.1. Schematic of climate space diagrams, showing representative American cities near the reference line intersections. Yuma, Arizona is a hot dry city in the desert along the California/Arizona border. Hilo, Hawaii is a wet windward city on the Big Island of Hawaii. Sitka, Alaska is on the windward coast of a cool rainforest island in Southeastern Alaska. El Paso, Texas is a dry cool (in Feb.) city in west Texas.

We plotted each of the climate records as 12-sided polygons, each vertex representing the mean conditions for one month of the year. The 12-sided polygons often doubled back on themselves to form figure 8s or other complex shapes. Interpretation of these 12-sided polygons depended on whether the species in question was known to hibernate or aestivate.

For species that hibernate or aestivate (for example, Indian Python), a minimum convex polygon of climate records could overstate the range of conditions suitable for the species to be active. For hibernating species, we treated the coldest vertices as representing the conditions prevailing during hibernation, and we considered at least two plausible hibernation temperature thresholds to quantify the likely duration of hibernation from the native range climate records. If these counts of months in hibernation did not conform to the hibernation durations in the literature, we inferred that the hibernation temperature threshold we hypothesized was in error and chose another temperature threshold that would produce a plausible hibernation duration. Once the quantified hibernation duration was in line with published values, we tentatively accepted the

hypothesized temperature threshold as plausible. Similarly, for species that are known or suspected to aestivate, we evaluated periods of extreme aridity in the same way.

By progressively flagging the first, second, and third months of greatest aridity or cold against the graphical background of the climate polygons, we inspected the aggregated 12-sided climate polygons to determine the number of arid or cold months that were largely confined to sparsely occupied climate space. In some cases we could identify no clear break between sparsely occupied and densely occupied climate space. In that case we relied on hibernation or aestivation *durations* from the literature. For example, Minton (1966) reported a four-month hibernation period for Indian Pythons in Pakistan; thus we evaluated alternate hypotheses of 3 (Clim3) or 4 (Clim4) months of hibernation.

For each hibernation hypothesis, we fit the closest convex polygon that included all points believed to represent climatic conditions experienced by active pythons (that is, excluding those points deemed hibernation or aestivation), and checked these climate hypotheses against field observations reported in the literature or by personal communication from appropriate experts.

For species that do not hibernate, we considered all points of the 12-sided polygons to represent climatically suitable conditions, and we fitted the closest convex polygon that enclosed all occupied climate space. We then mapped all locations of the United States that fell within minimum convex polygon's climate space and scored excluded localities by the feature (cold, hot, too wet, and too dry) that caused their exclusion. If there were climatically important disagreements among authorities regarding the native range boundaries (for example, Reticulated Python), we derived climate envelopes for both minimum and maximum estimates of the native range.

International Trade

To estimate the level of legal international trade in the giant constrictors, we queried the CITES (Convention on International Trade on Endangered Species) trade database (available at www.cites.org). All boas and pythons are listed under CITES in Appendixes I or II, and signatories to CITES are required to annually submit records of imports and exports of these species. We obtained CITES records of imports to the United States from 1977 through 2007 for the species of interest; results are presented in the Appendix and include records of over 1,100,000 individuals of these species imported to the United States during this period. Although we present records through 2007, the CITES website indicates that only records through 2005 are presently complete; more recent records should therefore not be considered definitive. We summed annual trade without regard to declarations of subspecies within any given species, as subspecific epithets are not required except for taxa listed under CITES Appendix I, and thus the subspecific identity of most individuals identified to species cannot be determined from the documentation. Many of these species are somewhat similar in appearance, and their taxonomy changes at alarmingly frequent intervals; such changes (for example, the splitting of the former *P. sebae* into *P. sebae* and *P. natalensis*) may not be reflected in import records. There are also LEMIS (Law Enforcement Management Information System) records from the U.S. Fish and Wildlife Service that provided some of the trade data we cite. However, there are many disagreements between LEMIS and CITES records, as has been documented for wildlife trade in general (Blundell and Mascia,

2005). Blundell and Mascia (2005) conclude that the records are “notoriously unreliable” for a host of reasons. We can confirm their unreliability, but know of no better source of information for quantifying the legal trade. Although the illegal trade in reptiles is considerable (Christy, 2008), we know of no means to quantify the level of the illegal trade and did not attempt to add the illegal trade volume to the CITES results. We are also chary of accepting as fact the declared country of origin for many records due to multiple anecdotal reports of cross-border smuggling and re-export of many of these taxa, so in this document we did not attempt to identify the main countries of origin or major trade routes. Accordingly, we consider the CITES import records to be the best available metric of the international trade in these species, but we recognize several potential shortcomings of the declared volume of trade.

Climate Matching

One controversial component of species-specific management is projection of the areas of the United States that are climatically suitable for each giant constrictor (section 10.2 of each species account). There are many proposed methods for “climate matching,” and we have chosen one that we believe most accurately portrays the regions of the country that may be at risk. However, there are other approaches, which have their own devotees. In particular, software designed for creating “Environmental Niche Models” are often used for climate matching, as the environmental niche data supplied with the software are primarily or exclusively climate measurements. In the following section of this chapter, we explain the method we used; in the concluding section of this chapter, we offer a brief defense of this selection. Please note that climate matching is a rapidly evolving field of endeavor and some methods will no doubt prove unreliable and be discarded in favor of methods not yet invented. We believe that current tools should be relied upon to give an indication of the relative size and location of the geographic area at risk, but should be used only with great circumspection to identify specific localities at risk.

We also applied our climate envelope hypotheses to current world climate data layers for monthly temperature and precipitation modeled from weather station data from around the world to a 1-km resolution (Hijmans and others, 2005) to verify if all occupied native range sites were identified as suitable.

Finally, we applied the identified climate envelopes to the current climate for the United States. We obtained average monthly precipitation (cm) and average monthly temperature (°C) data from the online Daymet database for the United States (<http://www.daymet.org>; Thornton and others, 1997). Thornton and others (1997) used daily observations from over 6,000 stations across the United States, collected from 1980 to 1997, to create the surfaces at a 1-km² resolution.

The equations defining the climate space minimum convex polygons were implemented using Visual Basic for Applications with ESRI’s ArcGIS 9.0 ArcObjects to produce the U.S. map of climate suitability. Where we considered alternative hibernation hypotheses, the final maps were compared using the Raster Calculator in ArcGIS to determine areas where the hibernation scenarios matched and differed.

Reasons for Preferring our Method to the use of Environmental Niche Models

Our method uses *a priori* identification of suitable climate metrics; Environmental Niche Models (see next paragraph) generally use automated selection of climate metrics. Both approaches incur the risk of selecting the wrong measure. We chose mean monthly precipitation and mean monthly temperature as adequately representing the climate attributes best associated with giant constrictor range limitations. The choice of monthly metrics insures that the climate will be suitable during every month of the active season, and that the inactive season length will not exceed that experienced in the native range. We do not believe that daily values are appropriate for snakes that have access to natural refugia, as the low metabolic demands of reptilian physiology, as well as the huge meals eaten by giant constrictors, insures that they do not need to venture out every day or even every week in order to maintain a net positive energy balance. We do not believe that annual climate averages are meaningful to a giant constrictor, as a low annual temperature average, for example, could reflect either continuously low temperatures (not acceptable to a giant constrictor) or warm summers and frigid winters (acceptable to hibernating species). A giant constrictor does not require that the conditions be continuously suitable, but conditions must be suitable for a sufficient number of months per year. Most species can probably aestivate for months to minimize exposure to seasonally inclement weather or food unavailability, but this is not known with assurance. While we chose mean monthly temperature and precipitation to represent the ecological conditions pertinent to giant constrictor population viability, there are many other climate metrics that could be used and may be plausible. For example, it may be that mean minimum January temperature is a better metric, or mean winter minimum, or mean dry season minimum or maximum, or extreme June maxima, number of frost-free days, or some other characterization. We could simply try every possibility until we discovered which one gave the most desired answer, but that would leave us guilty of the statistical error known as “fishing,” which often gives spurious correlations. If you try enough statistical tests, you will eventually discover one that “works,” but just by chance. Fishing is expressly invalid as a statistical procedure whenever the chosen metric was adopted *because* it gave the desired answer. *A priori* methods, in which the metrics are chosen for a biological reason in advance, without knowledge of the statistical outcome, are valuable because they offer statistical protection against spurious correlation, but they do not ordinarily discover the best possible fit between climate conditions and a species’ native range boundary.

A popular alternative to *a priori* identification of climate metrics is the use of automated programs that select the climate metrics on the basis of which metric gives the best fit to the native range distribution. Generically such programs are often called Environmental Niche Modeling programs, of which the current leader is MAXENT (Phillips and others, 2004, 2006; Phillips, 2008; see also BIOMOD: Thuiller, 2003). In the past GARP, BIOCLIM, CLIMEX were widely used (Nix, 1986; Sutherst and others, 1996, 1998; Stockwell and Peters, 1999; Peterson and Vieglais, 2001; Stockwell and others, 2005; Beaumont and others, 2005).

Environmental Niche Models were initially used to characterize the habitat features associated with plot data, wherein a particular species was encountered

(presence) or not (absence), so that nearby sites that were likely to support “presences” could be easily identified (geographic *interpolation*). For example, if one searched 50 plots in a nature reserve for the presence of one plant species, and the plant was found only on north-facing slopes at elevations between 2,000 and 2,100 m, it would be prudent to search for additional nearby populations of this plant on north-facing slopes at elevations of 2,000–2,100. This localized use is relatively robust against overfitting and lack of statistical independence among points, in that nearby sites are likely to have the same suite of statistical confounds and collinearity as did the original plots. Collinearity is said to exist when two variables covary; for example, mean January temperature and minimum January temperature covary among sites. Elevation and temperature have the same sort of collinearity. When interpolating geographically, the collinearity structure between various metrics remains largely the same and therefore doesn’t greatly bias the identification of suitable localities. However, if one chooses to use MAXENT to deduce climate drivers or *extrapolate* climate space from one part of the globe to another, the collinearity among climate attributes is very likely to have a different structure in the projection sites, and due to the overfitting that is characteristic of such programs (Beaumont and others, 2005), one is likely to get gross underprediction (too few sites match the *exact combination* of characters that was present in the source location) and erroneous identification of climate drivers (Randin and others, 2006). Using our plant example, it is possible that north-facing slopes at an elevation of 2,000–2,100 m at lat 40° N have a climate similar to a different locality (at say lat 50° N), where the same plants might be found on south-facing slopes at an elevation of 3,200–3,400 m. However, if the MAXENT model was calibrated on the original site only, it would overfit and fail to predict the species’ occurrence at the second site.

A strike against MAXENT (and comparable automated fitting algorithms, BIOCLIM, GARP, and others) is that it is methodologically opaque; the computations cannot be reproduced by hand, as the procedure is complex and not fully explained in any publication to date. Yet, it is so easy to use (software and data are available free on the internet, one isn’t responsible for identifying the biases in other peoples’ data, and it takes only a few minutes to crank out the maps) that many users accept the results and default settings without exploring the sensitivity of the result to the choices made. For example, we find MAXENT to be ultrasensitive to the boundary conditions set for selection of pseudo-absences. In several papers we have seen authors inappropriately take pseudo-absences from the entire rest of the globe. Others take them from unoccupied parts of entire continents. These gross distinctions provide really good apparent-model fits (see discussion of Area Under the Curve, or “AUC” below), but poor biological insight. The creator of MAXENT is clear, however (Phillips, 2008), that taking pseudo-absences from unrealistic localities is inappropriate; one should restrict pseudo-absences to those portions of the globe that are potentially occupiable by the species (that is, nearby and not separated from occupied range by dispersal barriers such as salt water, alpine zones, and so forth). If this is done, one gets much more realistic AUC values.

A brief digression into AUC. AUC is a good metric for evaluating models intended for binary judgments based on an uncertain threshold of a continuous variable. An example would be a model for estimating presence or absence (a binary trait) from a continuous habitat suitability score (for example, one that ranged from 1 to 10). Environmental Niche Models assume a single optimum condition for a species presence,

and every site is given a continuous score that reflects how close the site matches the deduced optimum. Yet a species can only be either present or absent. Perhaps “presences” would be best estimated for sites with habitat scores over 2.7, or maybe presences would be better discriminated using a threshold of 3.1. Different thresholds yield different binary selections, but which discrimination model works the best overall? AUC deals with this uncertainty by plotting the accumulation of true positives against false positives (that is, discrimination success) under *all* possible thresholds. The curve itself is called a “Receiver Operating Characteristic” or ROC curve; discrimination success is measured by the area under such an ROC curve, as the ROC curve bulges upward maximally when true positives most greatly exceed false positives (Hanley and McNeil, 1982). Thus the Area Under the Curve (AUC) is highest (on a scale of 0 to 1) for the mathematical models that discriminate best.

If the model is totally lacking in discriminatory power it will yield an AUC of 0.5 (false results accumulate as fast as true results); progressively better discriminators will have AUC values progressively closer to 1, and perfect reverse discrimination—for example, scoring all black sheep white—will give an AUC of zero. As computation of AUC is automated in MAXENT, and AUC often produces very satisfying values, it is widely reported. If the true negatives (that is, pseudo absences) are outrageous choices (for example, Siberia for tropical species), the model can be a really poor discriminator in delineating the native range, but it will encounter so few hard choices that it will yield a really good AUC. We’ve recently seen a suite of implausible models, none of which had a reported AUC of less than 0.96. AUC may depend more on the choice of pseudo-absences than on the fit of the model.

A very serious problem with MAXENT occurs when most of the native range is on islands (for example, Reticulated Python) from which there are no suitable adjoining land areas that are unoccupied. If the introduced or native range of a terrestrial species extends to saltwater or any other physical barrier to dispersal, there is no *climatic* interpretation to the range limit (absences should be given no statistical weight, Arntzen, 2006). All we can state is that the climate is suitable in the places where the species occurs. If the native range limit occurs somewhere without a dispersal barrier, we can infer that the species’ absence beyond the range limit is due to something, of which climate is a viable hypothesis.

MAXENT gives equal weight to each point. This is especially problematic if the data points were obtained from opportunistic museum collection localities (as is typically done for climate matching). Therefore, if museum collectors do not randomize their effort across the native range (and they don’t), MAXENT is biased by the same factors that bias the distribution of collecting locations. This is strikingly evident in many studies we have seen (for example, Stockwell and others, 2005) where major portions of a species’ range were undercollected and were therefore deemed unsuitable habitat by MAXENT, GARP, and so forth. Environmental Niche Models are often primarily inferring where collectors go to collect.

One reason why naïve application of MAXENT yields results with poor biological insight is that it automatically keeps adding more and more parameters as long as some improvement in the model fit can be obtained. Because each climate axis can be fit by any function (shape) that best matches the data set (*a posteriori* fitting), the model can include a potentially infinite number of parameters—even if the number of axes is

severely constrained (for example, five). This is a textbook case of statistical fishing, and it leads to overparameterization or overfitting. There are statistical tools that can be used to constrain the number of parameters (for example, *a priori* selection of hypotheses, parsimonious choice of function complexity, Akaike's Information Criterion; Burnham and Anderson, 2002), but in most geographic applications, these statistical protections are not invoked. Overfitting leads to underprediction, as is evident in many MAXENT-derived maps showing that parts (often large and important parts) of the occupied native range are projected to be unsuitable (for example, Pyron and others, 2008).

For an introduced population to survive and spread, the climate of the colonized site must be within the range of climate conditions under which the introduced species can survive and reproduce, *a necessary but not sufficient condition* (Guisan and Thuiller, 2005). Because population persistence is a complex interaction between the species and its predators, parasites, prey, competitors, dispersal barriers, and transient habitat conditions (Brown and others, 1996), the inferred climatic optima are context specific, not a single absolute optimum such as is computed by MAXENT. A climate that, on average, allowed a population to have a lambda of 0.98 in one place (a lambda slightly less than 1 indicates a population that is slowly disappearing) might sustain the same species in some other context (lambda = 1.01: a slowly increasing population). Thus we fundamentally are in pursuit of the relationship of climate to demographic persistence (lambda), a very complex, often indirect, and poorly understood function, which is likely to be limited by different conditions in different places. The climate-demography relation of an entire species cannot be adequately characterized as a single optimum in climate space. At the local scale, Environmental Niche Models work well because the demographic context is likely to be similar across the region used for small-scale geographic interpolation. Environmental Niche Models can produce wildly inaccurate results when applied to intercontinental extrapolation or deduction of climate drivers.

The ecological context prevailing in a species' native range is likely to differ from the context in its introduced range. Aside from habitat, topographic, and assemblage differences, an introduced species typically sheds many parasites and predators when it is translocated to a new environment. It is also likely to have passed through a genetic restriction, meaning the new population is not a carbon copy of the old gene pool and for this reason alone the outcome is likely to differ.

Given the contextual paradigm shift that may take place during a translocation from native to introduced range, our preference is that climate similarity be treated as the necessary but not sufficient condition (a one-sided prediction; on the correct side of a given criterion the climate is potentially suitable) rather than being rolled into an ecological black box to be inferred by automated data fitting (which assumes one optimal condition, with incremental degradation to either side of the optimum). That is, any occupied locality (whether native or introduced range), by definition, has a suitable climate; the suitable-climate envelope may be larger than the occupied climate space (indeed, additional climatically suitable but unoccupied localities are extremely likely for such poor dispersers as reptiles and amphibians), but the climate envelope cannot be smaller than that demonstrated by occupied areas. Some researchers distinguish a fundamental or potential niche (maximum occupiable climate space) from a realized niche (the actual climate space in a specific area, as constrained by biological factors such as dispersal barriers, predators, competitors, and so forth) (Guisan and Thuiller,

2005). Araujo and Pearson (2005) stated, “By relying on observed distributions (which inherently reflect multiple range determinants, both historical and ecological) to determine ecological requirements, this methodology is likely to underestimate the true range of climate variation that species are able to tolerate.”

If one accepts the *necessary but not sufficient* conceptualization of climate matching, the analytical goal would be to delineate the relevant climate characteristics that encompass all occupied range. The word “relevant” is included so as to omit climate characteristics that might apply to a particular locality but are not determining of the species’ presence. For example, elevation is sometimes included in climate matching algorithms, and it might correlate with a species’ boundary, but not determine it (perhaps temperature, which correlates with elevation, is determining). In another place, the temperature would still be determining, but the range limit would be at a different elevation. Inclusion of elevation in a climate-match model in this case would be an example of collinearity (temperature and elevation are *correlated*) and overfitting (because the collinearity is site-specific and may not extrapolate). When such an overfit model is projected to a different continent/context it gives an underprediction because the elevation would most likely be a mismatch.

An alternate to the necessary but not sufficient conceptualization is the black box approach, which holds that climate is a convenient proxy for many factors about habitat (prey abundance, vegetative structure of habitat, temperature tolerance, and so forth), and our analytical goal is to find the climate attributes that most closely correlate with the boundary of the occupied native range. Knowing the closest climatic correlate allows us to guess the likely spread of an invader without having to figure out the black box of habitat-species interactions. Unfortunately, a climate projection based on such a conceptualization will work well only if the demographically limiting factors in the native range are duplicated exactly in the introduced range.

In this study we do not use climate matching as a tool for determining which factors affect a species’ distribution; rather climate matching using plausible *a priori* climate axes provides one measure of the areas of the United States that may be at risk from a species invasion. Species with broad climate tolerances (for example, Indian Pythons) will exhibit a broader United States climate match than species with a narrow climate tolerance (for example, Reticulated Pythons). Such differences are visualized geographically by comparing maps in section 10.2 of the different species accounts. Demographically limiting factors that apply solely or primarily in the destination site alone will constrain actual range limits to less than that shown on the map, an example of overprediction. Conversely, demographically limiting factors that apply solely or primarily in the native range will induce underprediction in the map; thus the area actually at risk may be much larger than that shown. Current knowledge is insufficient to assess the relative probabilities of under- and overprediction of these maps. To the extent that all species accounts are vulnerable to the same magnitude of under- and overprediction, the maps can be profitably compared to infer the relative geographic risks associated with establishment in the United States.

Chapter Three–Synopsis of Eradication Tools

Introduction

The thrust of this risk assessment is to tabulate and assess the ecological and economic costs that could result from establishment in the United States of selected giant constrictors, so as to inform efforts to *prevent* that establishment. Why then is this chapter devoted to control of established snake populations rather than prevention of their arrival? The biodiversity losses and economic costs attributable to colonization of a mainland United States site by an invasive giant snake depend crucially on whether it is practical to eliminate (eradicate) the colonization through control measures (Bomford, 2003). If the cost of eradication is high, the penalty for failure to prevent a colonization includes the need to mount an expensive eradication program. If the cost of eradication is relatively low and new colonizations can be routinely eliminated, a higher risk of colonization may be tolerable. If eradication is not possible (or the cost is exorbitant), the risk of colonization may not be acceptable, even if the known impacts of an introduction are minor or few. Thus any risk assessment for a potential species introduction must consider the costs for eradicating unwanted colonizations, and the prospects that such an effort would be successful (Bomford, 2003).

The short answer is that no introduced populations of reptiles have been intentionally eradicated anywhere on Earth to the best of our knowledge (F. Kraus, personal commun., 2008). Thus, our toolbox of *proven* techniques is empty. One would have little confidence that a snake colonization could be eliminated if one chose to do so. However, few wildlife managers have made the decision to attempt eradication, and until recently little research effort was devoted to identifying and perfecting reptile eradication techniques (Rodda and others, 1999d). Based on the literature and our experience with the Brown Treesnake on Guam, local eradication (that is, in small areas) is possible, but may be costly. The prospects for success are strongly dependent on the geographic extent of the population (Rodda and others, 1999a); most observers feel that eradication of a large continental population (for example, Burmese Pythons in Florida) is impractical, but opinions on the level of difficulty vary. Certainly we have no examples to draw from, but ongoing research is producing a steady stream of innovations that might be tapped. Here we review potential techniques for reptile eradication.

Note that this chapter does not attempt to review or even consider management actions short of eradication. In the case of an established population, it may be prudent to undertake a variety of management actions short of eradication. We know that rats are controlled in every city in the world, even though there is no hope of eradicating rats from those cities or the world. Pythons may be controllable in the vicinity of bird rookeries for example, even if they cannot be eradicated from all of Florida. We may be able to protect isolated places like the Lower Florida Keys from giant constrictors. However, management recommendations for that sort of local control requires a careful study of local conditions and careful application of management expertise as it applies to

the particular constrictor species in question. Such a course of action could be described and evaluated in a management plan for a particular situation, but for the purposes of this work, we will limit the focus to whether and under what circumstances it is likely to be practical to *eradicate* a giant constrictor population.

Management commonalities among giant constrictors. In this synopsis of eradication tools, we do not provide separate analyses for the various giant constrictor species, as there is no management literature or experience upon which to base species distinctions. Furthermore, the giant constrictors share a suite of key traits that dictate similar eradication practices (see Epilogue in Rodda and others, 1999d, for examples of the relevance of such traits). For example, giant constrictors are notoriously cryptic and often hidden and immobile and are therefore difficult to detect. An invader such as an ibis is conspicuously colored and moves often; therefore it is very easy to spot if you are near it (that is, detection probability near 1), promoting effective control by shooting. In contrast, giant constrictors are routinely hidden from view inside soil, vegetation, or murky water (that is, detection probability often <0.001). The giant constrictors all rely heavily on ambush predation; thus control tools that rely on the snakes' movements (for example, traps) may be limited in application. The giant constrictors are all strongly attracted to endothermic prey and are likely to be vulnerable to similar endothermic food-based attractants (for traps or toxicants). The giant constrictors all eat infrequently, complicating their control by food-based attractants. Thus given the similarities in their natural histories, we anticipate that a similar suite of tools would be used for all of the giant constrictors, with accommodation for the more aquatic habits of the anacondas (though all of the giant constrictors spend time in aquatic environments, and those environments must be an important component of any eradication).

Introduction to primary eradication tools. Because there is no literature on eradication techniques or even control techniques for giant constrictors, we must cast a taxonomically wider net to find examples of control tools. Witmer and others (2007) reviewed all control tools for invasive terrestrial vertebrates in the United States. Veitch and Bell (1990) reviewed tools used for invasive endotherms in New Zealand. Both reviews note that the available tools are strongly dependent on taxon-specific attributes; Witmer and others (2007) list only four tools for invasive reptiles and amphibians: trapping, toxicants, dogs, and barriers. Barriers are used primarily to contain dispersal of an expanding population or prevent recolonization of areas already cleared of invaders, whereas trapping and toxicants are devices to collect targets or kill them. Dogs are not usually the direct agents of lethal control, but are used to enhance detection and localization of reptiles that can then be killed by some other method. Thus we can group tools on the basis of whether they limit spread (barriers), localize the targets (dogs, traps), or kill the targets (toxicants). To this list of four tools should be added visual searching by humans, which is used extensively for many herpetofauna, including Brown Treesnakes (Rodda and others, 1998; Campbell and others, 1999; Vice and Pitzler, 2002). Searching for many species, especially snakes, can be done at night with the aid of electric lights, and such direct searching is therefore often called spotlighting (Engeman and Vice, 2001). While dedicated searches are usually far more effective per person-hour than opportunistic detections by the general public, the general public has a vastly greater number of eyes with which to make detections. Thus we will discuss enlisting help from the general public as a tool for greatly increasing the number of detections.

Introduction to secondary eradication tools. In addition to these five primary eradication tools are several variations and some concepts that may have value in control of invasive snakes. Witmer and others (2007) mention: (1) Judas animals, (2) introduced predators, (3) habitat manipulation, (4) bounties, (5) frightening devices, (6) reproduction inhibition, and (7) egg/nest destruction. Pheromonal attractants (8) have frequently been mentioned as a tool for increasing the species specificity of trapping and toxicants. Introduced predators are an example of biocontrol, but diseases and parasites are another type of biocontrol that might be used to reduce (but not likely eradicate) an introduced snake population (Simberloff, 2001). We will consider both introduced predators (macropredators) and micropredators (diseases and parasites) in the section on biocontrol. We will review each tool in turn.

Standard of success. In this review, our standard of success is whether the tool would enable an incipient colonization to be eradicated. This is not a unitary threshold, as populations differ appreciably in the geographic extent that is infested at the time that the population is discovered or control is attempted. What works on a 2-ha colonization may not succeed with a 20,000-ha colonization. Thus we will also discuss in a relative way the geographic scale over which a control tool is likely to be successful (absolute geographic determinations must await more information). Keep in mind that the primary challenge of an eradication is not achieving a high body count or rapidly killing the bulk of the population, but getting to the last individual. Any eradication program that kills only the accessible animals, or the feeding ones, or the adults, or all but the largest few individuals will be an eradication failure. The individual that is the least accessible and the least vulnerable must be the defining focus of an eradication program—a standard that is very difficult to meet.

One *practical* concern in the application of snake control tools is fire. Control measures that involve the long-term placement in the field of control devices (especially traps, toxicant bait stations, and barriers) can be incinerated by a wild fire. Fire is not likely to eradicate any giant constrictor, as many individuals will escape the fire flames by refuging underground or in water, but plastic barriers or bait stations and trap attractants (such as live rats) may be impractical to relocate in advance of a rapidly spreading fire. This factor should be kept in mind when contemplating such devices in fire-prone areas.

Primary Tools

Primary Tool I—Limit Spread: Barriers

One can envision barriers as being physical (a fence), chemical (repellents), ecological (adverse habitat barrier), or a gauntlet of control tools (for example, five rings of toxicants/traps) that minimize the chances of a snake successfully passing through. Physical barriers are used extensively in the Ryukyu Islands to aid trap capture of Habu, *Protobothrops flavoviridis* (Shiroma and Akamine, 1999). Physical barriers have been used for Brown Treesnakes, primarily to minimize the contamination of cargo or enhance detection of snakes in potentially contaminated cargo leaving Guam (Perry and others, 1998). However, the large size of the giant constrictors suggests that the risk of undetected snakes in cargo will be much lower for the giant constrictors than for the

relatively diminutive Brown Treesnake. Numerous proposals have been floated for use on Guam of Brown Treesnake barriers to prevent the recolonization of natural areas from which Brown Treesnakes have been eliminated for restoration of endangered prey species (Rodda and others, 1999a). In this application, barriers would enclose a patch of habitat from which the extant population of invasive snakes can be eliminated. However, for giant constrictors in the United States mainland, barriers have been suggested for minimizing spread of the constrictors to previously uncolonized habitat (for example, protect Florida Keys or prevent northward spread of Burmese Pythons). Although the current management focus for giant constrictors emphasizes prevention of spread to novel areas, management emphasis may shift to local eradication in a fenced reserve if nationwide eradication proves impossible.

Are barriers effective, and if so, at what cost? Physical Brown Treesnake barriers have been extensively tested and can be effective (Perry and others, 1998, 2001), but other types of barriers (chemical, ecological, and control) have not been tested for Brown Treesnakes. No barriers of any type are known for giant constrictors, but the Brown Treesnake experience may be of value in anticipating the magnitude of costs and the circumstances under which physical barriers would be effective. Brown Treesnakes are much more slender than the giant constrictors; thus Brown Treesnakes can cantilever a higher proportion of their body across gaps (Jayne and Riley, 2007). Nonetheless, the reach of an ascending snake is primarily dependent on its length; longer snakes can ascend further. In this regard the longer and more slender Reticulated Python is apt to be a particular challenge for barrier design, whereas the shorter (Boa Constrictor) or more heavily bodied species (anacondas) would be less of a challenge. Species-specific testing would be needed, but it might be a reasonable first approximation to assume that a snake can extend itself vertically between one-half and three-fourths of its body length (the three-fourths value is based on Brown Treesnakes).

Left to their own devices, plants will grow onto a barrier and render it ineffective; thus, control of encroaching plants is a significant maintenance cost for all barriers (Perry and others, 1998, 2001). Maintenance costs can easily exceed construction costs over the life of a barrier; the ratio of these costs will depend on details of the barrier implementation.

Four environmental features are notable for sharply raising the construction cost of Brown Treesnake barriers: (1) salt content of the air, (2) hurricanes, (3) surface-water flow, and (4) steep terrain. Barriers can be established for areas lacking these attributes for relatively low cost (exact cost strongly dependent on size of area and other features) using metal mesh barriers. However, in areas with salty air, the metal mesh rusts within a few years. Hurricane frequency is very high on Guam, but hurricanes are also a consideration throughout the southeastern United States. If the purpose of a barrier is to keep exotic snakes out of a nature preserve permanently, the barrier must be designed to sustain the worst weather possible at the site, a costly consideration. Barriers can be rebuilt after a hurricane, but it is highly unlikely that they could be rebuilt fast enough to prevent surrounding snakes from penetrating the area and requiring an expensive reextermination. Surface-water flow is a dominant environmental characteristic of the south Florida areas that are most likely a point of original colonization for all of the giant constrictors. Conversely, steep terrain will rarely obstruct barrier construction in Florida.

In fire-prone areas such as the Everglades, it might be necessary to limit barrier designs to those using only nonflammable materials.

All of the giant constrictors swim (see Bioprofiles) and likely would be willing to enter water to bypass a barrier that terminated at the water's edge. There are no known snake barrier designs that prevent this (this is also a chronic problem for peninsular barriers for invasive mammals in New Zealand; see problems reported in Lovegrove and others, 2002).

Short lengths of hurricane-resistant physical barriers for Brown Treesnakes have been designed and installed in the Mariana Islands, but these routinely incur construction costs of >\$500 per linear meter (unpub. data). Presumably barriers for giant constrictors would be substantially more expensive (due to the greater height requirement), and costs could balloon further if the barrier needed to cope with surface-water flow. Barriers will interfere with the movement some non-target species. Thus physical barriers for giant constrictors are probably limited to protection of relatively small geographic areas. There are ample opportunities for research to identify and develop more cost effective physical barriers for giant constrictors, as well as to test chemical, ecological, and control tool barriers for these species.

Primary Tool IIa—Localize Targets: Visual Searching

Direct searching is the most widely used tool for locating reptiles and amphibians (Guyer and others, in press). Effective traps or toxicants have not been developed for most herpetofauna and thus visual searching is often the only tool available. For those species for which effective traps have been developed, such as for Brown Treesnakes or Habu (Rodda and others, 1999d), trapping tends to supersede visual searching as the most effective tool. However, visual searching for Brown Treesnakes remains the primary detection method under three circumstances: (1) on perimeter fences surrounding high value areas such as ports and airports (Vice and Pitzler, 2002), (2) for juvenile Brown Treesnakes (which are not easily trapped: Rodda and others, 2007), and (3) in high-prey environments, where traps work poorly (for example, on the island of Saipan, where prey have not yet been depleted by Brown Treesnakes; Gragg and others, 2007). As the two latter circumstances are defined by the capabilities (or lack thereof) of traps, and traps have not been developed for giant constrictors, it is unknown whether the same logic would apply to control of giant constrictors. Snakes climbing chain-link fences are relatively conspicuous, which is the attraction of that particular implementation for Brown Treesnakes, but chain-link fences are infrequent in Florida and many other mainland United States sites, and we expect relatively little use by the comparatively heavy-bodied giant constrictors.

It is notable that most giant constrictors are not systematically collected in their native ranges; most are taken when encountered by chance (Shine and others, 1998a). Thus there is not a body of native-range expertise to tap for refining visual search techniques.

Visual searching is very labor intensive and therefore costly, but its application to giant constrictors may be more constrained by limitations on physical access for visual searchers than by labor cost. The three primary challenges in Florida (the most likely site of colonization) are inundation, obstructing vegetation, and private property. Whereas the site of original colonization of Burmese Pythons was Everglades National Park (thus

private property is not an important factor in visual searching the area); dense low-level vegetation and chronic inundation block effective searching of most Everglades habitat. This is well illustrated by the low number of visual detections associated with the pythons that were known (2005–2008) to be in an area by virtue of their radiotransmitter signal. In 14.4 radiotelemetered python-years, we are aware of only four detections unaided by use of the radio signal (S. Snow, pers. commun., 2008). During the radiotracking period, there were visitors and searchers in a position to see pythons in the area every day. Despite this human presence, the average python was detected by searchers or the public about once per three years (4/5,270 days or 1/1,318 days). This implies that on any given day, the probability of anyone finding an arbitrary python without the assistance of radiotelemetry is only about one out of 1,318 days or 0.001 or 0.1 percent. This value should be considered trustworthy only to order of magnitude, but the order of magnitude has important implications for interpreting sighting rates and projecting control effectiveness. Whereas some of the pythons were undetected because no one was searching for them, and a few others were near a searcher but undetected due to obscuring vegetation, the vast majority of nondetections occurred simply because pythons rarely visit levees, roads or road berms, trails, or other locations frequented by humans (Mazzotti and others, unpub. data, 2009). In most cases a python went undetected simply because it was too far from any dry land or open water to be seen by any observer walking, driving, or boating.

Radiotelemetric data are not available to judge this phenomenon in the other giant constrictor species, although visual detections of insular Boa Constrictors in Honduras are biased towards microhabitats that are seldom used by telemetered individuals (Reed and others, 2007). The behavior of anacondas and Reticulated Pythons suggests that they would be even less inclined to spend time on land (see Bioprofiles). The other pythons and boas are less well known in this regard, though Boa Constrictors in some parts of their native range have little association with water (chapter Seven). Thus more information is needed to determine detection probabilities across a range of species and habitat types.

Extended wavelength searching. A concept that is intriguing to some researchers is that visual detection rates have the potential to be greatly enhanced through technological means, such as providing different wavelengths of nighttime illumination or extending human visual perception with tools such as FLIR (Forward Looking InfraRed) designed to detect infrared radiation (heat) or other special value wavelengths (R. Engeman, pers. commun., 2008). The prospects for extended wavelengths to enhance visual detection are highly sensitive to the reason for lack of visual detection with ordinary light. If the targets are within line of sight but are routinely overlooked (as a result of the snake's crypsis), a potentially productive approach might be technological aids to visual detection such as FLIR, but if the cause of the snakes' lack of detection is intervening vegetation or water, extended-spectrum aids would be of no use.

The use of infrared (heat) detection has not yet been tested on giant constrictors in the field. The fundamental problem with this approach is that nonbrooding giant constrictors are ectothermic, meaning that they do not generate appreciable heat. Whereas humans and other endothermic creatures are readily detected by the greater heat production of their surfaces relative to background, snakes will differ from background radiation levels only if they have recently moved from a medium with a different

temperature, or absorb solar radiation at a rate greater than background. Thus if a basking snake entered cooler water, it would present a thermal contrast with its surroundings (though not detectable with infrared sensing equipment once the snake submerged). Conversely, if a snake emerged from cooler water into vegetation or onto ground heated by sunshine, it would present a cooler signal than its surroundings, until thermal equilibrium was achieved (at which point the snake would disappear from a pure thermal image). The attainment of thermal equilibrium is a function of the mass of the snake and its thermal flux, which is itself a function of the starting temperature differential (Christy and others, 2007). A very large python would take hours to approach equilibrium if the starting temperature differential was large (for example, emerging from cold late-winter water and basking in strong sunlight), but a small snake would be close to equilibrium within a few minutes under the small environmental temperature differences that prevail at night and through much of the year. Because giant constrictors will generally attempt to achieve higher temperatures in the United States mainland in the winter, the best opportunities for thermal contrast are likely to occur at mid-morning with basking winter snakes. However, visual detection at mid-morning is already near maximal due to excellent visible-wavelength lighting conditions. In the evening, giant constrictors are apt to be in the water to take advantage of the daytime heat that is retained longer by the higher thermal mass of water. As a submerged snake is not detectable with infrared sensing equipment, the opportunities for enhanced detection at night seem pretty limited.

There are practical difficulties in using FLIR equipment to spot giant constrictors in daylight. Recall that snakes that have reached thermal equilibrium are not visible to FLIR and are best seen with unaided eyes. Snakes that have just emerged into sunlight from cooler water and those that have absorbed a lot of solar radiation and are basking next to damp (evapotranspiring) vegetation are maximally visible to FLIR. One presumes that the searcher wishes to detect all classes of snakes (those just arrived, those at equilibrium, and any that are hotter than background). This implies that detecting all snakes would require scanning each scene once with FLIR and once without. A plausible solution involves using two observers (each dedicated to their own wavelength—and a driver if conducted from a vehicle), but this increases costs over using a single observer. It remains to be seen if such an arrangement would be more cost-effective than using the excellent visible-wavelength light available at midday.

Brooding pythons showing shivering thermogenesis should be thermally detectable when they are shivering (among our giant constrictors, only *P. molurus* unequivocally exhibits shivering thermogenesis; Ellis and Chappell, 1987). Unfortunately, Burmese Pythons shiver only under certain circumstances. For example, the female may shiver if her clutch is somewhat cool, but not excessively so—if excessively so, the brooding mother gives up attempting to warm the eggs (Vinegar and others, 1970). We have no information on how often those circumstances would apply in the United States mainland. The more likely impediment to the use of thermal imaging, however, is that brooding pythons are usually hidden under dense and thick vegetative cover. Thus, there would most likely be few or no visual angles from which the temperature differential could be detected. Overall, the prospects for enhanced detection through infrared signals are likely to have strong seasonal and temporal limits when applied to giant constrictors in the United States mainland.

The relative difficulty of detecting giant pythons has vital implications for controlling the population using either trained searchers or volunteers. If the average per-day-detectability of a python is 0.001 and there is no heterogeneity among individuals in their detectability, only a very small proportion of the population would be removed with even a very substantial searching effort. With the number of searchers plausibly available for python control, the rate of removal would be so low that natural recruitment (roughly 50 eggs per female per year; see individual Bioprofiles) would presumably exceed the capture rate.

An additional inference from so low a detection rate is that one should generally assume that roughly 1,000 pythons are present for each one detected in habitats similar to the Everglades. This should not be taken to imply that any individual sighting represents a phalanx of undetected comrades; *on average* there will be many undetected individuals (to the nearest order of magnitude, about 1,000) for each one detected. Naturally, the exact detection probability is unknown and would presumably increase in areas that are more accessible (for example, the rangelands and agricultural lands of Central Florida), but the realized detectability may be lower on private lands that do not have the large number of visitors and searchers found in the Everglades region. The point is not to focus on the exact value, but to appreciate that all searching activity is seriously limited by the low visibility of snakes, even giant constrictors, in low visibility and inaccessible environments.

Detecting a giant constrictor is a key step in killing it, but one does need to consider the challenges of capturing a snake that has been seen but not yet secured. Our experience in Florida is largely limited to Burmese Pythons and Boa Constrictors, both of which are remarkably easy to subdue unless they are very large or poised to flee into deep murky water. They are “easy” in the sense that when on land they generally do not bolt in response to visual contact with a searcher (in contrast to racers and other snakes whose predator defense hinges on rapid flight). Though spectacularly muscular, most giant constrictors do not move quickly at the sight of a human. In many cases they will hold until they or the surrounding vegetation is contacted.

For safety reasons, no solitary searcher should touch a giant constrictor, but two people can safely handle giant constrictors up to about 3–4 m in total length. Larger snakes warrant additional handlers, though the basic approach is the same (noose or obtain a grip behind head, and use additional handlers to restrain coils). Several herpetoculturists have provided advice on the safe number of handlers needed for giant constrictors of various sizes (Barker and Barker, 1997; de Vosjoli and Klingenberg, 2005). The latter paper cites with approval a guideline from the American Federation of Herpetoculturists that solitary individuals should attempt handling only giant constrictors less than 2.4 m (8 ft) total length, with an additional person present for each additional 1.2 m (4 ft) in total length. These standards comport well with our personal experience.

Bites from giant constrictors can do considerable tissue damage (see a particularly ghastly wound from a Reticulated Python in Barker and Barker, 1997), so care is needed to avoid their many sharply recurved teeth. Rapid flight is rarely a problem with solitary Burmese Pythons on land. Individuals in shallow water can often be handled in the same way, with the additional challenge of determining where the head is located, as it is often obscured by murky water or vegetation. Capture of giant constrictors that are swimming

in deep water is probably best handled by noosing with the support of sufficient handlers to keep the struggling animal from endangering the stability of the handlers or their boat.

Shooting. Shooting has often been suggested for safety in capturing and restraining giant constrictors. Shooting is most attractive when the target is readily detectable but will not easily allow a searcher to get close enough to permit hand capture or noosing. Thus shooting is often used for ungulates, birds, and carnivores, but is rarely used for small mammals (for example, rodents, with the exception of nutria), reptiles, or amphibians (Witmer and others, 2007). Shooting is often restricted in National Parks or urban settings for reasons of safety or visitor equanimity. Shooting may be warranted for reptiles that are particularly dangerous to touch (for example, venomous snakes or crocodilians); very large individuals of the giant constrictor species will fall into the dangerous-to-touch category. An appreciable drawback of reliance on firearms is the restriction to ricochet-safe areas and to use trained shooters. Mortally wounded reptiles (even those shot through the head) are notorious for crawling some distance before dying, and the head of a giant constrictor is a relatively small target; shooting can be an unreliable method of euthanasia. Shooting with a stun gun is used in Australia to incapacitate large crocodilians and probably could be used to advantage on giant constrictors as well (G. Zug, pers. commun., 2009).

Primary Tool IIb—Localize Targets: Public Reporting

Trained searchers are the best for visual searching, but there are comparatively few of them (Stanford and Rodda, 2007). The general public is, or can be, well informed on the significance of sighting giant constrictors, and most people will eagerly submit such information to responsible authorities. Opportunistic sightings are presently being reported to the Python hotline in southern Florida (S. Snow: 305 815-2080). Hotlines of this sort have proven to be of enormous value in locating Brown Treesnakes on islands where Brown Treesnakes are not established (Hawley, 2007). In addition, volunteers can be induced to provide systematic searches in areas of special interest. Both approaches (opportunistic detections and volunteer searches) are powerful tools that not only address a crucial information need, but also generate interest and support among the public.

The pool of volunteers is not unlimited in number or stamina, however. The key is to ensure that public reporting is used *where* it is most effective. Maximal efficacy is likely to occur in areas where sightings are so rare that early detection is at a premium, and too few professional searchers are available to address the need. Thus opportunistic call-ins and volunteer searches are most productively steered towards areas at the fringe of the known occupied range of an invasive giant constrictor.

This focus on peripheral areas may conflict with the desires of volunteers. Volunteers are most enthusiastic about searches that result in many captures. Low reward rate is well known to diminish the efficacy of searchers, even trained searchers (Henke, 1998). The Brown Treesnake Rapid Response Team uses a variety of gambits to minimize the inherent problem of low reward rate; for example, the placement of physical target models (rubber snakes) in the search area with rewards for those who detect them. Volunteers also participate in training workshops conducted in high-target-density areas, with concomitant high-reward rates (Stanford and Rodda, 2007). Another approach is to ask the searchers to report other species of interest. In Florida, for example, searchers could be asked to report all snakes seen, so that the searchers' minds

stay focused on a vision of a slender cryptic reptile in the vegetation, while providing valuable baseline data on encounter rates with competing species at risk.

One would expect that enthusiasm for volunteer searches would be highest in areas where the presence of the snakes is novel. As the population of invaders becomes better established, one would expect the pool of volunteers to wane. Unlike bird watching, which is an established form of recreation often conducted from the comfort of an automobile, searching for dangerous snakes in a swamp at night has fewer steadfast devotees. During a high-profile snake hunting contest conducted on Guam at the peak of the Brown Treesnake irruption, a fully loaded four-wheel-drive pickup truck was awarded to the duo who collected the most snakes in one month (Rodda and others, 1998, 1999e). Out of a human population of more than 100,000 potential searchers, hundreds stepped forward to volunteer for snake searching, but at the end of the month 85 percent of the snakes had been brought in by just three pairs. The ecological consequence of this contest was that the island's snake population was reduced by only an estimated 0.2 percent (Rodda and others, 1998, 1999e).

Another consideration on the use of volunteers is that unlike Brown Treesnakes, giant constrictors are potentially dangerous to hunters, and misidentification of snake species in the southern United States can lead to fatalities. Legal liabilities need to be addressed forthrightly and in advance. Also, if volunteers are to be used in nature reserves (such as National Parks), some mechanism needs to be in place to ensure that volunteers do not collect native species opportunistically while they are on "patrol."

In summary, hunting for giant constrictors by sight probably offers the best opportunity to involve the public in reporting new locations for a spreading population. However, the low detectability of giant constrictor snakes in heavily vegetated environments (especially in the southeastern United States) probably precludes use of this tool for eradication. Searching may yet prove to be an important component for local control, especially in high visibility environments such as mowed grass on public property. Research opportunities exist to enhance the effectiveness of visual searching by new optical tools, careful selection of searching times and conditions (for example, only on days colder than X degree in sites with abundant basking sites, and so forth.), and detailed knowledge of the behavior of snakes with regard to their visibility.

Primary Tool III—Localize Targets: Trapping

In combination with toxicants, trapping is the backbone of control for most secretive animals (Veitch and Bell, 1990; Witmer and others, 2007). The majority of Brown Treesnakes are taken by traps (Vice and Pitzler, 2002). The vast majority of invasive rodents are taken with toxicants (Veitch and Clout, 2002). As both tools rely on food-based attractants, at least as now operationally deployed for snakes, the primary difference is that traps provide greater opportunity for the release of non-target species, but traps tend to be more expensive to build, deploy, and maintain.

The primary drawback for trap control of giant constrictor snakes is that there are not yet any designs for giant constrictor snake traps that have demonstrated effectiveness. A variety of ad hoc designs have been reported in the literature, but their effectiveness has neither been demonstrated nor quantified (for example, Auliya, 2006). Thus they may or may not be practical. Though traps have proven adequate for local eradication of Brown Treesnakes (Campbell, 1996), Brown Treesnake traps suffer from inability to

capture juvenile snakes (Rodda and others, 2007; Tyrrell and others, 2009). Thus discovery of an effective giant constrictor trap design does not guarantee that traps can be used efficiently for eradication (which requires the removal of all individuals).

The scope for improvement of giant constrictor traps is probably substantial, as the capture rate of Brown Treesnake traps was improved by about two orders of magnitude during research on that tool (Rodda and others, 1999b). However, there are several additional challenges associated with trapping giant constrictors. Most obviously, the traps must be much larger; this implies significantly greater challenges in fabricating, moving, deploying, and storing giant constrictor traps. Also, Guam is largely upland habitat, with no inundation at trap locations. Traps for use in South Florida, or for any species that is often found in water (that is, most of the giant constrictors) would need to accommodate a wide variety of water depths and periods of inundation. Giant constrictor traps used in the mainland United States would need to provide avenues for escape or release of the many species of non-targets present in the focal area. Among the key non-targets are rats (which are sometimes endangered and in all cases prone to damaging traps through gnawing), alligators (somewhat dangerous to remove from traps, and inclined to damage traps when trying to escape), raccoons (notorious for dexterous destructiveness), large species of protected snakes such as Indigo Snakes (cannot be automatically released without allowing small giant constrictors to leave), venomous snakes (dangerous), and birds (cannot be left in traps for extended periods). However, if traps are checked regularly (for example, daily), it should be relatively straightforward to release the non-targets safely.

A key consideration for traps is that giant constrictors appear to be primarily sit-and-wait or ambush foragers (Shiroma, 1999, discusses trapping implications). A fundamental premise of detection is that moving targets are best detected with stationary devices and stationary targets are best detected with moving devices (Koopman, 1946). To the extent that giant constrictors sit and wait for long periods of time, they may be ill-suited to control with stationary traps. However, some traps are designed to force the occasional movements of a target into the vicinity of a trap. When applied to reptiles, the forcing device is called a drift fence, and it works for many species because the moving animal tends to follow the line of the fence rather than change to an entirely new trajectory. Basically the traps are placed alongside long stretches of barrier fencing; a snake that runs into the barrier slithers along the barrier until it runs into a food-attraction or barrier trap, which effectively collects the snakes from an area defined by the length of the fence. As fences can be made very long, drift-fence traps can be highly effective, as they are for the sit-and-wait Habu (for example, Hayashi and others, 1999). Whether this concept will work for giant constrictors remains to be seen (anecdotal evidence suggests that this concept does not work for Brown Treesnakes; our unpub. data).

The primary limitation of traps as a large-scale management tool is that they provide no economies of scale. Two hundred traps cost about twice as much to run as one hundred traps, largely because the cost is mostly the labor of baiting, checking, and maintaining the traps. This limits the size of the area that can be controlled with trapping. We are aware of no snake trapping operations that exceed a few thousand traps. The size of the area covered by a few thousand traps depends on trap spacing. The successful use of traps for sit-and-wait snakes has required very short intertrap spacings, such as 10 m (presumably because sit-and-wait snakes move only short distances per day; see Shiroma

and Akamine, 1999; Katsuren and others, 1999). At 10-m spacing, each hectare requires 100 traps (Shiroma, 1999, suggests 200 traps per hectare), and thus 1,000 traps would service about 10 ha (about one-twenty-fifth of a square mile). In contrast, Brown Treesnake traps are fully effective when deployed at about 16/ha or one-eighth the trap density of Habu traps. In summary, traps may be a cost effective tool for local control of invasive giant constrictors, but they need R&D and probably cannot be used for eradication of extensive colonizations.

Primary Tool IV—Localize Targets: Detector Dogs

Detector dogs are widely used for transportation system interdiction of biological agents, including invasive snakes (Shiroma and Ukuta, 1999; Engeman and others, 2002). We can call such dogs cargo-sniffing dogs. Dogs are often used as an adjunct to hunting ungulates such as pigs or goats (hunting dogs). However, dogs are rarely used for landscape control of invasive reptiles, with the exception of some experimental use for Brown Treesnakes (USGS unpub. data) and Habu (Shiroma and Ukuta, 1999). Our experience with them is that they are reasonably good at finding Brown Treesnakes even when the snake is too high in the trees for the dog to physically contact, but there are challenges in searching dense vegetation with detector dogs (we have not attempted to locate snakes in association with water, but doubt its practicality for that application). Overall, USGS detector dogs on Guam have detected a known radiotelemetered snake in a defined search plot in about 35 percent of our trials. This indicates that a substantial fraction of the snakes was not located, but that dog teams are far more effective than human searchers (humans detect 7 percent of available snakes per search at 16-m search-transect spacing on Guam; Christy and others, unpub. data). Thus there may be a potent role for detector dogs in locating giant constrictors, at least in appropriately accessible habitat. This discussion is focused on dogs, but there is no compelling reason why other types of sniffer animals could not be used. However, the limitations on detector dogs would apply to a wide variety of other sniffer species as well (see below).

A likely drawback of sniffer dog detection of giant constrictors is that the dogs, which are remarkably expensive to train and maintain, could be killed by their targets. All of the giant constrictors have demonstrated an appetite for dogs. Even if an attempted ingestion were to be unsuccessful, the dog could become reluctant to hunt for giant constrictors if it had a bad experience with one. This was the outcome of a detector dog encounter with a Habu (Shiroma and Ukuta, 1999); after getting bitten it was unwilling to hunt snakes. Perhaps a large dog could be trained to signal the presence of a giant constrictor at a safe distance. Considering the various limitations on use of a sniffer dog for detection of giant constrictors in the United States (such as limited searchable habitat, time of day, size of snake, and so forth), it seems unlikely that detector dogs would play a large role in the landscape-level control of a giant constrictor. Where they might be indispensable is in detection of the last few snakes in an incipient colonization that was detected early enough to carry out an eradication by other means, or perhaps when attempting to define the limits of the expansion of a population. Training of a sniffer dog requires a substantial commitment of resources for facilities, and human and dog training. If the dog were to be used to determine if an eradication had been completed, the dog would have to be able to distinguish the target giant constrictor species from native snakes (false positives are unacceptable when the question is whether any of the targets

remain). Experience with detector dogs indicates that this capability is well within a good dog's abilities, but requires lengthy training (probably >1 yr). Training of detector dogs is unlikely to be justifiable for a giant constrictor species that is not yet known to be present in the United States. If training was delayed until the population was unequivocally established, the requisite training and testing time might be too much for the dog team to be available for the timely eradication of an incipient population. These factors warrant due consideration in any plan to use detector dogs for giant constrictor control.

Primary Tool V–Kill Unlocalized Snakes: Toxicants

Toxicants are the premier tool for eradicating introduced rodents (Wodzicki, 1978; Veitch and Bell, 1990), and they have also been used for invasive birds, mammals, and carnivores (Witmer and others, 2007). Rodents are particularly attractive targets for toxicants because rodents gnaw impulsively, some species cannot regurgitate, and their small size and high metabolism dictate nearly continuous feeding (Wodzicki, 1978). Snakes, on the other hand, often volunteer to go without eating for months at a time; this is especially true of giant constrictors (see Bioprofiles; Murphy and Henderson, 1997, recount multi-year fasts among most of the giant constrictors). Toxicants (acetaminophen) have been successfully applied on a local scale for Brown Treesnakes, and ongoing work may perfect aerial application for landscape scale use on Guam (Savarie and others, 2007). However, there are few or no non-target species on Guam; there are no native terrestrial snakes on Guam (Rodda and others, 1999c). The key challenge for toxicant application to invasive giant constrictors on the United States mainland is finding a way to prevent harm to non-target species, especially non-target snakes. In the southeastern United States, a special challenge is associated with protecting the Indigo Snake (*Drymarchon couperi*), both a State and Federally listed Threatened Species. Because the Indigo Snake is large (maximum total length 2.8 m) and has a diet that overlaps with that of the giant constrictors, it is challenging to identify a device that would exclude this particular non-target while poisoning all sizes of giant constrictors. The Indigo is of special interest, but many other vertebrates may take poison baits intended for giant constrictors, including most carnivorous or omnivorous birds, mammals, and reptiles (and larger frogs), and as far as is known all of these native species are vulnerable to acetaminophen toxicity. Brown Treesnakes are very slender, facilitating their exclusive entry into narrow cylindrical bait stations, but the giant constrictors are relatively, well, giant, making it more challenging to configure a bait station that would allow their unimpeded entry while defeating such clever and dexterous competitors as raccoons, or such numerous and relentless non-targets as crabs and rats. Scientific opinion is divided on whether this problem is surmountable, but no definite ideas for doing so have emerged. Toxicant developers routinely struggle with the issue of preventing non-target take of poison baits, and we see little evidence that any of the mechanisms proposed for other species would be applicable to acetaminophen use on giant constrictor snakes on the United States mainland.

Although we are not aware of any giant snake toxicants that are chemically harmless to the non-targets of concern, it is possible that such a compound may exist. The cost of identifying and registering such a product would be sensitive to the availability of appropriate pharmacological information. Acetaminophen was chosen for

Brown Treesnake poisoning because it was already registered for other uses and was associated with vast quantities of pharmacological data. At the time of acetaminophen's registration, the registrants judged that only known products were within the economic range of practicality for the substantial expense of obtaining a registration for use on Brown Treesnakes. Registering an entirely new product takes years of expensive testing and perhaps a decade of experimental documentation. Presumably the same fiscal constraints would apply for obtaining a registration for a giant constrictor toxicant. There is presently no toxicant registered for use on any snakes in the United States mainland.

An additional challenge for giant constrictors is that the dosage would need to be sufficient to poison snakes weighing up to about 150 kg (for anacondas; less for smaller species). This is crucial, because many of the non-targets have smaller body masses and would therefore be vulnerable, even if the toxin were to be relatively less toxic to them. For example, acetaminophen is highly toxic to felines including domestic cats, a non-target on Guam. Cats are protected to a degree on Guam because most cats are an order of magnitude or more heavier than a typical Brown Treesnake. Whereas cats may be sickened by ingestion of a Brown Treesnake bait on Guam, they would not receive a lethal dose, as each poison bait contains only enough to kill a Brown Treesnake. However, the non-targets on the United States mainland are uniformly *smaller* than an adult giant constrictor, creating an additional challenge for the identification of a safe toxin.

Summary of Primary Tools

Given current knowledge, the primary tools for eradicating invasive reptiles are traps and toxicants. Both have been used successfully for control but not eradication of invasive snakes. However, there are significant non-target challenges in using toxicants for giant constrictors on the United States mainland. It is very difficult to see how one would poison invasive snakes without considerable and possibly unacceptable ancillary damage to non-target carnivorous or omnivorous birds, mammals, amphibians, and reptiles. In the one use of snake toxicants to date (acetaminophen for Brown Treesnakes on Guam), the poison baits (dead neonatal mouse with acetaminophen tablet inserted inside) appear generally effective for adult snakes, but are not eaten by smaller Brown Treesnakes (our unpub. data). There is no reason to think that such a limitation would apply with equal force to giant constrictors, but the existence of such a limitation for the well-studied Brown Treesnake is a reminder that one cannot assume that any hypothesized tool for giant constrictors will be free of such constraints. Given the current state of knowledge and funding, it would be presumptuous to assume that any colonization of a giant constrictor could be eliminated through the use of toxicants, or even that an appropriate toxicant could be discovered and registered in time.

Traps are also likely to have significant limitations for eradication of an incipient colonization. Above all, the practical size of an area that could be trapped is small, and thus it would be necessary for an incipient colonization to be discovered and treated before the population spread very far. Successful traps for giant constrictors are presently unknown, with an unknown time interval needed to develop effective models, if that is even possible. Regardless, there may be serious constraints on their use, potentially including a high requisite trap density (as the giant constrictors are sit-and-wait predators and thus would be aware only of nearby traps), limitation of use to favorable substrates

(may not be practical in areas of inundation or impassible vegetation), vulnerability to wildland fires, and high labor and transportation costs needed with frequent monitoring to release non-targets unharmed. However, there appears to be no intrinsic obstacle to the development of cost-effective traps for effective local control, if timelines are sufficiently accommodating. For example, traps could be an essential component of keeping Burmese Pythons from spreading to the Lower Florida Keys, or to reduce their impacts on colonial bird rookeries.

Other tools that have been used for invasive snakes are visual searching (unlikely to result in eradication unless the infested area is very small) and detector dogs (most useful for monitoring the completion of an eradication using some other tool).

Secondary Tools

Secondary Tools I—Judas Snakes

Judas animals have been used most often for highly social ungulates, such as goats, as part of an eradication program based on shooting. The first several goats taken in such an eradication effort are live-trapped and radiocollared, then marked conspicuously (should be visible to any hunter) and released. The released goats seek out their own kind and accompany them, allowing radiotrackers to locate and decimate each Judas goat's herd at will. When its last compatriot is shot, the Judas goat will most likely seek out a new herd to accompany, with the same detrimental effect on its colleagues. The Judas animal approach has been invaluable for invasive goat removal, as it eliminates the need to find the herd, costs only one radiotransmitter per Judas animal, provides locality information for all goats, including both sexes and all sizes, and continues working as long as the radio works (and the Judas animal lives).

The application of the Judas animal stratagem to giant constrictors is more circumscribed, as giant constrictors seek out their own kind primarily or exclusively for mating. Thus juvenile snakes are not likely to be vulnerable to exposure by the Judas. However, many of the giant constrictors accompany their prospective mates for long periods of time during the mating season. Most notable are anacondas, Burmese Pythons, and Southern African Pythons (boas accompany their prospective mates in small parts of their range, and the other species may do so under some circumstances, but long-duration cohabitation appears limited to a few species). From a demographic perspective the most valuable targets are adult females; thus one would radio-mark adult males, which could lead one (at the appropriate season) to adult females. On an informal basis this has been done successfully with Burmese Pythons in Everglades National Park (S. Snow, pers. commun., 2007). A constraint on this approach with giant constrictors is that the Judas snake would generally lead one to only a single female at a time. Whereas several males might be accompanying this female (so the yield of captured snakes may be more than one per tracking event), the yield would rarely include more than one female. The cost of the requisite radiotracking is substantial (radios must be surgically implanted; snakes may need to be followed for weeks before one finds them with a mate), and the practicality of this approach will hinge on the "force multiplier": how many targets are killed for the cost of the radiotracking effort. As with trapping, it is difficult to obtain any economies

of scale when using Judas snakes, but the approach works and may benefit from research to make it more cost effective.

Secondary Tools II–Biocontrol

Biocontrol takes two forms: predator-based and pathogen-based. Predator-based biocontrol is the introduction of a higher order predator, which it is hoped will depress the population of the target. Pathogen-based biocontrol is the introduction of a disease, parasite, or fungus that one hopes will be fatal and highly contagious, and thereby depress the population. The primary advantage of biocontrol over other tactics is that the agent of control is self-sustaining. The primary disadvantage of biocontrol is that the agent of control is self-sustaining; if it has undesirable effects, there may be no way to eliminate it. If it fails to sustain itself, it would not continue to control the target. An ideal biocontrol agent would attack only one species and be just successful enough to sustain itself without impacting non-target species, and with enough demographic vulnerability itself that it could be destroyed if conditions warranted doing so. Caudell (2001) screened 57 potential Brown Treesnake predators, but found that none was socially acceptable as a biocontrol agent introduction to Guam. Vertebrate predator-based biocontrol has been attempted on numerous occasions, especially on islands (Davis and others, 1976; Howarth, 1999). The record of successes is small, and the number of catastrophic failures (non-target species decimated or even driven extinct by the predator) is large (Davis and others, 1976; Bykovskii and Kandybin, 1988; Howarth, 1991). As a result, it is against U.S. Fish and Wildlife Service policy to introduce predator-based biocontrol agents for vertebrates (there is also a question as to which higher order predator would qualify for preying on giant constrictors!), and we will not entertain that notion further.

Pathogen-based biocontrol has a stronger track record, but almost exclusively with invertebrate hosts (Davis and others, 1976; Bykovskii and Kandybin, 1988). For example, Waage (1997) (and Waage and Mills, 1992) as President of the International Association for Biological Control strongly promoted biocontrol agents for invertebrates, but opined that *no* acceptable agents were known for vertebrates, because the putative vertebrate agents lacked sufficient species specificity. Furthermore, whereas invertebrates have rudimentary immune systems, they lack the ability of vertebrates to rapidly mount immune responses triggered by pathogen-specific structures such as t-cells, and to produce new types of t-cells in response to a new pathogen (Davis and others, 1976). Vertebrate immune systems tend to interact with pathogens to produce progressively lower virulence in the biocontrol agent over generations (Dobson and others, 1992; Nokes, 1992). This has been a strong pattern, with few vertebrates that have been subjected to arguably successful pathogen-based biocontrol (Nokes, 1992). The most often cited example is the use of rabbit hemorrhagic fever and myxoma virus with rabbits in Australia (Mutze and others, 1998). Both resulted in a significant depression in the rabbit population immediately following the release of the disease agent, but in both cases the rabbits recovered in a few generations as the pathogen evolved lower virulence (Fenner, 1983; Bykovskii and Kandybin, 1988; see also Berthier and others, 2000).

Pathogen-based biocontrol has been studied by a number of researchers in Brown Treesnakes (primarily native range parasites and paromyxo virus) and Habu (primarily

Entamoeba invadens), with no appropriate agents yet identified. Nichols (1990, 1999; Nichols and Lamirande, 2001) studied captive Brown Treesnakes infused with paromyxo. Dobson (1988) proposed the use of *Entamoeba invadens* for use on Brown Treesnakes, but provided no data (see Telford, 1999, for support for use of parasites). Others have screened a variety of putative control agents from natural populations (classical biological control) of Brown Treesnakes (MacKerras, 1961; Schad, 1962; Ewers, 1968; Whittier and others, 1997; Caudell and others, 2002), but found no agent that appeared to lower populations. Ishii and coworkers have long pursued use of *Entamoeba invadens* for population reduction in Habu (Ishii and others, 1971, 1976, 1979, 1981; Ishii and Noboru, 1971; Ishii and Hayashi, 1978; Ishii and Sawai, 1999), without advancing to field trials or identifying a species-specific or highly virulent strain.

It is noteworthy that biocontrol has not been used for the *eradication* of invasive species (Simberloff, 2001). This is due to the unlikelihood of a disease agent causing the extinction of its own species-specific host (and therefore itself). In general, disease transmission slows and stops as the hosts become rare; thus pathogen-based biocontrol has not been known to extirpate an introduced host (Holmes, 1982). When a disease agent causes the extinction of a host, it is normally because the extirpated host is a secondary host (secondary in the sense of lesser importance), and the numbers of the pathogen are sustained by a persisting primary host (Holmes, 1982). However, one would rarely get permission to release a pathogen in order to kill a secondary host, as that implies a greater risk to a non-target species. If the primary host was also an undesirable invasive species, one can imagine that such a scenario could be approved by regulatory authorities, but we are hard pressed to envision such a scenario involving giant constrictors on the United States mainland.

One highly significant impediment to the application of biocontrol for giant constrictors or any snakes is that the science of snake epidemiology is primitive in the extreme. Virtually nothing is known about the virulence, spread, or pathways of diseases of snakes in the wild. Most snake diseases, such as the paromyxo studied in Brown Treesnakes in the 1990s (Nichols, 1999), are unknown in the wild and may not propagate there, though they do impact giant constrictors in captivity (Manvell and others, 2000). Viruses are also notoriously unstable and prone to jump to non-target hosts (Hoddle, 1998). Presumably one would have to conduct a very substantial body of research to obtain the necessary biological facts about a putative control agent. For example, in the early 2000s a blue-ribbon panel was convened (under pathologist Thierry Work, USGS, Honolulu) to guide research into pathogen-based biocontrol of the Brown Treesnake. The panel concluded that such a research program was warranted only if one could devote about 10 years and \$50M to the program, as lesser amounts were unlikely to progress to the point of a suitable agent. Many proponents of pathogen-based biocontrol have advocated the use of advanced genomic science to enhance the virulence of a pathogen-based agent (Interdisciplinary Center for Biotechnology Research, 1992). While we do not doubt that such an enhancement is possible, one has to presume that such an enhancement would engender substantial additional research cost, both for development and testing of the novel biological product. In most scenarios, the genetically modified enhancement would be vulnerable to the evolutionary pressures that tend to diminish a pathogen's virulence over generations. While pathogen-based

biocontrol of giant constrictors in the United States mainland might be possible, the requisite costs seem beyond that which would be available for this purpose.

Secondary Tools III–Habitat Manipulation

Habitat manipulation is a tool to manage pests, not eradicate them. Habitat manipulation of a gross sort is commonly used for control of Habu (Mishima and others, 1999) and Brown Treesnakes (Campbell and others, 1999), for example, by removing trees from the vicinity of transportation facilities. Brown Treesnakes are less inclined to cross mown grass to reach an objective, though they are capable of doing so. We can think of no habitat manipulation that would absolutely prevent incursion by a Brown Treesnake, and the same limitation is likely to apply to giant constrictors in the United States mainland.

Secondary Tools IV–Bounties and Adding Value

Bounties do not have a very favorable reputation for the management of invasive species, in that they tend to pay people for activities that the people would do anyway (hence there is no gain), and bounties rarely result in eradication of a colonization (Singleton and others, 1999). Typically bounties lose their potency as the target species becomes rare because the financial reward becomes an insufficient motivator for the progressively greater effort needed to capture the remaining individuals. Bounties have never been used successfully with invasive reptiles. Given the various restrictions on access inherent in the complex wetlands of southern Florida, it is difficult to see how a bounty could be raised to a high enough level to stimulate hunting of rare giant constrictor snakes in all suitable habitat.

If the bounty was raised to a level that would stimulate such hunting, one risks creating a perverse incentive for hunters to both distribute the pest to new areas (spread the wealth-yielding opportunities) and lobby for continuation of the lucrative business (that is, prevent the pest's extirpation). One can even imagine hunters holding a few individuals back to insure continuation of their business model. In St. Lucia, Lesser Antilles, bounty hunters turned to breeding *Bothrops* snakes (Fer-de-Lance) for the high bounty payments they could obtain from the litters of nearly 100 neonates (Devaux, 1995). The giant constrictors also have very large litters/clutches. This perverse potential of bounties can be generalized by noting that any feature that adds value to an invasive species (selling the hides for leather, making tourist trinkets of them, and promoting safaris to come see the novelty) creates economic pressure to assure the population's continuation, and further spread. If eliminating an invasive is a social good, one should not create economic incentives for its persistence.

Secondary Tools V–Frightening Devices

Snakes appear relatively insensitive to sound (they can hear, but do not seem to react to the sounds that startle humans, birds, and mammals; doesn't every visitor bang on the glass of snake cages at zoos, to no avail?), and thus audible frightening devices of the sort used to scare birds from airports or crops are unlikely to be successful. With reference to the Reticulated Python, Wall (1926) stated, "It lies for hours completely inert, treating contemptuously all efforts on the part of spectators to provoke a

movement.” Visual cues and chemical means are the primary sensory channels that have been suggested for repelling snakes. Both have been the subject of experiments with Brown Treesnakes (McCoid and others, 1993; Caprette, 1997), though only chemical sprays have been shown to have any effectiveness (see McCoid and others, 1993, for the failure of a static chemical barrier). Chemical sprays such as cinnamon oil (including cinnamon-scented air-freshening sprays) will induce Brown Treesnakes to flee from close confinement (Clark and Shivik, 2002), such as in cargo, but there has been no suggestion that this tool would have application on a landscape scale. We expect that the same limitation would apply to repellents/ejectants discovered for use on giant constrictors.

Secondary Tools VI—Reproductive Inhibition

The first question to ask of any reproductive inhibitor is, “In what way is contraception an improvement over a toxicant?” Bomford and O’Brien (1997) formalized the search for circumstances favoring contraception and found few applicable to Australia, as few contraceptive systems were effective or cost effective. When dealing with charismatic large mammals in urban settings (typically deer), reproductive inhibition may be chosen due to animal welfare promoters’ support for nonlethal tools (the public would prefer not to kill ‘Bambi,’ but they’re okay with deer being sterile) and concern for non-target death of pets (which is a risk with many toxicants in urban areas). There is a more subtle advantage of reproductive inhibitors that applies to social species in which the dominant male (typically a harem master) behaviorally suppresses the reproduction of same-sex social inferiors (Caughley and others, 1992; Kirkpatrick and others, 1997). In this case, one gets a multiplier; for every dominant male whose reproduction is suppressed, several subordinate males are also kept from reproducing. In contrast, if the dominant male in such a species were to be killed, the harem master would quickly be replaced by another sexually competent male. Thus there are three situations in which reproductive inhibition might be favored over ordinary toxicants (Guynn, 1997): (1) environments where non-target victims of a toxicant are highly valued (for example, Endangered Species); (2) target species that society values alive, even if they are sterile; and (3) behavioral dominance that keeps subordinates from breeding. Giant constrictors are not known to be a magnet for animal welfare concerns, nor are they deemed better alive and sterile than dead (pt. 2), and giant constrictor societies are not known to have harem masters² (pt. 3), but many of the non-targets associated with giant constrictor toxicant use are highly valued (for example, Indigo Snakes); thus point 1 might apply in some contexts.

Could a reproductive inhibitor be found that would impair the reproduction of giant constrictors in the United States mainland but not that of non-targets such as Indigo Snakes? If so, reproductive inhibitors would have a clear advantage over use of a toxicant. Unfortunately, nothing is known of reproductive physiology of giant constrictors that suggests a uniqueness that could be exploited for the purpose of contraception. Hormonal and immunological systems are thought to be relatively conserved in the evolution of snakes (Hoddle, 1998) and would likely be identical between giant constrictors and native American snakes.

² Subordinate individuals defer to the harem master, a pattern unknown in wild giant constrictors. Male-male scramble competition is routinely seen, but this does not appear to have an element of deferring to the dominant male except in captivity (Barker and others, 1979) where escape is impossible.

This would appear to leave only two options for reproductive inhibition of giant constrictors: (1) embark on a study of the reproductive physiology of giant constrictors in the hope of discovering a vulnerability specific to these species (basic research approach), and/or (2) prepare a delivery system that would keep native snakes from being exposed to a generalized inhibitor of snake reproduction (exclusive delivery system). Both approaches have potential, but the basic research approach runs a high risk of being time consuming, expensive, and fruitless, and a putative exclusive delivery system could just as easily be applied to toxicants (so why not apply it to toxicants?). As we discussed in the toxicant section, there is no intrinsic reason that such an approach would fail, but no one has yet suggested a plausible means to make it succeed.

In summary, reproductive inhibition remains a theoretical possibility, but would require a substantial investment in research to discover a physiological basis for distinguishing native snakes from giant constrictors, or invention of a non-target-excluding delivery system more likely appropriate for toxicant application.

Secondary Tools VII–Egg/Nest Destruction

Egg/nest destruction is normally used only for birds, usually colonial nesting birds whose nests are easy to find and destroy (but the birds themselves flee successfully). Python nests (the other giant constrictors are live bearers and do not have nests) are exceedingly difficult to find and are almost always guarded by the brooding female, which is unlikely to flee. If one can find brooding females, it would be more effective to destroy *them*.

Secondary Tools VIII–Pheromonal Attractants

Pheromonal attractants have been suggested as the solution to the non-target problem because they are species-specific. That is, if the attractant in a trap, toxicant, or reproductive inhibitor is a chemical messenger (pheromone) recognized only by the target species, few non-targets would fall prey to the trap/toxicant/reproductive inhibitor (Mason, 1999). Furthermore, if evolved resistance to the delivery system is a concern with long-term lethal control, one need not fear evolved resistance of a species to its own pheromone(s). Evolved resistance should not be a concern if the introduced population were to be eradicated, but could become a concern if eradication failed and chronic control of the invasive species were to become necessary. Thus chemical characterization and synthesis of a pheromone that draws giant constrictors into a trap or to a poison bait would be a scientific accomplishment of the first magnitude; we see no downside to this.

However, it could be difficult to do for the following reasons:

(1) Only one snake pheromone has been synthesized to date (Mason, 1992); considerable work on other snake systems including Brown Treesnake pheromones has failed to isolate the compound (Waye, 2007, was originally an attempt to isolate the Brown Treesnake courtship pheromone). No one is certain how to solve this problem of analytical chemistry. If the Brown Treesnake pheromone being pursued turns out to be a mixture (“bouquet”) of compounds rather than a single chemical, it could be very challenging to identify the appropriate mixture as the number of potential combinations is astronomical, and non-targets might respond to the mixture or some of its constituents.

(2) If a pheromone were to be successfully synthesized, it might induce a behavior that is not very useful. For example, Brown Treesnake mating pheromones clearly induce Brown Treesnake males to attempt copulation with a pheromone-containing substrate, but they have not been found to draw the snakes into a trap or ingest a bait.

(3) Most snake pheromones are believed to be nonvolatile (Mason, 1992). That is, instead of wafting through the air, there must be a trail of the pheromone leading to the target. In theory such a trail could lead a snake into a trap or to a bait, but to date no one has induced a snake to do that. Substrate-born attractants draw snakes in from only a very limited area (in contrast to airborne compounds), and there may be significant practical problems associated with laying the trails inexpensively and as often as required. Anecdotal suggestions that pheromones may be occasionally volatile in pythons (for example, Diamond Pythons, *Morelia spilota*; Brien and others, 2008) have not been confirmed by research.

(4) The leading model of snake attractant pheromones (Mason, 1999) has the pheromone being released by the skin of gravid females, inducing approach by sexually competent adult males. Though this has been studied and documented in Brown Treesnakes and other colubrid snakes, it very probably occurs in giant constrictors as well. A problem is that such a system captures only adult males. Adult males are the most demographically expendable stratum of the population. Unless one eliminates all adult males repeatedly until all of the juvenile males have matured and been killed, the population reduction may be minor.

(5) It makes biological sense that a sexual pheromone should decay very rapidly, as no male snake would want to be chasing a scent trail left weeks earlier (whose perpetrator may be long gone). An artificial scent trail that needed frequent renewal could be biologically successful but impractical.

(6) To be useful for managers, a pheromone must be species specific, but the discovery of a species-specific pheromone requires considerable work with each species. One has difficulty envisioning that the potentially large expense of discovering, isolating, characterizing, and synthesizing a novel pheromone would be funded unless a specific species were established in the United States to justify such a protracted research project. In that case, the pheromonal product would be unlikely to be available in time to play a role in eradicating an incipient colonization, and there is no guarantee that an appropriate pheromone exists. Whereas the pheromonal “bullet” is potentially silver, it is unlikely to be timely for the purpose of preventing establishment. If a synthetic pheromone becomes available but attracts only adult males, it may still be useful for early detection of individuals expanding the species’ range into new areas (for example, pheromonal “sentinel traps” in the Florida Keys).

The leading pheromone attractant model mentioned above (female scent draws adult males) is not the only possibility. It is theoretically possible for a pheromone to apply to both sexes and all ages. For example, some snakes are attracted to scent left by conspecifics of any age or sex (Burghardt, 1980, 1983). Wayne (2007) found evidence for the existence of a pheromone that promoted aggregation in Brown Treesnakes. Such social (as opposed to sexual) pheromones could prove very useful for population control. To our knowledge such social pheromones have not been isolated, much less characterized or synthesized for any snake species, but they remain a very attractive

scientific goal, especially if they should prove to be species specific, chemically stable, and inexpensive to make.

Summary of Secondary Tools

Of the various secondary tools we have considered, one is likely to be actively detrimental (bounties or adding value), and three are unlikely to be useful for landscape-scale control (habitat manipulation, frightening devices, and egg/nest destruction). A fourth (Judas snakes) has potential for local population control, but seems difficult to scale up to the level needed for landscape control. Biocontrol, reproductive inhibition, and pheromones are potentially applicable at almost any scale. Biocontrol is ill-suited for eradication and success would likely require an unprecedented investment in ophidian epidemiological research. Biocontrol has not had long-term success for vertebrate hosts, but it has the theoretical potential for reducing snake populations on a large scale. For reproductive inhibition to be species specific and an improvement over species-specific delivery of toxicants, it would require either an unexpected breakthrough in our understanding of basic snake reproductive physiology, or a delivery system that achieved species specificity in a way that would not be available for delivery of a toxicant. No such system has been suggested. Pheromones are a possible silver bullet, but the leading paradigm for their use would deplete only adult males. Research into species-specific social aggregation pheromones could solve this problem, but to date no such compound has been characterized for any reptile.

Overall Summary

Many tools have the potential to benefit from additional research, but none is ready for landscape-level control or eradication of giant constrictor populations. Pheromone research might open a new pathway for control or eradication, but would most likely require an appreciable increase in the level of research funding. It is highly likely that visual searching and traps will continue to be the primary tools for control of invasive giant constrictors. Improvement in these primary tools is probable as a result of continued research, but current methods exhibit capabilities to eradicate an incipient population only if the measures are vigorously invoked at the very beginning of a colonization. However, a monitoring and response program for timely detection of incipient colonizations of reptile invaders has not yet been established on the United States mainland, and thus eradication is unlikely to be successful.

Chapter Four–The Indian or Burmese Python, *Python molurus*

Biological Profile

1.0 Introduction

Each species in this risk assessment package is described and evaluated in three sections: the biological profile; the management profile; and the formal risk assessment. The former two sections are part of the respective species' chapters (Four–Nine), whereas the formal risk assessments for all species are merged in chapter Ten. Each bioprofile outlines the biology of the species, largely as it is manifest in the species' native range, though in some cases the biology is better documented where the species is introduced. Each management profile addresses the practical extent to which the species can be managed in the United States. This covers questions such as: Where might it occur in the U.S.? How soon are officials likely to be aware of a new population? Would it be difficult or expensive to eradicate a new population? These are questions germane to assessing the risk of establishment. However, the formal risk assessment is the third section (in chapter Ten), and it considers all nine species simultaneously, ranking each species in relation to each identified risk factor, following the format suggested by the Aquatic Nuisance Species Task Force (1996; see also Orr, 2003).

1.1 Species

The species *Python molurus* ranges widely over southern and southeastern Asia. At times the species has been divided into subspecies recognizable primarily by color pattern (Barten and others, 1985; Ross and Marzec, 1990). For example, the dark form in Sri Lanka was historically distinguished as *pimbura*, though that name is no longer in wide use. Today the form in India, Pakistan, Sri Lanka, and much of Bangladesh is generally recognized as the nominate subspecies *P. m. molurus*. It is generally distinguished from the form in the remainder of the range (*P. m. bivittatus*) by having a lighter overall coloration, an arrowhead marking on the top of the head that fades anteriorly, and the absence of a scale row between the supralabials (upper lip scales) and the oculars (single ring of scales at the margins of the eye). However, various researchers have found the distinguishing attributes to be incongruent (de Rooij, 1917; Mertens, 1930), and as the two forms are parapatric (abutting but not overlapping), introgression between the two forms is assumed to occur frequently enough for the combined population to qualify as a species (Underwood and Stimson, 1990; Kluge, 1993; Welch, 1994; Walls, 1998b; McDiarmid and others, 1999; the Reptile Database, accessed 2008;

ITIS (Integrated Taxonomic Information System) accessed 2008). However, the species concept is in flux and some herpetologists, especially those focused on herpetoculture (Daniel, 2002; O'Shea, 2007; Barker and Barker, 2008a), recommend splitting the population into two species at the contact line. Evidence that both forms occur in the same area without interbreeding would measurably strengthen the argument for splitting; in captivity, the taxa produce healthy crosses (Townson, 1980).

1.2 Common Names

The most widely used name for the entire species is Indian Python (Frank and Ramus, 1995; Murphy and Henderson, 1997; Reptile Database accessed 2007), with *P. m. bivittatus* routinely distinguished as the Burmese Python. As the pet trade is composed almost entirely of *P. m. bivittatus*, most popular references to the species refer to it simply as the Burmese Python. Previously popular names include Indian Rock Python (for example, Pope, 1961), Asian Rock Python (Walls, 1998b), or simply Rock Python (Ditmars, 1931). None of these names is entirely satisfactory. Indian Python is somewhat ambiguous, as it may refer to the nominate subspecies, or the full species, which has a distribution that extends well beyond India. Burmese Python suggests an origin in Burma (=Myanmar), but the species has become scarce in southern Burma (G. Zug, pers. commun., 2008), and the name Burmese Python is often incorrectly used to characterize the entire species. Indian Rock Python or Asian Rock Python or Rock Python suggests a limitation to rocky habitats, which is incorrect (see section 3.2). It also creates a potential confusion with *P. sebae*, which is also called the Rock Python, or more often the African Rock Python, though it too occupies many habitats bereft of rocks (Broadley, 1999).

1.3 Evolutionary Context

The sister taxon of the Indian Python is the Northern African Python, *P. sebae* (Underwood and Stimson, 1990; Rawlings and others, 2008) which is taxonomically clustered with the South African Python (*P. natalensis*). *P. molurus* is difficult to distinguish from *P. sebae*, as the morphology and range of coloration and scale patterns overlap extensively, and both African forms are reported to interbreed successfully with *P. molurus* in captivity (Branch and Erasmus, 1984; Coborn, 1991; Walls, 1998b). One can easily surmise that in a more mesic (wet) geological period the distributions of these sister taxa may have joined in the Middle East. Evidently they have not developed pre-zygotic reproductive isolating mechanisms since their separation, which is not surprising, as reproductive isolating mechanisms are thought to evolve more readily in species that overlap and therefore have a need to prevent lower viability hybrids (Mayr, 1974). The evolutionary position of the *P. molurus/sebae* group within the python clade is less certain (Kluge, 1993; Rawlings and others, 2008), but most observers agree that it is not closely related to the sympatric (geographically overlapping) Reticulated Python (*Broghammerus reticulatus*) and its sister taxon, *B. timoriensis* (Lesser Sundas Python).

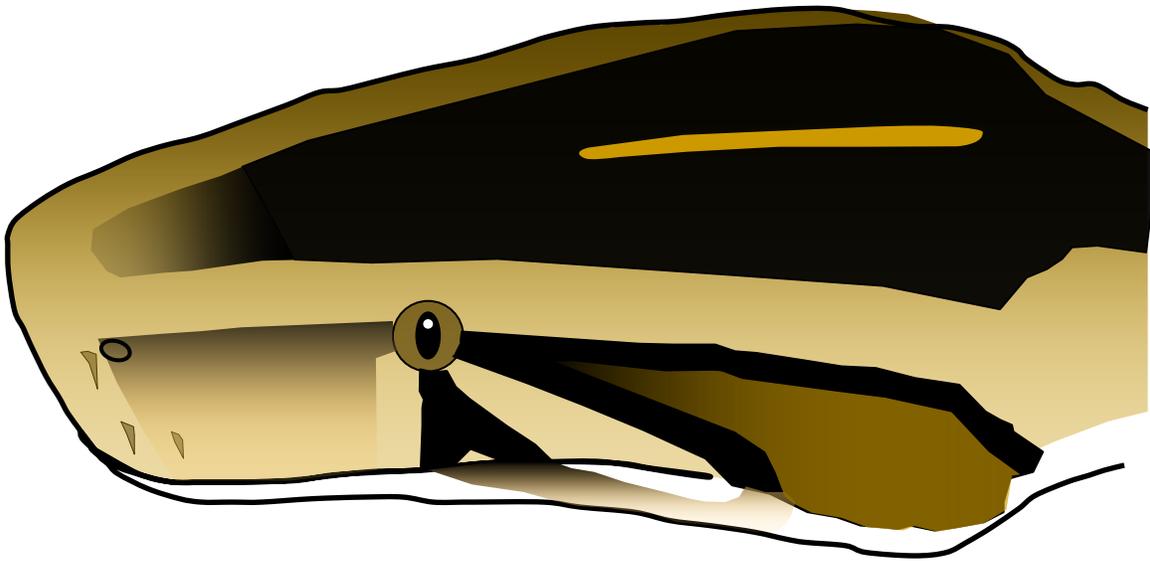


Figure 4.1. Schematic representation of the head of *P. molurus*.

2.0 Description

2.1 Unique Morphological Features

While details of the scalation differ somewhat among the giant constrictors, the functional features of the morphology of the Indian Python share more similarities than differences with other snakes of similar size. For example, all the giant snakes are nonvenomous constrictors having short prehensile tails (*P. molurus* tails about 12 percent of total length: Kabisch, 2002); heavy bodies; large, angular but supple skulls with high counts of small, severely recurved teeth; vertical pupils; temperature-sensing thermal pits in their lips (=labial scales; except *Eunectes*; note that *Boa* also lacks obvious labial pits, but we do not consider this species as a morphologically “giant” constrictor); narrow belly scales; bodies circular in cross section; flanks with many rows of tiny scales; and the blotchy color pattern characteristic of species that depend more on crypsis than mobility for prey capture and predator defense (Fig. 4.1). Vestigial pelvic girdles are used by the males for courting females (Gillingham and Chambers, 1982). The blotchy color patterns of Indian Pythons are individually unique (Bhupathy, 1990).

2.2 Size

Humans are fascinated by the large size of the Indian Python and have discussed the matter extensively (Oliver, 1959; Pope, 1961; Minton and Minton, 1973; Ernst and Zug, 1996; Murphy and Henderson, 1997; Walls, 1998b; Bellosa, 2003, 2004; Zug and Ernst, 2004; Bellosa and others, 2007), despite having relatively few data (large specimens rarely reach museums, for practical reasons). However the large size of the Indian Python may be its primary ecological adaptation. In combination with an extraordinary ability to recruit stomach tissue quickly to digest a large meal (Secor, 1995, 2003; Secor and Diamond, 1995, 1998; Secor and others, 1994, 2000), the large body

size of the Indian Python extends the size range of its predatory niche well beyond those of all sympatric snakes except the Reticulated Python (with which it shares some habitats in insular and mainland Southeast Asia). Estimates of the maximum size of a species depends on the size of the sample of measurements obtained (though rumors of rare but gargantuan snakes abound), and credible measurements are sparse when museums do not preserve a large series or large individuals (Zug and Ernst, 2004; Manthey and Grossman, 1997). Many experts state that Indian Pythons over 5 m in total length (all length measurements in this work are total length) are exceptionally rare (Ernst and Zug, 1996; Murphy and Henderson, 1997), though there is a recent record of a 8.22-m total length captive-reared Indian Python (Bellosa, 2003). Some typical benchmarks are given in Table 4.1. Useful references on this topic are: Wall, 1912, 1921; Smith, 1943; Lederer, 1956; Schmidt and Inger, 1957; Pope, 1961; Acharjyo and Misra, 1976, 1980; Van Mierop and Barnard, 1976; Ernst and Zug, 1996; Walls, 1998b; Cox and others, 1998; Zug and Ernst, 2004; Bellosa and others, 2007.

Table 4.1. Total lengths and masses of typical *P. molurus* (compiled from the literature sources listed in the text).

Sex	Hatchling		Maturation		Max. reported	
	Total (mm)	Mass (g)	Total (m)	Mass (kg)	Total (m)	Mass (kg)
M:	480-790	75-165	2.0	~5	~4.5	~50
F:	480-790	75-165	2.6	~10	8.22	182

2.3 Sexual Size Dimorphism

A diversity of metrics has been suggested for quantifying sexual size dimorphism (Lovich and Gibbons, 1992), but none of these has been applied to the Indian Python. Although hard data are absent, there appears to be a consensus that most very large Indian Pythons are females (for example, Walls, 1998b), which according to Lederer (1956), exceed the total length of males by 5 to 6 feet (1.5–1.8 m). A size difference of this magnitude probably allows large female Indian Pythons to eat prey items that would be unavailable to males.

2.4 External Sexual Differentiation

Both sexes of Indian Python exhibit vestigial remnants of pelvic girdle, visible externally as tiny protruding spurs, which are proportionately larger in males (Gillingham and Chambers, 1982). Pythons of exceptionally large size are generally females (section 2.3).

3.0 Distribution in Space and Time

3.1 Native Range

The range of the Indian Python is poorly documented, at least in part because such large snakes have not fared well amidst the dense human population that now occurs in its native range (Groombridge and Luxmoore, 1991). Thus the current distribution is likely to have shrunk over that occurring naturally (Minton, 1966; Khan, 2006). As our primary interest is in the ecological conditions under which it may occur, we have not dwelled on range shifts (presumably anthropogenic) reported within historic time. Groombridge and Luxmoore (1991) published the most recent compendium of native range distributions, though their interest was in trade regulation rather than biogeography, and the quality of their records was highly dependent on the caliber of trade monitoring in each country. Murphy and Henderson (1997) reviewed the relevant literature. Rodda and others (2009) reported the data also tabulated here (Fig. 4.2). Associated with a call for unrestricted importation, Barker and Barker (2008a) argued for a more restricted distribution, partially relying on nonpeer-reviewed or unpublished information about current distributions. The references cited in this paragraph are not repeated in the country by country summary below. Countries are listed in approximate order from west to east.

Pakistan—*P. molurus* has been recorded from mostly riparian zones in the lower and upper reaches of the Indus Valley, with only minor penetration into the highly arid lands in the west or the coldest portions of the extreme north (Wall, 1912; Smith, 1943; Minton, 1962, 1966; Khan, 2002, 2006). No explanation for its absence in the middle Indus has been published, though there seems to be agreement that it is not found there.

India—The Indian Python is found virtually throughout the country, though it is probably absent from higher elevations in the extreme north (for example, Kashmir, Arunachal Pradesh) and the extremely arid parts of the Thar or Great Indian Desert along the Pakistan border (Wall, 1912, 1921; Smith, 1943; Deoras, 1965; Whitaker, 1978, 1993; Das, 2002b).

Sri Lanka—Found throughout (Wall, 1921; Deraniyagala, 1955; de Silva, 1990).

Nepal—Found throughout the lowlands (Swan and Leviton, 1962; Malla, 1968; Zug and Mitchell, 1995; Kabisch, 2002); the maximum elevation is a matter of some uncertainty (see discussion in 3.2.1).

Bhutan—No unique literature, but presumed to have a distribution ecologically similar to that in neighboring Nepal.

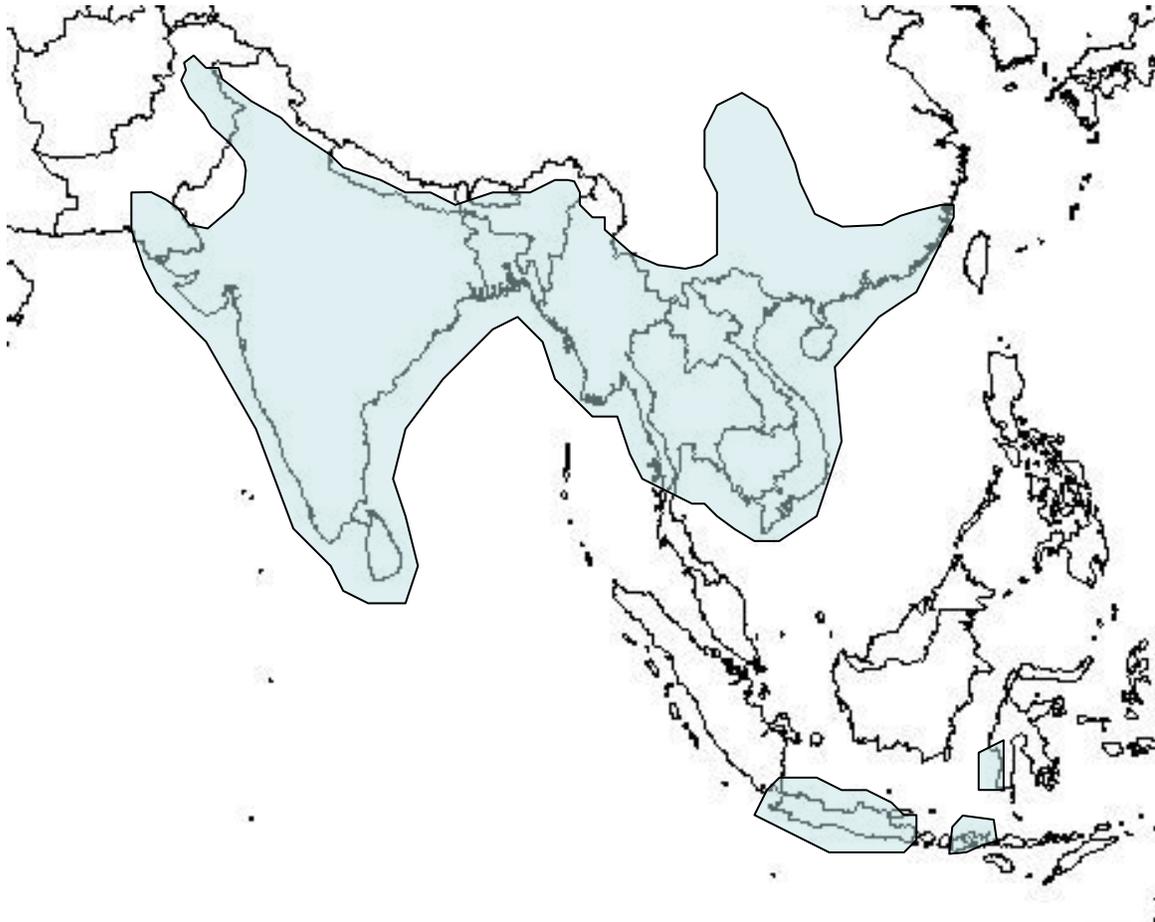


Figure 4.2. Native range of *P. molurus*, as deduced from the sources cited in text. The dividing line between the subspecies has not been subject of a recent review, but is believed to lie in the narrow neck of the range separating South Asia from Southeast Asia. Many specimens in the foothills of the Himalayas appear to be *P. m. bivittatus*, as are scattered specimens in lowland eastern India.

Bangladesh—Found throughout the country (Wall, 1912, 1921; Smith, 1943; Kock and Schröder, 1981; Das, 1996).

Burma (Myanmar)—Range poorly understood; may not reach the northernmost border (Wall and Evans, 1900; Wall, 1912; Smith, 1943; Dowling and Jenner, 1988; Auffenberg, 1994; Zug and others, 1998; Manthey and Grossman, 1997; Das, 2002a; Pauwels and others, 2003).

Thailand—Similar to Burma/Myanmar (Taylor and Elbel, 1958; Cox, 1991; Manthey and Grossman, 1997; Cox and others, 1998; Chan-ard and others, 1999) and does not extend south of the Isthmus of Kra (Pauwels and others, 2003).

Laos—Found throughout, with the possible exception of higher elevations at the northern border (Deuve, 1970; Manthey and Grossman, 1997).

Cambodia—Found throughout (Manthey and Grossman, 1997).

Vietnam—Found throughout, with the possible exception of high elevations at the northern border (Campden-Main, 1970; Manthey and Grossman, 1997; Ziegler, 2002).

China—Very poorly documented in publications of the West. The most authoritative recent source (Ji and Wen, 2001) does not explain the detailed range map presented (see also Pope, 1935; Vinegar and others, 1970; Lin, 1983; Liu, 1986; Zhao and Adler, 1993; Zhong, 1993).

Malaysia—The snake is believed absent from Borneo (see note under Indonesia) and if present in peninsular Malaysia, it would be so only at the most northern extreme (Boulenger, 1912; Manthey and Grossman, 1997; Cox and others, 1998; Inger and Voris, 2001).

Indonesia—The distribution in Indonesia is disjunct from the rest of the range, the snake being found only on the islands of Java, Sumbawa, and Sulawesi, and in Sulawesi only on the western side of the southwestern arm (de Rooij, 1917; Kopstein, 1930; Mertens, 1930; de Haas, 1950; David and Vogel, 1996; Inger and Tan, 1996; Manthey and Grossman, 1997; How and Kitchener, 1997; Stuebing and Inger, 1999; Inger and Voris, 2001; Malkmus and others, 2002; de Lang and Vogel, 2005; McKay, 2006; Das, 2006). Auliya (pers. commun., 2008) cited an unconfirmed report of this species on Lombok. Although a 19th century specimen attributed to Indonesian Borneo exists (Smith, 1943; Kabisch, 2002), the absence of any subsequent documentation casts doubt on the validity of the geographic attribution and modern authors do not recognize the presence of *P. molurus* on Borneo (Inger and Tan, 1996; Stuebing and Inger, 1999; Malkmus and others, 2002; Kabisch, 2002; Das, 2006; Auliya, 2006).

3.2 Habitat Range

A dedicated study of the habitat range of *Python molurus* has not been published. However, it is evident both from the wide range documented and the informal habitat descriptors mentioned in the literature that this species occurs in virtually every habitat from lowland tropical rainforest (Indonesia, Southeast Asia) to thorn-scrub desert (in Pakistan) and grasslands (Sumbawa, India) to montane warm temperate forests (Nepal, China). Zug and Ernst (2004) describe the habitat as mangrove to montane. Smith (1943) mentions both upland and riparian habitats. Murphy and Henderson (1997) state, "rain forest, mangrove swamps, savanna, scrub forests and semideserts." The most arid occupied habitats are near the species western limit (India, Pakistan), where Khan (2006) lists two habitat types: "Sind Kohistan and southern Baluchistan" ("clumps of cactus-like *Euphorbia* dominate the landscape") and "Dry Temperate Semi-evergreen Scrub Forests" ("*Olea cuspidata*, *Acadia modesta*, *Artemisia*...with occasional trees"). Wall (1921) emphasizes the degree to which this species is comfortable in water. Smith (1943) stresses this point and declares that it might even be considered semiaquatic in habit; however Wall (1921) notes that although it may remain in fresh water for long periods (potentially throughout a shedding period), "it shows no special affection for the sea." Whitaker (1978) claimed a preference of this species for relatively undisturbed habitats ("pythons require large undisturbed areas to hunt and hide in."); it is not clear whether absence from more developed sites is a product of direct human persecution (snake populations killed in developed areas), indirect human persecution (snakes may learn to remain away from settlements so as to avoid harassment), or a natural habitat preference (for example, snakes prefer mature forest). Whitaker's (1978) observation is reinforced by other observers only to the extent that the python seems to have disappeared from densely populated areas in recent history (Groombridge and Luxmoore, 1991). In a later paper (Whitaker, 1993), he stressed the ability of pythons to coexist with humans in disturbed habitats: "Because *P. molurus* can conceal itself in a remarkably small patch of live or dead vegetation and being nocturnal, it is sometimes able to dwell unnoticed for long periods near human habitation. However, as habitat loss increases by expanding human development, marginal forest and scrub forest zones favored by *P. molurus* are disappearing."

3.2.1 Maximum Elevation

No studies focused on this question have been published, but various authorities have asserted that they occur at elevations up to 2,500 m (Whitaker, 1993; Murphy and Henderson, 1997). Other mentioned limits include 1,500+ m (Pope, 1935), 1,650 m (Pope, 1961), 2,000 m (Whitaker, 1978; Kabisch, 2002; Whitaker and Captain, 2004; Khan, 2006), and 2,400 m (Ernst and Zug, 1996). As some of the highest occupied elevations in their native range are located at the highest occupied latitudes of their native range, the individuals present in such locations presumably hibernate (see 3.5, below).

3.3 Climate Range

The Indian Python shows an extraordinary range of climates, including both temperate and tropical, as well as both very wet and very dry environments (Fig. 4.3). The nominal subspecies (*P. m. molurus*) ranges into some very dry areas around the Thar

Desert of western India and Pakistan; both subspecies occupy cold areas in the neighborhood of the Tibetan Plateau and Himalaya Mountains (Fig. 4.3). Notice that the assumption of the shorter hibernation period implies a lower thermal tolerance (when active), whereas the assumption of a longer hibernation period spares active snakes from exposure to such low temperatures.

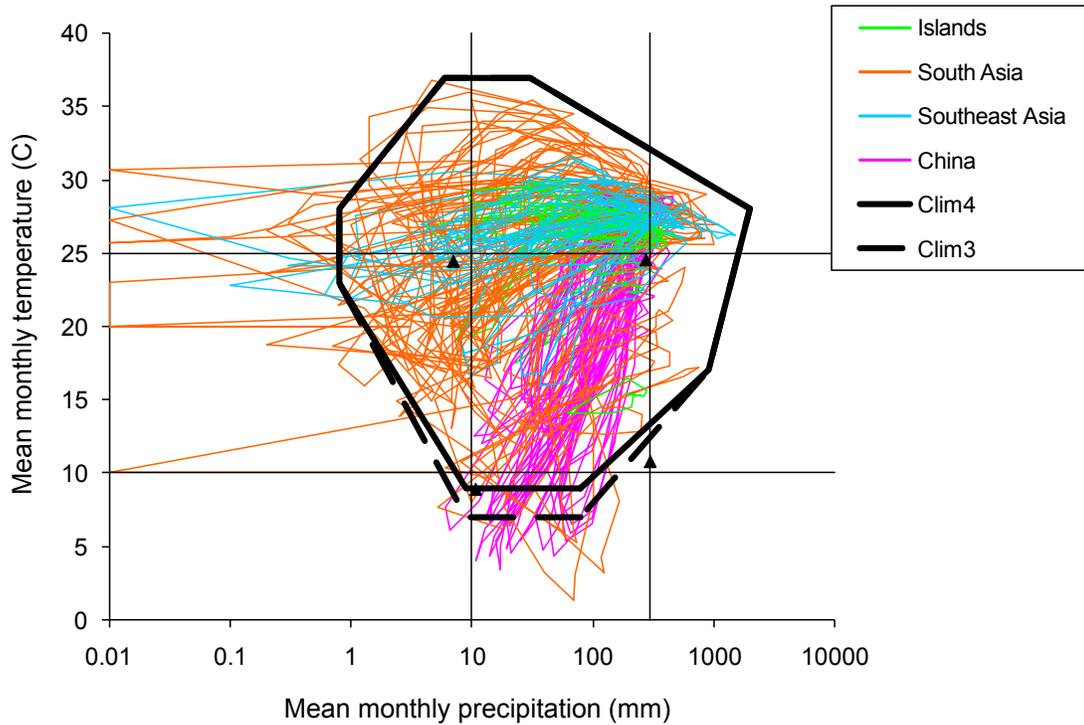


Figure 4.3. Climate space for *P. molurus*, with reference lines and localities as introduced in Fig. 2.1. The Chinese localities (magenta lines) and Southeast Asia (blue lines) are entirely within the subspecies *P. m. bivittatus*. Clim3 (heavy dashed line) presumes a hibernation period of 3 months whereas Clim4 (heavy solid black line) posits a hibernation period of 4 months.

3.4 Microhabitat

Very little information is available on microhabitat. Whitaker (1978) comments that “They live in rocky clefts and caves, abandoned mammal burrows, hollow trees, dense water reed and mangrove thickets, usually near a permanent water source.” Wall (1921) noted the prevalence of this species “partially or wholly submerged near the bank of a river or jheel. As in captivity, it will lie for hours showing nothing but the tip of its snout, which is pushed out to raise the nostrils above the surface, and permit breathing.” From the historical context, it is not clear whether such behavior is a preferred resting/foraging mode, or simply the best way to avoid excessive harassment by humans.

3.5 Introduced Ranges

Outside of Florida there are no known introduced populations of this species. Various commentators have speculated that disjunct (Walls, 1998b) or putatively disjunct (Barker and Barker, 2008a) populations might be introduced, but no direct evidence has been published to support this speculation.

3.6 Seasonal Activity

No studies on the seasonal activity of this species have been published. The species is understood to hibernate at the northern edge of its range (Wall, 1912, 1921; Shaw and others, 1939; Smith, 1943; Daniel, 2002). Minton (1966) gives approximate dates for entering and leaving hibernation, implying a hibernation duration of 3–4 months. It is not clear if hibernation in this species is equivalent to the deep burial associated with high latitudes in North America. Daniel (2002), for example, comments that hibernacula include “any convenient retreat such as a tree hole, a hole in a bank, or under rocks or grass heaps.” Bhupathy and Haque (1986) and Bhupathy and Vijayen (1989) describe intermittent winter activity near hibernacula, though their study site was not at the northern limit of the species range.

3.7 Daily Activity

Opinions differ with regard to the daily activity cycle of the Indian Python. This could reflect differing activity patterns in different localities or times of year. In areas where the python is subject to human persecution they may have learned to avoid daytime exposure. Whitaker (1978) stated, “Pythons sleep or bask in the sun during the daytime. At night they prowl in search of prey or lie in wait near a waterhole or a regular mammal pathway.” Bhatt and Choudhury (1993) studied the python in the cooler seasons in central India, where they found them to be largely diurnal in the coolest months and crepuscular in the warmer months. A similar pattern has been reported in Florida (Snow and others, 2007b). Many observers note that pythons will be inactive for a period of days to weeks following a large meal (Wall, 1912, 1921; Whitaker, 1978; Daniel, 2002).

3.8 Foraging Mode/Sensory Modalities

Dedicated studies on foraging mode or sensory modalities have not been published for this species. There is a consensus that pythons conceal themselves near pathways used by their prey (ambush site chosen on the basis of the snake’s detection of odor trails left by the prey species), which they strike when prey individuals walk in front of the snake’s mouth. Wall (1921) for example, opines that predatory strikes are visually guided and may be accompanied by tail movements that could constitute a distraction display (Mullin, 1999): “The snake, roused to activity by the sight of food, advances towards its prey often with quivering tail...” Given the sophisticated thermally sensitive pits in the head of pythons, they could presumably sense the passing prey by some combination of visual (Goris and others, 2007; Grace and Matushita, 2007), vibration, chemical, and thermal information (Wall, 1912; Bullock and Barrett, 1968; Auliya, 2006; Grace and Matushita, 2007). Auffenberg (1994) cites his own unpublished work showing an ability of pythons to commute between refugia and ambushing sites by following their

own scent trail from previous passages. Daniel (2002) suggests that pythons may actively acquire immobile prey under some circumstances: “Heronries, nesting colonies and large bird roosts usually have attendant pythons which take their toll at night.”

4.0 Life History

4.1 Reproductive Mode

The Indian Python shows a fairly standard snake-life history in that it hatches from an egg at a relatively small size, but is independent from birth, grows rapidly and matures in a few years, searches for mates (males search) or waits for males to find it (females) during the mating season, and females lay eggs to repeat the cycle. The primary uniqueness of the Indian Python is that females brood their eggs, enclosing the eggs inside their coils throughout incubation, raising the clutch’s temperature if needed by shivering thermogenesis (Valenciennes, 1841; Hutchinson and others, 1966; Vinegar and others, 1970; Müller, 1970; Vinegar, 1973; Van Mierop and Bernard, 1978). Wall (1921) reported “in all cases the dam has shown great solicitude for the fate of her eggs.” The female may raise the temperature of her clutch by 6–8°C (Hutchinson and others, 1966; Vinegar and others, 1970; Ernst and Zug, 1996).

4.2 Reproductive Phenology

Reproductive phenology (the time of year when reproductive events occur) is expected to vary with locality (especially latitude), but for the Indian Python has been quantified only in Florida (Snow and others, 2007a, b; Krysko and others, 2008) and South Asia (Wall, 1912, 1921; Bhupathy and Vijayan, 1989). The general pattern in areas of seasonally reduced activity seems to be for courtship to occur as air temperatures begin to warm. Mating aggregations or mating balls (Rivas and others, 2007a) form in south Florida in March/April (R.W. Snow, pers. commun., 2008); previous observations of this phenomenon were limited to captivity (Acharjyo and Misra, 1976), or inferred from aggregations seen in Dec.–Mar. in India (Shaw and others, 1939; Smith, 1943; Bhupathy and Vijayan, 1989; Daniel, 2002) or Pakistan (Minton and Minton, 1973).

Copulation in the Indian Python has not been carefully quantified, but appears to take typical snake form (Gillingham, 1987): (1) following shedding by the female, (2) males are incited to repeatedly and fairly rapidly rub ventrally against the dorsal surface of the newly shed female, and if she is receptive, (3) intromission follows the female’s gaping of her cloaca, which facilitates her cloacal grasping of the male’s nearest everted hemipene (Barker and others, 1979; Nakamoto and Toriba, 1983). If cloacal gaping by the female is required, the potential for forced copulation would seem to be quite limited in this species; we have found no reports of forced copulation in *P. molurus*. The one unique aspect of python courtship is that the vestigial hind limbs of the male are vibrated at a frequency of 30–80 movements per minute to stimulate the corresponding area on the female (base of tail; Gillingham and Chambers, 1982). Eighteen timed copulations (Pope, 1961; Barker and others, 1979; Nakamoto and Toriba, 1983) lasted 35–1,160 min (Nakamoto and Toriba, 1983, reported a median of 360 min for their 11 observations), though due to the intertwining of tails (and concomitant obstruction of view), there may be some uncertainty about whether intromission was present throughout.

Copulation by the male is not essential for development of viable eggs in the Indian Python (Durnford, 2003; Groot and others, 2003). Instead, the female apparently has the ability to fertilize her eggs with her own genetic material, though it is not known how often this occurs in the wild. Several captive studies reported viable eggs from females kept for many years in isolation. For example, Pope (1961) cites a 1951 report by C. Leigh of a python that laid eggs nine, ten, eleven, and thirteen years after mating. This was once interpreted as evidence for long-term sperm storage, but may instead be evidence for facultative parthenogenesis (self-fertilization).

The length of time between copulation and oviposition (gestation) has not been measured in the wild, and may vary with locality. Wall (1921) infers from anecdotes in the wild that 3–4 months elapses, but Stemmler-Morath (1956; cited in Pope, 1961) and Walls (1998b) reported only 2 months in captivity. Van Mierop and Barnard (1976) observed 113–114 d in captivity.

Most captive females stop eating at some point prior to oviposition (Acharjyo and Misra, 1980); Barker and others (1979) state that female reproductive aphagia (fasting) begins at the time of copulation. Presumably cessation of feeding is a reflection of competition from follicles/eggs for space within the narrow confines of a snake's body (Wagner, 1976; Van Mierop and Barnard, 1976, 1978; Barker and others, 1979). All observers agree that females also do not generally eat while they are brooding their eggs; thus the female may lose considerable weight during the lengthy period of reproductive aphagia (38 percent of pre-breeding mass lost (that is, includes mass lost through egg formation); Van Mierop and Barnard, 1976).

The mean date or degree of synchrony within a population of oviposition is not known with certainty for any site, but Wall (1921) reports anecdotes of Mar–Jun for India and as late as Aug for Sri Lanka. Harvey and others (2008) cites May–Jun for Florida. Wagner (1976) noted that females shed about 14 d prior to oviposition. Harvey and others (2008) give Jul–Aug as the dates for hatching in Florida, but comparable values are not apparently known for the native range.

4.3 Reproductive Effort/Fecundity

Reproductive effort is classically computed as the percentage of the female's body mass represented in the clutch (RCM or relative clutch mass). To our knowledge, this has not been computed for *Python molurus* (though see mass loss reported by Van Mierop and Barnard, 1976, in section 4.1).

4.3.1 Clutch or Litter Size/Frequency

Clutches of 8–107 have been reported (Wall, 1921; Smith, 1943; Stemmler-Morath, 1956, cited in Pope, 1961; Ernst and Zug, 1996; Cox and others, 1998), although the mean clutch size is towards the low end of that range (Pope, 1961, recognized only two clutches of more than 55). Karsen and others (1986) claimed a maximum number of 30, but that is inconsistent with recent records from Florida (mean 36, Brien and others, 2007), and does not approach two recent clutches of 79 and 85 from the Florida Everglades (Krysko and others, 2008). Ernst and Zug (1996) reiterate Wall's (1921) claim that the Indian Python's maximum of 107 is the maximum for all snake species, but Cox and others (1998) have a record of 124 for *B. reticulatus* and Zug (pers. commun., 2009) notes a Puff Adder (*Bitis arietans*) with 157.

Most observers assume that Indian Pythons produce only one clutch a year. Given the extreme physiological (clutch production, brooding, and reproductive aphagia) and temporal (months of brooding) cost of producing a clutch, and the absence of more than one reported breeding season per year for this species, the assumption of no more than one clutch per year seems sound. Indeed, it is possible that energetically challenged females may be unable to reproduce every year in some localities; this possibility has not been examined in the wild. It is probable that males attempt to reproduce annually in all localities.

4.3.2 Egg Size

Eggs are symmetrical, leathery, roughly 60 x 120 mm (Smith, 1943), and adherent when freshly laid (Pope, 1961; c.f. Walls, 1998b). Oviposition sites include open ground, tree holes, termite mounds, and under fallen logs (Wall, 1921). Eggs of minimum size (diameter as low as 47 mm in captivity, Acharjyo and Misra, 1980; length as low as 75 mm, Lederer, 1956) tend to have low viability and may be influenced by conditions of captivity. Mass of snake eggs is especially vulnerable to abnormal hydric conditions of captivity: reported values for *P. molurus* are 140–303 g (Lederer, 1956; Stemmler-Morath, 1956, cited in Pope, 1961; Walls, 1998b). Lederer (1956) pointed out that eggs shrink a few days before the eggs hatch.

4.4 Growth

Embryos are relatively advanced when oviposited, with total lengths of 25–83 mm (Pope, 1961; Van Mierop and Barnard, 1976). From that point on, the rate of growth will be highly dependent on ambient temperature, and captive observations may not reflect wild conditions. Unfortunately, all available data are from captivity (Wunder, 1934, cited in Pope, 1961; Lederer, 1956; Schmidt and Inger, 1957; Pope, 1961; Vinegar, 1973; Van Mierop and Barnard, 1976; Black and others, 1984). Pope (1961) noted a length of 275 mm after 43 d; Van Mierop and Barnard (1976) noted 289 mm (18 g) at 25 d, 580 mm at 47 d.

Hatchling lengths and masses are given in Table 1 (Section 2.2); key references are Wunder (1934) cited in Pope (1961), Smith (1943), Schmidt and Inger (1957), Pope (1961), Vinegar (1973), Van Mierop and Barnard (1976), Ernst and Zug (1996), and Cox and others (1998). Incubation time is highly sensitive to temperature, which is not always known or natural in captivity. Reported incubation times are in the range 55–80 d (Schmidt and Inger, 1957; Pope, 1961; Karsen and others, 1986; Clercq, 1988; Van Mierop and Barnard, 1976; Ernst and Zug, 1996). Hatchlings use an egg tooth to slit the shell one or more times (Lederer, 1956). Hatchlings shed 10–21 d after emergence, and probably rely on yolk until this first shed (Valenciennes, 1841; Schlott, 1935, cited in Pope, 1961; Lederer, 1956; Van Mierop and Barnard, 1976; Clercq, 1988).

Postemergence growth is among the fastest recorded for snakes, with captive individuals approaching 200 mm/mo, though typical rates are 70 mm/mo (Wall, 1921), 75 mm/mo (Acharjyo and Misra, 1980), 89 mm/mo (Pope, 1961), or 98–103 mm/mo (Van Mierop and Barnard, 1976). One extraordinary individual was recorded as growing 245 mm/mo (Frye and Mader, 1985). Growth rate declines with age; Parker (1963) expressed the trajectory as an increase in total length of 170 percent in the first year and 70 percent in the second. Acharjyo and Misra (1980) gave the mean growth rate as

declining from 76 mm/mo (1st year) to 45 mm/mo (2nd year) to 52 mm/mo (3rd year) to 15.5 mm/mo (4th year). Wall (1921) gave the mean monthly growth of a 3.6-m TL captive as 40 mm/mo.

Few data exist on the frequency of shedding in the Indian Python, which may scale with growth and would therefore decrease with increasing size. Wall (1921) states that a captive (size not given) shed 5–6 times per year (see also Daniel, 2002).

4.5 Maturation

Maturation in captivity is likely to be accelerated when captives are fed generously. Unfortunately, data are not available from the wild. Frye and Mader (1985) report on an extraordinary male captive that matured in five months, at a total length of 1.7 m. This is consistent with Wall's (1921) assessment of male maturation occurring at 1.7 m (all unqualified length measurements in this work are total length). However, females are reported (Wall, 1921; Lederer, 1956) to mature at around 2.6 m, which implies a greater age at female maturation or faster female growth. Pope (1961) argues that males may mature in 2 y and females in 3 y; Walls (1998b) asserts 3 y. Ross and Marzec (1990) state, "They can reach ten feet [3 m] in length by one year of age if overfed, and can reach sexual maturity at 18 months to two years. With more appropriate growth, sexual maturity is reached at 2 ½ to 3 years." These latter rates are a reasonable expectation for normally fed animals (Walls, 1998b). Acharjyo and Misra (1980) found two females kept out of doors in Orissa, India, to be mature at an age of 3 y 7.5 mo.

4.6 Longevity

Few records exist for long-term captives, and no data are available from the wild. Bowler (1977) gives two records for captives >28 y in captivity, the longest of 34 years, 2 months for an Indian Python acquired as an adult.

5.0 Diet/Trophic Role

5.1 Prey

With only a few reported exceptions, Indian Pythons eat terrestrial vertebrates, though they eat a very wide range of terrestrial vertebrates (lizards, frogs, crocodylians, snakes, birds, and mammals). Special attention has been paid to the large maximum size of prey taken from python stomachs; the most famous include a leopard (Begbie, 1907), alligators (Ditmars, 1912; Snow and others, 2007a), antelope (Wall, 1921; Raja of Jasden 1953, cited in Pope, 1961), dogs (Ernst and Zug, 1996), deer (Wall, 1921; Snow and others, 2007a), jackals (Wall, 1921), goat (Wall, 1921), porcupine (Wall, 1921), wild boar (Whitaker, 1978), pangolin (Pope, 1961), bobcat (Snow and others, 2007a), pea fowl (Wall, 1921), frigate birds (Snow, pers. commun., 2008), Great Blue Herons (Snow, pers. commun., 2008), Wood Stork (Snow, pers. commun., 2009), langur (Wall, 1921), and flying fox (Foster and Price, 1997). At the small end of the size spectrum are items such as wrens (Snow and others, 2007a), toads and frogs (Wall, 1921), and mice (Whitaker,

1978; Clercq, 1988). Within this prey size range are species of special concern³. In Florida, the species of special concern known to have been eaten include Endangered Key Largo Woodrats (*Neotoma floridana small*, Greene and others, 2007), Round-tail Muskrats (*Neofiber alleni*, Snow and others, 2007a), Limpkin (Snow and others, 2007a), and White Ibis (Snow and others, 2007a). It appears that Indian Pythons will eat any bird or mammal of an appropriate size.

While this statement may be an accurate characterization of the *population* of Indian Pythons, Wall (1921) presented evidence that *individual* pythons may be more idiosyncratic in dietary preferences. He noted a captive individual that consistently refused house rats (*Rattus*), while readily consuming jerboas (Dipodidae). Although lizards (Wall, 1921; Auffenberg, 1994), snakes (Wall, 1921), frogs (Wall, 1921) and toads (Wall, 1921) have been found in python stomachs, they do not appear to be common prey. Too few have been documented to assess the snake's prey range in those taxa, though it would appear that many North American reptiles and amphibians are too small to be of much interest to pythons. An exception is alligators (Snow and others, 2006, 2007a), which frequently interact with pythons in the Everglades, both as predator and prey.

Fish eating does not appear to be a common trait in Indian Pythons. Although Keays (1929) claimed it was common, at least at certain venues (see also Ernst and Zug, 1996), there are few other records documenting fish eating, despite the frequent close proximity of fish and pythons.

A number of vegetable items have been found in python stomachs (Wall, 1912, 1921); these fruits are presumed to be either ingestion errors (the rotting mango smelled of carrion) or secondary ingestion (the python swallowed a frugivore whose stomach contained some berries). The python's willingness to eat carrion or carrion analogues might facilitate the use of artificial attractants, as suggested by the observation of Pope (1961): "S. Mookerjee reported the discovery of four mangoes in the esophagus of an Indian python. Tooth marks were visible on the mangoes, which were infested with insect larvae, an indication that they were not fresh."

5.2 Predators

Predation on Indian Pythons has not been systematically documented. Presumably, eggs and hatchling pythons experience the greatest vulnerability due to their small size. Alligators (Snow and others, 2006), monitor lizards (Auffenberg, 1994), jackals (Bhupathy and Vijayan, 1989), and humans (Murphy and Henderson, 1997) are documented predators or scavengers of pythons. Adult pythons are relatively invulnerable to predators, except when they are digesting a large meal (Wall, 1921; Murphy and Henderson, 1997).

³ Our use of lower case letters in the phrase "species of special concern" indicates that we are using those words in their common English usage. Formal designation using the same words would be capitalized. For example, the State of Florida has a special legal category for species the Florida Wildlife Conservation Commission designates as Species of Special Concern (these are so noted under the Florida column in Table 4.2).

5.3 Diseases and Parasites

Little is known about the diseases or parasites of pythons in the wild. Morris (1932), Pope (1961), Frank and Haefner (1981), Riley and Self (1981), Ismail (1984), and Bhupathy and Vijayan (1989) mention the occurrence of internal parasites of the Indian Python, but none of these sources presents evidence that the parasites affect python populations.

6.0 Demography

6.1 Population Density

To our knowledge, there are no credible published estimates of population density of the Indian Python. Bhupathy and Vijayan (1989) summed the maximum number seen at different dens (over the course of a winter) from a 29-km² park in India, but they recognized that not all dens were known, and additional individuals were present away from dens. They also acknowledge that den switching may occur in midwinter, potentially leading to double counting. Accordingly, the bias of their ~5/km² estimate is difficult to assess. The density of the population studied by Bhupathy and Vijayan (1989) may have been depressed by losses to humans (well documented by Bhupathy and Vijayan).

6.2 Size Distribution

A satisfactory assessment of the size distribution of a population requires an understanding of the size dependence of detectability. Pythons donated to authorities by interested citizens are likely to have caught their attention because of the snake's large size, for example; conversely, preserved museum specimens are routinely selected for their small size (to save space and preservative). Although lengths are given for some individuals taken from the python's native range, these have not been aggregated into a usable size distribution; this has been done for the Florida population (Snow and others, 2007b). The Florida record indicates that the modal size class is 3.0–3.25 m in total length, with the majority of individuals below this mode (mean = 2.4 m).

7.0 Interactions with Humans

7.1 Human Utilization and Persecution

In South Asia, humans kill pythons in substantial numbers for their meat and skins, and for perceived improvements in human safety (Groombridge and Luxmoore, 1991). Due to legal protection associated with low python population density in South Asia, the documented hide trade is limited to Southeast Asia. At the time of Groombridge and Luxmoore's (1991) study, exports had peaked in 1985 in Thailand (at 188,000 skins plus an unquantified number of exports tabulated in terms of skin length, area, or weight). Following that peak year, trade in skins originating in Thailand was suspended, coincident with a surge in exports from Malaysia (where the species is not known to occur).

It is not possible to assess the impact of this trade on the health of wild stocks using available information; however, Groombridge and Luxmoore (1991) believed that the trend was not favorable. They cited evidence for population declines in Pakistan, India, Bangladesh, Sri Lanka, Nepal, Burma, Thailand, and Laos.

7.2 Human Health Risks

A full-grown female Indian Python constitutes a safety risk to humans, but virtually all known human fatalities are associated with pet manipulation (Minton and Minton, 1973; Chiszar and others, 1993; Murphy and Henderson, 1997; Flank, 1997; Associated Press, 2006), not unprovoked attacks. A remarkable exception occurred during production of this report (1 July 2009), in which an unattended 2-year-old in Florida was sought out and fatally constricted by the family's 2.5 m (5.5 kg) pet amelanistic Burmese Python (Miller, 2009). Events of this sort may have happened before, but gone unreported or underreported, as families are understandably reluctant to share details of so personal a tragedy with the media. Most putatively unprovoked attacks occur from an undocumented large constrictor in parts of Asia where the more likely perpetrator is a Reticulated Python (Minton and Minton, 1973), though the death of a Chinese baby near Hong Kong in 1900 (Wall, 1921) would be outside of the known range of *B. reticulatus* and was therefore most likely an Indian Python. Given the large number of humans living in the native range of the Indian Python, it is remarkable that more human fatalities have not been reported, as herpetoculturists believe that any python over 8 feet (2.4 m) in length is capable of killing an adult human (Flank, 1997). "Large constrictors have the ability to kill humans, and in areas of southern Florida where these snakes occur, children should be kept away from water edges and dense vegetation, which is a common precaution anyway because of the much higher likelihood of alligator attacks" (Snow and others, 2007b). Snow and others (2007b) also note that large constrictors crossing roads could cause traffic accidents.

7.3 Human Aesthetic Relations

7.3.1 Pet Trade

Indian Pythons are desirable because of their beauty and ease of handling. These attributes, combined with a very low cost for wild juveniles coming out of Southeast Asia, has long allowed the Burmese Python to be a mainstay of the exotic reptile trade. Groombridge and Luxmoore (1991) reported that export of live Burmese Pythons from Thailand peaked in 1985 at 25,000, after which Thailand curtailed the trade. The following year, Malaysian exports of the nonresident species jumped from 94 to 15,006, suggesting that much of the trade was rerouted in response to Thailand's export ban. Reed (2005) tabulated U.S. importation records for 24 species of boas and pythons during the period 1989–2000, which indicated that Burmese Pythons⁴ were the fourth most popular snake (behind *P. regius*, *B. constrictor*, and *B. reticulatus*), at 12,466 recorded importations. The number of snakes imported increased sharply over the last decade, with 99,000 individuals imported from 1996 through 2006 (Harvey and others, 2008,

⁴ There is no legal trade in Indian Pythons that are not of the Burmese subspecies; thus all importation records for the species are referred to *Python molurus bivittatus*.

based on LEMIS import records). It is notable that not all import records were identifiable to species (thus the cited figure is a minimum), and domestic sources (undocumented) are believed to constitute a significant additional source (unpub. records of Florida Wildlife Comm., Law Enforcement). CITES records (Fig. 4.4) show wide swings in annual imports, with a sharp decline in recent years that CITES notes may be at least partially due to incomplete records tabulated since 2005.

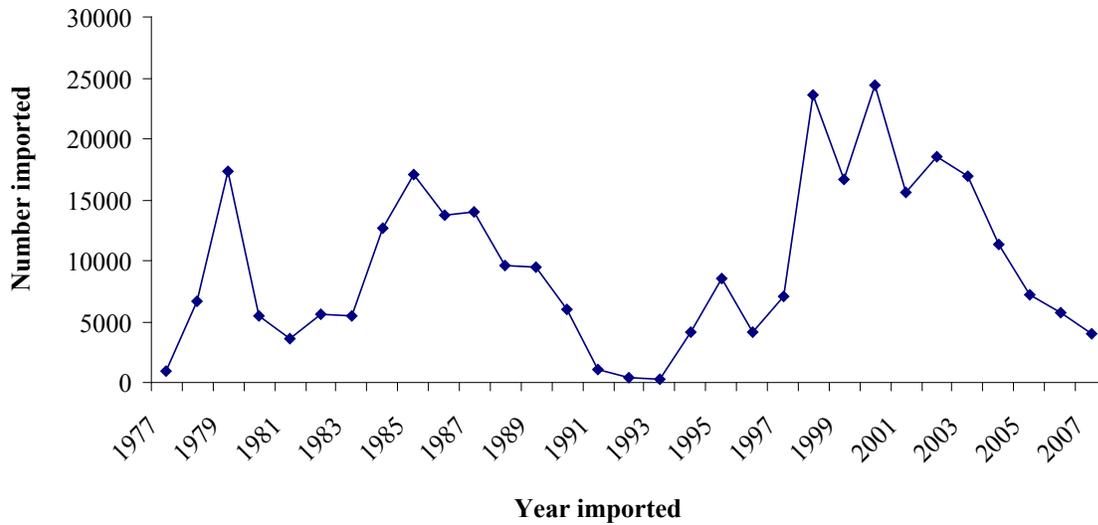


Figure 4.4. CITES records for importation to the United States of live *P. molurus*.

7.3.2 Other Uses

Pythons are valued in their native range for rodent control, religious symbols, entertainment, and medicinal value (Wall, 1921; Pope, 1961; Minton and Minton, 1973; Murphy and Henderson, 1997; Walls, 1998b). In the U.S., Burmese Pythons play a traditional role in zoos, circuses, carnivals, and roadside attractions; occasionally they are used as an accoutrement for exotic dancers (Pope, 1961; Coborn, 1991; Walls, 1998b).

Management Profile

This section follows the format suggested by the Aquatic Nuisance Species Task Force (1996) in which the first four elements review the sequential likelihood of species establishment (Pathway × Entry potential × Colonization potential × Spread potential), and the concluding three elements consider the sum of social, biological, economic, and political consequences that might occur if the species becomes established or legally regulated (Economic impact + Environmental impact + Social and political influences). These seven factors are rated and compiled for all giant constrictor species in the final

chapter (Ten) of this risk assessment. This section discusses the seven risk assessment areas as they apply to *P. molurus*.

8.0 Pathway Factors: Pet Trade

Although transport to the United States by another pathways is imaginable (for example, circuses, zoos, scientific study, food), the overwhelming preponderance of live Indian Pythons in the United States today arrive via the pet trade.

8.1 Volume of International Trade

As indicated in section 7.3.1 of this chapter, Indian Pythons are one of the most often imported snakes, routinely appearing in the top five species, with 99,000 imported from 1996 through 2006. Snakes in the international trade pathway constitute a somewhat higher risk than domestically bred animals, in that wild snakes often carry exotic parasites or pathogens that may transfer to other captive snakes during transport, sales, and pet ownership, or to native snakes or livestock once released. In addition, wild-caught snakes consist of genotypes that have proven ability to survive in the wild. Potentially, the survival experience or learning of the previously free-ranging animal is also of some value in improving the individual's prospects for subsequent survival in the wild.

8.2 Volume of Domestic Trade

The volume of domestic trade in *Python molurus* is unknown, but many experts believe it to be comparable or to exceed the volume of international trade (Florida Wildlife Commission law enforcement specialists, pers. commun., 2007). The Pet Industry Joint Advisory Council submitted testimony in 2008 to the Fish and Wildlife Service that domestic production of *P. molurus* greatly exceeded imports. The Burmese Python breeds readily in captivity and has been selectively bred for numerous “designer morphs” (Walls, 1998b; de Vosjoli and Klingenberg, 2005), which attract buyers with their beauty and novelty. Herpetoculture experts (for example, de Vosjoli and Klingenberg, 2005) routinely advise prospective buyers to purchase only captive-bred individuals as they are likely to be healthier. Accordingly, the captive-bred hatchlings generally command a higher price. Except for novel genotypes sought for breeding purposes, adult pythons do not command a high price, as supply exceeds demand for large individuals.

9.0 Entry Potential (Survival in Transit – Meant Mainly for Unintentional Transport)

This heading addresses the prospect of a species surviving in the pathway by which it might enter the United States. For species that arrive unintentionally as stowaways there is considerable uncertainty. But pythons arrive intentionally, in packages made up especially for their survival. As the pet trade makes no profit from the transport of any that die, survival of Indian Pythons in commerce is very high, approaching 100 percent for these sturdy animals.

10.0 Colonization Potential

10.1 Likelihood of Escape/Release

Pythons may be released either intentionally or unintentionally (see Reed and Rodda, 2008). Unintentional release is promoted by the impressive muscular strength and persistence of a confined python. Some indication of the frequency of python escape can be gleaned from the numerous newspaper accounts of escaped pythons reportedly terrorizing suburban neighborhoods. We are aware of no systematic compilation of such events, but they are familiar to any herpetoculturist.

Intentional releases appear to be motivated primarily by an owner's inability to properly care for such a large and voracious pet. Such owners are evidently unable or unwilling to find another owner for the undesirable giant constrictor (zoos are inundated with requests for taking over care of adult giant constrictors, requests that they are unable to satisfy), and may choose to release their pet in an area of biologically suitable habitat rather than kill the animal and protect the environment from potential invasion. For example, the initial colonization of the Burmese Python in Florida appears to have derived from animal(s) clandestinely released at the far end of the main entrance road in Everglades National Park (Snow and others, 2007b). Presumably the owner(s) of the pet(s) drove the >40 miles to the end of the dead-end road to ensure that their pet would be maximally surrounded by biologically suitable habitat.

10.2 Climate Match: Areas of the United States at Greatest Risk

Due to the wide rainfall tolerance and extensive semitemperate range of *P. molurus*, large areas of the southern United States mainland appear to have a climate suitable for survival of this species (Fig. 4.5). United States areas climatically matched at present ranged up the coasts and across the south from Delaware to Oregon, and included most of California, Texas, Oklahoma, Arkansas, Louisiana, Mississippi, Alabama, Florida, Georgia, and South and North Carolina. By the year 2100, projected areas of potential suitable climate extend northward beyond the current limit to include parts of the States of Washington, Colorado, Illinois, Indiana, Ohio, West Virginia, Pennsylvania, New Jersey, and New York. Thus a substantial portion of the mainland United States is potentially vulnerable to this ostensibly tropical invader. In addition to the mapped areas of the U.S. mainland, the territories of Guam, Northern Mariana Islands, American Samoa, Virgin Islands, and Puerto Rico would appear to have suitable climate. Areas of the State of Hawaii with elevations under about 2,500 m would also appear to be climatically suitable. Climate suitability is just one factor in the establishment of an invasive species, a necessary but not sufficient condition.

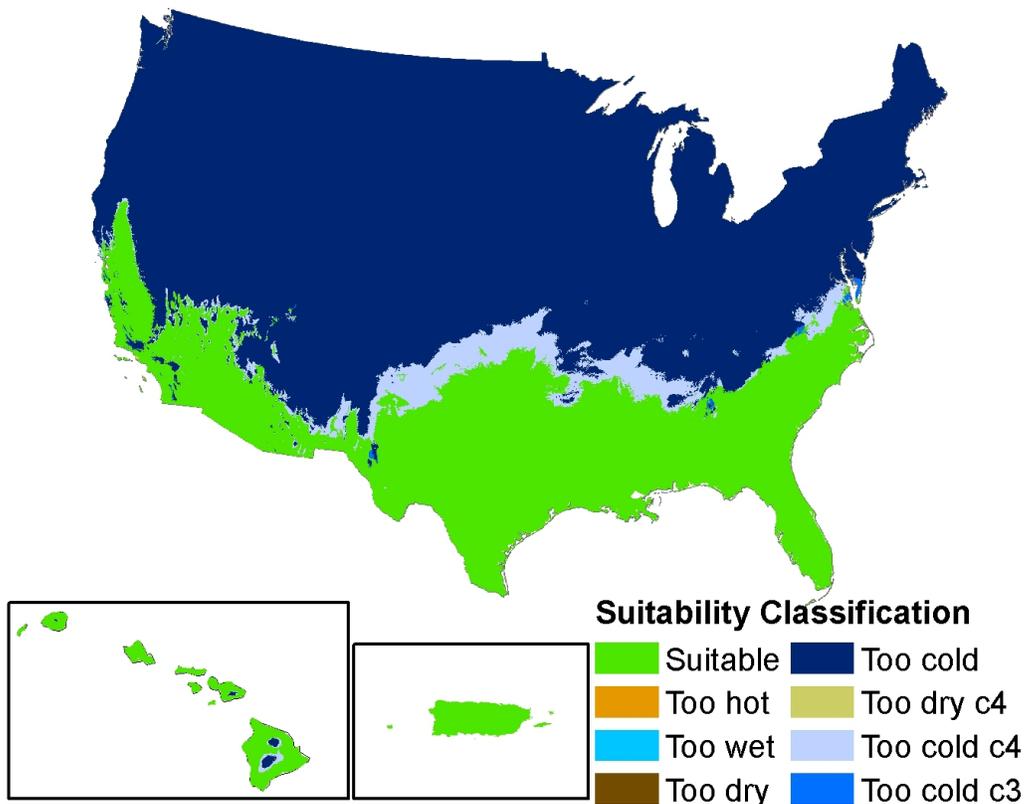


Figure 4.5. Areas of the United States matching the climate envelope expressed by *P. molurus* in its native range (Fig. 4.3) under two hypotheses of hibernation duration: clim3 (assumed duration of hibernation 3 months) and clim4 (assumed duration of hibernation 4 months). See chapter Two for details of analytical method.

10.3 Prey Availability

Dietary studies (see Biological profile 5.1) indicate that *P. molurus* will readily consume any terrestrial vertebrate of a size suitable for ingestion by the individual snake. In Florida, Burmese Pythons have eaten prey as small as wrens and as large as deer, with diet records that encompass multiple orders of mammals, birds, and reptiles excluding snakes and turtles. All indicated portions of the United States have prey of a suitable size, but some insular areas may lack prey of sufficient abundance in certain size ranges. For example, some islands in the Northern Mariana Islands have few terrestrial endotherms larger than rats. Rats are a key prey for juvenile and small adult pythons, but may not be sufficient for healthy growth of large adult females. Thus an invasive population of pythons in the Northern Mariana Islands might be subject to stunting, due to limited availability of large prey. On islands with feral cats, pigs, goats, and so forth, there would appear to be no such prey size limitation. A complete prey size distribution appears to be present in most of the U.S. mainland.

10.4 Predation Risk

Few predators on the U.S. mainland are of a size sufficient to safely engage an adult Burmese Python. Because of their size and predatory capabilities, panthers and crocodilians are likely to be especially effective. However, we know of no direct evidence on which to judge the probability of either species preying on pythons with sufficient frequency to depress the population of pythons or limit its spread. The circumstantial evidence from southern Florida is that the combination of panthers and alligators has not noticeably constrained establishment or spread. It is possible, however, that spread will accelerate if and when Burmese Pythons spread beyond the area densely inhabited by panthers and alligators.

10.5 Reproduction Requirements

As Burmese Pythons do not deposit their eggs in the ground, but hold and warm their eggs to protect them from cooling and perhaps from mold and predators, they appear capable of reproducing without further specialized features in any locality of suitably warm climate (Fig. 4.3), though it is possible that additional requirements exist but have not yet been identified.

10.6 Hibernation Requirements

Indian Pythons hibernate underground, but do not appear to dig their own hibernacula. In India they are most often associated with porcupine burrows (for example, see Bhupathy and Vijayan, 1989). Thus the existence of suitable animal-made or natural burrows would seem to be required for the persistence of *P. molurus* populations. We are aware of no systematic data collection on the availability of burrows in the United States, though natural crevices service the needs of hibernating snakes in localities such as Manitoba, well north of the area climatically suitable for *P. molurus* (Fig. 4.5). Much of the southeastern United States has Gopher Tortoise burrows that are probably suitable. Much of the southern United States has medium-size mammals (skunks, raccoons, foxes) that would provide suitable burrows. However, there well may be places where small burrows (for example, under wind-thrown root balls) are available, but climatically buffered large burrows (dug burrows or large natural crevices) are rare. For example, sandy areas in coastal Virginia and elsewhere (B. Savitsky, pers. commun., 2007) may have soils too weak to support large underground cavities and/or a paucity of large burrowing vertebrates. In such environments, pythons might not be able to overwinter, or they might be limited to riparian zones where beaver or other digging mammals create burrows.

10.7 Tools for Eradicating a Colonization

The prospects for preventing python colonization were outlined in the generic management chapter (Three). That chapter drew most heavily from the experience with the current *P. molurus* infestation in Florida and thus is most directly applicable to this species. To date there has been no evidence that a colonization could be eradicated by management activities.

11.0 Spread Potential

The localities into which pythons might spread are very similar to the localities in which pythons might survive (see section 4 above). However, the *rate* of spread (dispersal ability) is limited by python movement rate (vagility) and fecundity.

11.1 Dispersal Ability

Burmese Python vagility and fecundity are among the highest of any snake, with short-term (ca. 1 month) straight-line movements of 40 km recorded in Florida (S. Snow, pers. commun., 2008) with radiotelemetry, and the reported clutch sizes (max. 107) being third-ranked among snakes (second is the Reticulated Python). Thus the spread of Burmese Pythons is unlikely to be limited by dispersal ability. Indeed, the rate of spread is likely to be near maximal compared to other snake species.

11.2 Ability to Develop Races or Strains

Nothing is known about the viability of pythons of various strains or color morphs. At least three albino Burmese Pythons have been encountered in the wild in southern Florida, including those with wild prey in their stomachs, and an albino individual was found in an ambush posture under a bird feeder within a few days of escaping its cage (S. Snow, pers. commun., 2008). Thus albinism per se does not appear to be a lethal trait for wild individuals. Given the great diversity of native range localities that have contributed stock to the pet trade, it is likely that novel genetic combinations (that is, unrepresented in nature) could be created by existing or subsequent releases of captive stock (as was observed for introduced *Anolis sagrei* in Florida; Kolbe and others, 2004). However, no data are available on this topic.

11.3 Tools for Managing Spread

The chapter (Three) on generic management of giant constrictors specifically addressed the eradication of incipient colonizations. That chapter concluded that eradication has not been achieved for any giant constrictor and is unlikely on the U.S. mainland with the technology and early detection infrastructure presently implemented. However, spread and local population density may be somewhat more readily managed, especially if the area to be protected from spread is geographically isolated. Thus there are improved management opportunities associated with interdiction to islands such as Hawaii or the Florida Keys. Such interdiction would draw heavily from the vigorous interdiction program presently in place for Brown Treesnakes on Pacific Islands (Vice and Pitzler, 2002). Interdiction opportunities between geographically connected sites in the U.S. mainland would appear much less favorable, especially given the State-by-State variability in regulations on the ownership and transport of giant constrictors.

12.0 Economic Impact Potential

To the best of our knowledge, no one has undertaken a study of the economic impacts of *P. molurus* in either its native or introduced range. We are thus forced to speculate in an unquantified way on the basis of the known biological facts; many issues of great potential importance may be overlooked or mischaracterized by this approach.

12.1 Pathogen Vector

Very little is known about the disease vectors associated with Indian Pythons in the native range, and nothing is known regarding potential new interactions where introduced. It seems probable that ticks and other fairly general ectoparasites could be transmitted to native reptiles in the United States. Diseases borne by such parasites could potentially impact U.S. industry. The most famous possibility is heartwater disease, a potentially catastrophic disease of hoofed animals including cattle that is vectored by ticks found on African pythons (for example, *P. sebae*), but the ticks are capable of transferring to other species of the genus *Python* in captivity (see analysis of this phenomenon in *P. sebae* management chapter). If a tick bearing heartwater was to attach itself to a *P. molurus* that was subsequently released, there would be at least the possibility of introducing heartwater disease to North America. Alternately, if heartwater was to become established in North America by some other mechanism, newly resident pythons could support ticks that would harbor the disease (complicating management of the epidemic) or transmit the disease to previously unaffected areas by dispersing with infected ticks.

12.2 Predator on Livestock

Although cattle and adult sheep are unlikely to be taken often by *P. molurus*, all smaller livestock would be at risk if unconfined or confined in porous structures (for example, many barns have holes or crevices large enough for entry of pythons). Free-range poultry such as chickens and geese have already become victims (S. Snow, pers. commun., 2007). Newborn mammals are likely to be especially vulnerable, as they are with the much smaller Brown Treesnakes (Chiszar, 1990; Fritts and McCoid, 1991). Accounts of wild prey of *P. molurus* often mention wild pigs, so we expect that domestic pigs would be favored prey.

12.3 Predator on Pets

Loss of pet animals may be of greater psychological importance than what would be suggested by the raw number of individuals lost. Puppies and kittens are the pets most often taken by Brown Treesnakes (Rodda and others, 1999c), probably because they are the least able to defend themselves. Losses of caged birds are generally a one-off affair, as the snake is often unable to depart between the cage wires due to its excessively bulging stomach. This state of affairs may be distressing to the bird owner discovering the replete but only partially confined python.

12.4 Electrical Power Systems

Brown Treesnake economic damages are primarily a result of damage to electrical power circuits and supporting hardware such as transformers (Fritts and others, 1987; Burnett and others, 2006). Burnett and others (2006) projected potential Brown Treesnake annual power system losses of \$4.5B in Hawaii; thus the magnitude of potential losses is appreciable. However, juvenile Burmese Pythons are less capable climbers than are Brown Treesnakes (adult pythons are too stout and heavy for climbing on wires), and thus the economic loss per unit of land area is likely to be appreciably less from pythons than from Brown Treesnakes. We are not aware of any documented power

line problems from the large population of Burmese Pythons in south Florida, and thus this problem may be no more severe than that already associated with power line movements by rat snakes.

12.5 Traffic Accidents/Human Attacks

Although Burmese Pythons are the nonvenomous snake species most often associated with human fatalities, these generally involve interactions initiated by the pet owner (“illegitimate bites”); however, legitimate attacks have been documented and some visitors will find this disconcerting. In python-infested areas where American Alligators are also found, we expect that human health risks from reptiles would continue to be dominated by the risks from alligators. We do not anticipate *P. molurus* becoming a significant source of human mortality in the United States, though the loss of anxiety-free recreation space (terrestrial areas where alligators do not occur) may be important to some users.

As mentioned by Snow and others (2007b), pythons have a small potential for creating or contributing to traffic accidents by blocking traffic lanes or contributing to bystander accumulation. The economic cost associated with such activity would presumably be immeasurably small.

12.6 Tourism

The potential economic impacts on tourism can be exceedingly difficult to measure (Shwiff, 2008), as impacts that are large in aggregate magnitude may accumulate when immeasurably small antipython preferences are held by a large number of potential tourists. Furthermore, there may be some small offsetting benefits to tourism from the opportunity to witness novel predators. However, the potential exists for costly losses in tourist revenues if a high-profile encounter or fatality occurs and generates adverse publicity. The effect would likely be stronger in localities that do not presently have dangerous animals such as alligators. For example, several economic analyses of tourism in Hawaii have projected that colonization by the Brown Treesnake could cost Hawaiian businesses hundreds of millions of dollars. Presumably a colonization of Hawaii by the much larger and more dangerous Indian Python would engender a proportionately larger loss of tourism revenues.

12.7 Impacts on Commercially Important Wildlife

12.7.1 Species Hunted with Gun or Binoculars

South Florida ecotourism is heavily dependent on bird watching. Birds that are imperiled or visually striking are especially desired. Imperiled species are the ones most likely to be impacted by python predation (see section 5.1), as they are demographically least able to sustain a modest increase in predation pressure. Thus to the extent that visitation is tied to success at bagging a sighting of a rare bird, the presence of a novel predator on rare birds is likely to be detrimental to tourism.

South Florida is not heavily dependent on visitation by gun hunters, but hunting is an economically important activity further north, one that is potentially adversely

impacted by a stealthy predator that competes with hunters by eating desired species such as quail, turkey, feral hogs, and deer.

12.7.2 Species that Impact Forestry, Agriculture, or Horticulture

Burmese Pythons are unlikely to have a dramatic impact on forestry, agriculture, or horticulture. To the extent that managed lands are now impacted by rat, nutria, or beaver numbers, there might be a small positive effect related to rodent population reduction.

13.0 Environmental Impact Potential

13.1 Species of Special Concern as Prey or Competitors

A very large number of imperiled species are at risk from giant constrictors in the State of Florida. Table 4.2 lists all species tracked by the Florida Natural Areas Inventory (FNAI) that are of a size suitable for consumption by at least some ontogenetic stage of Burmese Pythons (10g–100kg) and that occur in suitable habitat within the State of Florida (139 taxa: species, subspecies, or populations judged by the Inventory to have taxonomic uniqueness). The FNAI tracks taxa that are either biologically imperiled or listed by a State or Federal agency as being of special conservation concern. The degree of imperilment is quantified by the number and size of discrete populations and is summarized on a scale of 1 to 5, where 1 is critically endangered (only a few individuals remain) and 5 is secure from a conservation perspective (many populations of many individuals). The number is preceded by various letters indicating the reference group: G stands for global and indicates that the reference group consists of all members of the same species found anywhere in the world; T indicates that the reference group is a special taxon (usually subspecies). A “Q” or “?” following the number indicates that there is some taxonomic or informational uncertainty afflicting the rating (see www.fnai.org for additional details on the assignment of rarity ratings). There are 75 biologically rare taxa within the State of Florida (Table 4.2) that are vulnerable to python predation and meet the Inventory’s rareness criteria 1–3, where 3 is either very rare and local throughout its range (21–100 occurrences or less than 10,000 individuals) or found locally in a restricted range or vulnerable to extinction from other factors. Using Federal or State listing as a metric of rarity, we find that 71 “listed” taxa from Florida are at risk of python predation (Table 4.2). We have not mapped out the global ranges of these 71, 75, or 139 imperiled taxa, but the majority appear to have distributions that would put them at risk of global extinction should the python spread throughout the area mapped to be climatically suitable in Figure 4.5.

Table 4.2. Imperiled wildlife potentially vulnerable to some ontogenetic stage of *P. molurus* or other giant constrictors in Florida, as tracked by the Florida Natural Areas Inventory (FNAI). Species with special legal status in either Florida or the United States are given in the last two columns respectively. See text for interpretation of the FNAI risk categories.

Class	Common Name	Scientific Name	FNAI	Florida	U.S.
Amphibians	Gopher Frog	<i>Rana capito</i>	G3	Spec. Conc.	-
Birds	Cooper's Hawk	<i>Accipiter cooperii</i>	G5	-	-
Birds	Bachman's Sparrow	<i>Aimophila aestivalis</i>	G3	-	-
Birds	Louisiana Seaside Sparrow	<i>Ammodramus maritimus fisheri</i>	T4	-	-
Birds	Macgillivray's Seaside Sparrow	<i>Ammodramus maritimus macgillivrayi</i>	T2	-	-
Birds	Cape Sable Seaside Sparrow	<i>Ammodramus maritimus mirabilis</i>	T1	Endangered	Endangered
Birds	Scott's Seaside Sparrow	<i>Ammodramus maritimus peninsulae</i>	T3Q	Spec. Conc.	-
Birds	Florida Grasshopper Sparrow	<i>Ammodramus savannarum floridanus</i>	T1	Endangered	Endangered
Birds	Brown Noddy	<i>Anous solidus</i>	G5	-	-
Birds	Florida Scrub Jay	<i>Aphelocoma coerulescens</i>	G2	Threatened	Threatened
Birds	Limpkin	<i>Aramus guarauna</i>	G5	Spec. Conc.	-
Birds	Great Egret	<i>Ardea alba</i>	G5	-	-
Birds	Great White Heron	<i>Ardea herodias occidentalis</i>	T2	-	-
Birds	Florida Burrowing Owl	<i>Athene cunicularia floridana</i>	T3	Spec. Conc.	-
Birds	Short-tailed Hawk	<i>Buteo brachyurus</i>	G4	-	-
Birds	Ivory-billed Woodpecker	<i>Campephilus principalis</i>	GH	Endangered	Endangered
Birds	Crested Caracara	<i>Caracara cheriway</i>	G5	Threatened	Threatened
Birds	Snowy Plover	<i>Charadrius alexandrinus</i>	G5	Threatened	-
Birds	Piping Plover	<i>Charadrius melodus</i>	G3	Threatened	Threatened
Birds	Wilson's Plover	<i>Charadrius wilsonia</i>	G5	-	-
Birds	Antillean Nighthawk	<i>Chordeiles gundlachii</i>	G4	-	-
Birds	Worthington's Marsh Wren	<i>Cistothorus palustris griseus</i>	T3	Spec. Conc.	-
Birds	Marian's Marsh Wren	<i>Cistothorus palustris marianae</i>	T3	Spec. Conc.	-
Birds	Mangrove Cuckoo	<i>Cossyzus minor</i>	G5	-	-
Birds	Florida Prairie Warbler	<i>Dendroica discolor paludicola</i>	T3	-	-
Birds	Kirtland's Warbler	<i>Dendroica kirtlandii</i>	G1	Endangered	Endangered
Birds	Cuban Yellow Warbler	<i>Dendroica petechia gundlachi</i>	T4	-	-
Birds	Little Blue Heron	<i>Egretta caerulea</i>	G5	Spec. Conc.	-
Birds	Reddish Egret	<i>Egretta rufescens</i>	G4	Spec. Conc.	-
Birds	Snowy Egret	<i>Egretta thula</i>	G5	Spec. Conc.	-
Birds	Tricolored Heron	<i>Egretta tricolor</i>	G5	Spec. Conc.	-
Birds	Swallow-tailed Kite	<i>Elanoides forficatus</i>	G5	-	-

Birds	White-tailed Kite	<i>Elanus leucurus</i>	G5	-	-
				Spec.	
Birds	White Ibis	<i>Eudocimus albus</i>	G5	Conc.	-
Birds	Merlin	<i>Falco columbarius</i>	G5	-	-
Birds	Peregrine Falcon	<i>Falco peregrinus</i>	G4	Endangered	-
	Southeastern American				
Birds	Kestrel	<i>Falco sparverius paulus</i>	T4	Threatened	-
Birds	Magnificent Frigatebird	<i>Fregata magnificens</i>	G5	-	-
Birds	Key West Quail-dove	<i>Geotrygon chrysia</i>	G3	Threatened	Threatened
				Spec.	
Birds	Whooping Crane	<i>Grus americana</i>	G1	Conc.	Endangered
Birds	Florida Sandhill Crane	<i>Grus canadensis pratensis</i>	T2	Threatened	-
				Spec.	
Birds	American Oystercatcher	<i>Haematopus palliatus</i>	G5	Conc.	-
Birds	Bald Eagle	<i>Haliaeetus leucocephalus</i>	G5	-	-
Birds	Worm-eating Warbler	<i>Helmitheros vermivorum</i>	G5	-	-
Birds	Least Bittern	<i>Ixobrychus exilis</i>	G5	-	-
Birds	Black Rail	<i>Laterallus jamaicensis</i>	G4	-	-
Birds	Wood Stork	<i>Mycteria americana</i>	G4	Endangered	Endangered
	Black-crowned Night-				
Birds	heron	<i>Nyctanassa nycticorax</i>	G5	-	-
	Yellow-crowned Night-				
Birds	heron	<i>Nyctanassa violacea</i>	G5	-	-
				Spec.	
Birds	Osprey	<i>Pandion haliaetus</i>	G5	Conc.	-
Birds	Painted Bunting	<i>Passerina ciris</i>	G5	-	-
Birds	White-crowned Pigeon	<i>Patagioenas leucocephala</i>	G3	Threatened	-
				Spec.	
Birds	Brown Pelican	<i>Pelecanus occidentalis</i>	G4	Conc.	-
	Red-cockaded				
Birds	Woodpecker	<i>Picoides borealis</i>	G3	Spec. Conc.	Endangered
Birds	Hairy Woodpecker	<i>Picoides villosus</i>	G5	-	-
				Spec.	
Birds	Roseate Spoonbill	<i>Platalea ajaja</i>	G5	Conc.	-
Birds	Glossy Ibis	<i>Plegadis falcinellus</i>	G5	-	-
		<i>Rallus longirostris</i>			
Birds	Mangrove Clapper Rail	<i>insularum</i>	T3	-	-
Birds	Florida Clapper Rail	<i>Rallus longirostris scottii</i>	T3?	-	-
Birds	American Avocet	<i>Recurvirostra americana</i>	G5	-	-
		<i>Rostrhamus sociabilis</i>			
Birds	Snail Kite	<i>plumbeus</i>	T3Q	-	-
				Spec.	
Birds	Black Skimmer	<i>Rynchops niger</i>	G5	Conc.	-
Birds	Louisiana Waterthrush	<i>Seiurus motacilla</i>	G5	-	-
Birds	American Redstart	<i>Setophaga ruticilla</i>	G5	-	-
	White-breasted				
Birds	Nuthatch	<i>Sitta carolinensis</i>	G5	-	-
Birds	Least Tern	<i>Sterna antillarum</i>	G4	Threatened	-
Birds	Caspian Tern	<i>Sterna caspia</i>	G5	-	-
Birds	Roseate Tern	<i>Sterna dougallii</i>	G4	Threatened	Threatened
Birds	Sooty Tern	<i>Sterna fuscata</i>	G5	-	-
Birds	Royal Tern	<i>Sterna maxima</i>	G5	-	-
Birds	Gull-billed Tern	<i>Sterna nilotica</i>	G5	-	-
Birds	Sandwich Tern	<i>Sterna sandvicensis</i>	G5	-	-
Birds	Bachman's Warbler	<i>Vermivora bachmanii</i>	GH	Endangered	Endangered
Birds	Black-whiskered Vireo	<i>Vireo altiloquus</i>	G5	-	-

Birds	Zenaida Dove	<i>Zenaida aurita</i>	G5	-	-
Mammals	Sherman's Short-tailed Shrew	<i>Blarina carolinensis shermani</i>	T1	Spec. Conc.	-
Mammals	Red Wolf	<i>Canis rufus</i>	G1Q	-	Endangered
Mammals	Rafinesque's Big-eared Bat	<i>Corynorhinus rafinesquii</i>	G3	-	-
Mammals	Big Brown Bat	<i>Eptesicus fuscus</i>	G5	-	-
Mammals	Florida Bonneted Bat	<i>Eumops floridanus</i>	G1	Endangered	-
Mammals	Hoary Bat	<i>Lasiurus cinereus</i>	G5	-	-
Mammals	Salt Marsh Vole	<i>Microtus pennsylvanicus dukecampbelli</i>	T1	Endangered	Endangered
Mammals	Southeastern Weasel	<i>Mustela frenata olivacea</i>	T4	-	-
Mammals	Florida Long-tailed Weasel	<i>Mustela frenata peninsulae</i>	T3	-	-
Mammals	Southeastern Bat	<i>Myotis austroriparius</i>	G3	-	-
Mammals	Gray Bat	<i>Myotis grisescens</i>	G3	Endangered	Endangered
Mammals	Northern Long-eared Myotis	<i>Myotis septentrionalis</i>	G4	-	-
Mammals	Indiana Bat	<i>Myotis sodalis</i>	G2	Endangered	Endangered
Mammals	Round-tailed Muskrat	<i>Neofiber alleni</i>	G3	-	-
Mammals	Key Largo Woodrat	<i>Neotoma floridana smalli</i>	T1	Endangered	Endangered
Mammals	Gulf Salt Marsh Mink	<i>Neovison vison halilmnetes</i>	T3	-	-
Mammals	Atlantic Salt Marsh Mink	<i>Neovison vison lutensis</i>	T3	-	-
Mammals	Southern Mink, So. FL pop	<i>Neovison vison pop 1</i>	T2Q	Threatened	-
Mammals	Key Deer	<i>Odocoileus virginianus clavium</i>	T1	Endangered	Endangered
Mammals	Pine Island Rice Rat	<i>Oryzomys palustris pop 1</i>	T1Q	-	-
Mammals	Sanibel Island Rice Rat	<i>Oryzomys palustris pop 2</i>	T1Q	Spec. Conc.	-
Mammals	Key Rice Rat	<i>Oryzomys palustris pop 3</i>	T2Q	Endangered	Endangered
Mammals	Key Largo Cotton Mouse	<i>Peromyscus gossypinus pop 1</i>	T1Q	Endangered	Endangered
Mammals	Choctawhatchee Beach Mouse	<i>Peromyscus polionotus allophrys</i>	T1	Endangered	Endangered
Mammals	Santa Rosa Beach Mouse	<i>Peromyscus polionotus leucocephalus</i>	T1	-	-
Mammals	Southeastern Beach Mouse	<i>Peromyscus polionotus niveiventris</i>	T1	Threatened	Threatened
Mammals	St. Andrews Beach Mouse	<i>Peromyscus polionotus peninsularis</i>	T1	Endangered	Endangered
Mammals	Anastasia Beach Mouse	<i>Peromyscus polionotus phasma</i>	T1	Endangered	Endangered
Mammals	Pedido Key Beach Mouse	<i>Peromyscus polionotus trissyllepsis</i>	T1	Endangered	Endangered
Mammals	Florida Mouse	<i>Podomys floridanus</i>	G3	Spec. Conc.	-
Mammals	Key Vaca Raccoon	<i>Procyon lotor auspicatus</i>	T1?	-	-
Mammals	Key West Raccoon	<i>Procyon lotor incautus</i>	T2	-	-
Mammals	Florida Panther	<i>Puma concolor coryi</i>	T1	Endangered	Endangered
Mammals	Mangrove Fox Squirrel	<i>Sciurus niger avicennia</i>	T2	Threatened	-
Mammals	Southeastern Fox Squirrel	<i>Sciurus niger niger</i>	T5	-	-
Mammals	Sherman's Fox Squirrel	<i>Sciurus niger shermani</i>	T3	Spec. Conc.	-

Mammals	Lower Keys Cotton Rat	<i>Sigmodon hispidus exsputus</i>	T2	-	-
Mammals	Insular Cotton Rat	<i>Sigmodon hispidus insulicola</i>	T1	-	-
Mammals	Lower Keys Rabbit	<i>Sylvilagus palustris hefneri</i>	T1	Endangered	Endangered
Mammals	Eastern Chipmunk	<i>Tamias striatus</i>	G5	Spec. Conc.	-
Mammals	Florida Black Bear	<i>Ursus americanus floridanus</i>	T2	Threatened	-
Reptiles	American Alligator	<i>Alligator mississippiensis</i>	G5	Spec. Conc.	-
Reptiles	Gulf Coast Smooth Softshell	<i>Apalone mutica</i>	T5	-	-
Reptiles	Spotted Turtle	<i>Clemmys guttata</i>	G5	-	-
Reptiles	American Crocodile	<i>Crocodylus acutus</i>	G2	Endangered	Threatened
Reptiles	Eastern Indigo Snake	<i>Drymarchon couperi</i>	G3	Threatened	Threatened
Reptiles	Red Rat Snake, Lower Keys pop	<i>Elaphe guttata, pop 1</i>	T2	Spec. Conc.	-
Reptiles	South Florida Rainbow Snake	<i>Farancia erythrogramma seminola</i>	T1	-	-
Reptiles	Gopher Tortoise	<i>Gopherus polyphemus</i>	G3	Threatened	-
Reptiles	Barbour's Map Turtle	<i>Graptemys barbouri</i>	G2	Spec. Conc.	-

The species most immediately in danger of extinction by the introduced *P. molurus* include the Key Largo Woodrat (*Neotoma floridana smalli*), whose global range is restricted to northern Key Largo in the Upper Florida Keys; the Key Largo Cotton Mouse (FNAI refers to this as *Peromyscus gossypinus* pop 1), similarly restricted in distribution; the Cape Sable Seaside Sparrow (*Ammodramus maritimus mirabilis*), whose global range is within Everglades National Park; and the Round-tailed Muskrat (*Neofiber alleni*), whose global distribution is limited to Florida and parts of southern Georgia. The seaside sparrow nests in low shrubs highly accessible to pythons. The muskrat has habits and habitats that put it maximally in harm's way, and though its resting platforms are conspicuous where present, the platforms have already become noticeably rarer in the areas occupied by the python (S. Snow pers. commun., 2008).

Should the python spread further into the Keys (presently it is known in Key Largo but does not clearly have a population established there), it would put several additional endemic populations or species at risk: Key Deer (*Odocoileus virginianus clavium*), Lower Keys Rabbit (*Sylvilagus palustris hefneri*), Lower Keys Cotton Rat (*Sigmodon hispidus exsputus*), Key Rice Rat (*Oryzomys palustris* pop 3), and Key Vaca Raccoon (*Procyon lotor auspicatus*). Should the python spread northward to Georgia, it would increase the risk on virtually all of the taxa listed in Table 4.2. Based on the experience of introduced prey sustaining artificially elevated introduced predator populations at the expense of native prey species (see references in Fritts and Rodda, 1998), the greatest biological impact of an introduced predator such as *P. molurus* is likely to be loss of imperiled native prey species. Species that are not presently listed as imperiled may become so or be extirpated. Species presently listed as at risk are in the greatest danger.

Although most endangerment from giant constrictors is likely to be associated with overt predation, it is possible that disturbance of birds at colonial roosts through

nighttime visitation by snakes could cause abandonment of dependent young and loss of recruitment, even without predation (P. Frederick, pers. commun., 2009).

13.2 Species of Special Concern as Predators (Giant Constrictors Augment Food Supply)

It is possible for an imperiled predator to benefit from the new prey species. For example, the Florida Panther (*Puma concolor coryi*) might obtain food by preying on Burmese Pythons. We have seen python carcasses in Everglades National Park that appeared to have been killed by predators, most likely panthers. However, this food supplementation effect is likely to be relatively minor and may be more than offset by competition between the two predators for food that is now diminished in abundance by the presence of the python, and by direct predation on panthers (especially panther cubs) by the python. Alligators and crocodiles may be in a similar situation of “intraguild predation”: individual predation events may favor one or the other predator, but the overall demographic effect is likely to be negative. We see no strong evidence for any predators that would consistently benefit from the presence of the python.

13.3 Vector for Disease Spread to or Within Native Faunas

Too few data exist to evaluate this consideration, though the risk of importation of parasites or pathogens cannot be excluded.

13.4 Species that Might be Adversely Impacted by Control Measures

If an indiscriminate control technique such as acetaminophen toxicants were to be applied to areas infested with Burmese Pythons, native species such as the Indigo Snake (*Drymarchon couperi*) or Florida panther (*Puma concolor coryi*) could be adversely impacted. It is difficult to project such ecological costs without a more distinctly enumerated set of management tools.

14.0 Perceived Impact (Social and Political Influences)

14.1 Pet Industry

14.1.1 Domestic Breeders Affected?

Domestic producers of Burmese Pythons for the pet industry and pet owners have raised objections to potential restrictions on the sale of this giant constrictor. Objections include concern for lost sales, concern that such a proposal would lead to other restrictions on pet ownership, and ideological objection to the concept of government regulation of pet ownership. If only importation of *P. molurus* were to be proscribed, domestic producers would presumably benefit via reduced competition from cheap imports.

There are a very large number (possibly exceeding 100,000) of Burmese Pythons in private ownership in the United States, though no one has data that would quantify the number or characterize the owners. Many are traded or exchanged in situations outside of conventional retail channels. Florida and Texas have begun to regulate ownership of

these animals, but it is too early to judge compliance with these measures (Environmental Law Institute, 2008).

Regulatory measures to restrict trade or ownership could have negative ecological effects in terms of dealers freeing stock (the release of multiple animals at the same time and same place enormously increases the risk over single releases such as those typically done by pet owners), owners releasing animals for which they don't have or cannot acquire appropriate licenses, and ecovandals determined to release animals as a imprecisely directed assault on the government.

14.1.2 International Trade/Alternate Pets

Companies that import Burmese Pythons would lose sales of these reptiles if importation restrictions were to be applied. As reptile importation has historically promoted both certain staple species (for example, Green Iguanas) and novelties (for example, Solomon Islands Monkey-tailed Skinks, amelanistic snakes), there is reason to believe that much of the importation effort associated with a particular species could be transferred to another species. In addition to likely economic impacts associated with such a shift, a large increase in importations of other species could significantly alter the risk environment associated with other potential invasive species. However, quantification of the economic impacts of trade regulations is a subject better handled by the economic impact report.

Chapter Five–The Reticulated Python, *Broghammerus reticulatus* or *Python reticulatus*

Biological Profile

1.0 Introduction

None of the giant constrictors is well known from field studies (though there is a substantial secondary literature), but the Reticulated Python stands out as poorly known even among these mysterious snakes. The few data come primarily from two sources: anecdotes from the colonial era (for example, Wall, 1926) and size, diet, and sex tabulations accumulated during the preparation of snakeskin leather (Shine and others, 1998a, b, 1999; Auliya, 2006). To date there is no body of literature based on field studies, with the conspicuous exception of one-third of one dissertation (Auliya, 2006). Though admirable in its scope and execution, Auliya was hampered by lack of preexisting information about field techniques and therefore was able to capture only 22 snakes, of which only one was a definite female. A recent compendium on the boas and pythons (Henderson and Powell, 2007) has no information from wild *Broghammerus reticulatus* and provides laboratory data only on the snake's digestive physiology. Therefore, though this report borrows heavily from the superb compendium provided by Auliya (2006), who synthesized all extant knowledge, we know very little about this species in the wild.

1.1 Species

Described by Schneider (1801) in the genus *Boa*, *Python reticulatus* or *Broghammerus reticulatus*, the Reticulated Python, is probably the world's longest snake (Bellosa and others, 2007). Although native range boundaries are disputed, the species conservatively ranges across much of mainland Southeast Asia, from Bangladesh to Vietnam, and virtually all of the islands between Asia and New Guinea (not found on New Guinea or the Aru Islands; it is found on Borneo, Sumatra, Java, Sulawesi, and the Lesser Sunda, Molucca, and Philippine Islands). The species is a giant constrictor characterized by a beautiful network (reticulations) of earth tones: white, tan, brown, yellow, and red.

There are three named subspecies of the Reticulated Python: *saputrai* (southwestern arm of Sulawesi and the island of Selayar), *jampeanus* (the island of Tanahjampea, south of Sulawesi), and *reticulatus* (the remainder of the range). Auliya (2006) opined that additional subspecies are likely to occur in the Sulawesi area.

1.2 Common Names

P. reticulatus or *B. reticulatus* is now almost always called the Reticulated Python in English (occasionally Reticulate Python, Wall, 1926; Pope, 1961; Frank and Ramus, 1995), though a century ago the name Regal Python was sometimes used for this species in honor of its grand size (Ditmars, 1931). However, the scientific name of the diminutive Ball Python (*Python regius*) carries a similar implication, and “Regal” or “Royal” descriptors are now used for the Ball Python or avoided entirely to preclude confusion.

The smaller subspecies are sometimes given distinctive common names for marketing purposes. In particular the *jampeanus* subspecies is often called a Dwarf Reticulated Python (commonly “Dwarf Retic”) to highlight its more manageable adult size (usually ~ 2-m total length).

1.3 Evolutionary Context

The Reticulated Python is very closely related to a smaller python, the Lesser Sundas Python (*Python timoriensis* or *Broghammerus timoriensis*), found on only a few of Indonesia’s Lesser Sunda Islands (but not Timor, despite the scientific name). The Reticulated Python and Lesser Sundas Python are clearly two twigs on the same evolutionary branch (“sister” taxa). However, the position of this branch in the evolutionary tree of pythons is less certain. The taxonomy of the Reticulated Python has been relatively stable (especially compared to Australasian Pythons), being located in the genus *Python* according to most 20th century observers (Underwood and Stimson, 1990; Kluge, 1993; Reptile Database, 2008). However, both evolutionary biologists and herpetoculturists (McDowell, 1975; Underwood and Stimson, 1990; Kluge, 1993; Walls, 1998b) pointed out that *P. reticulatus* was not only similar in several characters to *P. timoriensis* but it was also intermediate in many characters between the Afro-Asian pythons (for example, *P. molurus*, *P. sebae*, *P. curtus*) and the Australasian pythons (*Antaresia*, *Apodora*, *Aspidites*, *Bothrochilus*, *Leiopython*, *Liasis*, *Morelia*). Hoser (2004) recognized the unique intermediateness of the Reticulated Python by transferring it to the genus *Broghammerus*, in honor of one of his mentors. However, the justification for a monotypic genus of pythons was not widely accepted. Recently, Rawlings and others (2008) published a comprehensive molecular cladogram, which held that the phylogenetic grouping that included both the Reticulated Python and the other species in the genus *Python* also included all of the Australasian pythons, dictating that either the Reticulated Python + Lesser Sunda Python clade needed to be cleaved from the genus *Python*, or all of the Australasian pythons needed to be merged into *Python*. Rawlings and others (2008) opted for splitting, especially as a suitable name was already in use in the literature for the Reticulated Python. Adherents of this point of view will wish to use the name *Broghammerus reticulatus*. This name is not accepted by a number of prominent herpetologists (G. Zug, pers. commun., 2009), and conservative practice suggests retention of the older name *Python reticulatus*.

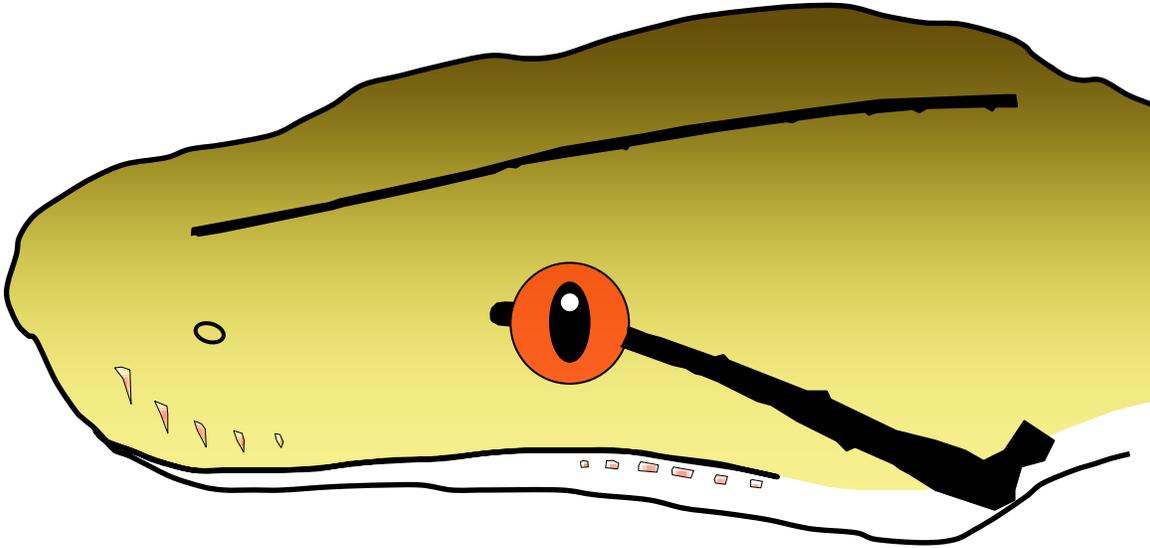


Figure 5.1. Schematic illustration of the head of a Reticulated Python.

2.0 Description

2.1 Unique Morphological Features

Whereas details of the scalation differ somewhat among the giant constrictors, the functional features of the morphology of the Reticulated Python share more similarities than differences with other snakes of similar size. For example, all the giant snakes are nonvenomous constrictors having short prehensile tails (*B. reticulatus* tails are 12–15 percent of total length); heavy bodies; large, angular but supple skulls with high counts of small, severely recurved teeth; vertical pupils; temperature-sensing thermal pits in their labial scales (except *Eunectes*); narrow belly scales; bodies circular in cross section; flanks with many rows of tiny scales; and the blotchy color pattern characteristic of species that depend more on crypsis than mobility for prey capture and predator defense. Vestigial pelvic girdles are present, as are spurs (pointed scales capping the pelvic girdles), which are proportionately longer in males than females (Shine and others, 1998a).

Reticulated Pythons differ from other giant constrictors and *Python* in having relatively lighter body mass (shared with *P. timoriensis*), lacking a wedge-shaped color marking (light or dark) on the top of the head (shared with *Eunectes* and some *P. brongersmai*); possessing a mid-sagittal dark line on the top of the head (Fig. 5.1; shared with *P. timoriensis*, and the blood python group *P. breitensteini*, *P. brongersmai*, and *P. curtus*); having a red/orange iris, especially when adult (Fig. 5.1; shared with blood python group); possessing a parallel-sided (as opposed to wedge-shaped) post-orbital dark mark (Fig. 5.1; shared with *P. anchietae* and *P. regius*); lacking a pre-orbital dark mark extending towards the nostril (shared with *Eunectes* and *P. timoriensis*); lacking posterior sutures in the rostral scale (shared with *Eunectes* and *P. timoriensis*); having a large number of subcaudal scales (55–102; no other *Python* species has more than 83,

though *P. timoriensis* is poorly known); and large size (0.6–9.7 m; shared with *Eunectes*). The genus *Broghammerus* (shared with *B. timoriensis*) is defined (Rawlings and others, 2008) externally “by having the supralabial thermoreceptive pits less well defined than the infralabial pits (converse arrangement in *Python*); by infralabial pits set in a longitudinal groove defined ventrally by a longitudinal fold [and] colour pattern of the suborbital supralabial region similar to the rest of the supralabials, compared with *Python*, in which there is a dark suborbital patch.” Mark Auliya (in litt., 2009) suggested that Rawlings and others (2008) accidentally reversed the polarity of the character comparing the depth of the supralabial and infralabial pits; our impression agrees with Auliya. The Reticulated Python is easily distinguished from *B. timoriensis* in possessing reticulated body coloration, lacking head shields darkened at the edges compared to the centers, and usually possessing a red iris.

Individual Reticulated Pythons can be distinguished on the basis of their blotch pattern (Vijayakumar, 1999) and the serial arrangement of paired and unpaired subcaudals (Auliya, 2006).

2.2 Size

As with all giant constrictors, the maximum length of the Reticulated Python is discussed far more than it is actually measured. In a rare exception, Cox (1991) measured a dead one, “a few centimeters less than ten meters.” Zug and Ernst (2004) acknowledged a 10-m Reticulated Python (presumably based on Raven, 1946), and most other authorities credit this value or list slightly lower figures (for example, Oliver, 1959; Pope, 1961; Murphy and Henderson, 1997; Tweedie, 1953; Walls, 1998b; O’Shea, 2007; Bellosa and others, 2007). However, specimens over 4 m in total length are rare in the wild (Shine and others, 1998a, b, 1999; Auliya, 2006), and even rarer in museum collections. Some benchmarks for wild populations are given in Table 5.1 (captives are not reported here, as they tend to be better fed and attain larger sizes, though Barker and Barker, 1997, give exceptionally small total lengths (457 mm) for some hatchlings). Useful references on size are: Wall, 1926; Smith, 1943; Ross and Marzec, 1990; Cox, 1991; Shine and others, 1998a, b, 1999; Walls, 1998b; Cox and others, 1998; Ziegler, 2002; Zug and Ernst, 2004; Auliya, 2006; and Bellosa and others, 2007. Note that different measurement samples (most were based on commercial collecting for skins) diverge appreciably in benchmarks such as size at maturation, and too few samples exist to generalize about the range of variation possible throughout the species.

Table 5.1. Total lengths and masses of typical *B. reticulatus* (compiled from the literature sources listed in the text).

Sex	Hatchling		Maturation		Max. reported	
	Total (mm)	Mass (g)	Total (m)	Mass (kg)	Total (m)	Mass (kg)
M:	550-850	95-210	1.6-3.5	1-10	~7	~90
F:	550-850	95-210	2.4-4.5	2.5-15	~10	~150

2.3 Sexual Size Dimorphism

Females mature at a larger size and attain a larger maximum size (see Table 5.1) than males, but the ratio of mean male and female size depends on the sexes' relative mortality schedules, which are not known for even one locality. Also, any size bias in sampling of the two sexes can skew estimates of sexual size dimorphism. Females are slightly longer in slaughterhouse samples, but they tend to be slightly lighter in weight for matched length samples (Shine and others, 1998a, b, 1999; Auliya, 2006). The degree to which female Reticulated Pythons exceed the size of their male counterparts is variable among samples; Shine and others (1998a) asserted that Reticulated Pythons show more extreme sexual size dimorphism than do most other snakes, with adult females 42 percent longer than adult males on average. However, Shine and others (1999) noted that the body size distributions of male and females were relatively similar (because more of the females in their sample were immature), and the sexual size dimorphism was not as extreme in the later sample from a different site on Sumatra (SSD not reported in the later study). Too few data exist to quantify the degree of SSD rangewide.

2.4 External Sexual Differentiation

Males have slightly longer tails and their spurs tend to be longer, but no definite method for external sexing has been derived, as the observed values have overlapping ranges between the sexes (Shine and others, 1998a, b, 1999; Auliya, 2006). Other body proportions (for example, head length) are relatively uniform between the sexes (Shine and others, 1998a, b; Auliya, 2006).

3.0 Distribution in Space and Time

3.1 Native Range

The southern limits of the native range of the Reticulated Python are relatively well known, but authorities disagree on the species' northern limits. Four published range maps (Groombridge and Luxmoore, 1991; Murphy and Henderson, 1997; Walls, 1998b; Auliya, 2006) differ in details of the northwest (India) and northeast (China) corners of the range, but the texts associated with these sources often suggest that the species may not be present in some northern areas. It is probable that the range of the python has contracted in response to human population expansion, but too few data are available to track range changes through time. We reprint the distribution of Auliya (2006; Fig. 5.2), as that is the authoritative rendition.

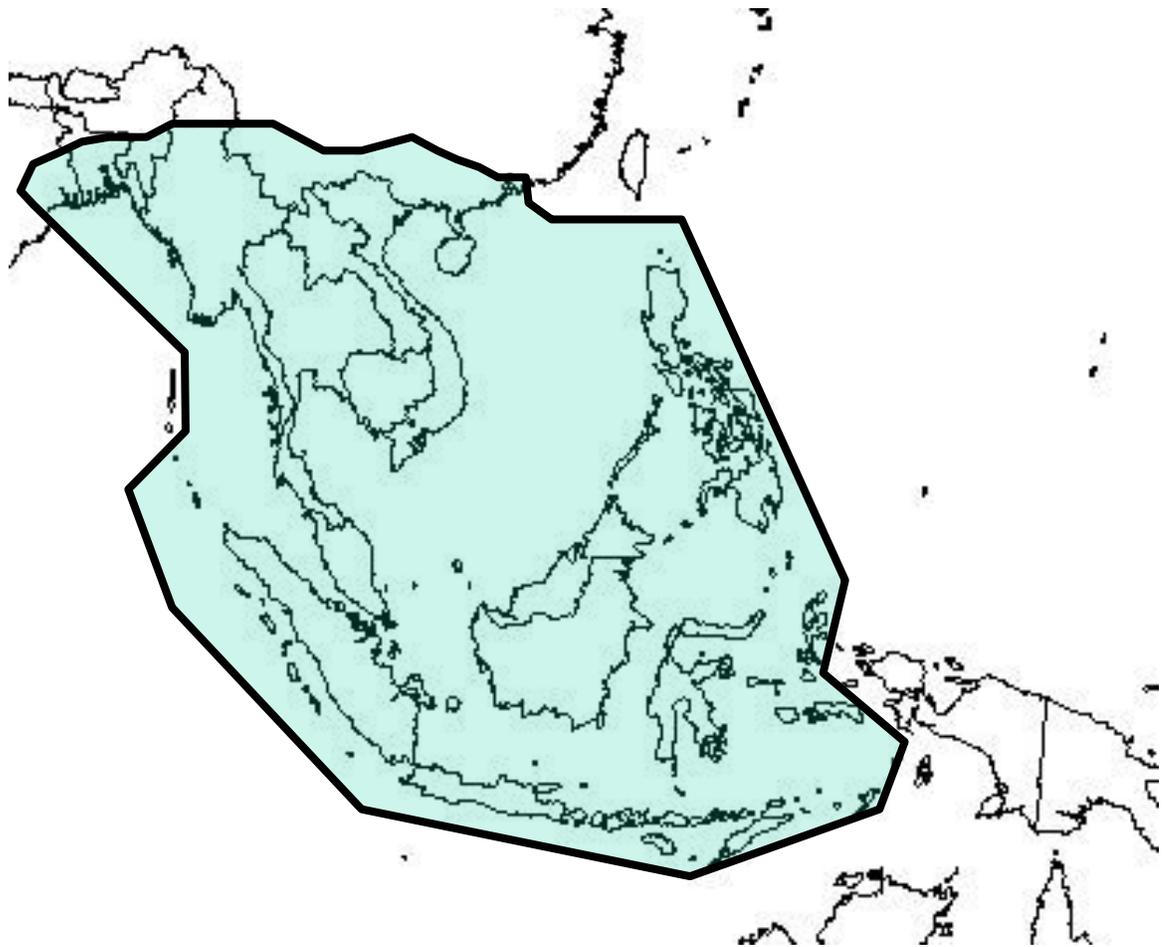


Figure 5.2. Native range of *B. reticulatus* as estimated by Auliya (2006), Auliya (in litt. 2009) and Bellosa and others (2007). Islands within the heavy outline are believed occupied by the Reticulated Python. Primary uncertainties include the entire northern periphery of the range, as well as the northwest and northeast corners of the range on the Asian mainland.

Bangladesh—Groombridge and Luxmoore (1991) accepted Khan’s (1982, cited in Groombridge and Luxmoore, 1991) assessment that Reticulated Pythons were found only in the southeastern “panhandle” of Bangladesh, or perhaps just inside the main unit east of the Ganges delta (see also Kock and Schröder, 1981). Noting the records of Daniel (2002), Khan (1988, cited in Groombridge and Luxmoore, 1991, but reference not given); Das (1994, 1996), and Islam and Islam (1997, cited in Auliya, 2006), Auliya (2006) maps out a more expansive distribution, including roughly the southern half of the country.

Brunei—Believed to be found throughout (Groombridge and Luxmoore, 1991).

Cambodia—Consensus is that it occurs throughout (all maps agree; Groombridge and Luxmoore, 1991; Murphy and Henderson, 1997; Walls, 1998b; Auliya, 2006), but Auliya (2006) notes that the only published locality is that of Trapeang Chan, north of 12° N. (Saint-Girons, 1972).

China—Records are few but most authors who doubt the presence of this snake in China rely on the undocumented assumption that its presence there is due to human transport. A specimen in the Leiden Natural History Museum from 25° N. is probably the most northern record for this species (tied with the record(s) from Arunachal Pradesh; below), but was found in a port city and may have been unintentionally from a more southerly locale. Wall (1903, cited in Auliya, 2006) and Stanley (1914, cited in Auliya, 2006) give records from China, but Auliya (2006) states that he agrees with Pope's (1935) conclusion that all records in mainland China are the result of introductions by humans; it is unclear whether any of these introductions have resulted in feral populations. In contrast, Walls (1998b) states that it "occurs through southern China (including Hainan [Island])." Auliya (in litt. 2009) concurred with occupation of Hainan Island. We consider all Chinese localities to be contested among authorities.

India—All sources agree that the Reticulated Python is resident in India's Nicobar Islands (off the northern tip of Sumatra) but not in the more northern extension known as the Andaman Islands (Deoras, 1965; Groombridge and Luxmoore, 1991; Das, 1994, 1996, 2002b; Murphy and Henderson, 1997; Walls, 1998b; Auliya and others, 2002; Auliya, 2006). However there is little consensus regarding the mainland distribution. Das (1994, 2002b) cites a specimen from Arunachal Pradesh, which is well north (26–27° N.) of any locality accepted (ca. 24° N.) by Auliya (2006), but consonant with the Assam limit stated by O'Shea (2007). Auliya (2006) accepts Deoras' (1965) locality in Madhya Pradesh (82° E; eastern peninsular India), which is nearly 1000 km west of most other records (for example, Groombridge and Luxmoore, 1991, recognize no mainland Indian localities). Whitaker and Captain (2004) considered its presence likely but unconfirmed in northeast India. We considered mainland Indian localities to be contested among authorities.

Indonesia—No serious dispute among authorities, except perhaps for a very small number of small Maluku islands at the eastern limit of the range. Auliya (2006) accepts as the limit Lydekker's line, which excludes New Guinea and several island groups near its western shore: Waigeo, Misool, and Aru Islands. The major islands included in the Indonesian native range of the Reticulated Python are Bali, Borneo, Buru, Flores, Halmahera, Java, Sumatra, Sumba, Sulawesi, Seram, Sumbawa, and Timor. All minor islands between these major islands are believed to be populated. Key references are: de Rooij, 1917; de Haas, 1950; Bosch, 1985; Underwood and Stimson, 1990; Groombridge and Luxmoore, 1991; Kluge, 1993; David and Vogel, 1996; Auliya and Abel, 2000a; Malkmus and others, 2002; Auliya and others, 2002; de Lang and Vogel, 2005; and Auliya, 2006. Koch (1926, cited in Auliya, 2006) asserted that the Reticulated Python was introduced to Ambon (small island south of Seram), though he did not cite evidence for this claim.

Laos—Although there is general agreement that it is found throughout (Deuve, 1970; Groombridge and Luxmoore, 1991; Auliya, 2006), specific localities are reported only by Stuart (1999, cited in Auliya, 2006), with most records occurring in central and southern parts of the country.

Malaysia—Observers agree that it is found throughout at suitable elevations. Key references are: Boulenger, 1912; Bourret, 1936 cited in Auliya 2006; Groombridge and Luxmoore, 1991; Stuebing, 1991; Malkmus, 1992; Inger and Tan, 1996; Barker and Barker, 1997; Stuebing and Inger, 1999; and Chan-ard and others, 1999.

Burma (Myanmar)—Authorities are uniform in accepting Myanmar as part of the native range, but they disagree somewhat as to the northernmost location in Myanmar. Without distinguishing between *P. molurus* and *B. reticulatus*, Salter (1983: cited in Auliya, 2006) claimed it was common throughout the country. Most other observers believe it present only in the southern half, though Salter (1983) notes a specific record for the Kyatthin (= Chatthin) Wildlife Sanctuary (23.6°N, 95.5°E) and this locality was confirmed by other sources (Zug et al. 1998, G. Zug, pers. comm., 2009). Localities to the north of this location are disputed among authorities.

Philippines—Found throughout, including the Batanes Islands (O’Shea, 2007), well north of the main archipelago: Taylor, 1922, cited in Auliya 2006; Bourret, 1936; de Haas, 1950; Leviton, 1963; Brown and Alcala, 1964; Groombridge and Luxmoore, 1991; Barker and Barker, 1997; Auliya, 2006; O’Shea, 2007.

Singapore—Resident (de Haas, 1950; Groombridge and Luxmoore, 1991; Lim and Lim, (1992, cited by Auliya, 2006; Paperna and others, 2004).

Thailand—Auliya’s (2006) map shows the Reticulated Python to be present throughout. This agrees with the other published maps (Groombridge and Luxmoore, 1991; Murphy and Henderson 1997; Walls 1998b), though Auliya seems to confirm de Haas’s (1950) assertion that it does not occur north of about 18°N, and Barker and Barker’s (1997) claim that it is limited to lower (unspecified threshold) elevations.

Vietnam—The northern limit of distribution in Vietnam is uncertain, though it appears to be common and widespread at least throughout the south (Campden-Main, 1970). A locality between 21° and 22° N. appears in Smith (1943), and other localities around Hanoi and further south are undisputed by most authors (Bourret, 1936; Darevsky, 1990; Ziegler and Hermann, 2000; Ziegler, 2002; Auliya, 2006). As this report went to press, a new volume on the herpetofauna of Vietnam was published (Nguyen and others, 2009); these authors do not recognize localities in the northern half of the country. If this assessment is accurate, then some of the climate loops currently considered “uncontested” in Fig. 5.3, should now be considered “contested.”

3.2 Habitat Range

Almost no information is available on habitat choices by Reticulated Pythons. Auliya (2006) made a valiant effort to compile anecdotal reports into a coherent description of the habitat and microhabitat (see below) preferences of this species, but the only strong generalizations to emerge were a penchant for inhabiting riparian zones (Smith, 1943; Campden-Main, 1970; Tweedie, 1953; David and Vogel, 1996; Auliya, 2006; and many others), and a willingness to utilize subterranean features in karst

landscapes (Hoogerwerf, 1970; Auliya, 2006). It is possible, however, that both of these attributes are induced or amplified by human persecution in more accessible places. David and Vogel (1996) summarize the habitat breadth of the species, “It is found from sea level up to more than 1300 m and it inhabits lowland primary and secondary tropical wet forests, tropical open dry forests, tropical wet montane forests, rocky scrublands, swamps, marshes, plantations and cultivated areas, and suburban and urban areas.” Several authors (for example, Manthey and Grossman, 1997; Malkmus and others, 2002) cite the 1,300-m maximum elevation figure reported by David and Vogel (1996), but Pope (1961) cited 1,200 m, Stuebing and Inger (1999) cited 1,000 m, and Cox and others (1998), Ziegler (2002), and O’Shea (2007) believe it reaches 1,500 m. McKay (2006) states that it reaches to 1,200 m on Bali but 1,300 m elsewhere.

The literature contains emphatic and yet contradictory views on the tolerance of *B. reticulatus* for populated places (Groombridge and Luxmoore, 1991). Wall (1926), for example, asserted that the “python is only met with in the densest jungles, places unknown to Europeans with the exception of a few forest officers, and an occasional sportsman.” In contrast, Wall (1926) cites Captain Stanley Flower (1899) who writes of a plethora of Reticulated Pythons living in the city of Bangkok, “Strange to say, it is not in the quiet jungle-forest that the python seems to prefer to live, but in the busiest spots along the Manam [River], where steamers and junks are loading and unloading, steam-launches whistling, steam-saws buzzing, rice-mill chimneys filling the air with smoke, and hundreds of noisy coolies passing to and fro...” Auliya (2006) attempts to reconcile these descriptions by suggesting that perhaps pythons in the 1–3 m size range are drawn to the high rat densities near human habitation, but that larger pythons find safety in more vegetated places. One must also be careful interpreting Captain Flower’s description of Bangkok of the 19th century in terms familiar to urban dwellers today. Flower noted that as Bangkok became a city the pythons grew scarce. Nonetheless, Cox (1991) asserts that occasional individuals continue to be caught within the city limits of Bangkok. Paperna and others (2004) found epidemiological data to suggest that Reticulated Pythons avoided densely populated areas of Singapore, even though rats were present.

From collections of pythons sold to tanners (Shine and others, 1998a, b, 1999; Auliya, 2006), it is evident that small (2–3 m) pythons remain numerous in oil palm plantations, rice fields, and other heavily developed agricultural landscapes (Inger and Colwell, 1977; Groombridge and Luxmoore, 1991; R. Rozar, pers. commun., 2009). However, they are also found in comparatively natural forests (Lim, 1981, cited in Groombridge and Luxmoore, 1991; Fredriksson, 2005; Auliya, 2006). The only consistent generality is that most individuals are found in association with water bodies.

3.3 Climate Range

Reticulated Pythons occur primarily in areas with a wet tropical climate (Fig. 5.3). Though they also occur in areas that are seasonally dry (Fig. 5.3), they do not occur in areas that are continuously dry, or very cold at any time.

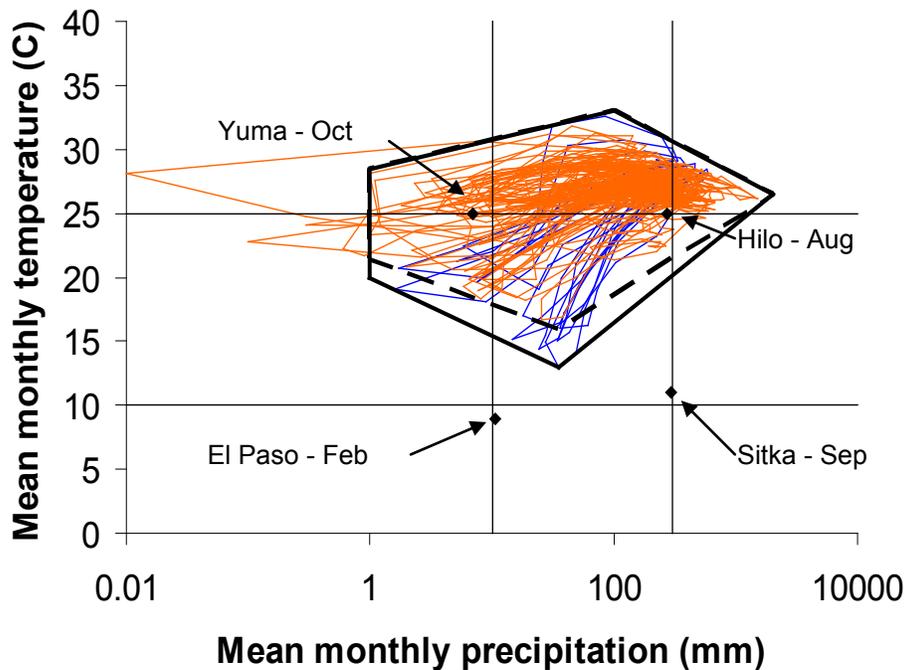


Figure 5.3. Climate space for *B. reticulatus*, with reference lines and localities as introduced in Fig. 2.1. The uncontested sites (orange lines) are those included in the native range maps of all peer-reviewed publications; inclusion of the contested sites (blue lines) expands the climate space (heavy black lines) from the dashed to the solid perimeter in a coldward direction.

3.4 Microhabitat

Pythons have been located in a wide range of microenvironments (especially near water) ranging from subterranean refuges, including the dark zone of caves, to moderate heights (6 m) in trees (van Rooijen and van Rooijen, 2002; Auliya, 2006). Auliya (2006) made the intuitively reasonable suggestion that arboreality might be more often expressed in the lighter weight juveniles (arboreality elevated in juveniles up to 2.0 m [presumably total length] according to O’Shea, 2007). Most pythons are found on the ground surface or at low perch heights, concealed in vegetation, but that is where most objects are found by human searchers. Without more information on the detection probabilities in different microenvironments, it is difficult to estimate the degree to which the range of observations is due to python behavior or human perception.

3.5 Introduced Ranges

We are aware of no strong evidence for any introduced population of the Reticulated Python. However, it is curious how often early observers concluded that Reticulated Python sightings at the edge of the known range must represent introductions. Such statements have been made for the northeastern (China), southeastern (Molucca or Maluku Islands), and northwestern (India) edges of the range. Part of the willingness of

these observers to ascribe the outlying records to human introduction may be due to observations of pythons appearing as stowaways in shipments (potentially attracted to the rats accompanying agricultural products). Several famous examples are reported by Wall (1926): four Reticulated Pythons were found in a shipment of coconuts from Rangoon; one in a ship arriving in Mumbai, India from Moulmein, Myanmar; another arriving alive on a ship docking in London (source locality unspecified). The paucity of recent records of this sort (in contrast to the persistence, until the last few decades, of *Boa constrictor* arriving in shipments of bananas) suggests that modern shipping methods have much reduced the likelihood of such accidental transport.

3.6 Seasonal Activity

Too few data exist to make any generalizations about seasonal locomotor activity. Given the aseasonal climate associated with most of the python's range, we would not expect there to be any seasonal limitations on activity in many areas. Nonetheless, Groombridge and Luxmoore (1991) cite statements from hide buyers that the majority in Sumatra are caught in the wet season (up to twice as many a month as in the dry season).

Several authors have commented on the propensity of Reticulated Pythons to be found in loose aggregations. Murphy and Henderson (1997) commented on the surprising absence of such observations in the literature, though as we noted in the introduction to this species, the relevant literature is quite sparse. David and Vogel (1996, probably based on Hagen, 1890) noted that aggregations may be found inside tree trunks or under plants during the day or in cool weather. A similar phenomenon was noted by van Rooijen and van Rooijen (2002) who found three aggregations (one of four individuals and two of two) among the 13 individuals they discovered during a short (Mar./Apr.) trip to a Malaysian island, Pulau Tioman. It would be helpful to know if their visit coincided with the local mating activity, as most aggregations of large constrictors have been associated with intermale competition for mates.

Several authors (Lederer, 1944; Barker and Barker, 1997; Walls, 1998b) have pointed out that unlike most snakes, Reticulated Pythons bite rival males, often inflicting very serious wounds. Nearly all authors comment on the willingness of some Reticulated Pythons to bite their human handlers. The word "vicious" is most commonly heard, though it is not clear that malice is motivating their behavior. Barker and Barker (1997) go to some length to argue that they have periodically encountered Reticulated Pythons with a disposition suitable for handling. However, these "pet-quality" individuals are evidently relatively rare; Walls (1998b) characterizes the species as "...one of the most feared. The Retic is notorious as an aggressive biter that often never tames. Though hatchlings and young specimens may have decent personalities, adulthood almost always brings with it an awful personality."

Several authors report evidence that Reticulated Pythons are either very sedentary in their habits or inclined to return to sites visited previously—philopatry (Kopstein, 1926, cited in Groombridge and Luxmoore, 1991; van Rooijen and van Rooijen, 2002; Auliya, 2006). As most pythons seem to be killed on first contact with humans, it is unlikely that many examples of philopatry would be documentable. In the absence of radiotelemetric studies, it is difficult to quantify or assess this propensity.

3.7 Daily Activity

No systematic data have been collected on daily patterns of activity or locomotion, though van Rooijen and van Rooijen (2002) found that five of seven became active after dusk (the remaining two were quiescent after large meals). Distinguishing resting behavior for alert but immobile ambush foragers is not easy to do in an animal lacking eyelids. Most anecdotes imply nocturnal activity (David and Vogel, 1996; Walls, 1998b; Auliya, 2006), but Ernst and Zug (1996) and Zug and Ernst (2004) suggest it may be more nocturnal where doing so would avoid conflicts with humans.

3.8 Foraging Mode/Sensory Modalities

Given the paucity of observations of Reticulated Pythons capturing prey (Auliya, 2006, reports one observation), it is plausible to assume that the pythons are primarily sit-and-wait or ambush foragers, as is believed characteristic of most large constrictors. What senses are used to identify prey are unknown; de Cock Buning and others (1978) found that it was easiest to arouse pythons with visual stimuli (movement brought a response in 87 percent of trials), though jets of prey-scented air were also effective in about 65 percent of trials. Thermal and vibratory cues were of ancillary importance; strikes were elicited only in the presence of visual cues. Newman and Hartline (1982) showed neurological overlap in processing of visual and thermal information. De Cock Buning and others (1978, 1981) and de Cock Buning (1979, 1983) explored the physiology of thermal reception in Reticulated Pythons.

4.0 Life History

4.1 Reproductive Mode

Like all pythons, the Reticulated Python lays eggs. The mother surrounds her eggs for most of their incubation period of 55–105 days (Wall, 1926; Smith, 1943; Branch and Patterson, 1975; Ross and Marzec, 1990; Cox, 1991; Manthey and Grossman, 1997; Cox and others, 1998; Walls, 1998b; Malkmus and others, 2002; Ziegler, 2002; Zug and Ernst, 2004; Auliya, 2006), presumably protecting them from light, desiccation, and predators (and potentially having some ability to limit mold or the spread of mold to healthy eggs). One would expect higher temperatures to expedite incubation, but hard data on incubation temperature in the wild are lacking for *B. reticulatus* (Shine, 1988; Ross and Marzec, 1990; Murphy and Henderson, 1997). As the reported incubation times usually lack information on incubation temperature, the incubation times are very difficult to interpret. Unlike some other pythons, however, the brooding mother python apparently does not warm the eggs with shivering thermogenesis (Wall, 1926; Vinegar and others, 1970; Honegger, 1970; La Panouse and Pellier, 1973; Cox, 1991; Walls, 1998b; Malkmus and others, 2002), though some observers have claimed that she does (Lederer, 1944 (equivocal); Hediger, 1968; Shine, 1985, 1988; Kluge, 1993). Apparently heat production, if it occurs, is minimal or contingent on specific conditions.

4.2 Reproductive Phenology

Given the paucity of data on pythons from the wild, it is difficult to make generalizations about the seasonal course of reproductive activities. Mating is rarely observed in the wild, and therefore little can be said about male reproductive phenology (though Shine and others, 1998a, found males to have larger testes in October 1994 than in April 1995); most inferences are made about female phenology, from the appearance of eggs or hatchlings. Within a species, the females can be synchronized throughout the range, synchronized within a locality but asynchronous across the native range (often associated with latitude as a proxy for onset of rains), or asynchronous within each locality. There are, of course, degrees of asynchrony; to our knowledge, uniform breeding throughout the year every year has not been documented in any reptile species. However, the degree of synchrony within a site can vary from strict seasonality (all local individuals breed simultaneously) to many months of some reproductive activity (some individuals breed much earlier than their peers), and the time of year for the breeding pulse can vary somewhat from year to year (perhaps in relation to local weather patterns). A definitive statement for even a single locality would require multiple years of data collection to ensure that the pattern observed in one year was representative of all years, and no research has been conducted continuously over the course of even one year. For example, Shine and others (1998a, b, 1999) made only short visits (about two weeks) three to four times a year at two sites in Sumatra. Nonetheless, they declared that reproduction is strongly seasonal in both sexes.

From the length of the gestation period (from mating to oviposition) and the length of the incubation period (from oviposition to hatching), we can roughly infer a locality's reproductive phenology from the knowledge of a single feature, such as peak oviposition date. Oviposition dates for wild pythons are given by five sources (Ross and Marzec, 1990; Shine and others, 1998a, 1999; Malkmus and others, 2002; Auliya, 2006). Auliya (2006) is the only source that gives dates for the four benchmarks: mating, oviposition, incubation, and hatching, though Malkmus and others (2002) also cites hatching dates. Groombridge and Luxmoore (1991) estimate gestation at two months; Ross and Marzec (1990) state 65 to 105 days, or two to three months. A large number of authors (see 4.1) estimate the incubation period at durations ranging from 55 to 105 d, or two to three months.

Reproduction in the tropics often tracks the onset of rainfall, which correlates with the movement of the sun (Intertropical Convergence), which is a function of latitude. From south to north the available oviposition dates are shown in Table 5.2.

The only source that is clear on the year-round pattern is Auliya (2006) in a relatively aseasonal environment with highly subjective and unquantified dates taken from local informants. In that environment, oviposition was not recorded only in May (the driest month) and July. The peak of oviposition at Shine and others' (1999) nearby and equivalently aseasonal site was in Apr.–May. Furthermore, the April peak appears in all study localities, suggesting that local variation in reproductive phenology may be extensive and may not be closely associated with latitude or rainfall.

Table 5.2. Peak oviposition dates of *B. reticulatus* by latitude (0 = no oviposition known; 1 = some oviposition known, but believed to be nonpeak; 2 = peak oviposition).

Authority	Lat	Seasonality	J	F	M	A	M	J	J	A	S	O	N	D
Shine and others, 1998a	S 2	Low				1				2	2	2		
Auliya, 2006	N 1	Very Low	1	2	2	1	0	1	0	1	1	2	2	2
Shine and others, 1999	N 2	Very Low			1	2	2	1		0				1
Malkmus and others, 2002	N 6	Low			2	2								
Ross and Marzec, 1990	N 10-18	Medium			2	2	2							

Taken in combination with the assumption that mating precedes oviposition by 2–3 months, these oviposition dates imply that we would expect mating activity to take place in midyear at the lat 2° S. site, the second half of the year at the lat 1° N. site, and near the beginning of year at the other sites. The only direct evidence is Auliya’s (2006) reasonably congruent estimate that mating occurred Aug.–Feb., with a peak in Nov.–Jan.

Taken with the assumption that oviposition precedes hatching by 2–3 months, these oviposition dates imply that hatching should peak at around Oct.–Dec. at the lat 2° S. site, Dec.–May at the lat 1° N site, and June–July at the other sites. The only direct evidence comes from Auliya’s (2006) figure showing peak hatching from Sept.–Nov. (which comports poorly with our estimate from oviposition dates and incubation duration), and Malkmus and others’ (2002) statement of a May–June hatching peak (which agrees reasonably with our June–July extrapolation). Considerable additional data collection will be needed to adequately describe the reproductive phenology of the Reticulated Python.

It is not unusual for reptiles to temporarily cease feeding during reproduction. The start and end triggers for this phenomenon have not been quantified in the Reticulated Python. A typical comment is that of Hagenbeck (letter cited by Taylor, 1965), “During the period of incubation I offered ducks, fowls, and geese to the python, but she refused all nourishment.” Honegger (1970) recorded that a captive male did not fast during his mate’s incubation (implying that she did so). In contrast, Barker and Barker (1997) stated that males “...cease feeding at the beginning of the breeding season...,” though no statement was made about the time of resumption of feeding or whether females also undergo reproductive aphagia. Lederer (1944) states that males fast during the period of mating and females fast during the period of brooding.

Williamson (1967) noted that a well-fed captive juvenile (of unspecified sex) fasted voluntarily at ages of about 12 months (8-week fast) and 24 months (17-week fast). Ditmars (1912) claimed that this was the pattern in tropical snakes, “This annual fasting period particularly appeals to the boas and pythons, which are of peculiarly delicate organization that responds quickly to changes of temperature and undoubtedly affects the feeding habits of these reptiles during the well-defined seasons in the tropics.” If this hypothesis is true, it may be difficult to infer the causes of anecdotes of aphagia observed in captivity.

4.3 Reproductive Effort/Fecundity

4.3.1 Clutch or Litter Size/Frequency

Individual females may not lay every year; Shine and others (1998a, b, 1999) judged Reticulated Pythons to be highly seasonal reproducers and thereby estimated from the peak observed fraction of reproductive females that females in Sumatra laid once every two or three years. Fitch (1970) comments that, “Unlike Indian pythons, females of this species that bred in captivity, seemed incapable of producing a clutch annually.”

The number of eggs produced is strongly dependent on the size of the female. Shine and others (1999) illustrated the relationship (their Fig. 3) and specified its strength ($r^2 = 0.88$), but did not provide the regression equation. As only one female in Shine and others (1999) exceeded 4 m in snout-vent length, it is difficult to judge the size–fecundity relationship for large females. Relative clutch mass (ratio of clutch mass to maternal carcass mass) of the one measured female was 0.39.

The clutch “sizes” (number of eggs laid at a time by one female) reported in the literature range from 8–124, with typical clutches of 20–40 (Hagenbeck, 1909; Wall, 1926; Kopstein, 1938; Smith, 1943; Lederer, 1944; Pope, 1961; Hoogerwerf, 1970; Groombridge and Luxmoore, 1991; Barker and Barker, 1997; Manthey and Grossman, 1997; Murphy and Henderson, 1997; Cox and others, 1998; Walls, 1998b; Shine and others, 1998a, 1999; Malkmus and others, 2002; Zug and Ernst, 2004; Auliya, 2006). We are not aware of any oviparous snake having a larger maximum clutch size.

4.3.2 Egg Size

The eggs are surprisingly large, sometimes described as grapefruit sized. Actual measurements of the smaller dimension range from 58–77 mm, the larger dimension from 89–115 mm, and the mass from 182–245 g (Wall, 1926; Kopstein, 1938; Lederer, 1944; Honegger, 1970; Groombridge and Luxmoore, 1991; Manthey and Grossman, 1997).

4.4 Growth

It is difficult to characterize growth of reptiles, as growth is generally size-, diet-, and season-specific. All things being equal, linear growth is maximal after hatching and declines thereafter. Therefore, although there are three data points on the growth of Reticulated Pythons in the wild (Auliya, 2006), these three points would be difficult to interpret without knowing the underlying size, diet, and seasonal patterns. Furthermore, none of the three is a strong point, as the three recaptures occurred over excessively short intervals (7–43 d) and two of the three report a reduction in total length (negative growth), probably due to reduced stretching on second capture.

Growth in captivity has a wide range (Lederer, 1944; Williamson, 1967; Honegger, 1970; Minton and Minton, 1973; Trutnau, 1980; Kingley, 1987), presumably as a result of differing thermoregulatory and caloric conditions. Some captive pythons grow only a tiny amount, but Shine and others (1998a) report that captive hatchlings have grown to over 4 m in total length in less than 12 months (~275 mm/mo); Barker and Barker (1997) imply a similar figure. Such growth may be the fastest that has been recorded for any snake (though Frye and Mader, 1985, recorded a similar growth rate of

245 mm/mo in a captive *P. molurus*), and far exceeds reasonable expectations for growth in the wild. Williamson (1967) recorded an initial (30 month) captive growth rate of 141 mm/mo, which itself is much faster than any growth recorded for a snake in the wild (for example, the rapidly growing Brown Treesnake, *Boiga irregularis*, has an initial average growth rate of 38 mm/mo; our unpub. data).

Shedding frequency in the wild is unknown; Honegger (1970) reported that three captive hatchlings shed about two weeks after birth (Wall, 1926, stated “about a month,” Williamson’s, 1967, python at 8 d) and at intervals averaging 54 days for their next four sheds. Williamson’s (1967) well-fed captive averaged 40 days between sheds over the first two years, slowing to a rate of once per 61 days in the third year. Pope (1961) cites a python that shed an average of every 55 days when it was in the 4–5 m size range. Lederer (1944) documented the decline in shedding frequency with age, stating young shed 5–9 times per year (40–73 d apart), subadults, 4–7 times (52–91 d apart), and adults, 3–7 times (52–121 d apart).

Length-weight relations in the wild are known for two samples of pythons with a snout-vent length up to about 5 m; southern Sumatra (Shine and others, 1998a) and western Borneo (Auliya, 2006).

4.5 Maturation

Shine and others (1998a) infer from captive growth that maturation is reached at age 2 years in males and 3 years in females. They explicitly based this on extraordinarily rapid captive growth. For example, Cox (1991) records maturation at an age of 5 years (unspecified whether this value is for captivity or in the wild). Barker and Barker (1997) state that captive males have been observed to court females as early as one year of age, but that successful captive breeding is attained only at 18 to 24 months for males and 30 to 36 months for females. Shine and others (1998a) also emphasized that Reticulated Pythons mature at a conspicuously small size relative to the size they might ultimately achieve (Table 5.1).

4.6 Longevity

There are no data on life expectancy in the wild; several captive specimens lived for nearly 30 years (maximum, 29 years 5 months; Schmidt and Inger, 1957; Pope, 1961; Minton and Minton, 1973; Groombridge and Luxmoore, 1991; Snider and Bowler, 1992; Walls, 1998b; Slavens and Slavens, web page, accessed 25 Nov. 08, available at <http://www.pondturtle.com/lsnakea.html#Python>). Barker and Barker (1997) refer to wild Reticulated Pythons “...with their 40- to 50-year life spans...” but do not cite a basis for this inference.

5.0 Diet/Trophic Role

5.1 Prey

Most of the available data are anecdotal, with emphasis on finding the largest item recovered from a stomach. Such records seem to emphasize wild boars (Ditmars, 1912; Shelford, 1917, cited in Murphy and Henderson, 1997; Jacobsen, 1936, cited in Auliya, 2006; Groombridge and Luxmoore, 1991; Shine and others, 1998b; Auliya, 2006),

though bears have also been documented (Domalain, 1991, cited in Auliya, 2006; Fredriksson, 2005). Ditmars (1912) is unusual in going beyond anecdote to report that 60 percent of a series of 40 large (criterion for large unspecified) wild-caught Reticulated Pythons had boar bristles or hooves in their excreta. He goes on to assert that “Many captive specimens of this great snake refuse all other food but swine, and examples twenty feet [6 m] in length, swallow a fifty-pound [22.5 kg] pig without difficulty.” More recent systematic data collection (Shine and others, 1998a, b, 1999; and Auliya, 2006) shows a heavy preponderance of chickens and rats, though perhaps the snakes turned in for the hide trade are more easily collected from agrarian landscapes where rats are exceptionally abundant. Other notable items include monitor lizards (Mertens, 1942; Auffenberg, 1994; Shine and others, 1998b), civet cats (Groombridge and Luxmoore, 1991; Shine and others, 1998b; Auliya, 2006), bats (Auliya, 2006), an immature cow (Barker and Barker, 1997; Auliya, 2006), various primates (Groombridge and Luxmoore, 1991; MacDonald, 1992, cited in Auliya, 2006; Shine and others, 1998b; Wiens and Zitzmann, 1999; Gursky, 2002), deer (Jacobsen, 1936; Ussher, 1979, both cited in Auliya, 2006; Wall, 1926; Hendrickson, 1966; Groombridge and Luxmoore, 1991; Shine and others, 1998b), goat (Kopstein, 1926; Wall, 1926), pangolins (Groombridge and Luxmoore, 1991; Shine and others, 1998b; Auliya, 2006), cats (Wall, 1926), dogs (Wall, 1926; Auliya, 2006), ducks (Wall, 1926), rabbits (Malkmus and others, 2002), tree shrews (Auliya, 2006), porcupines (Shine and others, 1998b), and many birds (Shine and others, 1998b). Frank Buck (1935, 1939, both cited in Murphy and Henderson, 1997) claims to have witnessed the capture of a leopard by a Reticulated Python, but unlike the other large animal accounts, this one does not appear to have gained credibility through frequent recitation. We also question its veracity, based on the unrealistic details provided. Walls (1998b) summarized the python’s diet by concluding, “most mammals and birds in its range.” However, it will also eat “large lizards [see also David and Vogel, 1996], frogs and fish” (Auliya and Abel, 2000b). Like *P. molurus*, the Reticulated Python recruits digestive tissue at the time of each large meal (Luz, 2002, cited by M. Auliya, in litt.; Secor and Ott, 2007; Ott and Secor, 2007a, b).

5.2 Predators

Many authors note that Reticulated Pythons habitually sleep over water, into which they plunge when disturbed (van Rooijen and van Rooijen, 2002; O’Shea and others, 2004). Though there are a number of accounts of dangerous prey animals that inflicted wounds on attacking pythons, there are few accounts that document Reticulated Pythons in the stomachs of higher order predators. Indeed we found no accounts specifically citing predation on Reticulated Pythons, though small individuals must be ready fare for large predatory crocodilians, birds, felids, pigs, and canids. In most areas, humans are presumably the most dangerous predator to pythons; this has been frequently documented (for example, Ditmars, 1912; Wall, 1926; Raven, 1946; Pope, 1961; Auliya, 2006).

5.3 Diseases and Parasites

A host of internal and external parasites plague wild Reticulated Pythons, as documented by Wall (1926), Shine and others, (1998b), and Auliya (2006). The pythons are especially hosts to various protozoans, nematodes, pentastomids, ticks, and lung

arthropods. There are no data to judge whether these infestations are of demographic significance. Pythons are known to carry ticks of agricultural significance while captive in Florida (Burridge and others, 2000, 2006). Kan and Hii (1979) found that Reticulated Pythons can transmit *Capillaria* (a cestode) that may result in the human disease capillariasis.

6.0 Demography

6.1 Population Density

There are no data on the density of wild Reticulated Python populations. Auliya (2006) noted that he caught 19 in a 4.4 km² area over six months, indicating that at least that many passed through the study area during the course of the study.

6.2 Size Distribution

The study of size distributions is severely plagued by sampling problems. For example, Shine and others, (1998a, b, 1999) and Auliya (2006) were able to document the size of pythons turned into skin dealers, but the dealers were uninterested in small snakes (and hatchlings are likely to be diverted into the more profitable live-animal trade). Furthermore, the skin buyers were located in agrarian areas where rat populations were likely to be subsidized by the availability of high-sugar-content crops (Shine and others, 1999); thus the size distributions submitted might reflect human disturbance of natural vegetation as much as snake availability. Nonetheless, the relative paucity of small snakes may suggest rapid initial growth, such as is seen in captive animals. The relative paucity of very large snakes may reflect natural and unnatural mortality of these long-lived animals.

7.0 Interactions with Humans

7.1 Human Utilization and Persecution

Reticulated Pythons are the premier source of leather from snakes. The most complete analysis of the trade (Groombridge and Luxmoore, 1991) covered only the years 1986–1989, when export records showed the international trade ranging from 200,000 skins per year to around 700,000. Internal organs from the snakes killed for their skins are used for medicinal purposes, especially the gall bladders (Shine and others, 1999; G. Zug, pers. commun., 2009). The number of snakes exported live is less well documented, but about an order of magnitude smaller (see 7.3.1). No doubt additional individual pythons are killed in areas too remote for transport to a buyer. Shine and others (1999) note that their informants reported that virtually all pythons encountered were killed, “because of the value of the meat and the advantages of removing nuisance animals that might otherwise devour chickens, dogs or children.”

7.2 Human Health Risks

The Reticulated Python is a particularly dangerous species of giant constrictor. Murphy and others (1994) is the only reputable source we found that argued that

Reticulated Pythons "...should not be considered a serious threat to human life." We can divide human fatalities into two categories on the basis of whether the snake was being potentially provoked by a human, usually the owner of a pet snake ("illegitimate bites"), as opposed to attacks on humans that were not interacting with the snake prior to the bite ("legitimate bites"). To our knowledge, illegitimate bites have never resulted in ingestion of the human, probably because the bites were defensive in nature, intended merely to cause the human to stop bothering the snake (lethal constriction is effective for this). Most of the giant constrictor bites clearly documented in the literature refer to illegitimate bites, but the Reticulated Python stands out as being the source of many legitimate bites, in which the snake often ingests the killed human (unless other humans intervene). Among the authorities who have weighed in on this distribution of deaths, Walls (1998b) is a minority of one for his assertion that Reticulated Pythons do not exhibit ingestion of adults: "...[although] it has been repeatedly charged with killing and eating children...[it] has been seen to kill, but not eat, adult humans." The most widely cited example of child eating is of a 14-year-old boy killed on the island of Salibabu, in the Talaud Islands north of Sulawesi (Kopstein, 1927). Incidents from this part of the world tend to be poorly documented, but this one was reported by a credible scientist and therefore has been very extensively cited (Smith, 1943; Tweedie, 1953; Schmidt and Inger, 1957; Pope, 1961; Campden-Main, 1970; Caras, 1975; Barker and Barker, 1997; Murphy and Henderson, 1997; Zug and Ernst, 2004; Auliya, 2006, among others).

Legitimate bites have not been limited to children; for example, Auliya (2006) cites a 60-kg adult removed from the stomach of a Reticulated Python in 1998 from the Philippines. Cox (1991) states that Reticulated Pythons are capable of killing adults. Muthusamy and Gopalakrishnakone (1990, cited in Murphy and Henderson, 1997) report two incidents with adults, at least one of which was unquestionably "legitimate." Barker and Barker (1997) cite a 29-year-old rubber tapper killed in peninsular Malaysia in 1995, as well as others earlier near Rangoon, and on Borneo, Sumatra, Sulawesi, and Halmahera. Murphy and Henderson (1997) recount numerous attacks and ingestions, both illegitimate and legitimate. Barker and Barker (1997) go so far as to aver that, "Of the species of giant snakes, there are more verified reports of man-eating reticulated pythons than of all the other species combined." They also assert that most go unreported, "with many cases classified simply as 'missing persons'." Headland and Greene (2007) presented data to show that in a preliterate hunter-gatherer society (Agta Negritos) in the Philippines in the 1970s, "...26% of adult males had survived predatory attacks by reticulated pythons and fatal attacks still occurred in the 1970s." A substantial number of the tribe's adults knew personally of a person who had been ambushed and killed. It is notable that claims to this effect are lacking for most other portions of the Reticulated Python's range; a possible exception is the undocumented assertion by the 19th century zoo collector Carl Hagenbeck (1909) that "It is said that in Borneo the natives are frequently attacked and devoured by giant serpents, and from what I have seen of their capacity for dealing with large prey I have no doubt that a full-grown Borneo python could easily swallow a man."

Davis (1980), Flank (1997), Murphy and Henderson (1997), and Day (2008) report some of the illegitimate fatalities.

7.3 Human Aesthetic Relations

7.3.1 Pet Trade

There are major discrepancies between reporting agencies on the number of Reticulated Pythons imported into the United States, though all sources acknowledge that undercounting occurs due to incomplete declarations, smuggling, and contradictory records. CITES records (Fig. 5.4) are acknowledged to be incomplete after 2005, but show fairly steady imports at around 4,000 per year. LEMIS records of the Fish and Wildlife Service for the period 1998–2005 averaged about 12,375 per year, roughly on parity with the number of *P. molurus* importations (C. Romagosa, pers. commun., 2008, from LEMIS records), and a dramatic increase from the 2,333 yearly average for the period 1989–2000 (Reed, 2005). We are unable to resolve these discrepancies, but all sources indicate that thousands of Reticulated Pythons are imported to the United States annually.

In addition to these sales of wild-caught or farmed/ranched individuals from the python's native range are added pythons that are captive bred in the United States, a substantial but unquantified number. As the captive-reared animals are often bred for unique colors, they are likely to be more expensive than the roughly \$100 retail price of an imported python (C. Romagosa, pers. commun., 2008, from LEMIS records).

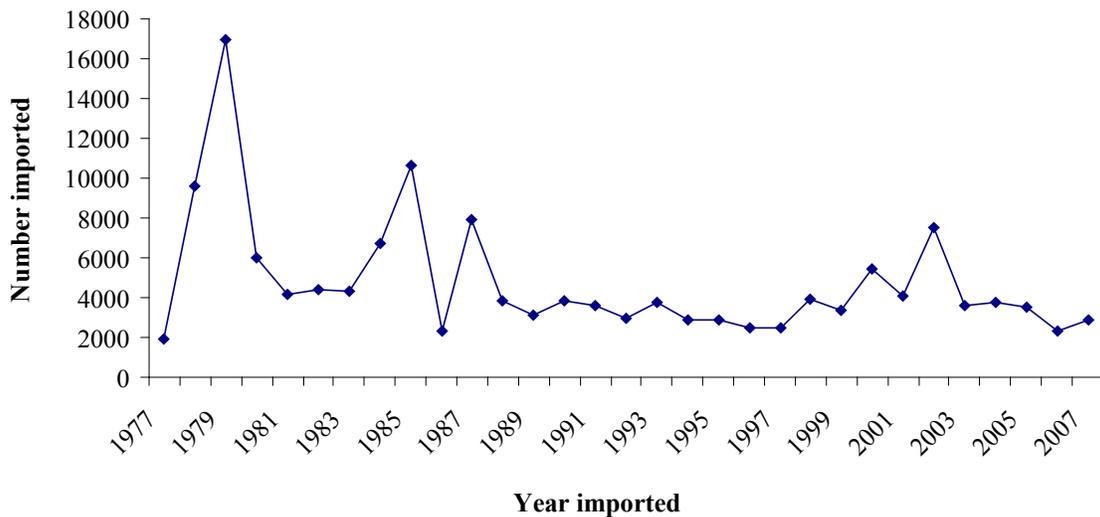


Figure 5.4. CITES records for importation to the United States of live *B. reticulatus*.

7.3.2 Other Uses

Major human uses of Reticulated Pythons are limited to leather, medicinals, meat (all section 7.1), and pets (7.3.1).

Management Profile

8.0 Pathway Factors: Pet Trade

As with the other giant constrictors, the overwhelming majority of live Reticulated Pythons reach the United States through the pet trade.

8.1 Volume of International Trade

As indicated in section 7.3.1, above, Reticulated Pythons are among the most often imported snakes, with thousands imported per year. Section 8.1 of chapter Four outlines reasons why imported snakes might constitute a slightly greater risk of establishment than captive-reared individuals, though hard data on this phenomenon are lacking.

8.2 Volume of Domestic Trade

We are aware of no estimates on the volume of domestic sales or breeding of Reticulated Pythons, but it seems to be increasing, especially for designer morphs or dwarf lineages. Our impression is that the domestic production is somewhat smaller than international trade for the United States, but we cannot verify this impression.

9.0 Entry Potential (Survival in Transit - Meant Mainly for Unintentional Transport)

As with all of the giant constrictors, survival in the pet-trade pathway is intentional and approaches 100 percent, as giant constrictors can routinely fast for the period of time between capture and sale, and the substantial expense associated with the purchase of a python generally induces care by owners that is sufficient for survival of these relatively robust snakes.

10.0 Colonization Potential

10.1 Likelihood of Escape/Release

The same set of factors that promote release of unwanted pet Burmese Pythons (see section 10.1 of Chapter Four) applies with equal or greater force to Reticulated Pythons. The only discernible difference is that Reticulated Pythons have a more fearsome reputation (which inhibits demand for adults), and they show slightly greater growth rate and maximum size than do Burmese Pythons, also limiting demand for adults. Reticulated Python individuals that are prone to attack their owners (behavior which appears to be more frequent in Reticulated Pythons) will likely induce owners to discard problematic individuals.

10.2 Climate Match: Areas of the Country at Greatest Risk

Reticulated Pythons have a more tropical distribution than Burmese Pythons. Accordingly, the area of the mainland United States showing a climate match of uncontested sites is smaller, exclusively tropical, and limited to southern Florida (Fig. 5.5; note that newly-available information for Vietnam, discussed in Section 3.1, could conceivably further reduce the area considered suitable in Florida, but we were unable to incorporate this information before going to press). However, if one includes those portions of the mainland Asia range that are judged occupied by some but not all observers, one obtains the climate match shown in Fig. 5.6, which also includes much of central Florida and the lower Rio Grande section of Texas. If the range limit of the Reticulated Python at the northern limit of the range reflects competition with Burmese Pythons, it is conceivable that additional portions of the United States would be at risk if they were not already occupied by Burmese Pythons. Given the current distribution of Burmese Pythons in Florida, and the ongoing spread of that species, such a scenario seems unlikely to become manifest in Florida, though there is a small chance that it could become so in extreme southern Texas. Low and mid-elevation sites in America's tropical territories (Guam, Northern Mariana Islands, American Samoa, Virgin Islands, Puerto Rico) and Hawaii would also appear to be climate matched to the requirements of the Reticulated Python, whether using all localities or the subset considered uncontested.

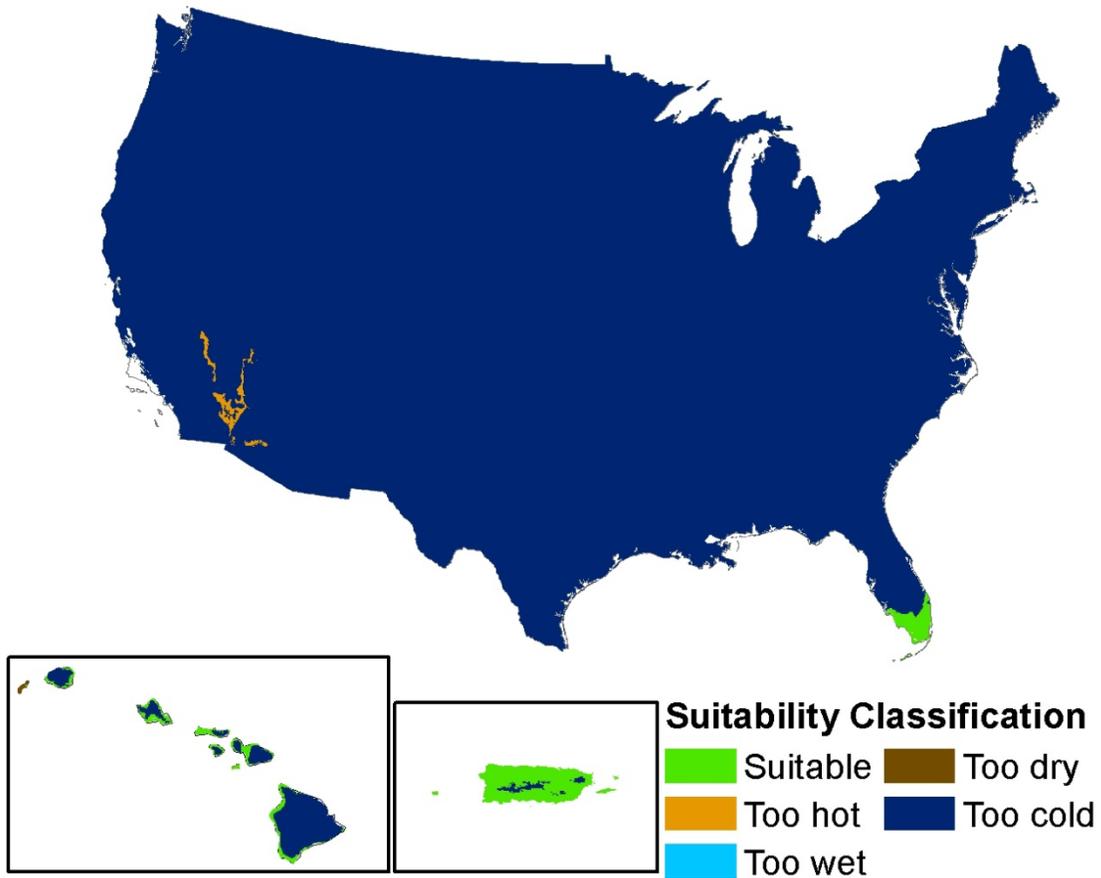


Figure 5.5. Areas of the United States matching the climate envelope expressed by *B. reticulatus* using only those portions of the range that are deemed occupied by all observers (see section 3.1).

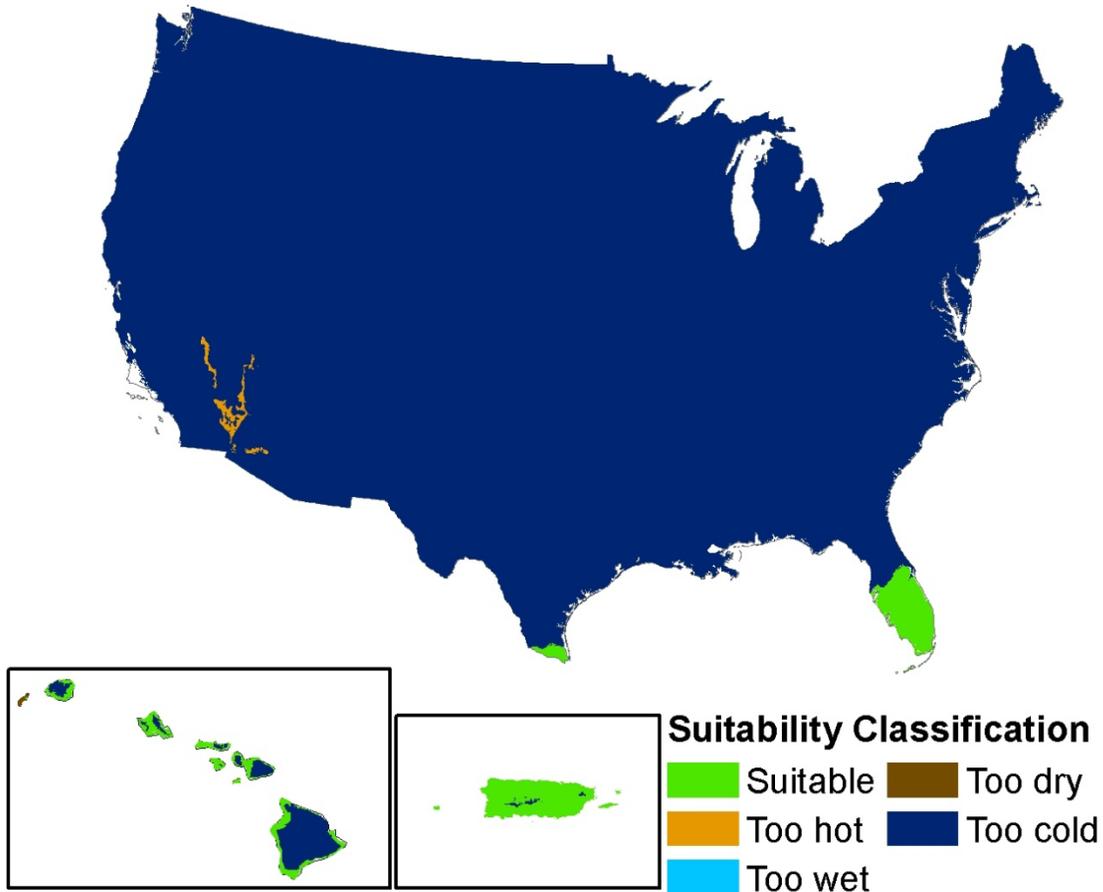


Figure 5.6. Areas of the United States matching the climate envelope expressed by *B. reticulatus* using all portions of the native range deemed occupied by any of the observers cited in section 3.1.

10.3 Prey Availability

The prey range of Reticulated Pythons is essentially the same as that of the Indian Python, as far as is known, including all birds, reptiles, and mammals of a size appropriate for the individual predator. Large frogs and fish are eaten less regularly, if at all, but might sustain an introduced population that had no alternative prey. Given the extreme generality of the Reticulated Python's diet, the mainland sites indicated in Figs. 5.5 and 5.6 would not appear to have any shortage of appropriately sized endotherms. Prey availability for large Reticulated Pythons could be a limiting factor in some insular situations, as noted in chapter Four, section 10.3.

10.4 Predation Risk

The Reticulated Python is the longest known snake, and the United States has no specialized predators that would take a large adult python. However, smaller generalized predators such as crocodilians or panthers would probably take small individuals, as noted for Indian Pythons in chapter Four, section 10.4. That narrative suggested that

such “intra-guild” predation would have an equivocal demographic outcome, with each predator prevailing where it was larger than an individual prey item, but with little demographic significance overall. In comparison to adult Burmese Pythons, Reticulated Pythons seem to be more aquatic, and thus adults might have fewer encounters with panthers. Hatchling Reticulated Pythons appear to be more arboreal than similar-sized Burmese Pythons (Retics are more slender, as befits a climber), and thus juveniles may have fewer encounters with crocodilians.

10.5 Reproduction Requirements

We are aware of no specialized reproduction requirements of this species, which broods its eggs but does not show shivering thermogenesis as far as we know. Thus it would probably have difficulty incubating eggs in colder climates, which should be reflected in the climate envelope and maps above.

10.6 Hibernation Requirements

As far as it known, Reticulated Pythons do not hibernate.

10.7 Tools for Eradicating a Colonization

The tools for eradication of this species are not known to differ from those specified in chapter Three, and section 10.7 of chapter Four. Because Reticulated Pythons do not hibernate, they might be especially vulnerable to capture while basking on cold days at the northern limit of their range.

11.0 Spread Potential

11.1 Dispersal Ability

To the best of our knowledge, there are no relevant data on dispersal ability. We have no reason to think that Reticulated Pythons would be less vagile than Indian Pythons. The record clutch size for Reticulated Pythons is 124, the largest known clutch of any oviparous snake, so they are unlikely to have their population-dispersal ability limited by fecundity.

11.2 Ability to Develop Races or Strains

There are no data to evaluate this issue in Reticulated Pythons. As the rare subspecies are highly sought after in the pet trade and are therefore disproportionately numerous in the trade, release of differing strains is a distinct possibility, though the rare subspecies presently command a premium price and attain smaller body sizes, which would presumably limit human motivation for release in the wild.

11.3 Tools for Managing Spread

There are no species-specific data germane to managing spread in this species. The highly aquatic adults may be difficult to constrain by barriers that end at the water’s edge. The arboreal habitats of juveniles suggest that barriers would also be more difficult to design and to maintain in forested habitats.

12.0 Economic Impact Potential

A formal economic analysis of the potential impacts of introduction of the Reticulated Python and possible regulation of the trade may be conducted pursuant to a variety of statutes and Exec. Order 13272, Proper Consideration of impact on small business. We defer to the economists for hard data; our narrative is provided only to cite relevant biological literature and identify germane sections of the bioprofiles.

12.1 Pathogen Vector

Reticulated Pythons are known to harbor a variety of pathogens or vectors that could potentially be of human health or agricultural significance; see discussion in section 5.3 regarding papers on Reticulated Python ticks (Burrige and others, 2000, 2006) and cestodes (Kan and Hii, 1979). The epidemiological significance of these carriers is unknown.

12.2 Predator on Livestock

Reticulated Pythons in their native range are reported to prey on all sizes of livestock. However, because the average Reticulated Python is relatively small, we infer that the greater predatory challenge would be on poultry (see chapter Four section 12.2).

12.3 Predator on Pets

Predation on all types of pets (except horses) is within the size range of known Reticulated Python predation, but the frequency of occurrence is probably sensitive to the snakes' willingness to reside in suburban situations. In its native range, the snake is heavily persecuted by a very high density of humans in mostly agrarian societies where few snakes of such a size would go undetected. It is less clear if that dynamic would have a similar outcome in American suburbs, which are often depopulated during business hours.

12.4 Electrical Power Systems

Juvenile Reticulated Pythons would presumably be capable of climbing overhead power lines, though their propensity for doing so is completely undocumented.

12.5 Traffic Accidents/Human Attacks

Human predation by Reticulated Pythons is sufficiently rare that it is not judged as a major public health problem in the snake's native range. Nonetheless, of all the giant constrictors, this species has the most abundant evidence for "legitimate" attacks (section 7.2). One imagines that such an attack in the United States would garner extensive press coverage due to its novelty and the iconic reputation of the Reticulated Python. This could have an appreciable negative influence on the serenity of residents and tourists. That this species does coexist with humans in urban or suburban settings would probably heighten anxieties in comparison to fear of species believed to stay in wild places.

12.6 Tourism

Of the two regions of the U.S. mainland showing potential evidence of a climate match with the native range of Reticulated Pythons (south Texas and southern Florida), southern Florida is probably the region most dependent on tourism and therefore most vulnerable to disruptions of tourism. However, southern Florida already has an acknowledged reputation for unsavory characters, both reptilian and otherwise. Thus the potential impact on tourism is probably relatively minor, given that southern Florida is already colonized by the Burmese Python. However, a widely publicized human-Reticulated Python encounter in an urban area of southern Florida could adversely impact tourism there.

Insular areas of the United States might be far more sensitive. For example, Hawaii is well known to be a tropical paradise, in part for the absence of snakes. Given the range of estimates associated with potential Brown Treesnake impacts on Hawaii tourism (up to \$3B/year; Shwiff, 2008), a legitimate Reticulated Python attack in Hawaii could be very costly. Whereas the dollar cost of an incident would be less in other U.S. insular areas (Guam, Northern Mariana Islands, Puerto Rico, Virgin Islands, American Samoa), the proportionate impact to those fragile island economies could be highly disruptive. The potential economic cost makes this improbable event worthy of serious consideration.

12.7 Impacts on Commercially Important Wildlife

12.7.1 Species Hunted with Gun or Binoculars

South Florida and south Texas ecotourism are associated with bird watching. Birds that are imperiled or visually striking are especially desired. Imperiled species are the ones most likely to be impacted by python predation (see section 7.1). Thus to the extent that visitation is tied to success at bagging a sighting of a rare bird, the presence of a novel predator on rare birds is likely to be detrimental to tourism. Gun hunting is relatively unimportant in southern Florida, and species that are most sought after in extreme southern Texas (for example, quail) are apt to be a bit small to be a primary prey of Reticulated Pythons. If southern Texas was to become colonized, there would be some impact to larger species (for example, deer).

12.7.2 Species That Impact Forestry, Agriculture, or Horticulture

Reticulated Pythons are unlikely to have a direct impact on forestry, agriculture, or horticulture, though one can imagine a scenario where agricultural workers might become disenthralled with field labor involving the chance of unexpectedly encountering a Reticulated Python (for example, sugar cane workers in south Florida; orchard workers in south Texas).

13.0 Environmental Impact Potential

13.1 Species of Special Concern as Prey or Competitors

See section 13.1 of the Burmese Python chapter (Four) for a listing of prey species that might be impacted by the Reticulated Python. The Reticulated Python would be expected to have a lower impact because (1) its anticipated range potential is substantially less (primarily southern Florida, but potentially also southern Texas and central Florida), and (2) the Burmese Python will likely have spread throughout the area of potential Reticulated Python colonization by the time the Reticulated Python would become established. Thus the two pythons are likely to be each other's most important competitor, and it is less likely that the second-arriving species would have as large an impact as the first (and therefore novel) giant constrictor.

13.2 Species of Special Concern as Predators (Giant Constrictors Augment Food Supply)

As indicated in section 13.2 of chapter Four, food supplementation by Reticulated Pythons is likely to be offset, or possibly more than offset, by intra-guild predation. For example, some alligators would no doubt get a meal from the presence of Reticulated Pythons in southern Florida, but it is equally likely that some Reticulated Pythons would make a meal of juvenile American Alligators, with no clear net result.

13.3 Vector for Disease Spread to or Within Native Faunas

Too few data exist to evaluate this consideration, though the risk of importation of parasites or pathogens cannot be excluded.

13.4 Species That Might be Adversely Impacted by Control Measures

If an indiscriminate control technique such as acetaminophen toxicants were to be applied to areas infested with Reticulated Pythons, native species such as the Indigo Snake (*Drymarchon couperi*) or Florida panther (*Puma concolor coryi*) could be adversely impacted (due to the lack of specificity of acetaminophen as a toxin). It is difficult to project such ecological costs without a more distinctly enumerated set of management tools.

14.0 Perceived Impact (Social and Political Influences)

14.1 Pet Industry

14.1.1 Domestic Production Affected?

Domestic producers of Reticulated Pythons for the pet industry and pet owners are likely to raise objections to potential restrictions on the sale of this giant constrictor. Objections include concern for lost sales, concern that such a proposal would lead to other restrictions on pet ownership, and ideological objection to the concept of government regulation of pet ownership. If only importation of *B. reticulatus* was to be

proscribed, domestic producers would presumably benefit via reduced competition from cheap imports.

There are a very large number of Reticulated Pythons in private ownership in the United States, though no one has data that would quantify the number or characterize the owners. Many retics are traded or exchanged in situations outside of conventional retail channels. Florida and Texas have begun to regulate ownership of these animals, but it is too early to judge compliance with these measures (Environmental Law Institute, 2008).

Regulatory measures to restrict trade or ownership could have negative effects in terms of dealers freeing stock (the release of multiple animals at the same time and same place enormously increases the risk over single releases such as those typically done by pet owners), owners releasing animals for which they don't have or cannot acquire appropriate licenses, and ecovandals determined to release animals as an imprecisely directed assault on the government.

14.1.2 International Trade/Alternate Pets

Companies that import Reticulated Pythons would lose sales of these reptiles if importation restrictions were to be applied. As reptile importation has historically promoted both certain staple species (for example, Green Iguanas) and novelties (for example, Solomon Islands Monkey-tailed Skinks, *Corucia zebrata*, amelanistic snakes), there is reason to believe that much of the importation effort associated with a particular species could be transferred to another species. Thus the industry would be less affected overall than specific breeders that have developed stock or expertise in this particular species. Quantification of the economic impacts of trade regulations would be the subject of an economic impact report (Exec. Order 13272), if needed. We defer to that economic analysis for assessment of this issue.

Chapter Six–The Northern African Python, *Python sebae*, and the Southern African Python, *Python natalensis*

Biological Profile

1.0 Introduction

See section 1.0 of the biological profile of the Indian Python (chapter Four) for a description of species-specific and overall components of the risk assessment package.

1.1 Species

Python sebae and *Python natalensis* are closely related, large-bodied pythons of similar appearance found in sub-Saharan Africa. *Python sebae* was described in 1789, while *Python natalensis* was described as a full species as 1840; within 25 years the latter taxon was considered a variant of the former, rather than a distinct species. This taxonomy held fairly steady for a century, until Broadley (1984) re-examined museum material and concluded that *P.s. sebae* and *P.s. natalensis* were valid subspecies. Broadley's (1984) work was partially stimulated by the description of *Python saxuloides* (Miller and Smith, 1979), which was described as a sister taxon to *P. sebae*, but which was later deemed a slightly aberrant population of *P. s. natalensis* by Broadley (1984, 1999).

Based on morphology, the presence of a single known hybrid individual from Tanzania, and an apparent zone of sympatry spanning 900 km from Kenya southwest into the Democratic Republic of the Congo, Broadley (1999) later raised *P.s. natalensis* to a full species. This conclusion has been widely accepted in the African herpetological community, as reflected in the names used in field guides and journal articles. Unfortunately, however, the geographical extent of overlap between these species is still only partially known, and many questions remain about how to refer older literature records to the correct species. This means that some aspects of African python ecology are difficult to tease apart at the species level, especially for observations from areas where both species may occur.

1.2 Common Names

The most common English name for this species complex has been African Rock Python. After *P. sebae* was nominally split from *P. natalensis*, some authors added 'Northern' and 'Southern' as a prefix to this common name (for example, Spawls and

others, 2002). Broadley (1999) opined, “I am unhappy about the use of ‘African Rock Python’ as these snakes show no particular association with rocky habitats, so I propose the use of ‘Northern African Python’ for *P. sebae* and ‘Southern African Python’ for *P. natalensis*.” In this document we have adopted Broadley’s recommendations, and refer to these snakes as the Northern and Southern African Pythons. When considered together, we will refer to both species as the giant African pythons.

As would be expected for species with such large distributions, local common names are legion. Auerbach (1987) lists 60 common names in 44 different languages in Botswana and its immediate surrounds alone. Of these, commonly encountered names include Afrikaanse reusslang, Luislang, or Gewone luislang (Afrikaans), Joboia africana (Portuguese), !na//ke: (!Kung), Ngoi (Kikomi), Chatu or Satu (Swahili), and Inhlwathi, uMonya, or imFundamo (Zulu). Farther north in Sudan, the Northern African Python is called Assalaa (El-Kamali, 2000); a wide range of common names can be expected in the northern and western parts of the range of the Northern African Python but are not enumerated here.

1.3 Evolutionary Context

The giant African pythons have long been considered members of an AfroAsian group, usually including *P. sebae*, *P. molurus*, and *P. regius*, but occasionally also including *B. reticulatus*, *P. anchietae*, the *P. curtus* complex (including *P. brongersmai* and *P. breitensteini*), and/or *B. timoriensis* (McDowell, 1975; Underwood and Stimson, 1990; Kluge, 1993; Lawson and others, 2004). None of these phylogenetic analyses have distinguished between the two giant African pythons, and some analyses (for example, Kluge, 1993) have used specimens of both species, while most GenBank records fail to give localities for the specimens from which tissues were collected.

More recently, Rawlings and others (2008) examined the phylogeny of pythons using nuclear and mitochondrial genes. They concluded that the Northern African Python (and by extension its putative sister taxon) is most closely related to *P. molurus*, the Asian python commonly referred to as the Indian or Burmese Python (depending on subspecies). Indeed, while the Northern and Southern African Pythons can be readily distinguished by head scalation, it is more difficult to distinguish the former from *P. molurus* using any surefire quantitative measure. Rawlings and others (2008) also concluded that the AfroAsian pythons (*P. sebae*, *P. molurus*, *P. brongersmai* and relatives, and *P. regius*) represent a basal clade within the python radiation, and that some species formerly included within the genus (*B. reticulatus* and *B. timoriensis*) should be assigned to a new genus (they proposed using the available genus *Broghammerus*).

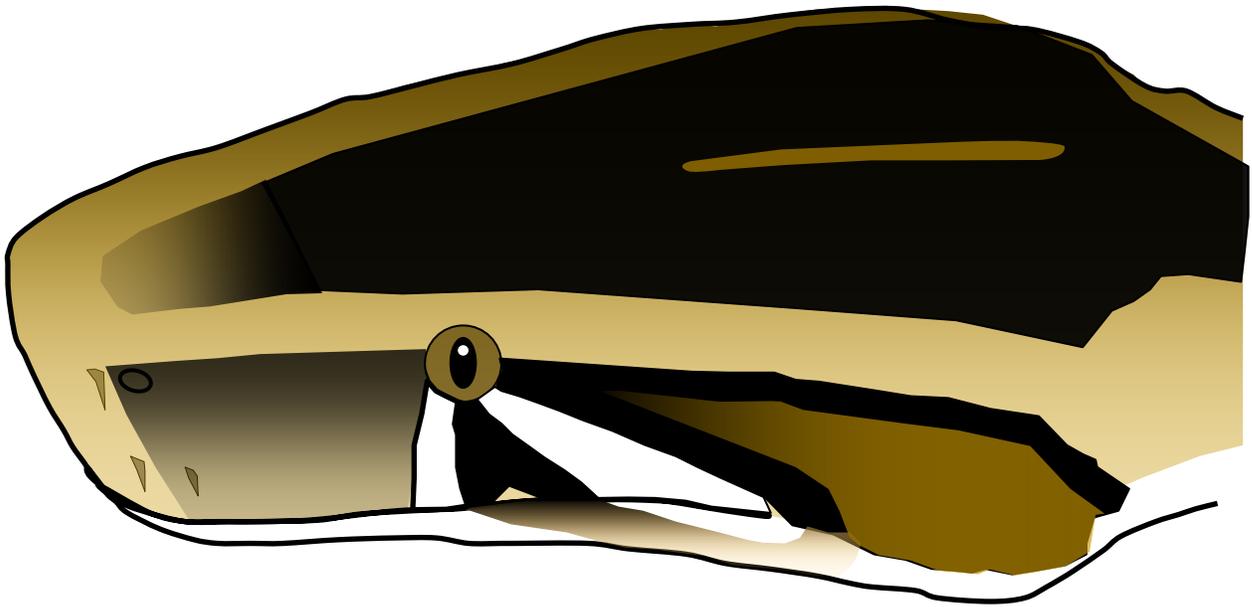


Figure 6.1. Schematic representation of the head of *P. sebae*.

2.0 Description

2.1 Unique Morphological Features

The following general description of body color pattern in the giant African pythons is based on descriptions in Branch (1988), Spawls and others (2002), Marais (2004), Lanza and Nistri (2005), Alexander and Marais (2007), and our personal observations. See below for more specific information on head pattern and means of discriminating between the two species. The overall impression when viewing these pythons is of a brown or grey python with numerous dark dorsal blotches and dark lateral spots. Dark brown to brownish-black saddles or bars are present dorsally, usually edged in black. These markings vary in size and shape and may be connected by complete or nearly complete dark paravertebral stripes on each side. When connected by paravertebral stripes, animals appear very dark on the dorsum, with regular “islands” of lighter ground color present mid-dorsally – these islands are often constricted in the middle, giving them the general shape of a number “8” oriented sideways to the long axis of the body. Lateral dark markings in the shape of a “C” are typically present on the anterior half of the body, with the open side of the C facing anteriorly. The center of the C may be filled with a darker color than the surrounding ground color, but the C itself is darker yet and typically edged in white or yellow. Posteriorly, these markings become more sharply defined and take the form of vertical or sinuous bars. Dark spots or dots are scattered across the lateral surfaces, often becoming larger on the lowermost scale rows adjacent to ventral scutes. The ventral surface is white to grey, with numerous dark grey to black blotches of varying size.

Schmidt (1923) stated that color pattern on the head was invariant among a series of 18 specimens of the Northern African Python from the Belgian Congo (Democratic

Republic of the Congo), and his description is applicable to most members of the species: “The top of the head is dark, with a straight light stripe from the supranasal over the nostril and eye on each side to the temporal region. The labial border, except posteriorly, is light, connected with the supraocular stripe on the neck, and anteriorly by a broad light area below the nostril and on the anterior labials and rostral. This area encloses a dark spot on the first and second labials. There are two distinct subocular light lines, one from the posterior lower corner to the ninth to twelfth labial, one from the lower anterior corner across the sixth labial. There is a median light mark behind the parietals.” In contrast to head pattern, however, Schmidt (1923) observed moderate variation in scalation, with individuals displaying 11-15 supralabials, 19-24 infralabials, 270-284 ventrals, 65-69 subcaudals, and dorsal scale formulae from 66-89-43 to 77-95-54. In both species, the first two supralabials have obvious thermoreceptive pits, with smaller pits visible on the first 4-6 infralabials. The rostral scale also has two lateral pits. In Southern African Pythons, there are 78-95 dorsal scale rows at midbody, 261-291 ventrals, 63-84 subcaudals, 12-15 supralabials, none contacting the eye, and 17-20 infralabials (Auerbach, 1987; Marais, 2004). Lanza and Nistri (2005) provide a fine summary of morphology and pattern for Northern African Pythons from Somalia, as well as some of the variation observed elsewhere in the range of the species.

Head scalation and lateral head pattern are used to distinguish Southern and Northern African Pythons, as described by Broadley (1984: see his Figure 1, p. 361). The frontal scales of the Southern African Python are fragmented, while those of the Northern African Python are entire, albeit sometimes fused; the latter situation is also true of *P. molurus*. The head markings of the Northern African Python are much better defined and strikingly contrasted than those of its sister taxon; the Northern African Python has a pale subnasal stripe, dark subocular and preocular patches, and a broad postocular stripe, whereas all of these are greatly reduced or fragmented in the Southern African Python. The body markings of the Southern African Python are less defined overall (and the Northern African Python in turn exhibits less definition than does *P. molurus*). Otherwise, most characters are similar among the African species, although old or incubating individuals of the Southern African Python can be almost solid black (Alexander and Marais, 2007). Both African species tend to have higher midbody, ventral, caudal, supralabial, and infralabial scale counts than does *P. molurus*, but the fields tend to overlap at least somewhat (Broadley, 1984).

2.2 Size

As is typical of giant snakes, estimates of the maximum body size attained by the giant African pythons are muddled by exaggeration, fable, and error. Some authors state that the Northern African Python reaches larger body sizes than does the Southern African Python, but we are unaware of any quantitative analysis of this supposition. Pope (1961) reported a maximum size of 9.8 m for a *P. sebae* killed in Ivory Coast in 1932 – this is perhaps the largest body size that has been given serious consideration by those summarizing the biology of the species, but this report lacks verification. To our knowledge, no individual snake of any species has ever been found to exceed 30 feet (9.14 m), either in the wild or in captivity. More realistic opinions on body sizes of the giant African pythons are provided by Ditmars (1931), who considered the maximum size of to be about 20 feet (6.1 m), and by Alexander and Marais (2007), who state that,

“It is doubtful that any specimens (of Southern African Python) of more than 6 m have existed, even in historical times.” Alexander (2007) stated that this species can exceed 55 kg body weight. Without distinguishing between the two species, Murphy and Henderson (1997) cited multiple accounts of African pythons over 6 m; while these claims generally lack verification, there seems to be a moderate amount of evidence to suggest the Northern African Python can reach 7 m and that maximal size of the Southern African Python is somewhat less.

The largest specimen in a series of 18 individual Northern African Pythons from Congo was 4.88 m (Schmidt, 1923), with no apparent size differences between rainforest and jungle specimens (in Schmidt’s era, the term “jungle” was applied to scrubby dry forest with high stem density, whereas “rainforest” was wet forest with a tall canopy and low stem density). In the Gambia, Starin and Burghardt (1992) stated that observed pythons ranged in size from 0.5 to about 7.5 m, but these were visual estimates of unknown accuracy. Two specimens of Northern African Pythons from southern Somalia were purportedly 5.72 m and 4.45 m total length, with girths of 0.41 and 0.46 m, respectively (Lanza and Nistri, 2005). In southern Nigeria this species averaged 3.4 m total length in natural habitats (n = 96, range 1.0-5.5 m) and 2.9 m in suburban habitats (n = 61, range 1.0-4.5 m; Luiselli and others, 2001), while three pythons captured on study plots in the same region averaged 2.39 m total length (Luiselli and others, 1998).

Auerbach (1987) said that specimens referable to the Southern African Python rarely reach 6.5 m, that specimens average 2-4 m, and that hatchlings average 600 mm. Alexander and Marais (2007) state that hatchlings of this species average 500-700 mm total length and weigh about 100 g.

Table 6.1. Total lengths and masses of typical *P. sebae* and *P. natalensis* (compiled/estimated from the literature sources listed in the text). Some values estimated from length/mass relationships (for example, Figure 6.8, below).

Sex	Hatchling		Maturation		Max. reported	
	Total (mm)	Mass (g)	Total (m)	Mass (kg)	Total (m)	Mass (kg)
M:	500-700	100	1.7-2.5	2.5-8	4.0?	30?
F:	500-700	100	1.7-3.0	2.5-10	7+ (<i>P. sebae</i>) 6 (<i>P. natalensis</i>)	65? 55

2.3 Sexual Size Dimorphism

Females of both species attain larger body sizes than do males. However, this size dimorphism may be somewhat less than what is seen in some of the other giant snakes. For example, females were larger in both SVL and mass among 24 Southern African Pythons used in a radiotelemetry study in South Africa (mass: one-tailed $t = 1.94$, $p = 0.03$; SVL: $t = 1.84$, $p = 0.04$; our calculations), but the largest female was less than 8 percent larger than the largest male: 4.6 vs. 4.2 m (4.07 m SVL vs. 3.78 m SVL):

Alexander, 2007). Females may be heavier than males at similar lengths (Lanza and Nistri, 2005).

2.4 External Sexual Differentiation

Pelvic spurs of males are larger than those of females, and the proximal portion of the tail is often visibly wider in males. While relative tail length (tail length/total length) among giant snakes tends to be significantly higher in males than in females, this trend may not be consistent for Southern African Pythons, at least using data provided by Alexander (2007) for 24 pythons greater than 1.53 m (1.35 m SVL). Among these snakes, relative tail length ranged from 0.07 to 0.15 for females and 0.11 to 0.13 for males (our calculations).

3.0 Distribution in Space and Time

3.1 Native Range

As with most other giant snakes, the giant African pythons are relatively under-represented in museum collections; this is due to the great size of adults and the associated labor and expense of preserving and maintaining large specimens. For example, Broadley (1984) stated that, “Because of the large size attained by this species, most museum specimens are juveniles or consist of the skins or severed heads of adults.” Distributional surveys based on museum surveys are thus likely to underestimate the overall geographic range of these snakes.

Without distinguishing between Northern and Southern African Pythons, Spawls and Branch (1995) stated that pythons are “found throughout sub-Saharan Africa, except for montane uplands above 2300 m, temperate regions in the south, and extreme desert in Namibia and adjacent Botswana, and Somalia and Ethiopia in the Horn.” Within this vast distribution, Northern African Pythons (Fig. 6.2) range from the coasts of Kenya and Tanzania across much of central Africa to Mali and Mauritania, as well as north to Ethiopia and Eritrea; in arid zones, their range is apparently limited to the vicinity of permanent water. The Southern African Python (Fig. 6.3) is found from Kenya southwest to Angola and south through parts of Namibia and much of eastern South Africa. Distributions of the species overlap somewhat, although the southern species tends to inhabit higher areas in regions where both species occur. The distributions of each species are treated separately by country, below.

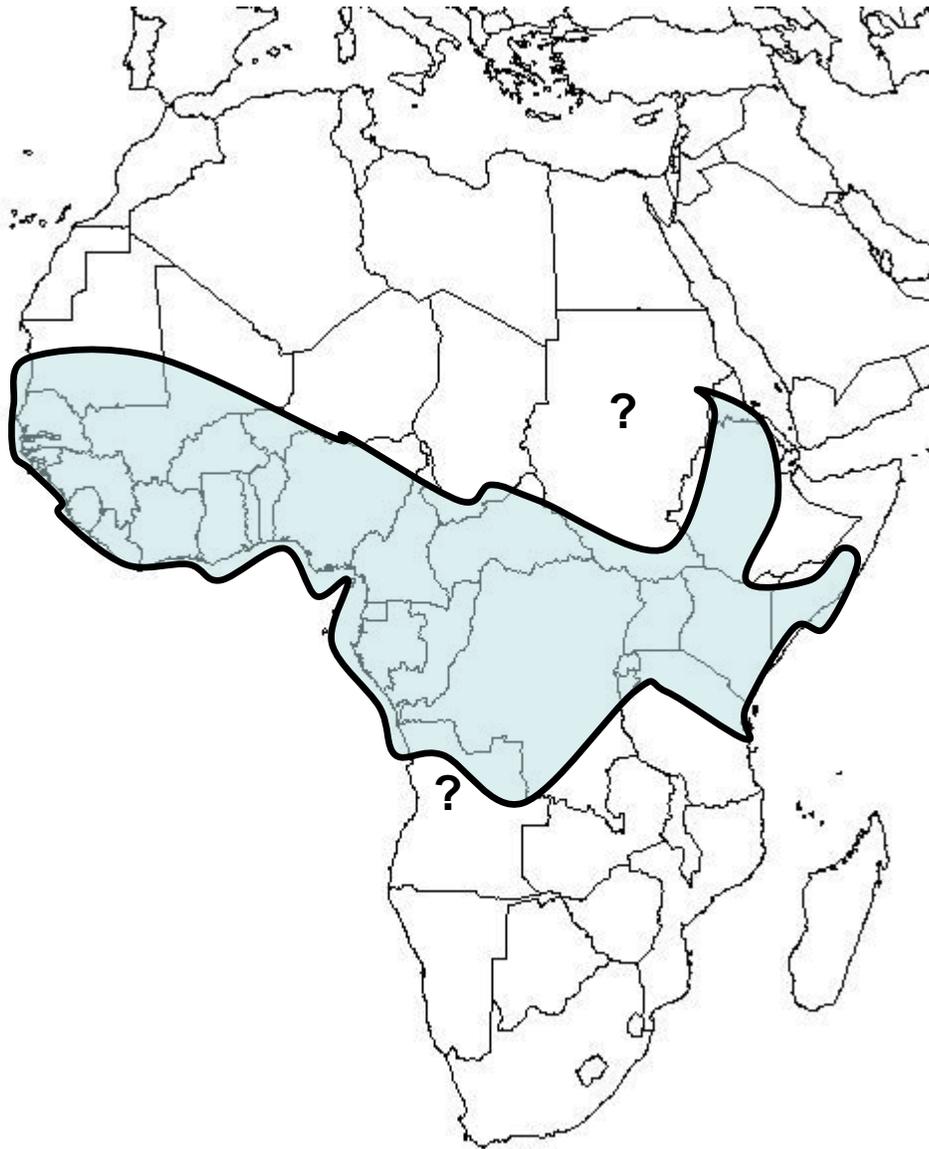


Figure 6.2. Native range of the Northern African Python, *Python sebae*, estimated using Broadley (1984) and additional sources cited in section 3.1.1. Primary uncertainties include the areas denoted with question marks, such as degree of python intrusion into arid zones in the northeastern part of the range (especially in Sudan), extent of the Angolan distribution, and areas of sympatry or parapatry with the Southern African Python, *Python natalensis*.

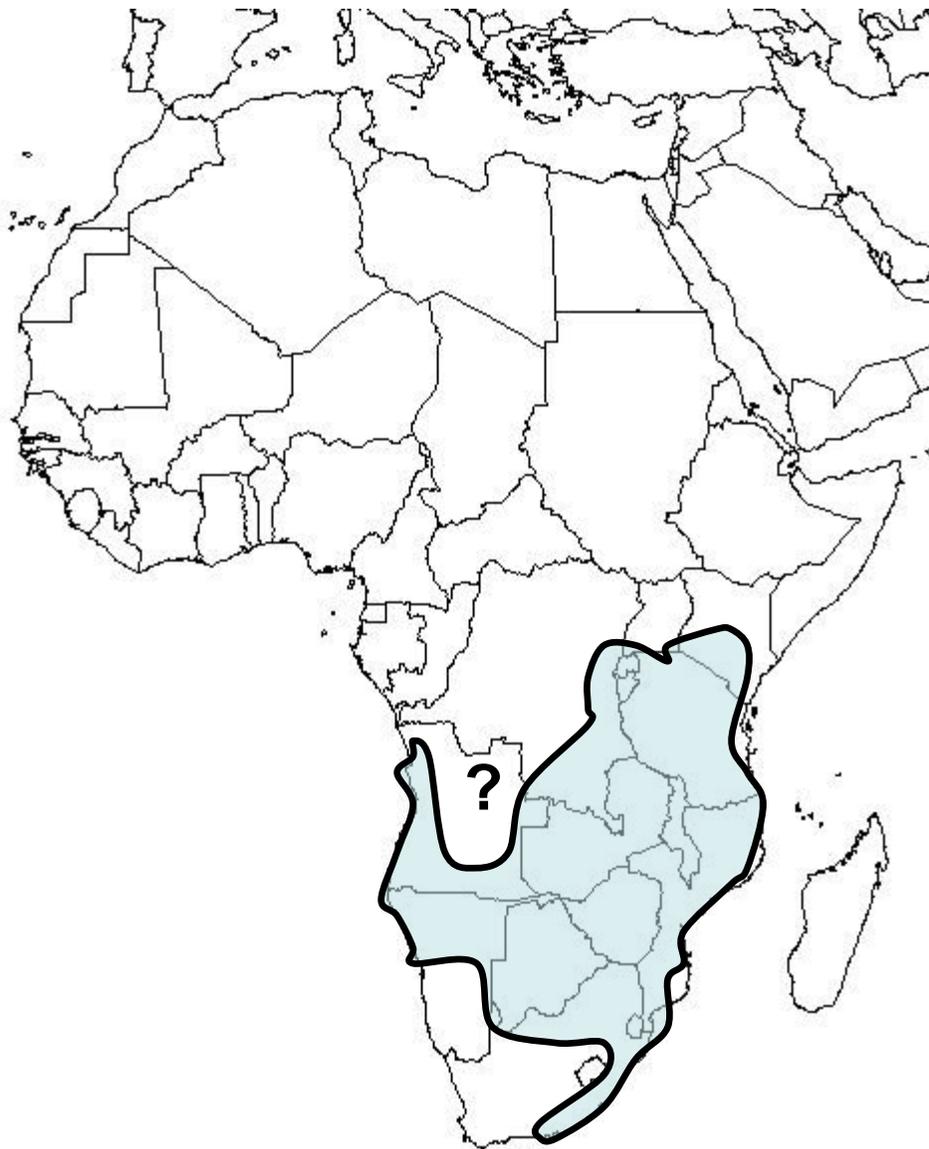


Figure 6.3. Native range of the Southern African Python, *Python natalensis*, estimated using Broadley (1984) and additional sources cited in section 3.1.2. Primary uncertainties include the area denoted with a question mark (primarily Angola) and areas of sympatry or parapatry with the Northern African Python, *Python sebae*.

3.1.1 Native Range of *Python sebae*

Angola—Present in the northernmost third of the country, although most records are from localities bordering the Democratic Republic of the Congo and Republic of the Congo (Broadley, 1984). Records from the south of the country are referable to *P. natalensis*.

Benin—Only one record in Broadley (1984) and three in Chippaux (1999), but apparently suitable habitat exists through most of the country. Benin has offered postal stamps featuring *P. sebae* and *P. regius* (<http://www.reptile-stamps.de/html/benin.html>; accessed 22 April 2009).

Burkina Faso (formerly Upper Volta)—Few records available (multiple observation localities reported by Chippaux (1999), and apparently suitable habitat exists through most of the country). The “python” is listed as Threatened in Burkina Faso, (<http://bch-cbd.naturalsciences.be/burkina/bf-eng/implementation/doc/monography/chap3-2-3-2.htm>; accessed 20 April 2009), but this could refer to *P. sebae* and/or *P. regius*.

Cameroon—Probably historically present through much of the country in suitable habitat, and known from multiple localities (Chippaux, 1999; LeBreton, 1999). Although considered rare by Gonwouo and others (2007) in the vicinity of Mt. Cameroon, it was found in lowland forest below 1500 m, as well as submontane forest from 1500 to 1800 m.

Central African Republic—Chirio and Ineich (2006) provided information on 23 specimens from 10 localities in the CAR and Chippaux (1999) reported 10 observations from across the country, while Joger (1989) reported specimens from Parc National Saint Floris and the vicinity of Bangoran, as well as several locations just across the border in Zaire. Probably historically present through much of the country in suitable habitat.

Chad—Known from Sar (Sahr), in southern Chad along the Chari River (Broadley, 1984). Probably historically present around aquatic habitats in southern Chad, especially the Logone and Chari Rivers and their tributaries.

Democratic Republic of the Congo (formerly Zaire and Belgian Congo, aka Congo-Kinshasa)—Apparently present or historically present through much of the country in suitable habitat. Largely replaced by *P. natalensis* in extreme southern DRC, but with possible areas of sympatry in parts of Shaba Province (Broadley, 1984).

Equatorial Guinea—Distribution poorly known and represented by only two localities in Broadley (1984), but likely was historically present in most suitable habitats. Individuals are regularly offered for sale in bushmeat markets on Bioko Island (Fa and others, 2000).

Eritrea—The few records from Eritrea are primarily from the Mareb, Gash, Barca, and Anseba River drainages, from the vicinity of Annesley Bay west to the border with Sudan (Lanza and Nistri, 2005; M. Largen, pers. commun., 2009). The species is probably more common than is reflected by museum records (M. Largen, pers. commun., 2009).

Ethiopia—Known from multiple localities in the southwest and extreme south near Mendera, as well as the Rift Valley, Lake Tana, Baro River, and near the northern border at Amba Aradam (Broadley, 1984; M. Largen, pers. commun., 2009). Most records are associated with watercourses.

Gabon—Represented by a small number of records scattered throughout the country (for example, Chippaux, 1999). Probably present, at least historically, in suitable habitat through much of this low-lying country.

The Gambia—Probably historically present in suitable habitat through much of this small country, which is a thin strip of land on each side of the lower Gambia River. Northern African Pythons were an obvious component of the vertebrate fauna during one ecological study in The Gambia (Starin and Burghardt, 1992), and were observed in savannah, marshland, and gallery forest by Hakansson (1981).

Ghana—Probably historically present through much of this low-lying West African country in suitable habitat, and represented by nearly 20 localities on the maps of Broadley (1984).

Guinea—Poorly known, but probably historically present through much of the country in suitable habitat.

Guinea-Bissau—Localities include the coastal city of Bissau and the offshore Bijagos Islands (Broadley, 1984), but suitable habitat appears to exist through much of the country.

Ivory Coast—Four localities mapped by Broadley (1984). Probably historically present through much of the country in suitable habitat

Kenya—Present in the Lake Victoria basin and along the eastern coast, but largely replaced by *P. natalensis* in the southern highlands (Broadley 1984, 1999; Spawls and others, 2002; Malonza and others, 2006).

Liberia—Multiple localities recorded (Broadley, 1984), probably historically present through much of the country in suitable habitat.

Mali—The only locality mapped by Broadley (1984) was from the vicinity of Bamako. Joger and Lambert (1996) added four more localities, all in the southwestern third of the country. Chippaux (1999) also provides four localities, including two in the southeast. Additional habitat may exist to the east along the Niger River corridor and its many drainages.

Mauritania—Recently confirmed to be present at multiple sites in the southern half of the country; appears to be confined to isolated wetlands in the Sahel (Padial, 2003, 2006).

Nigeria—Although represented by only a few localities in Broadley (1984) and Chippaux (1999), likely present through much of the country, including areas such as those in the state of Akwa-Ibom that experience extremely high annual rainfall during a well-specified wet season (May to October, 3146 mm/year: Luiselli and others, 1998). Considered vulnerable in all natural habitats in southern Nigeria, but persists better in suburbia (Akani and others, 2002).

Republic of the Congo (aka Congo-Brazzaville)—Recorded as “present or likely to occur” through all of five geographic sectors of the country (Broadley, 1998). Considered a common species along the Sangha River (Jackson and Blackburn, 2007) and reported by Chippaux (1999) from a few localities along the Congo River.

Rwanda—Poorly known, but present at elevations greater than 1300 m in the vicinity of Lake Ihema and Akagera National Park (Broadley, 1984).

Senegal—Represented by multiple specimens, largely around the edges of the country, including close to the northern border with Mauritania (Broadley, 1984; Chippaux, 1999) and in Niokola-Koba National Park in the southeast region of the country (Joger and Lambert, 2002).

Sierra Leone—Few records, but probably historically present through much of the country in suitable habitat.

Somalia—Present through a surprisingly large portion of the country, primarily associated with rivercourses and wadis that retain perennial pools; may be present as far north as the Wadi Nogal in the Horn of Africa (8.4° N latitude, 48° E longitude: Lanza and Nistri, 2005).

Sudan—Broadley (1984) listed four localities in Sudan, but mapped only two in the extreme southern part of the country. However, he listed Khartoum (over 1000 km to the north of these records) and White Nile (around 500 km north) as localities; both of these are along the Nile River corridor. Pythons are also known from the Mareb River drainage in Eritrea near the Sudanese border, as well as the headwaters of the Blue Nile; these populations may extend into Sudan. Existing populations appear to be limited to the vicinity of watercourses.

Tanzania—Both giant African Pythons are present in Tanzania. Northern African Pythons are known from the northwest of the country in the vicinity of Lake Victoria, as well as along the northern coastline and in a couple of locations between these regions. They are apparently sympatric with Southern African Pythons in part of this distribution, but are replaced by the latter in the southern half of the country.

Togo—Few records, but probably historically present through much of the country in suitable habitat.

Uganda—Occurs throughout Uganda, except for the northeast (Spawls and others, 2002), at elevations up to 2250 m (Spawls and Branch, 1995). Citing Charles R.S. Pitman, Pope (1961) stated that the species, “...can be found as high as 7,500 feet in Uganda. Extensive studies, chiefly by French workers, in the high country of the great lakes, extending from the borders of Uganda southward, indicate ascent to at least 5,900; as the 4,000-foot level is approached, the records grow more numerous and no doubt the

pythons themselves do. We may conclude that this reptile is certainly found at points lying between 6,000 and 7,000 feet, and possibly a little higher.”

Zambia—Probably not present, replaced by *P. natalensis*. However, Broadley (1984) lists a locality just across the border in the Democratic Republic of the Congo.

3.1.2 Native Range of *Python natalensis*

Angola—listed from several localities by Broadley (1984); most of these are in the southern third of the country except for a northern record from the vicinity of Luanda.

Botswana—Recorded from scattered locations in the country, with a concentration of records in the southeast corner (Auerbach, 1987). Also a reliable sight record from Twee Rivieren, South Africa, in an extremely arid region just across the Botswanan border (Haacke, 1984, cited in Auerbach, 1987). Most records from Auerbach (1987) are from elevations above 900 m.

Burundi—The only record in Broadley (1984) was from the vicinity of Bujumbura, which is on the shores of Lake Tanganyika at elevations below 800 m. Present across most of western Burundi according to Spawls and others (2002). Presence in the rest of the country (most of which is higher than 1500 m elevation) appears to be poorly known, although the species achieves similarly high elevations to the east in Tanzania and Kenya.

Democratic Republic of the Congo (formerly Zaire and Belgian Congo, aka Congo-Kinshasa)—Present through much of the southern third of the country, including areas of possible sympatry with Northern African Pythons (Broadley, 1984). Possibly present further north based on records of *P. natalensis* in Burundi close to the DRC border. Replaced in the northern portions of the country by *P. sebae*.

Kenya—Found in highlands of south-central Kenya, including elevations over 1800 m in the Lake Naivasha area (Spawls and others, 2002: this book includes much more detail on the species’ distribution in Kenya). Largely replaced by *P. sebae* in lower elevations in Kenya, including the Lake Victoria basin.

Lesotho—Probably not present, although specimens are known just to the east in South Africa (Marais, 2004; G. Alexander pers. commun., 2008).

Malawi—Known from Rumphu (or Rumpi) at fairly high elevations (higher than 1500 m) in the Northern Province (Nyasaland: Stewart, 1968), but likely present in historical times through much of the country in suitable habitats.

Mozambique—Known from scattered locations, including the northern coast, the southern tip, and along the Save (Sabi) River corridor (Broadley, 1984). However, some field guides consider it potentially present through all of southern Mozambique (for example, Alexander and Marais, 2007).

Namibia—Known to occur in the northern half of the country (Broadley, 1984), apparently associated with rivercourses and seasonal/permanent wetlands. Absent from extremely arid regions in southern Namibia (Auerbach, 1987).

South Africa—Now largely restricted to the northeast portion of the country, including coastal regions starting north of East London and northward, expanding inland to include Swaziland, the Northern Province and parts of Gauteng and Northwestern Provinces. Small disjunct populations were found east of Port Elizabeth and south of Kalahari Gemsbok National Park (Marais, 2004), but these may now be extirpated (G. Alexander pers. commun., 2008). A reliable sight record was obtained near Twee Rivieren on the Botswanan border (Auerbach, 1987). The species was historically found more widely in the Cape region, from which it is now largely absent (Auerbach, 1987). The species may have recently extended its range southwards in the area of Gauteng and the Northern Cape; Alexander and Marais (2007) speculate that this could be due to global warming. The southern range limits in South Africa may be determined by temperatures available to females when incubating eggs (Alexander, 2007).

Swaziland—Known from several specimens, mostly in the NE (Broadley, 1984). Occurs over the eastern half of Swaziland (Monadjem and others, 2003) in the middleveld, lowveld and Lubombos, reaching its western limits in the larger river valleys (Boycott, 1992).

Tanzania—Present across much of the country, but not in the Lake Victoria basin or along most of the coast (Spawls and others, 2002), where it is replaced by *P. sebae* (see above). Fairly common in Arusha National Park, especially in wet areas (Razzetti and Msuya, 2002). However, pythons were not observed in herpetofaunal surveys of the Southern Udzungwa Scarp Forest Reserve in southeast Tanzania at elevations between 900 and 1900 m (Menegon and Salvidio, 2005).

Zambia—Multiple specimens are known, and Broadley and others (2003) state that it is, “Found throughout the country in a variety of habitats, but usually close to water.”

Zimbabwe—Known from many specimens from throughout the country (Broadley, 1984).

3.2 Habitat Range

Various authors have opined on the habitat preferences of the giant African pythons, but these conclusions are often at odds with one another. For example, Spawls and Branch (1995) reported that the giant African pythons (which were not distinguished by species in this book) favor evergreen forest or moist savannah, often in rocky areas close to water, and Broadley (1990) stated, “Pythons favour moist, rocky, well-wooded valley, plantations or bush country, but seldom if ever far from permanent water, for which they have a great love...” The Northern African Python was also described as, “...widespread in a great variety of sub-Saharan habitats but seldom if ever occurring far from permanent water” (Lanza and Nistri, 2005). In arid regions such as the Kalahari,

pythons may have benefitted from the installation of watering holes for livestock and game (T. Hibbitts, pers. commun., 2008).

In Nigeria, Northern African Pythons are reported from suburban, forest, pond/stream, and swamp habitats (Butler and Reid, 1986), including extensive use of Nigerian mangrove habitats (Luiselli and Akani, 2002). In West Africa (The Gambia), pythons used savannah, marsh, and gallery forest habitats, usually close to water (Hakansson, 1981); pythons were also considered linked with aquatic habitats in the southwest portion of the Democratic Republic of the Congo (Trape, 1985).

In the arid northern parts of its range, Northern African Pythons appear to be limited to wetlands, including the headwaters of the Nile, isolated wetlands in the Sahel of Mauritania and Senegal, and various watercourses in Somalia, Ethiopia, and Eritrea (Broadley, 1984; Padial, 2003; Lanza and Nistri, 2005; M. Largen, pers. commun., 2009).

3.3 Climate Range

As would be expected by their relative latitudinal positions, the Southern African Python tends to inhabit slightly cooler regions than does its sister taxon. However, Northern African Pythons in some localities experience climates nearly as cool, indicating that they cannot be considered merely a tropical species. Drastic seasonal swings in precipitation are a striking feature of many localities for both species, although such seasonality does not necessarily appear to be a requirement, at least for Northern African Pythons which also inhabit less seasonal locales.

3.3.1 Climate Range of Northern African Pythons

The Northern African Python inhabits regions with some of the highest mean monthly temperatures that we identified for any of the giant constrictors' habitats, with means over 35 C in arid northern localities (Figure 6.4). However, many areas inhabited by this species are much cooler, especially in the higher elevations of Kenya, Tanzania, and Ethiopia. Seasonality in precipitation is a hallmark of many localities inhabited by Northern African Pythons; these localities often experience multiple months with little or no rainfall. This is true even in parts of western Africa, from which many of the animals in the international live animal trade originate. It is uncertain whether this seasonality is a requirement of the species, but this seems unlikely given the relatively aseasonal regimes experienced in other localities (including other parts of western Africa). Pythons also persist in extremely arid regions in the Sahel, but appear to be limited to the vicinity of watercourses in most arid climates.

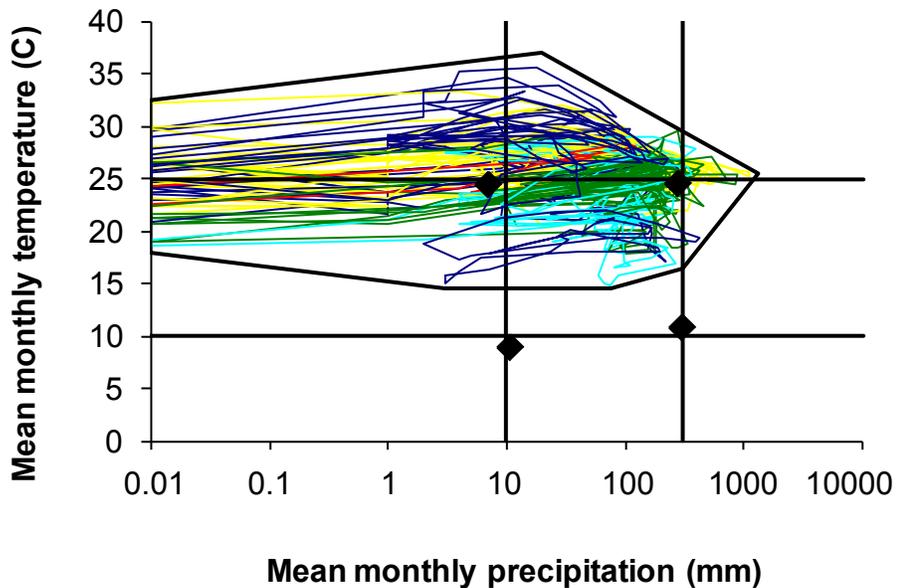


Figure 6.4. Climate space for *P. sebae*, with reference lines and localities as introduced in Fig. 2.1. Based on 109 known localities from the native range. Climate loops color-coded as follows: Red = Southern Africa (Angola, Zambia, Malawi, Mozambique and points south); Turquoise = Eastern Africa (Tanzania, Uganda, Kenya, southern Rift Valley countries); Yellow = Western Africa (Nigeria and countries to the west that are south of Mauritania, Mali, and Niger); Blue = Northern Africa (Mauritania, Mali, Niger, Chad, Sudan, Ethiopia, Eritrea, Somalia); Green = Central Africa (Cameroon, Central African Republic, Gabon, Rep. Congo, Dem. Rep. Congo).

3.3.2 Climate Range of Southern African Pythons

As would be expected for a species that attains significantly higher latitudes, Southern African Pythons generally inhabit cooler areas than do Northern African Pythons. In some localities, the mean monthly temperatures of the coolest months are among the lowest we observed for any of the giant constrictors' habitats. Other than persisting in cooler climates, the climate envelope of Southern African Pythons is similar to that of the northern species, including many localities with highly variable rainfall.

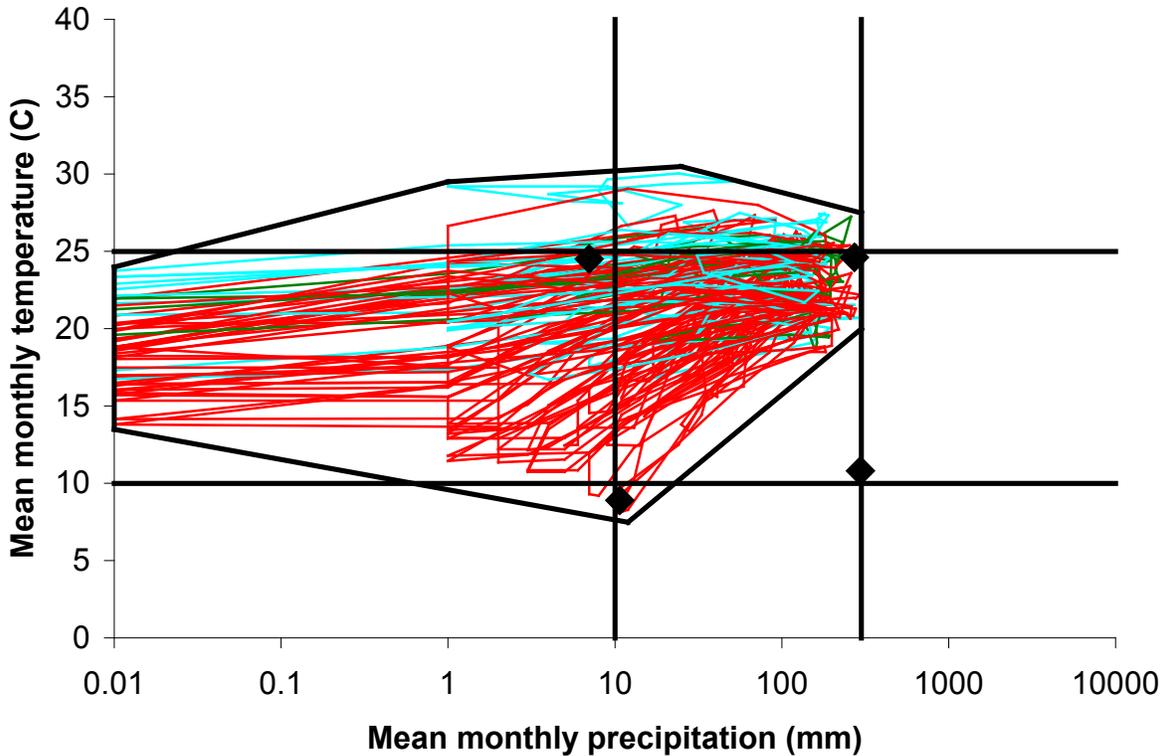


Figure 6.5. Climate space for *P. natalensis*, with reference lines and localities as introduced in Fig. 2.1. Based on 87 known localities from the native range. Climate loops color-coded as for *P. sebae*.

3.4 Microhabitat

See the biological profile for *Boa constrictor* for caveats about observed microhabitat use based on anecdotal observations. Radiotelemetric locations of free-ranging pythons would provide less biased information on microhabitat use, but we are aware of only two published radiotelemetric studies of the giant African pythons (Lawson, 2004; Alexander, 2007). The former had a sample size of one python, and the latter focused on thermoregulation rather than habitat use. Accordingly, few data are available to accurately assess fine-scale habitat use in the giant African pythons.

Southern African Pythons are reported to prefer rocky outcrops in both arid and moist savanna, as well as using lowland forest (Marais, 2004); we note that “preference” for rocky outcrops may simply reflect higher visibility to human observers in these habitats, and Broadley (1999) stated that these pythons exhibit no preference for rocky habitats. In Arusha National Park, Tanzania, the species is most often observed in or near aquatic habitats (Razzetti and Msuya, 2002). Burrows of porcupine, armadillo, and warthog are important refugia in northern South Africa (Alexander, 2007). African pythons readily climb trees (Broadley, 1990), and may use trees more often than is

commonly assumed (Lawson, 2004); juveniles may be more likely to use arboreal habitats (Luiselli and others, 2007).

In contrast to a number of general statements in the literature to the effect that the giant African pythons are usually associated with water, pythons in South Africa only immersed themselves in water on 3 percent of the days on which they were located via radiotelemetry (Alexander, 2007). Conclusions that pythons are reliant on aquatic habitats may therefore be biased by anecdotal data and detectability; for example, large pythons may be more prone to ambushing large-bodied mammalian prey from the water, and these large animals may be more obvious to human observers. It is also possible that the Northern African Python may be associated with water to a greater degree than is the southern species; 81 percent of locations of a radiotelemetered female *P. sebae* in Cameroon were within 10 m of a stream or river (Lawson, 2004), although we note that this area included many agricultural areas and thus the watercourse may have provided some of the only remaining forested landscape.

Observations of pythons in multiple habitats of southern Nigeria led Luiselli and others (2007) to conclude that they are most abundant in mangrove habitats, but that the species overall is a habitat generalist that is especially associated with riverine or other aquatic habitats. The apparent abundance of pythons in mangrove habitats in Nigeria may well represent higher abundances, but this perceived abundance could also be due to higher detectability of pythons in this habitat. A single snake in the adjacent country of Cameroon was located via radiotelemetry on 201 occasions over the course of a year, but was visually observed only *once* during this period (Lawson, 2004); on all other occasions, the python was concealed underground, in a log/debris, or in a tree. Such a difference between perceived and actual habitat use is a stark example of the dangers of assuming habitat use based solely on opportunistic observations.

3.5 Introduced Ranges

Several Northern African Pythons have been found in Florida and elsewhere in the United States, including observations going back over 100 years (for example, Moseley, 1901)—most of these have been assumed to be escaped or released pets. African pythons occasionally appear in other extralimital areas, almost certainly as a result of the international live animal trade; as an example, two Northern African Pythons were found in São Paulo, Brazil during the period 1995-2000 (Eterovic and Duarte, 2002). An attempt at re-establishing an extirpated population of Southern African Pythons in South Africa involved the release of 34 individuals, and discovery of a hatchling several years later was an indication of successful reproduction (Branch, 1988); we presume that releasing similar numbers of individuals in suitable extralimital habitats might result in extralimital populations.

Recently (August 2009), evidence has surfaced pointing to the presence of a population of Northern African Pythons along the western border of Miami adjacent to the Everglades. Four specimens, including hatchlings and adult females, have been confirmed from an area of about two kilometers in diameter, and three of these were found in 2009. Another large individual escaped from a credible observer in 2008, while a sixth record of a very large female had not been conclusively confirmed at the time of this document's production. A spatially concentrated cluster of sightings of pythons of various size classes is fairly strong evidence of a reproductive population, and planning is

underway to delineate and attempt control of this incipient population. This area is within the known distribution of Burmese Pythons in Florida, and hybridization between these species is known in captivity. The likelihood of hybridization among introduced Florida populations is unknown, as are the implications of genetic admixture for risk assessment and control purposes.

3.6 Seasonal Activity

Southern African Pythons north of Pretoria, South Africa, exhibited annual activity ranges that occasionally exceeded 500 ha. Even in winter, pythons rarely stayed below ground for more than a week, emerging to bask at regular intervals (Alexander, 2007). This study indicated that pythons had activity peaks in March (autumn) and August-September (late winter); the former may be due to hyperphagia before the winter fast, while the latter may be associated with reproductive behaviors such as mate-searching. In Nigeria, pythons exhibited weak activity peaks in January during the dry season and in August-September during the latter part of the wet season (Luiselli and others, 2007). These authors posited that the January activity peak was related to reproductive activity, as previously noted by Starin and Burghardt (1992). In Cameroon, a single radiotelemetered female confined her activities to about 7 ha during the rainy season but greatly expanded her activity range into forested habitats during the dry season (approx. 32 ha: Lawson, 2004). At a higher elevation, Southern African Pythons were rarely observed during the cool rainy season in Arusha National Park, Tanzania (Razzetti and Msuya, 2002). Pythons in equatorial zones are likely active to some degree throughout the year, while those at high elevations and in the south temperate zone appear to be relatively inactive during the winter.

3.7 Daily Activity

The giant African pythons may exhibit activity at any hour of the day. However, virtually all conclusions on diel activity cycles are based on opportunistic observations rather than on unbiased sampling methods. An exception to these biased conclusions was provided by Alexander (2007), who showed that most radiotelemetered pythons in South Africa sheltered in burrows at night and emerged to bask in the morning – basking frequency, duration, and target temperature varied significantly depending on size, sex, and reproductive status. In the Abuku Nature Reserve, The Gambia, pythons were commonly encountered during daylight hours (Hakansson, 1981), while juveniles (1.5-2.5 m) in Kenya became active near dusk (Spawls and others, 2002). Adults may be more nocturnal than juveniles (Spawls and Branch, 1995), and radiotelemetry of an adult female led Lawson (2004) to conclude that diurnal forays from secure retreats were uncommon.

Sightings of pythons in natural habitats ($n = 96$) of southern Nigeria were concentrated in the middle of the day (1000-1900), while suburban pythons ($n = 61$) were primarily sighted after dusk, especially after 2200 (Luiselli and others, 2001). However, these results are likely to have been somewhat biased by unequal sampling effort across years, seasons, and times of day. Of six predatory events recorded by Luiselli and others (2001), five occurred during the hours of 2115 - 2350, with the sixth at 1845; these results reflect the likely importance of nocturnal foraging, although it was unknown whether these occurrences reflect ambush predation or some level of active searching.

3.8 Foraging Mode/Sensory Modalities

The giant African pythons are primarily ambush foragers, lying in wait for prey in burrows, along animal trails, and in water (Branch, 1988; Spawls and others, 2002, Alexander and Marais, 2007). Pythons may also engage in active searching for prey to some extent (Alexander and Marais, 2007); this strategy appears to be more common among juveniles (Spawls and others, 2002). Adults are particularly prone to ambushing prey from the water. The African pythons have multiple thermoreceptive pits in the rostral and labial scales (see 2.1 Unique Features, above), allowing them to detect and strike endothermic prey even in darkness.

4.0 Life History

4.1 Reproductive Mode

Both the Southern and Northern African Pythons are oviparous.

4.2 Reproductive Phenology

Most available reproductive information is for the Southern African Python. In this species, males may trail females during the breeding season (Branch, 1988), and up to 13 males have been observed courting a single female (Alexander and Marais, 2007). Similar aggregations and trailing behavior were reported for Northern African Pythons in The Gambia (Starin and Burghardt, 1992), although these were smaller groups (six or fewer individuals). Captive males may engage in male-male combat (Barker and Barker, 1994), but this behavior has not been reported in the field.

In southern Africa, mating occurs during the winter [between June and September (Alexander, 2007; Alexander and Marais, 2007), July and August in Botswana (Auerbach, 1987)]. In contrast, Northern African Pythons are reported to mate and oviposit year-round around Lake Victoria (Spawls and others, 2002). Large diurnal or seasonal temperature variation may not be necessary to evoke reproductive behavior in captive Northern African Pythons (Ross and Marzec, 1990). Hybridization between *P. natalensis* and *P. molurus* has been observed in captivity (Branch and Erasmus, 1984).

Eggs may be laid in hollow trees, termite nests, or mammal holes, and the female coils around eggs during incubation (Branch, 1988; Stanford, 1994; Spawls and Branch, 1995). A female in northern South Africa oviposited in a burrow, approximately 7 m from the entrance and 1 m below ground (Alexander, 2007). Elsewhere in South Africa, however, a female was found coiled around eggs in open grassland (Porter, 1987). In South Africa, eggs are laid between September and December (Alexander, 2007; Alexander and Marais, 2007), although Pope (1961) reported a female captured in Natal that contained shelled eggs in June. Farther north in Tanzania, a female was observed coiled around eggs in early September (Stanford, 1994); based on the maps of Broadley (1984), this was most likely the Southern African Python.

Ditmars (1931) and Auerbach (1987) state that females are capable of shivering thermogenesis while brooding; the latter stated that this behavior can result in temperature increases of up to 6.5°C. However, most recent authors discount shivering thermogenesis in the giant African pythons (Pope, 1961; Vinegar and others, 1970; Spawls and Branch, 1995; Alexander and Marais, 2007). Instead, females may leave

their eggs to bask (sometimes attaining body temperatures over 40°C), returning to transfer body heat to the eggs (Marais, 2004; Alexander, 2007; Alexander and Marais, 2007). Alexander (2007) provided a summary of the arguments for and against thermiogenesis, including the intriguing possibility that Southern African Pythons are incapable of thermiogenesis but that Northern African Pythons may be capable. Body temperature data of radiotelemetered brooding females in South Africa provided no evidence of thermiogenesis (Alexander, 2007). The apparent lack of thermiogenesis in these species may mean that these species are less likely to succeed as invasive species in cool regions, as compared to thermiogenic pythons.

Incubation is typically 65 days (Spawls and Branch, 1995), similar to many other large pythons; although Branch (1988) stated that incubation of Southern African Pythons can vary between 60 (at 30-32°C) and 100 (at 25-27°C) days. In captivity, incubation is reported at 72-106 days, but typically 72-76 days, with longer incubation periods being associated with lower temperatures and resulting in the reduced fitness of hatchlings (Ross and Marzec, 1990). Broadley and others (2003) stated that eggs usually hatch in December in Zambia. A female in Zimbabwe was found with eggs and hatchlings on 24 December (Broadley, 1959, cited in Fitch, 1970), while a female in Angola was found with freshly-laid eggs at the end of January, and a female in Natal contained shelled eggs on June 2; this last observation appears to be an early outlier. A female Southern African Python (see above) in Tanzania incubated eggs for at least 78 days before they hatched around 20 November (Stanford, 1994). Alexander and Marais (2007) state that the hatching success of Southern African Python eggs is greatly decreased if incubation temperatures are maintained below 28°C, and only 29 percent of eggs hatched that were brooded by a female that was prohibited from basking normally for 10 days during incubation, as opposed to 85 percent hatching success for a female brooding normally (Alexander, 2007).

Juvenile Southern African Pythons in Tanzania stayed at their nest site for about 10 days, until shedding, after which they dispersed (Stanford, 1994); in this case the dam did not stay after her offspring hatched. Farther south, however, hatchlings may closely associate with their dam during the night in order to maintain higher body temperatures (Alexander and Marais, 2007).

4.3 Reproductive Effort/Fecundity

Reproductive effort of females is considerable, as clutch sizes can be large and females fast during incubation. Females may lose more than half of their body mass during this period, and spent females may die after incubation (Alexander, 2007; Alexander and Marais, 2007).

4.3.1 Clutch or Litter Size/Frequency

Branch (1988) stated that an “average” female of 3-4 m total length would be expected to lay 30-40 eggs, while Pope (1961) reported an average clutch of 46 eggs, individual clutches from 20 to “about 100,” and clutch size increasing with body length of the dam (Fig. 6.6). Other authors have reported clutch size as 30-50, occasionally up to 100 (Marais, 2004; Spawls and Branch, 1995; Alexander and Marais, 2007). Among specific observations of free-ranging females, a Southern African Python from Zimbabwe

was found with 39 eggs and hatchlings, and a female in Tanzania of the same species (approximately 2.75 m total length) incubated roughly 20 eggs.

Eggs of Southern African Pythons weigh 130-160 g and are about 10 cm in diameter (Marais, 2004). Females likely reproduce only every two to three years (Branch, 1988; Alexander and Marais, 2007).

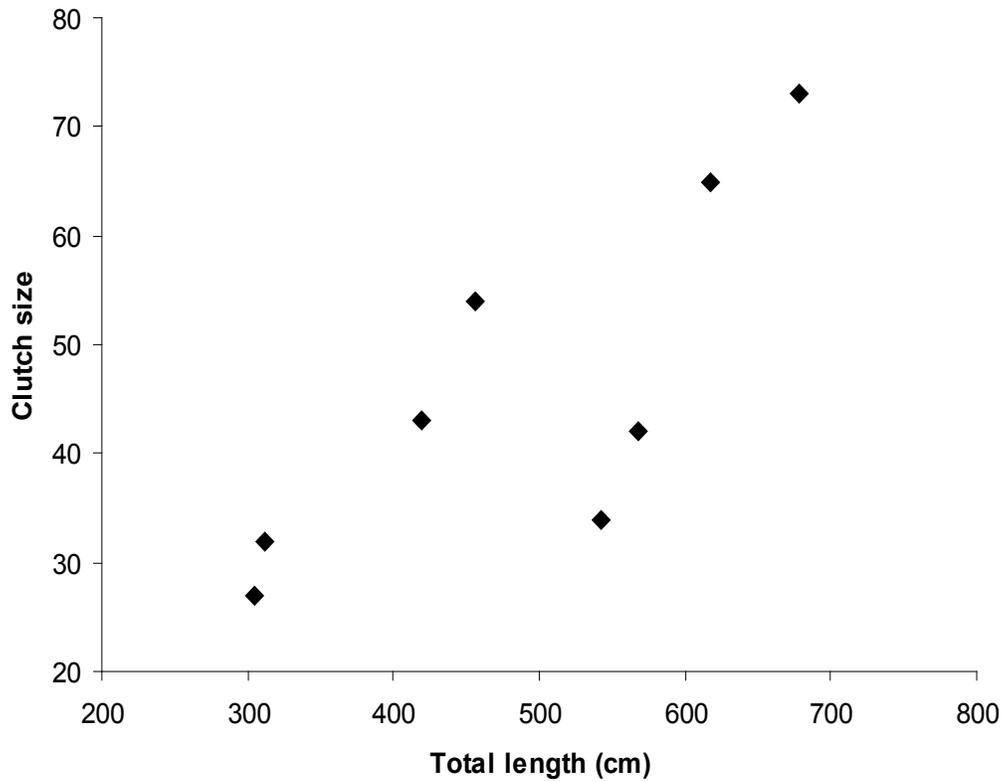


Figure 6.6. Relationship between dam body size and clutch size in 8 captive Northern African Pythons in Cameroon; adapted from data in Stucki-Stirn (1979).

4.4 Growth

We are unaware of any mark-recapture study of the giant African pythons that would allow estimation of growth rates among free-ranging pythons, and thus we are unfortunately reliant on growth records from individuals in captivity (for example, Fig. 6.7). Ross and Marzec (1990) stated that Northern African Pythons grow rapidly, but provided no accompanying data. A captive individual that grew from 0.53 m to 5.18 m in 5.5 years (approx. 70.5 mm/month; Whitworth, 1974) represents the fastest long-term growth rate of which we are aware. Lanza and Nistri (2005) provided a literature

summary of growth records from captive individuals, including some captives in the native range held under semi-natural environmental conditions.

Growth rates can be rapid among juveniles: Growth of three juveniles in one year averaged about 1.20 m (100 mm/month) and 3000 g (250 g/month: starting total lengths 0.60, 0.60, 0.69 m; starting mass 100, 100, 160; ending lengths 1.75, 1.80, 2.0 m; ending mass 3968, 3000, 3200 g), while another juvenile grew from 0.53 to 0.86 m in 14 weeks (94 mm/month). Slower growth was observed in 40 juveniles held in Cameroon, with length at one year ranging from 0.92 to 1.09 m, and Spawls and others (2002) observed growth from 0.50-0.55 m to 0.9-1.37 m in one year (n = 9). Juvenile growth rates are likely to be highly dependent on feeding frequency and food quality, as well as suitable conditions in captivity. Growth in body length decelerates as pythons get older, although body mass tends to continue to increase at a high rate. Lanza and Nistri (2005) provided the following observations on captives, culled from the literature: a 3.5 m female grew 1 m in 3 years, and captives in Cameroon had lengths of 1.80 m (2 years old), 2.50 m (3 years), 3.20 m (4 years), and a 6 year old specimen of 3.62 m.

In a field study of Southern African Pythons in South Africa, Alexander (2007) observed no pythons between 0.76 and 1.53 m (0.67 m and 1.36 m SVL; Fig. 6.9). This could indicate that hatchlings grow very quickly, but alternatively this observation could be a result of size-based heterogeneity in detectability.

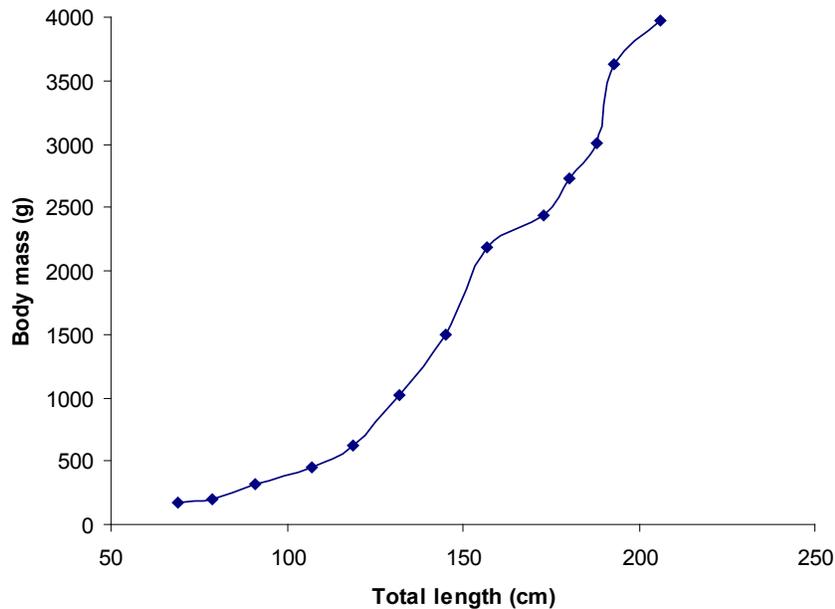


Figure 6.7. Growth of a captive juvenile *P. sebae* measured at monthly intervals, adapted from data tabulated by Raynis (1965). Measurements started when the individual was approximately two months old, and the animal was kept at constant temperatures of around 28°C.

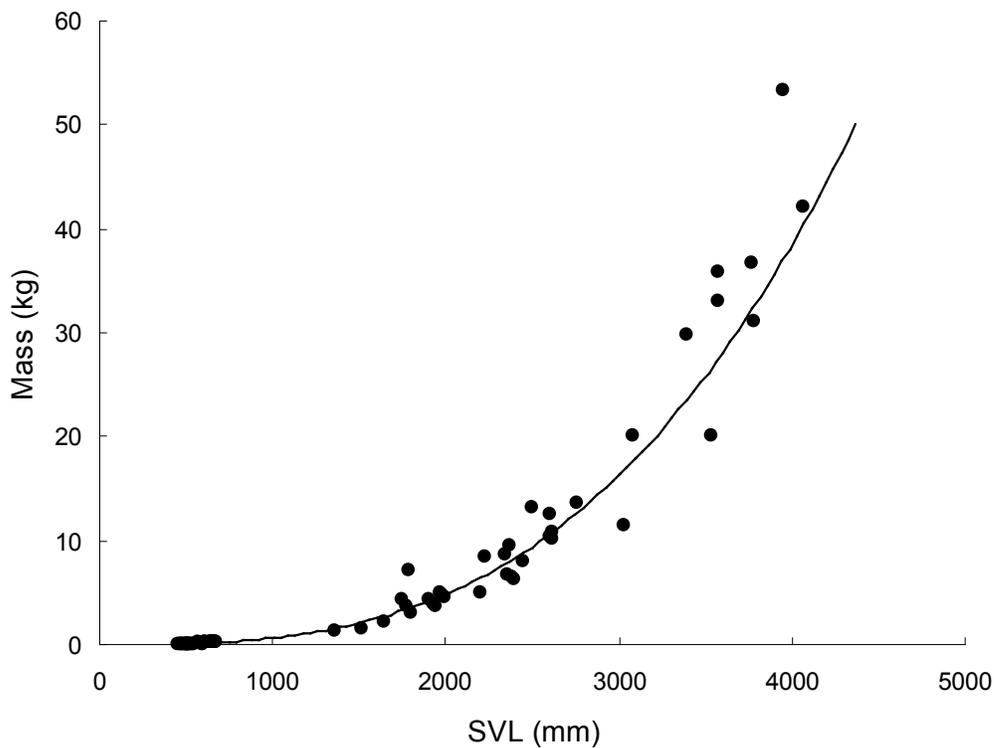


Figure 6.8. Relationship between snout-vent length and mass for a sample of *P. natalensis* from South Africa near the southern limits to the species' range. Graph courtesy G. Alexander, reproduced with permission.

4.5 Maturation

Females may mature at 2.5 m (this presumably refers to total length), which can occur in 3-4 years in captivity (Branch, 1988). Males likely mature at about 2 m total length. Age at maturity has been estimated at 10-15 years in free-ranging snakes (Broadley, 1990; G. Alexander, pers. commun., 2008), but captives in Cameroon matured at 5-6 years and 3-4 m (Stucki-Stirn, 1979). Luiselli and others (2007) estimated maturation of both sexes to occur at about 1.92 m (1.7 m SVL). Herpetoculturalists are regularly able to get male Northern African Pythons to breed at 2 years of age and females at 3 years, but this requires feeding large amounts of food to juveniles; similar growth rates are likely to be uncommon among free-ranging individuals.

4.6 Longevity

We are aware of no records for longevity among free-ranging individuals. In captivity, Northern African Pythons have lived for 27 yrs 4 mo (Snider and Bowler, 1992).

5.0 Diet/Trophic Role

Along with rare Nile crocodiles (*Crocodylus niloticus*), Northern African Pythons are considered a top predator in Nigerian mangrove habitats, especially since leopards (*Panthera pardus*) have been eliminated from this region (Luiselli and Akani, 2002).

5.1 Prey

As with most of the giant constrictors, adult giant African pythons primarily eat endothermic prey from a wide variety of taxa; Luiselli and others (2001) concluded that, “Pythons are opportunistic predators that take whatever suitably sized endothermic prey are available.” To this general statement on the palatability of endotherms can be added the observation that these pythons may also consume lizards (including monitor lizards, *Varanus* spp.), fish, crocodiles, and frogs (Spawls and Branch, 1995; Branch, 1998; Spawls and others, 2002; Marais, 2004). Endothermic prey has included various antelope (for example, kob, gazelle, and duiker), Warthog (*Phacochoerus africanus*), African Porcupine (*Hystrix cristata*), Caracal (*Caracal caracal*), a variety of rodents, various birds including pelicans and chickens, and even a Leopard (*Panthera pardus*: Wright, 1960; Branch, 1988 and references therein). Most authors state that juveniles consume small rodents and ground-dwelling birds, while adults largely subsist on medium-sized mammals.

Among notable diet records, a 47-kg Northern African Python consumed a 26-kg Uganda Kob (*Adenota kob*), and a 4.6-m individual ate a Thomson’s Gazelle (*Gazella thomsoni*), despite a horn briefly erupting from the snake’s body (Hay and Martin, 1966; Greene, 1997). A 4.8-m python ate an Impala (*Aepyceros melampus*) weighing 59 kg (Spawls and others, 2002), while a 3.79-m Southern African Python weighing 18 kg contained a 13.5-kg Bushbuck in Zimbabwe (*Tragelaphus scriptus*: D. Broadley, pers. commun., 2008). Another Southern African Python in Zimbabwe consumed a White Stork (*Ciconia ciconia*: D. Broadley, pers. commun., 2008). In The Gambia, known prey of Northern African Python included Bushbuck and possibly other harnessed antelope (*Tragelaphus* spp.), Red Colubus Monkeys (*Procolobus badius*), and several captive antelopes and monkeys (Starin and Burghardt, 1992). In southern Nigeria, pythons in suburban and natural areas consumed dogs, goats, rats, and poultry; rats were not found in snakes over 1.55 m, while the other prey classes were consumed by larger snakes (2.35-3.51 m: Luiselli and others, 2001). Prey items from three pythons captured in a matrix of rainforest/cultivated lands in Nigeria included a Gambian Giant Pouched Rat (*Cricetomys gambianus*), 3 macrochiropteran bats, and 2 guenon monkeys (*Cercopithecus* spp.: Luiselli and others, 1998), while pythons from the Congo consumed a rat and a female antelope measuring 1040 mm long and 480 mm high at the shoulder (Schmidt 1923). Pythons are considered an effective means of controlling small mammals such as Dassies (*Procavia capensis*) and Cane Rats (*Thryonomys swinderianus*: Marais, 2004). Domestic animals consumed by giant African pythons

include goats, dogs, attempted predation on a calf, and a domestic turkey consumed by an extralimital individual in suburban south Florida (Branch, 1988; Murphy and Henderson, 1997; S. Snow, pers. commun. 2008).

5.2 Predators

Marais (2004) lists mongooses, meerkats, crocodiles, wild dogs, hyenas, Ratels (honey badgers) and other snakes as potential enemies, and Pitman (1938: cited in Pope, 1961) reported that a warthog killed a Northern African Python 12 feet (3.66 m) in length. Crocodiles (*Crocodylus niloticus*) killed and consumed at least six pythons over several years at a reserve in The Gambia (Starin and Burghardt, 1992). Senter (2000) speculated that the slightly variant color pattern on the tails of hatchling pythons may function as a diversionary tail display to keep a predator's attention away from the snake's head. Branch (1988) stated that, "Man is now the python's main predator," and Alexander (2007) observed only one of 24 radiotelemetered Southern African Pythons lost to predators during over 2500 python-days of observation.

5.3 Diseases and Parasites

Broadley (1990) lists a number of ailments in African pythons, at least some of which are likely more prevalent in captivity than in the wild (for example, "mouthrot", fungal growth, etc.). Peirce (1984) observed haemogregarine and helminth parasites in a python (named as *P. sebae*, but probably referable to *P. natalensis*) in Zambia. The former was *Haemogregarina sebai*, which is apparently known only from African pythons. Peirce noted, "...both the nematode and cestode parasites in *P. sebae* occurred in large numbers and appeared to be causing some impaction of the intestine." A pentastomid has been identified from Northern African Pythons; this has been referred to as *Armillifer moniliformis* but may represent an undescribed species (Riley and Self, 1981). *Armillifer moniliformis* has also been isolated from *P. molurus*, *B. reticulatus*, and *Morelia amethystina*; effects of this parasite on python health are largely unknown. Infestations of *Armillifer* pentastomids are prevalent in pythons from South Africa and can interfere with respiration (Broadley, 1990). As boid snakes, the giant African pythons are probably susceptible to retrovirus-associated Inclusion Body Disease (Schumacher and others, 1994), but we are unaware of any known cases in these two species. In captivity, they are subject to a range of diseases and conditions, including paramyxovirus, cryptosporidiosis, etc., (Mader, 1996), but the extent to which such problems plague wild pythons is unknown.

Ticks capable of transmitting diseases of economic and veterinary importance are often associated with reptiles imported to the United States in association with the live animal trade (Burrige, 2001; Burrige and others, 2000, 2006). Northern and/or Southern African Pythons are known hosts of some of these ticks, including *Amblyomma nuttalli*, *Amblyomma marmoreum*, *Amblyomma sparsum*, *Aponomma exornatum*, *Aponomma flavomaculatum*, and *Aponomma latum* (Burrige, 2001). Once entering the country, ticks have proven capable of spreading to new host species (for example, African ticks found on Boa Constrictors from the Neotropics, Asian ticks on an African Ball Python, an African tick found on a domestic dog, etc.), establishing populations in Florida (Allan and others, 1998), and switching to feeding on native reptile species (Oliver and others, 1988).

At least eight exotic reptile-borne tick species are deemed capable of becoming established in Florida alone, based on climatic suitability and the presence of suitable native reptile hosts (Burrige, 2001), as has already happened with at least two species in the state. Four of the abovementioned eight species are known or suspected to be associated with mammalian diseases, including heartwater and Q fever, and some are vectors of reptile haemogregarine parasites and perhaps other pathogens. Heartwater is a devastating disease of wild and domestic ungulates, and estimates of ungulate mortality in the United States are 40-100 percent of all ungulates should the disease become established (Burrige, 2001). Unfortunately, tropical tick systematics, surveys of potential hosts, and the prevalence of tick-borne disease have received only modest attention in recent years; most of our knowledge of a species group of great medical/veterinary interest, for example, is based on a survey that is now 50 years old (Theiler and Salisbury, 1959).

6.0 Demography

6.1 Population Density

To our knowledge, there are no credible published estimates of population density of the giant African pythons. The only estimate of which we are aware resulted from long-term observational studies at a small study site in The Gambia, which produced density estimates of 0.6-0.75 pythons/ha (Starin and Burghardt, 1992). However, these numbers were based on tenuous visual recognition of individuals rather than mark-recapture or similar quantitative means of estimating population density, and the probable absence of top predators in this small and highly isolated nature reserve may have elevated prey abundances to an abnormal degree. Nonetheless, this is a surprisingly high density of large snakes.

There is little doubt that the giant African pythons can be obvious components of the vertebrate fauna of Africa, at least in some areas. In a study of snake community ecology in mangrove habitats of Nigeria, the Northern African Python ranked third in terms of number of individuals captured over four years (21 pythons/183 snakes total: Luiselli and Akani, 2002), and it would likely rank even higher in terms of relative biomass. The same species was considered common along the Sangha River in the Republic of the Congo by Jackson and Blackburn (2007: note, however, that these authors speculated that pythons may be present but difficult to detect in undisturbed forest), and as “very common” in forests along the lower Shebelli (Shabeele) River of Somalia, despite the overall aridity of this latter region near the northeastern limits of the species (Lanza and Nistri, 2005). However, the species was represented by only 3 individuals from a sample of 237 snakes captured in an area of southeast Nigeria characterized by rainforest patches and cultivated areas (Luiselli and others, 1998).

6.2 Size Distribution

See the equivalent section in the profile for *Python molurus* for problems associated with quantifying size distribution without accounting for detectability of various size classes. We are aware of no defensible size distribution for any population of either of the giant African pythons. Reports of average body sizes include 3-4 m

(Marais, 2004) and 2.8-4 m (max 5.5 m, hatchlings 0.45-0.60 m) in Southern African Pythons (Spawls and others, 2002), with similar estimates for the northern species. A large (n = 197) sample of Northern African Pythons from Nigeria averaged 3.4 ± 1.2 m total length and included snakes from 0.8 m to 5.0 m (Luiselli and others, 2007), while a sample of approximately 75 Southern African Pythons from north of Pretoria, South Africa, included lengths exceeding 4.5 m (4 m SVL) and 55 kg, but the majority were in the 2-3.4 m range (1.8-3 m SVL: Alexander, 2007).

7.0 Interactions with Humans

7.1 Human Utilization and Persecution

African pythons are collected for the skin trade. However, these pythons appear to represent a small portion of the overall international trade in python skins. African pythons do not represent a significant portion of the reptile skin trade involving tanneries in Mexico (Arroyo-Quiroz and others, 2007), and only 25 *P. sebae* skins entered the United States during 1996-2000 according to the USFWS LEMIS import database, while over 38,000 skins and skin products of *B. reticulatus* entered the United States during these years. Most African python skins are likely used within Africa.

Northern African Pythons are reported as declining in Nigeria due to intense hunting for food and skins (Akani and others, 1999). Pythons do not represent a large proportion of snakes observed to have been killed by people in southern Nigeria, but this may be because pythons are eaten after being killed and thus were not available for observation (Akani and others, 2002). In the Congo, Schmidt (1923) reported that pythons are often eaten by humans, and are taken by spearing or by placing nooses at the entrance of holes occupied by pythons. Southern African Pythons are protected from take in Botswana (Auerbach, 1987) and South Africa, where they are said to be declining in some areas, especially around Durban and the Eastern Cape where they may have been extirpated (Alexander and Marais, 2007). Causes of mortality for the giant African pythons include harvest for food, skins or fat (for medicinal purposes), killing pythons to protect livestock, habitat destruction, vehicular traffic when snakes are crossing roads, and possibly the rise in electrified fencing around game farms (Branch, 1988; Fa and others, 2000; El-Kamali, 2000; Alexander and Marais, 2007). Five of the six pythons encountered by Padiel (2003) in Mauritania had been killed by local people, and he considered these isolated populations to be in urgent need of protection. Juvenile pythons were often accidentally captured in fishing nets in the Republic of the Congo (Jackson and Blackburn, 2007). A survey of 17 traditional healers in a Johannesburg marketplace revealed products from 22 individual pythons, for which 14 different uses were described (T. Hibbitts, pers. commun., 2008).

A population of Southern African Pythons in the Eastern Cape of South Africa was reportedly extirpated by 1927, prompting a reintroduction project in the 1980s (Alexander and Marais, 2007). At a local scale, Northern African Pythons were reportedly translocated from a nature reserve to rice fields in The Gambia, presumably for rat control (Starin and Burghardt, 1992).

7.2 Human Health Risks

As with any large constricting snake, individuals over 3.5 m are potentially dangerous to children and/or adults, and some herpetoculturists consider any snake that can exceed 8 ft (2.43 m) as being potentially dangerous (Flank, 1997). However, most accounts of unprovoked attacks on humans by the giant African pythons are poorly substantiated, except for the well-documented deaths of a 13 year old boy in South Africa and an adult male who died of internal injuries a day after being constricted (Branch and Haacke, 1980; Spawls and Branch, 1995; Spawls and others, 2002). Among notable non-fatal injuries, a python bite to a herpetologist required 57 sutures, and a veterinarian lost an eye to a python bite (Spawls and others, 2002).

7.3 Human Aesthetic Relations

7.3.1 Pet Trade

According to USFWS import records, 8,245 live *P. "sebae"* (not distinguished from *P. natalensis* in import records) entered the United States between 1989 and 2000 (Reed, 2005). Most of these were likely to have been true *P. sebae*, based on examination of the declared countries of origin. Over a longer period of time (1977-2007), CITES records document 32,738 individuals imported, an average of 1,056 per year (range 5-3488; Fig 6.9). This rate has held fairly steady in recent years and is roughly 10 percent of the annual rate of imports of Indian Pythons during the same period.

The giant African pythons are not particularly popular as pets in the United States, especially as compared to Indian Pythons and Reticulated Pythons. This is likely due to three observations: 1) the African pythons are commonly perceived as a fairly "vicious" snake that is prone to striking with little warning, although this trait has not been quantified; 2) whereas *P. molurus* and *B. reticulatus* exhibit a bewildering range of color/pattern/size "morphs" (named with terms such as albino, granite, green, labyrinth, tiger, sunfire, dwarf, etc.), only three such morphs (hypomelanistic, patternless and striped) are known for Northern African Pythons (de Vosjoli and Klingenberg, 2005), and none are known for Southern African Pythons to our knowledge; and 3) relative to *molurus* and *reticulatus*, Northern African Pythons have less contrast between ground colors and overlying pattern, resulting in a "duller" appearance. The species can be easily bred in captivity, but is bred infrequently as compared to other giant pythons, likely implying that a greater proportion of African pythons sold in the United States are wild-caught.

7.3.2 Other Uses

Major human uses of giant African pythons include meat, skins, medicinals, and the live animal trade (see above).

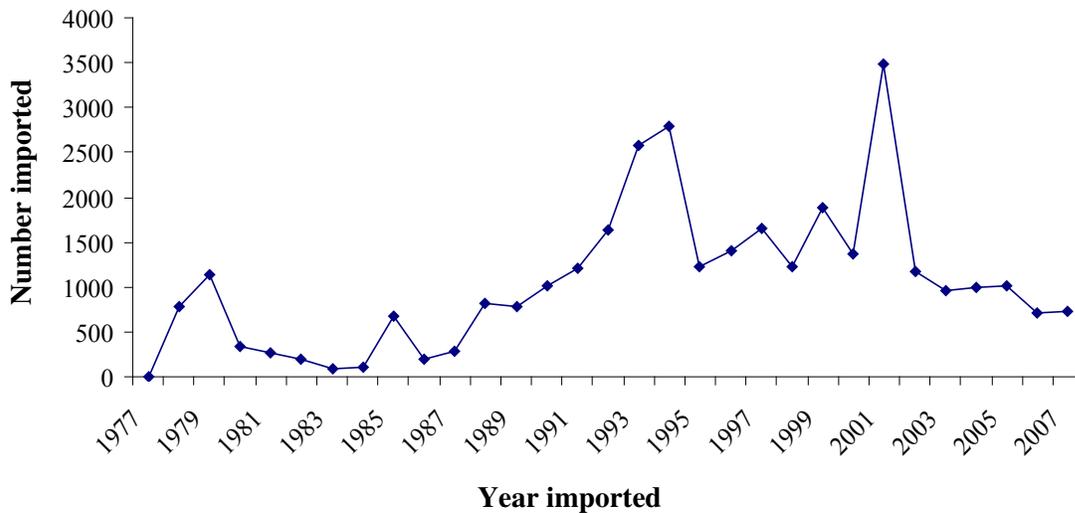


Figure 6.9. Annual imports of giant African pythons, *Python sebae*/*P. natalensis* (not distinguished in trade) to the United States during the period 1977-2007. Data from CITES.

Management Profile

See the introduction to the management profile for the Indian Python (chapter Four) for an explanation of the format of this section of the risk assessment.

8.0 Pathway Factors: Pet Trade

8.1 Volume of International Trade

As indicated in section 7.3.1, above, and in the Appendix, the giant African pythons represent a fairly small proportion of the overall trade in live giant constrictors as compared to perennial favorites such as Boa Constrictor. Although the trade in giant African pythons appears low compared to the more popular species, the long-term average of about 1,000 imports per year ranks them well above the average for all boid/pythonid species in the live animal trade. The annual volume of imported giant African pythons has been fairly constant over the past three decades, generally lacking the drastic year-to-year changes evident for some other species. Section 8.1 of chapter Four outlines broad reasons why imports may constitute higher risk as invasive species than captive-reared individuals.

We are uncertain as to the specific identity of some individuals in the trade, as *P. natalensis* was split from *P. sebae* fairly recently and pythons have been imported with declared origins in countries with both species. This means that older CITES records and those involved in the export/import business may not distinguish between these species in international trade. Further examination of CITES export records could be helpful in

elucidating the species identity of giant African pythons entering the United States, assuming that the declared country of origin is accurate.

8.2 Volume of Domestic Trade

We are aware of no credible estimates of the volume of domestic sales or captive propagation of the giant African pythons. Surveys of storefront and online reptile dealers appear to indicate a relatively low rate of captive propagation; we strongly suspect that this rate is lower than the declared import rate, but have no means to quantify this suspicion.

9.0 Entry Potential (Survival in Transit – Meant Mainly for Unintentional Transport)

As with all of the giant constrictors, survival in the pet trade pathway is likely to be high, as animals are packed and shipped using methods designed to maximize the rate of survival in transit. While mortality rates of some reptiles have historically been very high during international transport (Franke and Telecky, 2001; Christy, 2008), large hardy species of snakes would appear to be among the taxa most likely to survive the travails of international transport. Once in the United States and purchased by an endpoint consumer, the python is likely to be housed in conditions that are designed to meet its needs. Survival in captivity is likely to be high except for snakes possessed by extremely negligent owners.

10.0 Colonization Potential

10.1 Likelihood of Escape/Release

Those factors promoting release of pet Indian Pythons (see section 10.1 of chapter Four) are likely to apply to the giant African pythons. Because the majority of giant African pythons in the United States live animal trade appear to be imports, they may be more subject to ailments caused by parasites, other pathogens, or captivity stress. These species also have a reputation of being prone to biting their owners, even as compared to other giants such as Reticulated Pythons, and wild-caught imports may be especially likely to bite. Both poor health and a temperament poorly suited to captivity may increase the odds that problematic individuals are discarded. Observations of multiple individuals in a small area of south Florida indicate that release(s) (whether unintentional or intentional) have certainly occurred.

10.2 Climate Match: Areas of the Country at Greatest Risk

We extrapolated climate from the native range and mapped it to the United States for Northern (*P. sebae*: Fig. 6.10) and Southern (*P. natalensis*: Fig. 6.11) African Pythons separately. When considered separately, Northern and Southern African Pythons both exhibit a climate match to the United States that includes a large portion of peninsular

Florida, extreme south Texas, and parts of Hawaii and Puerto Rico. To this can be added apparently suitable conditions for the Southern African Python extending slightly further to the north in Florida and also including portions of Texas from about the Big Bend region to the southeasternmost extent of the state.

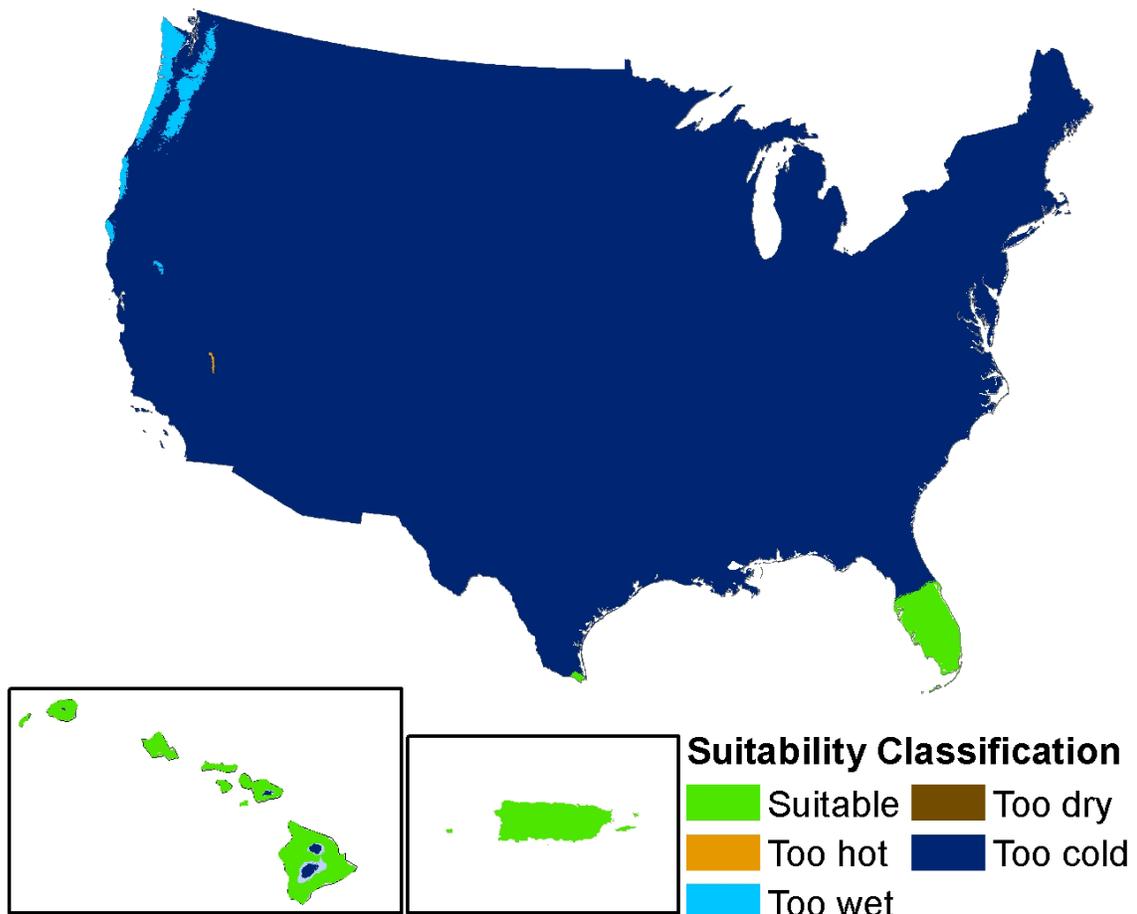


Figure 6.10. Areas of the United States matching the climate envelope expressed by *P. sebae* in its native range (Fig. 6.5), based on 109 known localities. See chapter Two for details of analytical method.

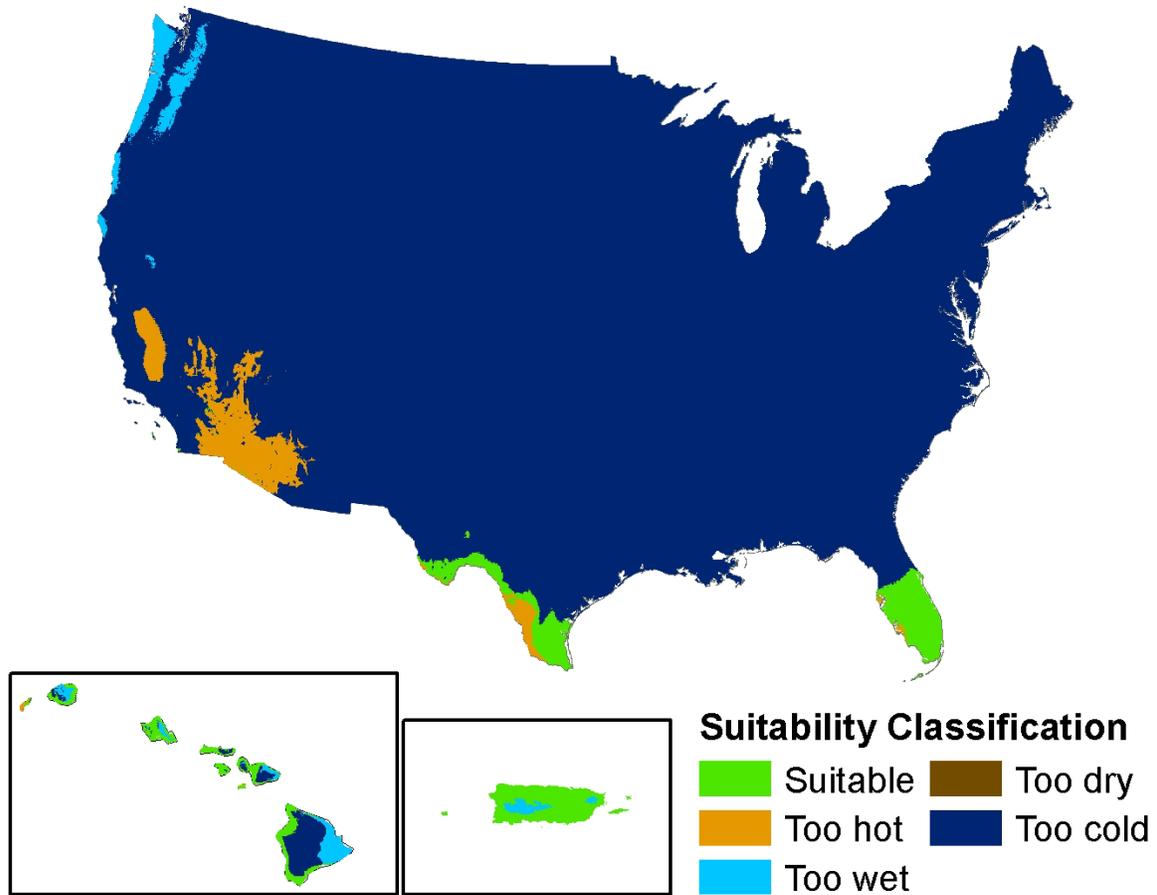


Figure 6.11. Areas of the United States matching the climate envelope expressed by *P. natalensis* in its native range (Fig. 6.5), based on 87 known localities. See chapter Two for details of analytical method.

10.3 Prey Availability

As with Reticulated and Indian Pythons, the prey of the giant African pythons includes all endotherms of a size appropriate for consumption by an individual snake, as well as many reptiles (primarily lizards and crocodiles) and the rare inclusion of amphibians (frogs). Fish appear to be an inconsequential part of the diet. The mainland areas indicated in Figures 6.10 and 6.11 do not appear to be lacking in prey species of suitable sizes and taxonomic affiliations. In fact, if successfully established in south Texas, giant African pythons might come into contact with prey species from their native distribution (including many species of small to medium-sized antelope), given the prevalence of exotic game ranches in this region. Because islands tend to exhibit a relative lack of large-bodied mammals, large pythons might be food-limited in insular situations such as Hawaii, Puerto Rico, Guam, Northern Mariana Islands, etc.

10.4 Predation Risk

The United States has no specialized predators capable of keying in on large adult giant African pythons (for that matter, no such predator exists anywhere in the world, to our knowledge). More generalized predators, including panthers and alligators, would certainly take some large individuals, but would likely be repaid in kind by pythons consuming juveniles or adults. Smaller pythons are likely to fall prey to a range of potential predators, including birds of prey, mammalian mesocarnivores, a few ophiophagous snakes, feral hogs, etc. Not enough is known about microhabitat use across the range of the giant African pythons for inferences on whether they are more or less likely than other giant constrictors to make use of aquatic, arboreal or terrestrial microhabitats. Energetic losses associated with moving up through trophic levels means that adding a new predator (python) to an ecosystem is unlikely to represent a net benefit to native predators, as a python would represent a lower energetic benefit as a prey item than the native animals they had consumed to reach any particular body size. Introduced pythons would thus be likely to reduce the overall prey biomass available to a predator.

10.5 Reproduction Requirements

Giant African pythons do not appear to exhibit any specialized reproductive requirements; they commonly brood their eggs, but the consensus is that neither species employs shivering thermogenesis to warm eggs. The inability to warm eggs by shivering would appear to limit their ability to successfully reproduce in cool climates, but for the observation that the Southern African Python leaves its eggs to bask, after which it returns to the eggs and warms them using heat acquired passively. Most, but not all, observations of nesting appear to be associated with underground microhabitats (burrows created by other species); nesting underground may further buffer the eggs from cool ambient temperatures.

10.6 Hibernation Requirements

Whereas the giant African pythons do not appear to undergo true hibernation, they do appear to be less active during the cool season. At moderate elevations in Tanzania, fewer pythons were observed surface-active during the cool season, and pythons spent most of their time underground during the South African winter (Razzetti and Msuya, 2002; Alexander, 2007). However, pythons were generally surface-active at least once per week in the South African study, and late winter saw an increase in python activity associated with the onset of the breeding season. The preceding observations apply to the Southern African Python; we are unaware of evidence to support hibernation or extended aestivation in the Northern African Python, although it would be unsurprising if individuals of this species aestivate during the dry season in arid habitats bordering the Sahel.

10.7 Tools for Eradicating a Colonization

Available tools for eradication of either species of giant African python are likely to be similar to those described in chapter Three and section 10.7 of chapter Four. Many observers claim that the Northern African Python is often associated with aquatic habitats, implying that development of control tools might be complicated by the

necessity of deploying them in aquatic or seasonally flooded habitats. Observations of African pythons basking on cool days might make them vulnerable to capture resulting from visual surveys during the cool season.

11.0 Spread Potential

11.1 Dispersal Ability

We are unaware of relevant data on dispersal capacity in these species. A single individual of the Northern African Python exhibited an activity range of about 30 ha over a year of observations, while activity ranges of Southern African Pythons can approach 500 ha. Given the relatively close relationship among the giant African Pythons and the Indian Python, there appears to be no convincing reason why the former would not be capable of movements of similar magnitude to those observed for the latter in Florida. Clutch sizes of the giant African pythons average 30-50 eggs, but often exceed this number and clutch sizes can approach 100 eggs. The upper end of this clutch size range puts the species very close to the maximal observed for giant constrictors (107 in *P. molurus*, 124 in *B. reticulatus*), and the rate of population dispersal is thus unlikely to be limited by fecundity.

11.2 Ability to Develop Races or Strains

There are no native species in the United States with which either giant African python would be capable of interbreeding, negating the risk of developing new races or strains by that route. However, the African species are capable of hybridizing with the Indian Python, which is already established in south Florida. The fertility and long-term viability of such hybrids is unexplored. It is conceivable that introduction of African genes to the Indian Python population could result in increased genetic variability that could allow exploitation of new ecological or physiological niches and/or result in some other type of hybrid vigor. Such a scenario has become more likely in the face of recent evidence for a population of Northern African Pythons along the western edge of Miami, an area within the introduced range of Indian (Burmese) Pythons.

11.3 Tools for Managing Spread

No species-specific tools are available to combat spread. The apparent propensity to use aquatic habitats, especially in the Northern African Python, may complicate deployment of barriers to dispersal.

12.0 Economic Impact Potential

Regulatory agencies have not decided whether a formal economic analysis of the potential impacts of introduction of, and regulation of trade in, the giant African pythons will be separately conducted pursuant to a variety of statutes and Executive Order 13272 (Proper consideration of impact on small business). Our narrative below is provided only to cite relevant biological literature and identify germane sections of the biological profiles.

12.1 Pathogen Vector

There is more information on giant African pythons as potential pathogen vectors than for any of the other giant constrictors (see section 5.3 of this chapter), but this information is still woefully inadequate. A range of pathogens of medical, veterinary, or agricultural importance are known or suspected to be vectored by tick species that use giant African pythons as hosts, and these pythons may harbor parasites or other pathogens capable of being transmitted to vertebrates in the United States; the level of threat is difficult to predict given existing knowledge gaps.

12.2 Predator on Livestock

In their native range, giant African pythons have been reported to kill livestock up to the size of a 43-kg calf, and one python contained six goats. Such events are unlikely to be common, as very large individuals would be expected to represent a small proportion of any given python population. Smaller domestic animals (poultry, etc.) are more likely to experience predation by the average-sized python, and an escaped/released *P. sebae* consumed a domestic turkey in south Florida (S. Snow, pers. commun., 2007). If Northern African Pythons are closely associated with aquatic habitats as suggested by some observers, then domestic waterfowl production may suffer in areas with introduced python populations.

12.3 Predator on Pets

Dogs have been recorded in the diet of giant African pythons, and it is likely that virtually any endothermic household pet, from gerbils to pot-bellied pigs, could be consumed by a python of sufficient size. Akani and others (2002) suggested that in recent years pythons actually persist better in suburban situations than in natural areas, and the average suburban python is about 3.0 m long. A snake of this size would be capable of consuming domestic cats, small dogs, etc., but whether a Nigerian suburb bears any resemblance to the typical American suburb is another question, which renders direct comparisons problematic.

12.4 Electrical Power Systems

The frequency with which giant African pythons would be expected to reach elevated power lines is unknown, although radiotelemetry of a single Northern African Python revealed extensive use of arboreal habitats. Pythons are unlikely to be nearly as adept at climbing utility poles as are Brown Treesnakes or other snake species with specialized adaptations for climbing. We expect python-associated damages to electrical grids to be minimal.

12.5 Traffic Accidents/Human Attacks

Legitimate attacks on humans that result in fatalities are exceedingly rare in the native range of the giant African pythons, but such attacks are not unknown. If an attack were to occur in the United States, the negligible public health risk would likely be far outstripped by media-induced panic among the populace.

Both African species reach body sizes large enough to cause automobile accidents, should a vehicle traveling at a high rate of speed impact a large python; this type of accident occurs with unfortunate regularity in the southeast United States when vehicles hit alligators, but its potential frequency is difficult to predict.

12.6 Tourism

Potential impacts to tourism are likely to be similar to those associated with introduction of Reticulated Pythons (see section 12.6 in chapter Five), although the higher propensity for Reticulated Pythons to attack humans in their native range means that they might have a greater impact on tourism after such an attack takes place. While there are some tourists who might travel to an area for the express purpose of viewing an introduced giant African python, experience with Indian Pythons in south Florida suggests that these will represent a tiny fraction of the overall visitation rate.

12.7 Impacts on Commercially Important Wildlife

12.7.1 Species Hunted with Gun or Binoculars

Bird watching in south Florida and south Texas is a major contributor to local economies. Many of the most sought-after birds are endemic to these areas and/or are of conservation concern, and pythons are likely to have the greatest impacts on imperiled species (see section 5.1). The presence of a novel predator on rare birds is likely to be detrimental to bird watching tourism if pythons reduce populations and thus reduce sighting rates. Birds are a predictable component of the diet of African pythons in their native range. Numerous ungulates considered trophy game species have been recorded in the diet of both giant African pythons. Potential impacts to similar species in the United States would likely be limited to white-tailed deer and introduced game ungulates (many of which are from Africa themselves), although important non-ungulate game species (for example, turkey) could be impacted as well.

12.7.2 Species that Impact Forestry, Agriculture, or Horticulture

We do not anticipate that giant African pythons would have a direct impact on these industries. However, the presence of giant constricting snakes in forested or agricultural habitats could certainly reduce the available pool of laborers willing to work in such habitats. Presence of such species in natural landscapes might also induce employers to institute measures such as are used in bear country, including special training, requirements for safety equipment, and/or requirements to travel in pairs in predator-occupied habitat. Such requirements could increase costs associated with some industries. It is possible that pythons would suppress populations of rats or other crop pests in agricultural settings.

13.0 Environmental Impact Potential

13.1 Species of Special Concern as Prey or Competitors

See section 13.1 of chapter Four for a list of prey species that might be impacted by the Indian Python, and the same section of chapter Five for a discussion of why another invasive giant constrictor might be expected to have lower impacts. The giant African pythons could potentially occupy a larger area than the Reticulated Python based solely on climatic variables, but their potential range is smaller than that of the Indian Python. Overall impacts of African pythons to species of special concern are therefore likely to fall between the other two species, assuming similar densities and dietary preferences.

13.2 Species of Special Concern as Predators (Giant Constrictors Augment Food Supply)

As indicated in section 13.2 of chapters Four and Five, food supplementation provided by giant African pythons is likely to be offset or upset by intra-guild predation. Furthermore, native predators are likely to experience a net loss of prey biomass after the introduction of a novel predatory snake, as discussed above in section 10.4.

13.3 Vector for Disease Spread to or Within Native Faunas

Too few data exist to evaluate this consideration, but the risk of importation of parasites and pathogens cannot be discounted. Tick species that use giant African pythons as hosts have been documented to survive the pet trade pathway to the United States, move to new hosts once transported, and establish populations in Florida. Some of these tick species are known or suspected to be vectors for diseases that could be devastating to native vertebrates.

13.4 Species that Might be Adversely Affected by Control Measures

Control measures for giant African pythons would likely be similar to those envisioned for giant constrictors in general (see chapter Three). Some possible avenues of control, such as acetaminophen toxicants, are likely to result in non-target mortality to native species, especially large snakes capable of accessing toxicant delivery devices designed for giant constrictors. Traps, drift fences, and other potential tools may also impede movements of non-target native taxa or result in their inadvertent capture. As no management tools have been adequately field-tested, however, it is not possible to estimate potential ecological costs.

14.0 Perceived Impact (Social and Political Influences)

14.1 Pet Industry

14.1.1 Domestic Production Affected?

Domestic production of the giant African pythons in herpetoculture is relatively low, almost certainly less than 500 offspring produced per year in the United States, although we have no means of verifying this estimate. Restrictions on sales of these species are thus likely to impact a relatively small number of producers, at least in economic terms, although those who specialize on breeding these species would be disproportionately impacted. Such considerations would be better addressed by a formal economic analysis. As with Reticulated Pythons (section 14.1.1 of chapter Five), however, imposing regulations on trade in giant African pythons would likely result in much wider concern over whether such steps are precursors to more general restrictions for other species.

As with Reticulated Pythons, regulations on trade or ownership of the giant African pythons might result in importers or dealers releasing unsalable stock, owners releasing animals for which they cannot acquire permits, etc. Releases by importers, breeders, and dealers are of greatest concern, as they are likely to involve multiple individuals at the same time and place (= high propagule pressure).

14.1.2 International Trade/Alternate Pets

While the long-term average of 1,000 giant African pythons per year is dwarfed by average imports of Boa Constrictors, Indian Pythons, Ball Pythons, etc, the average retail price of \$100-250 per individual giant African python adds up to a moderate income stream for importers even considering retail mark-ups. Restrictions on trade in these species would thus produce some economic hardship, but would likely be offset to some degree by importers switching to different species that lack such restrictions.

Restrictions on certain taxa are also likely to result in taxonomic loopholes that could be exploited by importers, breeders, and retailers. For example, the state of Florida recently imposed regulations related to permitting processes for certain large constricting snakes, including the Northern African Python (*P. sebae*). However, the regulations do not cover the Southern African Python (*P. natalensis*), nor several other species of slightly smaller body size but which present potentially serious threats as invasive species (for example, Boa Constrictor, Yellow Anaconda). It is possible that trade in non-regulated species could increase as a means of circumventing species-specific attempts to regulate trade. If the numbers of certain species in trade increase greatly as a means of getting around regulations, then the relative risk associated with propagule pressure for those species increases as well.

Chapter Seven–The Boa Constrictor, *Boa constrictor*

Biological Profile

1.0 Introduction

See section 1.0 of the biological profile of the Indian Python for a description of species-specific and overall components of the risk assessment package.

1.1 Species

The species *Boa constrictor* ranges widely over North, Central, and South America and dozens of marine and lacustrine islands, and has one of the widest latitudinal distributions of any snake in the world. The species displays extensive variation in size, color, pattern, scalation, and other traits, and some populations are also noticeably divergent in terms of diet, ecology, and/or behavior. Various authors have recommended splitting the taxon into several species, but the lack of a thorough revision of the species (see below) has kept such recommendations from being widely adopted.

Peters and Orejas-Miranda (1986) listed eight subspecies (Table 7.1), which have been largely adopted by some in the academic community and most in the herpetocultural community (for example, Fogel, 1997; Russo, 2007; but see Ross and Marzec, 1990 for a more conservative viewpoint). Both Walls (1998a) and Peters and Orejas-Miranda (1986) gave a synonymy for the species, and the latter included a key to subspecies. Smith (1999) provided a rough review of the taxonomy of *B. constrictor*, including references to much of the important literature. Price and Russo (1991) reviewed subspecies of *B. constrictor*, described a new subspecies *Boa constrictor longicauda*, suggested that *B. c. nebulosa* and *B. c. orophias* warrant specific status, and downgraded *B. c. melanogaster* (Langhammer, 1983) to a *nomen dubium*. Savage (2002) briefly commented on some potential problems with the approach of Price and Russo (1991) in describing *B. c. longicauda*, but concurred with their castigation of Langhammer (1983). Lazell (1964) gave full descriptions and ecological information for *B. c. orophias* from Saint Lucia and *B. c. nebulosus* from Dominica, comparing both to *B. c. constrictor* from the mainland. More recently, some authors (Walls, 1998a; Bonny, 2007) have considered the Saint Lucia and Dominica boas as full species, based on their allopatry and apparently independent evolutionary lineages, while others have suggested that the Argentine subspecies (*B. c. occidentalis*) should be considered a full species as well (M. Chiaraviglio, pers. commun., 2007).

We suspect that raising *B. c. orophias* and *B. c. nebulosus* to full species could render some other subspecies paraphyletic with respect to these island populations, necessitating the erection of additional species; the consequences of raising *B. c. occidentalis* would likely have similar repercussions. Pending a phylogeographical review of the genus, we consider the lineage to represent a single wide-ranging species for the purposes of this document.

Despite a fairly large body of literature basing intraspecific taxonomic differentiation on the subspecies described in Table 7.1, it is important to note that a more nuanced view of geographic variation in Boa Constrictors is likely to emerge with further study, and that the current named subspecies may be insufficient to describing this variation. Wilson and Meyer (1985) stated that “*Boa constrictor* is a widespread, common and variable species with a taxonomy existing in an abysmal state...it is obvious from (a perusal of the literature) that numerous potentially interesting patterns of character variation are disarticulated by the application of the subspecies category...if we are to understand the systematics of this logistically-difficult-to-study snake, we will have to jettison the archaic system of subspecies categories now masquerading as a systematic framework.” Similarly, Savage (2002) concluded, “No adequate study of individual and geographic variation in this wide-ranging and common species has ever been published,” and instead of recognizing traditional subspecies, Savage hesitantly offered only four “poorly diagnosable geographic variants...often regarded as races of this boa that intergrade in geographically intermediate areas.”

Table 7.1. Subspecies of *Boa constrictor* as recognized by Peters and Orejas-Miranda (1986), with the addition of the disputed *B. c. longicauda* as proposed by Price and Russo (1991). Data from sources listed in text. See text for comments on legitimacy of subspecific epithets. For dorsal blotch and scale row counts, we give ranges as the recorded minima to recorded maxima; numbers that are contradictory among sources are indicated with *.

Subspecies	Common name	Geographic distribution	Dorsal blotches	Dorsal scale rows	Ventral scale count
<i>B. c. constrictor</i>	Red-tailed Boa	S. America, inc. Amazon Basin	14*-22*	77*-95	231*-250*
<i>B. c. imperator</i>	Common Boa	Mexico, C. America, NW S. America	22-30	55-79	225-260*
<i>B. c. orophias</i>	St. Lucia Boa	St. Lucia, Lesser Antilles	25-31	65-75	258*-288
<i>B. c. occidentalis</i>	Argentine Boa	Portions of Bolivia, Paraguay, Argentina	22-30	64*-87	242-251
<i>B. c. sabogae</i>	Pearl Islands Boa	Islands of Gulf of Panamá	?	65-67	241-247
<i>B. c. nebulosus</i>	Clouded Boa	Dominica, Lesser Antilles	31-35	59-69	258-273
<i>B. c. amarali</i>	Bolivian Boa	Portions of S. Brazil, Paraguay, Bolivia	22-28	71-79	226-237
<i>B. c. ortonii</i>	Peruvian Boa	NW Peru	15*-28*	57*-80*	246-252
<i>B. c. longicauda</i>	Long-tailed Boa	Peru, vicinity of Tumbes	19-21	60-76	223-247

1.2 Common Names

Common names for the Boa Constrictor are legion, as would be expected of a species with such an enormous geographic distribution. In English, this species is one of the few with a common name identical to its scientific name. A few examples of regional common names include Béquer (Costa Rica: Savage, 2002), Mazacuate, Waula, and Ugrwe (Honduras: McCranie and others, 2006), Lampalagua (Argentina: M. Chiaraviglio, pers. commun., 2008), Mboi-roy (Paraguay: Waller and others, 1995), Macajuel (Trinidad: Boos, 2001), Jumbo Jocko (Tobago: Boos, 2001), and Wowla (Belize: Stafford and Meyer, 1999).

1.3 Evolutionary Context

Boa Constrictors have long been placed within the family Boidae, which traditionally included boine, erycine, and pythonine snakes. In recent years, however, pythons have been split off to form the Pythonidae, leaving erycines and boines in the Boidae. The boine snakes are currently composed of at least 32 species of snakes, primarily found in the Neotropics but with two genera in Madagascar and one genus in southeast Asia (Kluge, 1991; McDiarmid and others, 1999; Burbrink, 2005). Numerous phylogenetic hypotheses of relationships within and among these higher taxa have been erected over the decades.

Based on examination of morphological characters, Kluge (1991) hypothesized that the two Madagascan taxa are more closely related to Boa Constrictors than any of the three are to other New World boines. This hypothesis was accepted by many herpetologists and led to much bewilderment among those attempting to decipher the historical biogeography of the subfamily. More recently, Burbrink (2005) explicitly examined the phylogenetic position of *B. constrictor* among other boine snakes, incorporating molecular analyses, re-examination of Kluge's morphological data, and a combined analysis. He rejected the hypothesis that Madagascan taxa are the closest relatives of Boa Constrictors, and instead proposed a clade that includes all the New World boines as a natural grouping, with *Boa* as the sister taxon to a group that includes *Corallus*, *Epicrates*, and *Eunectes*. The informal name "boa" is often applied to the boines in general and it may be a component of the common names of many individual species (for example, Pacific Island Boa), but in this work we are referring specifically to *Boa constrictor* whenever we use the unmodified term "boa."

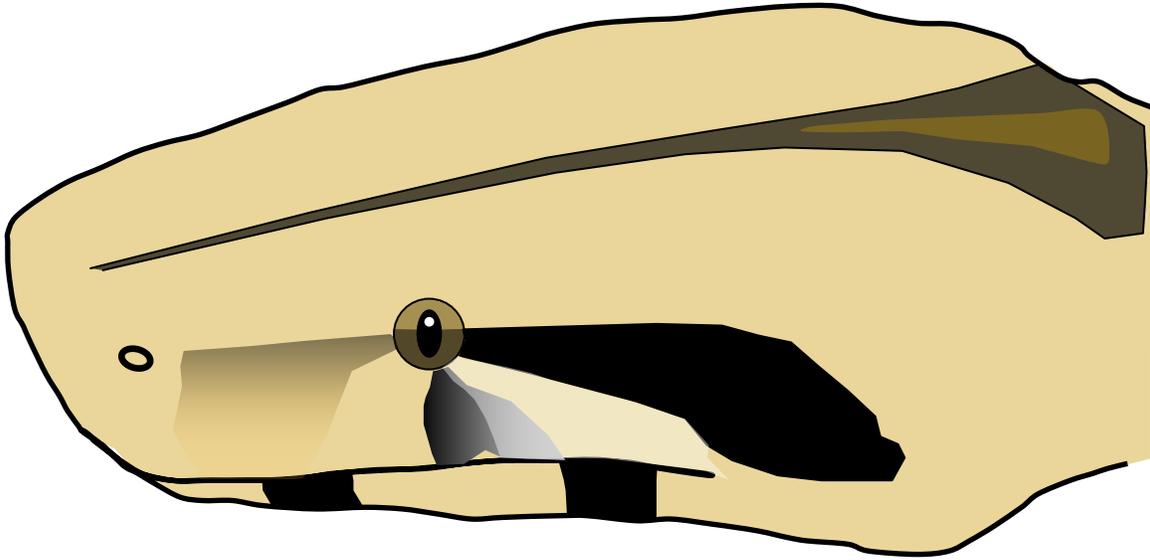


Figure 7.1. Schematic representation of the head of *B. constrictor*

2.0 Description

2.1 Unique Morphological Features

See the biological profile for *P. molurus* for characters that tend to be shared among giant constrictor snakes, including *B. constrictor*. Boa constrictors are easily distinguished from pythons because boas have no enlarged head shields or internasals. Unlike the pythons, boas also lack thermoreceptive labial pits. In contrast to the four species of anacondas (genus *Eunectes*) boas have laterally-directed eyes, as is characteristic of most terrestrial snakes.

2.1.1 Color and Pattern

This species is extremely variable in color and pattern, but distinguishing Boa Constrictors from other large-bodied constrictors is straightforward. Boas have no visible thermoreceptive pits that open to the environment and no enlarged scales on the top or lateral head surfaces, other than slightly enlarged nasals near the tip of the snout. Boas also lack the four or five longitudinal head stripes that are present in the anacondas (see section 2.1 of chapters Eight and Nine); instead, boas tend to have a single narrow dark stripe on the top of the head, which may or may not widen into a narrow arrowhead shape towards the back of the head and neck. There is usually a dark band (width varies among individuals) from the eye posteriad (we term this the ocular stripe), and this band typically extends through the bottom half of the eye and forward to the snout, usually becoming wider and angling down to the supralabials—the combination of these bands often appears as a single stripe originating on the snout and continuing to the neck. There is usually another dark blotch below the eye (often appearing as a triangle with the narrower end pointed toward the eye), and two more blotches are typically present on the

infralabials (sometimes lined up with the subocular blotch and the anterior end of the ocular stripe where it contacts the supralabials, but offset in many parts of the range).

In most parts of the range, the dorsal ground color is light tan to brown, and the venter is nearly immaculate and white or off-white in color, although *B. c. occidentalis* exhibits extensive dark ventral coloration (T. Waller, pers. commun., 2009), as do some individuals in other parts of the range (Langhammer, 1983). The dorsal pattern is variable, but usually consists of well-defined dark hourglass-shaped dorsal saddles on a lighter background. The size, number, and shape of the saddles are extremely variable. Most boas also have less distinct lateral markings that are offset from the dark saddles, consisting of wide vertical bars or ocelli with lighter centers. In many populations, the dorsal saddles become much wider and assume the form of rectangles or oval blotches on the tail, with bright chestnut to red colors (hence the common term “red-tailed boas”).

In a description that will distinguish most mainland South American boas from other potentially confusing taxa, Lazell (1964) described *B. c. constrictor* as having “15 to 22 rather neat, geometric, dark dorsal saddles to the level of the anus; the ground color is fawn-brown to tan; the venter white to yellow with little dark marking; a dark stripe proceeds from the eye directly to the supralabials (subocular stripe), and a second proceeds from the eye anteriorly in the loreal region, then curves down onto the supralabials (loreal stripe); both stripes correspond to two dark blotches on the infralabials and chin.” In El Salvador, *B. c. imperator* was described as “dorsal ground color gray, grayish brown, brown, or yellowish brown, with a series of darker saddle-like blotches becoming more reddish brown and contrasting on the tail, where they form dark brown rings alternating with cream rings; another series of smaller creamish centered and rhomboidal blotches laterally; top of head shares dorsal ground color; a narrow dark brown median stripe originating on the snout and extending onto neck” (Köhler and others, 2006). Mainland boas from Venezuela have 16-20 dorsal blotches, plus 3-5 on the tail (Lancini, 1986), while Dixon and Soini (1986) reported 17 body blotches (range 14-21) and 4.8 tail blotches (range 4-6) among boas from the Iquitos region of Peru. Beebe (1946) described variation in iris color in *B. c. constrictor* from S. America, and stated that in Kartabo, Guyana, there were “two more or less distinct and definite color phases, independent of age or sex. One was characterized by rich, warm hues of chestnut and browns, and the other was darker and colder in general color, with drab and olive greens replacing the warmer tones.”

Insular *B. c. orophias* from Saint Lucia have “27 to 31 distinct, subrectangular, dark dorsal saddles to the level of the anus; dorsal ground color rich brown; venter white with black or grey spotting pronounced; subocular stripe distinct and complete; loreal strip largely obsolete; dark pigment on chin and infralabials not closely corresponding to the facial stripes” (Lazell, 1964). Insular *B. c. nebulosus* from Dominica have “32 to 35 very obscure, irregular transverse markings to the level of the anus; dorsal ground color very dark, clouded, grey-brown; venter ash to slate grey, blotched and mottled with black; both loreal and subocular stripes absent, or, at most, partially indicated and largely obsolete; infralabials and chin merely grey” (Lazell, 1964). Dominican boas occasionally exhibit extreme melanism (Malhotra and Thorpe, 1999), and Porras (1999) further describes coloration of various insular boas, including their tendency to change color.

2.1.2 Scalation and Meristics

As would be expected for such a wide-ranging species, *B. constrictor* exhibits considerable geographic variation in scale pattern and number. According to Walls (1998a), *B. constrictor* has 17-25 supralabials and 20-28 infralabials, 55-91 dorsal scale rows at midbody, 225-288 ventrals, and 45-69 subcaudals (however, he later listed subspecies with counts that do not agree with some of these numbers). This summary was from across the entire range of the species and excluded boas from St. Lucia and Dominica, which he recognized as full species. Scalation ranges for various subspecies, including questionable subspecies, of *B. constrictor* have been tabulated and/or discussed by various authors (Peters and Orejas-Miranda, 1986; en Ben Lotte, 1996, Walls, 1998a; Smith, 1999; Monzel, 2005: see also Table 7.1 and discussion of the validity of these subspecies in the section 1.1), and Gomes and others (1989) provided line drawings of *B. constrictor* anatomy.

Considerable meristic and morphological divergence can exist between mainland and island boas. For example, Lazell (1964) found that *B. c. constrictor* from northeastern South America have a “slightly prominent snout and straight or nearly straight canthus; there are 81 to 95 dorsal scale rows at midbody, [and] 234-243 ventrals.” In contrast, he found that insular *B. c. orophias* from Saint Lucia have a “prominent snout and a convex canthus; 65 to 75 dorsal scale rows at midbody, 270 to 288 ventrals,” and *B. c. nebulosus* from Dominica have a “prominent snout and strikingly convex canthus; 59 to 69 dorsal scale rows at midbody, 258 to 273 ventrals.” Similarly, insular *B. constrictor* from Belize have a narrow head, longer labial length, longer nares-ocular distance, shorter internares distance, and larger eyes compared to mainland boas, and island snakes were also shorter and lighter at the same length (Boback, 2006).

2.2 Size

As with most giant constrictors, the maximum size of the Boa Constrictor has been subject to exaggeration, especially in the older literature. Unfortunately, many of these claims of gigantic boas have been perpetuated by more recent authors, and ascertaining the actual maximum size is difficult. Part of the confusion stems from misapplication of the name Boa Constrictor to other giant snakes, including anacondas and even some Old World pythons (Ditmars, 1931). A 5.7 m specimen from Trinidad turned out to be a misidentified Green Anaconda (*Eunectes murinus*: Boos, 1992). Lancini (1986) stated that he measured a skin in “an institution in Brazil” that measured 5.45 m; however, skins can be stretched by over 20 percent as compared to live snake length (RNR, pers. obs., 2003). In a review of the species, Greene (1983) stated that *B. constrictor* reaches 5 to 6 m, but Martins and Oliveira (1998) state that the maximum size for the species is 4.2 m, and minimum is 0.65 m. Savage (2002) stated that maximum size is 4.5 m, but that most adults are 2-3 m. Pope (1961) gave maximum length as 5.5-5.8 m. Porras (1999) noted that he handled several boas over 4.0 m, including individuals of 4.4 m and over 4.88 m, while unpacking a shipment of animals imported from Peru.

The maximum body size based on an available specimen is 4.45 m (Watkins-Colwell and Leenders, 2003), but this measurement is from a dried skin from Brazil. Although the authors claim that a visual inspection revealed no apparent effects of stretching, they provide no quantification of this claim, which we consider dubious based

on our experience with skins removed from boid snakes (RNR, pers. obs., 2008) and the published observation that two Boa Constrictors over 3 m total length in life yielded skins that were 13.7 percent and 30 percent longer than the live length (Field Naturalists' Club, 1893, 1894: cited in Boos, 2001). These findings imply that the maximum size of *B. constrictor* may be in the neighborhood of 4 m.

Table 7.2. Total lengths and masses of typical *B. constrictor* (compiled/estimated from the literature sources listed in the text).

Sex	Hatchling		Maturation		Max. reported	
	Total (mm)	Mass (g)	Total (m)	Mass (kg)	Total (m)	Mass (kg)
M:	430-575	34-80	0.9-1.6	0.225-1.75	3.0	~15
F:	430-575	34-80	1.2-2.3	0.8-5	4.45	~35

The largest boas tend to be from northern South America, with body size generally decreasing to the north and south of the Amazon Basin, as well as numerous examples of dwarfed insular forms on Caribbean, Pacific, and Atlantic islands. Mexican specimens are generally small, with average lengths generally between 1.0 and 1.75 m (Bogert and Oliver, 1945; Davis and Smith, 1953; Myres and Eells, 1968; Gonzalez-Baca and Cuaron, 2003), while Central American specimens more commonly reach and sometimes exceed 3.0 m (Campbell, 1998; Leenders and Watkins-Colwell, 2004; Guyer and Donnelly, 2005; Köhler and others, 2006; Holtzman and others, 2007). Juveniles and adults from insular populations near Central America are often smaller than those on adjacent mainland areas (Barbour and Loveridge, 1929; Boback, 2005, 2006; Reed and others, 2007). Mainland neonates from Belize were 42 ± 4.7 g and 0.48 m (0.42 m SVL: Boback, 2005; Boback and Carpenter, 2007). Insular neonates from Belize were 34 ± 3.6 g and 0.44 m (0.39 m SVL: Boback, 2005; Boback and Carpenter, 2007), while 13 neonates from Utila, in the Bay Islands of Honduras, were 0.49-0.52 m and weighed approximately 52 g (Köhler, 2003). There was a captivity effect for island *B. constrictor* from Belize, as captive-bred females had longer babies than did wild-bred females (Boback, 2005; Boback and Carpenter, 2007).

Body size in South America is variable, but most reports corroborate the observation that northern South American boas reach larger body sizes than do boas to the north or south. Beebe (1946) found fairly small boas in Venezuela, but at Kartabo (Guyana), "...among the twenty or thirty collected, eight were from eleven feet to twelve feet six inches in total length" (3.35-3.81 m). Boas from Tumbes Province, Peru, can exceed 2.80 m (Price and Russo, 1991), while boas from Cusco Amazónico, Peru, were between 1.2 and about 3 m (Duellman, 2005). On Trinidad, off northeastern South America, Mole and Urich (1894) stated that the largest boa with which they were familiar was a 3.51 m female, containing 41 "eggs," and that, "It is probable that Boas (in Trinidad, at any rate) never exceed 12 feet" (3.66 m). Mean neonatal size of Brazilian *B. c. amarali* was 0.47 m (0.41 m SVL) and that of *B. c. constrictor* was 0.52 m (0.45 m SVL: Pizzatto and Marques, 2007). Neonatal sizes given by Pizzatto and Marques (2007) appear to be somewhat smaller than most values recorded for mainland South

American snakes, probably because they included values from near-term embryos. Alternatively, it could be that post-parturient neonates hide in refugia while absorbing remaining yolk, emerging only after growing past their lengths at parturition.

Lazell (1964) collected boas up to 2.36 m on Saint Lucia and 1.85 m on Dominica, but saw larger (to about 3 m) boas in the field and in captivity. In Argentina, adult male *B. c. occidentalis* averaged 2.1 m (1.80 m SVL) and 4.1 kg and adult females 2.28 m (2.05 m SVL) and 6.1 kg (Bertona and Chiaraviglio, 2003). Some authors (Ceï 1993, cited in Chiaraviglio and others, 2003) have stated that the largest *B. c. occidentalis* were over 4.0 m in the past, but the largest animals found since 1995 in Córdoba, Argentina, were 3.16 m (2.85 m SVL: female) and 2.59 m (2.23 m SVL: male), possibly reflecting the intensive harvest pressure on large snakes (or exaggerated claims of body size in the past). Tomás Waller (pers. commun., 2009) stated that he is unaware of any individuals of this subspecies that exceeded 3.2 m total length and around 18 kg body mass, even in areas that have not been harvested. Argentine neonates are 0.47-0.66 m and 70-80 g (Monguillot, 1988; Bertona and Chiaraviglio, 2003).

2.3 Sexual Size Dimorphism

As with the majority of species of large boid snakes, *B. constrictor* exhibits female-biased sexual size dimorphism (SSD). Females tend to reach longer absolute lengths, and in many cases are relatively heavier than males of similar body lengths. The very largest boas are undoubtedly female. Section 2.2, above, includes some relative lengths of male and female boas from various parts of the species' geographic distribution. Unfortunately, few studies have sample sizes large enough for estimation of average SSD in a population, and SSD based on small samples and museum specimens are likely biased by differences in detection probability among sizes and sexes, and by the tendency for only relatively small specimens to be accessioned into museums (thus underestimating SSD for a species where females attain appreciably larger sizes).

Among available records, SSD (calculated as [SVL of larger sex/SVL of smaller sex] – 1; Lovich and Gibbons, 1992) was 0.01 and 0.02 among preserved Brazilian *B. c. amarali* and *B. c. constrictor*, respectively, but only 0.01 among neonate *B. c. constrictor*; females of both subspecies had relatively larger heads and shorter tails than did males, based on preserved specimens (Pizzatto and Marques, 2007). Other records of SSD in length, with varying sample sizes, include 0.142 among Argentine boas (Bertona and Chiaraviglio, 2003), -0.03 (males slightly larger: length SSD) and 0.01 (mass SSD) among boas on Ometepe Island, Nicaragua (Holtzman and others, 2007), and 0.11 (length SSD) and 1.0 (mass SSD) among dwarfed insular boas on Cayo Pequeño, Honduras (Reed and others, 2007). In Belize, insular boas did not exhibit appreciable SSD, but insular males had comparatively longer tails than did mainland males (Boback, 2006). Although preserved neonatal females from Brazil had shorter tails (Pizzatto and Marques, 2007), Boback and Carpenter (2007) found no evidence of SSD at birth and no sex differences in any skeletal elements, including the skull.

2.4 External Sexual Differentiation

As with most boas and pythons, the Boa Constrictor exhibits vestigial remnants of a pelvic girdle, including externally visible pelvic spurs. These are larger in males than in females (Pope, 1961). Very large individuals are virtually always female. In captive

individuals, male tail length averages 11.55 percent of total length, while the equivalent proportion for females is 9.85 percent (Smith, 1999).

3.0 Distribution in Space and Time

3.1 Native Range

Henderson and others (1995) presented what is perhaps the best-supported range map of Boa Constrictor for S. America; this map was based on museum and literature surveys. They noted that *B. constrictor* has a latitudinal range of 66°, nearly twice that of any other New World boine, and that its altitudinal range is 0-1500 m. The species is present on a great number of islands in the Caribbean, Atlantic, and Pacific, including some populations that may be introduced (for example, Islas San Andres, Santa Catalina, and Providencia in the Atlantic, claimed by Colombia: Porras, 1999). Walls (1998a) provided a map showing the distributions of the traditional subspecies, and Köhler (2003) provided a fairly detailed range map for Central America. Steadman and others (1984) found fossils from *B. constrictor* on Antigua in the Lesser Antilles, indicating a former presence of the species—however, these authors cautioned that this could have been a human introduction to the island.

Argentina—Bertona and Chiaraviglio (2003) and Cardozo and Chiaraviglio (2008) studied *B. c. occidentalis* in the District of Pocho in the west plain of Córdoba Province of Argentina. This is close to the southernmost extent of the species (M. Chiaraviglio, pers. commun., 2007), although Chiaraviglio (2006) previously stated that the genus *Boa* is distributed from 30° N to 36° S. Chiaraviglio and others (1998) provided more information on geographic range in Córdoba Province, and DiCola and others (2008) modeled the distribution of *B. c. occidentalis* in the Gran Chaco (which extends from 22° to 31° S) of Argentina, at or near the southernmost extent of the species' distribution. As a result of their model, they provided a dot-distribution map for 93 *B. c. occidentalis* in Argentina, and a probability area for the occurrence of *B. c. occidentalis*. They concluded that boas are continuously distributed across the plains of the Gran Chaco, and that suitable habitat extends from 60 to 1600 m.

In contrast, T. Waller (pers. commun., 2009) states that the species does not exceed 1120 m in Argentina. Giraudo and Scrocchi (2002) also summarized the species' distribution in Argentina, describing it as being present in the provinces of Catamarca, Córdoba, Chaco, Jujuy, Formosa, La Rioja, Mendoza, Salta, San Juan, San Luis, Santa Fe, Santiago del Estero and Tucumán. Chiaraviglio (2006) stated that *B. constrictor* inhabits the Chaco, Monte, and Espinal phytogeographic provinces of Argentina, but within these it is largely restricted to Dry Chaco forests. Giraudo and Scrocchi (2002) stated that only *B. c. occidentalis* is present in Argentina and discussed the lack of specimens from La Pampa province, such that reports of the species' presence south of about 34° S are suspect.



Figure 7.2. Estimated native range of the Boa Constrictor (*Boa constrictor*), with approximate Mexican range in inset box. Intervening Central American range is nearly continuous at suitable elevations. Arrow indicates presence on St. Lucia and Dominica; species is present on many other islands, but this is not reflected on this map. Maps follow Henderson and others (1995) and references in section 3.1 of this chapter.

Belize—Present through most lowland areas. Neill and Allen (1962b) mentioned a *B. constrictor* caught on Cockroach Cay, Turneffe Group, Belize, and stated, "Boas are common on some of the cays, and on the mainland the species seems to find its optimum habitat in red mangrove swamp." They stated that mangrove boas from Belize have more dark red/cinnamon coloration than do lowland boas from Honduras. Boback (2005) collected *B. constrictor* from several mangrove islands off the Belize coast and from mainland areas around Belmopan.

Bolivia—Present throughout the lowlands of Amazonia, Beni, and Chaco, including both *B. c. amarali* and *B. c. occidentalis* (T. Waller, pers. commun., 2009), but apparently absent from western highlands (Henderson and others, 1995).

Brazil—Found throughout the Amazon Basin and throughout much of the rest of the country, excepting only the extreme southeast (Henderson and others, 1995; Walls, 1998a; Bartlett and Bartlett, 2003). Strüssmann and Sazima (1993) found two boas during snake surveys in the Pantanal in western Brazil, but the species appears to be more common in the Manaus region (Martins and Oliveira, 1998). Andrade and Abe (1998) found color, morphology, and scutellation abnormalities in neonate *B. c. amarali* from a dam captured in the state of São Paulo that was bred in captivity and kept at 18-26°C during gestation. They suggested that temperature may limit the southern extent of this subspecies' range, although we note that their captive regime did not allow thermoregulation by the dam.

Colombia—Present in both Caribbean and Amazonian lowlands, Pacific Choco forest, some offshore islands (T. Waller, pers. commun., 2009; Henderson and others, 1995).

Costa Rica—Apparently present throughout, except for high elevations (Savage, 2002; Köhler, 2003). While some authors have claimed that the species reaches its altitudinal limits at about 900 m in Costa Rica (Pope, 1961; Leenders, 2001), Savage (2002) provided a dot-distribution map for Costa Rica and stated that *B. constrictor* reaches 1360 m (this record is surprisingly similar to the 1370 m cited for Honduras by McCranie and others, 2006).

Dominica—Lazell (1964) discussed *B. c. nebulosus* on Dominica, under the former genus *Constrictor*. He stated that boas are found throughout the island and to at least 350 m elevation, but that they are confined to wet ravines in the driest areas of the island.

Ecuador—Apparently found throughout the lower elevations on both the Pacific coast and in Amazonia on the eastern slope of the Andes, including one possibly isolated subspecies in the Tumbes region (Price and Russo, 1991). Boas were considered uncommon at Santa Cecilia, Ecuador, at an elevation of 340 m (Duellman, 1978).

El Salvador—Historically, probably present through much of the country up to about 1200 m. The fewer than 20 records in Köhler and others (2006) are from widely-

distributed lowlands (less than 600 m) and areas between 600 and 1200 m. Some of these records are higher than the limits proposed in earlier literature (for example, 650 m: Pope, 1961).

French Guiana—Documented by Chippaux (1986) in most of his field sites, although most of these were located along the coast [many of the localities given by Starace (1998) derived from Chippaux (1986)]. Probably found throughout the lower elevations.

Guatemala—Present along the Pacific coast and in the northern third of the country; possibly absent from much of Sierra Madre (Köhler, 2003). Stuart (1948) collected one *B. constrictor* from Finca Canihor and 3 from Finca Chamá, Alta Verapaz, Guatemala. The species attains about 1200 m in the vicinity of Petén, Guatemala (Stuart, 1935; Campbell, 1998).

Guyana—Apparently found throughout the lower elevations, but poorly documented in the literature.

Honduras—Wilson and Meyer (1985) provided a dot-distribution map for Honduras, and stated that boas are found in Tropical Moist Forest, Tropical Dry Forest, and Subtropical Moist Forest at elevations to 800 m. McCranie and others (2006) extended the elevational range in Honduras to 1370 m and described the species as widespread throughout much of the mainland, as well as on the islands of Barbareta, Guanaja, Roatán, Utila, and Cayo Cochino Grande. Boas are present in the Cayos Cochinos (both Cayo Grande and Cayo Pequeño, referred to as Hog Island boas in the live animal trade: Lundberg, 2002; Reed and others, 2007), although Wilson and Cruz Díaz (1993) previously failed to find them on either island.

Mexico—Found in most of the tropical regions of the country, as well as north into portions of the Sonoran Desert and northeast into Tamaulipan scrub and on many islands (Oliver, 1937; Duellman, 1954; Martin, 1958; Pope, 1961; McGinnis and Moore, 1969; Lemos-Espinal and Ballinger, 1994; Lee, 1996; Walls, 1998a). In the northwest, localities include Hermosillo (Allen, 1933) and Guirocoba in Sonora (the latter at about 453 m where they were described as common in valleys and rare in the hills), 79 km north of Hermosillo (Zweifel and Norris, 1955; Pope, 1961), and southeast of Alamos, Sonora, at around 250 m elevation (Myres and Eells, 1968), while the most northeasterly record is from Tamaulipas, Mexico, at 23°23'25" N, 99°30'30" W and 1040 m (Farr and others, 2007). Pope (1961) stated that *B. constrictor* reaches 792 m in Michoacán, Mexico.

Nicaragua—Apparently present throughout, possibly excepting a small portion of the north-central highlands (Gaige and others, 1937; Köhler, 2003). Holtzman and others (2007) studied *B. constrictor* on Ometepe Island, Nicaragua. A dwarfed form of *B. constrictor* is present on the Nicaraguan-owned Islas de Maíz, off the east coast of Central America (Barbour and Loveridge, 1929).

Panamá—Found throughout the lower elevations (Henderson and others, 1995; Köhler, 2003).

Paraguay—In Paraguay, *B. constrictor* is present in most areas except the central wetlands (Waller and others, 1995); *B. c. occidentalis* is found in the west, and *B. c. amarali* in the east, with little apparent intergradation even in the northeast in ecotones where the taxa abut one another (T. Waller, pers. commun., 2009).

Peru—Found through much of the country except at very high elevations in the departments of Amazonas, Huánaco, Lambayeque, La Libertad, Loreto, Madre de Dios, Pasco, Piura, San Martín, and Ucayali (Lehr, 2002; Bartlett and Bartlett, 2003, T. Waller, pers. commun., 2009). Lehr (2002) personally observed specimens between 320 and 900 m above sea level. *B. c. longicauda* was described from east of Tumbes, Tumbes Province, Peru (Price and Russo, 1991), and, if the taxon is valid, it is likely confined to Tumbes Province, which is surrounded to the north, east, and south by mountains rising to 3000 m.

Saint Lucia—*B. c. orophias* is apparently confined to the leeward and windward coasts in the northern two thirds of the island, including moderately dry lowlands and to at least 350 m elevation. Boas are absent from southern and central highlands and from the south coast (Lazell, 1964).

Suriname—Apparently found throughout the lower elevations (Henderson and others, 1995), but poorly documented in the literature and represented by only a few museum specimens, despite being highly valued in the live animal trade (“Suriname red-tailed boas” are prized). Individuals are regularly encountered in the interior (N. Hawley, pers. commun., 2008).

Trinidad and Tobago—Found throughout the major islands (Mole and Urich, 1894; Boos, 2001), as well as smaller outliers such as Gaspar Grande and Monos Islands, southwest of Trinidad (Boos, 1984).

Venezuela—Probably present through much of the country, but Kornacker (1999) did not provide localities. La Marca and Soriano (2004) stated that *B. constrictor* reaches 1500 m in the Andes of Venezuela. *B. constrictor* can be found on the arid Paraguana Peninsula (GHR, pers. obs., 1983), and on Isla de Margarita (Brongersma, 1940).

3.2 Habitat Range

As part of a short review of the species, Greene (1983) stated that, “Boas inhabit a remarkable range of environments from sea level to 1,000 m, including wet and dry tropical forest, savanna, very dry thorn scrub, and cultivated fields.” Henderson and others, (1995) reported that *B. constrictor* uses all available vegetative/edaphic zones present in S. America (16 categories in all, based on overlaying their range map on the vegetation map of Campbell and Lamar, 1989), and that the species also occupies more “morphoclimatic domains” than any other New World boine. They concluded that it is “...a habitat and diet generalist that has successfully colonized many islands and remains

common in human-disturbed habitat,” and also reported that *B. constrictor* has been reported by fishermen in Belize to float in the Caribbean between small islands. Both Porras (1999) and Henderson and others (1995) provided lists of occupied islands in both Central and South America, including islands of less than 0.5 km².

In Argentina, *B. c. occidentalis* were studied in the “driest territory of Occidental Chaco. It is characterized by a xeric forest of *Aspidosperma quebrachoblanco* and *Prosopis nigra* and shrublands of *Larrea divaricata* and *Mimozyanthus carinatus*” (Bertona and Chiaraviglio, 2003). Di Cola and others (2008) described boa habitat in the Gran Chaco as the “largest dry forest in South America and its vegetation comprises a mosaic of xerophytic forests, woodlands, scrubs, savannas, and grasslands,” and T. Waller (pers. commun., 2009) confirmed that Argentine boas are habitat generalists within the Dry Chaco forests.

In Venezuela, *B. constrictor* was described as inhabiting all low and warm areas of the country, up to 1500 m elevation (Lancini, 1986), while boas are present in lower montane dry evergreen forest, humid submontane forest, and semideciduous montane forest of the Venezuelan Andes (La Marca and Soriano, 2004). Stuart (1948) stated that “in Alta Verapaz (Guatemala) this species is apparently restricted to the lower Tropical zone, where it is more frequently taken in second-growth than it is in the virgin forest.” In Manaus, Brazil, and outskirts, boas were often found in disturbed areas (Martins and Oliveira, 1998); these authors also summarized previous literature and concluded that the species is found in multiple habitats, is primarily terrestrial, and may be active by day or night.

In Sonora, Mexico, Myres and Eells (1968) found *B. constrictor* in deciduous thornscrub with rainfall near 508 mm per year. The rainy season at this site is in late summer (August–September), but winters are relatively dry. Martin (1958) stated that in southern Tamaulipas, Mexico, *B. constrictor* “...has not been found north of Tropical Deciduous Forest, its typical habitat in the Gómez Farías region.” However, Farr and others (2007) reported that *B. constrictor* inhabits Tamaulipan tropical thornscrub in the Jaumave Valley to the north, where the thornscrub blends with Chihuahuan Desert.

There were no differences in apparent boa abundance among the three main vegetative types on Cozumel, leading to the conclusion that these invasive boas are habitat generalists. Overall, more boas were seen in uninhabited areas than in inhabited areas on Cozumel (Romero-Nájera and others, 2007). Boos (1984) described the habitat of Gaspar Grande Island, apparently inhabited by *B. constrictor*, as extremely dry and scrub-covered. At the Deering Estate at Cutler (Miami-Dade County, Florida), invasive *B. constrictor* were found in multiple habitats, including tropical hardwood hammocks, dirt roads/trails, landscaped areas, and pine rocklands (Snow and others, 2007b), while invasive boas are established in sparsely vegetated arid habitats across Aruba (Quick and others, 2005; RNR pers. obs., 2008).

3.3 Climate Range

The Boa Constrictor inhabits a wide range of climate spaces (Figure 7.3). While the mean monthly temperatures experienced by most South, Central, and North American boas generally range above 15°C, the Argentine Boa (*B. constrictor occidentalis*) inhabits several localities with mean monthly winter temperatures well below 10°C (Di Cola and others, 2008). Multiple localities in various parts of the range exhibit a pronounced dry

season, suggesting that boas do not require aseasonal conditions even in South American localities. The more recent results of Di Cola and others (2008) extend the climatic limits described by Henderson and others (1995), who stated that, “mean winter temperature of 10°C appears to determine the northern and southern geographic limits for the species,” and that the species occurs in areas that receive fewer than 500 mm of rainfall annually (Peninsula de Paraguana, Venezuela), in areas receiving 100-200 mm of rain in evergreen shrubland of western Argentina, and in areas receiving less than 100 mm in western Peru. In contrast, a survey by T. Waller (pers. commun., 2009) recorded no Argentine boas in areas with less than 250 mm annual precipitation.

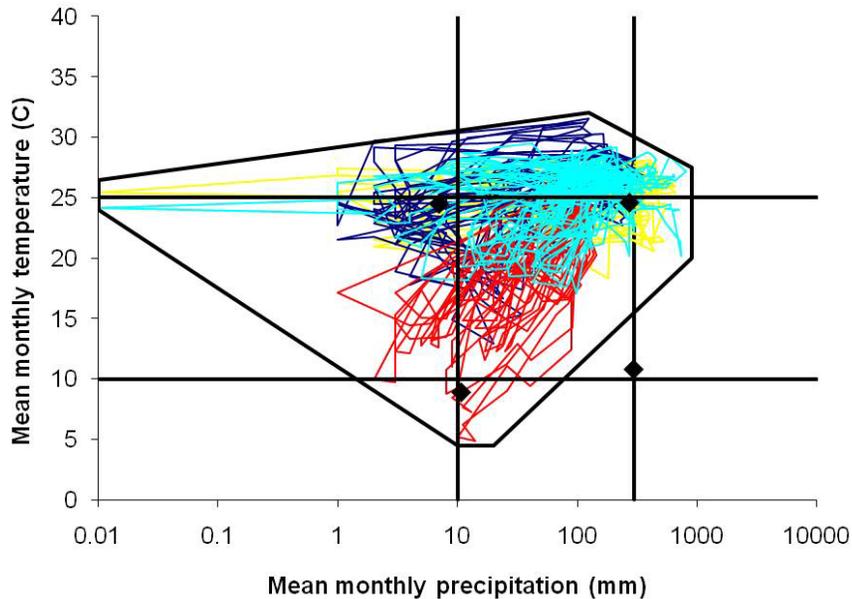


Figure 7.3. Climate space for the Boa Constrictor (*B. constrictor*) with reference lines and localities as introduced in Figure 2.1, based on 131 known localities from the native range. Climate loops color-coded as follows: Yellow = Central America; Dark blue = Mexico; Turquoise = South America; Red = Argentina and all other *B. c. occidentalis*.

3.4 Microhabitat

Generalizations about the macrohabitat use of the Boa Constrictor are easy to come by in the available literature, but microhabitat descriptions are infrequent. This is partially due to the low sample sizes of boas in most mainland herpetological studies, such that microhabitat observations tend to be anecdotal and based on only a few individuals. These anecdotes are further complicated in that microhabitats are only recorded for snakes that are seen by humans, in places that may not typify microhabitats actually selected by boas. In contrast, radiotelemetric studies on several islands have yielded relatively more information on actual microhabitat use over longer periods of time.

Based on the observation that boas consume bird species that occupy all forest strata, from the ground to the canopy (Boback and others, 2000), it may be safe to assume that boas also inhabit these strata. On small mangrove offshore islands of Belize, 96

percent of boas were found in trees and tree hollows, compared to 18 percent of mainland boas (Boback, 2006). On Ometepe Island, Nicaragua, most radiotelemetered snakes used overgrown fields and forest environments; resident snakes were more likely to use rocky outcrops, while displaced snakes were more likely to use trees/logs. With one exception, all locations in trees were less than 1 m above ground (Holtzman and others, 2007).

Juvenile *B. c. orophias* from Saint Lucia were often found in trees, once as high as 12 m (Lazell, 1964). *B. c. nebulosus* from Dominica (mostly small individuals) were also frequently found in trees, and boas occurred throughout the island to elevations of at least 350 m, but in arid areas their habitat appeared to be confined to wet ravines (Lazell, 1964). Vandeventer (1992) found *B. c. nebulosus* on Dominica aggregated in tunnels or rock piles in the vicinity of hot springs and sulfur gas vents along volcanic mountain streams and stated that these dens hold snakes year round.

In the Cayos Cochinos, Honduras, *B. constrictor* captures resulting from visual surveys were highest in areas where snakes were most detectable, rather than where snakes spent most of their time. For example, radiotelemetered snakes tended to occupy microhabitats with higher leaf and branch density and smaller diameter trees than did the individuals detected by sight (Reed and others, 2007).

Chiaraviglio and Bertona (2007) found that reproductive female *B. c. occidentalis* in Argentina preferred sites with greater arboreal cover. Reproductive females used this heavy cover, but also basked more frequently than did nonreproductive females or reproductive males, and thus required thick vegetative cover interspersed with open areas. Overall, reproductive females maintained higher body temperatures than nonreproductive females or reproductive males, and they appeared to be better thermoregulators (Chiaraviglio, 2006). All *B. c. occidentalis* studied using radiotelemetry were located under heavy cover (logs, caves, etc.) over 50 percent of the time (Chiaraviglio and Bertona, 2007), and all reproductive individuals were associated with burrows.

Twelve neonate boas were captured in 1996 by children along the oolitic limestone walls of the C-100 canal adjacent to the known invasive population at the Deering Estate at Cutler, Miami, Florida, and *B. constrictor* were observed to use gopher tortoise burrows in pine rocklands (Snow and others, 2007b).

3.5 Introduced Ranges

The Boa Constrictor has established more introduced populations than any other boa or python species of which we are aware, with at least three known populations. There are also multiple records and anecdotes of individual boas found far from their native range all over the world, largely as a result of released or escaped pets or individuals transported by another means. As an example of the latter type of pathway, at least seven *B. constrictor* specimens currently held in museums in the United States were found among bananas shipped from Central America or Mexico (RNR, unpubl. data). There are clearly multiple means by which the species could be transported to an area outside its range, with risk of establishment varying with factors such as propagule pressure, climate match with native range, etc.

The invasive population on Cozumel, off the coast of the Yucatán Peninsula in the state of Quintana Roo, Mexico, was described by Romero-Nájera and others (2007) and Martínez-Morales and Cuarón (1999). This population apparently became established as

a result of boas being discarded in 1971 by a film crew after their use in a movie being filmed on the island. The founding population may have consisted of two to six large individuals. Boas achieved high densities by 1989-1990 (Martínez-Morales and Cuarón, 1999). Of the seven boas observed by Martínez-Morales and Cuarón (1999) during approximately 400 km of pedestrian transects, all but one were "...about 1.5 meters long, the exception being about 2.5 meters."

Snow and others (2007b) reported on a population of *B. constrictor* on and around the Deering Estate at Cutler, a Miami-Dade County park property. Ninety-six individuals were captured between 1989 and 2005, including an individual found 2.1 km to the southwest of the park. Other individuals have been found in areas within 2.5 km of the park, and a large female was found dead after a recent prescribed burn in the park (S. Snow, pers. commun., 2008). However, most (around 70 percent) of the Deering snakes were found in 1996, when at least two females must have given birth in the park. The longest of 91 *B. constrictor* from the invasive population at the Deering Estate was 2.79 m (2.51 m SVL), and 66 percent of individuals were young-of-year. Snow and others (2007b) also provided records of three individual *B. constrictor* found elsewhere in southern Florida and gave a list of other large constrictors that have been found in the Miami area.

A population of *B. constrictor* has rapidly colonized the entire island of Aruba in less than a decade (Quick and others, 2005). The first boa was discovered in 1999, with annual capture rates increasing from 36 in 2000 and 40 in 2001 to 74 in 2002 and 118 in 2003 (Quick and others, 2005); population growth rates may have slowed since then (H. Reinert, pers. commun., 2008). Three scenarios have been proposed for how the boas arrived on Aruba: (a) natural dispersal from the mainland (the arid Paraguana Peninsula is only 17 km away); (b) stowing away in ornamental plants from the mainland; or (c) as a result of released/escaped pets (Quick and others, 2005). These boas tend to exhibit the small body size of island boas but exhibit head morphology and color pattern more typical of mainland boas (RNR, pers. obs., 2008). Further examination of the morphology and/or genetics of island and nearby mainland populations might be able to distinguish among these hypotheses to some extent, as boas from captivity might not exhibit traits from the nearby mainland, instead representing a more distant or inland source population.

3.6 Seasonal Activity

In Córdoba Province, Argentina, at the southern end of the species' range, average annual temperatures vary from 18-23 °C and rainfall varies from 300-550 mm with "distinct dry (April to September) and wet (October to March) seasons" (Capitanelli, 1979: cited by Bertona and Chiaraviglio, 2003). Maximum summer temperatures exceed 40 °C, and "...frosts occur commonly from May through early September" (Chiaraviglio and Bertona, 2007). Chiaraviglio and others (2003) found 125 of 153 *B. constrictor* during the dry season (local winter), and 56 percent of individuals captured in the dry season were found between 1300 and 1500 hr. Wet season air temperature during captures was 28 ± 5 °C, dry season was 22 ± 4 °C. Overall mean annual temperature was 19.5 °C, and annual activity appears to be primarily driven by temperature rather than by precipitation (T. Waller, pers. commun., 2009).

There were no differences in apparent activity of invasive boas by month or season on Cozumel (Romero-Nájera and others, 2007) as determined from road-cruising, but this conclusion was based on a small sample size. These authors found most boas at night while road-cruising, but they “did not systematically survey during daytime,” and noted that “we know that boas are also diurnally active on Cozumel.”

On Saint Lucia, *B. c. orophias* was considered extremely sedentary, and “...a specimen seen a week, two weeks, or even a month previously is usually in the same vicinity” (Lazell, 1964). Some boas were rumored to use the same den site for multiple years, but young boas were less predictable. Similarly, *B. c. nebulosus* from Dominica were considered “basically lethargic and prone to remaining in the same place for long periods of time” (Lazell, 1964).

In a series of short-term experiments, McGinnis and Moore (1969) used captive snakes, mesocosm trials, and radiotelemetry ($n = 1$) to examine thermoregulation in *B. constrictor* from Nayarit, Mexico. Juveniles in a mesocosm could maintain body temperature (T_b) as much as 7°C below shaded ground temperature by moving to subterranean retreats, while conversely these retreats allowed T_b to remain above ambient levels during cool rainstorms. No basking was observed, although basking was inferred via radiotelemetry in a free-ranging 2.3 m *B. constrictor* which experienced a 15°C rise in T_b over a 2.5 hour period. This snake experienced a peak voluntary T_b of 38.5°C , but mean T_b was 26.4°C .

In Sonora, Mexico, Myres and Eells (1968) found an aggregation of 5 boas (4 males and 1 larger female) in the foothills of the Sierra Madre Occidental, with body temperatures of $25.8\text{--}30.4^\circ\text{C}$ at the time of capture. T_b was higher than substrate or air temperatures. Temperatures as low as 11°C were recorded in this area during 17-20 December 1965.

Brattstrom (1965) reported that the T_b of a basking boa on Barro Colorado Island, Panamá, was 34°C (air: 27.0 , log: 30.8) at 1030 hrs. A larger *B. constrictor* emerging from a stream had a T_b of 26.0°C (water: 25.5 , air: 26.0). Boas in the Cayos Cochinos, Honduras, were captured at ambient temperatures between 24.5 and 36.2°C , with most captures occurring between 29 and 30.9°C . Body temperatures of 7 adult females averaged $29.3 \pm 1.8^\circ\text{C}$ (range $24.4\text{--}34.9$), and body temperatures averaged 1.3°C below ambient temperatures (Reed and others, 2007). Beebe (1946) found most of his *B. constrictor* at night on trails or low branches, and 88 percent of captures were “at the height of the long rainy season, May through July.”

Snow and others (2007b) suggested that the invasive population at the Deering Estate at Cutler may be limited by climate, and that reproduction may be successful only during years with especially warm winters, such as occurred in 1996; they support this idea by saying that the boas appear to be of northern South American stock and thus unlikely to be adapted to cooler temperatures.

Rivera and others (2005) stated that high dispersal capability is postulated for *B. c. occidentalis* based on measures of gene flow between populations and sexes. They found low levels of protein polymorphism between two populations separated by 200 km in Córdoba, Argentina, but no evidence of inbreeding.

3.7 Daily Activity

Daily activity is best studied by radiotelemetry because opportunistic observations of boas are typically biased by human activity cycles—this can result in artificially high numbers of observations of diurnal activity. Despite this potential bias, numerous records from the native range indicate that boas can be found active during virtually any time of day. However, records of daily activity cycles for *B. constrictor* are few, and once again the majority of studies are from islands or from a well-studied population in Argentina.

A single 2.4-m, 11.3-kg *B. constrictor* on Barro Colorado Island, Panamá, moved a total of 135 m over 12 days (Montgomery and Rand, 1978), moving from burrow to burrow. Tracking at hourly intervals showed that the snake did not make intradiel excursions from burrows and then return. Boback (2006) found most mainland boas at night, either crossing roads after rains or moving in garbage dumps.

Holtzman and others (2007) radiotracked 6 translocated and 14 untranslocated snakes on Ometepe Island, Nicaragua. Mean distance per move was 241 m for displaced snakes and 73 m for resident snakes, and all displaced snakes moved directionally back towards their capture sites. Overall, translocated snakes moved 1872 ± 388 m after relocation, but resident snakes moved only 887 ± 322 m (both groups' dispersal quantified from release point to position 5-10 months later).

In the Cayos Cochinos, Honduras, during the dry summer season, a small number ($n = 4$) of boas implanted with radiotransmitters moved on 23 percent of days they were located. Movements averaged 13.7 m from the previous location (range 1.6–59.1 m), and the total distance moved over the course of the approximately five week study ranged from 18.5 m to 208 m (Watson, 2004).

In Argentina, during the breeding season, radiotelemetry revealed that over 6-8 weeks (4-22 fixes) reproductive female *B. c. occidentalis* moved a total of 41 ± 19 m (range 0-97, $n = 5$), while non-reproductive females moved 628 ± 238 m (range 0-1598, $n = 6$), and reproductive males moved 388 ± 172 m (range 0-1362, $n = 8$; Chiaraviglio and Bertona, 2007).

3.8 Foraging Mode/Sensory Modalities

The Boa Constrictor is typically described as an ambush predator, using a sit-and-wait strategy to capture prey. However, there is considerable evidence that boas spend significant time searching for optimal ambush sites, such as burrows used by prey species, logs or other runways used by prey, or waterholes that might be visited by prey. For example, Montgomery and Rand (1978) reported a sit-and-wait hunting strategy in a radiotelemetered boa on Barro Colorado Island, Panamá. The snake used four different mammal burrows over 12 days and was seen once about 5 m from the mouth of the burrow, facing out. A boa was sighted regularly in a *Cecropia* tree for one month before it was seen to capture a blue-grey tanager (Greene, 1983), and a snake coiled at the entrance to a tree cavity captured a bat that was clambering up the inner wall of the cavity (Arendt and Anthony, 1986). Juvenile *B. constrictor* in captivity have been reported to engage in caudal luring behavior when a live mouse was introduced to their cage (Radcliffe and others, 1980), but the frequency with which this tactic is used in the wild remains unknown.

B. constrictor has 3 visual pigments, with peak absorbances at 495 ± 2 nm (rod), 549 ± 1 nm (cone), and 357 ± 2 nm (small rare cone); the latter has sensitivity in the

ultraviolet (Sillman and others, 2001). These authors suggest that ultraviolet vision may improve hunting efficiency, and that, "...on the basis of cone packing density, it is reasonable to conclude that the photopic visual resolution of *B. constrictor* is similar to that of the cat." Ultraviolet vision might allow snakes to see scent trails left by prey and would increase the contrast of lizards and birds with ultraviolet reflectance (Sillman and others, 2001).

B. constrictor also has dense arrays of infrared-sensitive neurons beneath the surface of labial scales (Grace and Matsushita, 2007). Bullock and Barrett (1968, cited by Goris and others, 2007) found that infrared stimuli produce responses in branches of the trigeminal nerve; Goris and others (2007) reviewed other evidence for infrared reception in *B. constrictor*. However, de Cock Buning (1983) opined that Boa Constrictors could likely detect a mouse at only 50-100 mm using thermal cues only, and hypothesized that substrate-borne vibrations from prey are more important in detecting prey in the absence of light.

Secor and Ott (2007) found that mass of the small intestine approximately doubled in *B. constrictor* between 24 and 48 hrs post-feeding of a meal approximately 25 percent of snake mass, and nutrient uptake rates went up several-fold. These trends are similar to those observed in pythons, and support the notion of a generalized intestinal response among large-bodied, infrequently-feeding snakes.

In the Cayos Cochinos, Honduras, large females are apparently highly susceptible to starvation; it is possible that they require at least one large ctenosaur or iguana per year to meet reproductive and maintenance requirements (Reed and others, 2007).

4.0 Life History

4.1 Reproductive Mode

Boa Constrictors are live-bearing. The extent of post-parturient parental care in the wild is unknown, although Köhler (2003) described finding a spent female in a log, associated with neonates. Similarly, a female on Crawl Cay, Belize, was found in association with seven neonates (S.M. Boback, pers. commun. 2008).

4.2 Reproductive Phenology

4.2.1 Seasonality

There are few records of observed mating or parturition in the native range of *B. constrictor*, possibly because females appear to seek refugia during latter stages of ovulation and pregnancy and are thus largely unavailable for observation or capture. Much of the available information on reproduction is thus based on captive animals, which may experience highly artificial conditions.

Because Boa Constrictors experience such a dizzying range of latitudes, habitats, and climatic regimes across their native distribution, it is fruitless to attempt to pigeonhole the species into generalities such as "winter breeder, summer parturition." Overall, boas at higher latitudes tend to breed in the cool season and give birth in the warm season, but seasonality in precipitation may be more important in low-latitude areas (Table 7.3). The primary message is that reproductive seasonality is incredibly

variable across the range of *Boa constrictor*. Furthermore, extended gestational durations mean that an entire reproductive cycle may take at least a year for females, considering follicular growth, mating, ovulation, gestation, and parturition.

Copulation is rarely observed in the field, and it is difficult to tell whether groups of boas constitute mating aggregations. For example, Myres and Eells (1968) found an aggregation of boas (four male, one larger female) in the foothills of the Sierra Madre Occidental, Sonora, Mexico on December 18, 1965. They inferred that the aggregation was for thermoregulatory purposes, but we suggest that a mating aggregation cannot be ruled out. The absence of data from the field leaves us to be somewhat reliant on data from captive individuals and museum specimens, but neither of these is without its drawbacks. Ronne (1996) gave an overview of reproduction in captivity, including data on the number of days between post-ovulatory shed and parturition (104-111, $n = 6$), a table of gestation periods for Colombian boas, and the observation that parturition seemed to occur on days when the barometer drops appreciably.

The best data on reproductive seasonality come from the Argentine boa, which inhabits the coolest climate occupied by the species. Reproduction in Argentina is strongly seasonal—reproductive females were found in the dry season (April-August, winter), with large ovarian follicles (Bertona and Chiaraviglio, 2003). Reproductive males were found in March to August, with low testicular volume during March-May compared to June-August. However, only 50 percent (19 of 38) of adult females and 64 percent (29 of 45) of adult males were reproductive – the overall operational sex ratio was thus 1.53:1. While reproductive females were in better body condition than non-reproductive females, no similar effect was noted in males (Bertona and Chiaraviglio, 2003), although males with good body condition had larger testes (Cardozo and Chiaraviglio, 2008). Overall, reproduction occurs in winter and is synchronized, resulting in mid-spring ovulation. Although based on a small number of neonates, parturition is inferred to be at the end of the wet season (Feb-March: Monguillot, 1988; Bertona and Chiaraviglio, 2003); Waller (pers. commun., 2009) extends this period through April.

Table 7.3. Recorded and inferred seasonality of reproductive activity in *Boa constrictor* from various parts of the range. Mating and parturition seasons marked with an * are inferred using an estimated average gestational period of 110 days.

Location	Latitude	Mating	Parturition	Source	Notes
Miami, FL	25°N	Apr-May*	Aug-Sep	Snow et al 2007b	Many infertile ova/embryos
Yucatán, Mexico	~18-21°N	Mar-Apr*	July-Aug	Dundee and others 1986; Lee 1996	
Guatemala	~13-17°N	Jan-Apr*	May-Aug	Smith 1994; Campbell 1998	
Cayos Cochinos, Honduras	15°N	Apr*	Aug	S. Green, pers. commun. 2007	1 litter
Dominica	15°N	Mar-Apr	Jul-Aug	Vandeventer 1992	Wild-caught females
Trinidad	10°N	Feb-Mar	Jun-Jul*	Mole and Urich 1894	
Iquitos, Peru	3.5°S	July-Oct*	Nov-Feb	Dixon and Soini 1986	
São Paulo, Brazil	23°S	Apr-Jul	Aug-Nov*	Pizzatto and Marques 2007	
Brazil	~5°N-18°S	Jun-Feb	Sep-Apr	Pizzatto and Marques 2007	<i>B. c. constrictor</i>
Brazil (SE)	~14-29°S	Mar-Oct	Aug-Jan	Pizzatto and Marques 2007	<i>B. c. amarali</i>
Argentina	~21-32°S	Jun-Oct	Feb-Apr	Monguillot 1988; Bertona and Chiaraviglio 2003, Waller, pers. commun. 2009	<i>B. c. occidentalis</i> . Some disagreement over timing b/w Chiaraviglio and Waller

4.2.2 Reproductive Behaviors

Mole and Urich (1894) were apparently the first to note that males used spurs during courtship, and stated that “the claws scratching the scales of his mate make a noise which can be distinctly heard two yards off.” Chemoreception of conspecific cues is likely important during identification of potential mates. Chiaraviglio and Briguera (2001) showed that male *B. c. occidentalis* respond much more strongly (higher rate of tongue-flicking) to female skin and glandular chemical cues than to male cues, while females respond more strongly to cues from other females.

In Argentina (Bertona and Chiaraviglio, 2003), aggregations of one adult female and one to three adult males (presumed to be mating-related, with the first aggregations found in April and the last in August) accounted for a majority (43 of 84) of boas captured during the dry season. Of these, 33 were reproductively mature as indicated by ultrasonography. Most (16 of 19) reproductive females were found in aggregations. No male combat or copulations were observed. These authors concluded that reproductive activity in *B. c. occidentalis* is seasonal and associated (following terminology of Whittier and Crews, 1987), and that females reproduce less than annually. Additional potential mating aggregations have been observed on St. Lucia, consisting of one large female and five smaller males (Malhotra and Thorpe, 1999) and Sonora, Mexico (Myres and Eells, 1968).

Sillman and others (2001) suggests that *B. constrictor* might be able to use its vision in the ultraviolet spectrum to locate lipid trails left by conspecifics.

4.2.3 Vitellogenesis and Ovulation

Pizzatto and Marques (2007) examined 442 preserved *B. constrictor* from Brazil, including adults and juveniles. Although their text indicated that vitellogenesis occurs from summer (Jan-Feb) to winter (Jul-Sep) in both *B. c. constrictor* and *B. c. amarali*, an accompanying graph depicts significantly enlarged follicles during Jun-Sept (both with very small sample sizes). They observed a female reproductive frequency of 13.6 percent of *B. c. amarali* and 16.7 percent in *B. c. constrictor*; such a low proportion of reproductive females is probably due to decreased detectability of gestating females combined with the generally low frequency with which very large snakes are accessioned into museum collections. Among males, testes volume and deferent duct diameter were constant in *B. c. amarali*, but in *B. c. constrictor* testes appeared to be larger in Jan-Feb (summer) and duct diameter was larger in Apr-May (autumn). They concluded that female and male gametogeneses are asynchronous in *B. c. constrictor*, with mating season occurring after sperm production and possible short-term, over-winter sperm storage by males. As discussed in section 4.2.1, however, generating overall conclusions from such a vast area as Brazil is likely to swamp out regional differences in the seasonal timing of reproductive events, possibly giving the impression of extended reproductive periods even though such periods may be markedly shorter in any one location.

Vitellogenic follicles of captive Argentine females were 10-28 mm in diameter, while post-ovulatory follicles were over 28 mm and aligned in a row. Gravid females were not found in the field, probably because they stayed in Plains Viscacha burrows (Bertona and Chiaraviglio, 2003).

4.3 Reproductive Effort/Fecundity

4.3.1 Clutch or Litter Size/Frequency

In a very general review of *B. constrictor*, Greene (1983) gave litter size as 20-64, with neonate size of approximately 0.50 m; these figures are generally concordant with those provided by other authors. In Mexico and Central America, litter sizes reported by Fitch (1985) averaged 17.8 ± 3.4 (range 10-36, n = 6: Fitch 1985); these numbers are corroborated for a record from Guatemala (Stuart, 1948: 11 eggs in a female) and mainland Belize (Boback, 2005; Boback and Carpenter, 2007: 11 litters averaged 30 ± 18 , with relative clutch mass of 17 percent of female mass). However, other reports exceed these numbers. For example, litter sizes are 20-50 in Chiapas, Mexico (Alvarez del Toro, 1960), and a female at La Selva, Costa Rica, gave birth to 52 young (Guyer and Donnelly, 2005). Insular boas in Central America tend to have reduced litter sizes. A female on Utila, in the Bay Islands of Honduras, was associated with 13 neonates with umbilical remnants, and insular females from Belize had litter sizes of 4.6 ± 1.9 , with mean relative clutch mass of 15 ± 4 percent (Boback, 2005; Boback and Carpenter, 2007).

Litter sizes in South America are generally larger, as would be expected for the larger maximum sizes attained by South American females. Boas from Trinidad and Peru had litters averaging 30.3 ± 7.3 (range 6-63: Fitch, 1985). The maximum litter size of 63 appears to be derived from Mole (1924) for a snake from Trinidad. *B. c. constrictor* from Brazil had mean litter size of 27 ± 8.15 (range 18-41), while *B. c. amarali* from Brazil had mean litter sizes of 14.5 ± 6.9 (range 5-30: range listed by Pizzatto and Marques (2007) as 5-10 but cleared up by first author in a pers. commun. in 2008). In the Iquitos Region, Peru, four adult females gave birth to 6-28 young (Dixon and Soini, 1986), and wild-caught *B. c. nebulosa* from Dominica gave birth to litters of 7-11 after a few months in captivity (Vandeventer, 1992). Four dissected boas (of putatively South American origin) from the invasive population at the Deering Estate at Cutler had litter sizes between 24 and 47, most of which were infertile ova or slugs (Snow and others, 2007b). Litter sizes in Argentina averaged 25.05 ± 1.25 (range 11-33), and litter size was positively correlated with dam size (Bertona and Chiaraviglio, 2003; Chiaraviglio and others, 2003: dam sizes in the latter ranged from 1.92 to 2.7 m [1.73-2.43 m SVL]).

Estimates of female reproductive frequency in free-ranging populations are rare. In Argentina, only 36 percent of females 1.82-2.28 m (1.64-2.05 m SVL) were reproductive, while 69 percent of females over 2.28 m (2.05 m SVL) were reproductive (Cardozo and Chiaraviglio, 2008). This implies variation in reproductive frequency among female size classes, even though the overall reproductive frequency might be close to 0.5. However, these observations are complicated by the observation that both body condition and clutch size of females decreased during the period 1995-2003, presumably as a result of deteriorating habitat conditions. The hypothesis of biennial reproduction among females in Argentina is supported by T. Waller (pers. commun., 2009), who found 15 of 28 females with secondary follicles.

4.4 Growth

Growth rates of wild *B. constrictor* are almost entirely undocumented. Growth rates have been reported in the herpetocultural literature, but these rates typically involve sedentary snakes that are often fed large amounts of food, and are thus likely to be extremely poor indicators of growth in the wild. In a captive colony, growth of males and females slowed appreciably after three and five years of age, respectively (Smith, 1999); based on Smith's (1999) graphs and tables and assuming neonate length of 0.55 m, male growth averaged about 45 mm/month for the first 24 months after birth, while female growth averaged about 40 mm/month for the first 40 months. In both sexes, growth in length slowed appreciably after these ages, but weight continued to increase for a longer period of time. Males reached their near-asymptotic weights at about 36 months (inferred average monthly weight gain of around 280 g/month over this period), but female continued a high rate of weight gain for over 48 months (inferred average monthly weight gain of about 380 g/month).

Schuett and others (2005) found no effect of prey size on growth of the skull in captive *B. constrictor*, but found that females grew faster in terms of snout-vent and total length, while males grew faster in tail length. In captivity, mainland snakes grew faster than island snakes, and females grew faster than males in both SVL and mass, but there were no effects of prey diameter on growth of skull elements (Boback and Carpenter, 2007).

4.5 Maturation

In a general review, Greene (1983) stated that, "Sexual maturity evidently occurs at a length of 1.5-2 m," and this range appears to be a workable rule of thumb for most mainland populations of *B. constrictor*. However, males of some insular populations mature at considerably smaller sizes, and in some populations may fail to exceed 1.2 m even as adults (for example, Reed and others, 2007).

Pizzatto and Marques (2007) reported body size at maturity of Brazilian boas to be 0.74 (*B. c. amarali*) and 0.61 (*B. c. constrictor*) of mean adult male sizes, which were 1.418 and 1.903 m respectively. Similar ratios for females were 0.85 and 0.70 of mean adult size (1.501 and 2.030 m). In the Córdoba Province of Argentina, males mature at 1.73 m (1.49 m SVL), females at 1.82 m (1.64 m SVL: Chiaraviglio and others, 2003). Male *B. c. longicauda* from Tumbes Province, Peru, mature at 1.50 m in captivity (Price and Russo, 1991).

4.6 Longevity

We are aware of no longevity records from wild populations. Greene (1983) stated that longevity in captivity can be 38 years, 10 months. Snider and Bowler (1992) extended this record to 40 years, 4 months for a wild-caught adult *B. c. constrictor* and gave known longevity records for *B. c. imperator* (29 yrs), *B. c. occidentalis* (14 yrs), *B. c. ortonii* (18 yrs), and *B. c. amarali* (15 yrs); of these, all but the *B. c. imperator* were wild-caught adults.

5.0 Diet/Trophic Role

5.1 Prey

The Boa Constrictor has a catholic diet, consuming prey from a wide variety of higher vertebrate taxa. Henderson and others (1995) reported that *B. constrictor* eats “fishes, lizards (iguanids, teiids), birds, [and] mammals (including Marsupialia, Chiroptera, Edentata, Lagomorpha, Carnivora, Artiodactyla)”, and Boback (2005) stated that 54 diet items were reported in the literature for mainland *B. constrictor*, from Greene (1983), Smith (1994), and Sironi and others (2000). Greene (1983) summarized prey known for the species up to that time, including ctenosaurs (*Ctenosaura*), Green Iguanas (*Iguana iguana*), opossums (*Didelphis*), Neotropical fruit bats (*Artibeus*), vampire bats (*Desmodus*), Eurasian rats (*Rattus*), agouti (*Dasyprocta*), prehensile-tailed porcupine (*Coendou*), rabbits (*Sylvilagus*), deer (*Odocoileus/Mazama*), coatis (*Nasua*), Ocelot (*Leopardus pardalis*), Small Asian Mongoose (*Herpestes javanicus*), and tamandua (*Tamandua*).

Sironi and others (2000) reported on diet of 28 boas in the Chaco region of Córdoba Province, Argentina. Diet records were supplemented with interviews with rural inhabitants. Results included 11 species of mammals, 7 spp. of birds, and 1 reptile; Plains Viscacha (*Lagostomus maximus*) were an important prey item for boas of 2.35 m TL or longer, and their burrows provided refuge to snakes. Boas were used as viscacha control agents by farmers. Invasive boas were considered generalist predators on Cozumel (Gonzalez-Baca and Cuaron, 2003). Beebe (1946) found the following in boas from Guyana and Venezuela: two large jungle whiptail lizards (*Ameiva*) and an *Ameiva* tail, one small whiptail lizard (*Cnemidophorus*), a large antbird (Thamnophilidae), and two spiny rats (Echimyidae).

Martins and Oliveira (1998) stated that no diet data are available for the Manaus region, but they summarized diet based on the literature and stated that a boa killed a South American Squirrel Monkey (*Saimiri sciureus*) and another constricted a Nine-banded Armadillo (*Dasypus novemcinctus*). In the Cayos Cochinos, Honduras, prey items of dwarfed insular boas included grackles (*Quiscalus*), Green Iguanas (*Iguana iguana*), and Black-chested Ctenosaurs (*Ctenosaura melanosterna*: Reed and others, 2007); these authors posited that the historically high-density population of *B. constrictor* was responsible for the absence of small mammals on these islands. Of 65 boas examined from the recently-established population on Aruba, 47 (72.3 percent) contained prey, consisting of birds (40.4 percent), lizards (34.6 percent), and mammals (25 percent: Quick and others, 2005). Some assertions on the diet of boas are of a dubious nature; for example, Goulding (1990) stated that boas eat fish and shrimp, based solely on the observation that boas are sometimes found in fish traps placed in flooded forests in the Amazon Basin.

Additional diet records for higher vertebrate taxa follow:

5.1.1 Mammals

Borland (1855) described ingestion of a rabbit by a captive boa that “measured about 20 feet in length;” these observations include refutation of the myth that snakes lick

their prey to coat it with saliva prior to ingestion. Bakkegard and Timm (2001) reviewed the rodent prey recorded for *B. constrictor* (Black rats [*Rattus rattus*], agoutis [*Dasyproctus*], prehensile-tailed porcupine [*Coendou rothschildi*]) and reported a Big-eared Climbing Rat (*Ototylomys phyllotis*) in a 0.96 m boa (0.84 m SVL, 450 g without prey) from Costa Rica. They also reported observing a Costa Rican boa consuming a Virginia Opossum (*Didelphis virginianus*). Records from El Salvador include another Big-eared Climbing Rat and a Deppe's Squirrel (*Sciurus deppei*: Leenders and Watkins-Colwell, 2003). Lazell (1964) considered *B. constrictor* to eat almost exclusively rats on Dominica, but stated that it probably takes agoutis as well. Davis and Smith (1953) reported on a large *Rattus rattus* taken from a specimen in Morelos, Mexico.

Mole and Ulrich (1894) reported that Ocelots and young Wood-Broquets (*Cariacus nemorivagus*, a small deer) had been taken from boas on Trinidad, but that “their droppings contain evidences of the fact that they feed largely on agouti.” A boa imported from Panamá had porcupine quills imbedded in its mouth, and the snake later passed feces containing claws, quills and fur from a juvenile prehensile-tailed porcupine (*Coendou rothschildi*: species name misspelled in original paper: Tschambers, 1949). A snake in Brazil apparently died as a result of ingesting a tree porcupine of unknown species (Cherubini and others, 2003). A boa from the invasive population near Miami, Florida had eaten a Virginia Opossum (*Didelphis virginianus*), and captured adults accepted dead Raccoons (*Procyon lotor*: Snow and others, 2007b). In northwest Costa Rica, a boa killed but did not consume an adult White-Nosed Coati (*Nasua narica*: Janzen, 1970). A boa at La Selva, Costa Rica, consumed a Three-Toed Sloth (*Bradypus variegatus*: S.M. Boback, pers. commun., 2009). Mid-sized mammals are reported as the primary prey in Venezuela (Lancini, 1986), but this author pointed out that deer are not eaten.

Arendt and Anthony (1986) reported on *B. c. orophias* (397 g, 1.1 m TL, head width 53 mm) eating an Antillean Fruit-eating Bat (*Brachyphyllum cavernarum*: 67 g) on St. Lucia. Bat remains were found in fecal samples from the same boa. A boa in the Cayos Cochinos, Honduras was observed falling from a palm tree while simultaneously constricting four phyllostomatid bats (possibly *Artibeus phaeotis*); the snake subsequently consumed two of them (RNR, pers. obs., 2007 G. Sorrell, unpub. data). A boa in the state of Mato Grosso, Brazil, inserted its head into a cavity in a *Ficus* tree and emerged with a Lesser Bulldog Bat (*Noctilio albiventris*) in its mouth (Esbérard and Vrcibradic, 2007); these authors also summarized previous bat prey known for *B. constrictor*, including Common Vampire Bats (*Desmodus rotundus*) and Jamaican Fruit Bat (*Artibeus jamaicensis*).

Tello and others (2002) reported attempted predation by a 1.5 m *B. constrictor* on a subadult male Moustached Tamarin (*Saguinus mystax*). Ferrari and others (2004) reported a *B. constrictor* (over 3 m long, approximately 8 m up in tree) killing a 2-3 kg female Bearded Saki (*Chiropotes satanas*) in Brazil, while Chapman (1986) reported on a 2-m *B. constrictor* killing a 1.7-kg juvenile White-faced Capuchin (*Cebus capucinus*) in northwestern Costa Rica. Also in Costa Rica, Perry and others (2003) reported another attack by a 2-m *B. constrictor* attacking a 3-year-old *C. capucinus*, but the snake was driven off after being mobbed and bitten by the rest of the capuchin troupe.

5.1.2 Birds

Boback and others (2000) reviewed passerine birds taken from *B. constrictor*, and added to this list the Bright-rumped Attila (*Attila spadiceus*: 39 g) from a 0.87-m (0.76 m SVL), 240-g (without prey) boa at La Selva, Costa Rica. On Cozumel, an invasive *B. constrictor* ate a Caribbean Dove (*Leptotila jamaicensis*: Martínez-Morales and Cuarón, 1999), and a 1.50-m (1.32 m SVL), 1.1-kg *B. constrictor* constricted an adult Great-tailed Grackle (*Quiscalus mexicanus*) in Belize (Greene and others, 2003). Greene (1983) reported a Blue-grey Tanager (*Thraupis episcopus*) in the diet of a boa on Perico Island, Panamá, and boas at La Selva, Costa Rica, consumed an Orange-billed Sparrow (*Arremon aurantiirostris*: Guyer and Donnelly, 2005) and a Wood Thrush (*Hylocichla mustelina*: Wasko and Roberts, 2008). Boback (2005) found prey in 16 of 88 (18 percent) of boas from small mangrove cays off the coast of Belize; 18 of the 19 prey items were Grey-breasted Martins (*Progne chalybea*). Mean prey mass was 7.3 percent of mean snake mass. A 6.8-kg *B. constrictor* in Belize contained feathers and bones of an adult Black Vulture (*Coragyps atratus*: Boback, 2004), and Argentine boas have been observed to climb 3–4 m into trees to consume juvenile Blue-fronted Amazon parrots (*Amazona aestivus*; T. Waller, pers. commun., 2009).

5.1.3 Reptiles

Lizards constitute the majority of the reptilian prey recorded for *B. constrictor*, especially large iguanid and teiid lizards. However, this may be due to the fact that boa/iguana interactions are likely to involve large individuals of both species and thus may be more apparent to human observers (RNR, pers. obs., 2005). Small lizards can also be difficult to feel when palpating boas for prey, so they may be overlooked as prey items.

A 2.44-m, 6.85-kg *B. constrictor* from the mainland of Belize contained a 2.2-kg Green Iguana (*I. iguana*: Boback, 2004). Gutsche (2005) observed a 1.4-m boa fall from a tree while constricting a 0.192-m SVL, 235-g Utila Ctenosaur (*Ctenosaura bakeri*) on Utila, Honduras. Similarly, a 1.48-m (1.33 m SVL), 1267-g female boa fell from a tree while constricting a 0.316 m SVL, 996-g Black-chested Ctenosaur (*Ctenosaura melanosterna*) on Cayo Cochino Pequeño, Honduras; the snake subdued but did not kill the lizard, and two more *C. melanosterna* were reported in the diet of boas from the Cayos Cochinos (Reed and others, 2006). In Mexico, a 1.6 m boa killed a Mexican Ctenosaur (*Ctenosaura pectinata*: 0.34 m SVL, 1.03 m TL: Lemos-Espinal and Ballinger, 1994). Bakkegard and Timm (2001) reported a Costa Rica boa that ate an adult Black Spiny-tailed Ctenosaur (*Ctenosaura similis*). Further south, Argentine boas regularly consume Red Tegus (*Tupinambis rufescens*; T. Waller, pers. commun., 2009).

5.2 Predators

Due to their large body size, adult boas from the mainland are likely to have few predators, and records of predation on boas are rare. Likely predators of adults include Jaguars (*Panthera onca*), Pumas (*Felis [Puma] concolor*), caimans (*Caiman*) and crocodiles (*Crocodylus*), the largest raptors, feral hogs, and perhaps peccaries. Juveniles likely fall victim to a range of mesopredators, raptors, and ophiophagous snakes, but

observations of such attacks are few. Insular boas typically exist on islands with low mammalian biodiversity, and predation rates on these snakes are likely even lower.

Savage (2002) stated that large birds, mammals, and crocodilians are the primary predators on boas. Gerhardt and others (1993) observed six boas among prey fed to nestling Giant Black Hawks (*Buteogallus urubitinga*) in Guatemala. Beebe (1946) reported on a Mussurana (*Clelia clelia*) attacking a small boa in South America. Campbell (1998) reported that a 2.95-m Black-tailed Cribo (*Drymarchon melanurus*) ate a 1.68-m *B. constrictor*, and Duellman (1963) reported on the same species eating *B. constrictor* in Guatemala.

5.3 Diseases and Parasites

Pathogens of *B. constrictor* are largely known from captive individuals in the pet trade, but most of these are not specific to boas, or even to boas/pythons in general. For example, Russo (2007) has an entire chapter on parasites and pathogens of Boa Constrictors, but all are largely associated with captivity, and to our knowledge few of these ailments have ever been recorded in the wild for any snake. An apparently snake-specific parvovirus was isolated from a captive Boa Constrictor in Europe (Farkas and others, 2004). Lia and others (1999) described a pentastomid, *Porocephalus clavatus*, in a captive *B. constrictor* imported from Colombia to Italy, and heavy pentastomid loads are often observed in the lungs of captive *B. c. occidentalis* in Argentina (T. Waller, pers. commun., 2009). Wild-caught *B. c. nebulosa* from Dominica were found to harbor ticks, tapeworms, roundworms, protozoans, and pentastomes (Vandeventer, 1992), and both Central American (Ditmars 1931) and South American (M. Chiaraviglio, pers. commun., 2008) boas are often heavily infested with ticks. Oda and others (1971) successfully transferred hemogregarine parasites from an infected *B. constrictor* to various other reptile species by feeding the recipients mosquitoes that had fed on the boa.

Boas are apparently susceptible to Inclusion Body Disease, as are other boas and pythons (Schumacher and others, 1994). However, many putative cases of this fatal retrovirus-associated disease are diagnosed based on clinical symptoms and histology rather than isolation/identification of the causative agent (for example, Knotek and others, 2007). More information on parasites and pathogens can be found in the Risk Assessment portion of this report.

6.0 Demography

6.1 Population Density

Despite having one of the widest geographic distributions of any snake, there are few estimates of population abundance or density for *B. constrictor*. Mainland boas tend to be found in relatively low numbers, such that rigorous population estimates based on mark-recapture would require monumental effort. In the Pantanal of Western Brazil, for example, *B. constrictor* constituted only about 1 percent (two individuals) of the apparent snake community (Strüssmann and Sazima, 1993). Relative abundance of mainland boas may vary by site, however, as boas were described as “fairly common” at two sites in northern South America by Beebe (1946). T. Waller (pers. commun., 2009) described

finding over two dozen Argentine boas near a village in a few days during periods when they were concentrated around viscacha burrows.

Insular boas, on the other hand, can achieve high densities. *B. c. nebulosus* on Dominica was described by Lazell (1964) as “amazingly abundant.” Boas were fairly common on small (4.5–24 ha) mangrove islets off the coast of Belize (Boback, 2006), with individual islets yielding between 4 and 40 boas. Reed and others (2007) roughly estimated population size of *B. constrictor* on Cayo Pequeño (0.64 km²), Honduras to be 632 boas (approximately 1000 boas/km²), and suggested that densities had been considerably higher prior to overcollection for the pet trade. On Cozumel, 49 invasive boas were found via road-cruising and haphazard encounters by Romero-Nájera and others (2007) over 17 months of intermittent searching. Road-cruising yielded abundance index of 0.11 ± 0.03 boas/10km, slightly lower than a previous estimate of 0.18/10km (Martínez-Morales and Cuarón, 1999) based on diurnal line-transects along trails. Over 273 boas were captured on the 175 km² island of Aruba in less than a decade after they became established (Quick and others, 2005).

6.1.1 Spacing and Aggregation

Most boas found on the mainland are singletons, and aggregations are rarely reported. Pizzatto and Marques (2007) stated that there are no records of aggregation in Brazilian boas but noted that reproduction in captivity only occurred when more than one male is present. Aggregations of individuals have been observed in Sonora, Mexico (Myres and Eells, 1968), and in Argentina during the local winter and at the onset of the reproductive period (Bertona and Chiaraviglio, 2003). It is notable that these observations are near the northern and southern range limits, respectively, for the entire species, and that aggregations were concentrated around refugia (rock crevice in Sonora, viscacha burrows in Argentina) that may be spatially limited. Boas in most of the tropical regions of the species’ range may not commonly need to find refugia from adverse climatic conditions. Boas on Dominica engage in communal “denning,” with 3 to 12 individuals sharing a hollow log or tree stump (Lazell, 1964), and aggregations have also been observed on nearby St. Lucia (Malhotra and Thorpe, 1999).

6.2 Size Distribution

To our knowledge, estimates of detectability for *B. constrictor* are available only for the insular dwarfed population in the Cayos Cochinos of Honduras, and those results are as yet unpublished (S. Green, pers. commun., 2009). Without estimates of detectability across ages, sexes, and sizes, any attempt to quantify size distribution based on opportunistic captures will likely be biased. In the Cayos Cochinos (without taking detectability into account), the distribution of female body lengths was highly right-skewed, due to a small number of extremely large females, while male body lengths largely fit a normal distribution. Similar trends were seen for snake mass, especially at the largest female sizes, and females were relatively heavier than males of the same length. Captures of invasive boas at the Deering Estate at Cutler, Miami, Florida were heavily biased towards neonates and juveniles, apparently due to a couple of large litters produced during one year (Snow and others, 2007b). Of 130 boas captured in Argentina, 106 were considered adult (56 male, 50 female: Bertona and Chiaraviglio, 2003).

Chiaraviglio and others (2003) divided captures into four size classes and found even sex ratios and relatively few small individuals (their Figure 1).

7.0 Interactions with Humans

7.1 Human Utilization and Persecution

Because of the historically large trade in skins of boas and pythons for decorative items, all of these species are listed under CITES Appendix II (and a few under Appendix I), requiring declaration of species type and individual numbers as a requirement of the import process among CITES signatories. Theoretically, this makes it easier to estimate the numbers of boas that are in the skin and pet trade, but in reality the level and quality of reporting by member states is highly variable.

Schlaepfer and others (2005) reported that 8,182 wild-caught *B. constrictor* skins were imported to the United States between 1998 and 2002. *B. constrictor* represented a very small proportion of reptile skin products exported from Mexico, totaling 12 skins and 2,035 skin products during the period 1980-2001 (Arroyo-Quiroz and others, 2007). In contrast, Mexico exported 31,769 skins and 86,689 skin products of *Python reticulatus* during this period. A large part of the skin trade in *B. constrictor* is not accounted for by CITES records, however; as an example, a huge variety of skin products from boas were available from curio vendors in Manaus, Brazil, during brief trips in 2003 and 2008 (Reed and Rodda, pers. obs.). This indicates that international records of the boa trade seriously underestimate local trade, undeclared tourist curios, and cross-border trade in the native range that does not involve shipping.

B. c. occidentalis is in Appendix I of CITES, due to hunting for the skin and pet trade and habitat loss from intense farming and cattle ranching; this is the only New World boine to be assigned Appendix I status. Chiaraviglio and Bertona (2007) stated that forest cutting for charcoal production is likely to disproportionately impact reproductive females, which are dependent on forested areas. Cardozo and others (2007) documented the severity of habitat loss in Argentina using GIS, with implications for levels of gene flow but apparently not for loss of genetic diversity.

7.2 Human Health Risks

Despite their fairly large size, wide distribution in their native range, and prevalence in the pet trade, we are unaware of any verified fatal attacks of a Boa Constrictor on a human being. Herpetoculturists have stated that any python over 8 feet (2.4 m) in total length may be capable of killing an adult human (Flank, 1997), and boas certainly exceed that length, so we do not exclude the possibility. A widely-disseminated news story (BBC News, 2006; Associated Press, 2006; and other sources) reported a fatal attack of a 3.96-m boa on its owner, an adult male residing in Cincinnati, Ohio. However, further investigation revealed that the snake had been misidentified and was in fact an underweight, 3.35-m Burmese Python (*Python molurus*: Damian, Arrowhead Reptile Rescue, pers. commun. to RNR, 2006).

The largest, and thus presumably most dangerous, boas (*B. c. constrictor* from mainland S. America) have the reputation of being relatively docile in captivity, at least as compared to smaller northern (*B. c. imperator*) and southern (*B. c. occidentalis*) forms.

We have additionally noticed that bites from both wild and captive *B. c. imperator* tend to consist of a quick defensive bite, but that ensuing attempts at constriction are either half-hearted or absent (Reed and Rodda, pers. obs., over many years). Only occasionally are bites from captive snakes of medical concern (for example, Kleinman and others, 1998). Taken together, these observations tend to downplay the risk of fatalities from boas, although the risk does exist.

7.3 Human Aesthetic Relations

7.3.1 Pet Trade

Due to its attractive coloration, impressive size, hardiness, and relative docility, Boa Constrictors have long been a popular animal in the pet trade. In recent years, literally dozens of locality-specific lines of boas have been available, along with selectively bred color morphs (Fogel, 1997; Bonny, 2007; Russo, 2007; Gilbert, 2008). These include albinos, dwarfs, and a myriad of other naturally occurring and artificially selected types.

United States importation records for the period 1989-2000 totaled 115,131 individuals, a sum that was second only to Ball Pythons (*Python regius*: 366,808 individuals) among 24 species of boid/pythonid snakes imported (Reed, 2005). To this total can be added the 36,746 live individuals imported during 1983-1988 (Hoover, 1998), summing to 151,877 individuals. However, imports were extremely variable among years, ranging from fewer than 2,000 to over 40,000 individuals (Fig. 7.4, also see Appendix). Based on similar sources of data, Franke and Telecky (2001) reported that 21,209 *B. constrictor* were imported from Colombia and 7,326 from Nicaragua in 1997 alone.

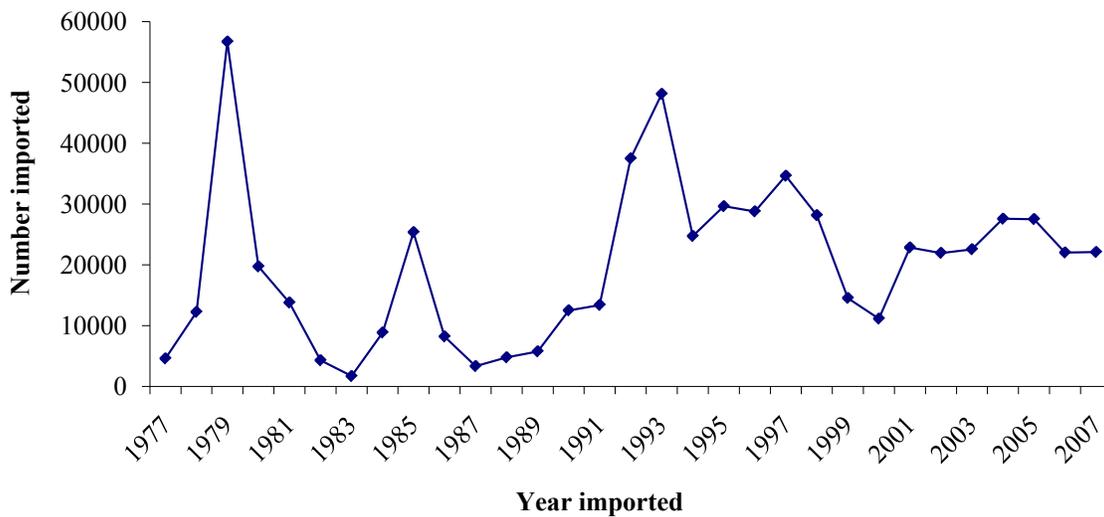


Figure 7.4. Annual imports of Boa Constrictors, *Boa constrictor*, to the United States during the period 1977-2007. Data from CITES.

Many of the boas imported from S. America are declared as “ranchled” or “farm bred” individuals, especially those from Colombia. Ideally, these ranches collect pregnant females from the wild and hold them in captivity until they give birth, then release the females and sell the offspring. However, there are numerous questions about this practice. The estimated numbers of ranchled boas imported are based on statements of the origin of snakes made by exporters and importers, and there are no checks on the validity of declarations of boa origins. Fogel (1997) stated that spent females are often slaughtered for their skins, and cautioned that farm bred animals were essentially wild-caught, as they represent neonates that would under normal circumstances contribute to population recruitment.

Reed and others (2007) reported on the population status and historical exploitation of insular boas from the Cayos Cochinos, Honduras, and concluded that at least 5,000 boas were removed from two islands, totaling 1.66 km² in about a decade of collecting for the pet trade. They also claimed that poaching is ongoing, a claim that has been bolstered by the recent prosecution of an individual in Honduras selling wild-caught boas from the Cayos Cochinos, as well as additional evidence of wild-caught Cayos boas for sale in the United States (S. Green, pers. commun., 2007). Wilson and Cruz Díaz (1993) gave additional history on exploitation of boas in the Cayos Cochinos.

The United States domestic trade in captive-bred boas is largely unquantified, thus complicating any attempt to estimate the number of boas in captivity in the country. Hoover (1998) reported 8,320 boas exported from the United States between 1983 and 1995, but this total included an unknown number of re-exported individuals. Using USFWS Law Enforcement Management Information System (LEMIS) data, Reed (2005) concluded that import/export declarations of whether snakes were wild-caught or captive-bred were largely unreliable. A prominent snake breeder estimates that “probably between one and two thousand common boas are now captive-bred and born in the U.S. each year” (Barker and Barker, 2008b); if true, then sales of domestically-produced boas are still dwarfed by sales of imported boas.

7.3.2 Other Uses

Major human uses of Boa Constrictors include meat, skins, medicinals, and the live animal trade. They may also be used in religious services in areas of the United States where use of venomous snakes for such purposes has been banned (RNR, pers. obs., 1996).

Management Profile

See the introduction to the management profile for Indian Pythons (chapter Four) for an explanation of the format and content of this section of the risk assessment.

8.0 Pathway Factors: Pet Trade

8.1 Volume of International Trade

Boa Constrictors are imported to the United States in huge numbers, usually in the tens of thousands per year. This species is imported at a long-term average rate higher than that observed for any other species addressed in this document. See section 8.1 of chapter Four for reasons why imported individuals may be of especially high risk as potential invasive species. Although many boas entering the United States are declared as captive-bred offspring of farmed or ranched individuals, the veracity of such claims is difficult to judge.

8.2 Volume of Domestic Trade

The volume of domestic trade is poorly documented. If breeders produce only a couple of thousand boas per year as suggested by Barker and Barker (2008b), then domestic production is about an order of magnitude lower than the import volume. This would imply that production may be lower than that of Indian Pythons or Reticulated Pythons but higher than the giant African pythons or any of the anacondas.

Breeders have produced numerous “designer morphs” based on aberrant individuals, including varieties that routinely sell for over \$1000 per individual. Prices for these morphs tend to decrease over time as more breeders acquire adult stock, but usually stay above the priceline for individuals with wild-type patterns. Albino and similar genotypes may exhibit reduced fitness if released to natural habitats, but this is speculative.

9.0 Entry Potential (Survival in Transit – Meant Mainly for Unintentional Transport)

This category focuses on the prospect of a species surviving in a pathway that was not intended to convey the individual (stowaways). As the live animal trade is premised upon live animals, Boa Constrictors tend to be shipped using methods that ensure high survival, probably approaching 100 percent for such sturdy snakes. However, there are also numerous records of unintentional transport of Boa Constrictors, usually in fruit shipments, and the species appears to be hardy regardless of whether transportation is intentional or unintentional.

10.0 Colonization Potential

10.1 Likelihood of Escape/Release

In the public mind, Boa Constrictors are considered a giant snake, but they are not particularly large in comparison to some of the true giants. As a consequence, we consider them somewhat less likely to be released due to reaching unmanageable sizes, or to escape substandard caging by brute force. However, the reduced per-animal risk is offset by the high volume of trade, as the latter increases the potential pool of keepers likely to exhibit poor husbandry techniques or to have a lower threshold for dumping an

unwanted animal. Introduced populations in Florida and Aruba are likely the result of released or escaped pets (Snow and others, 2007b; H. Reinert, pers. commun., 2008), and free-ranging individuals are regularly reported in various parts of the United States.

10.2 Climate Match: Areas of the United States at Greatest Risk

We extrapolated the native-range climate space of *Boa constrictor* to the United States using (a) records from all localities (Fig. 7.5); and (b) all localities except those occupied by the Argentine Boa (*B. c. occidentalis*; Fig. 7.6). We include the latter map because the Argentine Boa is phenotypically distinct and is considered by some to be a candidate for description as a full species. The Argentine Boa is present in the live animal trade in the United States, albeit in low numbers, and we cannot predict whether adding genes from an escaped/released Argentine Boa to an established population of Boa Constrictor in the United States would allow the population to better withstand cold temperature. Because Fig. 7.5 depicts the United States extrapolation using climate space from the entire known native range (that is, the limits to which the species was capable of dispersing on its own) using the more inclusive species definition as used by a majority of current workers in the field, we use this map for the overall risk assessment in chapter Ten.

Using all localities, apparently suitable climate in the United States includes a large swath of land in the southern United States. This area includes mesic areas such as peninsular Florida and a corner of southeast Georgia, but also includes more arid zones including the southern half of Texas and portions of New Mexico and Arizona. Much of Hawaii and Puerto Rico also appear climatically suitable. When localities of Argentine boas are removed, however, the suitable area is much smaller and includes peninsular Florida south of about Orlando and extreme south Texas, as well as parts of Hawaii and Puerto Rico.

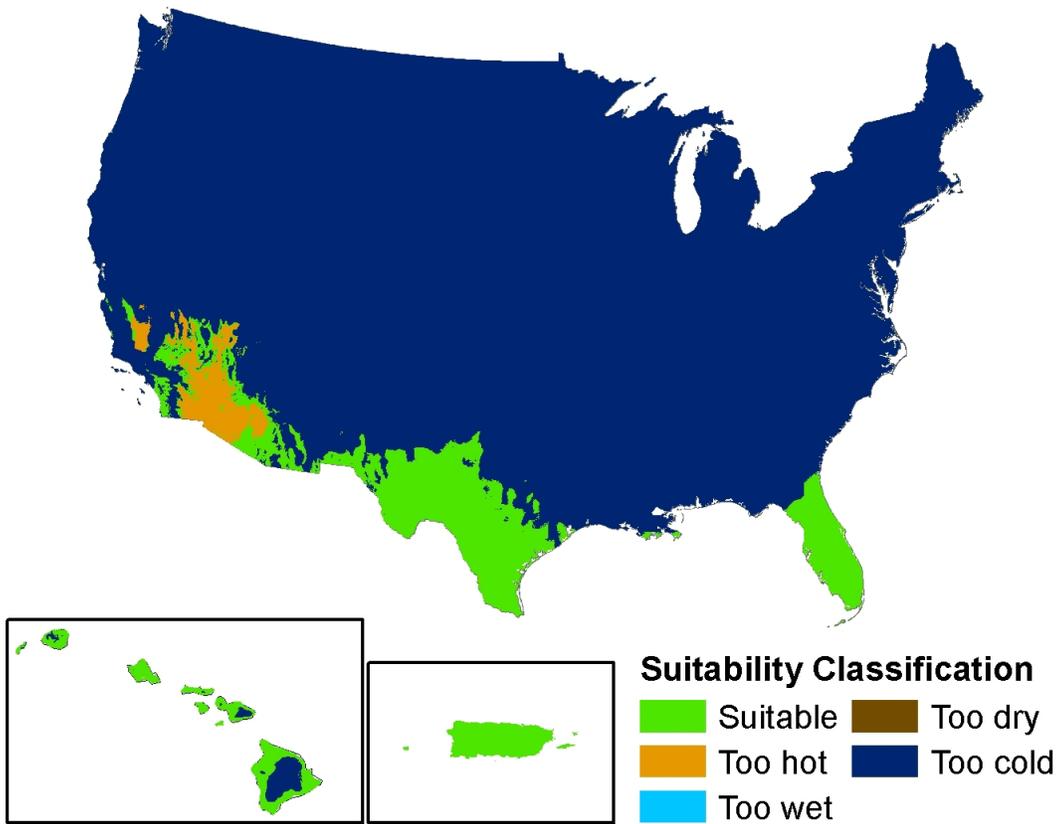


Figure 7.5. Areas of the United States matching the climate envelope expressed by *B. constrictor* in its native range (Fig. 9.3), based on 131 known localities. See chapter Two for details of analytical method.

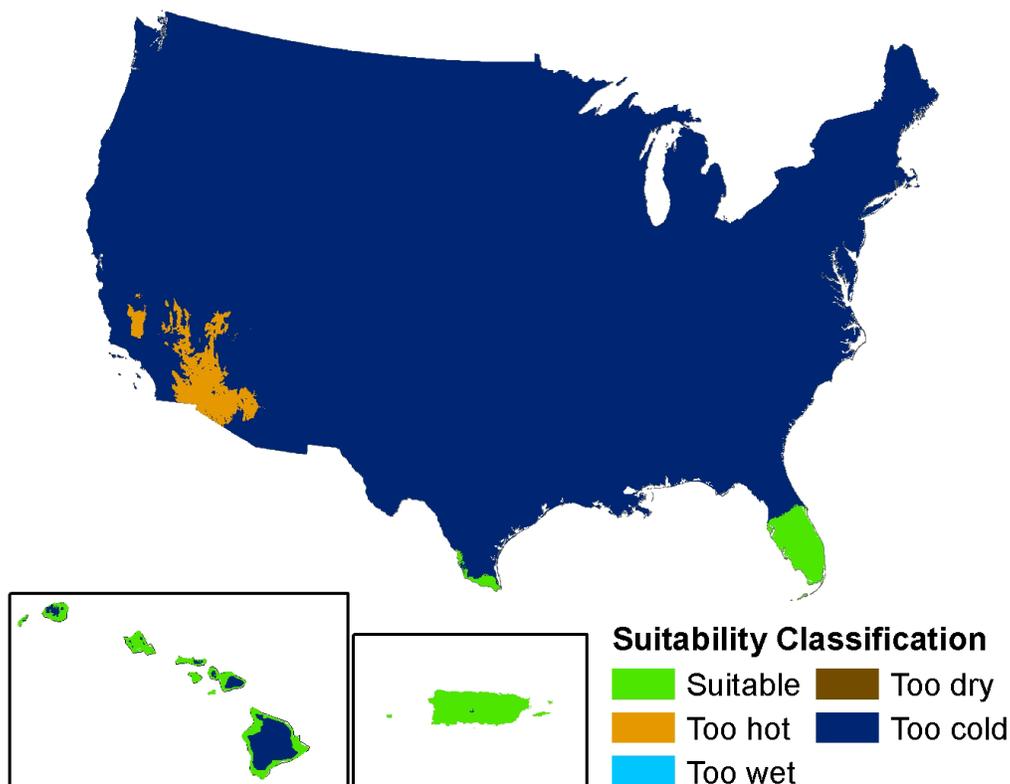


Figure 7.6. Areas of the United States matching the climate envelope expressed by *B. constrictor* in its native range (Fig. 9.3), excluding records for the Argentine Boa (*B. c. occidentalis*). See chapter Two for details of analytical method.

10.3 Prey Availability

The Boa Constrictor is capable of consuming prey from a variety of higher taxa and is unlikely to be limited by availability of suitable prey species in most areas of the United States with apparently suitable climate for the species. The introduced population on Aruba consumes many types of prey, including dogs, rats, birds, iguanas, etc. (Quick and others, 2005; H. Reinert, pers. commun., 2008), and introduced boas on Cozumel are considered to pose a threat to several endemic mammals and birds (Romero-Nájera and others, 2007).

The species is amazingly plastic in body size (Boback and Carpenter, 2007), with numerous examples of insular dwarfism evident in the lineage. Such dwarfism is likely a result of food limitation on species-poor islands, and boas are able to persist even on tiny islets by exploiting seasonally abundant prey such as migratory birds (Boback, 2005, 2006; Reed and others, 2007). Reductions in body size may occur over a remarkably short number of generations, as evidenced by apparent dwarfism in boas introduced to

Aruba only a couple of decades ago (Quick and others, 2005; RNR pers. obs., 2008). Moreover, dwarfed populations often exist at high densities and may exert top-down influences on prey species composition on these islands (Reed and others, 2007). The ability of boas to adapt to limited food by reducing body size and their propensity to achieve high densities in insular situations suggest that they may be able to become successfully established in insular states and territories including Puerto Rico, the Mariana Islands, Hawaii, etc.

10.4 Predation Risk

Because of their smaller body size and use of terrestrial/arboreal habitats, Boa Constrictors are likely to be exposed to a wider range of predators than some of the giant pythons or more exclusively aquatic species such as anacondas (see chapters Eight and Nine). A range of predators consume boas in their native distribution, and some of the same taxa (raptors, mesocarnivores, snakes, big cats, etc.) would be likely to at least occasionally consume boas introduced to the United States. None of these would be expected to specialize on consuming boas, however, and native predators have had no observable impacts on any invasive boa population. The potential for native predators to appreciably limit the growth or expansion of introduced boa population appears relatively slim, but is perhaps greater than the equivalent potential to limit Green Anacondas, Reticulated Pythons, or other giants.

10.5 Reproduction Requirements

Boa Constrictors do not exhibit specialized requirements for reproduction such as lekking, multiple male attendance of females, specific microhabitats for parturition, etc. Gravid females likely require access to basking sites for behavioral thermoregulation during embryonic development. Although herpetoculturists routinely expose boas to cool temperatures before breeding them, the species does not naturally endure such low temperatures in much of its range, and boas introduced to the United States would likely be naturally exposed to a cool winter anyway.

10.6 Hibernation Requirements

So far as we are aware, Boa Constrictors do not engage in behaviors resembling long-term hibernation anywhere in their native distribution. Even in the coldest parts of the species' distribution in Mexico and Argentina, individuals are observed engaging in reproductive, thermoregulatory, and/or other behaviors during the winter, although these are often conducted in the vicinity of a refugium to which snakes retreat at night or during particularly adverse weather.

10.7 Tools for Eradicating a Colonization

In chapter Three, we reviewed the tools available for eradicating large continental populations of giant constrictors and concluded that no tools that are currently available are likely to be dependable for such a task. This conclusion is likely to hold for Boa Constrictors as well, and limited control activities on Aruba appear to have had little effect on the introduced population (RNR, pers. obs., 2008). Small, localized populations that can be easily accessed, such as the population near Miami, Florida, are more

promising candidates for eradication, and in at least two small islands in the native range, intensive visual searching by collectors for the pet trade has resulted in drastic declines of island populations (Reed and others, 2007; S.M. Boback, pers. commun., 2009). Developers of tools for eradicating a colony of Boa Constrictors would need to be especially cognizant of the need to target snakes that forage and refuge in arboreal microhabitats.

11.0 Spread Potential

11.1 Dispersal Ability

Movement activity of Boa Constrictors has been studied in a few sites, but with generally low sample sizes and of relatively short-term durations. Furthermore, some of the radiotelemetric studies are of island populations for which dispersal is limited by the size of the island. It is therefore difficult to assess how far individuals in an introduced population might disperse. Genetic evidence from Argentine boas suggests that individuals disperse between distant populations within the state of Córdoba at fairly frequent intervals (Cardozo and others, 2007). The introduced population in south Florida has not dispersed widely over the past three decades, but it is unknown whether this is due to unsuitable surrounding habitat, whether we are currently observing the pre-expansion lag phase typical of many invasive species (Crooks and Soule, 1999), or for some other reason. Maximal litter size is greater than 60, indicating that dispersal is unlikely to be limited by female fecundity. However, most boas produce fewer offspring than the maximal number, and even maximal boa litter sizes do not compare with equivalent maximal clutch sizes of giant pythons.

11.2 Ability to Develop Races or Strains

There are no native species in the United States with which boas would be capable of breeding. However, certain aspects of the herpetoculture trade increase the odds of new strains developing in an introduced population. To a greater degree than for any other species assessed in this document, boa aficionados tend to seek out snakes from known localities, and many forms in the pet trade are known by the locality name (for example, Hog, Crawl Cay, Saboga, and Corn Island boas, Suriname red-tails, etc.). Such locality-specific individuals may be bred with boas of aberrant patterns to produce new variations, such as hypomelanistic boas produced from Colombian and Panamanian boas. These boas possess genotypes that are distinct from those found in the native range, and thus expand overall genotypic variation beyond that found in any one population across the massive geographic range of the species (for example, Kolbe and others, 2008). Lacking effective eradication tools, we consider it a high probability that new genes would eventually be incorporated into a large established population of Boa Constrictors, but the effects of such new genetic contributions to the population are largely unknown.

11.3 Tools for Managing Spread

Existing control tools appear inadequate for the eradication of large established populations of Boa Constrictors (see chapter Three). In the absence of proven control tools, an effective interdiction program might hold the most promise for preventing

establishment (for example, Vice and Pitzler, 2002), combined with a well-organized rapid response capacity to respond to sightings of colonizers (Stanford and Rodda, 2007). A multi-agency rapid response capacity for giant constrictors was recently developed in the Florida Keys and resulted in capture of a large (over 3.0 m) female Boa Constrictor in early 2009 (A. Higgins, pers. commun., 2009), offering evidence that developing such capacity can be effective. However, interdiction within the continental United States would be difficult under current regulatory regimes, which largely fail to effectively monitor interstate transport of large reptiles.

12.0 Economic Impact Potential

Regulatory agencies have not decided whether a formal economic analysis of the potential impacts of introduction of, and regulation of trade in, Boa Constrictors will be separately conducted pursuant to a variety of statutes and Executive Order 13272 (Proper consideration of impact on small business). Our narrative below is provided only to cite relevant biological literature and identify germane sections of the biological profiles.

12.1 Pathogen Vector

Very little is known of the pathogens of Boa Constrictors in their native range, or whether these pathogens exert demographic effects on boa populations. In captivity, boas are subject to a wide variety of ailments (Walls, 1998a; Mader, 1996; Smith, 1999; Russo, 2007), but many of these appear to be artifacts of captivity or exacerbated by captivity. For example, one of us (RNR) has handled well over 100 Boa Constrictors in the field in their native range and has never witnessed maladies common in captivity (including respiratory distress, “mouthrot”, skin blisters, etc.). Numerous ticks of potential medical or veterinary import readily use giant constrictors as hosts (see chapter Six for more information on these ticks and the economically-crippling pathogens they can vector), and readily transfer to new hosts in captivity. The common practice of co-housing multiple species of giant constrictors during importation, transport, or husbandry could facilitate such transfers. Overall, more knowledge of boa pathogens and parasites is required to understand the potential economic impacts of boa-vectoring pathogens becoming established in the United States.

12.2 Predator on Livestock

Boas are unlikely to prey on large hoofstock, although juveniles (for example, lambs) may be taken occasionally. However, boas are perhaps more likely to impact domestic fowl such as chickens than are more aquatic species like anacondas, and the boa’s tendency to climb means that it is more likely to surmount fences or otherwise achieve ingress to domestic poultry operations. Boas that achieve high densities (similar to the situation on some Neotropical islands) could potentially have moderate impacts on poultry production; high densities are most likely to be achieved in areas with few native predatory competitors (for example, United States insular areas within the suitable climatic conditions).

12.3 Predator on Pets

As with many of the large constricting snakes, boas would be capable of attacking and consuming a variety of companion animals, from caged birds to cats and dogs. We would not expect these attacks to be particularly common, but such an attack would almost certainly garner extensive media attention and widespread consternation among pet-owners.

12.4 Electrical Power Systems

The Boa Constrictor is perhaps the most arboreal of the species reviewed in this document, and in Central and South America we have observed boas of all sizes using habitats far above the ground. Boas may thus be the most likely species to cause power outages as a result of climbing electrical lines and spanning insulators. However, the areas of the United States where boas might conceivably become established already have fairly large arboreal snakes (genus *Elaphe* or *Pantherophis*) that have even better climbing abilities. We do not expect introduced Boa Constrictors to appreciably elevate the rate of snake-caused power outages above the background level caused by native snakes.

12.5 Traffic Accidents/Human Attacks

While an extremely large Boa Constrictor is probably capable of killing an adult human under some circumstances, we are aware of no legitimate attacks anywhere in the species' native range. Children would be at higher risk of attempted predation than adults, but a boa attacking a human of any size would appear to be a very low-odds proposition. Loss of control of a vehicle after hitting a very large boa on the road is possible but unlikely, and the odds of losing control would approximate the odds associated with striking an alligator of similar girth. Overall, we judge boas to pose low risks to human health and safety.

12.6 Tourism

To many residents of the United States, the term "Boa Constrictor" brings to mind images of giant people-eating snakes, despite a complete lack of evidence that a boa has ever attempted to consume a human. Such misplaced fear is exacerbated by well-known ditties such as, "Oh, I'm being swallowed by a Boa Constrictor..." While it may be true that oh, gee, he could get to your knee, the odds of such an event happening are extremely low. Illogical fears about snakes being what they are, however, some tourists might be dissuaded from visiting an area with a well-publicized introduced population of boas.

Conversely, a small proportion of potential tourists might travel for the purposes of viewing introduced boas. However, the cryptic nature of the species would probably result in a very low reward rate, and we doubt that the desire to see boas would motivate many potential tourists.

12.7 Impacts on Commercially Important Wildlife

12.7.1 Species Hunted with Gun or Binoculars

As compared to the giant pythons or Green Anaconda, boas are unlikely to frequently consume big game animals such as deer or pigs, although boas in the species' native range have successfully consumed both these taxa. Waterfowl that are hunted by humans (primarily ducks and geese) would probably experience some level of predation by boas, but this snake is generally less aquatic than are anacondas and (probably) the large pythons, so the relative risk to waterfowl might be lower.

Among species of watchable wildlife, we consider birds to be at greatest risk of predation from introduced Boa Constrictors. Birds are an important part of the diet of some populations of boas, especially those on islands. On the mainland, the addition of predatory boas to the suite of existing stressors is most likely to impact species that are already of conservation concern, and boas would be capable of ingesting all threatened birds in Florida, from Cape Sable Seaside Sparrows to Wood Storks. Birds of conservation concern constitute an especially large proportion of the avifaunas of insular states and territories of the United States, and boas have proven capable of persisting on tiny islands by consumption of birds, even those that only briefly stop on islands during migration (Boback, 2005: this situation is repeated on several islands with high-density snake populations across the globe, for example, Shine and others, 2002). We consider boas to pose a significant risk to avian faunas that have not experienced snake predation in recent evolutionary time, including Hawaii and the Northern Mariana Islands.

12.7.2 Species that Impact Forestry, Agriculture, or Horticulture

We do not expect boas to significantly impact these industries. However, the arboreal habits of boas would make them more likely to be encountered in horticultural settings as compared to more terrestrial or aquatic snakes. Such encounters would be startling to a human, but would entail low risk.

13.0 Environmental Impact Potential

13.1 Species of Special Concern as Prey or Competitors

Boa Constrictors would be capable of consuming most of the species considered to be potentially at risk from Indian Pythons (see chapter Four, section 13.1), although boas rarely, if ever, exceed 4 m in length and would be less of a risk to the largest prey species. Among mammals, species from the size of rats to rabbits would be expected to compose the majority of prey for introduced boas, and unfortunately this size range includes a number of imperiled mammals in the areas of the United States (such as the Florida Keys) that appear to be climatically suitable for the snake.

Along with medium-sized mammals, a wide variety of imperiled birds would be at risk of consumption by introduced Boa Constrictors. Among the species profiled in this document, boas are probably the most arboreal and take birds from all forest strata in their native range. Moreover, they manage to persist on tiny mangrove islets with little fresh water and low prey availability, primarily by targeting birds during some parts of

the year. This observation suggests that the list of potential prey provided in chapter Four, section 13.1 could be expanded to include all imperiled bird species that migrate through an area occupied by introduced boas, especially on small islands.

13.2 Species of Special Concern as Predators (Giant Constrictors Augment Food Supply)

As with the other species profiled in this document, it is unlikely that introduced boas would provide a net benefit as prey items to native predators. Intraguild predation would probably balance any benefit, and benefits would be further decreased by adding another predator to the ecosystem (see sections 10.4 and 13.2 of chapter Six). Although willing to forage in the water, boas are less aquatic than many of the other large constrictors, so crocodylians would probably encounter them at a low rate.

13.3 Vector for Disease Spread to or Within Native Faunas

Our conclusions on the probability of Boa Constrictors vectoring pathogens to native faunas are subject to the same uncertainties described above in section 12.1, namely that there is insufficient evidence to rigorously assess risk. We can say with confidence that: (1) Parasites known or suspected to vector virulent vertebrate pathogens are found on large snakes in their native range; (2) These parasites readily transfer among reptile species and to mammalian hosts; (3) Multiple species of these parasites have survived importation to the United States on live reptiles; (4) At least some of these parasites can successfully switch to feeding on native reptiles; and (5) At least one of these species has become established in the United States as a result of the international trade in live reptiles (Oliver and others, 1988; Allan and others, 1998; Burrige, 2001, Burrige and others, 2000, 2006).

13.4 Species that Might be Adversely Affected by Control Measures

Control measures for Boa Constrictors would likely be similar to those envisioned for giant constrictors in general (see chapter Three), but would probably be deployed in fewer aquatic habitats, instead concentrating on terrestrial and arboreal habitats. Some possible avenues of control, such as toxicants, are likely to result in non-target mortality to native species. Because boas attain smaller sizes than the giant constrictors, it would be more difficult to design traps or toxicant delivery systems that would be accessible to boas yet repel native species. If control tools were to be used in arboreal habitats, it would be particularly difficult to design control tools that would thwart native climbing snakes. As no management tools have been adequately field-tested, however, it is not possible to estimate potential ecological costs.

14.0 Perceived Impact (Social and Political Influences)

14.1 Pet Industry

14.1.1 Domestic Production Affected?

Domestic production of Boa Constrictors probably exceeds 1,000 individuals per year (Barker and Barker, 2008b), although there are no means of verifying this estimate. Captive-bred boas are often from locality-specific lineages and/or “designer morphs” with aberrant colors and patterns, and are typically more expensive than imported boas from Central and South America. Individuals very often sell for hundreds of dollars, occasionally thousands of dollars, so the overall value of domestic production is likely to be a large sum relative to many herpetocultural activities. It is our subjective impression that domestic production of boas is lower than production of Indian Pythons or Reticulated Pythons, perhaps because of the continued availability of inexpensive wild-caught imports and slightly more involved husbandry methods required for predictably successful captive propagation of boas. Captive production is spread across far more breeders than is the case for the anacondas or the giant African pythons, and regulations on trade in Boa Constrictor would probably cause economic hardship for a greater number of breeders, but quantification of producer impacts would be better handled in a formal economic analysis.

14.1.2 International Trade/Alternate Pets

Boa Constrictors constitute one of the mainstays of the reptile import trade, with tens of thousands imported per year for at least the last three decades. Colombia is the declared origin of the bulk of imports, but CITES records include declarations from nearly every country in the native range. Many of these are juvenile snakes declared as “farmed” or “ranching” and described as the offspring from wild-caught and/or long-term-captive dams. The veracity of these declarations has never been adequately investigated and much of the documentation associated with the live animal trade is unreliable (Blundell and Mascia, 2005). Regardless, implementation of restrictions on importation of Boa Constrictors would cause importers to lose the associated revenue stream. We cannot speculate whether such a loss could be compensated for by switching to different species, or whether a switch might actually result in importation of species with even more potential to be injurious as invasive species in the United States.

Chapter Eight–The Yellow Anaconda, *Eunectes notaeus*, and DeSchauensee’s Anaconda, *Eunectes deschauenseei*

Biological Profile

1.0 Introduction

See section 1.0 of chapter Four for a description of species-specific and overall components of the risk assessment package.

1.1 Species

As currently understood, the yellow anacondas comprise two species with entirely disjunct distributions. The northern form, DeSchauensee’s Anaconda (*E. deschauenseei*), is known from a small number of specimens and has a limited range in northeast South America. The southern form, the Yellow Anaconda (*E. notaeus*), has a larger distribution in subtropical and temperate areas of South America, and has received more scientific attention. Subspecies are not recognized for either species (Peters and Orejas-Miranda, 1986; McDiarmid and others, 1999), although the Yellow Anaconda exhibits significant genetic differentiation among disjunct populations that are within a few hundred kilometers of each other (Mendez and others, 2007). Because *E. deschauenseei* is so poorly known, general statements about yellow anaconda biology in this bioprofile refer to *E. notaeus* except where specifically noted as applicable to *E. deschauenseei*.

The literature on the Yellow Anaconda is fairly slim, and that on DeSchauensee’s Anaconda even more so. In preparing this bioprofile, we leaned heavily on the work of Christine Strüssmann and colleagues (Strüssmann and Sazima, 1991, 1993; Strüssmann, 1997) for information concerning Yellow Anacondas in the Pantanal of Brazil, and relied on the taxonomic review and associated literature on the genus *Eunectes* by Lutz Dirksen and colleagues (Dirksen and others, 1998; Dirksen and Böhme, 1998, 2005; Dirksen, 1999, 2002; Dirksen and Henderson, 2002). The most ecologically revealing data on Yellow Anacondas, however, come from the research of Tomás Waller, Patricio Micucci, and their colleagues, who amassed a large sample size of anacondas from a harvested population in the Formosa Province of Argentina (Waller and Micucci, 1993, 2008; Waller and others, 1995, 2001, 2007; Waller, 2000; Micucci and others, 2006; Micucci and Waller, 2007). Many of our conclusions on body size, reproduction, and many other topics were drawn directly from their work.

1.2 Common Names

In this report we will refer to the more widespread southern form, *Eunectes notaeus*, as the Yellow Anaconda, and the geographically limited northern form, *Eunectes deschauenseei*, as DeSchauensee's Anaconda. We term them the yellow anacondas when describing features likely to be common to both species. DeSchauensee's Anaconda is sometimes referred to as the Dark-Spotted Anaconda in English-language popular publications and websites, but we deem this name unsatisfactory as both *E. notaeus* and *E. deschauenseei* have extensive dark coloration, including spots. Because they are confined to smaller geographic areas than are wide-ranging species such as Boa Constrictor or Green Anacondas, the two yellow anacondas tend to have fewer common names ascribed to them in their native range. DeSchauensee's Anaconda may be called Sucuri or Sucuriju in its native range (Dirksen and Henderson, 2002), but the former local name fails to distinguish it from the sympatric *E. murinus*. Common names for *E. notaeus* include Anaconda Amarilla (Uruguay: Achaval and Olmos, 2003), Curiyú or Boa Curiyú (Paraguay: Waller and others, 1995; Argentina: Micucci and others, 2006), Sakobo, Aboma, Watra-Aboma, or couleuvre d'eau (French Guiana: Starace, 1998), Southern Anaconda (United States: Pope, 1961), Paraguay-Anakonda (Germany: Dirksen, 2002), and Kochokor (Paraguay: Waller and others, 1995). See Dirksen (2002) for an exhaustive list of common names.

1.3 Evolutionary Context

See the biological profile for *Eunectes murinus* for a discussion of placement of *Eunectes* in the New World boid snakes and hypothesized relationships of the four species within the genus. The two yellow anacondas addressed herein appear to represent a monophyletic lineage most closely related to *E. beniensis* and more distantly related to *E. murinus* (Dirksen, 2002; Dirksen and Böhme, 2005). In captivity, *E. notaeus* has been reported to readily hybridize with *E. murinus*, and hybrid offspring are reported by herpetoculturalists to exhibit a strong feeding response but to display unpredictable temperaments.

The herpetocultural stance on hybridization is somewhat contradicted by Dirksen and Henderson (2002), who stated that most hybrid matings between Green and Yellow Anacondas produce no viable offspring and that reproductive competence of the few viable offspring is unknown. However, successful captive breeding of Green Anacondas appears to remain relatively uncommon, at least in Europe (Bisplinghoff and Bellosa, 2007), such that it is difficult to tell whether low success of hybrid breedings is due to interspecific incompatibilities or to the reproductively intransigent nature of the Green Anaconda in the putative pairing. There are no records of hybridization between *E. notaeus* and *E. deschauenseei*, probably due to the rarity/absence of the DeSchauensee's Anaconda in herpetoculture. Although the two species are almost indistinguishable in terms of scale counts and morphology, they exhibit divergent color patterns and unique genetic identities, and are allopatric; these differences have been used to justify their continued recognition as separate species (Dirksen, 2002).

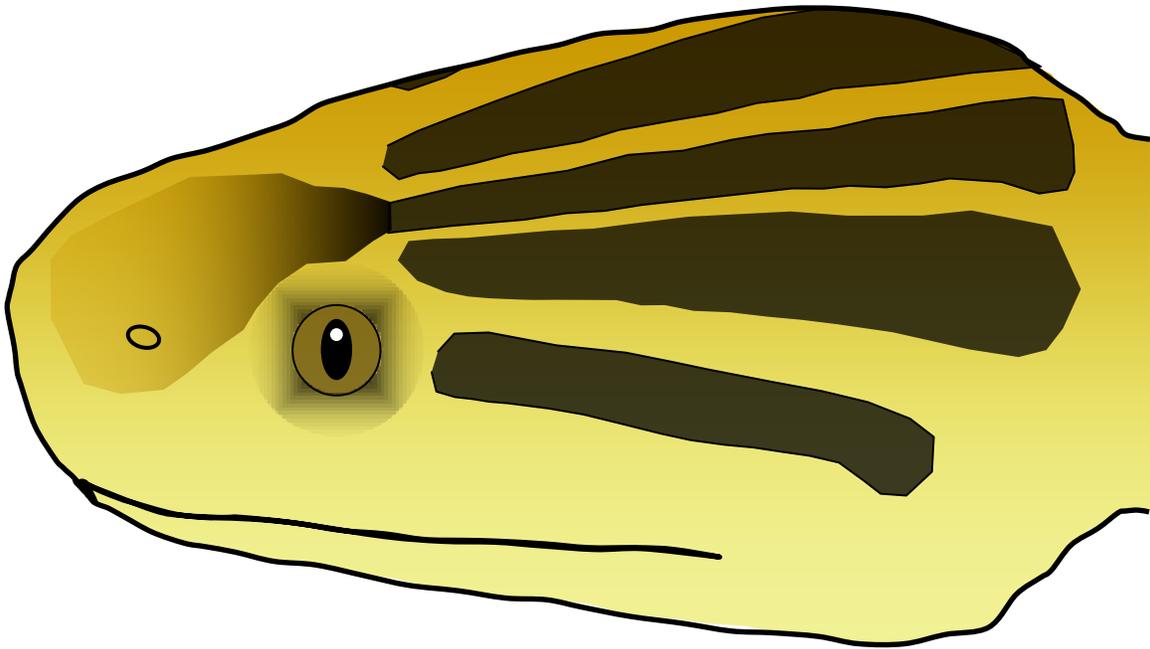


Figure 8.1. Schematic representation of the head of *E. notaeus*.

2.0 Description

2.1 Unique Morphological Features

The yellow anacondas typically exhibit a more complicated dorsal pattern than does the Green Anaconda (see Bioprofile of *E. murinus*), but to distinguish them from other large constrictors is still a relatively trivial task. Most casual observers would agree that the ground pattern of the Yellow Anaconda is strongly yellow across much of its range, as suggested by its common name. However, the ground color can range from olive yellow to brownish yellow both among and between populations across the species' range (T. Waller, pers. commun., 2009). The yellow ground color is somewhat muted (sometimes to yellowish-green to light brown) in DeSchauensee's Anaconda, and tends to be more confined to the lateral surfaces, but is still fairly visible and can be strongly yellow in some individuals. Strong yellow coloration is shared with very few non-albino constrictors, although "jungle" morph carpet pythons (*Morelia spilota*) and a few other taxa may exhibit considerable yellow coloration; the pythons, however, can be easily distinguished by their large thermoreceptive facial pits.

After noticing the yellow ground color, an observer will likely notice the many black dorsal blotches and smaller lateral blotches present in the yellow anacondas. The number and size of blotches is usually, but not always, sufficient to differentiate between the species. DeSchauensee's Anaconda has fewer (87-126) and larger dorsal oval blotches (usually solid) separated by two or three scales, as well as small lateral irregular blotches. The Yellow Anaconda has 101-175 dorsal blotches, separated by only one or two scales; the dorsal blotches tend to have lighter centers. This species also has

numerous irregular lateral blotches which tend to form complete or incomplete ocelli on the upper flanks below the dorsal blotches, below which are numerous black flecks. The two yellow anacondas exhibit very similar scale counts, including 43-54 dorsal scale rows at midbody and 213-237 ventrals (Dirksen, 2002; Dirksen and Henderson, 2002; Dirksen and Böhme, 2005). In the field within either species' native range, geography alone should be sufficient to allow determination of which species has been encountered.

Where either of the two species of yellow anacondas is sympatric with the Green Anaconda, the former can be reliably distinguished by any of the following: (1) the presence of fewer than 50 dorsal scale rows (Green Anacondas exhibit more than 50 rows); (2) no scales present between the supralabials and the oculars (present in Green Anaconda); and (3) the presence of five dark head stripes (the Green Anaconda has only four; Fig. 8.1; Starace, 1998; Dirksen, 2002).

2.2 Size

The Yellow Anaconda attains considerably smaller body sizes than does its congener the Green Anaconda. A large sample (n = 908) from northeast Argentina included no males over 2.93 m (2.55 m SVL; Waller and others, 2007). The largest female was 3.80 m (3.35 m SVL; n = 647). Male mass in this study topped out at 10.5 kg, while females attained 29 kg. Of the female sample, less than 9 percent were over 3.0 m (2.6 m SVL), and Waller and others (2007) suggested that large females are rare. However, 40 percent of females were longer than 3 m in another region of Argentina (T. Waller, pers. commun., 2009), indicating regional differences in body size distributions, the causes of which remain poorly understood. Maximum lengths above were corroborated by Dirksen (2002), who surveyed museum specimens and wild-caught individuals from across the species' range and found no females over 3.76 m or males over 2.34 m.

In the field or in semi-captive conditions in their native range, neonatal Yellow Anacondas are typically 0.48-0.65 m and 61-140 g (Waller and others, 1995, 2007); these values are appreciably larger than an estimate (0.40 ± 0.01 m, range 0.39–0.41 m) derived from a single Brazilian litter (possibly removed pre-term from a preserved female; Pizzatto and Marques, 2007). Neonates from captive females may be larger, with records of individuals ranging from 0.65 to 0.78 m total length and body masses up to 210 g (Bisplinghoff and Bellosa, 2007), but it is possible that some of these were measured and weighed well after parturition.

Table 8.1. Total lengths and masses of typical *E. notaeus* (compiled from the literature sources listed in the text).

Sex	Hatchling		Maturation		Max. reported	
	Total (mm)	Mass (g)	Total (m)	Mass (kg)	Total (m)	Mass (kg)
M:	405-593	95-210	1.3-1.45	1.5-2.5	2.9	~15
F:	440-540	95-210	1.4-1.85	2.3-5	4.25	~50

There may be a moderate amount of variability in body size in different parts of the distribution of the Yellow Anaconda, but few observers report wild-caught individuals over 4.0 m. The species was reported to reach 4.0 m in the Pantanal of western Brazil (Strüssmann and Sazima, 1993), and Dirksen (2002) similarly estimates maximum body size to be about 4.0 m; both of these estimates are only marginally larger than the published 3.79 m maximum size reported for Argentina by Waller and others (2007) and 3.95 m for a female from Corrientes, Argentina (T. Waller, pers. commun., 2009). Most of the larger body sizes reported for the Yellow Anaconda (for example, a 5-m specimen from Misiones, Argentina) are typically derived from skins, which can be stretched by as much as 30 percent over the actual length of the animal (Dirksen, 2002). Females occasionally exceed 4 m in captivity, and attain body weights in excess of any specimens known from the wild (approx. 50 kg; Bisplinghoff and Bellosa, 2007).

DeSchauensee's Anaconda appears to be the smallest of the anacondas, although the extremely limited number of available specimens does not allow unequivocal determination of maximal body sizes. Dirksen and Henderson (2002) record maximum total length of available specimens as 1.92 m in males and 3.0 m in females; three females from Marajo measured 1.89, 1.91, and 1.60 m (Belluomini and others, 1959). A juvenile from French Guiana measured 0.75 m (Starace, 1998) and offspring from the three Marajo females mentioned above were 0.37–0.55 m (Belluomini and others, 1959), while dissections of gravid females in museums yielded a neonatal size estimate of 0.49 m (0.42 m SVL, range 0.29-0.53; Pizzatto and Marques, 2007).

2.3 Sexual Size Dimorphism

As with most giant boids, females attain larger body sizes (Strüssmann and Sazima, 1993; Waller and others 2007); see above for differences in male and female body size from one population in Argentina.

2.4 External Sexual Differentiation

Males exhibit proportionally longer tails and larger pelvic spurs (Dirksen, 2002), and adults can be visually sexed in the field with some reliability by examining the width of the tail base (wider in males) in combination with tail/body proportions (T. Waller, pers. commun., 2009). In northeast Argentina, male tail length averages 17.1 percent of SVL (range 14.3-20.0; equivalent to 15.1 percent of TL), while female tail length is 15.1 percent of SVL (range 13.5-16.6; equivalent to 13.0 percent of TL); note that these ranges overlap to a significant degree, and the overlap among neonatal males and females was even greater (Waller and others, 2007). Examination of specimens from across the range of the species yielded tail lengths averaging 14.3 percent of total length among male Yellow Anacondas and 12.7 percent among females (Dirksen, 2002).

3.0 Distribution in Space and Time

3.1 Native Range

3.1.1 Yellow Anaconda, *Eunectes notaeus*

Waller and others (1995) described the overall range of the Yellow Anaconda as including the Pantanal in Bolivia and Brazil from 15°S latitude, south through aquatic habitats of the Paraguay and Parana River Basins below 250 m elevation in Paraguay and Argentina, and reaching 32°S latitude in the Parana Basin. The species' range includes about 400,000 km² overall (Micucci and others, 2006), but populations are confined to aquatic habitats within this range. Dirksen (2002) provided both dot-distribution maps for specimens and range maps showing the estimated extent of occurrence for both species.

Argentina—Found in the states of Corrientes, Chaco, Entre Rios, Formosa, Misiones, and Santa Fe over an area of 120,000 km² (Giraud and Scrocchi, 2002; Micucci and others, 2006; Waller and others, 2007), but Yellow Anacondas occupy only aquatic habitats within these extent-of-occurrence maps. The species reaches its southernmost range limits in Argentina at approximately 31°S latitude (Micucci and others, 2006), and persists in areas with an average annual temperature of 23°C, a maximum recorded temperature of 45°C and with occasional winter freezes (minimum temperature of -7°C (Waller and others, 2007).

Bolivia—Known from the northeast bordering Brazil (Itenex-Guaporé river drainage) and the eastern edge of the country south to the Paraguayan border associated mainly with the Pantanal (Paraguay River drainage; T. Waller, pers. commun., 2009). In the north, Yellow Anacondas appear to be somewhat sympatric with Green Anacondas (Dirksen, 2002), but the degree to which they may overlap with the Beni or Bolivian Anaconda (*E. beniensis*; see biological profile for Green Anaconda) is unknown (Dirksen, 2002).

Brazil—Present in the western Pantanal and in tributaries of the Río Paraguay in the states of Mato Grosso and Mato Grosso do Sul. Most Brazilian specimens are known from a region within a few hundred kilometers of the eastern Bolivian border, which extends south nearly to the Paraguayan border. However, an apparently disjunct population is located in São Paulo Province, well to the east of the rest of the known range (Dirksen, 2002); the two localities in this province may represent localized relictual populations or may be part of a poorly-sampled population covering a wider area.

Paraguay—Widespread through the Paraguay, Parana, and Pilcomayo River Basins (Waller and others, 1995). In the Paraguayan Chaco, it is found only in wetlands of the Eastern Chaco region and tributaries around the Paraguay River, but in the Western (dry) Chaco the species is found only in the Pilcomayo floodplain (Norman, 1994; T. Waller, pers. commun., 2009).

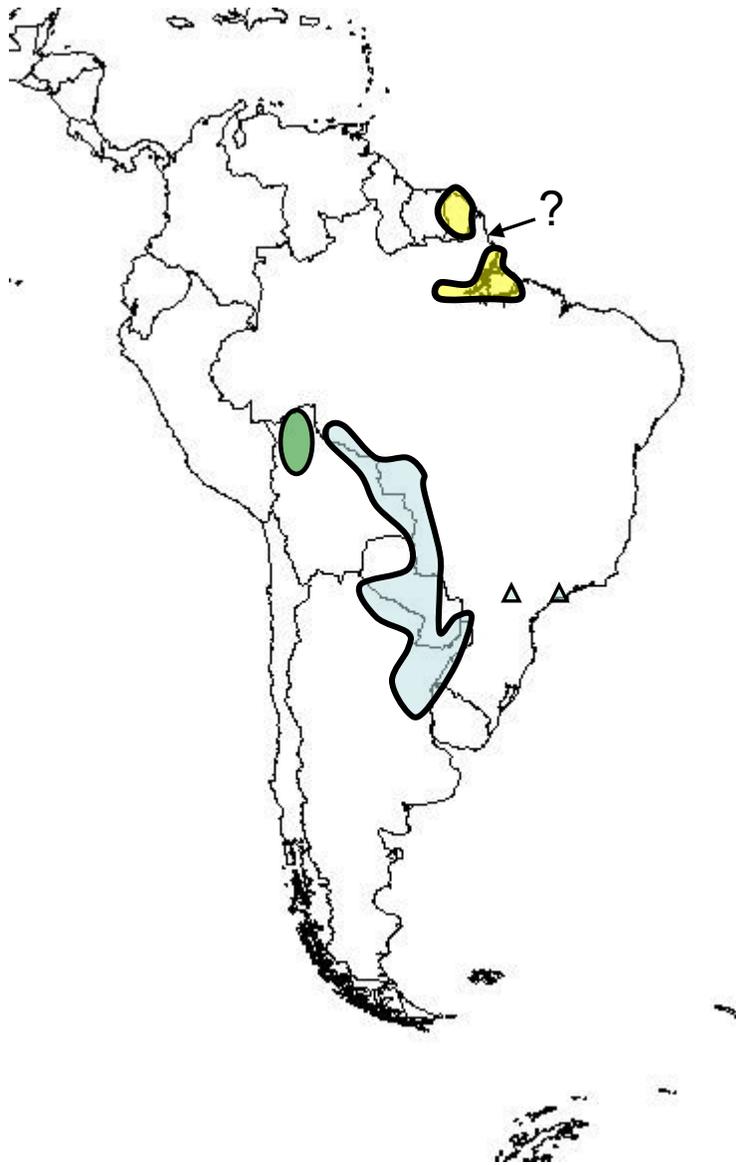


Figure 8.2. Estimated native range of the Yellow Anaconda (*Eunectes notaeus*, shown in blue) and DeSchauensee's Anaconda (*Eunectes deschauenseei*, shown in yellow). Blue triangles indicate apparently disjunct populations of *E. notaeus*. The range of the Beni Anaconda, *E. beniensis*, is shown in green for geographical reference; see chapter Nine for more information on the Beni Anaconda. All ranges follow Dirksen (2002: his Fig. 4.15) and Dirksen and Henderson (2002), with additional input from T. Waller (pers. commun., 2009).

Uruguay–Yellow Anacondas are found only in the far northern province (Achaval and Olmos, 2003), but this is apparently based on a single specimen from the delta of the Cuareim River. Individuals may be transported by floods into Uruguay down the Uruguay River, but appear to represent single waifs rather than established populations (Dirksen, 2002).

3.1.2 DeSchauensee's Anaconda, *Eunectes deschauenseei*

This species has a much smaller range than does *E. notaeus*, and is largely confined to the Brazilian island of Marajó, nearby areas around the mouth of the Amazon River, and several drainages in French Guiana. The large gap between the Brazilian and French Guianan populations may be a result of undersampling or may reflect disjunct or relictual populations.

Brazil–Present in the states of Amapá and Pará, from Santarem to the mouth of the Amazon River (Chippaux, 1986; Starace, 1998; Dirksen, 2002). However, the species is known from few specimens, and its distribution may include smaller rivers draining to the north or south, and/or slightly higher reaches of the Amazon River.

French Guiana–Considered rare by both Chippaux (1986) and Starace (1998) and known from only three museum specimens and a few additional sightings/captures in French Guiana. The museum specimens were found in the Maroni, Mana, and Approuague drainages. These localities are widely spaced, including the northeast of the country near Kaw, the western border and a locality approximately 100 km inland from the coast. Although the Maroni borders Suriname, no specimens are known from the latter country. The area around Kaw is a large open wetland surrounded by mountains, with similarly isolated populations of Black Caiman (*Melanosuchus niger*; T. Waller, pers. commun., 2009), which suggests that Deschauensee's Anacondas in this area represent a relictual population.

3.2 Habitat Range

The Yellow Anaconda appears to be restricted to swampy, seasonally flooded, or riverine habitats throughout its range (Dirksen, 2002, Strüssmann and Sazima, 1993, Waller and others, 2007). In the Pantanal of Brazil, individuals spend the wet season in seasonally flooded habitats and spend the dry season near permanent water (Strüssmann and Sazima, 1993). In the Formosa Province of Argentina, the two primary habitats are: (1) palm savanna interspersed with creeks and rivers that abut marshes and riparian forest; and (2) the Paraguay River basin, which includes seasonally flooded forest, palm savannah and oxbow lakes (Waller and others, 2007). Although not as well known, DeSchauensee's Anaconda apparently prefers swampy and riverine habitats that may be seasonally flooded (Starace, 1998; Dirksen and Henderson, 2002).

3.3 Climate Range

3.3.1 Climate Range of Yellow Anacondas

The Yellow Anaconda inhabits a fairly temperate climate range, including localities with cold-season monthly mean temperatures around 10°C and no localities with monthly means exceeding 30°C in the warm season. Most localities experience moderate variation in rainfall during the year, but overall the climate range of this species is considerably smaller than that of some of the other species reviewed in this document that range across large tropical and temperate areas. Yellow Anacondas are able to largely escape extremely cold temperatures in the native range by moving to deeper water that stays warmer than ambient water does; while parts of their range in Argentina experience winter lows below -5°C, individuals with implanted temperature data loggers did not display body temperatures below 6°C (T. Waller, pers. commun., 2009).

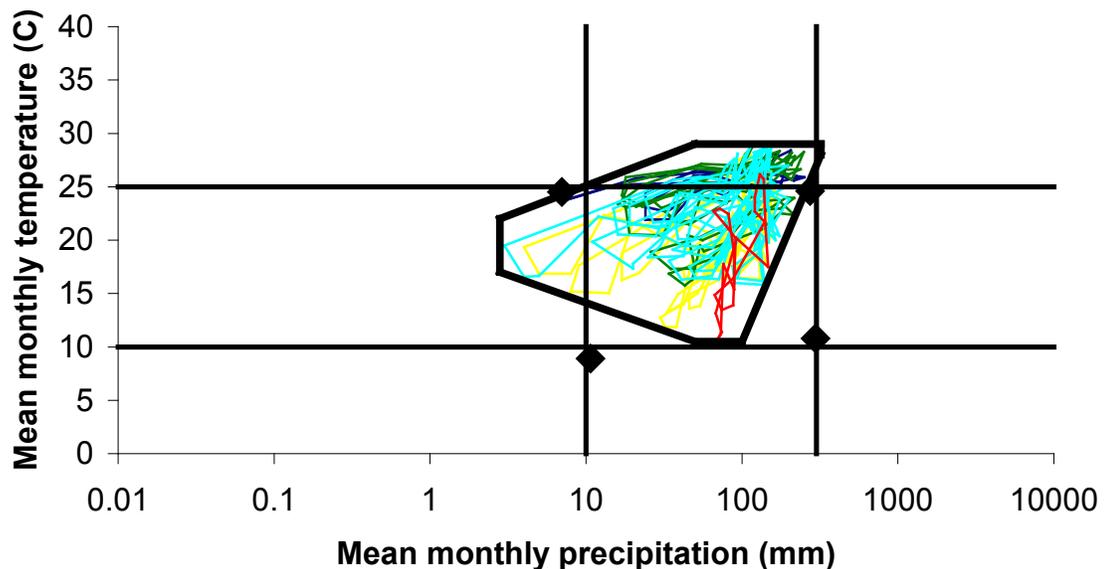


Figure 8.3. Climate space for *E. notaeus*, with reference lines and localities as introduced in Fig. 2.1. Based on 37 known localities from the native range. Climate loops color-coded as follows: Yellow = Argentina; Dark Blue = Bolivia; Green = Brazil; Turquoise = Paraguay; Red = Uruguay.

3.3.2 Climate Range of DeSchauensee's Anaconda

DeSchauensee's Anaconda is known from only a few localities in northeast South America, and its known climate range is accordingly very small. While the occupied range exhibits moderate variation in precipitation across the year, annual temperatures tend to range between 25°C and 30°C. Whether the species could tolerate greater climatic variation is unknown.

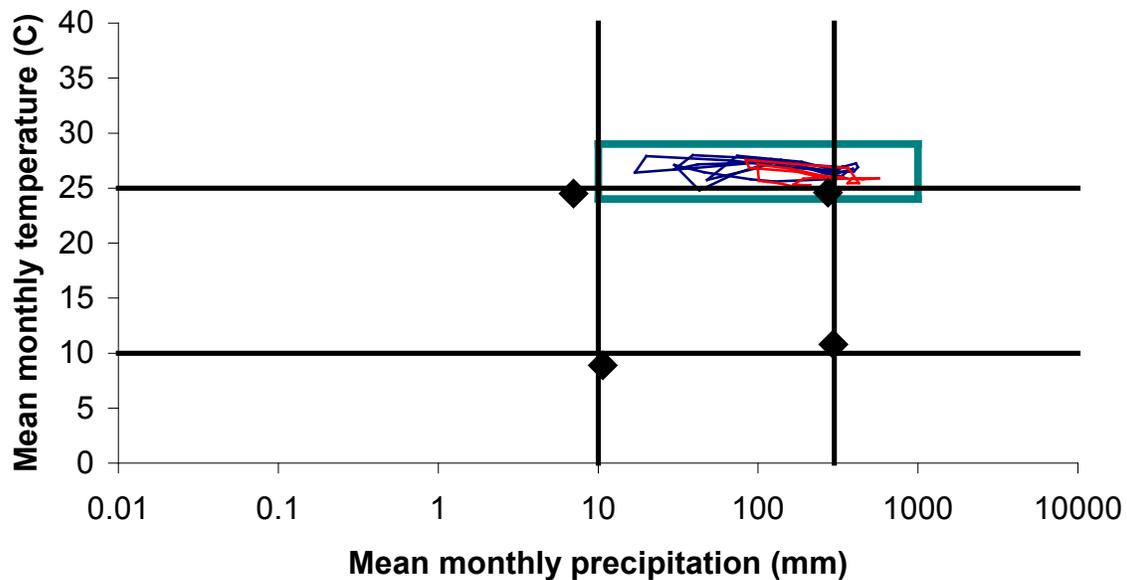


Figure 8.4. Climate space for *E. deschaeunseei*, with reference lines and localities as introduced in Fig. 2.1. Based on six known localities from the native range. Climate loops color-coded as follows: Blue = Brazil; Red = French Guiana.

3.4 Microhabitat

Data that could be used to determine the type and frequency of microhabitat use have not been published for the yellow anacondas. Both species appear to spend a large proportion of their time submerged, resulting in few visual detections by humans. By far the best available ecological data for the species come from populations in Argentina (Micucci and others, 2006; Micucci and Waller, 2007; Waller and others, 2007), but the majority of these data originate with anacondas collected for the commercial skin trade (see 7.1, below), which is done by local hunters. These hunters would be expected to have the ability to predict when and where Yellow Anacondas of salable size can be collected using visual searching during the legal harvest season, but are perhaps less likely to know precisely where snakes spend their time during the rest of the year.

During the winter harvest season when their habitats are flooded, anacondas from this population are collected from basking sites on emergent logs/palm trunks and vegetation mats, often covered with vines and other vegetation (Micucci and Waller, 2007; Waller and others, 2007). During the dry season (local spring and early summer), these individuals appear to congregate and seek refuge in pockets of dense vegetation (*Typha latifolia*) that retain moisture (Waller and others, 2007); overall, Argentine individuals spend virtually all of their time in heavily vegetated areas, especially along the shores of marshes and lagoons (T. Waller, pers. commun., 2009). Yellow Anacondas appear to select warm, shallow water for reproductive behaviors and fairly shallow water during spring and summer, but move to deeper water with more stable temperatures during the winter (T. Waller, pers. commun., 2009, based on unpublished radiotelemetric data). The microhabitats used for foraging, reproduction, and other activities have thus

far not been identified for this population, and radiotelemetric studies would likely be required to quantify such microhabitat use.

3.5 Introduced Ranges

We are aware of no established introduced populations of either species. An adult Yellow Anaconda was collected from Big Cypress National Reserve in south Florida in January 2007 (S. Snow, pers. commun., 2007), and another individual was photographed basking along a canal about 25 km north of this location in January 2008 (A. Flanagan, pers. commun., 2008). More recently (2008), an unnamed observer reportedly captured two anacondas that most closely fit the description of the Yellow Anaconda farther to the east near the Palm Beach County Line; these were reported to have been sold to a snake dealer/breeder (S. Snow, pers. commun., 2008).

3.6 Seasonal Activity

Dirksen (2002) concluded that the Yellow Anaconda in the Pantanal of Brazil was most active in the dry season (July-November), largely based on Strüssmann's (1997) observation that 76 percent of prey removed from Yellow Anacondas was recovered during this period. However, anacondas are likely to be less detectable during the wet season when they are dispersed across seasonally-flooded wetlands, which may have led to under-representation of wet-season Yellow Anacondas containing prey in Strüssmann's (1997) sample.

Yellow Anacondas in Argentina are active year-round, including confirmed feeding activity throughout the year. However, individuals become somewhat sedentary in the winter and spend much of their time basking to elevate body temperatures above the threshold required for gonadal processes and digestion (Waller and others, 2007). Basking primarily occurs when water temperatures fall below 15°C. Snake captures in Argentina decrease markedly when temperatures warm in the spring (October) and snakes reduce the amount of time spent basking. Radiotelemetered individuals move more than 2 km in a season and stay in one spot for several days before moving on (T. Waller, pers. commun., 2009). Adults of ca. 2 m body length exhibit activity ranges averaging 15 ha, while large (ca. 3.5 m) females have ranges of about 50 ha (T. Waller, pers. commun., 2009).

3.7 Daily Activity

Strüssmann and Sazima (1993) observed Yellow Anacondas actively foraging at night in Brazil, but the species appears to frequently exhibit both diurnal and nocturnal foraging behaviors (Strüssmann, 1997; Dirksen, 2002), with indications of crepuscular activity peaks in more temperate parts of the distribution (T. Waller, pers. commun., 2009). In Argentina, individuals bask during the cold season and during cool days in summer, initiating basking around 10 AM; during extended cool periods, Yellow Anacondas move to vegetated deeper water and become inactive (T. Waller, pers. commun., 2009, based on unpublished radiotelemetric data). DeSchauensee's Anaconda is reported as being nocturnal (Starace, 1998), but insufficient data are available to assess this conclusion. See the Green Anaconda biological profile for more discussion of the pitfalls of inferring diel activity based on opportunistic sightings of highly aquatic snakes.

3.8 Foraging Mode/Sensory Modalities

The Yellow Anaconda appears to employ both ambush predation and active searching for its prey (Dirksen, 2002), and may use active searching to a greater extent than is commonly credited. Although Yellow Anacondas are considered to be strongly aquatic in their foraging behavior, Strüssmann and Sazima (1991) reported observing individuals in Brazil taking birds from trees at heights of about 2.5 m.

4.0 Life History

4.1 Reproductive Mode

Both yellow anacondas are live-bearing. There is no evidence of parthenogenesis in these species, but we would not be surprised by its existence given anecdotal evidence for facultative parthenogenesis in three other genera of New World boid snakes (see Green Anaconda biological profile in chapter Nine).

4.2 Reproductive Phenology

Timing of reproductive events is likely to exhibit some variation among populations of the Yellow Anaconda, as would be expected of a species with a wide latitudinal range. In temperate parts of the species' range, temperature appears to be the primary factor that drives reproductive seasonality, with most reptiles in the area exhibiting synchronized spring copulation and late spring/summer oviposition or parturition (T. Waller, pers. commun., 2009).

Females in Formosa, Argentina exhibited seasonal and synchronous reproductive cycles, with follicle size slowly increasing from March to June (while their habitats are flooding in the antipodean fall) and then accelerating rapidly until October. Formosan males were also largely synchronous in reproductive condition, with testicular recrudescence from February to April. Virtually all adult males contained turgid testes and/or sperm-containing efferent ducts during the pre-reproductive months of April-September (winter, flooded season). Argentine Yellow Anacondas bask on emergent logs and vegetation when water temperatures drop below 15°C during the winter, and such basking is required for both sexes to complete gonadal cycles before the spring mating season (Micucci and Waller, 2007).

Copulation occurs in October-November and parturition in February-March (Achaval and Olmos, 2003); these dates are apparently based on Brazilian data, as phenology is unknown for Uruguay. "Semi-captive" specimens (freshly captured) in Argentina copulated in September-November (onset of dry season, spring/summer), but mating behaviors dropped off sharply after October (Waller and others, 2007). While copulation was not observed in the field in Argentina, male efferent ducts attained maximal sperm scores from July to October, the tail end of which coincides with anecdotal reports of mating in the field as well as copulations in the semi-captive individuals (above). Field-collected females contained oviductal (fertilized) embryos starting in early October also. Anecdotal evidence supports the notion that Yellow Anacondas at least occasionally engage in breeding aggregations of multiple males and a single female (Waller and others, 2007), but the numbers of males involved and the

duration of such aggregations have not been quantified as they have been for Green Anacondas (Rivas, 1999).

As with many other captive boids/pythonids, captive Yellow Anacondas are typically induced to mate by cooling them to 18-24°C for a couple of months (Bisplinghoff and Bellosa, 2007). Such experience with captives should not be used to justify any inference that the species requires ambient temperatures in this range to achieve reproductive readiness; whereas the lower temperature limit at which reproductive readiness can be achieved is unknown, the species appears to regularly experience much colder temperatures in parts of its native range (for example, Waller and others, 2007) and employs behavioral strategies (basking) to raise its body temperature above ambient during the pre-reproductive period.

The duration of gestation is 4-6 months, with a maximum recorded gestation of 9 months (Waller and others, 1995). Gestation was 160-180 days in seven semi-captive, wild-caught females maintained in Argentina, with parturition occurring between 12 and 28 April.

Reproductive phenology of DeSchauensee's Anaconda is largely unknown. Based on dissections of five preserved females, vitellogenesis has been inferred to be from August through February and gestation from June into April (Pizzatto and Marques, 2007). If accurate, these extended reproductive periods may be due to a less seasonal tropical climate producing more asynchronous reproductive periods, as compared to the Yellow Anaconda.

4.3 Reproductive Effort/Fecundity

4.3.1 Clutch or Litter Size/Frequency

Various authors give the number of Yellow Anaconda offspring as 12-40 (Achaval and Olmos, 2003), 10-20 with a maximum of 33 (Waller and others, 1995), 10-30 (Walls, 1998a), 13 (Belluomini and others, 1959), 12-22 (Norman, 1994), maximum of 37 (Williams and Scrocchi, 1994), "up to 56" (Bisplinghoff and Bellosa, 2007, citing an unpublished zoo report), etc. Many of the more general sources do not distinguish between wild and captive females (for example, the tabulated data of Bisplinghoff and Bellosa, 2007), even though litter sizes of the latter might be expected to be larger on average due to more generous feeding. Similarly, most sources provide little information on the relationship between dam size and offspring number. For example, captive females of about 2.5 m total length have been recorded to give birth to 13, 16, and 18 young (Belluomini and others, 1959; Holmstrom, 1982; Luttenberger, 1984), but similar information is lacking for most wild populations.

As with other reproductive variables, the best available data on litter size come from the work of Waller and others (2007) in the Formosa Province of Argentina. Mean litter size among 11 wild-caught females that reproduced in "semi-captive" conditions was 19.5, with a range of 7-42. The upper end of this range is higher than the maximum recorded in all but one previous report, and higher than any litter sizes outside of captivity (see above). Female SVL was positively related to litter size, albeit with a small sample size of litters, and the increase in litter size with female body size appeared to be linear rather than allometric. Both the maximal number of vitellogenic follicles (around 80) and the maximal numbers of oviductal scars (around 50) significantly exceeded

maximal observed litter size, perhaps indicating that some follicles are resorbed and/or unfertilized.

In the Formosa Province of Argentina, 54 percent of mature female Yellow Anacondas contained vitellogenic follicles, indicating that about half of females are capable of breeding in any given year (Waller and others, 2007). This proportion would be expected to exhibit temporal variability both within and between populations depending on local climatic, hydric, and other conditions. The presence in this population of virgin females well above the average size at maturity also implies that not all females capable of breeding end up producing offspring.

Clutch size of DeSchauensee's Anaconda ranged from 3 to 27 (mean 10.6 ± 9.6) in a sample of five museum specimens (Pizzatto and Marques, 2007), a range far greater than reported in some general works (for example, 3-7 offspring; Walls, 1998a).

4.4 Growth

No mark-recapture data are available to assess individual growth rates in the wild, but anecdotal evidence suggests that growth rates can be rapid. Free-ranging Yellow Anacondas can double their body mass in less than a year after birth, and can mature in the second or third spring after birth (T. Waller, pers. commun., 2008; Waller and others, 2007). Growth rates can be even higher in captivity; captives can attain 1.8 m TL and 2.6 kg within two years (Norman, 1994), thus roughly tripling their neonatal length and increasing mass by 20-40 times over the neonatal body sizes provided by Waller and others (1995).

4.5 Maturation

In males from Formosa, Argentina, sexual maturity typically occurred between 1.48 and 1.66 m (1.28 and 1.43 m SVL), and average length of the ten smallest mature males in a sample of several hundred individuals was 1.57 m (1.35 m SVL). Females exhibited a much wider range of body sizes at maturity, including a pre-reproductive individual of 1.69 m (1.47 m SVL) and a virgin non-reproductive female of 2.96 m (2.57 m SVL). The latter, however, does not equate with immaturity as a mature female may not have mated in previous years (Waller and others, 2007). Using the presence of 5-mm follicles to determine maturity, Waller and others (2007) inferred maturity from 1.67 to 2.13 m (1.45 to 1.85 m SVL), and proposed 1.9 m (1.65 m SVL) as a general threshold for maturity. Males in the Formosa population may mature as early as 17 months after parturition. Females may be physiologically mature in their second season after birth but require a second full year to attain energetic reserves required to reproduce, thus reproducing as early as 29 months.

A captive-born female appeared to be gravid at 3 years, 10 months of age, and gave birth to 18 young at 4 years, 2 months of age (Holmstrom, 1982). This is roughly concordant with Walls (1998a), who estimated maturation in captivity at "about" 4 years of age. A male captive reached 1.5 m and a female 2.1 m in their first year (Lederer, 1942; Brandes, 1971: both cited in Waller and others, 2007), which places both specimens at or above the threshold of maturity identified by Waller and others (2007) in Argentina.

4.6 Longevity

We are aware of no records for longevity among free-ranging Yellow Anacondas or DeSchaunsee's Anacondas. In captivity, Yellow Anacondas have lived for over 20 years, and DeSchaunsee's Anacondas for 17 years, 11 months (Snider and Bowler, 1992).

5.0 Diet/Trophic Role

5.1 Prey

The yellow anacondas appear to be generalist predators on a range of vertebrates. In the Pantanal of Brazil, the diet of the Yellow Anaconda includes fish, turtles, caimans, aquatic birds (ducks, herons, storks), rodents (Nutria and Capybara), and carrion (Strüssmann and Sazima, 1991; Strüssmann, 1997; Dirksen, 2002). This pattern was repeated among Yellow Anacondas in Argentina, which consumed fish, snakes, birds, and mammals (Waller and others, 2007); notable items in this sample included three False Water Cobras (*Hydrodynastes gigas*, a large colubrid snake), multiple Neotropical Cormorants (*Phalacrocorax olivaceus*), a Roseate Spoonbill (*Platalea ajaja*), a Capybara (*Hydrochoerus hydrochaeris*), and many rodents the size of rats.

Both the Brazilian and Argentine samples included a preponderance of birds in the diet, accounting for over 50 percent of the Brazilian sample and around 50 percent of the Argentine sample. Fish did not figure prominently in either sample, but most of these snakes were collected from seasonally flooded wetlands where fish would be expected to be at low densities. Individuals in riverine habitats may eat more fish, and Strüssmann and Sazima (1991) mention a young Yellow Anaconda that was observed consuming small fish, while T. Waller and colleagues have observed anacondas scavenging dead fish from drying ponds during droughts (T. Waller, pers. commun., 2009).

The diet of Yellow Anacondas in Uruguay is unknown (Achaval and Olmos, 2003), while in the Paraguayan Chaco an individual was observed consuming a Wood Stork (*Mycteria americana*; Norman, 1994). A series of Yellow Anacondas collected from the Paraná River during the winter contained rodents (Brazilian Guinea Pig [*Cavia aperea*] and Waterhouse's Swamp Rats [*Scapteromys tumidus*], a Lutrine Opossum [*Lutreolina crassicaudata*], a Unicolored Blackbird [*Agelaius cyanopus*] and unidentified feathers: Waller and others, 2001). As with Green Anacondas, the Yellow Anaconda exhibits durophagy (eating hard-shelled items), which is relatively uncommon among snakes (Savitsky 1983); hard-shelled items recovered from Yellow Anacondas have included turtles such as the Pantanal Swamp Turtle (*Platemys macrocephala*), Vanderhaege's Toad-Headed Turtle (*Phrynops vanderhaegei*), and eggs of the Limpkin, *Aramus guarana* (Strüssmann and Sazima, 1991; Waller and others, 2007). This observation of egg-eating is noteworthy because the juvenile Yellow Anaconda (1.9 m; 1.65 m SVL, 3.2 kg) had eaten three Limpkin eggs, each of which was only ca. 2 percent of the snake's mass—these are very small prey items for a booid snake (Greene, 1997). In the Formosa province of Argentina, anacondas have consumed eggs of South American Screamers (*Chauna torquata*), as well as an aquatic snail (Ampullaridae) of about 5 cm diameter (T. Waller, pers. commun., 2009).

DeSchauensee's Anaconda is reported to consume mammals, fish, and birds (Starace, 1998), and its overall diet may be similar to that of the Yellow Anaconda.

5.2 Predators

Predation on the yellow anacondas is poorly documented in the literature, although Yacare Caiman (*Caiman yacare*) are reported to consume them, and there have been rare observations of cannibalism (T. Waller, pers. commun., 2009). We assume that the documented and suspected predators of Green Anacondas (see biological profile of *E. murinus*, chapter Nine) would also be capable of subduing and consuming yellow anacondas, at least for those predatory taxa sympatric with the latter. As with other anacondas, *E. notaeus* and *E. deschauenseei* engage in protective balling posture when harassed by humans (Dirksen and others, 1998).

5.3 Diseases and Parasites

While general information on the identification and treatment of reptile parasites and some viral/bacterial pathogens is readily available (Jacobsen, 1986a, 1986b; Klingenberg, 1993; Köhler, 1996; Mader, 1996), specific information for the Yellow Anaconda and DeSchauensee's Anaconda appears to be lacking. Wild-caught anacondas imported to Europe are reported to be riddled with parasites (Bisplinghoff and Bellosa, 2007), but the average veterinarian simply identifies parasites at a gross level (nematode, haemogregarine, cestode, etc.) and administers treatment according to gross taxon rather than identifying them to species. Similarly, while many ailments appear to be especially common among captive anacondas (respiratory infections, fungal problems, etc.), the demographic significance of such ailments in natural populations is unknown, and could range from minor (for example, Brown and others, 2006) to potentially severe (for example, Schumacher and others, 1994).

6.0 Demography

6.1 Population Density

As discussed in the biological profiles for other constrictor species, population density is difficult to quantify without rigorous mark-recapture or intensive censuses of bounded areas. No such studies have been pursued for the yellow anacondas to our knowledge.

In a collection of snakes from the Pantanal of western Brazil, the Yellow Anaconda was represented by 35 individuals, or 15.1 percent of the total number of snakes captured; it was second in abundance only to *Hydrodynastes gigas* (Strüssmann and Sazima, 1993). In Argentina, Waller and others (2007) amassed a sample size of over 1,500 individuals while sampling snakes harvested for the commercial skin trade, and Micucci and Waller (2007) estimated 30–60 anacondas per km² at one study site. Neither of these studies used mark-recapture to estimate population size, nor were detectibilities estimated. Regardless, the relatively large numbers of snakes captured in each of the two aforementioned studies appear to reflect the species' ability to achieve high population densities in suitable aquatic habitats (H.W. Greene, pers. commun.,

2008), as well as the ability to sustain viable populations in the face of moderate harvest by humans.

6.2 Size Distribution

Although Strüssmann and Sazima (1993) reported capturing several dozen Yellow Anacondas in the Pantanal of western Brazil, they did not provide size distributions. The sole available data based on adequate sample sizes therefore come from the results of Waller and others (2007), obtained from northeast Argentina. Among 449 individuals collected in 2002, the distribution was strongly unimodal, with a peak in the 1.86-2.09 m class (1.6-1.8 m SVL) and 72 percent of anacondas fell into the 1.62-2.56 m size classes (1.4-2.2 m SVL). As expected for a snake with sexual size dimorphism, male size distributions differed from those of females. Males dominated (81% of individuals) size classes between 1.62 and 2.09 m (1.4-1.8 m SVL), but larger size classes (1.84-3.06 m, or 1.6-2.6 m SVL) are composed primarily of females, but 75 percent of females falling into the 1.84-3.06 m size classes (1.6-2.6 m SVL). Juveniles comprised only 13.4 percent of the sample, and female juveniles outnumbered male juveniles. Although these data were collected as part of an examination of anaconda harvest for the skin trade, snake hunters were paid equally for snakes of all sizes during accumulation of data for size distributions, thus minimizing the possibility that hunters were preferentially targeting large snakes. Any remaining biases are thus likely to be due to differences in detectability across individuals rather than due to preferential harvest of certain size classes.

7.0 Interactions with Humans

7.1 Human Utilization and Persecution

Yellow Anacondas represented a large proportion of the historical trade in skins of New World boid snakes. From 1980 to 1999, several hundred thousand skins were exported from Paraguay and Argentina, mostly to the United States and Europe (Waller and Micucci, 1993; Dirksen, 2002; Micucci and others, 2006), and the trade was largely unregulated for over 60 years (Micucci and Waller, 2007). The Argentine trade was halted in 1999 due to conservation concerns, and an experimental harvest was initiated in the state of Formosa in 2002, overseen by biologists. This program resulted in harvest of 16,517 skins averaging 2.6 m long during the first three years (Micucci and others, 2006; Waller and others, 2007). The program allows collection of snakes over 2.32 m (2.0 m SVL) during the winter (June-August) when they are basking above water (Micucci and Waller, 2007). Extended from 2002 through 2007, the long-term average harvest was 3,800 skins per year (Micucci and Waller, 2007). This level of take has been deemed sustainable by the scientists supervising the harvest, who estimate that fewer than 5 percent of adult females are removed annually (Waller and others, 2007), although this judgment has not been without controversy (Rivas, 2007; Waller and Micucci, 2008). The Argentine harvest is currently the only legal source of Yellow Anaconda skins in international trade (T. Waller, pers. commun., 2009).

In French Guiana, killing DeSchauensee's Anaconda is considered to bring misfortune on one's family (Starace, 1998). We are unaware of any international trade in skins of DeSchauensee's Anaconda.

7.2 Human Health Risks

Because they attain smaller sizes than do some of the truly giant constrictors, the yellow anacondas present a low risk level to humans. We are unaware of any well-documented attacks by free-ranging yellow anacondas on humans. In captivity, the Yellow Anaconda is often considered irascible and less predictable than other large snakes (for example, Boa Constrictor from South America, Indian/Burmese Pythons; RNR, pers. obs. of captive animals), but injuries from Yellow Anaconda bites to their keepers are usually minor. However, given that some herpetoculturists consider any python over 8 feet (2.4 m) in total length to be capable of killing an adult human (Flank, 1997), caution should be exercised when capturing or handling adult Yellow Anacondas, especially large females approaching 4 m in length and over 30 kg body mass.

7.3 Human Aesthetic Relations

7.3.1 Pet Trade

The Yellow Anaconda is an attractive animal, and is considered by some to be a more appropriate choice as a pet than the related Green Anaconda; this judgment is generally due to the mammoth size attained by the latter. However, anacondas in general are relatively uncommon in captivity as compared to many members of the genera *Boa* and *Python*. About 790 live Yellow Anacondas were imported to the United States during 1989-2000 according to USFWS Law Enforcement Management Information System records (Reed, 2005), an average rate of about 70 per year. Over a slightly longer period of time, CITES records revealed an average rate of 63 live Yellow Anacondas per year imported to the United States from 1977 through 2007. However, there was considerable variation among years (range 0-249 individuals/year). This is about 15 percent of the rate at which Green Anacondas were imported during this time period, and less than 1 percent of the importation rate of taxa including Ball Pythons, Boa Constrictors, and Reticulated Pythons.

Dirksen (2002) reported that exports of live animals from Paraguay fell off after 1996, but that the volume of intra-European trade reflects continued imports to Europe and that there appears to be a thriving illegal trade. While CITES records documented only two individuals imported to the United States during 2005-2007, over 50 per year were imported over the previous decade; we also note that CITES says that 2005 is the most recent year for which data are complete. Captive breeding of the Yellow Anaconda is being accomplished more and more frequently in the United States and Europe, but overall production appears to be low (Bisplinghoff and Bellosa, 2007), and we are aware of no credible estimates of the volume of domestic production. We are unaware of any international trade in live DeSchauensee's Anacondas.

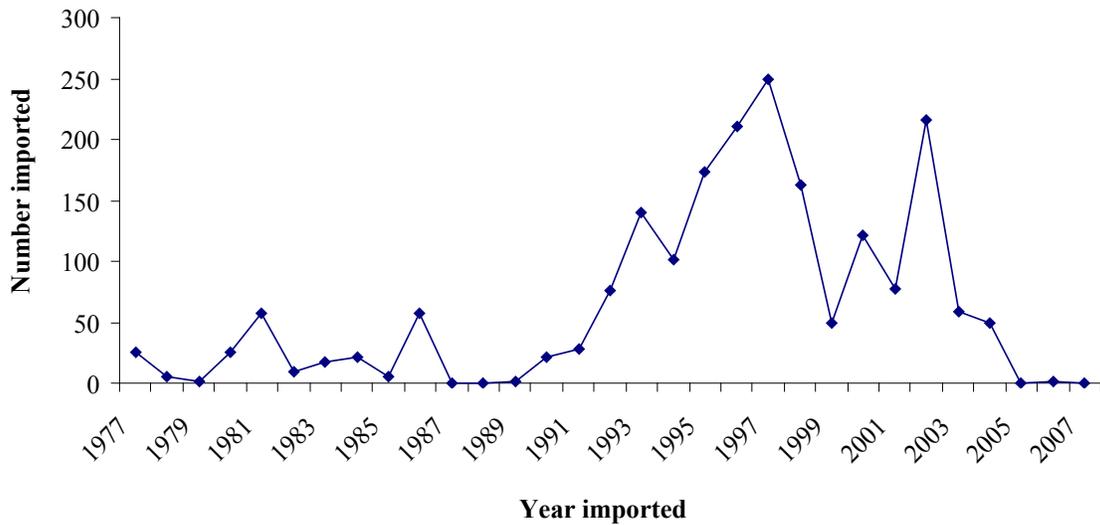


Figure 8.5. Annual imports of Yellow Anacondas, *Eunectes notaeus*, to the United States during the period 1977-2007. Data from CITES.

7.3.2 Other Uses

Major human uses of Yellow Anacondas appear to be limited to skins and the live animal trade, although their meat may be consumed in some parts of the native range.

Management Profile

See the introduction to the management profile for Indian Pythons (chapter Four) for an explanation of the format of this section of the risk assessment.

8.0 Pathway Factors: Pet Trade

8.1 Volume of International Trade

The volume of international trade in the Yellow Anaconda is low, with a range of 0 to about 250 snakes per year entering the United States. Within this range, trade volume changes drastically from year to year, implying that the few imports documented in recent years are not necessarily a good indicator of what to expect in the future. Furthermore, the observations of Dirksen (2002) regarding apparently high levels of smuggling in Europe may also be applicable to the United States import trade, although there is insufficient evidence. Section 8.1 of chapter Four outlines some reasons why imports may constitute higher risk as invasive species than captive-reared individuals.

International trade in DeSchauensee's Anaconda appears to be virtually non-existent, although the high volume of Green Anacondas exported from Suriname leads to questions of whether DeSchauensee's Anacondas from next-door French Guiana might find their way into the export market at some point.

8.2 Volume of Domestic Trade

We are unaware of any credible estimates of the volume of domestic sales or captive propagation of the Yellow Anaconda. Informal surveys of online and storefront reptile dealers lead us to suspect that only a few successful breedings of Yellow Anacondas occur per year in the United States and that domestic production is likely to be under 200 neonates per year, but we have no means of verifying this suspicion.

9.0 Entry Potential (Survival in Transit—Meant Mainly for Unintentional Transport)

As with most species assessed in this document, survival of yellow anacondas in international transport is likely to be very high, as animals are packed and shipped via means designed to ensure their survival. While mortality rates of some reptiles have historically been very high during international transport (Christy, 2008), large, hardy species of snakes would appear to be among the taxa most likely to survive the travails of international transport. Once in the United States and purchased by an endpoint consumer, the anaconda is likely to be housed in conditions that are designed to meet its needs. Survival in captivity is likely to be high except for snakes possessed by extremely negligent owners.

10.0 Colonization Potential

10.1 Likelihood of Escape/Release

Most of the factors promoting the release of pet Indian Pythons (see section 10.1 of chapter Four) are likely to apply to yellow anacondas. The smaller size attained by the latter may result in a lower rate of escape by breaking out of cages by brute force, and lower rate of release due to individuals becoming unmanageably large in captivity. Indeed, Yellow Anacondas are occasionally promoted in the herpetoculture literature as being more suitable pets than their truly giant relatives capable of exceeding five meters in body length. Although the volume of domestic trade/production is unquantified, it may equal or exceed the volume of imports. If so, then a lower proportion of captive Yellow Anacondas would be expected to harbor high parasite/pathogen levels.

Although the preceding factors may reduce the odds of captives escaping or being released, they may be countered by other factors. As compared to “calm” species like Indian Pythons and South American Boa Constrictor, Yellow Anacondas are often described as prone to biting and exuding a foul-smelling musk when handled (T. Waller, pers. commun., 2009). Furthermore, the necessity of providing water in which the snake can submerge greatly complicates the captive husbandry of the species; snakes can develop fungal or bacterial infections if the water is not cleaned regularly, and large Yellow Anacondas require a large amount of water. Both chronic illness and

expensive/complex caging requirements may increase the odds of a captive being released.

10.2 Climate Match: Areas of the Country at Greatest Risk

The Yellow Anaconda has a native-range distribution that includes highly seasonal and fairly temperate regions in South America. When projected to the United States, the climate space occupied by *E. notaeus* maps to a fairly large area, including virtually all of peninsular Florida and a corner of southeast Georgia (to about the level of Brunswick), as well as large parts of southern and eastern Texas and a very small portion of southern California. Large areas of Hawaii and Puerto Rico appear to exhibit suitable climates, and additional insular United States possessions (Guam, Northern Marianas, American Samoa, etc.) would probably be suitable as well. Within the areas deemed suitable, however, the Yellow Anaconda would be expected to occupy only habitats with permanent surface water.

The Yellow Anaconda is able to escape temporary air temperatures below freezing in its native range by moving to deeper waters, and cold-season body temperatures of 6°C have been recorded in free-ranging individuals. The ability of the species to similarly escape cold temperatures by behavioral means if introduced to the United States would likely depend on a poorly-explored interaction between the duration of such periods of cold body temperature and the absolute water temperature minima.

Rainfall has only an indirect effect on the life of an aquatic snake; it could be a misleading indicator of seasonal climate suitability. Much of the area described as “too wet” has a combination of rainfall characteristics and cool winter temperatures that are outside of the climate space that we bounded in Fig. 8.3. This zone includes mean monthly rainfall values between 100 and 300 mm and mean monthly temperature values below about 25°C (in other words, the area just to the right of, and below, the bounded climate space of Fig. 8.3). Although our climate space algorithm deemed this area unsuitable according to the boundaries we identified from native range climate records, we have no a priori ecological reason to believe that Yellow Anacondas would be adversely affected by additional rainfall up to a monthly maximum of 300 mm. Therefore, it seems very likely that the species could persist in areas with additional rainfall so long as these areas were within the temperature limits known from the native range. If so, then Coastal Plain portions of the area identified as too wet would actually be suitable. Similarly, areas in the Southwest deemed “too dry” under this climate space extrapolation could be thermally suitable so long as aquatic habitats are present. If these suggestions are valid, then Fig. 8.6 would be a significant underprediction of suitable regions of the United States.

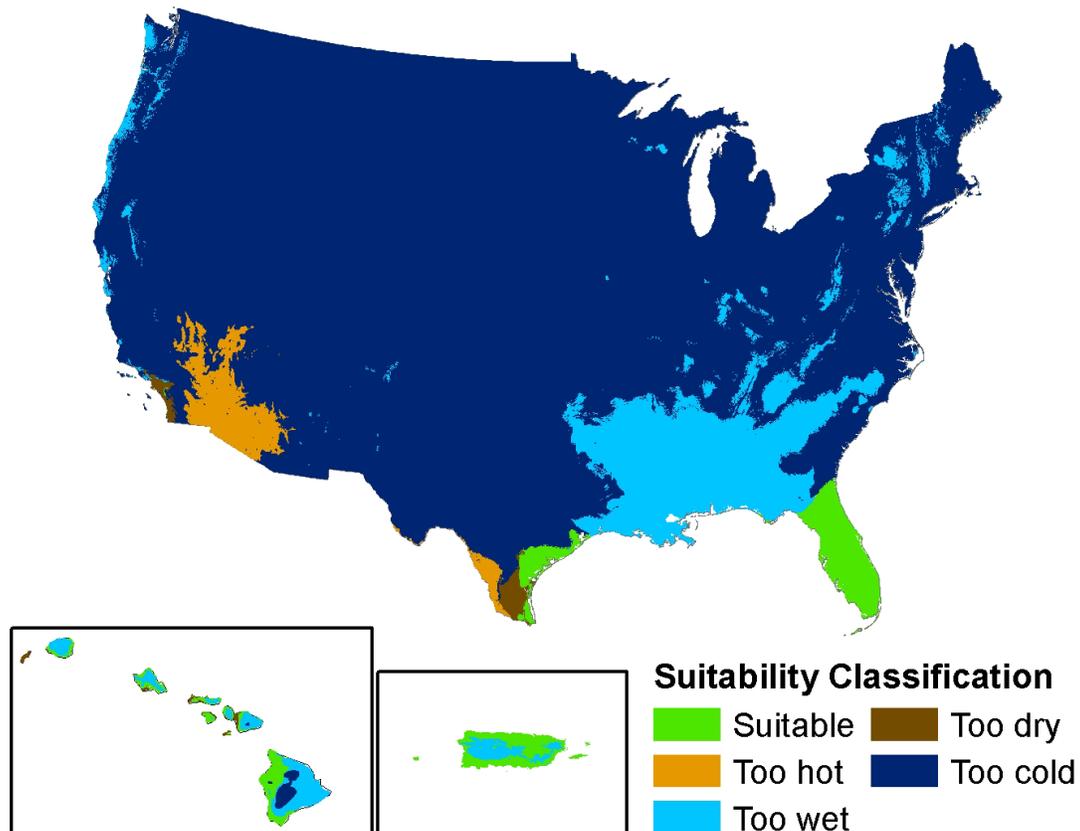


Figure 8.6. Areas of the United States matching the climate envelope expressed by *E. notaeus* in its native range (Figure 8.3). See chapter Two for details of analytical method.

As would be expected of an exclusively tropical reptile with a small geographic range, DeSchauensee’s Anaconda appears to have a poor climate match with the United States (Fig. 8.7.). We identified no areas of the continental United States or Hawaii that appear to have precipitation and temperature profiles similar to those observed in the species’ native range, although the southern margin of Puerto Rico and adjacent islands (for example, Vieques) appear suitable. However, extending the climate match to the globe (not depicted) indicates that much of the Amazon Basin and some other tropical areas of the world appear to be climatically suitable. Such a result indicates that the native range of DeSchauensee’s Anaconda does not appear to be bounded by unsuitable climate, but may instead be due to other factors (biogeography, climate change, competition or other ecological factors, etc.). If the current range reflects historical or ecological limitations rather than climatic tolerances of the species, then Figure 8.7 could be a significant underestimate of actual suitable climate in the United States.

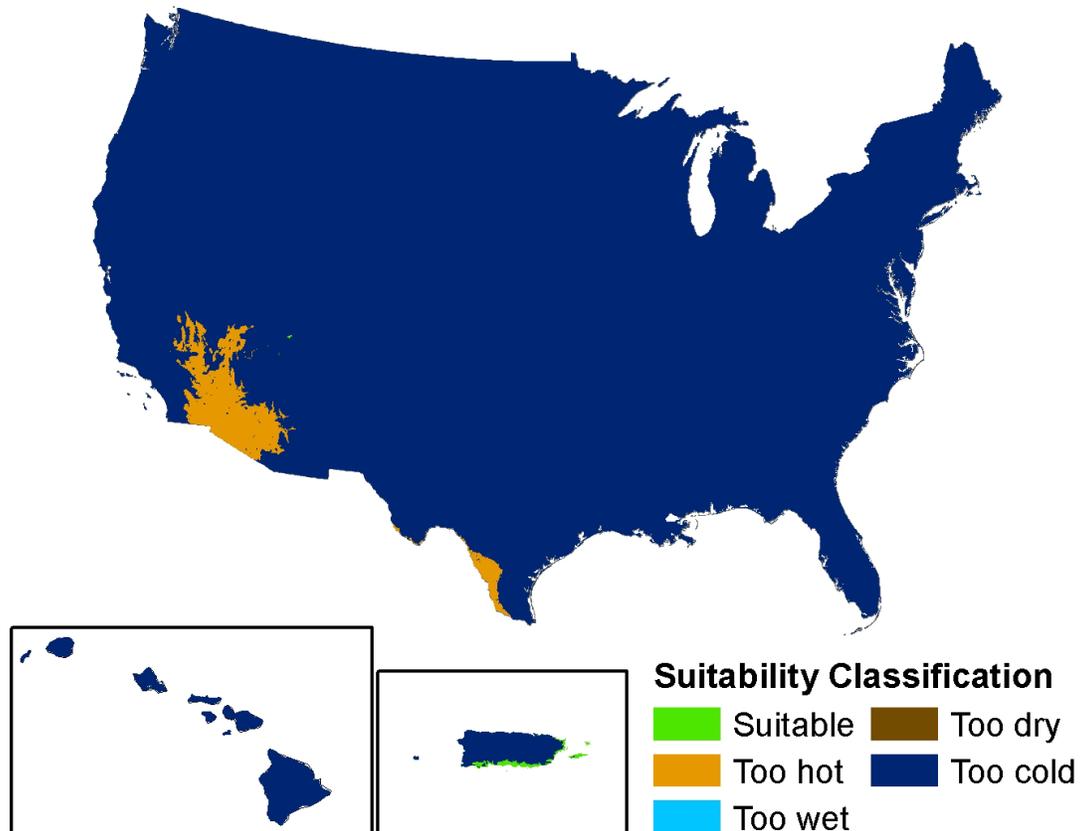


Figure 8.7. Areas of the United States matching the climate envelope expressed by *E. deschauenseei* in its native range (Figure 8.4). See chapter Two for details of analytical method.

10.3 Prey Availability

The anacondas in general exhibit among the broadest diet range of any snake, including ectotherms (lizards, crocodilians, turtles, snakes, fish) and endotherms (birds, mammals). All but the largest species considered at risk of potential predation by the Indian Python (see section 10.3 and Table 4.1, chapter Four) could be considered potential prey for the yellow anacondas, with the possible addition of more species of turtles, aquatic and semi-aquatic snakes, and perhaps a higher proportion of crocodilians.

The Yellow Anaconda appears to be especially prone to consuming birds, which are omnipresent in the aquatic habitats in the United States that appear to have suitable climate for the snake. Whereas aquatic and semi-aquatic organisms would likely constitute the bulk of the diet of the Yellow Anaconda were the species to become established in the United States, we see no obvious limitations on prey availability. The ability to persist on smaller prey items implies that the species could fare better in insular situations than would the true giants, were adequate freshwater habitats to be available.

10.4 Predation Risk

There are no predators in the United States that are likely to specialize in consuming yellow anacondas. However, this species does not attain the stupendous proportions of the Green Anaconda or some pythons, so a larger proportion of an introduced population might be vulnerable to predation by native predators. Aquatic and semi-aquatic predators would be the most likely to consume yellow anacondas, and adult alligators in particular would likely be effective predators on all but the largest individuals. Avian predators might also consume some juveniles. However, the anaconda's tendency to remain submerged much of the time would likely render it nearly invisible to most visual predators during much of the year.

10.5 Reproduction Requirements

There appear to be no specialized reproductive requirements of this species, which is a live-bearer. Bearing live young allows pregnant females to use behavioral thermoregulation (for example, basking, shuttling between habitats with different temperatures) in order to maintain relatively high and constant body temperatures during embryonic development. Live-bearing anacondas may be able to successfully reproduce in cooler climates as compared to egg-laying giant constrictors with similar temperature requirements for embryonic development (excluding those species that employ shivering thermogenesis).

10.6 Hibernation Requirements

So far as is known, the yellow anacondas do not hibernate to escape cold temperatures anywhere in their native ranges. In fact, individuals near the southernmost (coldest) parts of the range of *E. notaeus* engage in exposed basking to raise body temperatures during the coldest winter months, and this is the time during which they are most vulnerable to collection by humans. During longer periods (1-2 weeks) of cold weather or overcast skies, snakes submerge in deeper water and rest among aquatic plants. Prey items have been found in Yellow Anacondas year-round, indicating some level of activity even in winter. Individuals may seek out and congregate in moist vegetated refugia during the dry season in seasonally flooded habitats, and long-term use of such refugia may approach a physiological/behavioral state that could be considered aestivation, but not hibernation.

10.7 Tools for Eradicating a Colonization

Tools for eradicating a population of yellow anacondas are likely to be similar to those described in chapter Three and section 10.7 of chapter Four, but no tools have been developed specifically for highly aquatic snakes such as anacondas. In its native range, the species is targeted via visual searching while individuals are basking during the winter, but the limited harvest does not appear to reduce population size appreciably. Over 800 snakes per year are harvested from sites of 2000-3000 ha in Argentina, with no evidence of reduction after seven years of the harvest program (T. Waller, pers. commun., 2009). If the area occupied by an introduced population were a largely inaccessible wetland (such as the Everglades, Okefenokee, etc.), we doubt that visual searching alone would be sufficient for eradication.

11.0 Spread Potential

11.1 Dispersal Ability

We are unaware of data sufficient to evaluate dispersal ability in yellow anacondas, although Argentine individuals are reported to move over 2 km in an active season. Yellow anacondas are highly aquatic, and there is no reason to think that they would be less effective at aquatic locomotion than Burmese Pythons of equivalent body size (see section 11.1 of chapter Four). Tomás Waller (pers. commun., 2009) reported that Argentine individuals move extensively in response to the constantly changing water bodies in the dynamic Pilcomayo River floodplain, and that he considers this species “a very able disperser.” Litter sizes of yellow anacondas are lower than the Green Anaconda or the giant pythons, but the upper end of the known fecundity range (over 40 neonates for *E. notaeus*) is well above the maximum for most species of snakes.

11.2 Ability to Develop Races or Strains

There are no native species in the United States with which the yellow anacondas would be capable of interbreeding, negating the risk of developing new races or strains by that route. However, Yellow and Green anacondas appear capable of interbreeding, although the frequency and fertility of hybridization events is largely unknown and hybrids have not been observed in the native range to our knowledge. If hybrids are fertile and exhibit characteristics of both species (for example, cold tolerance of Yellow Anacondas but increased size from Green Anaconda genetic contributions), the resulting hybrid might represent higher risk as an introduced species. However, we judge such a scenario to be fairly unlikely.

11.3 Tools for Managing Spread

Generic management of giant constrictors was addressed in chapter Three, including opportunities for eradication of incipient colonizations. That chapter concluded that eradication has not been achieved for any giant constrictor and is unlikely on the U.S. mainland with the technology and early detection infrastructure presently implemented. However, spread and local population density may be somewhat more readily managed, especially if the area to be protected from spread is geographically isolated. In areas where water bodies are isolated from one another, isolation and eradication of yellow anacondas colonies would be more feasible than for species with good terrestrial dispersal capacities. The converse of this conclusion is that containment of yellow anacondas would be extremely difficult in large wetlands such as the Everglades or Okefenokee. There may be improved management opportunities associated with interdiction to islands such as Hawaii or the Florida Keys which tend to lack large wetland areas.

12.0 Economic Impact Potential

Regulatory agencies have not decided whether a formal economic analysis of the potential impacts of introduction of, and regulation of trade in, the yellow anacondas will be separately conducted pursuant to a variety of statutes and Executive Order 13272

(Proper consideration of impact on small business). Our narrative below is provided only to cite relevant biological literature and identify germane sections of the biological profiles.

12.1 Pathogen Vector

There is insufficient evidence to evaluate whether the yellow anacondas regularly vector pathogens of zoonotic, veterinary, or agricultural importance, or whether they host parasitic vectors of such pathogens. So far as we are aware, the native-range pathogens and parasites of the species are virtually unknown. The yellow anacondas are likely to be vulnerable to many pathogens known from boid/pythonid snakes, but their aquatic habits may reduce the rate at which they are colonized by ectoparasites such as ticks. Tomás Waller (pers. commun., 2009) has never seen a tick on a Yellow Anaconda, despite seeing them on *Boa* and *Epicrates* in nearby areas.

12.2 Predator on Livestock

Because yellow anacondas are smaller than the giant constrictors, they are less likely to attempt predation of domestic ungulates, although predation on lambs (Dirksen, 2002) and young pigs (T. Waller, pers. commun., 2009) has been reported. Domestic fowl that are housed and maintained away from water are also unlikely to experience impacts from Yellow Anacondas (although locals in Argentina report loss of chicks; T. Waller, pers. commun., 2009), but domestic waterfowl would be more vulnerable. Commercial production of fish, turtles, or other aquaculture species could conceivably be impacted by yellow anacondas, and mitigation for these impacts would likely be expensive (draining ponds, erecting snake barriers, etc.).

12.3 Predator on Pets

Most yellow anacondas do not attain sizes sufficient to ingest large breeds of dogs, but would be capable of consuming many smaller companion animals. As compared to more terrestrial constrictors, water-dwelling yellow anacondas would appear to be less likely to regularly encounter household pets. However, this risk could be somewhat elevated for pets in neighborhoods that include extensive freshwater habitats (around golf courses, canals, water features, etc.).

12.4 Electrical Power Systems

Yellow Anacondas have been observed climbing trees to consume birds, but none has been observed more than a few meters above the water to our knowledge and adults are less likely to climb. The heavy build of this snake likely precludes it from being a particularly good climber, and we would expect minimal impacts to electrical power delivery networks.

12.5 Traffic Accidents/Human Attacks

The smaller size of the yellow anacondas as compared to the truly giant constrictors means that only the very largest individuals in an introduced population might be large enough to cause vehicle accidents if a snake were struck by a car moving at a high rate of speed. To our knowledge there are no records of attacks on humans in

the native range of this species, although large captives can inflict serious lacerations through defensive bites.

12.6 Tourism

The yellow anacondas attain smaller body sizes than do true giants such as Reticulated Pythons, and are responsible for no human deaths that we are aware of. It should by rights therefore have minimal impacts on tourism should the species become established in the United States. However, most citizens do not differentiate between Yellow and Green Anacondas and the word “anaconda” is associated with giant anthropophagic snakes in the public mind, such that potential tourists hearing of the establishment of Yellow Anacondas might reconsider their travel plans. Such fears could be allayed by education and outreach efforts, but these might be expensive. Overall, however, establishment of Yellow Anacondas would be unlikely to have major impacts on tourism.

12.7 Impacts on Commercially Important Wildlife

12.7.1 Species Hunted with Gun or Binoculars

Predation by yellow anacondas is unlikely to result in population declines of upland game species such as deer or turkey, but the snakes would frequently come into contact with, and certainly consume, waterfowl such as ducks or geese. Of these, it is likely that dabbling ducks that forage in habitats with extensive aquatic vegetation would be more likely to fall prey to anacondas than would diving ducks. Whether introduced anacondas could attain densities capable of exerting demographic impacts on ducks is unknown, but does not appear out of the question. Yellow Anacondas are known to consume wading birds such as herons and egrets, and may climb trees in or near the water to forage for birds. They would thus be capable of impacting many species of “watchable wildlife,” which are the mainstays for birdwatching and other nonconsumptive uses of wildlife.

12.7.2 Species that Impact Forestry, Agriculture, or Horticulture

We foresee no major impacts to these industries if yellow anacondas were to be introduced to the United States, although workers might be reluctant to venture into aquatic habitats containing a species with the word “anaconda” in its name (see section 12.6, above).

13.0 Environmental Impact Potential

13.1 Species of Special Concern as Prey or Competitors

As generalist predators on ecto- and endothermic prey, the yellow anacondas are capable of ingesting the same kinds of prey as Indian Pythons (chapter Four, section 13.1), albeit the former would be unlikely to consume the very largest species on this list. The highly aquatic habits of anacondas reduce predation risk for potential prey that do not require regular access to water. On the other hand, the anacondas are more likely to

consume aquatic ectotherms including fish and turtles; we judge predation on fish to be of low demographic significance for the majority of fish populations, but regular predation on turtles could have demographic impacts on species of conservation concern. Bird species that nest communally near aquatic habitats (for example, Wood Storks) might be vulnerable to Yellow Anacondas, as these snakes are known to occasionally climb trees to forage for birds.

13.2 Species of Special Concern as Predators (Giant Constrictors Augment Food Supply)

Introduced yellow anacondas would be suitable prey for native predators such as American alligators, and juvenile anacondas would likely fall prey to a range of predators ranging from ospreys to indigo snakes. However, such benefits would probably be balanced by anaconda predation on the native predators (for example, consuming juvenile and subadult alligators). Furthermore, adding predatory anacondas to United States ecosystems would likely reduce overall biomass available to a native predator by reducing populations of other prey species (see sections 10.4 and 13.2 of chapter Six).

13.3 Vector for Disease Spread to or Within Native Faunas

Insufficient data are available to evaluate the likelihood of transmission of pathogens or parasites to native faunas. The yellow anacondas are likely to be suitable hosts for some of the same ectoparasites known from other taxa (for example, the giant African pythons) and which are known or suspected to be carriers of zoonotic disease. However, because they spend much of their time submerged, anacondas might be less suitable hosts for such ectoparasites, as evidenced by an apparent lack of ticks on Yellow Anacondas from Argentina.

13.4 Species that Might be Adversely Affected by Control Measures

Control measures for yellow anacondas would likely be similar to those envisioned for giant constrictors in general (see chapter Three). Some possible avenues of control, such as acetaminophen toxicants, are likely to result in non-target mortality to native species, especially those species capable of accessing toxicant delivery devices designed for giant constrictors. Traps, drift fences, and other potential tools may also impede movements of non-target native taxa or result in their inadvertent capture. Because yellow anacondas attain smaller body sizes than do some of the truly giant constrictors, control measures could likely be designed to exclude large non-target species, but conversely it would be more difficult to exclude small-bodied non-targets. Control measures for yellow anacondas would largely be deployed in or adjacent to aquatic habitats, implying that species using such habitats are at highest risk of being adversely affected by control measures. Depending on geography, these species might include Alligators, American Crocodiles, aquatic snakes, River Otters, etc. As no management tools have been adequately field-tested, however, it is not possible to estimate potential ecological costs.

14.0 Perceived Impact (Social and Political Influences)

14.1 Pet Industry

14.1.1 Domestic Production Affected?

Domestic production of Yellow Anacondas is trivial compared to species such as Reticulated Pythons or Boa Constrictors, and production of DeSchauensee's Anaconda appears to be non-existent. Regulations on trade in species would disproportionately impact a small number of breeders specializing in anacondas.

14.1.2 International Trade/Alternate Pets

The declared import rates of Yellow Anacondas are variable across years but are uniformly low as compared to other species of giant constrictors, and there are no declared imports of DeSchauensee's Anaconda. If recent records are an indication of future imports, then regulating trade in Yellow Anacondas would have minimal impact on reptile importers.

Chapter Nine–The Green Anaconda, *Eunectes murinus*, and Beni Anaconda, *Eunectes beniensis*

Biological Profile

1.0 Introduction

See section 1.0 of chapter Four for a description of species-specific and overall components of the risk assessment package.

1.1 Species

As currently understood, the Green Anaconda is a single wide-ranging species, *Eunectes murinus*, and is the world's heaviest snake. Although it has an extensive distribution in South America, its ecology is known only from a small number of study sites, such as the seasonally flooded savanna wetlands called the “llanos” of Venezuela (Rivas, 1999).

Dunn and Conant (1936) described two new anaconda species from the island of Marajó in northeastern Brazil; the newly-described *E. barbouri* was very similar to *E. murinus*, and the former species was shortly thereafter considered invalid by Amaral (1944). After further examination, both Strimple and others (1997) and Dirksen (2002) concluded that *E. barbouri* is simply a color morph of *E. murinus*, and not a valid taxon. A species closely related to *E. murinus* has recently been described from Bolivia (*E. beniensis*; Dirksen, 2002); see section 1.3 Evolutionary Context, below, for more information.

A parallel situation exists within *E. murinus* itself, as the species has historically been considered to comprise two subspecies (*E. m. murinus* and *E. m. gigas*). However, based on morphology and color pattern, Dirksen and Böhme (1998) sank *E. m. gigas* into synonymy with *E. murinus murinus*, resulting in a single wide-ranging species with no subspecific differentiation. This German-language publication has failed to achieve wide penetration in the United States, where *E. m. gigas* is still often mentioned as a valid taxon, especially among herpetoculturists.

The vast majority of literature on the Green Anaconda consists of anecdotal observations of single individuals in the field, comments on small series of specimens, and observations on captive snakes. While the biology of anacondas has been reviewed in past decades (for example, Petzold, 1984; Strimple, 1993), two recent authors have made especially important contributions to our knowledge of the genus. Lutz Dirksen compiled a thorough review of the genus, re-defined the taxonomy of anacondas, and provided insights on a variety of topics (Dirksen and others, 1998; Dirksen and Böhme,

1998, 2005; Dirksen, 1999, 2002; Dirksen and Henderson, 2002). Jesús Rivas conducted the only long-term study of any population of Green Anacondas, resulting in sample sizes at least an order of magnitude larger than any previously available and providing the first reliable data on myriad aspects of Green Anaconda behavior and ecology (Rivas, 1998, 1999; Rivas and Burghardt, 2001; Rivas and others, 1997, 2007a, 2007b). We relied heavily on the literature produced by both of these authors during the production of this bioprofile, and we feel fortunate to have such sturdy shoulders upon which to stand.

1.2 Common Names

Most English-language publications refer to *Eunectes murinus* as the Green Anaconda (for example, Rivas and others, 2007a), although some call it the Common Anaconda (for example, Holmstrom, 1982). In cases where a species is simply called Anaconda, authors are typically referring to the Green Anaconda (for example, Pope, 1961). Minton and Minton (1973) reported that “anaconda” is a Sinhalese word translating to “elephant killer” that was originally applied to *Python molurus*, and that the name was brought by the Portuguese to the New World. Regional names are various, and include Water Camoodie or Kamudi (Creole, Guyana: Beebe, 1946; Pope, 1961), Ow-oo-rah and Sal-urrying mah (Akawai Indian, Venezuela/Guyana: Beebe, 1946), Sucuriú, Sucuri, Sicurí, or Sucurijúba (Brazil, Bolivia: Ditmars, 1931; Pope, 1961; Strimple, 1993), Guio de Agua, Petaca, or Guio Petequero (Colombia: Strimple, 1993), Huilla or Huile (Trinidad: Mole and Urich, 1894; Mole, 1924), Culebra de Agua (Venezuela: Lancini, 1986), and many others (see Dirksen, 2002 for an extensive list). There is thus far no English-language common name for *E. beniensis* in wide usage, although some herpetoculturists refer to it as the Beni Anaconda (Bisplinghoff and Bellosa, 2007).

1.3 Evolutionary Context

Green Anacondas are members of the family Boidae, which includes species found in the Americas, Africa, Asia, Europe, and many islands. The genus *Eunectes* is part of the South American radiation of boid snakes, which also includes the genera *Boa*, *Epicrates*, and *Corallus*; this group is distantly related to North American boids of the genera *Charina* and *Lichanura*. Phylogenetic analysis of molecular genetic data places *Eunectes* as the sister group to *Epicrates* (Burbrink, 2005; Noonan and Chippindale, 2006). There are four species within the genus *Eunectes* as currently understood. The yellow anacondas, *E. notaeus* and *E. deschauenseei* appear to be sister species (Dirksen and Böhme, 2005). *Eunectes beniensis* is a recently-described species (Dirksen, 2002) from northern Bolivia, previously considered to be contained within *E. murinus*. However, Dirksen and Böhme (2005) reappraised the relationships within the genus, and proposed that the members are related as: *E. murinus* (*E. beniensis* [*E. deschauenseei*, *E. notaeus*]). Because *E. beniensis* is known from only six specimens, is not known from the pet trade, and has a limited range, we will not consider it separately in this risk assessment. To the extent that the risk is dependent on the natural history traits of the species, *E. murinus* will be the best proxy for *E. beniensis*.

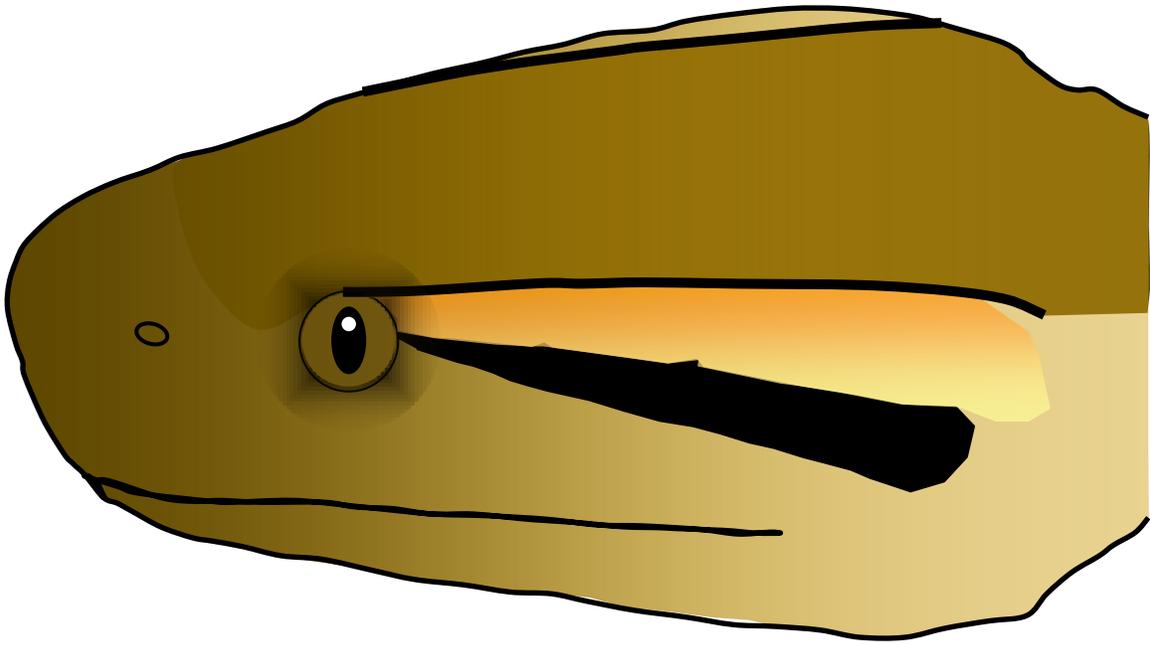


Figure. 9.1. Schematic representation of the head of *E. murinus*

2.0 Description

2.1 Unique Morphological Features

The Green Anaconda is probably the easiest to identify among the giant constrictors due to its relatively simple color pattern. The ground color is typically olive green, upon which are scattered dark (black to blackish-brown) ovoid blotches of varying size; these blotches can be single, paired, joined, or alternating down the midline, depending on the individual. There are typically no saddles or other types of dorsal patterns, making for a very “clean” appearance of black blotches on a solid background. A second lateral series of irregular dark markings is typically present, sometimes presenting as small circles with centers that are lighter, usually yellow, than the ground color.

There is some color variation across the range of the species—for example, individuals from southern Brazil have more and smaller dark dorsal blotches than do those in Peru, dorsal blotches tend to be round in Peru and more ovoid elsewhere (L. Dirksen, pers. commun., 2009), and ground color can be dark brown to blackish-brown in the Manaus area (Martins and Oliveira, 1998). The ground color in the upper Amazon Basin was reported as bluish-grey, with spots that can be dark olive rather than black (Dixon and Soini, 1986), but some individuals from the same area appear olive green (L. Dirksen, pers. commun., 2009). Although Boos (2001) cites Fawcett (1953) in support of the notion that the eyes of Green Anacondas reflect light, this notion is dismissed by others with more field experience with the species (J. Rivas, pers. commun., 2009).

The massive build of large specimens is also indicative of the Green Anaconda, and large individuals can have midbody diameters exceeding 0.30 m (Coborn, 1991). In comparison to pythons and *Boa constrictor*, the eyes and nostrils of all anacondas are positioned more dorsally, as is typical of many semi-aquatic vertebrates.

Dirksen and Böhme (2005) defined the Green Anaconda as having 239-269 ventrals, 53-81 dorsal scale rows, 4 black head stripes, suborbitals between the oculars and supralabials, black dorsal blotches *usually* (our emphasis; look at the entire animal, as individual spots may well be more round than this standard) half as long as dorsal width (dorsal blotches sometimes lighter in center), and black lateral spots with yellowish centers that are lighter than the ground color. In contrast, the other three species of *Eunectes* all have five head stripes, no scales between the oculars and labials, and lower dorsal scale counts (Dirksen, 2002, pers. commun., 2009). For descriptions of additional morphological characters useful in defining boid snakes, see Kluge (1991; however, note that Kluge's conclusions are incorrect with regard to *E. deschauenseei* vs. *E. notaeus*, due to errors in specimen identification; Dirksen, 2002).

2.2 Size

The Green Anaconda is truly a giant snake, with fairly reliable records of lengths over 7 m. Moreover, it is a very stout snake, such that very large anacondas are almost certainly the heaviest snakes in the world, even though more gracile species (for example, *Broghammerus reticulatus*) may attain greater lengths. Murphy and Henderson (1997) and Bellosa and others (2007) provide tabulated data on body size in Green Anacondas from a variety of sources. As with other giant snakes, many a tall tale has been related about maximum size. Ditmars (1931) considered the maximum length to be just over 25 feet (7.62 m), based on a personal communication from A. do Amaral. In the apparent absence of confirmed specimens longer than Ditmars' estimate, we consider his conclusion to be as valid today as it was nearly 80 years ago. One of the largest snakes measured in recent decades by a reliable observer (W.W. Lamar) was 7.49 m, taken from a shallow stream in Colombia in 1978 (Murphy and Henderson, 1997), while a specimen found crossing the road in Amazonas, Brazil was 6.2 m total length (Martins and Oliveira, 1998).

Bisplinghof and Bellosa (2007) considered the largest verified specimen to have been "...just short of 9 m (29.5 ft.) and a maximum weight of 180-200 kg (397-441 lbs.)," but they did not cite their sources for this statement and did not differentiate between captive and free-living individuals. Their maximum length of nearly 9 m may be based on Robertson (1998), who reported a Green Anaconda skin from Brazil that was nearly 29 ft. without the head and tail. As discussed for other species in their bioprofiles, however, we consider skins to be highly dubious sources of information on body size of giant constrictors, as skins typically stretch extensively during removal and tanning.

Size variation across the range of the Green Anaconda has not been adequately addressed. Some authors consider snakes in riverine rainforest habitat to attain greater lengths than those in the llanos (for example, Murphy and Henderson, 1997), but this may be due to more intensive study of the species in the llanos, producing more reliable and more realistic insights on maximum size. However, Rivas (1999) noted that several males from a Venezuelan river were larger than any of the several hundred males captured in the adjacent seasonally-flooded llanos, and males in captivity often exceed

the maximum sizes observed in the llanos by Rivas (1999). On Trinidad, Mole and Urich (1894) stated that “specimens have been frequently killed 18 and 20 feet in length” (5.49, 6.10 m); however, the longest specimen from Trinidad actually measured by Mole (1924) was 5.26 m and weighed 47.63 kg, while the heaviest was 5.03 m and 105.23 kg. Beebe (1946) shot a Green Anaconda measuring 5.23 m in Kartabo, Guyana, and stated that the maximum “accredited” size of the species is 8.8 m. At the other end of the scale, a specimen measuring 0.92 m total length weighed 280.4 g, while a 0.67 m specimen weighed 69 g (Beebe, 1946); the latter is somewhat smaller than the minimum size of 0.73 m cited in a review by Martins and Oliveira (1998).

In the field, neonates average 0.70-0.90 m total length and 200-300 g (Waller and others, 1995); French Guianan neonates are reported to be 0.65-0.85 m (Starace, 1998). Neonates from four captive females were 0.73-0.90 m total length and 192-303 g (but length and mass were generally more consistent within litters than between litters; Holmstrom, 1980). Variation in body mass by sex was not observed among male and female neonates in Venezuela (Rivas, 1999); several hundred neonates measured in Rivas’ study averaged 0.68 ± 0.04 (SD) m SVL, 0.790 ± 0.040 m total length, and 217 ± 36 g at birth. Average neonate size from the Venezuelan llanos is somewhat larger than the mean of 0.618 ± 0.055 m SVL (range 0.435-0.685) recorded for embryonic Brazilian Green Anacondas (Pizzatto and Marques, 2007), perhaps because the latter had not fully completed their development. The majority of information on neonate sizes, however, comes from captive situations. Recent reviews of neonate body sizes based largely on captives (Dirksen, 2002; Bisplinghoff and Bellosa, 2007) reported total neonatal lengths from 0.508 to 0.965 m and body masses from 153 to 454 g, indicating a potentially wider range of neonatal sizes in the Green Anaconda than in other giant constrictors such as *B. reticulatus* (see biological profiles in chapters Four to Eight).

Table 9.1. Total lengths and masses of typical *E. murinus* (compiled/estimated from the literature sources listed in the text).

Sex	Hatchling		Maturation		Max. reported	
	Total (mm)	Mass (g)	Total (m)	Mass (kg)	Total (m)	Mass (kg)
M:	508-965	150-400	1.8-2.8	2.5-7?	4.5	>50
F:	508-965	150-400	2.4-3.5	5-12?	8+	180-200

2.3 Sexual Size Dimorphism

With the possible exception of the Australopapuan *Morelia amethystina* complex, all of the truly large snakes appear to exhibit female-biased sexual size dimorphism. This is certainly true of the Green Anaconda, in which females are capable of attaining much greater length and larger mass than do males. This has been best documented in the llanos of Venezuela, where females average 3.70 ± 0.71 m and 32.6 kg, while males average 2.63 ± 0.28 m and 7 kg (Rivas and others, 2007a).

It is not unlikely that large female body size is a result of fecundity selection (large females can have larger numbers of offspring, possibly increasing their fitness) and/or selection to allow females to take advantage of large prey items (for example, Capybaras, caiman). Male size, on the other hand, may have undergone stabilizing selection, in which large males are favored during mating aggregations but smaller males are of an optimal size for consuming prey of moderate size classes, low predatory risk, and high abundances. See Rivas and others (2007a) and Rivas and Burghardt (2001) for extended discussions and alternative viewpoints on body size evolution in anacondas.

2.4 External Sexual Differentiation

Other than the massive size attained by some female Green Anacondas, there is no reliable means of determining sex of anacondas at a distance. In hand, males have relatively longer tails and pelvic spurs than do females (for example, Rivas and others, 2007a).

3.0 Distribution in Space and Time

Despite its large geographic range and relative abundance in parts of this range, the Green Anaconda is not well represented in museum collections, and many parts of its distribution are assumed rather than documented by preserved material. In large part, this is because the large body size of the species necessitates large amounts of space and supplies in a museum collection, as is true for many of the giant constrictors. For example, Dixon and Soini (1986) stated, “Many specimens have been observed over the last 8 years but the large size of most specimens makes it impossible to maintain an adequate preserved series.”

3.1 Native Range

Waller and others (1995) summarized the range of the Green Anaconda as including aquatic habitats in much of South America below 850 m elevation plus the insular population on Trinidad, encompassing the Amazon and Orinoco Basins, major Guianan rivers, the San Francisco, Parana and Paraguay Rivers in Brazil, and extending south as far as the Tropic of Capricorn in northeast Paraguay. Dirksen (2002) provides the most thorough review of the distribution of members of the genus *Eunectes*, as reflected in our frequent citation of his work below. Although anacondas are not present in Central America, Lutz Dirksen stated to us that he believes that this is solely due to their inability to surmount the Andes to access areas to the north (pers. commun., 2008)

Argentina—Probably not present. While a specimen of the Green Anaconda was reported from Argentina by Correa and Pautassi (1986, cited in Giraudo and Scrocchi, 2002), Giraudo and Scrocchi (2002) considered this to be an erroneous locality and stated that the Green Anaconda is likely not found in Argentina.



Figure 9.2. Estimated native distribution of the Green Anaconda (*Eunectes murinus*, shown in blue) and the Beni Anaconda (*Eunectes beniensis*, cross-hatched oval). Distributions follow Dirksen (2002, his Fig. 4.15).

Bolivia—Known from the Itenez/Guaporé River along the border with Brazil, as well as the Baures River drainage in northeast Bolivia. Another species of anaconda with similar appearance, *Eunectes beniensis*, is known from a few specimens in the state of Beni (Dirksen, 2002).

Brazil—Likely throughout the Amazon Basin, as well as throughout rivers that drain to the eastern coastline from the state of Paraná northward and southward flowing rivers in the Mata Grosso do Sul (Dirksen, 2002; Bisplinghoff and Bellosa, 2007).

Colombia—Known from a few specimens from lowland drainages to the east of the Andes, including upper reaches of the Amazon and Orinoco drainages (Dirksen, 2002). Although there are rumors of anacondas in the Magdalena Valley in northern Colombia (J. Rivas, pers. commun., 2009), their presence has not been confirmed by herpetologists familiar with the area (J. Maldonado, J. Daza, pers. commun., 2009).

Ecuador—A few specimens are known in the lowlands of extreme eastern Ecuador, including the Napo and Tiputini Rivers and other drainages to the Amazon (Dirksen, 2002).

French Guiana—Known from a few specimens and a larger number of sightings, including the Maroni and Oyapock (Oiapoque) Rivers that respectively border the country to the west and east, as well as several drainages in between (Dirksen, 2002). Probably historically present in most lowland drainages.

Guyana—Known from the Essequibo River and adjacent drainages along the coast, as well as farther south along the Takatu and upper Essequibo River (Dirksen, 2002). Probably historically present in most lowland drainages.

Paraguay—Presence confirmed only by a couple of specimens from the extreme northeast of the country east of the Paraguay River, plus anecdotal reports from this area (Waller and others, 1995). These authors surmise that the species may be present in the Concepción, Canindeyú and Alto Paraná Departments.

Peru—Known from multiple specimens in northern and central Peru along the Ucayali and Marañon Rivers downstream to the upper Amazon River. In the south, specimens are known from the Madre de Dios River drainage near the Bolivian border (Dixon and Soini, 1986; Dirksen, 2002).

Suriname—Known from multiple specimens and sight records in drainages within 50 km of the coast, as well as scattered locations in the interior (Dirksen, 2002). A number of sight records from the vicinity of Kwakoeqron, roughly 90 km inland (N. Hawley, pers. commun., 2008). Gaps in the known Suriname distribution are likely the result of incomplete sampling; the species may be present in most lowland drainages.

Trinidad and Tobago—Currently found in estuary lagoons and swamps of various parts of Trinidad, but not in apparently suitable habitat in the Caroni River drainage and now absent from some historically-occupied areas and rare elsewhere (Murphy, 1997; Boos, 2001). Absent on Tobago. Boos (1984) reported a juvenile Green Anaconda found at sea on a floating mat of vegetation, and surmised that it was a waif that rafted from

Venezuela; Boos (2001) provided additional examples of rafting in the Green Anaconda. The species' aquatic habits may facilitate such rafting events to previously uncolonized islands.

Venezuela—Found throughout the seasonally flooded areas (Rivas, 1999) and waterways of the Orinoco River system and other rivers of the states of Sucre, Guárico, Cojedes, and Portuguesa (Lancini, 1986), as well as Zulia, Amazonas, Bolivar, Anzoategui, Monagas, Barinas, and Apure (Roze, 1966; J. Rivas, pers. commun., 2009: anacondas in Zulia may represent a disjunct population). The species has received intensive study in the Venezuelan llanos of the state of Apure (Rivas, 1999).

3.2 Habitat Range

Eunectes is Greek for “good swimmer,” and the habitat range of the Green Anaconda is largely defined by availability of aquatic habitats. Depending on location within the wide distribution of the species, these appear to include deep, shallow, turbid, and clear waters, and both lacustrine and riverine habitats.

3.3 Climate Range

The Green Anaconda inhabits areas delineated by a wide range of rainfall and precipitation regimes (Fig. 9.3). The coldest mean monthly winter temperatures (around 14°C) are in several south Brazilian localities, while a few localities in Brazil, Venezuela, and Bolivia also experience periods with little rain. However, seasonal variation in rainfall is probably not as important to the Green Anaconda as is the year-round availability of surface water. Anacondas may also be able to escape both daily and seasonal temperature decreases by retreating to aquatic habitats when water temperatures exceed air temperatures.

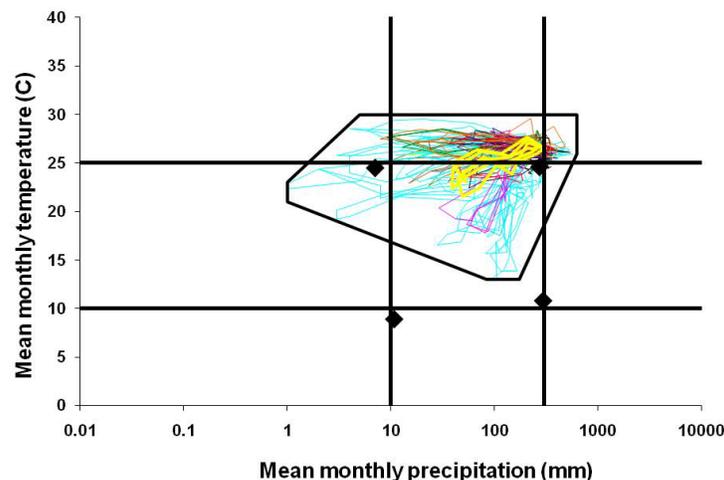


Figure 9.3. Climate space for *E. murinus* based on 77 known localities from the native range, and for *E. beniensis* based on three known localities. Reference lines and localities as introduced in Fig. 2.1. Climate loops color-coded as follows: Brown = Bolivia; Turquoise = Brazil; Green = Colombia; Dark blue = Ecuador; Black = French Guiana; Red = Guyana; Pink = Paraguay; Gray = Peru; Violet = Suriname; Dark Red = Trinidad; Orange = Venezuela; Yellow = *E. beniensis* from Bolivia (the latter is completely contained within the climatic envelope of *E. murinus*).

3.4 Microhabitat

In the llanos of Venezuela, radiotelemetered anacondas were found in the water 86 percent of the time and at the water's edge the remaining 14 percent. Most (92 percent) locations of telemetered snakes were in shallow water covered in aquatic vegetation, and snakes apparently preferred still water with aquatic vegetation over areas with flowing water (Rivas, 1999). Basking behavior was observed in reproductive females and wounded or diseased individuals, but rarely among other age, sex, or stage classes.

Microhabitat use in rainforest habitats such as much of the Amazon Basin is poorly understood, and almost entirely reliant on chance observations of basking or otherwise visible anacondas. This trend is exemplified by a few records from central Amazonas, including a 4-m individual observed in tree roots near a stream, an adult female found crossing a road, two snakes observed basking by water, two more active along the aquatic margin, and two incidental captures in fishing nets (Martins and Oliveira, 1998). Radiotelemetric studies in Venezuela (above) suggest that the encounters in other parts of the species' range are unlikely to represent "typical" anaconda behavior, and instead are the result of higher detectability to humans when snakes make infrequent jaunts to terrestrial or arboreal microhabitats. Nonetheless, such scattered anecdotes have often been used as evidence that the Green Anaconda is a nocturnal species that often exhibits diurnal basking. Around-the-clock monitoring of radiotelemetered snakes in the llanos of Venezuela showed no preference for nocturnal activity, and indeed showed very little activity from 0200 to about 0800 (J. Rivas, pers. commun., 2009).

3.5 Introduced Ranges

We are unaware of any established extralimital populations of the Green Anaconda. An individual (around 2.5 m total length) was found dead on US41 in the vicinity of Fakahatchee Strand Preserve State Park, FL, in December 2004, and there are reports of two medium-sized adults and a juvenile observed but not collected in this general area (S. Snow, pers. commun. 2008).

3.6 Seasonal Activity

Green Anacondas exhibited marked seasonal changes in their activity ranges and movement behavior in the Venezuelan llanos (Rivas 1999), but equivalent information is lacking for any other population. In the llanos, activity ranges were small (about 25 ha) during the dry season when water bodies are isolated, but snakes migrated (1.3 km on average) to slightly higher elevations at the onset of the wet season, and activity ranges were somewhat larger during the latter (about 37 ha). Breeding females provided an exception to this trend, as their wet season activity range was very small (about 0.01 ha) and they spent much of their time basking on emergent ground (levees, river banks, etc.). Adult males increased their movement activity prior to the mating season, including movement during mid-day when other age and sex classes were inactive.

3.7 Daily Activity

Rivas (1999) opined that Venezuelan anacondas were somewhat crepuscular in their activity, but that movement, predatory, and reproductive behaviors were seen throughout the day and night. Most individuals in this study sought shelter during the warmest parts of the day, although male mate-searching activity was apparent throughout the day if skies were overcast. Nocturnal activity was not notably elevated above diurnal activity, and snakes often went a week or more without moving (Rivas and others, 2007a).

In the Venezuelan llanos during the wet season, female Green Anacondas were often observed basking for extended periods during daylight hours, while radiotelemetered animals were usually found under vegetation or submerged (Strimple, 1993; Rivas, 1999). This disparity may reflect judgments on daily activity based on where humans observe snakes (usually diurnal and basking) versus activity patterns gained from radiotelemetry (often submerged). Overall, conclusions that the Green Anaconda primarily exhibits nocturnal activity appear to be poorly supported.

3.8 Foraging Mode/Sensory Modalities

Mole and Ulrich (1894) noted over a century ago that anacondas ambush most prey from the water, a conclusion that has been largely corroborated by more recent observers. However, a 3-m individual was observed actively “chasing” a rallid bird in a flooded area in Brazil (Martins and Oliveira, 1998), and the extent to which the Green Anaconda uses chemosensory, visual, or other cues to locate prey is poorly known.

The violence of the strike and the power of the subsequent constriction by large anacondas may be enough to kill prey by physical damage by dislocating or fracturing vertebrae, as evidenced by examination of prey species including Capybara, White-tailed Deer, Spectacled Caiman, and White-lipped Peccary that had been killed by Green Anacondas (Valderrama and Thorbjarnarson, 2001; Rivas, 2004).

As with *Boa constrictor*, anacondas lack the thermoreceptive labial/facial pits that are typical of most pythons, although *B. constrictor* exhibits labial thermoreceptors that are not housed in pits (de Cock Buning, 1983). We are unaware of unequivocal evidence for the presence of such receptors in *Eunectes*, but their presence would be relatively unsurprising given the prevalence of thermoreceptors among boid snakes.

4.0 Life History

4.1 Reproductive Mode

The Green Anaconda is live-bearing. While reproduction is typically sexual, a recent report noted that a female that was five years old in 1976 and kept in captivity for 26 years without any access to males produced 23 female offspring in 2002 (only three of which were alive) and 20 atresic eggs (Lamonica and others, 2007). Although the authors did not comment on the implications of this event, it raises the possibility that *E. murinus* exhibits facultative parthenogenesis, as has been reported in female *Python molurus*, *Epicrates cenchria*, and several other snake species (including *Boa constrictor*)—these rare events typically produce only female offspring that are clones of

the mother (Schuett and others, 1997; Groot and others, 2003; G. Schuett, pers. commun., 2008).

4.2 Reproductive Phenology

4.2.1 Seasonality

In the seasonally-flooded llanos of Venezuela (8° N), mating peaked before the onset of rains (late April–early May), with no breeding aggregations observed before mid-Feb (mid dry season) or after mid-June (early wet season: Rivas, 1999). Earlier in the year (January–March), males appeared to engage in long distance movements in order to locate females. It is possible that the timing of breeding in the llanos is due to the spatial predictability of females during the dry season.

Based on dissections of Brazilian (10°S - 5°N) Green Anaconda museum specimens, Pizzatto and Marques (2007) inferred vitellogenesis during late wet to dry seasons (roughly September to February), gestation from dry to early wet (January to July) and parturition from late dry to early wet (April to July). These inferences roughly correspond to observations by Mole (1924), who reported mating in December and January (early dry) on Trinidad (10.5° N) in a relatively aseasonal climate. Timing of reproduction in the Green Anaconda is apparently divergent from the pattern seen in a variety of bovid and pythonid species, in which gestation/incubation primarily occur in wet/early dry and parturition/hatching in early-mid dry (Pizzatto and Marques, 2007). Instead, these authors suggest that parturition in Green Anacondas is related to low water levels during the dry season in much of Brazil (as contrasted with Rivas' assertion that low water levels induced mating in Venezuela).

We caution, however, that generalities on the timing of reproduction based on specimen dissections remain tenuous, as Pizzatto and Marques (2007) used specimens from across the range of the species in Brazil, and their sample sizes did not permit examination of seasonal variation by latitude or other factors that would be expected to vary across such a vast area (these authors also had inadequate material available for any inferences on male reproductive cycles). Timing of reproduction does, in fact, appear to exhibit a strong latitudinal signal, as populations in northern South America mate from December to April, while equatorial populations mate from June to September and southern populations mate in September and October (Dirksen, 2002; Bisplinghoff and Bellosa, 2007).

4.2.2 Reproductive Behaviors

Breeding aggregations consisting of a single adult female and several males appear to be common in the Green Anaconda, at least in northern populations such as those in the llanos of Venezuela. Rivas and others (2007a) reported aggregations averaging 3.8 males per female, with a maximum of 13 males in attendance. Aggregations can occur in water or on land and were of surprisingly long duration, with none under four days duration and some lasting as long as 40 days (18 day average). Rivas (2007a; pers. commun., 2009) never observed male-male combat as described in some other giant constrictors, but observed tail wrestling and “pushing tournaments” among males in mating aggregations. Aggregations of Green Anacondas have also been

reported from rivers in Brazil (Pope, 1961), indicating that the phenomenon is relatively widespread. On Trinidad, a single male courted a female from 24 December to 13 January (Mole, 1924).

4.2.3 Vitellogenesis and Ovulation

Duration of gestation has been summarized as typically about six months, with a recorded maximum of ten months (Waller and others, 1995). The mean duration of gestation was inferred to be about nine months across the range of the species in Brazil (Pizzatto and Marques, 2007), but was only 202 ± 15 (SD) days or ~ 6.75 months in the Venezuelan llanos (Rivas, 1999).

4.2.4 Parturition

Parturition may occur on land or in the water, and was observed at the end of the wet season (October to late December) in Venezuela (Rivas, 1999). A female was observed giving birth on 01 July 1892 at the mouth of the Orinoco River in Venezuela (Mole and Urich, 1894). These are among the only verified records of parturition in the wild. In the upper Amazon Basin of Peru, a neonate was found in February, and two wild-caught females gave birth in early March (Dixon and Soini, 1986), whereas females from Guyana and French Guiana gave birth in January (Neill and Allen, 1962a; Starace, 1998). Pizzatto and Marques (2007) report parturition during April through July (early wet). Given that these observations include parturition over ten months of the year (available data do not as yet support parturition in August or September), the timing of parturition is obviously highly variable. Further complicating the matter, a small individual that is judged to be a “neonate” may actually have been born several months previously but achieved little growth in body size, depending on its foraging success.

Females may consume infertile eggs and stillborn young after parturition (Neill and Allen, 1962a); Rivas (1999) observed post-parturient females ($n = 8$) moving their snout across the neonates, consuming those that did not respond by moving.

Many wild female Green Anacondas retain moderate fat reserves and decent body condition even after producing a large litter (Rivas, 1999). While some captive females accept food through all but the last month or so of gestation (Bisplinghoff and Bellosa, 2007), wild-caught females held in Venezuela refused food before parturition, after which they readily accepted food (J. Rivas, pers. commun., 2009).

4.3 Reproductive Effort/Fecundity

4.3.1 Clutch or Litter Size/Frequency

The maximum recorded litter size is 82, removed from a Brazilian specimen (Belluomini and Hoge, 1958), but the typical range is 28 to 42 (Waller and others, 1995). Among 36 litters in Venezuela, mean litter size was 29.4, with litter size strongly correlated with mass of the dam, litter sizes ranging from 5 to 75, and total litter mass averaging about half the dam’s body mass (Rivas, 1999). Additional litter size data are available from wild and captive anacondas (Mole and Urich, 1894; Ditmars, 1931; Holmstrom, 1980, 1982; Dixon and Soini, 1986; Hero and dos Santos, 1987; Martins and Oliveira, 1998; Starace, 1998; Bisplinghoff and Bellosa, 2007).

Reproductive frequency is poorly understood in the Green Anaconda. Only about half (57 percent) of females greater than 2 m SVL captured in the llanos of Venezuela were reproductive (Rivas, 1999), and all reproductive females exhibited high body condition, whereas all but a few non-reproductive females exhibited lower body condition. However, reproductive females were more detectable than were non-reproductive females, which may artificially inflate conclusions on relative abundances of breeders and non-breeders. These results suggest that females typically exhibit a biennial or longer reproductive cycle in this population, and that it takes females over a year to recoup energetic stores depleted by reproduction. Rivas estimated overall female reproductive frequency to be 0.38 among snakes captured in multiple years, but that breeding frequency decreases among very large females. There may be exceptions to the typical trend, as exemplified by two females that were inferred to be reproductive in successive years based on their condition index (these were not, however, observed to breed). Equivalent data are lacking for any other population of Green Anacondas.

4.4 Growth

Rivas (1999) provided the only available growth rates for free-ranging anacondas, from a sample of females captured from a population in Venezuela. Growth rates were highly variable; many individuals ranging from about 2.3 to over 5.5 m (2.0-4.75 SVL) exhibited zero growth between captures, while the highest growth rates (averaged over 12 months) were observed in fairly large snakes (for example, the four highest rates were from females of 4.1-5.2 m (3.5-4.5 m SVL), whose growth averaged 34-49 mm/mo (29-42 mm/mo SVL). In contrast, extremely slow growth (less than 3 mm/mo; 25 g/mo) was observed in an adult female originally captured in 1994 at 3.76 m (3.24 m SVL) and 21 kg and recaptured in 2007 (thirteen years later) at 4.25 m (3.66 m SVL) and 25 kg (Rivas and Corey, 2008); these authors suggested that free-ranging anacondas may require more than a decade to reach 3.7 m (3.2 m SVL).

Growth rates can be high in captivity. A captive female grew from 1.42 m and 1.35 kg to 3.2 m and 25.5 kg in just under four years (about 38 mm/mo: Holmstrom, 1980), while a 0.60-m hatchling reached 2.05 m in 21 months (69 mm/mo), with mass increasing by roughly 30-fold from 160 g to 5000 g. Three captives held at a constant temperature of 26°C grew from an average of 183 g and 0.717 m to 4.01 kg and 1.87 m over a period of 445 days, during which time they exhibited about 78.8 mm/mo growth (66.5 mm/mo SVL) and an assimilation efficiency of 42.5 percent of the prey mass consumed (Lamonica and others, 2007). Growth rates of 17-25 mm/mo can be sustained for up to a decade after a captive individual reaches 3 m total length (Bisplinghoff and Belloso, 2007), a number which may also be reasonable for some free-ranging snakes when compared to the results of Rivas (1999), above.

The herpetoculture literature often discusses the slower growth rate of anacondas as compared to other giant snakes such as Reticulated Pythons; for example, Bisplinghoff and Belloso (2007) stated that it takes 8-15 years for a captive Green Anaconda to reach 5 m total length, but only 5-8 years for *B. reticulatus* or *P. molurus* to reach this length. If this difference in growth rate is real, it may perhaps be ascribed to the greater mass per unit length of anacondas, necessitating significant energetic investment in production of somatic tissue without appreciably increasing body length.

4.5 Maturation

In the Venezuelan llanos, the smallest females observed participating in breeding aggregation were 2.42 m and 9.25 kgs (Rivas and others, 2007a; length and mass were not reported by individual, so these numbers may or may not represent the same individual). Equivalent numbers for males were 1.88 m and 2.45 kg. Most other reported sizes at maturation for free-living Green Anacondas appear to be crude estimates. Waller and others (1995) stated that individuals typically mature at about 3.2 m after 4-6 years, while Pizzatto and Marques (2007) inferred maturity at 3.45 m (2.97 m SVL) in females (n = 6) and 1.54 m (1.33 m SVL) in males (n = 35); the latter appears to be an outlier for male reproductive size, as most authors state that males mature at body sizes larger than this.

Holmstrom (1982) reported that a captive female Green Anaconda (3.63 m, 25 kg post-partum mass) fed ad libitum reproduced at the age of three years and ten months, and this interval has been repeated elsewhere in the literature (for example, Ross and Marzec, 1990). This is the fastest time to maturity reported for the species, and is notable primarily because many of the other giant constrictors can reach maturity in a much shorter time, especially in captivity (see biological profiles for *P. molurus* and *B. reticulatus*). In contrast, more typical ages at maturity among captives were reported by the same author, who estimated sexual maturity for three females at 6 or 7 years of age and a male at 5 years (Holmstrom, 1982).

4.6 Longevity

There are no data to document longevity of Green Anacondas in the wild (Rivas, 1999) except for a single record of an adult female captured in 1994 and recaptured thirteen years later (Rivas and Corey, 2008). A wild-caught individual lived 28 years in captivity under zoo conditions (Snider and Bowler, 1992), and Waller and others (1995) stated that longevity can be at least 32 years; this record may be based on Stemmler (1963, cited by Strimple, 1993). Dirksen (2007) reported a captive that lived about 33.5 years, based on a personal communication with the snake's owner.

5.0 Diet/Trophic Role

5.1 Prey

Most reviews of the diet of the Green Anaconda indicate that the species is euryphagic (Beebe, 1946; Henderson and others, 1995; Murphy and Henderson, 1997; Martins and Oliveira, 1998). As examples, Strimple (1993) summarized the literature by stating that the species eats “fish, amphibians, reptiles (including turtles and caimans), birds, and mammals such as agoutis, pacas, peccaries, capybaras, tapirs, and deer,” and prey records on Trinidad included caiman, dogs, deer, tamandua, turtle, sheep, and “...rodents and almost any animal which comes down to drink of the water in which it is lying” (Mole 1924). Large prey items have included birds such as Jabirú (*Jabiru mycteria*) and mammals as large as tapirs (*Tapirus terrestris*), White-lipped Peccary (*Tayassu pecari*), a young zebu (*Bos primigenius*) and deer (*Odocoileus* and *Mazama* sp.: Martins and Oliveira, 1998 and references therein; Starace, 1998; Valderrama and

Thorbjarnarson, 2001; Rivas, 2004). The Green Anaconda can certainly be considered a top predator in South American ecosystems.

A partial analysis of dietary data from over 100 Green Anacondas in Venezuela yielded 63 individuals of 27 prey species, most of which were represented by only a single record (Rivas, 1999). Seventeen of the 27 species were birds, followed by reptiles (6 spp., including Green Iguana [*Iguana iguana*] and Common Tegu [*Tupinambis teguixin*]), mammals (3 spp.) and fish (1 spp.). Anacondas occasionally killed prey too large to consume, and there were reports and circumstantial evidence of carrion consumption. Small anacondas appeared to consume primarily birds, and as they matured underwent an ontogenetic prey shift to large mammals and reptiles (Rivas, 1999; Rivas and others, 2007a). Somewhat surprisingly, Savannah Side-Necked Turtles (*Podocnemis vogli*) were the most abundant (n = 10) among observed prey in the Rivas (1999) sample, followed by Northern Jacanas (*Jacana jacana*; n = 7), Spectacled Caiman (*Caiman crocodilus*; n = 5, with additional information on caiman predation in Rivas and others, 1999), Capybara (*Hydrochaeris hydrochaeris*; n = 5), whistling ducks (*Dendrocygna* sp.; n = 5) and White-tailed Deer (*Odocoileus virginianus*, n = 5). The large number of turtles observed may have been partially due to the ease of identifying osseous turtle remains in the voided contents of anaconda digestive tracts.

The wide range of prey consumed by Green Anacondas in Venezuela is largely mirrored by diet records for other parts of the range, to which can be added Moustached Tamarin (*Saguinus mystax*: Greene, 1997), Neotropical Mud Turtles (*Kinosternon scorpioides*: Boos, 2001), jungle runner lizards (*Kentropyx* sp.: Martins and Oliveira, 1998), domestic pigs (*Sus scrofa*: Macedo-Bernarde, 2006), Lesser Anteaters (*Tamandua tetradactyla*: Valderrama and Thorbjarnarson, 2001), a large dog (Neill and Allen, 1956), a Boa Constrictor (*Boa constrictor*: De Freitas, 2009), a Brown-Banded Watersnake (*Helicops angulatus*; Infante-Rivero and others, 2008) and occasionally conspecifics (Rivas and Owens, 2000). Despite the assertion by Ditmars (1912) that *E. murinus* does not eat fish, 27 fish, including sharp-spined catfish and armored catfish, were taken from the stomachs of three anacondas in Venezuela and Guyana (Beebe, 1946). Indeed, the regular inclusion of fish in the diet of the anacondas (including other members of the genus *Eunectes*) increases their dietary niche breadth in relation to the other giant constrictors, which very rarely consume fish.

5.2 Predators

Green Anacondas likely occasionally fall prey to a variety of predators, including felid, canid, procyonid, and mustelid mammals, birds including raptors and herons, and reptiles such as crocodylians and some large ophiophagous snakes. However, few such predation events are documented, and juvenile anacondas likely suffer most such predation. A Crab-Eating Fox (*Cerdocyon thous*) harassed a 1.87-m female Green Anaconda on dry land (Rivas and others, 2001), and the authors surmised that the fox would have eventually killed the snake had the authors not intervened. Two more radiotelemetered juveniles in this study may have fallen victim to a Common Tegu (*Tupinambis teguixin*) and a Crested Caracara (*Polyborus plancus*: Rivas and others, 2001). Caimans were implicated in the deaths of at least a dozen Green Anacondas during a seven year study in Venezuela, with male snakes at particularly high risk of predation (Rivas, 1999; Rivas and others, 1999), but it was difficult to assign the

predatory role to the players in some of these incidents, as a caiman may represent either predator or prey to an anaconda. The same author recorded numerous severe wounds on anacondas inflicted by prey species such as Capybara, and females were observed to have a higher injury rate than did males (Calle and others, 1994; Rivas and others, 2007a). Large female Green Anacondas occasionally cannibalize smaller males (Rivas and Owens, 2000), but this is unlikely to be of demographic significance unless predation on males occurs regularly (as is the case among some crocodylians, for example, Rootes and Chabreck, 1993).

All members of the genus *Eunectes* appear to adopt a balling posture when attacked or when harassed by humans (Mole and Urich, 1894; Dirksen and others, 1998). This posture protects the head, which is held in the center of the ball. Anacondas may also burrow into mud to escape predators, including humans attempting to capture the snake (Strimple and Dirksen, 2001).

5.3 Diseases and Parasites

As with most of the giant constrictors, the range and impacts of pathogens and parasites of the Green Anaconda are known primarily from captive individuals (for example, McNamara and others, 1994; Miller and others, 2004). However, results of a health assessment of 24 wild Green Anacondas in Venezuela (Calle and others, 1994) provided more information for this population than is available for most giant constrictors. Observed parasites included ticks (*Amblyomma dissimile*; 6 individuals; note also that *A. fulvum* was described from a *E. murinus*: Keirans, 1972), tapeworms (*Crepidobothrium* sp.), subcutaneous nematodes (*Dracunculus* sp.), an unidentified trematode, and an intraerythrocytic protozoan (*Hemoproteus* sp.; all individuals). Cestodes and trematodes were abundant in two dissected individuals (Calle and others, 1994), but Rivas (1999) noted that many individuals with known endoparasite loads survived and reproduced for years after the parasites were initially detected. A follow-up study revealed low or undetectable serum levels of antibodies for a variety of diseases including paramyxovirus, *Leptospira*, and *Cryptosporidium* among ten anacondas from the same site (Calle and others, 2001).

An apparent respiratory infection was observed in a free-ranging Green Anaconda in Venezuela, and another individual may have succumbed to lymphatic cancer (Rivas, 1999; Rivas and others, 2007a), but no similar maladies were observed among the rest of nearly 800 animals examined during this study.

6.0 Demography

6.1 Population Density

Rivas (1999) reported capturing 780 Green Anacondas during a seven year study in the Venezuelan llanos, which is by far the largest sample size reported for any scientific study of the species. Sample sizes increased during dry years, reflecting the fact that snakes were concentrated in smaller areas, and additional detection biases were noted for juveniles and females. One of the Rivas' study sites yielded 550 snakes from about 1500 ha, for a density of 0.37 individuals/ha, but the low rate of recaptures at this site led him to believe that only about a third of resident snakes were captured. If correct,

densities may have approached 1/ha. At a micro-scale, densities can be very high when suitable habitat is limiting, exemplified by 34 anacondas found in a 200 m² pool after surrounding areas had dried (Rivas, 1999).

In the Iquitos region of Peru, the Green Anaconda was considered "...common in and around flooded forests, large and small streams, and bodies of water where aquatic vegetation is dense" (Dixon and Soini, 1986). In contrast, only one individual, found dead in a fishing net strung across a river, was recorded by Duellman (2005) during intensive studies at Cusco Amazónico in southeast Peru. However, little time was spent sampling riverine habitats or large snakes during this study and thus abundance was likely underestimated.

6.2 Size Distribution

Sample sizes are insufficient to produce reliable size distributions for most published reports on populations of the Green Anaconda, with the sole exception of the long-term studies of Rivas and colleagues in the llanos of Venezuela (for example, Rivas, 1999). In Rivas' study, the male size distribution was leptokurtotic (exceptionally peaked), with a strong peak at about 2.7 m (2.3 m SVL) and a maximum of about 4.1 m (3.5 m SVL). In contrast, the female size distribution was largely platykurtotic (exceptionally flat), with a weak peak around 3.1 m (2.7 m SVL) but numerous individuals in the 3.36-4.52 m (2.9- 3.9 m SVL) size classes and a maximum of nearly 5.8 m (5 m SVL). However, even this distribution is biased by detectability issues, as small anacondas were very difficult to detect using any method and radiotelemetry results revealed differences in individual detection rates by size, sex, and season (Rivas, 1999).

Although Rivas (1999) did not provide a histogram of body mass, a regression of mass on length for 660 snakes (his p. 55) provided some insight on mass distribution. The majority of captured snakes were less than 20 kg, but about 60 individuals (roughly 9 percent) were between 20 and 40 kg, about 35 (roughly 5 percent of sample) were between 40 and 60 kg, about 12 (roughly 1.8 percent) were between 60 and 80 kg, and about 3 were between 80 and 100 kg. These results are suggestive of the notion that females with very large body masses are a predictable component of natural Green Anaconda populations, rather than representing extremely uncommon giants.

7.0 Interactions with Humans

7.1 Human Utilization and Persecution

Populations of the Green Anaconda have been impacted by the leather and live animal trade in some areas (Strimple, 1993), but this conclusion does not appear to be supported by any rigorous population estimates. Green Anacondas are occasionally consumed by humans (Gasc and Rodriguez, 1980, cited in Strimple, 1993; Rivas, 1999). Anaconda fat may be used in traditional medicine, but demand in Venezuela is low (Rivas, 1999).

Anaconda skins were formerly exported in significant numbers from South America (ranging between 4,781 and 21,936 per year from 1980-1987), but this trade has effectively ceased since the species was listed by CITES (a maximum of 2,030 skins in 1989 and only two in the period 1994-1997; Dirksen, 2002; Dirksen and Böhme, 2005).

One of us (RNR, pers. obs.) observed no curios made from anaconda skins during visits to marketplaces in Manaus, Brazil in 2003 and 2008, although these markets included a wide variety of curios incorporating skins of *Boa constrictor*. Over 2,000 Green Anaconda skins were confiscated in Venezuela in 1988 and 1990 combined; continued trade in skins was suspected but its extent was unknown (Rivas, 1999). Dixon and Soini (1986) stated that “live anacondas and raw skins were shipped in considerable numbers from Iquitos to animal dealers and tanneries around the world” prior to their study, which occurred before the CITES listing.

In Trinidad, young anacondas are occasionally caught on fishing hooks baited with whole fish (Boos, 2001), and large individuals were recorded as by catch in fishing nets in Brazil and Peru (Martins and Oliveira, 1998; Duellman, 2005).

7.2 Human Health Risks

Although some authors state that several humans have been attacked or killed by anacondas (especially after provoking the snake: Lancini, 1986; Goulding, 1990), there are no well-documented fatal attacks by Green Anacondas on humans (Murphy and Henderson, 1997; Rivas, 1998). Mole (1924) cited a personal communication from a S.M. Klages, who said that he saw a young man in Venezuela killed by an anaconda that he had placed on his shoulders; this would not be considered a “legitimate” attack, as it involves a manipulated animal. Boos (2001) reported several incidents, some of which were anecdotal, in which anacondas attacked or attempted to attack humans. Rivas (1998) reported two apparently unprovoked attempted attacks on humans by Green Anacondas in Venezuela during the course of fieldwork on the snakes. The snakes were 5.04 m total length and 54 kg and 4.45 m and 39 kg respectively, and the ratio of attempted human prey mass to snake mass was about 1.0 for the first attack and 1.46 for the second. Rivas (1998) concluded, “The potential exists for anacondas to prey on people.”

7.3 Human Aesthetic Relations

7.3.1 Pet Trade

The Green Anaconda is relatively uncommon in the pet trade as compared to some of the pythons (*P. molurus*, *B. reticulatus*) or *Boa constrictor*. From 1989 through 2000, about 1,400 live Green Anacondas were imported to the United States, an average rate of approximately 125/year (Reed, 2005). However, the import rate picked up in the 2000s, and examination of CITES documentation revealed a longer-term average of 427 per year (range 0-1,413). This average is about 10 percent of the average rate at which Reticulated Pythons are imported, and is an even smaller fraction of the annual trade in *Boa Constrictor* and *Burmese Python*. The major exporting countries are Guyana and Suriname, which together accounted for 98.6 percent of live exports during 1980-1997 (Dirksen, 2002).

According to Bisplinghoff and Bellosa (2007), most Green Anacondas offered for sale in Germany are exports from Guyana or Peru (the latter seems dubious based on CITES records), and captive breeding is relatively uncommon compared to many other giant constrictors. However, only a single live specimen was legally imported to

Germany between 1980 and 1997 according to CITES documents, and most imports are smuggled from eastern Europe and are of largely unknown geographic origins (L. Dirksen, pers. commun., 2009). Wild-caught and captive-bred juveniles in the United States typically sold for \$150-225 in 2008, based on our review of online dealers. The relatively low popularity of anacondas as pets may be attributed to the necessity of providing enough water for the immersion of a large animal, combined with perceived predilections towards skin infections and unpredictable defensive behaviors including biting and exuding a vile-smelling musk.

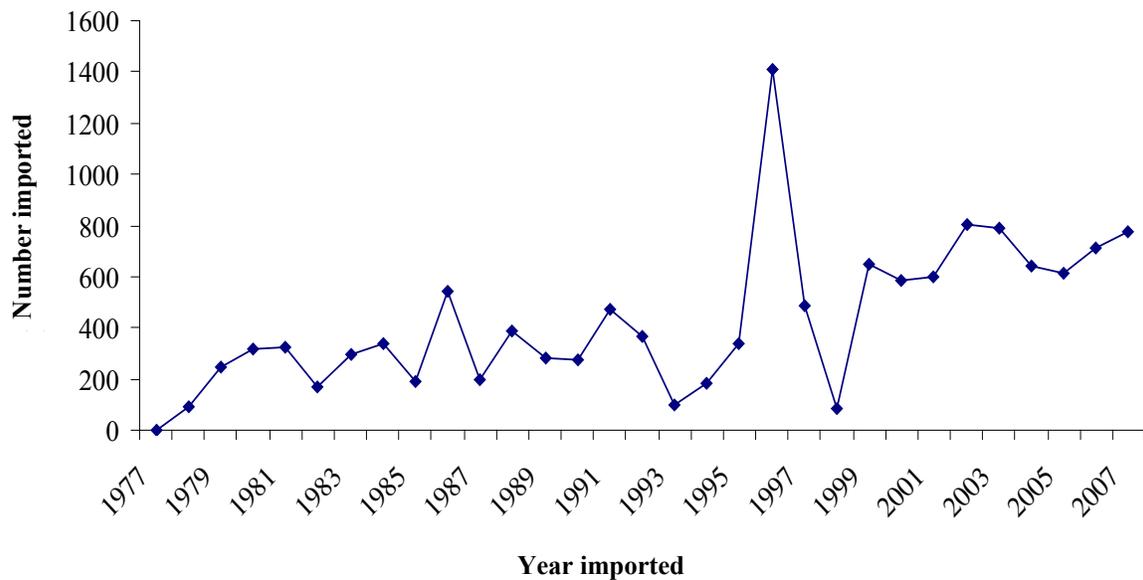


Figure 9.4. Annual imports of Green Anacondas, *Eunectes murinus*, to the United States during the period 1977-2007. Data from CITES.

7.3.2 Other Uses

Major human uses of Green Anacondas appear to be limited to meat, skins, medicinals, and the live animal trade.

Management Profile

See the introduction to the management profile for Indian Pythons (chapter Four) for an explanation of the format of this section of the risk assessment.

8.0 Pathway Factors: Pet Trade

8.1 Volume of International Trade

The number of Green Anacondas entering the United States represents a relatively low volume (an average of 427 individuals per year) as compared to species such as Boa Constrictor and Indian Python, and is somewhat lower than the import rate of the giant African pythons. However, the annual rate of imports in recent years has not exhibited drastic interannual swings as observed for some other taxa (for example, Yellow Anacondas), and the mean rate of imports over the last decade has increased as compared to the previous decade. Exporting countries are essentially limited to Suriname and Guyana; if these countries halt exports or other countries initiate exports, the numbers of individuals entering the United States could change dramatically. Section 8.1 of chapter Four outlines some reasons why imports may constitute higher risk as an invasive species than captive-reared individuals.

Imports spiked in 1997 as compared to levels in preceding or ensuing years. It is likely that this spike was related to the 1997 release of the horror movie *Anaconda*, in which larger-than-life anthropophagous anacondas consumed a variety of B-list movie stars. If the apparent relationship between the movie and import rates is more than a remarkable coincidence, such a spike implies that demand, not availability, drives the import rate of anacondas, and that suppliers can obtain more snakes from wild populations even within a short time period.

The Beni or Bolivian Anaconda (*E. beniensis*) does not appear to be represented in international trade.

8.2 Volume of Domestic Trade

We are unaware of any credible estimates of the volume of domestic sales or captive propagation of the Green Anaconda. Informal surveys of online and storefront reptile dealers lead us to suspect that Green Anacondas are infrequently bred in captivity in the United States and that annual domestic production may be less than the average number of individuals imported per year, but we have no means of verifying this suspicion.

9.0 Entry Potential (Survival in Transit—Meant Mainly for Unintentional Transport)

As with most species assessed in this document, survival of Green Anacondas in international transport is likely to be very high, as animals are packed and shipped via means designed to ensure their survival. While mortality rates of some reptiles have historically been very high during international transport (Christy, 2008), large hardy

species of snakes would appear to be among the taxa most likely to survive the travails of international transport. Once in the United States and purchased by an endpoint consumer, the anaconda is likely to be housed in conditions that are designed to meet its needs. Survival in captivity is likely to be high except for snakes possessed by extremely negligent owners.

10.0 Colonization Potential

10.1 Likelihood of Escape/Release

See section 10.1 of chapter Four for factors that might increase the rate at which captive snakes escape or are released; the same factors are likely to apply to Green Anacondas. The massive build of adult Green Anacondas increases requirements for caging size and strength, even above that required for pythons of the same body length, and this species regularly reaches body sizes that many owners would consider difficult to manage. As with Yellow Anacondas, the necessity of providing water in which to submerge complicates the captive husbandry of the Green Anaconda; snakes can develop fungal or bacterial infections if the water is not cleaned regularly, and large Green Anacondas require bathtub- or larger-sized basins. Both chronic illness and expensive/complex caging requirements may increase the odds of a captive being released.

10.2 Climate Match: Areas of the Country at Greatest Risk

Much of peninsular Florida (roughly south of Gainesville) and extreme south Texas exhibit climatic conditions similar to those experienced by Green Anacondas somewhere in their large South American native range. Lower elevations in Hawaii and all of Puerto Rico have apparently suitable climates, but the rest of the country appears to be too cool and/or too arid. Within the climate-matched area, however, anacondas would not be at risk of establishment in sites lacking surface water. Conversely, the areas of the American Southwest that are deemed “too hot” by our algorithm could conceivably represent suitable climatic conditions if aquatic habitats with cooler water conditions are available as thermal refugia. However, such habitats are few and far between in much of this region. Climate suitability is just one factor in the establishment of an invasive species—a necessary but not sufficient condition. As regards climate tolerance in southern Florida, Lutz Dirksen told us, “There is no environmental reason why anacondas could not survive in the Everglades” (L. Dirksen, pers. commun., 2009).

The Beni Anaconda is known from few specimens in a small part of Bolivia, and we judged the number of available localities to be insufficient for an attempt to delineate its climate space or extrapolate this space to the United States. Beni Anacondas are known from sites with fairly low seasonality (mean monthly temperatures approximately 22.5°C-27.5°C, mean monthly precipitation about 50-300 mm; see Fig. 9.3 for an idea of the small size of this climate space as compared to that of *E. murinus*) and as such very little of the continental United States would appear to be climatically suitable (although insular states and territories may be at some risk). However, it is unknown whether the species’ native distribution is limited by factors other than climate; if the small native range is attributable to ecological (for example, competition with *E. murinus*), or

historical (for example, climate change) factors, then our subjective estimate of the climatically suitable areas of the United States would represent underprediction.

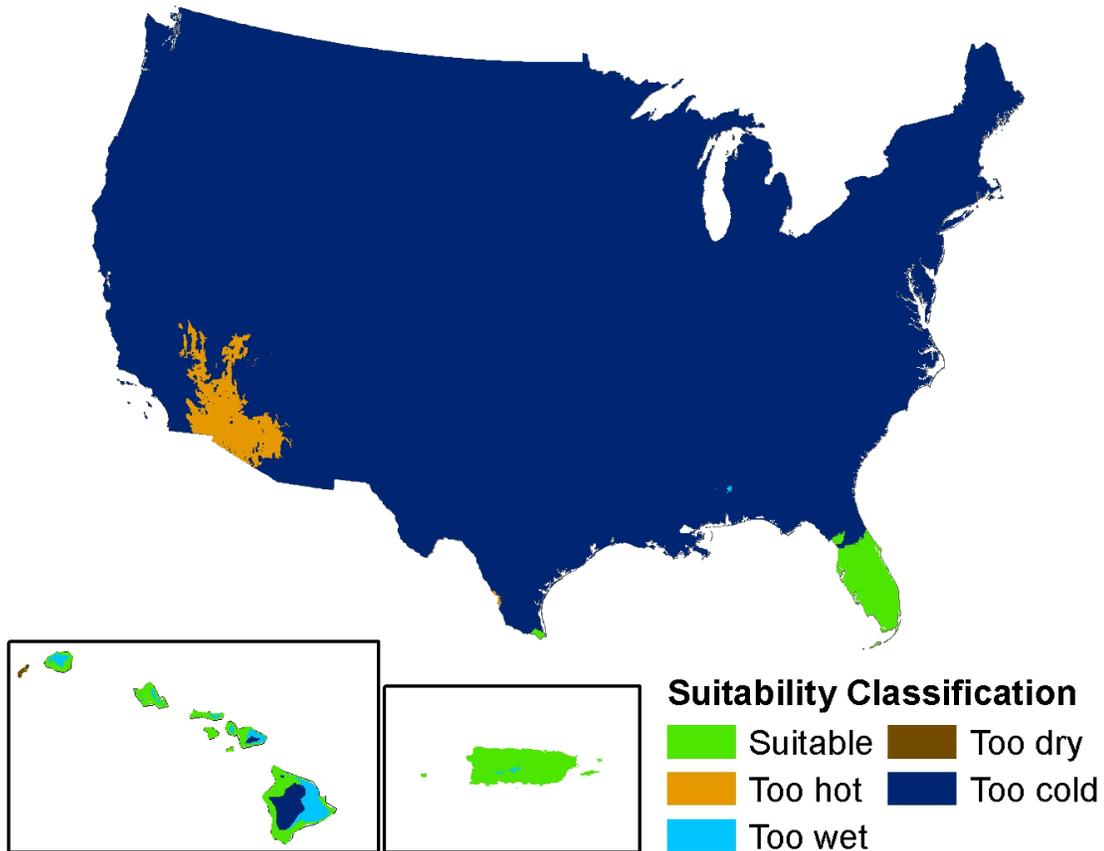


Figure 9.5. Areas of the United States matching the climate envelope expressed by *E. murinus* in its native range (Fig. 9.3), based on 77 known localities. See chapter Two for details of analytical method.

10.3 Prey Availability

Green Anacondas are highly euryphagic, and consume endotherms and ectotherms from a wide variety of higher taxa, including large prey such as deer and crocodilians. The regular inclusion of fish, turtles, and other aquatic organisms in their diet increases their range of prey even beyond that of Reticulated or Indian Pythons. Organisms that regularly come in contact with aquatic habitats are likely to be most commonly consumed by Green Anacondas, but this does not appreciably truncate their available range of prey. The mainland sites above would not appear to have any shortage of prey for Green Anacondas of a variety of body sizes, although in insular situations (Hawaii, etc.) adults may be limited by low availability of large-bodied prey.

10.4 Predation Risk

There are no predators in the United States that are likely to specialize in consuming Green Anacondas. Aquatic and semi-aquatic predators would be the most likely to consume Green Anacondas, but very large adults would be virtually invulnerable to attack by all native predators except in unusual situations (for example, animals stranded away from water that could be tired out by harassment), with the exception of very large alligators. Avian predators might also consume some juveniles, although submerged anacondas would be nearly invisible to visual predators except when snakes are basking above the waterline or when swimming near predatory wading birds (herons, etc.) or raptors.

Any losses to native predators would probably be balanced by intraguild predation (for example, alligators eat anacondas, but the converse also happens), as discussed in section 10.4 of chapters Four and Six. The odds of terrestrial predators foraging in Green Anaconda habitat is probably low, but these same predators might be vulnerable to attack by anacondas when they traverse or otherwise need to use aquatic habitats; all in all the rate of predation *on* Green Anacondas would probably be outweighed by predation on native predators *by* Green Anacondas.

10.5 Reproduction Requirements

There appear to be no specialized reproductive requirements among Green Anacondas, which are live-bearing snakes. Bearing live young allows pregnant females to use behavioral thermoregulation (for example, basking and shuttling between habitats with different temperatures) in order to maintain relatively high and constant body temperatures during embryonic development. Live-bearing anacondas may thus be able to successfully reproduce in cooler climates as compared to egg-laying giant constrictors with similar temperature requirements for embryonic development (excluding those species that employ shivering thermogenesis).

10.6 Hibernation Requirements

So far as is known, the Green Anaconda does not escape cold temperatures by hibernating anywhere in its range. Individuals may seek out isolated mudholes during the dry season in seasonally flooded habitats, and long-term use of such refugia may approach a physiological/behavioral state that could be considered aestivation.

10.7 Tools for Eradicating a Colonization

Tools for eradicating a population of Green Anacondas are likely to be similar to those described in chapter Three and section 10.7 of chapter Four, but no tools have been developed specifically for highly aquatic snakes such as anacondas. Because Green Anacondas spend much of their time submerged, visual searching is unlikely to be very effective for eradicating an introduced population unless most individuals need to bask above the waterline in cooler months and all individuals are accessible to human searchers. Meeting both of these requirements seems unlikely.

11.0 Spread Potential

11.1 Dispersal Ability

Nothing is known of the dispersal rates of Green Anacondas in their native range, but it is likely that individuals could move efficiently through aquatic habitats. Green Anacondas are unlikely to engage in long-distance dispersal through entirely terrestrial habitats. This could potentially retard their rate of spread if introduced to the United States, especially in areas with widely-spaced bodies of water. Unfortunately, much of the potentially colonizable area (section 10.2) in the Southeast United States is characterized by numerous riverine, lacustrine, and/or seasonally flooded habitat. Green Anacondas exhibit large litter sizes; although these do not attain the maximal clutch sizes of some pythons, viviparity may allow high embryo survival as compared to oviparous snakes.

11.2 Ability to Develop Races or Strains

There are no native species in the United States with which the Green Anaconda would be capable of interbreeding, negating the risk of developing new races or strains by that route. However, Yellow and Green Anacondas appear capable of interbreeding, although the frequency and fertility of hybridization events is largely unknown and hybrids have not been observed in the native range to our knowledge. If hybrids are fertile and exhibit characteristics of both species (for example, cold tolerance of Yellow Anacondas but increased size from Green Anaconda genetic contributions), the resulting hybrid might represent higher risk as an introduced species. However, we judge such a scenario to be fairly unlikely.

11.3 Tools for Managing Spread

As with the other giant constrictors (see chapter Four, section 11.3), we judge existing control tools to be inadequate for the eradication of large, established populations of Green Anacondas. In the absence of proven control tools, an effective interdiction program might hold the most promise for preventing establishment (for example, Vice and Pitzler, 2002), combined with a well-organized rapid response capacity to respond to sightings of colonizers (Stanford and Rodda, 2007). Because interstate transport of anacondas and other giant constrictors is poorly monitored, interdiction within the continental United States would be difficult.

12.0 Economic Impact Potential

The Fish and Wildlife Service has not decided whether a formal economic analysis of the potential impacts of introduction of, and regulation of trade in, the anacondas will be separately conducted pursuant to a variety of statutes and Executive Order 13272 (Proper consideration of impact on small business). Our narrative below is provided only to cite relevant biological literature and identify germane sections of the biological profiles.

12.1 Pathogen Vector

An amazing knowledge gap exists with regard to the ability of Green Anacondas to vector pathogens to native or domestic animals in the United States. A single health assessment of a few individuals in Venezuela (Calle and others, 1994, 2001) found Green Anacondas to harbor a number of internal parasites of unknown medical or veterinary importance, but failed to find antibodies to a limited range of diseases. Ticks known or suspected to act as pathogen vectors (see chapter Six, sections 5.3 and 12.1) which were observed using other giant constrictors as hosts could almost certainly infest Green Anacondas as well. While the highly aquatic habits of anacondas may reduce their susceptibility to external air-breathing parasites, at least two species of *Amblyomma* ticks are known to use Green Anacondas as hosts in their native range, as are species of ticks commonly found on cattle (J. Rivas, pers. commun., 2009).

12.2 Predator on Livestock

Green Anacondas are capable of preying on most species of domestic livestock, although reports of predation on cattle and horses are rare and often dubious. Domestic waterfowl and other livestock kept near water would appear to be at highest risk of attack from Green Anacondas. The tendency of adult anacondas to ambush large prey from water means that livestock victims may be quickly submerged and drowned without attracting the attention of human owners, thereby reducing the odds of rescue before the animal succumbs. Alligator and turtle farming might be somewhat impacted by established populations of Green Anacondas, but we would expect losses to be minimal to moderate.

12.3 Predator on Pets

Green Anacondas are certainly capable of successfully consuming nearly all species of companion animals, and have eaten dogs in their native range. As with the Yellow Anacondas, however, Green Anacondas would be most likely to attack companion animals in close proximity to aquatic habitats. Well-publicized attacks on companion animals would result in public concern that would almost certainly be out of proportion to the actual threat posed to such animals.

12.4 Electrical Power Systems

Heavy-bodied adult anacondas are unlikely to climb high enough to impact electrical delivery systems, although a single 5 m long individual was observed 5 m up in a tree and attempted to climb higher when disturbed (De Freitas, 2009). Juveniles may occasionally climb (for example, several juveniles were observed in trees over water on Trinidad; R. Rozar, pers. commun., 2009), but this habit appears to be less common among Green Anacondas than among many giant constrictors, even as compared to Yellow Anacondas.

12.5 Traffic Accidents/Human Attacks

Legitimate attacks on humans in the native range of Green Anacondas are incredibly rare, and poor documentation of such attacks makes their likelihood difficult to

assess. A constricting aquatic predator of this size could conceivably overpower and drown an adult human without much associated noise or commotion, so it is possible that persons disappearing in the native range could be victims of anacondas without their disappearances being linked to this species. Compared to species with a better-documented history of attacks on humans (for example, Reticulated Pythons), the Green Anaconda appears to be a relatively low risk as an attempted predator on humans.

Green Anacondas can attain huge sizes and girths greater than other constrictors of the same body length. They may therefore pose a slightly higher risk of causing auto accidents, should a fast-moving automobile strike a large anaconda on a road.

12.6 Tourism

As discussed above, Green Anacondas are fairly unlikely to attack humans. Perhaps more than any other species of giant constrictor, however, the Green Anaconda likely has the worst perception as a marauding terror among the general public, and “anaconda” is the common name most likely to evoke images of mammoth snakes. This misconception has been reinforced in recent years by a series of horror movies portraying gigantic (over 20 m) anacondas consuming entire boatloads of innocent and not-so-innocent humans. Establishment of Green Anacondas in the continental United States would likely have an overall negative impact on tourism, as the small proportion of the public who would be likely to visit an area to see anacondas would be far outnumbered by the ophiophobic majority who assume that their families would be in extreme danger from anacondas.

12.7 Impacts on Commercially Important Wildlife

12.7.1 Species Hunted with Gun or Binoculars

Upland game species such as deer, feral hogs, turkeys, etc. would be expected to largely escape predation by Green Anacondas. However, even upland species occasionally use aquatic habitats, and Green Anacondas would represent a novel large-bodied predator of native game species. In the Southeast, such species would presumably be somewhat adapted to the presence of alligators, another large aquatic predator that often attacks from submerged ambush positions; if so, then Green Anacondas might not represent a completely novel class of predators.

Waterfowl are the birds most likely to be jeopardized by established populations of Green Anacondas, as discussed for Yellow Anacondas in chapter Eight, section 12.7.1. Wading birds are a mainstay of birdwatching in Florida, and Green Anacondas could potentially hasten population declines of species that are already of conservation concern, such as Wood Storks. Duck hunting is an economically important activity in some parts of the Southeast; Green Anacondas commonly take anseriform birds in their native range, and would no doubt do so in the United States, but it is difficult to predict the demographic significance of this predation on huntable wildlife.

12.7.2 Species that Impact Forestry, Agriculture, or Horticulture

Green Anacondas would be unlikely to have drastic impacts on these industries, although safety considerations associated with the presence of giant introduced snakes

might affect costs for business owners (see chapter Six, section 12.7.2), especially those overseeing work in aquatic habitats.

13.0 Environmental Impact Potential

13.1 Species of Special Concern as Prey or Competitors

We consider all of the species of special conservation concern in Florida that are potential prey of Burmese Pythons (chapter Four, Table 4.2) to also be potential prey for Green Anacondas. Truly giant anacondas might be capable of eating even larger prey, but extremely large individuals would likely be uncommon in introduced populations.

13.2 Species of Special Concern as Predators (Giant Constrictors Augment Food Supply)

As discussed in this section in previous chapters, a range of native predators would be capable of consuming Green Anacondas of varying sizes. Alligators are the most obvious of these, although panthers might take some adults and a variety of smaller predators could consume juveniles. However, such benefits to predators are likely to be balanced or outweighed by intraguild predation and/or overall energetic losses associated with eating prey that are themselves high on the food chain (see chapter Six, section 10.4). There is no evidence to suggest that any native predator would experience a net demographic benefit from the presence of Green Anacondas.

13.3 Vector for Disease Spread to or Within Native Faunas

Insufficient data are available to evaluate the likelihood of transmission of pathogens or parasites to native faunas. The sole survey for infectious diseases in the species examined a sample of Green Anacondas from Venezuela and failed to find antibodies to any of a range of pathogens. Green Anacondas are likely to be suitable hosts for some of the same ectoparasites known from other taxa (for example, the giant African pythons) and which are known or suspected to be carriers of zoonotic disease. However, Green Anacondas might be less suitable hosts for such ectoparasites, as anacondas spend much of their time submerged.

13.4 Species that Might be Adversely Affected by Control Measures

Control measures for Green Anacondas would likely be similar to those envisioned for giant constrictors in general (see chapter Three). Some possible avenues of control, such as acetaminophen toxicants, are likely to result in non-target mortality to native species, especially large snakes capable of accessing toxicant delivery devices designed for giant constrictors. Traps, drift fences, and other potential tools may also impede movements of non-target native taxa or result in their inadvertent capture. Control measures for Green Anacondas would largely be deployed in or adjacent to aquatic habitats, implying that species using such habitats are at highest risk of being adversely affected by control measures. Depending on geography, these species might include alligators, American crocodiles, aquatic snakes, river otters, etc. As no

management tools have been field-tested, however, it is not possible to estimate potential ecological costs.

14.0 Perceived Impact (Social and Political Influences)

14.1 Pet Industry

14.1.1 Domestic Production Affected?

Domestic production of Green Anacondas by herpetoculturists is relatively miniscule as compared to some of the other large constrictors. Based on our examination of online dealers, stock available at reptile shows, and the herpetocultural literature, we estimate that domestic production is typically less than 250 neonates per year, but we have no means to verify this estimate. Breeding Green Anacondas is largely confined to a few specialty herpetoculturists. Prohibition on interstate transport or sales would disproportionately affect these individuals but would have a small impact on the overall domestic reptile trade.

14.1.2 International Trade/Alternate Pets

In a typical year, fewer than 500 Green Anacondas are imported to the U.S., and most of these originate in northern South America. Trade at this volume would be worth perhaps \$50,000-100,000 annually to importers at the wholesale level, and two to three times that amount at the retail level. While a considerable sum, these estimates pale in comparison to species that are traded in the thousands (for example, Reticulated Pythons) or tens of thousands (for example, Ball Pythons), and represent a tiny fraction of the overall value of the reptile import trade. Were importation regulated, dealers would likely switch to other species to make up for the loss of Green Anacondas in the international trade, rather than experiencing major economic losses.

Chapter Ten–The Risk Assessment

Introduction

The Risk Assessment is in two parts: (1) Four factors evaluating the risk of establishment, and (2) three factors evaluating the consequences of establishment. For each of these seven factors we begin by noting the relevant traits shared by the nine giant constrictor species, and then the traits that differentiate them. Each part concludes with a table summarizing the risk scores and producing an overall component risk score for each species. In turn, these will be combined into a single Organism Risk Potential (ORP) score for each species, presented in a table at the end of the chapter, following the guidance established by the Aquatic Nuisance Species Task Force (ANSTF, 1996).

Risk of Establishment

1. Organism with Pathway

This element establishes the likelihood that the species occurs in the pathway under consideration. As noted in the species accounts, the overwhelmingly dominant pathway for the entry of these giant constrictors into the United States is commercial trade in pets, consistent with the global pattern for reptiles (Kraus, 2009). The amount of commercial pet trade traffic is fairly easily assessed on the international scale, as the international regulatory authority CITES (the Convention on International Trade in Endangered Species) maintains the trade records we reported in each species account (tabulated in Appendix). However, there is a substantial additional but unknown amount of domestic trade, and a presumably small amount of clandestine trade (both international and domestic).

In aggregate, there is a very large trade in giant constrictors, with over one million of these snakes imported to the United States in the last 30 years and many of these bred domestically and traded in even larger numbers. Thus, as a group, the nine giant constrictors constitute a high risk relative to those taxa with lower trade volumes. But not all of the nine species are equally represented; about 60 percent of the trade in our focal group consists of *Boa constrictor*. On the basis of the number being traded, and the assumption that the proportion being released is constant from species to species, it would be possible to rank the relative risk of release, but to assign risk categories to each species we need to identify thresholds for distinguishing the high, low, and medium risk categories required. The ANSTF provides minimal guidance on this challenge, presumably because the thresholds vary among taxa (for example, giant constrictor snakes may all be higher than typhlopid [worm] snakes). It is possible that although the risks vary among the giant constrictors, all giant constrictor species would have an absolutely low or high risk.

One of the rarely traded species (fewer than 2000 individuals total over 30 years) is the Yellow Anaconda; is the overall risk low because it is less frequently traded than most of the other giant constrictors? No unequivocal answer is apparent. We can get some indication from the appearance in Florida of multiple reports of Yellow Anacondas in or near the Big Cypress National Preserve. The occurrence of this species in the wild, in a location far from most human sources of this pet suggests that the risk of establishment of this rarely-traded species is substantial. If the risk of Yellow Anaconda “Organism With Pathway” is high (multiple individuals appearing at the same site in the same time period is a strong indication that enough are in the pet trade to constitute a significant pathway risk: Risk High), the species with greater trade volume would presumably be High also (Indian Pythons, Northern African Pythons, Reticulated Pythons, Green Anacondas, and Boa Constrictors). The level of certainty for these five species is Very Certain (certainty codes established by ANSTF, 1996, and reprinted on pp. 10-16).

The remaining species (De Schauensee’s Anaconda, Beni Anaconda, and potentially Southern African Python) have low levels of reported importation, and if these levels are accurate, and past performance is a guarantee of future prospects, the risk of their presence in the pet pathway would be Low. However, past performance is not a guarantee of future prospects, and importation reports for the United States wildlife trade are “notoriously unreliable” (Blundell and Mascia, 2005). In this case, the low levels of reported importation may be low by virtue of similarity of appearance (misreported or misidentified), but also because the closely related taxa of these lesser-known species are readily and inexpensively available in the pet trade. Should the species that currently dominate the trade become less readily available, one would expect a compensatory increase in sales and interest in the related taxa, as has been seen in response to export bans of particular species from several countries in recent decades. This is a question of human behavior, with the attendant high level of uncertainty. By virtue of similarity of appearance these species may warrant a High risk of presence in the pathway, though at present there appears to be only limited commercial traffic in these three species.

2. Entry Potential

This risk element is primarily relevant to unintentional pathways, for which the survival of the species in transit is variable or low. In the case of our nine giant constrictor species, transport is intentional and survival is therefore High, an assessment that is Very Certain.

3. Colonization Potential

Colonization potential depends on a wide range of elements, including propagule pressure (how many of the same species are released in the same area in a short period of time); the probability of release or escape; and the likelihood of the released pets finding suitable food, environmental conditions (for example, climate match: Bomford and others, 2009), lack of competition from similar species, and conditions suitable for reproduction (ANSTF, 1996). For a more comprehensive list of the elements hypothesized to promote the establishment of reptiles and amphibians see Table 3 in Rodda and Tyrrell (2008), which provides references for each of the hypotheses. The hypotheses are grouped into sets relating to the survival and reproduction of released

animals. For example, dietary characteristics primarily affect survival, and number of offspring primarily affects the species' likelihood of successful reproduction.

Survival: Of the eleven hypotheses related to survival, ten apply with roughly equal force to all of the giant constrictors. Of these ten, two suggest that giant constrictors are not likely to establish: (1) Establishment is facilitated for insectivores (none of the giant constrictors are insectivorous), and (2) establishment is promoted for species that actively modify their environment in their favor (for example, digging tortoises). As far as is known, the giant constrictors' requirement for burrows is dependent on other species digging them.

Four additional survival hypotheses are equivocal with regard to giant constrictors, at least with the information available: (1) Establishment is promoted for island/tropical/maritime destinations (equivocal because some American destinations are, and some aren't), (2) establishment is more likely on islands (Kraus, 2009), at least in part because islands have maritime climates, unexploited niches, etc. (equivocal because some American destinations are islands and some are not), (3) establishment of adaptable species is facilitated compared to species that are more fixed in their ways (insufficient information about the behavioral adaptability of the giant constrictors), and (4) establishment of highly heterozygous species is more likely (insufficient information; although some of the giant constrictors are drawn from diverse localities and are therefore likely to have a deep gene pool, other giant constrictor individuals are likely to have been intensely inbred for purposes of obtaining "designer morphs").

The four remaining hypotheses apply similarly to all of the giant constrictors and suggest that giant constrictors are likely to establish: (1) High longevity combined with early maturation leads to a high overlap between generations, with enhanced opportunities for benefitting from peers and finding a suitable mate, (2) empty niches at destinations make it unlikely that native species will outcompete the newcomers, (3) broad diets increase the opportunities for finding suitable prey, and (4) introduced snakes are likely to have very few parasites relative to the overall parasite fauna that afflicts the species in its native distribution, because there is a lack of suitable alternate hosts in the United States for the complete lifecycle of the parasite, and because many snakes are well-maintained and treated for parasites while in captivity prior to release.

The one survival attribute that varies greatly among the giant constrictors is that of climate match. Some species (for example, Indian Python, Yellow Anaconda, Southern African Python, Boa Constrictor) would find suitable habitat over a broad swath of the American landscape, whereas others (Northern African Python, Reticulated Python, Green Anaconda), would likely be limited to the warmer fringes of the continent. The remainder (DeSchauensee's Anaconda, Beni Anaconda) might be able to survive in very small portions of the mainland or on America's tropical islands (Hawaii, Puerto Rico, American Samoa, Guam, Northern Mariana Islands, Virgin Islands). Although these islands are only a small proportion of the United States, they are especially important for biodiversity preservation.

We have summarized this assessment of survival prospects in Table 10.1.

Table 10.1. Hypothesized attributes affecting survival of potential invaders during establishment (from Rodda and Tyrrell, 2008), as applied to giant constrictors. Y = yes; N = No; H = High; M = Medium; L = Low; - = equivocal; ? = insufficient information. Species names are coded by the first two letters of the genus and species name.

Hypothesized attribute	PyMo	BrRe	PySe	PyNa	BoCo	EuNo	EuDe	EuMu	EuBe
Longevity	Y	Y	Y	Y	Y	Y	Y	Y	Y
Climate match	H	M	M	H	H	H	L	M	L
Tropical destination	-	-	-	-	-	-	-	-	-
Island destination	-	-	-	-	-	-	-	-	-
Empty niche	Y	Y	Y	Y	Y	Y	Y	Y	Y
Adaptable	?	?	?	?	?	?	?	?	?
Heterozygous	?	?	?	?	?	?	?	?	?
Insectivorous	N	N	N	N	N	N	N	N	N
Broad diet	Y	Y	Y	Y	Y	Y	Y	Y	Y
Parasites absent	Y	Y	Y	Y	Y	Y	Y	Y	Y
Modify environment	N	N	N	N	N	N	N	N	N

Reproduction: The most obvious attribute influencing reproductive success in an incipient colonization is “propagule pressure” (how many breeders are present). The more individuals of the same species (or a closely-related species that when bred with the focal species produces viable offspring) that are present in an area, the greater the likelihood of successful reproduction (Reaser and others, 2008; Bomford and others, 2009). The commercial trade statistics provide one component of propagule pressure (discussed above); another is the willingness of human owners to discard their pets, or the owners’ abilities to keep the pets from escaping. The more owners that are willing to release or unable to contain, the greater likelihood that two or more releases of the same species will occur in the same area. For most of the giant constrictors, there is a high likelihood of release of unwanted adult giant constrictors, as evidenced by dozens of media reports of individuals found across the country. Market value has some predictive value in this regard, as species that are inexpensive as juveniles are more likely to be dumped as juveniles. Most of these species lose market value as adults, because the demand for large adult giant constrictors of most species is far exceeded by the supply.

Rodda and Tyrrell (2008) enumerated eight reproduction traits that have been hypothesized to influence the establishment success of reptiles and amphibians. These eight are expressed to much the same degree in the giant constrictors under consideration:

Two giant constrictor attributes are potentially associated with reduced probability of establishment: (1) Gregariousness increases the chances of encountering a suitable mate at the season of reproduction (giant constrictors are not ordinarily considered to be gregarious, though they possess highly effective olfactory means of

finding suitable mates when needed), and (2) sexual monomorphism increases effective population size (number of individuals making a genetic contribution to the next generation) compared to species with strong sexual dimorphism or dominance hierarchies (most giant constrictors are sexually dimorphic, but the influence of this on gene transmission is unknown and may not apply at low population densities characteristic of incipient populations). This trait was hypothesized to influence invasive-species colonization primarily with reference to birds, for which monomorphism refers primarily to plumage coloration, and dimorphism connotes male dominance hierarchies (which diminish effective population size). It is not clear that this phenomenon is relevant to giant constrictors, for which sexual size dimorphism is primarily manifest in large female size to promote larger clutches or litters, a consequence that does not diminish effective population size.

Two traits are equivocal with regard to giant constrictors: (1) Ability to shift between *r* and *K* demographic strategies (Pianka, 1970) in response to prevailing conditions (intended mainly for fish that can adaptively alter their mating system; the application of this phenomenon to giant constrictors is uncertain—too little is known about their reproduction to exclude adaptive fecundity modification—but they are not known to switch sexes), and (2) short interclutch intervals expedite population expansion (insufficient information, though giant constrictors achieve the same fecundity increase with large clutch sizes).

Four reproductive traits of giant constrictors appear to facilitate population establishment: (1) Early maturation, (2) parthenogenesis (facultative parthenogenesis is firmly documented in Indian Pythons, suspected in Boa Constrictor and Green Anaconda, possible in the other species: see chapters Four–Nine), (3) sperm storage (probable, as it is present in many snakes but not known with certainty in these species), and (4) high fecundity (variable among these species, but with clutch/litter sizes that are all larger than the average for snakes).

We have summarized this assessment of reproductive attributes in Table 10.2.

Table 10.2. Hypothesized attributes affecting reproduction of potential invaders during establishment (from Rodda and Tyrrell, 2008), as applied to giant constrictors. Symbols as in Table 10.1.

Hypothesized attribute	PyMo	BrRe	PySe	PyNa	BoCo	EuNo	EuDe	EuMu	EuBe
Shift r to K	?	?	?	?	?	?	?	?	?
Early maturation	Y	Y	Y	Y	Y	Y	Y	Y	Y
Parthenogenesis	Y	Y?							
Sperm storage	Y?								
Gregariousness	N	N	N	N	N	N	N	N	N
High fecundity	Y	Y	Y	Y	Y	Y	Y	Y	Y
Short interclutch interval	?	?	?	?	?	?	?	?	?
Sexual monomorphism	N	N	N	N	N	N	N	N	N

4. Spread Potential

To quantify Spread Potential, the ANSTF (1996) guidelines mention: ability for natural dispersal, ability to use human activity for dispersal, ability to readily develop races or strains, and the estimated range of probable spread. Rodda and Tyrrell (2008) expand this list substantially, with specific reference to reptiles and amphibians, and point out that attributes that enable a species to spread aggressively are likely to be similar to traits that increase the success of the bearer at the expense of native wildlife. In other words, these traits correlate with the environmental impact potential (see subsequent section on Environmental Impact Potential). A potential additional complication is that traits that promote the *speed* of spread may be incompatible with the traits that promote the *ability* to spread (equal to environmental impact potential). In classical “r versus K” conceptualization of adaptation, a species that is adapted to rapidly occupy a vacant patch (r selected) may be poorly adapted for the competition inherent in behaviorally dominating resident individuals in an already-occupied patch. Evolutionary ecologists are divided on the relevance of the r versus K conceptualization, but it is notable that if that sort of trade-off has any basis in ecological reality, it may have a manifestation in a trade-off between speed of spread and ability to spread against biotic resistance (Rodda and Tyrrell, 2008).

In relation to the elements enumerated in the ANSTF (1996) guidelines, giant constrictors are probably similar to one another in the ability for natural dispersal (very high), ability to use human activity for dispersal (low as inadvertent stowaways; high if one includes intentional transport via the pet trade), and ability to develop races or strains (unknown, though hybridization between species is known in captivity and new genotypes could be formed by multiple releases of individuals from disparate parts of the native range, see Kolbe and others [2004] for an example). The estimated range of

probable spread differs among species, in keeping with the sizes of the climate-match areas outlined in the previous section (Colonization Potential).

Rodda and Tyrrell (2008) tabulate and describe 23 traits that have been hypothesized to influence spread (rate or success) in reptiles and amphibians. Twelve of these appeared in the two previous tables, and are worth reconsideration only to be reminded that traits that favor colonization may also favor spread: (1) Ability to shift between r and K strategies (insufficient information), (2) adaptability (insufficient information), (3) broad diet (Yes for giant constrictors), (4) heterozygosity (insufficient information), (5) sexual monomorphism (No for giant constrictors), (6) gregariousness (No for giant constrictors), (7) species that modify environment (No for giant constrictors), (8) insectivorous (No for giant constrictors), (9) climate match (varied by species), (10) tropical destination (equivocal: depends on which part of United States under consideration), (11) island destination (equivocal: depends on which part of the United States is under consideration), and (12) empty niches (Yes for giant constrictors).

In addition to the twelve repeated traits, Rodda and Tyrrell (2008) listed eleven novel attributes hypothesized to influence spread potential, of which eight are relatively consistent among the giant constrictor species: (1) Continental native range (Yes for giant constrictors) is thought to imbue the denizens of continents with more competitive ability (relative to island species), (2) disturbed habitat preference is thought to facilitate spread of invaders, probably due to a concurrent tendency to disperse rapidly to discover new habitat patches (insufficient information on giant constrictors), (3) high density in native range (insufficient information on most giant constrictors, but some species are capable of reaching high densities in some habitats), (4) fire-adapted (No for giant constrictors, except insofar as they refuge underground and in water and would survive fires in those refugia), (5) being a lizard (No for giant constrictors), (6) being a predator (Yes for giant constrictors), (7) large adult size (Yes for giant constrictors), and (8) arboreality opens up additional potential prey for predators (all of the giant constrictors are somewhat arboreal in their youth, and become less so as they gain weight).

The three remaining traits differ among the giant constrictors, and are scored in the following table (Table 10.3): (1) Wide latitudinal range of native range is thought to reflect wide ecological tolerances, (2) size of native range is another metric of ecological tolerance, and (3) tolerant of a wide range of climates is a third metric of ecological amplitude.

Table 10.3. Eleven traits not previously mentioned that have been hypothesized to influence spread success in reptiles and amphibians (for source information see Table 5 in Rodda and Tyrrell 2008). Symbols as in Table 10.1. In this case arboreality is expressed primarily in juveniles.

Hypothesized attribute	PyMo	BrRe	PySe	PyNa	BoCo	EuNo	EuDe	EuMu	EuBe
Continental native range	Y	Y	Y	Y	Y	Y	Y	Y	Y
Disturbed habitat preference	?	?	?	?	?	?	?	?	?
High pop density in native range	?	?	?	?	Y	Y	?	?	?
Wide lat. range of native range	H	M	M	H	H	M	L	H	L
Size of native range	H	H	H	H	H	M	L	H	L
Wide climate range	H	M	M	H	H	H	L	H	L
Arboreal	Y	Y	Y	Y	Y	Y	Y	Y	Y
Fire adapted	N	N	N	N	N	N	N	N	N
Lizard	N	N	N	N	N	N	N	N	N
Predator	Y	Y	Y	Y	Y	Y	Y	Y	Y
Large adult size	Y	Y	Y	Y	Y	Y	Y	Y	Y

The overall guidance for the subscore Spread Potential is: “Estimate probability of the organism spreading beyond the colonized area” (ANSTF, 1996). This is relatively straightforward, as all of the giant constrictors most likely have the ability to spread beyond the colonized area if the colonized area is within the area that is climatically suitable. However, the ANSTF (1996) provides additional guidance to consider the estimated range of probable spread. On the one hand it is clear that an invasive species that is limited to a small part of the United States constitutes a lesser risk, all things being equal, than a species that could spread throughout the United States. However, not all things are equal, and some of the most egregious examples of invasive reptiles have been manifest in only a very limited area (albeit with catastrophic impacts in that limited region) (for example, Savidge, 1987; Romero-Najera and others, 2007; Cheke and Hume, 2008). Consideration of the degree of impact is, however, more properly considered in the second part, Consequences of Establishment. Thus, for the purposes of scoring Spread Potential we focused on the overall guidance “Estimate probability of the organism spreading beyond the colonized area” with the implicit proviso that the colonized area was within the area deemed climatically suitable. We presume that a species would be unable to colonize areas that were not climatically suitable, although this is conservative given that many invasive species have expanded beyond the climatic profile of their native range (Williamson, 2006; Randin and others, 2006; Broennimann and others, 2007).

Probability of Organism Establishment

The ANSTF (1996) guidelines establish that the reviewer has considerable latitude in assessing the four factors—(1) organism with pathway, (2) entry potential, (3) colonization potential, and (4) spread potential—making up the probability of establishment, but the product of the four subscores rigidly determines the overall probability of organism establishment. Thus, the guidelines specify, “the probability of establishment is assigned the value of the element with the lowest risk rating (example: a high, low, medium, and medium estimate for the above elements would result in a low rating).” A separate evaluation of uncertainty is not computed for Probability of Establishment. In the following table (Table 10.4) we give our best estimates of the four factors and derive the final probability of organism establishment following ANSTF guidelines. Below each species’ subscore is our assessment of our uncertainty, using the intuitive abbreviations and verbal descriptions established in ANSTF (1996):

VC = Very Certain (“As certain as we are going to get”)

RC = Reasonably Certain (“Reasonably certain”)

MC = Moderately Certain (“More certain than not”)

RU = Reasonably Uncertain (“Reasonably uncertain”)

VU = Very Uncertain (“A guess”).

Table 10.4. Probability of organism establishment for nine giant constrictor species, and constituent values. Constituent subscores are for the four specified factors: (1) Estimate probability of the nonindigenous organism being on, with, or in the pathway (**Organism With Pathway**), (2) estimate probability of the organism surviving in transit (**Entry Potential**), (3) estimate probability of the organism successfully colonizing and maintaining a population where introduced (**Colonization Potential**), and (4) estimate probability of the organism spreading beyond the colonized area (**Spread Potential**). Uncertainty codes following the abbreviations given in the immediately preceding text. * = by similarity of appearance.

Species	Organism With Pathway	Entry Potential	Colonization Potential	Spread Potential	Probability of Establishment
<i>Python molurus</i>	High VC	High VC	High VC	High VC	High
<i>Broghammerus reticulatus</i>	High VC	High VC	Medium MC	High RC	Medium
<i>Python sebae</i>	High VC	High VC	High RC	High RC	High
<i>Python natalensis</i>	High* MC	High VC	High VC	High RC	High*
<i>Boa constrictor</i>	High VC	High VC	High VC	High VC	High
<i>Eunectes notaeus</i>	High VU	High VC	High RC	High RC	High
<i>Eunectes deschauenseei</i>	High* VU	High VC	Medium MC	Medium MC	Medium*
<i>Eunectes murinus</i>	High VC	High VC	Medium RC	High RC	Medium
<i>Eunectes beniensis</i>	High* VU	High VC	Medium MC	Medium MC	Medium*

Consequence of Establishment

5. Economic Impact Potential

The Economic Impact Potential is the most difficult component to assess accurately, perhaps because the modern economy is so large and complex relative to our ability to accurately project ecological outcomes. Economic impacts that are negligible at normal snake population densities (for example, in native range) can become extreme at higher population densities, and ecologists have very limited ability to predict the densities that will be achieved during irruptions of introduced species. We defer to any potential economic evaluation to quantify the potential costs associated with giant constrictor colonization.

To appreciate the inherent uncertainty in economic analyses, consider the ability to judge the economic impact of the Brown Treesnake prior to its arrival on Guam. At that time, the snake was not known to be a threat to wildlife, children, pets, or electrical systems. It was known to eat domestic fowl. We now know that the negative economic impacts are greatest to electrical systems, and constitute a multi-billion dollar risk to Hawaii should it become invaded (Burnett and others, 2006). An equivalent economic threat darkens the prospects of tourism in Hawaii (Shwiff, 2008). By comparison, the economic risks for the other factors are relatively small, and at present the impact on Guam to the poultry industry is minimal, in part because the industry has been largely abandoned on Guam, reportedly in response to snake predation (Fritts and McCoid, 1991). Similarly, the economic cost associated with zebra mussel impacts on power plant water intakes was underestimated prior to the mussel's arrival in the Great Lakes because the mussel did not achieve such high densities in its native range (Benson and Boydston, 1995). Thus, all economic impact predictions have low certainty.

Based on the Brown Treesnake experience and the relatively weak arboreality of the giant constrictors, the largest economic costs are likely to be associated with damage to tourism. All of the giant constrictors would be unpopular with some potential tourists, though the impact is likely to be greater in places that are heavily dependent on tourism, such as Florida, southern California, or Hawaii. Though the uncertainty is great, the potential economic costs to tourism are also very high (see species accounts section 12.6). If tourism impacts were based solely on an objective appraisal of the human health risks likely to be associated with interactions between tourists and giant constrictors, the tourism impact would be minimal and would be primarily associated with one species—the Reticulated Python. However, fear of snakes is not entirely rational and one well-publicized attack on a human could jeopardize considerable tourism business.

Although all of the giant constrictors are capable of climbing trees and some, such as the Boa Constrictor and Reticulated Python, readily forage in trees (at least when young), our impression is that these giant constrictors are unlikely to frequently climb power lines. Though we can claim only very high uncertainty with this prediction, we do not anticipate large power grid infrastructure losses due to giant constrictors (see species accounts section 12.4).

A potentially devastating impact to the nation's agriculture could occur if the deadly cattle disease heartwater or some other tick-borne disease were to become established in the United States and be transmissible through reptile ticks (see species

accounts section 12.1). African tick species that use pythons as hosts may be vectors of heartwater, and these ticks have been observed to transfer to other hosts, including other giant constrictors, other reptiles, and dogs. Because multiple python species are held captive together in the commercial trade, such transmission has ample opportunities to occur prior to retail sales.

Direct predation on livestock will occur if any of the giant constrictors become established in the United States (see species accounts sections 12.2). This prediction is very certain, in part because livestock losses have been widely documented in Florida (by Burmese Pythons, Northern African Pythons, and Reticulated Pythons). However, the extent of the damage is much less certain. Free-ranging, small-to-medium livestock, especially poultry, would be expected to be most heavily impacted. Pigs may be favored prey for some species, especially the Asian pythons. We anticipate that the anacondas would be relatively less detrimental to livestock, in part because of limited exposure of livestock to the anaconda's preferred watery habitat. Most Boa Constrictors and yellow anacondas will be too small to greatly impact mammalian livestock, as will all but very large individuals of the remaining species.

Predation on pets is likely to be of limited economic importance, but acutely felt by the bereaved pet owner. If experience with alligators has predictive value for understanding other large reptile-human exchanges, encounters between companion animals and snakes have the potential to escalate into a human health risk (because aggrieved pet owners sometimes unwisely choose to defend their pets against the reptile).

With the possible exception of the Reticulated Python, most giant constrictors' impact on human health will be in the realm of feared attacks rather than actual unprovoked events. Most of the area of the United States mainland that is likely inhabitable by Reticulated Pythons is lightly populated, except for cities and towns along the Florida and Texas coasts. Though the number of actual attacks is likely to be small, such events as do take place could significantly degrade the already angst-ridden psychological relationship between people and wetlands.

All of the giant constrictors could further endanger watchable wildlife species that presently constitute a significant draw for eco-tourists. Colonial bird rookeries (for example, Wood Storks) are a particular tourist draw, and are potentially vulnerable to depredation by a new nocturnal and opportunistically arboreal predator. Where their ranges overlap, all of the giant constrictors could significantly reduce stocks of economically-important fur-bearers such as beaver and muskrats. None of the giant constrictors seems likely to have a large direct impact on forestry, non-livestock agriculture, or horticulture.

6. Environmental Impact Potential

The natural history attributes that predict a species' environmental impact were discussed under the section "Spread Potential" and summarized in Tables 10.3 and 10.4.

Based on experience with the Brown Treesnake (Fritts and Rodda, 1998) and other introduced snakes, the greatest environmental impact of invasion by giant constrictors would be predation on endangered species, either via further endangerment or outright extinction. Table 4.2 tabulates the large number of imperiled wildlife that presently occur in Florida and would be put at greater risk by the establishment in that state of any of the giant constrictors. The amount of damage probably correlates with the

novelty of the invader's predatory tactics: the larger giant constrictor species have predatory tactics that diverge more from the predator defenses of native wildlife than do the smaller species. For example, a native mouse may have evolved movement patterns and senses for detecting a native snake that is a sit-and-wait predator, but such skills are likely to be lacking in beaver, which have not evolved with such a threat.

Giant constrictors would be novel predators in much of the area of the United States that is at risk of establishment. Because novelty is an important element of the predatory impact of giant constrictors, and the giant constrictors use largely the same predatory tactics as each other, a second colonization event (for example, if Reticulated Pythons were to become established in Florida in 2010, after Burmese Pythons had already spread throughout the area) would likely have considerably less impact on endangered species than the first colonization.

Novelty is an attribute that is hard to quantify; all large reptilian carnivores have some degree of overlap in their predatory tactics. Giant constrictors exhibit predatory tactics that partially overlap with a variety of native wildlife such as rat snakes, pit-vipers, and alligators. Alligators, for example, are also sit-and-wait predators on a very diverse suite of prey appearing near water. However, in comparison to most pythons and boas, alligators specialize on prey resistant to crushing (durophagy), such as turtles and mollusks; alligators tend to ambush from relatively deep water (especially in the summer when shallow marshes become too hot); and alligators rarely ambush prey on land (pythons and boas ordinarily do so). Juveniles of the giant constrictors will climb to extract prey from bird nests or capture perching or sleeping birds, a tactic not used by alligators. Nonetheless, some prey will obtain a degree of protection through their evolutionary experience with alligators and other large reptiles native to North America.

Although the novelty of sit-and-wait predation is likely to be most acutely felt by the larger prey species, the majority of giant constrictor individuals are juveniles or small adults. Thus, to the extent that predatory impacts reflect the numerical relationship between predators and prey (all things being equal, one expects a larger number of predators and predatory attacks, to result in a larger number of predatory successes), the potential harm to endangered species might be most immediately or acutely felt by small- or medium-sized mammals and birds. The Brown Treesnake eliminated or assisted with the elimination of most of the birds, bats, and lizards native to the island of Guam (Fritts and Rodda, 1998), with the smaller prey species showing the most immediate declines. Only after several generations of diminished recruitment did the larger prey species become extirpated (Wiles and others, 2003).

A most difficult aspect of this threat is its irreversibility. Once an introduced giant constrictor becomes well-established, there is no known method for removing the threat (see chapter Three), and thus recovery of endangered species in an infested area is a prospect likely to be diminished or even eliminated permanently. In this respect, invasive species constitute a more enduring threat than pollution, overexploitation, or habitat degradation.

The giant constrictors are unlikely to appreciably supplement the diets of native wildlife. Too little information is available to assess the likelihood of giant constrictors vectoring new diseases or indirectly impacting native wildlife if control programs inadvertently harm non-target species. It is possible that giant constrictors could have a positive impact by reducing populations of exotic pest species such as rats or Nutria.

However, our experience with Brown Treesnakes suggests that such non-native species allowed the snakes to achieve and maintain high densities, and snakes at these densities were able to cause the decline of many native species even though native species may not have comprised the majority of their diet (Fritts and Rodda, 1998). Therefore consumption of non-native prey species leads to more predation on natives, rather than less.

7. Perceived Impact (Social and Political Influences)

The ANSTF risk analysis guidelines (ANSTF, 1996) state that perceived impacts may include aesthetic damage, consumer concerns, and political repercussions, and this category thus appears to be a catch-all for potential impacts that are not specifically environmental or economic in nature. The guidelines also consider political forces unleashed by regulatory action or control measures on the invader, not just the direct consequences of establishment. Were giant constrictors to become established, the potential dampening effect on tourism would have obvious social overtones, but these impacts can to some degree be better quantified by considering the economic impacts associated with drops in tourism (see the Economics Impact section of this chapter). Similarly, the loss of wading birds and other watchable wildlife would be an aesthetic impact, but the effect on birdwatching can be translated into economic terms and is more appropriately examined in that section. Political repercussions could include conflict between regional, state, and federal philosophies of invasive-species interdiction and control (such as occurred with Black Carp in the Southeast and Asian oysters in Chesapeake Bay), but we see no means of predicting the nature or intensity of such conflict.

Although it is difficult, or perhaps impossible, to fully quantify perceived impacts that have no overt economic or ecological impacts, it is notable that colonization by giant constrictors would affect human relations to the rural landscape significantly, and not in a good way. Perhaps a mother would no longer allow her children to explore the woods unescorted, or to swim in a creek. Perhaps a child would have fewer opportunities to experience the full range of native wildlife. Loss of these pivotal developmental opportunities comes at a cost that we can appreciate even if we cannot readily measure it.

In light of the preceding observations, we have largely addressed perceived impacts (both in the management profiles and here) as those that would accrue to the live animal trade, were regulations on this trade enacted by state or federal agencies in response to the risk of establishment of giant constrictors in the United States. These would best fall under the “consumer concerns” listed as a component of this section by ANSTF (1996), but we acknowledge that the concerns of importers, breeders, and retailers would also need to be quantified as part of any possible regulatory evaluation.

As noted throughout this risk assessment, the only significant pathway for importation of live giant constrictors at present is the pet trade. Opposition to regulation of reptile commerce is likely to arise from both the commercial pet-trade interests and the pet-buying public. More-experienced buyers of exotic reptiles are often motivated by the opportunity to acquire a species or color morph that is unique. To such buyers, any restriction on the range of purchasing choices is likely to diminish the prospective scope of their acquisitions. There is also a widely-publicized fear that regulation of one type of import could facilitate subsequent regulations on other species. This concern may

motivate regulatory resistance from ordinary buyers that do not have a strong personal stake in preserving purchasing options for the more unusual or gigantic forms.

Countries such as Australia and New Zealand limit reptile commerce to a modest number of species deemed unlikely to become invasive (Bomford, 1991, 2003, 2008; Shine and others, 2000). Several countries (for example, Brazil, Venezuela, Australia) also broadly limit the keeping of native wildlife (Shine, 1991; Honegger, 1993). Although there is widespread concern that these regulations may be excessive with regard to the keeping of native wildlife (Reed, 2002), less concern has been voiced regarding the diminished range of exotic species available.

Commercial trade interests have proven nimble with regard to redirecting imports among species and countries to accommodate export restrictions from countries of origin (Christy, 2008). Few doubt that giant constrictor import restrictions would not be accommodated in a similarly nimble manner. A much greater concern originates from those domestic producers who have invested considerable effort and resources in producing designer morphs of particular species whose sales might be proscribed. Although the novelty-seeking nature of this market dictates that new lines be introduced continually, most of the new lines are derivative from existing stock. Full prohibition of trade in selected species would greatly impact those producers who have spent years developing novel morphs in proscribed species.

The continuous search for novelty in exotic snake species also raises a regulatory challenge in that a black-list-only approach (identifying the worst offenders progressively, and prohibiting their importation and interstate transport through Federal regulation) is likely to drive a novelty-motivated market in unpredictable and potentially detrimental directions, possibly focusing trade on species that are more problematic than the common species previously considered. New Zealand and Australia reptile-importation regulators also maintain a white list of permanently allowable species, from which pet buyers can confidently identify choices that are not candidates for importation restrictions.

The Consequences of Establishment element in the ANSTF (1996) risk assessment are computed as the sum of the economic, ecological, and perceived impacts. Unlike the establishment factors, which are multiplied together (thus a zero in any contributory factor dictates a zero for overall establishment), the impacts are additive (thus a zero in any contributory factor merely diminishes the sum by that amount). Step 2b in ANSTF (1996; see also Orr, 2003) directs how the Low, Medium, and High subscores are to be combined. Our subscores and confidence ranges are given in Table 10.5, along with the Consequences of Establishment summation as specified in ANSTF (1996).

Table 10.5. Consequences of establishment for nine giant constrictor species, with their associated confidence ranges.

Species	Economic impacts	Environmental impacts	Perceived impacts	Consequences of Establishment
<i>Python molurus</i>	High MC	High VC	High RC	High
<i>Broghammerus reticulatus</i>	Medium MC	Medium RU	Medium RC	Medium
<i>Python sebae</i>	High MC	High MC	Medium RC	High
<i>Python natalensis</i>	High MC	High RC	Medium RC	High
<i>Boa constrictor</i>	High MC	High RC	High VC	High
<i>Eunectes notaeus</i>	Medium RU	Medium RU	Low MC	Medium
<i>Eunectes deschauenseei</i>	Low VU	Low VU	Low VU	Low
<i>Eunectes murinus</i>	Medium RU	Medium RU	Medium RC	Medium
<i>Eunectes beniensis</i>	Low VU	Low VC	Low VU	Low

Organism Risk Potential

The Organism Risk Potential (ORP) is an overall assessment based on the combination of Probability of Establishment (Table 10.4) and Consequences of Establishment (Table 10.5), following the algorithm of Step 2c (ANSTF, 1996), which is duplicated in Table 10.6. Table 10.7 restates the summary judgments from the preceding tables (10.4 and 10.5), and provides the ORP scores for each giant constrictor species. Most species warranted a “High” ORP, though two look-alike anacondas (*Eunectes deschauenseei* and *Eunectes beniensis*) and the Reticulated Python (*Broghammerus reticulatus*) were “Medium.” The two look-alike anacondas are readily distinguishable on the basis of differences in scalation and pattern from the regularly-traded anacondas, but based on their similarity of appearance may not be distinguished from other species in commerce. Based on the ANSTF (1996) guidelines, “mitigation” is warranted for species evaluated as High or Medium. However, the ANSTF guidelines provide no direction as to what form mitigation should take.

Table 10.6. Organism Risk Potential (ORP) algorithm adopted by the Aquatic Nuisance Species Task Force (ANSTF, 1996).

Probability of Establishment	Consequences of Establishment	Organism Risk Potential (ORP)
High	High	High
Medium	High	High
Low	High	Medium
High	Medium	High
Medium	Medium	Medium
Low	Medium	Medium
High	Low	Medium
Medium	Low	Medium
Low	Low	Low

Table 10.7. Organism Risk Potential (ORP) for nine giant constrictor species. * = by similarity of appearance.

Species	Probability of Establishment	Consequences of Establishment	Organism Risk Potential (ORP)
<i>Python molurus</i>	High	High	High
<i>Broghammerus reticulatus</i>	Medium	Medium	Medium
<i>Python sebae</i>	High	High	High
<i>Python natalensis</i>	High*	High	High*
<i>Boa constrictor</i>	High	High	High
<i>Eunectes notaeus</i>	High	Medium	High
<i>Eunectes deschauenseei</i>	Medium*	Low	Medium*
<i>Eunectes murinus</i>	Medium	Medium	Medium
<i>Eunectes beniensis</i>	Medium*	Low	Medium*

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References Cited

- Acharjyo, L.N., and Misra, Ch.G., 1980, Growth rate of Indian *Python molurus molurus* (Serpentes Boidae) in captivity with special reference to age at first egg-laying: *Journal of the Bombay Natural History Society*, v. 77, p. 344–350.
- Acharjyo, L.N., and Misra, R., 1976, Aspects of reproduction and growth of the Indian Python, *Python molurus molurus*, in captivity: *British Journal of Herpetology*, v. 5, p. 562–565.
- Achaval, F., and Olmos, A., 2003, *Anfibios y reptiles del Uruguay*: Montevideo, Uruguay, Facultad de Ciencias, 136 p.
- Akani, G.C., Eyo, E., Odegbune, E., Eniang, E.A., and Luiselli, L., 2002, Ecological patterns of anthropogenic mortality of suburban snakes in an African tropical region: *Israel Journal of Zoology*, v. 48, p. 1–11.
- Akani, G.C., Luiselli, L., and Politano, E., 1999, Ecological and conservation considerations on the reptile fauna of the eastern Niger Delta (Nigeria): *Herpetozoa*, v. 11, p. 141–153.
- Alexander, G.J., 2007, Thermal biology of the Southern African Python (*Python natalensis*): does temperature limit its distribution?, in Henderson, R.W., and Powell, R., eds., *Biology of the boas and pythons*: Eagle Mountain, Utah, Eagle Mountain Publishing, p. 50–75.
- Alexander, G.J., and Marais, J., 2007, *A guide to the reptiles of southern Africa*: Cape Town, Struik, 408 p.
- Allan, S.A., Simmons, L.A., and BurrIDGE, M.J., 1998, Establishment of the tortoise tick *Amblyomma marmoratum* (Acari: Ixodidae) on a reptile-breeding facility in Florida: *Journal of Medical Entomology*, v. 35, p. 621–624.
- Allen, C.R., 2006, Predictors of introduction success in the South Florida avifauna: *Biological Invasions*, v. 8, p. 491–500.
- Allen, M.J., 1933, Report on a collection of amphibians and reptiles from Sonora, Mexico, with the description of a new lizard: *Occasional Papers of the Museum of Zoology, University of Michigan*, v. no. 259, p. 1–16.
- Alvarez del Toro, M., 1960, *Los reptiles de Chiapas*: Chiapas, Mexico, Tuxtla Gutiérrez, 204 p.
- Amaral, A.d., 1944, Notas sôbre a ofiologia neotrópica e Brasileira. VI. Formas de boíneos de recente registro: *Papeis Avulsos, São Paulo*, v. 10, p. 41–48.
- Andrade, D.V., and Abe, A.S., 1998, Abnormalities in a litter of *Boa constrictor amarali*: *The Snake*, v. 28, p. 28–32.
- Aquatic Nuisance Species Task Force, 1996, *Generic nonindigenous aquatic organisms risk analysis review process (for estimating risk associated with the introduction of nonindigenous aquatic organisms and how to manage for that risk)*: Washington, D.C., Aquatic Nuisance Species Task Force, 32 p.
- Araújo, M.B., and Pearson, R.G., 2005, Equilibrium of species' distributions with climate: *Ecography*, v. 28, p. 693–695.
- Arendt, W.J., and Anthony, D., 1986, Bat predation by the St. Lucia boa (*Boa constrictor orophias*): *Caribbean Journal of Science*, v. 22, p. 219–220.
- Arntzen, J.W., 2006, From descriptive to predictive distribution models: a working example with Iberian amphibians and reptiles: *Frontiers in Zoology*, v. 3, p. 8.

- Arroyo-Quiroz, I., Péres-Gil, R., and Leader-Williams, N., 2007, Mexico in the international reptile skin trade: a case study: *Biodiversity and Conservation*, v. 16, p. 931–952.
- Associated Press, 2006, Pet boa constrictor strangles owner at home: *Edmonton Sun*, v. 18 Dec 2006.
- Auerbach, R.D., 1987, *The amphibians and reptiles of Botswana: Botswana, Gaborone Printing Works*, 295 p.
- Auffenberg, W., 1994, *The Bengal Monitor: Gainesville, Florida, Univ. Press Florida*, 560 p.
- Auliya, M.A., 2006, Taxonomy, life history and conservation of giant reptiles in West Kalimantan (Indonesian Borneo): *Munich, Natur und Tier Verlag*, 432 p.
- Auliya, M.A., and Abel, F., 2000a, Zur Taxonomie, geographischen Verbreitung und Nahrungsökologie des Netzpythons (*Python reticulatus*). Teil 1: Taxonomie und geographische Verbreitung: *Herpetofauna (Weinstadt)*, v. 22, no. 127, p. 5–18.
- Auliya, M.A., and Abel, F., 2000b, Zur Taxonomie, geographischen Verbreitung und Nahrungsökologie des Netzpythons (*Python reticulatus*). Teil 2: Nahrungsökologie: *Herpetofauna (Weinstadt)*, v. 22, no. 128, p. 19–28.
- Auliya, M.A., Mausfeld, P., Schmitz, A., and Böhme, W., 2002, Review of the Reticulated Python (*Python reticulatus* Schneider, 1801) with the description of a new subspecies from Indonesia: *Naturwissenschaften*, v. 89, p. 201–213.
- Bakkegard, K.A., and Timm, R.M., 2001, Boa constrictor (*Boa constrictor*). Diet: *Herpetological Review*, v. 32, p. 261–262.
- Barbour, T., and Loveridge, A., 1929, Reptiles and amphibians. Vertebrates of the Corn Islands: *Bulletin of the Museum of Comparative Zoology*, v. 69, p. 138–146.
- Barker, D.G., and Barker, T.J., 1994, The African giants: *The Vivarium*, v. 6, p. 18–21.
- Barker, D.G., and Barker, T.J., 1997, Big & beautiful: the Reticulated Python: *Reptiles*, v. 5, no. 6, p. 48–67.
- Barker, D.G., and Barker, T.J., 2008a, The distribution of the Burmese Python, *Python molurus bivittatus*: *Bulletin of the Chicago Herpetological Society*, v. 43, p. 33–38.
- Barker, D.G., and Barker, T.J., 2008b, Common Boa Constrictors, information and care: Available online at <http://www.vpi.com/publications/boa-constrictor>, accessed 30 Apr 2008.
- Barker, D.G., Murphy, J.B., and Smith, K.W., 1979, Social behavior in a captive group of Indian Pythons, *Python molurus* (Serpentes, Boidae) with formation of a linear social hierarchy: *Copeia*, v. 1979, p. 466–471.
- Barten, S.L., Frye, E., Evans, R., and Ihrke, P., 1985, *Python molurus bivittatus* (Burmese python). Coloration.: *Herpetological Review*, v. 16, p. 57.
- Bartlett, R.D., and Bartlett, P.P., 2003, *Reptiles and amphibians of the Amazon: an ecotourist's guide: Gainesville, Fla., Univ. Press of Florida*, 291 p.
- BBC News, 2006, Pet boa constrictor chokes owner: Available online at <http://news.bbc.co.uk/2/hi/americas/6191305.stm>, accessed 30 April 2008.
- Beaumont, L.J., Hughes, L., and Poulsen, M., 2005, Predicting species distributions: use of climatic parameters in BIOCLIM and its impact on predictions of species' current and future distributions: *Ecological Modelling*, v. 186, p. 250–269.
- Beebe, W., 1946, Field notes on the snakes of Kartabo, British Guyana, and Caripito, Venezuela: *Zoologica*, v. 31, p. 11–64.

- Begbie, A., 1907, The food of pythons: Journal of the Bombay Natural History Society, v. 17, p. 1,021.
- Belloso, H., 2003, Record snake fascination: Reptilia (Great Britain), v. no. 27, p. 28–30.
- Belloso, H., 2004, Faszination Rekerschlange. Teil 3. Lass dich nicht beissen: Reptilia, v. 9, no. 3, p. 42–44.
- Belloso, H., Dirksen, L., and Auliya, M.A., 2007, Faszination Riesenschlangen-Mythos, Fakten und Geschichten: Munich, BLV Buchverlag, 160 p.
- Belluomini, H.E., and Hoge, A.R., 1958, Operação cesariana realizada em *Eunectes murinus* (Linnaeus, 1758) (Serpentes): Memorias do Instituto Butantan, v. 28, p. 187–194.
- Belluomini, H.E., Maranhao Nina, A.F., and Hoge, A.R., 1959, Contribuicao a biologia do genero *Eunectes* Wagler, 1830. (Serp., Boidae). Estudo de seis ninhadas de "sucuris": Memorias do Instituto Butantan, v. 29, p. 165–174.
- Benson, A.J., and Boydstun, C.P., 1995, Invasion of the Zebra Mussel in the United States, in LaRoe, E.T., Farris, G.S., Puckett, C.E., Doran, P.D., and Mac, M.J., eds., Our living resources: a report to the nation on the distribution, abundance, and health of U.S. plants, animals, and ecosystems: Washington, D.C., U.S. Dept. of Interior-National Biological Service, p. 445–446.
- Berthier, K., Langlais, M., Auger, P., and Pontier, D., 2000, Dynamics of a feline virus with two transmission modes within exponentially growing host populations: Proceeding of the Royal Society of London, Series B, v. 267, p. 2,049–2,056.
- Bertona, M., and Chiaraviglio, M., 2003, Reproductive biology, mating aggregations, and sexual dimorphism of the Argentine Boa Constrictor (*Boa constrictor occidentalis*): Journal of Herpetology, v. 37, p. 510–526.
- Bhatt, K., and Choudhury, B.C., 1993, The diel activity pattern of Indian python (*Python molurus molurus* LINN.) at Keola National Park, Bharaptur, Rajasthan: Journal of the Bombay Natural History Society, v. 90, p. 394–403.
- Bhupathy, S., 1990, Blotch structure in individual identification of the Indian python *Python molurus molurus* and its possible usage in population estimation: Journal of the Bombay Natural History Society, v. 87, p. 399–404.
- Bhupathy, S., and Haque, M.H., 1986, Association of rock python (*Python molurus*) with porcupine (*Hystrix indica*): Journal of the Bombay Natural History Society, v. 83, p. 449–450.
- Bhupathy, S., and Vijayan, V.S., 1989, Status, distribution and general ecology of the Indian Python, *Python molurus molurus* Linn. in Keoladeo National Park, Bharatpur, Rajasthan: Journal of the Bombay Natural History Society, v. 86, p. 381–387.
- Bisplinghoff, H., and Belloso, H., 2007, Professional breeders series: Anacondas: Frankfurt am Main, Germany, Edition Chimaira, 127 p.
- Black, C.P., Birchard, G.F., Schuett, G.W., and Black, V.D., 1984, Influence of incubation water content on oxygen uptake in embryos of the Burmese Python (*Python molurus bivittatus*), in Seymour, R.S., ed., Respiration and metabolism of embryonic vertebrates: Dordrecht, The Netherlands, Dr. W. Junk Publ., p. 137–145.
- Blackburn, T.M., Cassey, P., Duncan, R.P., Evans, K.L., and Gaston, K.J., 2004, Avian extinctions and mammalian introductions on oceanic islands: Science, v. 305, p. 1,955–1,958.

- Blundell, A.G., and Mascia, M.B., 2005, Discrepancies in reported levels of international wildlife trade: *Conservation Biology*, v. 19, p. 2,020–2,022.
- Boback, S.M., 2004, *Boa constrictor* (*Boa constrictor*). Diet.: *Herpetological Review*, v. 35, p. 175.
- Boback, S.M., 2005, Natural history and conservation of island boas (*Boa constrictor*) in Belize: *Copeia*, v. 2005, p. 880–885.
- Boback, S.M., 2006, A morphometric comparison of island mainland boas (*Boa constrictor*) in Belize: *Copeia*, v. 2006, p. 261–267.
- Boback, S.M., Burroughs, E., Ugarte, C., and Watling, J., 2000, *Boa constrictor* (*Boa constrictor*). Diet: *Herpetological Review*, v. 31, p. 244–245.
- Boback, S.M., and Carpenter, M., 2007, Body size and head shape of island *Boa constrictor* in Belize: environmental versus genetic contributions, in Henderson, R.W., and Powell, R., eds., *Biology of the boas and pythons*: Eagle Mountain, Utah, Eagle Mountain Publishing, p. 102–117.
- Bogert, C.M., and Oliver, J.A., 1945, A preliminary analysis of the herpetofauna of Sonora: *Bulletin of the American Museum of Natural History*, v. 83, p. 297–426.
- Bomford, M., 1991, Importing and keeping exotic vertebrates in Australia; criteria for the assessment of risk: Canberra, Australia, Bureau of Rural Resources, Dept. Primary Indust. Energy, Bulletin No. 12, 92 p.
- Bomford, M., 2003, Risk assessment for the import and keeping of exotic vertebrates in Australia: Canberra, Australia, Bureau of Rural Sciences, 136 p.
- Bomford, M., 2008, Risk assessment models for establishment of exotic vertebrates in Australia and New Zealand: Canberra, Australia, Invasive Animals Coop. Res. Centre, 198 p.
- Bomford, M., Kraus, F., Barry, S.C., and Lawrence, E., 2009, Predicting establishment success for alien reptiles and amphibians: a role for climate matching: *Biological Invasions*, v. 11, p. 713–724.
- Bomford, M., and O'Brien, P., 1997, Potential use of contraception for managing wildlife pests in Australia, in Kreeger, T.J., ed., *Contraception in wildlife management*: Fort Collins, Colo., U.S. Department of Agriculture, APHIS Technical Bulletin 1853, p. 205–214.
- Bonny, K., 2007, *Die Gattung Boa*: Taxonomie und Fortpflanzung: Rheinstetten, Germany, KUS-Verlag, 262 p.
- Boos, H.E.A., 1984, A consideration of the terrestrial reptile fauna of some offshore islands north west of Trinidad: *Living World*, v. 1983/1984, p. 19–26.
- Boos, H.E.A., 1992, A report on the 18.5 foot boa constrictor from Trinidad: *Bulletin of the British Herpetological Society*, v. 40, p. 15–17.
- Boos, H.E.A., 2001, *The snakes of Trinidad and Tobago*: College Station, Texas, Texas A&M University Press, 270 p.
- Borland, J.N., 1855, Account of the feeding of a large *Boa Constrictor*, measuring about twenty feet in length: *Proceedings of the Boston Society of Natural History*, v. 5, p. 210–211.
- Bosch, H.A.J.i.d., 1985, Snakes of Sulawesi: Checklist, key, additional biogeographical remarks: *Zoologische Verhandelingen. Uitgegeven Door Het Rijksmuseum Van Nat.Hist.te Leiden*, v. 217, p. 3–50.

- Boulenger, G.A., 1912, A vertebrate fauna of the Malay Peninsula from the Isthmus of Kra to Singapore, including the adjacent islands, Reptilia and Batrachia: London, Taylor and Francis, 294 p.
- Bourret, R., 1936, Les serpents de l'Indochine, vol. 1, Études sur la fauna: Roulouse, France, Henri Basayau and Cie 141 p.
- Bowler, J.K., 1977, Longevity of reptiles and amphibians in North American collections: Soc. Stud. Amphib. Rept./Phila. Herpetol. Soc., 32 p.
- Boycott, R.C., 1992, A herpetofaunal survey of Swaziland: Durban, South Africa, Univ. of Natal, 175 p.
- Branch, W.R., 1988, South Africa red data book—Reptiles and amphibians: Pretoria, South Africa, Foundation for Research Development, 241 p.
- Branch, W.R., and Erasmus, H., 1984, Captive breeding of pythons in South Africa, including details of an interspecific hybrid (*Python sebae natalensis* x *Python molurus bivittatus*): Journal of the Herpetological Association of Africa, v. 1984, no. 30, p. 1–10.
- Branch, W.R., and Hacke, D., 1980, A fatal attack on a young boy by an African Rock Python *Python sebae*: Journal of Herpetology, v. 14, p. 305–307.
- Branch, W.R., and Patterson, R.W., 1975, Notes on the development of embryos of the African Rock Python, *Python sebae* (Serpentes: Boidae): Journal of Herpetology, v. 9, p. 243–248.
- Brandes, C.-H., 1971, Über die Ernährung und das Wachstum der Gattung *Eunectes* Wagler in der Gefangenschaft: Veröff.Überseemus.Bremen, Reihe A, v. 4, p. 63–70.
- Brattstrom, B.H., 1965, Body temperatures of reptiles: American Midland Naturalist, v. 73, p. 376–422.
- Brien, M.L., Brien, C.H., and Reed, R.N., 2008, *Morelia spilota spilota* (Diamond python), Reproduction: Herpetological Review, v. 39, p. 355.
- Brien, M.L., Cherkiss, M.S., Johnson, V.M., Mazzotti, F.J., and Snow, R.W., 2007, *Python molurus bivittatus* (Burmese Python), Clutch size: Herpetological Review, v. 38, p. 342–343.
- Broadley, D.G., 1959, The herpetology of southern Rhodesia, Part 1, Snakes: Bulletin of the Museum of Comparative Zoology, v. 120, no. 1, p. 1–100.
- Broadley, D.G., 1984, A review of geographical variation in the African python, *Python sebae* (Gmelin): British Journal of Herpetology, v. 6, p. 359–367.
- Broadley, D.G., 1990, FitzSimon's snakes of southern Africa: Johannesburg, South Africa, Delta Books, 376 p.
- Broadley, D.G., 1998, Introduction to Reptilia: Karl Patterson Schmidt and the reptile volumes based on the collections of the American Museum of Natural History Congo Expedition 1909–1915, in Schmidt, K.P., and Noble, G.K., eds., Contributions to the herpetology of the Belgian Congo: Soc. Study Amphibians Reptiles, p. ix–xxxiii.
- Broadley, D.G., 1999, The Southern African Python, *Python natalensis* A. Smith 1840, is a valid species: African Herp News, v. 29, p. 31–32.
- Broadley, D.G., Doria, C.T., and Wigge, J., 2003, Snakes of Zambia: An atlas and field guide: Frankfurt, Germany, Edition Chimaira, 280 p.
- Broennimann, O., Treier, U.A., Müller-Schärer, H., Thuiller, W., Peterson, A.T., and Guisan, A., 2007, Evidence of climatic niche shift during biological invasion: Ecological Letters, v. 10, p. 701–709.

- Brongersma, L.D., 1940, Snakes from the Leeward group, Venezuela and eastern Colombia: Studies on the fauna of Curacao, Aruba, Bonaire and the Venezuelan Islands, v. no. 8, p. 115–137.
- Brown, G.P., Shilton, C.M., and Shine, R., 2006, Do parasites matter?: Assessing the fitness consequences of haemogregarine infection in snakes: *Canadian Journal of Zoology/Revue Canadienne de Zoologie*, v. 84, p. 668–676.
- Brown, J.H., Stevens, G.C., and Kaufman, D.M., 1996, The geographic range: size, shape, boundaries, and internal structure: *Annual Review of Ecology and Systematics*, v. 27, p. 597–623.
- Brown, W.C., and Alcala, A.C., 1964, Relationship of the herpetofaunas of the non-dipterocarp communities to that of the dipterocarp forest of southern Negros Island, Philippines: *Senckenbergiana Biologica*, Frankfurt, v. 45, p. 591–611.
- Buck, F., 1935, Fang and claw: New York, Simon & Schuster, 239 p.
- Buck, F., 1939, Animals are like that: New York, R.M. McBride, 240 p.
- Bullock, T.H., and Barrett, R.H., 1968, Radiant heat reception in snakes: *Communications in Behavioral Biology, Part A*, v. 1, p. 19–29.
- Burbrink, F.T., 2005, Inferring the phylogenetic position of *Boa constrictor* among the Boinae: *Molecular Phylogenetics and Evolution*, v. 34, p. 167–180.
- Burghardt, G.M., 1980, Behavioral and stimulus correlates of vomeronasal functioning in reptiles: feeding, grouping, sex and tongue use, *in* Müller-Schwarze, D., and Silverstein, R.M., eds., *Chemical signals: vertebrates and aquatic invertebrates*: New York, Plenum Press, p. 275–301.
- Burghardt, G.M., 1983, Aggregation and species discrimination in newborn snakes: *Zeitschrift für Tierpsychologie*, v. 61, p. 89–101.
- Burnett, K.M., Kaiser, B.A., Pitafi, B.A., and Roumasset, J.A., 2006, Prevention, eradication, and containment of invasive species: illustrations from Hawaii: *Agricultural and Resources Economics Review*, v. 35, p. 63–77.
- Burnham, K.P., and Anderson, D.R., 2002, Model selection and multimodel inference; a practical information-theoretic approach, 2nd edn.: New York, Springer, 488 p.
- Burridge, M.J., 2001, Ticks (Acari: Ixodidae) spread by the international trade in reptiles and their potential roles in dissemination of diseases: *Bulletin of Entomological Research*, v. 91, p. 3–23.
- Burridge, M.J., Berube, L.R., and Holt, T.J., 2006, Invasive ticks: introduction of *Amblyomma kraneveldi* (Anastos) and other exotic ticks (Acari: Ixodidae) into Florida on imported reptiles: *International Journal of Acarology*, v. 32, p. 315–321.
- Burridge, M.J., Simmons, L.-A., and Allan, S.A., 2000, Introduction of potential heartwater vectors and other exotic ticks into Florida on imported reptiles: *Journal of Parasitology*, v. 86, p. 700–704.
- Butler, J.A., and Reid, J., 1986, Habitat preferences of snakes in the Southern Cross River State, Nigeria, *in* Rocek, Z., ed., *Studies in herpetology*: Prague, Czech Republic, Charles University, p. 483–488.
- Bykovskii, V.A., and Kandybin, N.V., 1988, Biological principles, development, and perspectives of the use of bacteria and viruses. Rodent pest management: Boca Raton, Fla., CRC Press, p. 377–389.
- Calle, P.P., Rivas, J.A., Muñoz, M., Thorbjarnarson, J., Dierenfeld, E.S., Holmstrom, W., Braselton, W.E., and Karesh, W.B., 1994, Health assessment of free-ranging anacondas

- (*Eunectes murinus*) in Venezuela: *Journal of Zoo and Wildlife Medicine*, v. 25, p. 53–62.
- Calle, P.P., Rivas, J., Muñoz, M., Thorbjarnarson, J., Holmstrom, W., and Karesh, W.B., 2001, Infectious disease serologic survey in free-ranging Venezuelan anacondas (*Eunectes murinus*): *Journal of Zoo and Wildlife Medicine*, v. 32, p. 320–323.
- Campbell, E.W., III, 1996, The effect of Brown Tree Snake (*Boiga irregularis*) predation on the island of Guam's extant lizard assemblages: Columbus Ohio, Ohio State Univ., Ph.D. dissertation, 83 p.
- Campbell, E.W., III, Rodda, G.H., Fritts, T.H., and Bruggers, R.L., 1999, An integrated management plan for the Brown Treesnake (*Boiga irregularis*) on Pacific islands, in Rodda, G.H., Sawai, Y., Chiszar, D., and Tanaka, H., eds., *Problem snake management: the Habu and the Brown Treesnake*: Ithaca, N.Y., Cornell Univ. Press, p. 423–435.
- Campbell, J.A., 1998, *Amphibians and reptiles of northern Guatemala, the Yucatán, and Belize*: Norman, Oklahoma, Univ. of Oklahoma Press, 380 p.
- Campbell, J.A., and Lamar, W.W., 1989, *The venomous reptiles of Latin America*: Ithaca, N.Y., Comstock Publ. Association, 425 p.
- Campden-Main, S.M., 1970, *A field guide to the snakes of South Vietnam*: Washington, D.C., Smithsonian Institution, 114 p.
- Capitanelli, R.G., 1979, Clima, in Vasquez, J.R., Miatello, A., and Roqué, M.E., eds., *Geografía de la Provincia de Córdoba*: Buenos Aires, Argentina, Ed. Boldt, p. 45–138.
- Caprette, C.L., 1997, Pilot studies of the effects of illumination on trapping brown tree snakes, *Boiga irregularis*: Columbus, Ohio, report to Ohio State University, 3 p.
- Caras, R.A., 1975, *Dangerous to man; the definitive story of wildlife's reputed dangers*, revised edition: New York, Holt, Rinehart and Winston, 422 p.
- Cardozo, G., and Chiaraviglio, M., 2008, Landscape changes influence the reproductive behaviour of a key 'capital breeder' snake (*Boa constrictor occidentalis*) in the Gran Chaco region, Argentina: *Biological Conservation*, v. 141, p. 3,050–3,058.
- Cardozo, G., Rivera, P.C., Lanfri, M., Scavuzzo, C.M., Gardenal, C.N., and Chiaraviglio, M., 2007, Effects of habitat loss on populations of the Argentine Boa Constrictor (*Boa constrictor occidentalis*), in Henderson, R.W., and Powell, R., eds., *Biology of the boas and pythons*: Eagle Mountain, Utah, Eagle Mountain Publishing, p. 300–310.
- Caudell, J.N., 2001, *Pathophysiology and predation of Brown Tree Snakes in Australia*: Logan, Utah State Univ., Jack H. Berryman Institute for Wildlife Damage Management Ph.D. dissertation, 61 p.
- Caudell, J.N., Whittier, J.M., and Conover, M.R., 2002, The effects of haemogregarine-like parasites on Brown Tree Snakes (*Boiga irregularis*) and Slatey-grey Snakes (*Stegonotus cucullatus*) in Queensland, Australia: *International Biodeterioration and Biodegradation*, v. 49, p. 113–119.
- Caughley, G., Pech, R.P., and Crice, D., 1992, Effect of fertility control on a population's productivity: *Wildlife Research*, v. 19, p. 623–627.
- Cei, J.M., 1993, *Reptiles del nordeste y este de Argentina. Herpetofauna de las Selvas Subtropicales, Puna y Pampa*: Museo Regionale di Scienze Naturali Torino, Monografia, v. 14, p. 1–949.

- Chan-ard, T., Grossmann, W., Gumprecht, A., and Schulz, K.-D., 1999, Amphibians and reptiles of peninsular Malaysia and Thailand; an illustrated checklist: Wuersele, Germany, Bushmaster Publ., 240 p.
- Chapman, C.A., 1986, Boa constrictor predation and group response in White-Faced Cebus Monkeys: *Biotropica*, v. 18, p. 171–172.
- Cheke, A.S., and Hume, J., 2008, Lost land of the Dodo: London, Y & AD Poyser, 464 p.
- Cherubini, A.L., Barrella, T.H., and Da Silva, R.J., 2003, Death of *Boa constrictor amarali* (Serpentes, Boidae) after ingestion of a tree porcupine (Rodentia): *Journal of Venomous Animals and Toxins including Tropical Diseases*, v. 9, available online at http://www.scielo.br/scielo.php?script=sci_arttext&pid=S1678-919920030001000009&long=pt&nrm=iso, accessed 01 Jun 2008.
- Chiaraviglio, M., 2006, The effects of reproductive condition on thermoregulation in the Argentina boa constrictor (*Boa constrictor occidentalis*) (Boidae): *Herpetological Monographs*, v. 20, p. 172–177.
- Chiaraviglio, M., and Bertona, M., 2007, Reproduction and thermoregulation are principal factors that influence habitat selection in the Argentine boa constrictor (*Boa constrictor occidentalis*), in Henderson, R.W., and Powell, R., eds., *Biology of the Boas and Pythons*: Eagle Mountain, Utah, Eagle Mountain Publishing, p. 76–86.
- Chiaraviglio, M., Bertona, M., Sironi, M., and Cervantes, R., 1998, Distribucion de *Boa constrictor occidentalis* (Serpentes: Boidae) en el noroeste de la Provincia de Cordoba, Argentina: *Gayana Zoología*, v. 62, p. 75–77.
- Chiaraviglio, M., Bertona, M., Sironi, M., and Lucino, S., 2003, Intrapopulation variation in life history traits of *Boa constrictor occidentalis* in Argentina: *Amphibia-Reptilia*, v. 24, p. 65–74.
- Chiaraviglio, M., and Briguera, V., 2001, Participation of chemical cues in conspecific detection and sexual discrimination in *Boa constrictor occidentalis* (Serpentes: Boidae): *Gayana*, v. 65, p. 5–10.
- Chippaux, J.-P., 1986, Les serpents de la Guyane française: Paris, Editions de l'ORSTOM, 65 p.
- Chippaux, J.-P., 1999, Les serpents d'Afrique occidentale et centrale: Lyons, France, Editions de l'IRD, 278 p.
- Chirio, L., and Ineich, I., 2006, Biogeography of the reptiles of the Central African Republic: *African Journal of Herpetology*, v. 55, p. 23–59.
- Chiszar, D., 1990, The behavior of the Brown Tree Snake, *Boiga irregularis*: a study in applied comparative psychology, in Dewsbury, D.A., ed., *Contemporary issues in comparative psychology*: Sunderland, Mass., Sinauer Assoc., p. 101–123.
- Chiszar, D., Smith, H.M., Petkus, A., and Dougherty, J., 1993, A fatal attack on a teenage boy by a captive Burmese Python (*Python molurus bivittatus*) in Colorado: *Bulletin of the Chicago Herpetological Society*, v. 28, p. 261–262.
- Christy, B., 2008, The lizard king: the true crimes and passions of the world's greatest reptile smugglers: New York, Twelve (Hatchett Book Group, U.S.A.), 241 p.
- Christy, M.T., Savidge, J.A., Bischof, R., and Rodda, G.H., 2007, Can temperature be used as a tool for limiting Brown Treesnake invasion via transportation pathways?, in Witmer, G.W., Pitt, W.C., and Fagerstone, K.A., eds., *Managing vertebrate invasive species: Proceedings of an international symposium*: Fort Collins, Colo., USDA-APHIS Wildlife Services, National Wildlife Research Center, p. 246–256.

- Clark, L., and Shivik, J.A., 2002, Aerosolized essential oils and individual natural product compounds as Brown Treesnake repellents: *Pest Management Science*, v. 58, p. 775–783.
- Clercq, P.d., 1988, Note on breeding *Python molurus bivittatus*: *Litteratura Serpentina*, v. 8, p. 50.
- Coborn, J., 1991, *The atlas of snakes of the world*: Neptune City, N.J., T.F.H. Publ., Inc., 591 p.
- Correa, A., and Pautassi, C.V., 1986, *Catálogo sistemático de la Colección de Ofidios. Primera parte.*: Museo de Ciencias Naturales Universidad Nacional de Salta, 44 p.
- Cox, M.J., 1991, *The snakes of Thailand and their husbandry*: Malabar, Fla., Krieger Publ., 526 p.
- Cox, M.J., van Dijk, P.P., Nabhitabhata, J., and Thiraklupt, K., 1998, *A photographic guide to snakes and other reptiles of peninsular Malaysia, Singapore and Thailand: Sanibel Island, Fla.*, Ralph Curtis Books, 144 p.
- Crooks, K.R., and Soulé, M.E., 1999, Mesopredator release and avifaunal extinctions in a fragmented system: *Nature*, v. 400, p. 563–566.
- Daniel, J.C., 2002, *The book of Indian reptiles and amphibians*: Mumbai, India, Bombay Natural History Soc./Oxford Univ. Press, 238 p.
- Darevsky, I.S., 1990, Notes on the reptiles (Squamata) of some offshore islands along the coast of Vietnam, *in* Peters, G., and Hutterer, R., eds., *Vertebrates in the tropics*: Bonn, Museum Alexander Koenig, p. 125–129.
- Das, I., 1994, *The reptiles of South Asia: checklist and distributional summary*: *Hamadryad*, v. 19, p. 15–40.
- Das, I., 1996, *Biogeography of the reptiles of South Asia*: Malabar, Fla., Krieger Publ., 87 p.
- Das, I., 2002a, *An introduction to the amphibians and reptiles of tropical Asia*: Kota Kinabalu, Natural History Publ. (Borneo), 207 p.
- Das, I., 2002b, *Snakes and other reptiles of India*: Sanibel Island, Fla., Ralph Curtis Publ., 144 p.
- Das, I., 2006, *A photographic guide to snakes and other reptiles of Borneo*: Sanibel Island, Fla., Ralph Curtis Publ., Inc., 144 p.
- David, P., and Vogel, G., 1996, *The snakes of Sumatra: an annotated checklist and key with natural history notes*: Frankfurt am Main, Germany, Edition Chimaira, 260 p.
- Davis, D.E., Myers, K., and Hoy, J.B., 1976, Biological control among vertebrates, *in* Huffaker, C.B., and Messenger, P.S., eds., *Theory and practice of biological control*: New York, Academic Press, p. 501–519.
- Davis, R.A., 1980, Handler beware! Large constrictors can kill!: *Herpetological Review*, v. 11, p. 91.
- Davis, W.B., and Smith, H.M., 1953, Snakes of the Mexican state of Morelos: *Herpetologica*, v. 8, p. 133–143.
- Day, S., 2008, Police blame snake in Tuesday death—Virginia Beach Police believe 13-foot Reticulated Python strangled its owner when she tried to give it medication: *Virginian-Pilot*, v. Oct. 25, 2008.
- de Cock Buning, T., 1979, Feeding behavior and the morphology of thermoreceptors in *Python reticulatus*: *Japanese Journal of Herpetology*, v. 8, p. 64.

- de Cock Buning, T., 1983, Thermal sensitivity as a specialization for prey capture and feeding in snakes: *American Zoologist*, v. 23, p. 363–375.
- de Cock Buning, T., Poelmann, R.E., and Dullenmeijer, P., 1978, Feeding behavior and the morphology of the thermoreceptors in *Python reticulatus*: *Netherlands Journal of Zoology*, v. 28, p. 62–93.
- de Cock Buning, T., Terashima, S., and Goris, R.C., 1981, Python pit organs analyzed as warm receptors: *Cellular and Molecular Neurobiology*, v. 1, p. 271–278.
- De Freitas, D., 2009, *Eunectes murinus* (Green Anaconda). Diet: *Herpetological Review*, v. 40, p. 98.
- de Haas, C.P.J., 1950, Checklist of the snakes of the Indo-Australian archipelago (Reptiles, Ophidia): *Treubia*, v. 20, p. 511–625.
- de Lang, R., and Vogel, G., 2005, The snakes of Sulawesi; a field guide to the land snakes of Sulawesi with identification keys: Frankfurt am Main, Germany, Edition Chimaira, 312 p.
- de Rooij, N., 1917, The reptiles of the Indo-Australian archipelago. II. Ophidia: Leiden, E. J. Brill, 334 p.
- de Silva, A., 1990, Colour guide to the snakes of Sri Lanka: Portishead, Avon, R & A Publ., 130 p.
- de Vosjoli, P., and Klingenberg, R., 2005, Burmese Pythons plus Reticulated Pythons and related species: Irvine, Calif., Advanced Vivarium Syst., 79 p.
- Deoras, P.J., 1965, Snakes of India: New Dehli, India, National Book Trust, 148 p.
- Deraniyagala, P.E.P., 1955, A coloured atlas of some vertebrates from Ceylon, vol. 3, Serpentine Reptilia: Colombo, Ceylon National Museum, 121 p.
- Deuve, J., 1970, Les serpents du Laos: Paris, Office de al Recherche Scientifique et Technique Outre-Mer, 251 p.
- Devaux, R.J., 1995, Extermination of the cribo in St. Lucia, in Underwood, G.L., ed., A tale of old serpents: Castries, St. Lucia, West Indies, St. Lucia National Trust, p. 17–29.
- Di Cola, V., Cardozo, G., Lanfri, M., Scavuzzo, C.M., and Chiaraviglio, M., 2008, Modelling the distribution of the boid snakes, *Epicrates cenchria alvarezi* and *Boa constrictor occidentalis* in the Gran Chaco (South America): *Amphibia-Reptilia*, v. 29, p. 299–310.
- Dirksen, L., 1999, Zur Kenntnis der Anakonda-Arten (Serpentes: Boidae: Eunectes) I. *Eunectes deschauenseei* Dunn & Conant, 1936: *Herpetofauna*, v. 21, p. 12–21.
- Dirksen, L., 2002, Anakondas: Monographische Revision der Gattung *Eunectes* Wagler, 1830 (Serpentes, Boidae): Münster, Germany, Natur-und-Tier-Verl., 189 p.
- Dirksen, L., 2007, Rekordalter einer großen Anakonda in Gefangenschaft: *Ophidia*, v. 1, p. 6.
- Dirksen, L., and Böhme, W., 1998, Studien an Anakondas 2: Zum taxonomischen Status von *Eunectes murinus gigas* (Latreille, 1801) (Serpentes: Boidae), mit neuen Ergebnissen zur Gattung *Eunectes* Wagler 1830: *Salamandra*, v. 34, p. 1–16.
- Dirksen, L., and Böhme, W., 2005, Studies on anacondas III: A reappraisal of *Eunectes beniensis* Dirksen, 2002, from Bolivia, and a key to the species of the genus *Eunectes* Wagler, 1830 (Serpentes: Boidae): *Russian Journal of Herpetology*, v. 12, p. 223–229.
- Dirksen, L., Buongermini Palumbo, E., Strüssmann, C., and Waller, T., 1998, Protective balling-posture behavior in the genus *Eunectes* Wagler, 1830 (Serpentes: Boidae): *Herpetological Natural History*, v. 6, p. 151–155.

- Dirksen, L., and Henderson, R.W., 2002, *Eunectes deschauenseei* Dunn and Conant: de Schauensee's Anaconda: Catalogue of American Amphibians and Reptiles, v. 755, p. 1–3.
- Ditmars, R.L., 1912, The feeding habits of serpents: Zoologica: Scientific Contributions of the New York Zoological Society, v. 1, no. 11, p. 196–238.
- Ditmars, R.L., 1931, Snakes of the world: New York, Pyramid Publ., 208 p.
- Dixon, J.R., and Soini, P., 1986, The reptiles of the upper Amazon Basin, Iquitos region, Peru, Part 1, Lizards and amphisbaenians; Part 2, Crocodylians, turtles and snakes: Milwaukee, Wis., Milwaukee Public Museum, 154 p.
- Dobson, A.P., 1988, Restoring island ecosystems: the potential of parasites to control introduced mammals: Conservation Biology, v. 2, p. 31–39.
- Dobson, A.P., Hudson, P.J., and Lyles, A.M., 1992, Macroparasites: worms and others, in Crawley, M.J., ed., Natural enemies: the population biology of predators, parasites and diseases: Oxford, Blackwell Sci., p. 329–348.
- Domalain J.-Y., 1991, Panjamon–Ich war ein Kopffjäger: Munich, R. Ppiper GmbH & Co., 310 p.
- Dowling, H.G., and Jenner, J.V., 1988, Snakes of Burma: Checklist of recorded species and bibliography: Smithsonian Herpetological Information Service, v. 76, p. 1–19.
- Duellman, W.E., 1954, The amphibians and reptiles of Jorullo volcano, Michoacan, Mexico: Occasional Papers of the Museum of Zoology, University of Michigan, v. 560, p. 24.
- Duellman, W.E., 1963, Amphibians and reptiles of the rainforests of southern El Peten, Guatemala: University of Kansas Publications, Museum of Natural History, v. 15, p. 205–249.
- Duellman, W.E., 1978, The biology of an equatorial herpetofauna in Amazonian Ecuador: University of Kansas Museum of Natural History Miscellaneous Publications, v. 65, p. 1–352.
- Duellman, W.E., 2005, Cusco Amazónico: the lives of amphibians and reptiles in an Amazonian rainforest: Ithaca, N.Y., Comstock Publ., 433 p.
- Dundee, H.A., White, D.A., and Rico-Gray, V., 1986, Observations on the distribution and biology of some Yucatán Peninsula amphibians and reptiles: Bulletin of the Maryland Herpetological Society, v. 22, p. 37–50.
- Dunn, E.R., and Conant, R., 1936, Notes on anacondas, with descriptions of two new species: Proceedings of the Academy of Natural Sciences of Philadelphia, v. 88, p. 503–506.
- Durnford, L. 2003, World's first self-cloning snake, www.rnw.nl/science/html/030224snake.html, accessed June 2003.
- El-Kamali, H.H., 2000, Folk medicinal use of some animal products in Central Sudan: Journal of Ethnopharmacology, v. 72, p. 279–282.
- Ellis, T.M., and Chappell, M.A., 1987, Metabolism, temperature relations, maternal behavior, and reproductive energetics in the ball python (*Python regius*): Journal of Comparative Physiology B, v. 157, p. 393–402.
- Ben Lotte, J., 1996, Taxonomy and determination of Boa constrictor: Litteratura Serpentiaria, v. 16, no. 3, p. 78–81.

- Engeman, R.M., and Vice, D.S., 2001, A direct comparison of trapping and spotlight searches for capturing Brown Tree Snakes on Guam: *Pacific Conservation Biology*, v. 7, p. 4–8.
- Engeman, R.M., Vice, D.S., York, D.L., and Gruver, K.S., 2002, Sustained evaluation of the effectiveness of detector dogs for locating Brown Tree Snakes in cargo outbound from Guam: *Int.Biodegrad.Biodeter.*, v. 49, p. 101–106.
- Environmental Law Institute, 2008, Cooperative prevention of invasive wildlife introduction in Florida: Environmental Law Institute Technical Report, 58 p.
- Ernst, C.H., and Zug, G.R., 1996, *Snakes in question*: Washington, D.C., Smithsonian Institution Press, 203 p.
- Esbérard, C.E.L., and Vrcibradic, D., 2007, Snakes preying on bats: new records from Brazil and a review of recorded cases in the Neotropical region: *Revista Brasileira de Zoologia*, v. 24, p. 948–953.
- Eterovic, A., and Duarte, M.R., 2002, Exotic snakes in São Paulo City, southeastern Brazil: why xenophobia?: *Biodiversity and Conservation*, v. 11, p. 327–339.
- Ewers, W.H., 1968, Blood parasites of some New Guinea reptiles and amphibians: *Journal of Parasitology*, v. 54, p. 172–174.
- Fa, J.E., Garcia Yuste, J.E., and Castelo, R., 2000, Bushmeat markets on Bioko Island as a measure of hunting pressure: *Conservation Biology*, v. 14, p. 1,602–1,613.
- Farkas, S.L., Zádori, Z., Benko, M., Essbauer, S., Harrach, B., and Tigssen, P., 2004, A parvovirus isolated from royal python (*Python regius*) is a member of the genus Dependovirus: *Journal of General Virology*, v. 85, p. 555–561.
- Farr, W.L., Lavín Murcio, P.A., and Lazcano, D., 2007, New distributional records for amphibians and reptiles from the state of Tamaulipas, México: *Herpetological Review*, v. 38, p. 226–233.
- Fawcett, P.H., 1953, *Exploration Fawcett*: Essex, U.K., Arrow Books, 312 p.
- Fenner, F., 1983, Biological control, as exemplified by smallpox eradication and myxomatosis: *Proceedings of the Royal Society of London B Biological Sciences*, v. 218, p. 259–285.
- Ferrari, S.F., Pereira, W.L.A., Santos Ricardo R., and Veiga, L.M., 2004, Fatal attack of a Boa Constrictor on a Bearded Saki (*Chiropotes satanas utahicki*): *Folia Primatologica*, v. 75, p. 111–113.
- Field Naturalists' Club, 1893, Report of club meeting for March 1893: *Journal of the Trinidad Field Naturalists' Club*, v. 1, p. 155.
- Field Naturalists' Club, 1894, Report of club meeting 4th May 1894: *Journal of the Trinidad Field Naturalists' Club*, v. 2, p. 26.
- Fitch, H.S., 1970, Reproductive cycles of lizards and snakes: University of Kansas Museum of Natural History Miscellaneous Publications, v. 52, p. 1–247.
- Fitch, H.S., 1985, Variation in clutch and litter size in New World reptiles: University of Kansas Museum of Natural History Miscellaneous Publications, v. 76, p. 1–76.
- Flank, L., 1997, Playing with the big boys: handling large constrictors: *Reptiles*, v. 5, no. 6, p. 33–37.
- Flower, S.S., 1899, Notes on a second collection of reptiles made in the Malay Peninsula and Siam, from November 1896 to September 1898, with a list of the species recorded from those countries: *Proceedings of the Zoological Society (London)*, v. 1899, p. 600–697.

- Fogel, D., 1997, Captive husbandry and propagation of the boa constrictors and related boas: Melbourne, Fla., Krieger Publ., 98 p.
- Foster, J., and Price, P., 1997, A case of predation by Python on a fruit bat *Pteropus giganteus* with notes on bat-snake interactions: *Hamadryad*, v. 22, p. 58–61.
- Frank, N., and Haefner, U., 1981, Host range and host specificity of *Sarcosystis singaporensis*: *Parasitology*, v. 250, p. 355–360.
- Frank, N., and Ramus, E., 1995, A complete guide to scientific and common names of reptiles and amphibians of the world: Pottsville, Pa., Reptile and Amphibian Magazine, 377 p.
- Franke, J., and Telecky, T.M., 2001, Reptiles as pets; an examination of the trade in live reptiles in the United States: Washington, D.C., Humane Society of the U.S., 146 p.
- Fredriksson, G.M., 2005, Predation on Sun Bears by Reticulated Python in East Kalimantan, Indonesian Borneo: *Raffles Bulletin of Zoology*, v. 53, p. 165–168.
- Fritts, T.H., and McCoid, M.J., 1991, Predation by the Brown Tree Snake on poultry and other domesticated animals in Guam: *The Snake*, v. 23, p. 75–80.
- Fritts, T.H., and Rodda, G.H., 1998, The role of introduced species in the degradation of island ecosystems: a case history of Guam: *Annual Review of Ecology and Systematics*, v. 29, p. 113–140.
- Fritts, T.H., Scott, N.J., Jr., and Savidge, J.A., 1987, Activity of the arboreal Brown Tree Snake (*Boiga irregularis*) on Guam as determined by electrical power outages: *The Snake*, v. 19, p. 51–58.
- Frye, F.L., and Mader, D.R., 1985, Precocious sexual maturity in a juvenile male python: *Journal of Zoo and Animal Medicine*, v. 16, p. 69–72.
- Gaige, H.T., Hartweg, N., and Stuart, L.C., 1937, Notes on a collection of amphibians and reptiles from eastern Nicaragua: *Occasional Papers of the Museum of Zoology, University of Michigan*, v. no. 357, p. 1–20.
- Gasc, J.-P., and Rodriguez, M.T., 1980, Liste préliminaire des serpents de la Guyane française: *Bulletin Museum National d'Histoire Naturelle*, v. Series 4, Section A, 2, p. 559–598.
- Gerhardt, R.P., Harris, P.M., and Marroquin, M.A.V., 1993, Food habits of nesting great black hawks in Tikal National Park, Guatemala: *Biotropica*, v. 25, p. 349–352.
- Gilbert, C. 2008, The boa list: Available online at <http://www.boalist.com/>, accessed 30 Apr 2008.
- Gillingham, J.C., 1987, Social behavior, in Seigel, R.A., Collins, J.T., and Novak, S.S., eds., *Snakes: ecology and evolutionary biology*: New York, Macmillan, p. 184–209.
- Gillingham, J.C., and Chambers, J.A., 1982, Courtship and pelvic spur use in the Burmese python, *Python molurus bivittatus*: *Copeia*, v. 1982, p. 193–196.
- Giraud, A.R., and Scrocchi, G.J., 2002, Argentinian snakes: an annotated checklist: *Smithsonian Herpetological Information Service*, v. 132, no. 1, p. 53.
- Gomes, N., Puerto, G., Buononato, M.A., and Ribeiro, M.d.F.M., 1989, Atlas anatómico de Boa constrictor Linnaeus, 1758 (Serpentes; Boidae): *Instituto Butantan Monografias 2*: 1-60, v. 2, p. 1–60.
- Gonwouo, N.L., LeBreton, M., Chirio, L., Ineich, I., Tchamba, N.M., Ngassam, P., Dzikouk, G., and Diffo, J.L., 2007, Biodiversity and conservation of the reptiles of the Mt. Cameroon area: *African Journal of Herpetology*, v. 56, p. 149–161.

- Gonzalez-Baca, C., and Cuaron, A.D., 2003, Foraging ecology of Boa constrictor, an introduced predator to a Caribbean island Manaus, Brazil: Joint Meeting of Ichthyologists and Herpetologists, p. 3.
- Goris, R.C., Nakano, M., Atobe, Y., and Funakoshi, K., 2007, The infrared sight of boas and pythons, *in* Henderson, R.W., and Powell, R., eds., *Biology of the boas and pythons*: Eagle Mountain, Utah, Eagle Mountain Publishing, p. 286–296.
- Goulding, M., 1990, *Amazon: the flooded forest*: New York, Sterling Publ., 208 p.
- Grace, M.S., and Matushita, A., 2007, Neural correlates of complex behavior: vision and infrared imaging in boas and pythons, *in* Henderson, R.W., and Powell, R., eds., *Biology of the boas and pythons*: Eagle Mountain, Utah, Eagle Mountain Publishing, p. 271–285.
- Gragg, J.E., Rodda, G.H., Savidge, J.A., White, G.C., Dean-Bradley, K., and Ellingson, A.R., 2007, Response of brown treesnakes to reduction of their rodent prey: *Journal of Wildlife Management*, v. 71, p. 2,311–2,317.
- Greene, D.U., Potts, J.M., Duquesnel, J.G., and Snow, R.W., 2007, *Python molurus bivittatus* (Burmese Python): *Herpetological Review*, v. 38, p. 355.
- Greene, H.W., 1983, Boa constrictor (Boa, Béquer, Boa Constrictor), *in* Janzen, D.H., ed., *Costa Rican natural history*: Chicago, Univ. Chicago Press, p. 380–382.
- Greene, H.W., Fogden, M., and Fogden, P., 1997, *Snakes: the evolution of mystery in nature*: Berkeley, Calif., Univ. California Press, 351 p.
- Greene, M.P., Boback, S.M., and Guyer, C., 2003, Boa constrictor (*Boa constrictor*). Diet: *Herpetological Review*, v. 34, p. 146.
- Groombridge, B., and Luxmoore, R., 1991, *Pythons in South-east Asia: A review of distribution, status, and trade in three selected species*: Lausanne, Switzerland, Report to CITES Secretariat, 127 p.
- Groot, T.V.M., Bruins, E., and Breeuwer, J.A.J., 2003, Molecular genetic evidence for parthogenesis in the Burmese python, *Python molurus bivittatus*: *Heredity*, v. 90, p. 130–135.
- Guisan, A., and Thuiller, W., 2005, Predicting species distribution: offering more than simple habitat models: *Ecology Letters*, v. 8, p. 993–1,009.
- Gursky, S., 2002, Predation on a wild Spectral Tarsier (*Tarsius spectrum*) by a snake: *Folia Primatologica*, v. 73, p. 60–62.
- Gutsche, A., 2005, *Ctenosaura bakeri*: Predation: *Herpetological Review*, v. 36, p. 317.
- Guyer, C., and Donnelly, M.A., 2005, *Amphibians and reptiles of La Selva, Costa Rica, and the Caribbean slope: a comprehensive guide*: Berkeley, Calif., Univ. of Calif. Press, 299 p.
- Guyer, C., Rodda, G.H., and Donnelly, M.A., in press, Visual encounter surveys, *in* Foster, M.S., McDiarmid, R.W., Guyer, C., Gibbons, J.W., and Chernoff, N., eds., *Measuring and monitoring biological diversity: standard methods for reptiles*: Berkeley, Calif., Univ. Calif. Press.
- Guynn, D.C., Jr., 1997, Contraception in wildlife management: reality or illusion?, *in* Kreeger, T.J., ed., *Contraception in wildlife management*: Fort Collins, Colo., U.S. Department of Agriculture, Animal and Plant Health Inspection Service, *Tech. Bulletin 1853*, p. 241–246.
- Haacke, W.D., 1984, The herpetology of the Southern Kalahari domain: Koedoe, v. supplement, p. 171–186.

- Hagen, B., 1890, Die Pflanzen-und Thierwelt von Deli auf der Ostküste Sumatras: Tijdschrift van het Koninklijk Nederlandsch Aardrijkskundig Genootschap, Amsterdam, v. 2, p. 1–240.
- Hagenbeck, C., 1909, Beasts and men; being Carl Hagenbeck's experiences for half a century among wild animals (an abridged translation by H. S. R. Elliot and A. G. Thacker): London, Longmans, Green, and Co., 299 p.
- Hakansson, N.T., 1981, An annotated checklist of reptiles known to occur in The Gambia: *Journal of Herpetology*, v. 15, p. 155–161.
- Hanley, J.A., and McNeil, B.J., 1982, The meaning and use of the area under a receiver operating characteristic (ROC) curve: *Radiology*, v. 143, p. 29–36.
- Harvey, R.G., Brien, M.L., Cherkiss, M.S., Dorcas, M.E., Rochford, M., Snow, R.W., and Mazzotti, F.J., 2008, Burmese Pythons in South Florida: Scientific support for invasive species management: Gainesville, University of Florida, p. 8.
- Hawley, N.B., 2007, Custom trucks, radio snake jingles, and temporary tattoos: an overview of a successful public awareness campaign related to Brown Treesnakes in the Commonwealth of the Northern Mariana Islands, *in* Witmer, G.W., Pitt, W.C., and Fagerstone, K.A., eds., *Managing vertebrate invasive species: Proceedings of an international symposium: Fort Collins, Colo., USDA-APHIS Wildlife Services, National Wildlife Research Center*, p. 53–56.
- Hay, P.W., and Martin, P.W., 1966, Python predation on a Uganda kob: *African Journal of Ecology*, v. 4, p. 151–152.
- Hayashi, Y., Sawai, Y., Tanaka, H., and Mishima, S., 1999, Development of electric fence barriers for Habu, *Trimeresurus flavoviridis*, in the Amami Islands, *in* Rodda, G.H., Sawai, Y., Chiszar, D., and Tanaka, H., eds., *Problem snake management: the Habu and the Brown Treesnake: Ithaca, N.Y., Cornell Univ. Press*, p. 319–326.
- Headland, T., and Greene, H.W., 2007, Primates and pythons as predators, prey, and potential competitors: St. Louis, Mo., Joint Meeting of Ichthyologists and Herpetologists, CD.
- Hediger, H., 1968, Der Akademiestreit über die brütende Pythons: *Neue Zürcher Zeitung*, v. 11-6-1968, no. 351.
- Henderson, R.W., and Powell, R., 2007, *Biology of the boas and pythons: Eagle Mountain, Utah, Eagle Mountain Publishing*, 438 p.
- Henderson, R.W., Waller, T., Micucci, P., Puerto, G., and Bourgeois, R.W., 1995, Ecological correlates and patterns in the distribution of Neotropical boines (Serpentes: Boidae): a preliminary assessment: *Herpetological Natural History*, v. 3, p. 15–27.
- Hendrickson, J.R., 1966, Observations on the fauna of Pulau Tioman and Pulau Tulai, 5, The reptiles: *Bulletin of the National Museum of Singapore*, v. 34, p. 53–71.
- Henke, S.E., 1998, The effect of multiple search items and item abundance on the efficiency of human searchers: *Journal of Herpetology*, v. 32, p. 112–115.
- Hero, J.-M., and dos Santos, A., 1987, *Eunectes murinus* (Anaconda), Reproduction: *Herpetological Review*, v. 18, p. 36.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., and Jarvis, A., 2005, Very high resolution interpolated climate surfaces for global land areas: *International Journal of Climatology*, v. 25, p. 1,965–1,978.

- Hoddle, M.S., 1998, Biological control of vertebrate pests, *in* Fisher, T.W., Bellows, T.S., Caltagirone, L.E., Dahlsten, D.L., Huffaker, C.B., and Gordh, G., eds., *Handbook of biological control*: London, Chapman and Hall, p. 1–68.
- Holmes, J.C., 1982, Impact of infectious disease agents on the population growth and geographical distribution of animals, *in* Anderson, R.M., and Mar, R.M., eds., *Population biology of infectious diseases*: Berlin, Springer-Verlag, p. 37–51.
- Holmstrom, W.F., Jr., 1980, Observations on the reproduction of the common anaconda, *Eunectes murinus*, at the New York Zoological Park: *Herpetological Review*, v. 11, p. 32–33.
- Holmstrom, W.F., Jr., 1982, *Eunectes* (anacondas): Maturation: *Herpetological Review*, v. 13, p. 126.
- Holtzman, D.A., Shifley, S., and Sisson, D., 2007, Spatial ecology of resident and displaced boa constrictors (*Boa constrictor imperator*) on Ometepe Island, Nicaragua: implications for conservation, *in* Henderson, R.W., and Powell, R., eds., *Biology of the boas and pythons*: Eagle Mountain, Utah, Eagle Mountain Publishing, p. 364–372.
- Honegger, R.E., 1970, Beitrag zur Fortflanzungsbiologie von *Boa constrictor* und *Python reticulatus* (Reptilia, Boidae): *Salamandra*, v. 6, p. 73–79.
- Honegger, R.E., 1993, Amateurs–conservation and captive care: Adelaide, Second World Congress of Herpetology, p. 122.
- Hoogerwerf, A., 1970, *Udjung Kulon: the land of the last Javan rhinoceros*: Leiden, Brill, 512 p.
- Hoover, C., 1998, *The U.S. role in the international live reptile trade: Amazon Tree Boas to Zululand Dwarf Chameleons*: Washington, D.C., TRAFFIC North America, 59 p.
- Hoser, R.T., 2004, A reclassification of the pythoninae including the descriptions of two new genera, two new species and nine new subspecies, Part II: *Crocodylian: Journal of the Victorian Association of Amateur Herpetologists*, v. 4, no. 4, p. 21–40.
- How, R.A., and Kitchener, D.J., 1997, Biogeography of Indonesian snakes: *Journal of Biogeography*, v. 24, p. 725–735.
- Howarth, F.G., 1991, The environmental impacts of classical biological control: *Annual Review of Entomology*, v. 36, p. 485–509.
- Howarth, F.G., 1999, Environmental risks of biological control of vertebrates, *in* Rodda, G.H., Sawai, Y., Chiszar, D., and Tanaka, H., eds., *Problem snake management: the Habu and the Brown Treesnake*: Ithaca, N.Y., Cornell Univ. Press, p. 399–410.
- Hutchison, V.H., Dowling, H.G., and Vinegar, A., 1966, Thermoregulation in a brooding female Indian Python, *Python molurus bivittatus*: *Science*, v. 151, p. 694–696.
- Infante-Rivero, E., Natera-Mumaw, M., and Marcano, A., 2008, Extension of the distribution of *Eunectes murinus* (Linnaeus, 1758) and *Helicops angulatus* (Linnaeus, 1758) in Venezuela, with notes on ophidophagia : *Herpetotropicos*, v. 4, p. 39.
- Inger, R.F., and Colwell, R.K., 1977, Organization of contiguous communities of amphibians and reptiles in Thailand: *Ecological Monographs*, v. 47, p. 229–253.
- Inger, R.F., and Tan, F.L., 1996, *The natural history of amphibians and reptiles in Sabah: Kota Kinabalu, Sabah, Malaysia*, Natural History Publ. (Borneo) Sdn. Bhd., 101 p.
- Inger, R.F., and Voris, H.K., 2001, The biogeographical relations of the frogs and snakes of Sundaland: *Journal of Biogeography*, v. 28, p. 863–891.
- Interdisciplinary Center for Biotechnology Research, 1992, Research proposal: *Biological control of the Brown Tree Snake, Boiga irregularis through application of*

- new biotechnologies: Madison, proposal to U.S. Fish and Wildlife Service, National Wildlife Health Research Center, 32 p.
- Ishii, A., and Hayashi, Y., 1978, Attempt to transmit *Entamoeba invadens* by tortoise to Habu, *Trimeresurus flavoviridis*, in an enclosure [in Japanese with English summary]: *The Snake*, v. 10, p. 16–17.
- Ishii, A., Kawaguchi, E., and Hayashi, Y., 1979, Attempt to transmit *Entamoeba invadens* by tortoise to Habu, *Trimeresurus flavoviridis* [in Japanese with English summary]: *The Snake*, v. 11, p. 25–27.
- Ishii, A., and Noboru, Y., 1971, Attempts to infect laboratory rats and mice and the snake Habu, *Trimeresurus flavoviridis*, with *Entamoeba invadens*: *The Snake*, v. 3, p. 24–29.
- Ishii, A., Noboru, Y., Ono, T., and Sawai, Y., 1971, Experimental oral inoculation of *Entamoeba invadens* in some snakes of the Amami Islands [in Japanese with English summary]: *The Snake*, v. 3, p. 30–34.
- Ishii, A., Owhashi, M., Kawaguchi, E., Hayashi, H., and Nakai, H., 1981, Experimental transmission of *Entamoeba invadens* from tortoise to the venomous snake Habu, *Trimeresurus flavoviridis* [in Japanese with English summary]: *The Snake*, v. 13, p. 1–5.
- Ishii, A., and Sawai, Y., 1999, Biological control of Habu with *Entamoeba invadens*, in Rodda, G.H., Sawai, Y., Chiszar, D., and Tanaka, H., eds., *Problem snake management: the Habu and the Brown Treesnake*: Ithaca, N.Y., Cornell Univ. Press, p. 391–398.
- Ishii, A., Takaoka, M., Kano, R., Suzuki, H., and Ori, M., 1976, Experimental oral inoculation of *Entamoeba invadens* in some amphibians and reptiles [in Japanese with English summary]: *The Snake*, v. 8, p. 64–68.
- Islam, M.Z., and Islam, M.S., 1997, Wildlife status in the evergreen forests between Ramu and Ukhia of Cox's Bazar Forest Division: *Tiger Paper*, v. 24, p. 9–13.
- Ismail, S., 1984, Life history of the tick *Amblyomma cordifernum* under laboratory conditions: *Malaysian Nature Journal*, v. 38, p. 73–78.
- ITIS, 2008, International taxonomic information system: Available online at <http://www.catalogueoflife.org/search.php>, accessed Jun. 2007–Dec. 2008.
- Jackson, K., and Blackburn, D.G., 2007, The amphibians and reptiles of Nouabale-Ndoki National Park, Republic of Congo (Brazzaville): *Salamandra*, v. 43, p. 149–164.
- Jacobsen, E., 1936, Reuzenslangen en hun prooi: *Tropical Natuur Jub. Uitg.*, v. p. 49–51.
- Jacobson, E.R., 1986a, Viruses and viral associated diseases of reptiles, in Bels, V.L., and Van Den Sande, A.P., eds., *Maintenance and reproduction of reptiles in captivity*, vol. II, *Diseases*: *Bulletins de al Societe Royale De Zoologie D'Anvers, Acta Zoologica et Pathologica Antverpiensia.*, p. 73–89.
- Jacobson, E.R., 1986b, Parasitic diseases of reptiles, in Fowler, M.E., ed., *Zoo and wild animal medicine*: Philadelphia, Pa., W. B. Saunders, p. 162–181.
- Janzen, D.H., 1970, Altruism by coatis in the face of predation by Boa constrictor: *Journal of Mammalogy*, v. 51, p. 387–389.
- Jayne, B.C., and Riley, M.A., 2007, Scaling of the axial morphology and gap-bridging ability of the Brown Tree Snake (*Boiga irregularis*): *Journal of Experimental Biology*, v. 210, p. 1,148–1,160.
- Ji, D.-M., and Wen, S.-S., 2001, *Atlas of the reptiles of China* [in Chinese]: Henan, China, Henan Sci. Technol. Press, 347 p.

- Joger, U., 1989, The herpetofauna of the Central African Republic, *with* description of a new species of Rhinotyphlops (Serpentes: Typhlopidae), *in* Peters, G., and Hutterer, R., eds., *Vertebrates in the tropics*: Bonn, Germany, Museum Alexander Koenig, p. 85–102.
- Joger, U., and Lambert, M.R.K., 1996, Analysis of the herpetofauna of the Republic of Mali, I, Annotated inventory, *with* description of a new Uromastyx (Sauria: Agamidae): *Journal of African Zoology*, v. 110, p. 21–51.
- Joger, U., and Lambert, M.R.K., 2002, Inventory of amphibians and reptiles in SE Senegal, including the Niokola-Koba National Park, *with* observations on factors influencing diversity: *Tropical Zoology*, v. 15, p. 165–185.
- Kabisch, K., 2002, Family Boidae, *in* Schleich, H.H., and Kästle, W., eds., *Amphibians and reptiles of Nepal*: Ruggell, Germany, A.R.G. Gantner Verlag K.G., p. 785–802.
- Kan, S.K.P., and Hii, J.L.K., 1979, Helminth eggs from faeces of *Python reticulatus* with special reference to *Capillaria* and its public health significance in Sabah, Malaysia: *Southeast Asian Journal of Tropical Medicine and Public Health*, v. 10, p. 155–157.
- Karsen, S.J., Wai-neng Lau, M., and Bogadek, A., 1986, *Hong Kong amphibians and reptiles*: Hong Kong, Urban Council, 136 p.
- Katsuren, S., Yoshida, C., and Nishimura, M., 1999, A ten-year trapping program to eradicate Habu, *Trimeresurus flavoviridis*, from Minnajima, a small island in the Okinawa Islands, Japan, *in* Rodda, G.H., Sawai, Y., Chiszar, D., and Tanaka, H., eds., *Problem snake management: the Habu and the Brown Treesnake*: Ithaca, N.Y., Cornell Univ. Press, p. 340–347.
- Keays, R.W., 1929, An unpleasant experience with a python: *Journal of the Bombay Natural History Society*, v. 33, p. 721–722.
- Keirans, J.E., 1972, Redescription of *Amblyomma fulvum* Neumann 1899 (Acarina: Ixodidae), a parasite of the giant anaconda in northern South America: *Journal of Medical Entomology*, v. 9, p. 138–139.
- Khan, M.A.R., 1982, On the endangered snakes of Bangladesh: Meeting IUCN/SSC Snake Specialist Group, Madras, India, IUCN, 4 p.
- Khan, M.S., 2002, *A guide to the snakes of Pakistan*: Frankfurt am Main, Germany, Edition Chimaira, 265 p.
- Khan, M.S., 2006, *Amphibians and reptiles of Pakistan*: Melbourne, Fla., Krieger Publ., 311 p.
- Kingley, K.J., 1987, Potential growth rate of pythons and boas: *Snake Keeper*, v. 1, no. 6, p. 4–5.
- Kirkpatrick, J.F., Turner, J.W. Jr, and Liu, I.K.M., 1997, Contraception of wild and feral equids, *in* Kreeger, T.J., ed., *Contraception in wildlife management*: Fort Collins, Colo., U.S. Department of Agriculture., APHIS Tech. Bulletin 1853, p. 161–169.
- Kleinman, D.M., Dunne, E.F., and Taravella, M.J., 1998, Boa Constrictor bite to the eye: *Archives of Ophthalmology*, v. 116, p. 949–950.
- Klingenberg, R.J., 1993, *Understanding reptile parasites: A basic manual for herpetoculturists and veterinarians*: Mission Viejo, Calif., Advanced Vivarium Systems, 83 p.
- Kluge, A.G., 1991, Bione snake phylogeny and research cycles: *Miscellaneous Publications Museum of Zoology, University of Michigan*, v. 178, p. 1–58.

- Kluge, A.G., 1993, Aspidites and the phylogeny of pythonine snakes: Sydney, Records of the Australian Museum, Supplement 19, 77 p.
- Knotek, Z., Jekl, V., Dorrestein, G.M., Blahak, S., and Knotkova, Z., 2007, Presumptive viral infections in captive populations of *Boa constrictor* in the Czech Republic: *Veterinarni Medicina*, v. 52, p. 512–520.
- Koch, W., 1926, Brehms Tierleben. Kriechtiere, Lurche, Fische, Vierter Band: Leipzig, Schlüter & Co., GmbH, 428 p.
- Kock, D., and Schröder, H., 1981, Die Gattung Python in Bangladesh (Reptilia: Serpentes: Boidae): *Salamandra*, v. 17, p. 112–118.
- Köhler, G., 1996, Krankheiten der reptilien und amphibien: Stuttgart, Germany, DATZ Terrarienbücher, 166 p.
- Köhler, G., 2003, Reptiles of Central America: Offenbach, Germany, Herpeton Verlag, 368 p.
- Köhler, G., Veselý, M., and Greenbaum, E., 2006, The amphibians and reptiles of El Salvador: Melbourne, Fla., Krieger Publ., 248 p.
- Kolbe, J.J., Glor, R.E., Rodríguez Schettino, L., Chamizo Lara, A., Larson, A., and Losos, J.B., 2004, Genetic variation increases during biological invasion by a Cuban lizard: *Nature*, v. 431, p. 177–181.
- Kolbe, J.J., Larson, A., Losos, J.B., and de Queiroz, K., 2008, Admixture determines genetic diversity and population differentiation in the biological invasion of a lizard species: *Biology Letters*, v. 4, p. 434–437.
- Koopman, B.O., 1946, Search and screening: Center for Naval Analyses (OEG Report No. 56), available online at <http://www.cna.org/documents/1100005600.PDF>, accessed 8 Sep 2009.
- Kopstein, F., 1926, Reptilien von den Molukken und den benachbarten Inseln: *Zoologische mededeelingen (Leiden)*, v. 9, no. 2-3, p. 71–112.
- Kopstein, F., 1927, Over het verslinden van menschen door *Python reticulatus*: *Tropical Natuur*, v. 16, p. 65–67.
- Kopstein, F., 1930, Herpetologische Notizen, III, Reptilien des östlichen Preanger (West Java): *Treubia*, v. 12, p. 273–276.
- Kopstein, F., 1938, Ein beitrage zur Eierkunde und zur Fortpflanzung der Malaiischen reptilien: *Bulletin of the Raffles Museum*, v. 14, p. 81–167.
- Kornacker, P.M., 1999, Checklist and key to the snakes of Venezuela: Rheinbachk, Germany, Pako-Verlag, 270 p.
- Kraus, F., 2009, Alien reptiles and amphibians; a scientific compendium and analysis: New York, Springer Ser. in Inv. Ecol. 4, 563 p.
- Krysko, K.L., Nifong, J.C., Snow, R.W., and Enge, K.M., 2008, Reproduction of the Burmese Python (*Python molurus bivittatus*) in southern Florida: *Applied Herpetology*, v. 5, p. 93–95.
- La Marca, E., and Soriano, P.J., 2004, Reptiles de los Andes de Venezuela: Merida, Venezuela, Fundacion Polar, Conservacion Internacional, CODEPRE-ULA, Fundacite Merida, BIOGEOS, 173 p.
- La Panouse, R., and Pellier, C., 1973, Ponte d'un python reticule (*Python reticulatus*) eleve en terrarium, et incubation des oeufs [in French with English summary]: *Bulletin Musee National d'Historie Naturel*, v. 79, p. 37–48.

- Lamonica, R.d.C., Abrahão-Charles, H., de Castro Loguercio, M.F., and Rocha-Barbosa, O., 2007, Growth, shedding and food intake in captive *Eunectes murinus* (Linnaeus, 1758) (Serpentes: Boidae): *International Journal of Morphology*, v. 25, p. 103–108.
- Lancini V., A.R., 1986, *Serpientes de Venezuela*: Caracas, Edit. Ernesto Armitano, 264 p.
- Langhammer, J.K., 1983, A new subspecies of Boa Constrictor, *Boa constrictor melanogaster*, from Ecuador (Serpentes: Boidae): *Tropical Fish Hobbyist*, v. 32, no. 4, p. 70–79.
- Lanza, B., and Nistri, A., 2005, Somali Boidae (genus *Eryx* Daudin 1803) and Pythonidae (genus *Python* Daudin 1803) (Reptilia Serpentes): *Tropical Zoology*, v. 18, p. 67–136.
- Lawson, D.P., 2004, *Python sebae* (African Rock Python): Habitat use and home range: *Herpetological Review*, v. 35, p. 180–181.
- Lawson, R., Slowinski, J.B., and Burbrink, F.T., 2004, A molecular approach to discerning the phylogenetic placement of the enigmatic snake *Xenophidion schaeferi* among the Alethinophidia: *Journal of Zoology (London)*, v. 263, p. 285–294.
- Lazell, J.D., Jr., 1964, The Lesser Antillean representatives of Bothrops and Constrictor: *Bulletin of the Museum of Comparative Zoology*, v. 132, p. 245–273.
- LeBreton, M., 1999, A working checklist of the herpetofauna of Cameroon: Amsterdam, IUCN, 141 p.
- Lederer, G., 1942, Fortpflanzung und Entwicklung von *Eunectes notaeus* Cope (Boidae): *Zoologischer Anzeiger*, v. 139, p. 162–172.
- Lederer, G., 1944, Nahrungserwerb, Entwicklung, Paarung und Brutfürsorge von *Python reticulatus* (Schneider): *Zoologische Jahrbücher (Anatomie)*, Jena, v. 68, p. 363–398.
- Lederer, G., 1956, Fortpflanzungsbiologie und Entwicklung von *Python molurus molurus* (Linné) und *Python molurus bivittatus* (Kühl): *Die Aquarien-und Terrarien-Zeitschrift*, v. 9, p. 243–248.
- Lee, J.C., 1996, *The amphibians and reptiles of the Yucatán Peninsula*: Ithaca, N.Y., Cornell Univ. Press, 512 p.
- Leenders, T.A.A.M., 2001, *A guide to amphibians and reptiles of Costa Rica*: Miami, Fla., Zona Tropical, 305 p.
- Leenders, T.A.A.M., and Watkins-Colwell, G., 2003, *Boa constrictor (Boa constrictor)*. Diet: *Herpetological Review*, v. 34, p. 146–147.
- Leenders, T.A.A.M., and Watkins-Colwell, G.J., 2004, Notes on a collection of amphibians and reptiles from El Salvador: *Postilla*, v. no. 231, p. 1–31.
- Lehr, E., 2002, *Amphibien und reptilien in Peru*: Munster, Germany, Natur-und Tier-Verlag GmbH, 206 p.
- Lemos-Espinal, J.A., and Ballinger, R.E., 1994, *Ctenosaura pectinata* (Mexican spiny-tailed iguana): predation: *Herpetological Review*, v. 25, p. 26.
- Leviton, A.E., 1963, Remarks on the zoogeography of Philippine terrestrial snakes: *Proceedings of the California Academy of Sciences*, v. 31, p. 369–416.
- Lia, R., Tarsitano, E., and Orsini, O., 1999, Pentastomids causing zoonosis: Report on *Porocephalus clavatus* Sambon, 1992 in a captive *Boa constrictor* from Apulia region: *Rivista di Idrobiologia*, v. 38, p. 63–72.
- Lim, F.L.K., 1981, The Reticulated Python: *Nature malaysiana*, v. 6, no. 4, p. 14–17.
- Lim, K.K.L., and Lim, F.L.K., 1992, *A guide to the amphibians and reptiles of Singapore*: Singapore, Singapore Science Centre, 160 p.

- Lin, L., 1983, On the python from Zhang autonomous region of Guangxi [entirely in Chinese]: Chinese Journal of Zoology, Beijing, v. 18, p. 8–10.
- Liu, D., 1986, *Python molurus bivittatus* occurred in Qingchuan County of Sichuan Province [in Chinese]: Acta Sinica Herpetologica, v. 5, p. 198.
- Lovich, J.E., and Gibbons, J.W., 1992, A review of techniques for quantifying sexual size dimorphism: Growth, Development and Aging, v. 56, p. 269–281.
- Luiselli, L., and Akani, G.C., 2002, An investigation into the composition, complexity and functioning of snake communities in the mangroves of south-eastern Nigeria: African Journal of Ecology, v. 40, p. 220–227.
- Luiselli, L., Akani, G.C., and Capizzi, D., 1998, Food resource partitioning of a community of snakes in a swamp rainforest of south-eastern Nigeria: Journal of Zoology (London), v. 246, p. 125–133.
- Luiselli, L., Akani, G.C., Eniang, E.A., and Politano, E., 2007, Comparative ecology and ecological modeling of sympatric pythons, *Python regius* and *Python sebae*, in Henderson, R.W., and Powell, R., eds., Biology of the boas and pythons: Eagle Mountain, Utah, Eagle Mountain Publishing, p. 88–100.
- Luiselli, L., Angelici, F.M., and Akani, G.C., 2001, Food habits of *Python sebae* in suburban and natural habitats: African Journal of Ecology, v. 39, p. 116–118.
- Lundberg, M., 2002, Herpetofaunan på Hog Islands, Honduras: Snoken Nat.Swed, Herp.Assoc.[Snoken utgiven av Sverigea Herpetologiska Riksförening], v. 2002, no. 1, p. 4–13.
- Luttenberger, F., 1984, Nachzucht der Paraguay-Anakonda (*Eunectes notaeus* Cope 1862) im Tiergarten-Schönbrunn, Wien: Aquaterra, v. 10, p. 15–21.
- Luz, S., 2002, Adaptive Veränderungen im Verdauungstrakt des Netpython (*Python reticulatus*) in Abhängigkeit von der Nahrungsaufnahme: Hannover, Germany, School of Veterinary Medicine, 306 p.
- MacDonald, D., 1992, Expedition to Borneo: Kuala Lumpur, Season Printers Sdn Bhd, 180 p.
- Macedo-Bernarde, L.C., 2006, *Eunectes murinus* (Linnaeus) (Serpentes, Boidae), preying activity: Pan-American Journal of Aquatic Sciences, v. 1, p. II.
- MacKerras, M.J., 1961, The haematozoa of Australian reptiles: Australian Journal of Zoology, v. 9, p. 61–122.
- Mader, D.R., 1996, Reptile medicine and surgery (1 ed.): St. Louis, Mo., Saunders Elsevier, 512 p.
- Malhotra, A., and Thorpe, R.S., 1999, Reptiles and amphibians of the eastern Caribbean: Bangor, U.K., Univ. of Wales, 134 p.
- Malkmus, R., 1992, Herpetologische Beobachtungen am Mount Kinabalu, Nord-Borneo. III: Mitteilungen aus dem Zoologischen Museum im Berlin, v. 68, p. 101–138.
- Malkmus, R., Manthey, U., Vogel, G., Hoffmann, P., and Kosuch, J., 2002, Amphibians and reptiles of Mount Kinabalu (North Borneo): Ruggell, Liechtenstein, A.R.G. Gantner Verlag K.G., 424 p.
- Malla, Y.K., 1968, Reptiles of Nepal: The faunal studies of Nepal: Nepal National Comm. for UNESCO, Region. seminar on the ecology of tropical highlands: Kathmandu, HMG & UNESCO, p. 12–15.

- Malonza, P.K., Wasonga, V.D., Muchai, V., Rotich, D., and Bwong, B.A., 2006, Diversity and biogeography of herpetofauna of the Tana River Primate National Reserve, Kenya: *Journal of East African Natural History*, v. 95, p. 95–109.
- Manthey, U., and Grossmann, W., 1997, *Amphibien & Reptilien südostasiens*: Berlin, Natur und Tier-Verlag, 512 p.
- Manvell, R.J., Drury, S.E., Geach, M., and Lewis, J.C.M., 2000, Isolation of ophidian paramyxovirus type 7 from a Reticulated Python in the UK: *Veterinary Record*, v. 147, p. 696.
- Marais, J., 2004, *A guide to the snakes of southern Africa*: Cape Town, Struik, 312 p.
- Martin, P.S., 1958, A biogeography of reptiles and amphibians in the Gomez Farias region, Tamaulipas, Mexico: *Miscellaneous Publications of the Museum of Zoology, University of Michigan*, v. no. 101, p. 1–124.
- Martins, M., and Oliveira, M.E., 1998, Natural history of snakes in forests of the Manaus region, Central Amazonia, Brazil: *Herpetological Natural History*, v. 6, p. 78–150.
- Martínez-Morales, M.A., and Cuarón, A.D., 1999, Boa constrictor, an introduced predator threatening the endemic fauna on Cozumel Island, Mexico: *Biodiversity and Conservation*, v. 8, p. 957–963.
- Mason, R.T., 1992, Reptilian pheromones, in Gans, C., and Crews, D., eds., *Biology of the Reptilia*, vol. 18, *Physiology E: Hormones, brain, and behavior*: Chicago, Univ. Chicago Press, p. 114–228.
- Mason, R.T., 1999, Integrated pest management: the case for pheromonal control of Habu (*Trimeresurus flavoviridis*) and Brown Treesnakes (*Boiga irregularis*), in Rodda, G.H., Sawai, Y., Chiszar, D., and Tanaka, H., eds., *Problem snake management: the Habu and the Brown Treesnake*: Ithaca, N.Y., Cornell Univ. Press, p. 196–205.
- Mayr, E., 1974, *Populations, species, and evolution an abridgment of animal species and evolution*: Cambridge, Mass., The Belknap Press of Harvard University Press, 453 p.
- McCoid, M.J., Campbell, E.W., III, and Alokoa, B.C., 1993, Efficacy of a chemical repellent for the Brown Tree Snake (*Boiga irregularis*): *The Snake*, v. 25, p. 115–119.
- McCranie, J.R., Wilson, L.D., and Townsend, J.H., 2006, *The amphibians and reptiles of the Honduran Mosquitia*: Melbourne, Fla., Krieger Publ., 291 p.
- McDiarmid, R.W., Campbell, J.A., and Touré, T.A., 1999, *Snake species of the world; a taxonomic and geographic reference*, vol. 1: Washington, D.C., The Herpetologists' League, 511 p.
- McDowell, S.B., 1975, A catalogue of the snakes of New Guinea and the Solomons, with special reference to those of the Bernice P. Bishop Museum, Part II, Anilioidea and Pythoninae: *Journal of Herpetology*, v. 9, p. 1–79.
- McGinnis, S.M., and Moore, R.G., 1969, Thermoregulation in the boa constrictor, *Boa constrictor*: *Herpetologica*, v. 25, p. 38–45.
- McKay, J.L., 2006, *A field guide to the amphibians and reptiles of Bali: Malabar Fla.*, Krieger Publ., 148 p.
- McNamara, T.S., Cook, R.A., Behler, J.L., Ajello, L., and Padhye, A.A., 1994, Cryptococcosis in a common anaconda (*Eunectes murinus*): *Journal of Zoo and Wildlife Medicine*, v. 25, p. 128–132.
- Mendez, M., Waller, T., Micucci, A., Alvarenga, E., and Morales, J.C., 2007, Genetic population structure of the Yellow Anaconda (*Eunectes notaeus*) in northern Argentina:

- Management implications, *in* Henderson, R.W., and Powell, R., eds., *Biology of the Boas and Pythons: Eagle Mountain, Utah*, Eagle Mountain Publishing, p. 405–414.
- Menegon, M., and Salvidio, S., 2005, Amphibian and reptile diversity in the Southern Udzungwa Scarp Forest Preserve, south-eastern Tanzania, *in* Huber, B.A., Sinclair, B.J., and Lampe, K.-H., eds., *African biodiversity: Netherlands*, Springer, p. 205–212.
- Mertens, R., 1930, Die Amphibien und Reptilien der Inseln Bali, Lombok, Sumbawa und Flores (Beiträge zur Fauna der Kleinen Sunda-Inseln, I): *Abhandlungen der Senchenbergischen Naturforschenden Gesellschaft*, v. 42 and 43, p. 115–344.
- Mertens, R., 1942, Die Familie der Warane (Varanidae): *Abhandlungen der Senchenbergischen Naturforschenden Gesellschaft*, v. 462, 465, 466, variously paged.
- Micucci, P.A., and Waller, T., 2007, The management of yellow anacondas (*Eunectes notaeus*) in Argentina: From historical misuse to resource appreciation: *Iguana*, v. 14, p. 160–171.
- Micucci, P.A., Waller, T., and Alvarenga, E., 2006, Programa Curiyú: Para la conservación y aprovechamiento sustentable de la boa curiyú (*Eunectes notaeus*) in la Argentina. Etapa experimental piloto 2002–2004, Formosa, *in* Bolkovic, M.L., and Ramadori, D., eds., *Manejo de fauna silvestre en la Argentina. Programas de uso sustentable*, Dirección de Fauna Silvestre, Secretaría de Ambiente y Desarrollo Sustentable, p. 77–92.
- Miller, A.L., 2009, Pet python blamed in child's death: *Gainesville Sun*, v. 2, July 2009, p. 1,045.
- Miller, D.L., Radi, Z.A., Stiver, S.L., and Thornhill, T.D., 2004, Cutaneous and pulmonary mycosis in green anacondas (*Eunectes* (sic) *murinus*): *Journal of Zoo and Wildlife Medicine*, v. 35, p. 557–561.
- Miller, T.J., and Smith, H.M., 1979, The Lesser African Rock Python: *Bulletin of the Maryland Herpetological Society*, v. 15, p. 70–84.
- Minton, S.A., Jr., 1962, An annotated key to the amphibians and reptiles of Sind and Las Bela, West Pakistan: *American Museum Novitates*, v. no. 2081, p. 1–60.
- Minton, S.A., Jr., 1966, A contribution to the herpetology of West Pakistan: *Bulletin of the American Museum of Natural History*, v. 134, p. 29–184.
- Minton, S.A., Jr., and Minton, M.R., 1973, *Giant reptiles*: New York, Chas. Scribner's Sons, 345 p.
- Mishima, S., Hayashi, Y., Tanaka, H., and Sawai, Y., 1999, The effectiveness of habitat modifications for controlling Habu populations on Tokunoshima, *in* Rodda, G.H., Sawai, Y., Chiszar, D., and Tanaka, H., eds., *Problem snake management: the Habu and the Brown Treesnake*: Ithaca, N.Y., Cornell Univ. Press, p. 365–371.
- Mole, R.R., 1924, The Trinidad snakes: *Proceedings of the General Meetings for Scientific Business of the Zoological Society of London*, v. 1924, p. 234–278.
- Mole, R.R., and Urich, F.W., 1894, Biological notes upon some of the Ophidia of Trinidad, B.W.I., with a preliminary list of the species recorded from the island: *Journal of Zoology (Proceedings of the Zoological Society of London)*, v. p. 499–515.
- Monadjem, A., Boycott, R.C., Parker, V., and Culverwell, J., 2003, Threatened vertebrates of Swaziland; Swaziland red data book: fishes, amphibians, reptiles, birds and mammals: Swaziland, Ministry of Tourism, Environment and Communications, 256 p.

- Monguillot, J.C., 1988, Contribución al conocimiento de *Boa constrictor occidentalis* (Phil) (Reptilia: Boidae). Observaciones biológicas sobre viboreznos en condiciones de cautividad: Fundación Vide Silvestre Argentina. Amphibia y Reptilia (conservación), v. 1, p. 99–104.
- Montgomery, G.G., and Rand, A.S., 1978, Movements, body temperature and hunting strategy of a Boa constrictor: Copeia, v. 1978, p. 532–533.
- Monzel, M., 2005, A snake with many faces: Boa constrictor variability and subspecies differentiation: Reptilia (G.B.), v. no. 38, p. 79–81.
- Morris, R.C., 1932, Intestinal parasites of the python: Journal of the Bombay Natural History Society, v. 36, p. 513.
- Moseley, E.L., 1901, The python in Pennsylvania: Science, v. 14, p. 852–853.
- Müller, P., 1970, Einige Beobachtungen zur Fortpflanzungsbiologie bei Riesenschlangen im Zoologischen Garten Leipzig: Aquarien und Terrarien Zeitschrift, v. 17, p. 162–164.
- Mullin, S.J., 1999, Caudal distraction by rat snakes (Colubridae, Elaphe): a novel behavior used when capturing mammalian prey: Great Basin Naturalist, v. 59, p. 361–367.
- Murphy, J.C., 1997, Amphibians and reptiles of Trinidad and Tobago: Malabar, Fla., Krieger Publ., 245 p.
- Murphy, J.C., and Henderson, R.W., 1997, Tales of giant snakes: a natural history of anacondas and pythons: Malabar, Fla., Krieger Publ., 221 p.
- Murphy, J.C., Voris, H.K., and Karns, D.R., 1994, A field guide and key to the snakes of the Danum Valley, a Bornean tropical forest ecosystem: Bulletin of the Chicago Herpetological Society, v. 29, p. 133–151.
- Muthusamy, E., and Gopalakrishnakone, P., 1990, Python bites—case reports [in English with Japanese summary]: The Snake, v. 22, p. 113–119.
- Mutze, G., Cooke, B., and Alexander, P., 1998, The initial impact of rabbit hemorrhagic disease on European rabbit populations in South Australia: Journal of Wildlife Diseases, v. 34, p. 221–227.
- Myres, B.C., and Eells, M.M., 1968, Thermal aggregation in Boa constrictor: Herpetologica, v. 24, p. 61–66.
- Nakamoto, E., and Toriba, M., 1983, Some observations on mating behavior of Burmese python, *Python molurus bivittatus* Kuhl: The Snake, v. 15, p. 110–112.
- Neill, W.T., and Allen, E.R., 1956, Secondarily ingested food items in snakes: Herpetologica, v. 12, p. 172–174.
- Neill, W.T., and Allen, E.R., 1962a, Parturient anaconda, *Eunectes gigas* Latreille, eating own abortive eggs and foetal membranes: Quarterly Journal Florida Academy of Sciences, v. 25, p. 73–75.
- Neill, W.T., and Allen, E.R., 1962b, Reptiles of the Cambridge expedition to British Honduras, 1959–1960: Herpetologica, v. 18, p. 79–91.
- Newman, E.A., and Hartline, P.H., 1982, The infrared "vision" of snakes: Scientific American, v. 246, p. 98–107.
- Nguyen, V.S., Ho, T.C., and Nguyen, Q.T., 2009, Herpetofauna of Vietnam: Frankfurt am Main, Germany, Edition Chimaira, 768 p.
- Nichols, D.K., 1990, Pathogenesis of ophidian paramyxovirus infection in the Brown Tree Snake (*Boiga irregularis*): Washington, D.C., grant proposal to U.S. Office of Insular Affairs, 5 p.

- Nichols, D.K., 1999, Pathogenesis of ophidian paramyxovirus infection in the Brown Tree Snake (*Boiga irregularis*), progress report for the Office of Insular Affairs, Department of the Interior, October 1, 1998 through February 28, 1999: Report to U.S. Department of the Interior, Office of Insular Affairs, p. 2.
- Nichols, D.K., and Lamirande, E.W., 2001, Ophidian viruses as potential biological control agents for the Brown Treesnake (*Boiga irregularis*): *Micronesica*, v. 37, p. 170.
- Nix, H., 1986, A biogeographic analysis of Australian elapid snakes, *in* Longmore, R., ed., Snakes; atlas of elapid snakes of Australia: Canberra, Australian Bureau of Flora and Fauna, Australian Flora and Fauna Series No. 7, p. 4–15.
- Nokes, D.J., 1992, Microparasites: viruses and bacteria, *in* Crawley, M.J., ed., Natural enemies: the population biology of predators, parasites and diseases: Oxford, Blackwell Sci., p. 349–374.
- Noonan, B.P., and Chippindale, P.T., 2006, Dispersal and vicariance: The complex evolutionary history of boid snakes: *Molecular Phylogeny and Evolution*, v. 40, p. 347–358.
- Norman, D.R., 1994, Amphibians and reptiles of the Paraguayan Chaco, vol. 1 [in English and Spanish]: San José, Costa Rica, David Norman, 281 p.
- Oda, S.N., Chao, J., and Ball, G.H., 1971, Additional instances of transfer of reptile hemogregarines to foreign hosts: *Journal of Parasitology*, v. 57, p. 1,377–1,378.
- Oliver, J.A., 1937, Notes on a collection of amphibians and reptiles from the state of Colima, Mexico: *Occasional Papers of the Museum of Zoology, University of Michigan*, v. no. 360, p. 1–34.
- Oliver, J.A., 1959, Snakes in fact and fiction: New York, Macmillan, 199 p.
- Oliver, J.H., Owsley, M.R., and Claiborne, C.M., 1988, Chromosomes, reproductive biology, and developmental stages of *Aponomma varanensis* (Acari: Ixodidae): *Journal of Medical Entomology*, v. 25, p. 73–77.
- Orr, R., 2003, Generic nonindigenous aquatic organisms risk analysis review process, *in* Ruiz, G.J., and Carlton, J.T., eds., Invasive species: vectors and management strategies: Covelo, Calif., Island Press, p. 415–431.
- O'Shea, M.T., 2007, Boas and pythons of the world: New Jersey, Princeton Univ. Press, 160 p.
- O'Shea, M.T., Tamsiripong, Y., and Lynam, A.J., 2004, *Python reticulatus* (Reticulated Python): Site selection, sleeping, and escape behavior: *Herpetological Review*, v. 35, p. 71–72.
- Ott, B.D., and Secor, S.M., 2007a, Adaptive regulation of digestive performance in the genus Python: *Journal of Experimental Biology*, v. 210, p. 340–356.
- Ott, B.D., and Secor, S.M., 2007b, The specific dynamic action in boas and pythons, *in* Henderson, R.W., and Powell, R., eds., Biology of the boas and pythons: Eagle Mountain, Utah, Eagle Mountain Publishing, p. 298–310.
- Padial, J.M., 2003, On the presence of *Python sebae* Gmelin, 1788 (Ophidia: Pythonidae) in Mauritania: *Herpetological Bulletin*, v. no. 84, p. 30–31.
- Padial, J.M., 2006, Commented distributional list of the reptiles of Mauritania (West Africa): *Graellsia*, v. 62, p. 159–178.
- Paperna, I., Peh Kelvin, S.-H., Martelli, P., Koh, L.P., and Sodhi, N.S., 2004, Factors affecting Sarcocystis infection of rats on small tropical islands: *Ecological Research*, v. 19, p. 475–483.

- Parker, H.W., 1963, Snakes: New York, Norton, 191 p.
- Pauwels, O.S.G., David, P., Chimsunchart, C., and Thirakhupt, K., 2003, Reptiles of Phetchaburi Province, Western Thailand: a list of species, with natural history notes, and a discussion on the biogeography at the Isthmus of Kra: Natural History Journal of Chulalongkorn University, v. 3, p. 23–53.
- Peirce, M.A., 1984, Some parasites of reptiles from Zambia and Indian Ocean islands with a description of *Haemogregarina zambiensis* sp. nov. from *Dispholidus typus* (Colubridae): Journal of Natural History, v. 18, p. 211–217.
- Perry, G., Campbell, E.W., III, Rodda, G.H., and Fritts, T.H., 1998, Managing island biotas: Brown Treesnake control using barrier technology, in Baker, R.O., and Crabb, A.C., eds., Proceedings 18th vertebrate pest conference: Davis, Calif., Univ. of California, p. 138–143.
- Perry, G., Rodda, G.H., Fritts, T.H., and Qualls, F.J., 2001, Snake control using barrier technology: a final report on studies to develop temporary and permanent barriers for blocking movement of Brown Treesnakes (*Boiga irregularis*): Report to U.S. Department of the Interior, p. 36.
- Perry, S., Manson, J.H., Dower, G., and Wikberg, E., 2003, White-faced capuchins cooperate to rescue a groupmate from a Boa constrictor: Folia Primatologica, v. 74, p. 109–111.
- Peters, J.A., and Orejas-Miranda, B., 1986, Catalogue of the Neotropical Squamata, Part I, Snakes (2nd ed.): Washington, D.C., Smithsonian Institution Press, 347 p.
- Peterson, A.T., and Vieglais, D.A., 2001, Predicting species invasions using ecological niche modeling: new approaches from bioinformatics attack a pressing problem: Bioscience, v. 51, p. 363–371.
- Petzold, H.-G., 1984, Die Anakondas: Wittenberg Lutherstadt, A. Ziemsen Verlag, 143 p.
- Phillips, S.J., 2008, Transferability, sample selection bias and background data in presence-only modelling: a response to Peterson et al. (2007): Ecography, v. 31, p. 272–78.
- Phillips, S.J., Anderson, R.P., and Schapire, R.E., 2006, Maximum entropy modeling of species geographic distributions: Ecological Modelling, v. 190, p. 231–259.
- Phillips, S.J., Dudlik, M., and Schapire, R.E., 2004, A maximum entropy approach to species distribution modeling: Proc.21st International Conference on Machine Learning, v. 21, unpaginated reprint.
- Pitman, C.R.S., 1938, A guide to the snakes of Uganda: Kampala, Uganda Soc., 326 p.
- Pizzatto, L., and Marques, O.A.V., 2007, Reproductive biology of boine snakes with emphasis on Brazilian species and a comparison to pythons: South American Journal of Herpetology, v. 2, p. 107–122.
- Pope, C.H., 1935, The reptiles of China: turtles, crocodylians, snakes, lizards; Natural History of Central Asia, Volume 10: New York, American Museum of Natural History, p. 604.
- Pope, C.H., 1961, The giant snakes: New York, Alfred A. Knopf, 290 p.
- Porrás, L.W., 1999, Island boa constrictors (*Boa constrictor*): Reptiles, v. (1999), no. 7, p. 48–61.
- Porter, B.W., 1987, *Python sebae natalensis*, Africa Rock Python, Reproduction: Journal of the Herpetological Association of Africa, v. 34, p. 44.

- Price, R.M., and Russo, P., 1991, Revisionary comments on the genus *Boa* with the description of a new subspecies of *Boa constrictor* from Peru: *The Snake*, v. 23, no. 29-35.
- Pyron, R.A., Burbrink, F.T., and Guirer, T.J., 2008, Claims of potential expansion throughout the U.S. by invasive python species are contradicted by ecological niche models: *PLoS ONE*, v. 3, no. 8, p. e2931.
- Quick, J.S., Reinert, H.K., de Cuba, E.R., and Odum, R.A., 2005, Recent occurrence and dietary habits of *Boa constrictor* on Aruba, Dutch West Indies: *Journal of Herpetology*, v. 39, p. 304–307.
- Radcliffe, C.W., Chiszar, D., and Smith, H.M., 1980, Prey-induced caudal movements in *Boa constrictor* with comments on the evolution of caudal luring: *Bulletin of the Maryland Herpetological Society*, v. 16, p. 19–22.
- Raja of Jasden, 1953, Python capturing chinkara: *Journal of the Bombay Natural History Society*, v. 51, p. 945–946.
- Randin, C.F., Dirnböck, T., Dullinger, S., Zimmermann, N.E., Zappa, M., and Guisan, A., 2006, Are niche-based species distribution models transferable in space?: *Journal of Biogeography*, v. 33, p. 1,689–1,703.
- Raven, H.C., 1946, Adventures in python country: *Natural History*, v. 55, p. 38–41.
- Rawlings, L.H., Rabosky, D.L., Donnellan, S.C., and Hutchinson, M.N., 2008, Python phylogenetics: inference from morphology and mitochondrial DNA: *Biological Journal of the Linnean Society*, v. 93, p. 603–619.
- Raynis, E.A., 1965, Notes on the growth of an immature African Rock Python: *Herpetologica*, v. 21, p. 150–151.
- Razzetti, E., and Msuya, C.A., 2002, Field guide to the amphibians and reptiles of Arusha National Park (Tanzania): *Pubblinova Edizioni Negri and Istituto OIKOS*, 84 p., available online at <http://www-1.unipv.it/webshi/images/files/tanzie2002.pdf>.
- Reaser, J.K., Meyerson, L.A., and Von Holle, B., 2008, Saving camels from straws: how propagule pressure-based prevention policies can reduce the risk of biological invasion: *Biological Invasions*, v. 7, p. 1,085–1,098.
- Reed, R.N., 2002, Review of Joseph Franke and Teresa M. Telecky: Reptiles as Pets: A review of the trade in live reptiles in the United States (2001): *Journal of International Wildlife Law and Policy*, v. 4, p. 315–317.
- Reed, R.N., 2005, An ecological risk assessment of non-native boas and pythons as potentially invasive species in the United States: *Risk Analysis*, v. 25, p. 753–766.
- Reed, R.N., Boback, S.M., Montgomery, C.E., Green, S., Stevens, Z., and Watson, D., 2007, Ecology and conservation of an exploited insular population of *Boa constrictor* (Squamata: Boidae) in the Cayos Cochinos, Honduras, *in* Henderson, R.W., and Powell, R., eds., *Biology of the boas and pythons*: Eagle Mountain, Utah, Eagle Mountain Publishing, p. 389–403.
- Reed, R.N., Green, S., Boback, S.M., and Montgomery, C.E., 2006, *Ctenosaura melanosterna* (Black-chested ctenosaur). Predation: *Herpetological Review*, v. 37, p. 84.
- Reed, R.N., and Rodda, G.H., 2008, Why do people release exotic reptiles and amphibians?: Manaus, Brazil, Sixth World Congress of Herpetology, CD.
- Reptile Database, 2008, The TIGR Reptile Database: Available online at <http://www.reptile-database.org>, accessed Jun 2007–Aug 2009.

- Riley, J., and Self, J.T., 1981, Some observations on the taxonomy and systematics of the pentastomid genus *Armillifer* in southeast asian and Australian snakes: Systematic Parasitology, v. 2, p. 171–180.
- Rivas, J.A., 1998, Predatory attacks of Green Anacondas (*Eunectes murinus*) on adult human beings: Herpetological Natural History, v. 6, p. 157–159.
- Rivas, J.A., 1999, The life history of the Green Anaconda (*Eunectes murinus*), with emphasis on its reproductive biology: Knoxville, Univ. Tennessee, Ph.D. dissertation, 168 p.
- Rivas, J.A., 2004, *Eunectes murinus* (Green Anaconda); Subduing behavior: Herpetological Review, v. 35, p. 66–67.
- Rivas, J.A., 2007, Conservation of Green Anacondas: How Tylenol conservation and macroeconomics threaten the future of the world's largest snake: Iguana, v. 14, p. 74–85.
- Rivas, J.A., and Burghardt, G.M., 2001, Understanding sexual size dimorphism in snakes: wearing the snake's shoes: Animal Behaviour, v. 62, p. F1–F6.
- Rivas, J.A., and Corey, S.J., 2008, *Eunectes murinus* (Green Anaconda); Longevity: Herpetological Review, v. 39, p. 469.
- Rivas, J.A., Muñoz, M.D.C., Burghardt, G.M., and Thorbjarnarson, J.B., 2007a, Sexual size dimorphism and the mating system of the Green Anaconda (*Eunectes murinus*), in Henderson, R.W., and Powell, R., eds., Biology of the boas and pythons: Eagle Mountain, Utah, Eagle Mountain Publishing, p. 312–325.
- Rivas, J.A., Muñoz, M.D.C., Thorbjarnarson, J.B., Burghardt, G.M., Holmstrom, W., and Calle, P.P., 2007b, Natural history of the Green Anaconda (*Eunectes murinus*) in the Venezuelan llanos, in Henderson, R.W., and Powell, R., eds., Biology of the boas and pythons: Eagle Mountain, Utah, Eagle Mountain Publishing, p. 128–138.
- Rivas, J.A., Muñoz, M.D.C., Thorbjarnarson, J.B., Holmstrom, W., and Calle, P., 1997, Mating system of the green anaconda (*Eunectes murinus*) in the Venezuelan Llanos in Rocek, Z., and Hart S., eds., Herpetology '97: Abstracts of the Third World Congress of Herpetology, 2-10 August 1997, Prague, p. 173–174.
- Rivas, J.A., and Owens, R.Y., 2000, *Eunectes murinus* (Green Anaconda); Cannibalism: Herpetological Review, v. 31, p. 45–46.
- Rivas, J.A., Owens, R.Y., and Calle, P., 2001, *Eunectes murinus* (Green Anaconda). Juvenile predation: Herpetological Review, v. 32, p. 107–108.
- Rivas, J.A., Thorbjarnarson, J.B., Muñoz, M.C., and Owens, R.Y., 1999, *Eunectes murinus* (Green Anaconda); Caiman predation: Herpetological Review, v. 30, p. 101.
- Rivera, P.C., Chiaraviglio, M., Pérez, G., and Gardenal, C.N., 2005, Protein polymorphism in populations of *Boa constrictor occidentalis* (Boidae) from Córdoba Province, Argentina: Amphibia-Reptilia, v. 26, p. 175–181.
- Robertson, M.M.K., 1998, Coro de Sucuri (Anaconda snake skin): Reptiles, September, p. 37–39.
- Rodda, G.H., Fritts, T.H., and Campbell, E.W., III, 1999a, The feasibility of controlling the Brown Treesnake in small plots, in Rodda, G.H., Sawai, Y., Chiszar, D., and Tanaka, H., eds., Problem snake management: the Habu and the Brown Treesnake: Ithaca, N.Y., Cornell Univ. Press, p. 468–477.

- Rodda, G.H., Fritts, T.H., and Chiszar, D., 1997, The disappearance of Guam's wildlife; new insights for herpetology, evolutionary ecology, and conservation: *Bioscience*, v. 47, p. 565–574.
- Rodda, G.H., Fritts, T.H., Clark, C.S., Gotte, S.W., and Chiszar, D., 1999b, A state-of-the-art trap for the Brown Treesnake, *in* Rodda, G.H., Sawai, Y., Chiszar, D., and Tanaka, H., eds., *Problem snake management: the Habu and the Brown Treesnake*: Ithaca, N.Y., Cornell Univ. Press, p. 268–305.
- Rodda, G.H., Fritts, T.H., McCoid, M.J., and Campbell, E.W., III, 1999c, An overview of the biology of the Brown Treesnake, *Boiga irregularis*, a costly introduced pest on Pacific Islands, *in* Rodda, G.H., Sawai, Y., Chiszar, D., and Tanaka, H., eds., *Problem snake management: the Habu and the Brown Treesnake*: Ithaca, N.Y., Cornell Univ. Press, p. 44–80.
- Rodda, G.H., Fritts, T.H., Perry, G., and Campbell, E.W., III, 1998, Managing island biotas: can indigenous species be protected from introduced predators such as the Brown Treesnake?, *in* Wadsworth, K.G., ed., *Trans. 63rd No. Amer. Wildl. Natur. Resour. Conf.*: Washington, D.C., Wildlife Management Institute, p. 95–108.
- Rodda, G.H., Jarnevich, C.S., and Reed, R.N., 2009, What parts of the US mainland are climatically suitable for invasive alien pythons spreading from Everglades National Park?: *Biological Invasions*, v. 11, p. 241–252.
- Rodda, G.H., Savidge, J.A., Tyrrell, C.L., Christy, M.T., and Ellingson, A.R., 2007, Size bias in visual searching and trapping of Brown Treesnakes on Guam: *Journal of Wildlife Management*, v. 71, p. 656–661.
- Rodda, G.H., Sawai, Y., Chiszar, D., and Tanaka, H., 1999d, *Problem snake management: the Habu and the Brown Treesnake*: Ithaca, N.Y., Cornell Univ. Press, 534 p.
- Rodda, G.H., Sawai, Y., Chiszar, D., and Tanaka, H., 1999e, Snake management, *in* Rodda, G.H., Sawai, Y., Chiszar, D., and Tanaka, H., eds., *Problem snake management: the Habu and the Brown Treesnake*: Ithaca, N.Y., Cornell Univ. Press, p. 1–23.
- Rodda, G.H., and Tyrrell, C.L., 2008, Introduced species that invade and species that thrive in town: are these two groups cut from the same cloth?, *in* Mitchell, J.C., Jung Brown, R.E., and Bartholomew, B., eds., *Urban herpetology: Salt Lake City, Utah, Herpetological Conservation*, vol. 3, Soc. Study Amphibians and Reptiles, p. 327–341.
- Romero-Najera, I., Cuarón, A.D., and González-Baca, C., 2007, Distribution, abundance, and habitat use of introduced Boa constrictor threatening the native biota of Cozumel Island, Mexico: *Biodiversity and Conservation*, v. 16, p. 1,183–1,195.
- Ronne, J., 1996, Revelations of a boa breeder: *Reptiles*, November 1996, p. 24–43.
- Rootes, W.L., and Chabreck, R.H., 1993, Cannibalism in the American Alligator: *Herpetologica*, v. 49, p. 99–107.
- Ross, R.A., and Marzec, G., 1990, *The reproductive husbandry of pythons and boas*: Stanford, Calif., Inst. for Herpetological Research, 270 p.
- Rozé, J.A., 1966, *La taxonomía y zoogeografía de los ofidios de Venezuela*: Caracas, Edic. Bibl. Univ. Central Venezuela 362 p.
- Russo, V., 2007, *The complete Boa Constrictor: A comprehensive guide to the care, breeding, and geographic races*: unk. (printed in China), ECO Herpetological Publishing, 281 p.

- Saint-Girons, H., 1972, Les serpents du Cambodge: Paris, Mém. Mus. Nat. D'Hist. Natur. Sér. A, 74, 170 p.
- Salter, R.E., 1983, Summary of currently available information on internationally threatened wildlife species in Burma: Rangoon, FAO Nature conservation and National Park Project Burma, FAO Rome Field Document 7/83, BUR/80/006, 79 p.
- Savage, J.M., 2002, The amphibians and reptiles of Costa Rica: Chicago, University of Chicago Press, 934 p.
- Savarie, P.J., Mathies, T.C., and Fagerstone, K.A., 2007, Flotation materials for aerial delivery of acetaminophen toxic baits to Brown Treesnakes, *in* Witmer, G.W., Pitt, W.C., and Fagerstone, K.A., eds., Managing vertebrate invasive species: Proceedings of an international symposium: Fort Collins, Colo., USDA-APHIS Wildlife Services, National Wildlife Research Center, p. 218–223.
- Savidge, J.A., 1987, Extinction of an island forest avifauna by an introduced snake: *Ecology*, v. 68, p. 660–668.
- Savitzky, A.H., 1983, Coadapted character complexes in snakes: fossoriality, piscivory, and durophagy: *American Zoologist*, v. 23, p. 397–409.
- Schad, G.A., 1962, Studies on the genus *Kalicephalus* (Nematoda: Diaphanocephalidae), II, A revision of the genus *Kalicephalus* Molin, 1861: *Canadian Journal of Zoology/Revue Canadienne de Zoologie*, v. 40, p. 1,035–1,165.
- Schlaepfer, M.A., Hoover, C., and Dodd, C.K., Jr., 2005, Challenges in evaluating the impact of the trade in amphibians and reptiles on wild populations: *Bioscience*, v. 55, p. 256–264.
- Schleich, H.H., and Kästle, W., 2002, Amphibians and reptiles of Nepal: Ruggell, Germany, A.R.G. Gantner Verlag K.G., 1,201 p.
- Schlott, M., 1935, Nachrichten aus dem Zoologischen Garten Breslau: *Der Zoologische Garten (N.F.)*, v. 8, p. 74–77.
- Schmidt, K.P., 1923, Contributions to the herpetology of the Belgian Congo based on the collection of the American Museum Congo Expedition, 1909–1915, Part II: snakes: *Bulletin of the American Museum of Natural History*, v. 49, p. 146.
- Schmidt, K.P., and Inger, R.F., 1957, Living reptiles of the world: Garden City, N.Y., Doubleday, 287 p.
- Schneider, J.G., 1801, *Historiae amphibiorum naturalis et literariae, Fasciculis secundus: continens Crocodilos, Scincos, Chamaesauras, Boas, Pseudoboas, Elapes, Angues, Amphisbaenas et Caecilias*: Jena, Frommann, 364 p.
- Schuett, G.W., Fernandez, P.J., Jr., Gergits, W.F., Casna, N.J., Chiszar, D., Smith, H.M., Mitton, J.B., Mackessy, S.P., Odum, R.A., and Demlong, M.J., 1997, Production of offspring in the absence of males: evidence for facultative parthenogenesis in bisexual snakes: *Herpetological Natural History*, v. 5, p. 1–10.
- Schuett, G.W., Hardy, D.L., Jr., Earley, R.L., and Greene, H.W., 2005, Does prey size induce head skeleton phenotypic plasticity during early ontogeny in the snake *Boa constrictor*?: *Journal of Zoology (London)*, v. 267, p. 363–369.
- Schumacher, J., Jacobsen, E.R., Homer, B.L., and Gaskin, J.M., 1994, Inclusion body disease in boid snakes: *Journal of Zoo and Wildlife Medicine*, v. 25, p. 511–524.
- Secor, S.M., 1995, Digestive response to the first meal in hatchling Burmese Pythons (*Python molurus*): *Copeia*, v. 1995, p. 947–954.

- Secor, S.M., 2003, Gastric function and its contribution to the postprandial metabolic response of the Burmese python *Python molurus*: *Journal of Experimental Biology*, v. 206, p. 1,621–1,630.
- Secor, S.M., and Diamond, J.M., 1995, Adaptive responses to feeding in Burmese pythons: pay before pumping: *Journal of Experimental Biology*, v. 198, p. 1,313–1,325.
- Secor, S.M., and Diamond, J.M., 1998, A vertebrate model of extreme physiological regulation: *Nature*, v. 395, p. 659–662.
- Secor, S.M., Hicks, J.W., and Bennett, A.F., 2000, Ventilatory and cardiovascular responses of a python (*Python molurus*) to exercise and digestion: *Journal of Experimental Zoology*, v. 203, p. 2,447–2,454.
- Secor, S.M., and Ott, B.D., 2007, Adaptive correlation between feeding habits and digestive physiology for boas and pythons, *in* Henderson, R.W., and Powell, R., eds., *Biology of the boas and pythons*: Eagle Mountain, Utah, Eagle Mountain Publishing, p. 256–268.
- Secor, S.M., Stein, E.D., and Diamond, J.M., 1994, Rapid upregulation of snake intestine in response to feeding: a new model of intestinal adaptation: *American Journal of Physiology*, v. 266, p. G695–G705.
- Senter, P., 2000, *Python sebae* (African rock python); Caudal displays: *Herpetological Review*, v. 31, p. 179.
- Shaw, G.E., Shebbeare, E.O., and Barker, P.E., 1939, The snakes of northern Bengal and Sikkim: *Journal of the Darjeeling Natural History Society*, v. 13, no. 3, p. 64–73.
- Shelford, R.W., 1917, *A naturalist in Borneo*: Singapore, Oxford Univ. Press, 331 p.
- Shine, C., Williams, N., and Gündling, L., 2000, *A guide to designing legal institutional frameworks on alien invasive species*: Gland, Switzerland, IUCN-Environmental Law Centre, 152 p.
- Shine, R., 1985, The evolution of viviparity in reptiles: an ecological analysis, *in* Gans, C., and Billett, F., eds., *Biology of the Reptilia*, volume 15: New York, John Wiley and Sons, p. 605–694.
- Shine, R., 1988, Parental care in reptiles, *in* Gans, C., and Huey, R.B., eds., *Biology of the Reptilia*, volume 16, *Ecology B*: New York, Alan R. Liss, p. 275–330.
- Shine, R., 1991, *Australian snakes: a natural history*: Ithaca, N.Y., Cornell Univ. Press 223 p.
- Shine, R., Ambariyanto, Harlow, P.S., and Mumpuni, 1999, Reticulated Pythons in Sumatra: biology, harvesting and sustainability: *Biological Conservation*, v. 87, p. 349–357.
- Shine, R., Harlow, P.S., Keogh, J.S., and Boeadi, 1998a, The allometry of life-history traits: insights from a study of giant snakes (*Python reticulatus*): *Journal of Zoology (London)*, v. 244, p. 405–414.
- Shine, R., Harlow, P.S., Keogh, J.S., and Boeadi, 1998b, The influence of sex and body size on food habits of a giant tropical snake, *Python reticulatus*: *Functional Ecology*, v. 12, p. 248–258.
- Shine, R., Sun, L., Zhao, E., and Bonnet, X., 2002, A review of 30 years of ecological research on the Shedao Pitviper, *Gloydus shedaoensis*: *Herpetological Natural History*, v. 9, p. 1–14.

- Shiroma, H., 1999, Population biology highlights, *in* Rodda, G.H., Sawai, Y., Chiszar, D., and Tanaka, H., eds., Problem snake management: the Habu and the Brown Treesnake: Ithaca, N.Y., Cornell Univ. Press, p. 492–494.
- Shiroma, H., and Akamine, H., 1999, Complete removal of Habu, *Trimeresurus flavoviridis*, from a residential area by trapping, *in* Rodda, G.H., Sawai, Y., Chiszar, D., and Tanaka, H., eds., Problem snake management: the Habu and the Brown Treesnake: Ithaca, N.Y., Cornell Univ. Press, p. 327–339.
- Shiroma, H., and Ukuta, H., 1999, Training a dog to detect Habu, *Trimeresurus flavoviridis*, *in* Rodda, G.H., Sawai, Y., Chiszar, D., and Tanaka, H., eds., Problem snake management: the Habu and the Brown Treesnake: Ithaca, N.Y., Cornell Univ. Press, p. 348–352.
- Shwiff, S.A., 2008, An evaluation of the potential economic impacts of the introduction of the Brown Treesnake on tourism in Hawaii: Honolulu, Hawaii, U.S. Fish and Wildlife Service, p. 19.
- Sillman, A.J., Johnson, J.L., and Loew, E.R., 2001, Retinal photoreceptors and visual pigments in Boa constrictor: Journal of Experimental Zoology, v. 290, p. 359–365.
- Simberloff, D., 2001, Eradication of island invasives: practical actions and results achieved: Trends in Ecology & Evolution, v. 16, p. 273–274.
- Singleton, G.R., Sudarmaji, Jumanta, Quang Tan, T., and Hung, N.Q., 1999, Physical control of rats in developing countries: Ecologically-based management of rodent pests: Canberra, Australian Centre for International Agricultural Research, p. 178–242.
- Sironi, M., Chiaraviglio, M., Cervantes, R., Bertona, M., and Rio, M., 2000, Dietary habits of *Boa constrictor occidentalis*, in the Cordoba Province, Argentina: Amphibia-Reptilia, v. 21, p. 226–232.
- Smith, C.R., 1999, Boa Constrictors: Austin, Texas, Siar Anthranir Reptiles, 20 p.
- Smith, E.N., 1994, Biology of the snake fauna of the Caribbean rainforest of Guatemala: Arlington, Univ. of Texas at Arlington, MS thesis, 138 p.
- Smith, M.A., 1943, The fauna of British India, Ceylon and Burma; Reptilia and Amphibia, Vol. III–Serpentes: London, Taylor and Francis, 583 p.
- Snider, A.T., and Bowler, J.K., 1992, Longevity of reptiles and amphibians in North American collections (2nd ed.): Soc. Study Amphibians and Reptiles, Herpetological Circular 21, 40 p.
- Snow, R.W., Brien, M.L., Cherkiss, M.S., Wilkins, L., and Mazzotti, F.J., 2007a, Dietary habits of Burmese Python, *Python molurus bivittatus*, from Everglades National Park, Florida: Herpetological Bulletin, v. 101, p. 5–7.
- Snow, R.W., Krysko, K.L., Enge, K.M., Oberhofer, L., Warren-Bradley, A., and Wilkins, L., 2007b, Introduced populations of *Boa constrictor* (Boidae) and *Python molurus bivittatus* (Pythonidae) in southern Florida, *in* Henderson, R.W., and Powell, R., eds., Biology of the boas and pythons: Eagle Mountain, Utah, Eagle Mountain Publishing, p. 416–438.
- Snow, R.W., Oberhofer, L., and Mazzotti, F.J., 2006, *Alligator mississippiensis* (American Alligator); Feeding: Herpetological Review, v. 37, p. 80–81.
- Spawls, S., and Branch, B., 1995, The dangerous snakes of Africa: natural history, species directory, venoms and snakebite: Sanibel Island, Fla., Ralph Curtis—Books, 192 p.

- Spawls, S., Howell, K., Drewes, R., and Ashe, J., 2002, A field guide to the reptiles of East Africa; Kenya, Tanzania, Uganda, Rwanda and Burundi: San Diego, Calif., Academic Press, 543 p.
- Stafford, P.J., and Meyer, J.R., 2000, A guide to the reptiles of Belize: London, Natural History Museum/Academic Press, 356 p.
- Stanford, C.B., 1994, *Python sebae* (African Rock Python); Reproduction: Herpetological Review, v. 25, p. 125.
- Stanford, J.W., and Rodda, G.H., 2007, The Brown Treesnake Rapid Response Team, in Witmer, G.W., Pitt, W.C., and Fagerstone, K.A., eds., Managing vertebrate invasive species: Proceedings of an international symposium: Fort Collins, Colo., USDA-APHIS Wildlife Services, National Wildlife Research Center, p. 175–217.
- Stanley, A., 1914, The collection of Chinese reptiles in the Shanghai Museum: Journal of the New China British Royal Asiatic Society, v. 1914, p. 21–31.
- Starace, F., 1998, Guide des serpents et amphisbènes de Guyane française: Guadeloupe-Guyane, Ibis Rouge Editions, 449 p.
- Starin, E.D., and Burghardt, G.M., 1992, African Rock Pythons (*Python sebae*) in the Gambia: observations on natural history and interactions with primates: The Snake, v. 24, p. 50–62.
- Steadman, D.W., Pregill, G.K., and Olson, S.L., 1984, Fossil vertebrates from Antigua, Lesser Antilles: Evidence for late Holocene human-caused extinctions in the West Indies: Proceedings of the National Academy of Sciences, v. 81, p. 4,448–4,451.
- Stemmler, O., 1963, Eine Anaconda (*Eunectes murinus* L.) 32 Jahre in Gefangenschaft: Aquaria, v. 10, p. 30–31.
- Stemmler-Morath, C., 1956, Beitrag zur Gefangenschafts-und Fortpflanzungsbiologie von *Python molurus* L.: Der Zoologische Garten (Leipzig), v. 21, p. 347–364.
- Stewart, M.M., 1968, Notes on reptiles from Northern Malawi, Africa: Journal of Herpetology, v. 2, p. 163–164.
- Stockwell, D.R.B., and Peters, D., 1999, The GARP modeling system: problems and solutions to automated spatial prediction: International Journal of Geographic Information Science, v. 13, p. 143–158.
- Stockwell, D.R.B., Shaner, S., Tate, D.J., Bork, K., and Dougherty, S., 2005, Integrating transportation network data into predictive models for invasive species: Report to U.S. Dept. of Transportation, 15 Nov. 2005, p. 1–19.
- Strimple, P.D., 1993, Overview of the natural history of the Green Anaconda: Herpetological Natural History, v. 1, no. 1, p. 25–35.
- Strimple, P.D., and Dirksen, L., 2001, *Eunectes murinus* (Green Anaconda); Escape behavior and respiration: Herpetological Review, v. 32, p. 106–107.
- Strimple, P.D., Puerto, G., Holmstrom, W.F., Jr., Henderson, R.W., and Conant, R., 1997, On the status of the anaconda *Eunectes barbouri* Dunn and Conant: Journal of Herpetology, v. 31, p. 607–609.
- Strüssmann, C., 1997, Hábitos alimentares da sucuri-amarela, *Eunectes notaeus* Cope, 1862, no pantanal Matogrossense: Biociencias, v. 1, p. 35–52.
- Strüssmann, C., and Sazima, I., 1991, Predation on avian eggs by the boid snake, *Eunectes notaeus*: Herpetological Review, v. 22, p. 118–120.

- Strüssmann, C., and Sazima, I., 1993, The snake assemblage of the Pantanal at Poconé, Western Brazil: Faunal composition and ecological summary: Studies on Neotropical Fauna and Environment, v. 28, p. 157–168.
- Stuart, B.L., 1999, Amphibians and reptiles, in Duckworth, J.W., Salter, R.E., and Khouboline, K., eds., Wildlife in Lao PDR, 1999 status report: IUCN, WCS & CPAWN, p. 43–67.
- Stuart, L.C., 1935, A contribution to a knowledge of the herpetology of a portion of the savanna region of central Petén, Guatemala: Miscellaneous Publications Museum of Zoology, University of Michigan, v. 29, p. 1–74.
- Stuart, L.C., 1948, The amphibians and reptiles of Alta Verapaz Guatemala: Miscellaneous Publications Museum of Zoology, University of Michigan, v. 69, p. 1–118.
- Stucki-Stirn, M.C., 1979, Snake report 721; A comparative study of the herpetological fauna of the former West Cameroon/Africa, with a classification and synopsis of 95 different snakes and description of some new sub-species: Teuffenthal, Switzerland, Herpeto-Verlag, 650 p.
- Stuebing, R.B., 1991, A checklist of the snakes of Borneo: Raffles Bulletin of Zoology, v. 39, p. 323–362.
- Stuebing, R.B., and Inger, R.F., 1999, A field guide to the snakes of Borneo: Kota Kinabalu, Sabah, Malaysia, Natural History Publ. (Borneo) 254 p.
- Sutherst, R.W., Floyd, R.B., and Maywald, G.F., 1996, The potential geographical distribution of the Cane Toad, *Bufo marinus* L. in Australia: Conservation Biology, v. 10, p. 294–299.
- Sutherst, R.W., Maywald, G.F., Yonow, T., and Stevens, P.M., 1998, CLIMEX; Predicting the effects of climate on plants and animals; Users guide: Melbourne, CSIRO Publ., CD.
- Swan, L.W., and Leviton, A.E., 1962, The herpetology of Nepal: a history, check list, and zoogeographical analysis of the herpetofauna: Proceedings of the California Academy of Science, Fourth Series, v. 32, p. 103–147.
- Taylor, E.H., 1922, The snakes of the Philippine Islands, in Taylor, E.H., ed., The herpetology of the Philippine Islands: Amsterdam, A. Asher & Co. (1955 reprint), 312 p.
- Taylor, E.H., 1965, The serpents of Thailand and adjacent waters: University of Kansas Science Bulletin, v. 45, p. 609–1096.
- Taylor, E.H., and Elbel, R.E., 1958, Contribution to the herpetology of Thailand: University of Kansas Science Bulletin, v. 38, p. 1,033–1,189.
- Telford, S.R., Jr., 1999, The possible use of haemogregarine parasites in biological control of the Brown Treesnake (*Boiga irregularis*) and the Habu (*Trimeresurus flavoviridis*), in Rodda, G.H., Sawai, Y., Chiszar, D., and Tanaka, H., eds., Problem snake management: the Habu and the Brown Treesnake: Ithaca, N.Y., Cornell Univ. Press, p. 384–390.
- Tello, N.S., Huck, M., and Heymann, E.W., 2002, Boa constrictor attack and successful group defence in moustached tamarins, *Saguinus mystax*: Folia Primatologica, v. 73, p. 146–148.

- Theiler, G., and Salisbury, L.E., 1959, Ticks in the South African zoological survey collection—part IX "The *Amblyomma marmoreum* group": *Onderstepoort Journal of Veterinary Research*, v. 28, p. 47–124.
- Thorton, P.E., Running, S.W., and White, M.A., 1997, Generating surfaces of daily meteorology variables over large regions of complex terrain: *Journal of Hydrology*, v. 190, p. 214–251.
- Thuiller, W., 2003, BIOMOD: optimising predictions of species distributions and projecting potential future shifts under global change: *Global Change Biology*, v. 9, p. 1,353–1,362.
- Tomanovic, B., and Paunovic, S., 1976, Parazitoloski nalaz kod anakonde (*Eunectes murinus*) uginule u Beogradskom zooloskom vrtu: *Veterinarski glasnik*, v. 30, p. 1,051–1,055.
- Townson, S., 1980, Observations on the reproduction of the Indian Python in captivity with special reference to the interbreeding of two subspecies *Python molurus molurus* and *Python molurus bivittatus*, in Townson, S., Millichamp, N.J., Lucas, D.G.D., and Millwood, A.J., eds., *The care and breeding of captive reptiles*, British Herpetological Society, p. 69–80.
- Trape, J.F., 1985, Les serpents de la region de Dimonika (Mayombe, Republique Populaire du Congo): *Revue Zoologie Africain*, v. 99, p. 135–140.
- Trutnau, L., 1980, Über die Lebensweise und Pflege des Netzpythons *Python reticulatus* (Schneider): *Herpetofauna* (Weinstadt), v. 2, p. 26–31.
- Tschambers, B., 1949, Boa constrictor eats porcupine: *Herpetologica*, v. 5, no. 141.
- Tweedie, M.W.F., 1953, *The snakes of Malaya*: Singapore, Government Printing Office, 139 p.
- Tyrrell, C.L., Christy, M.T., Rodda, G.H., Yackel Adams, A.A., Ellingson, A.R., Savidge, J.A., Dean-Bradley, K., and Bischof, R., 2009, Evaluation of trap capture in a geographically closed population of Brown Treesnakes on Guam: *Journal of Applied Ecology*, v. 46, p. 128–135.
- Underwood, G.L., and Stimson, A.F., 1990, A classification of pythons (Serpentes: Pythoninae): *Journal of Zoology* (London), v. 221, no. 4, p. 565–604.
- Ussher, C.A., 1979, Brunei's largest snake: *Brunei Museum Journal*, v. 4, p. 180–181.
- Valderrama, X., and Thorbjarnarson, J., 2001, *Eunectes murinus* (Green Anaconda); Diet: *Herpetological Review*, v. 32, p. 46–47.
- Valenciennes, A., 1841, Observations faites pendant l'incubation d'une femelle du python a deux raies (*Python bivittatus*, Kuhl) pendant les moises de mai et de juin 1841: *Comptes Rendus, Academie Sciencias*, Paris, v. 13, p. 126–133.
- Van Mierop, L.H.S., and Barnard, S.M., 1976, Observations on the reproduction of *Python molurus bivittatus* (Reptilia, Serpentes, Boidae): *Journal of Herpetology*, v. 10, p. 333–340.
- Van Mierop, L.H.S., and Barnard, S.M., 1978, Further observations on thermoregulation in the brooding female *Python molurus bivittatus* (Serpentes, Boidae): *Copeia*, v. 1978, p. 615–621.
- Van Rooijen, J., and Van Rooijen, M., 2002, Einige Ergänzungen, Berichtigungen und Neue Beobachtungen zur Herpetofauna von Pulau Tioman, West Malaysia: *Sauria*, v. 24, p. 3–12.

- Vandeventer, T.L., 1992, In search of the Tete'Chein: observations on the natural history of *Boa constrictor nebulosus*: Clinton MS, privately printed, 4 p.
- Veitch, C.R., and Bell, B.D., 1990, Eradication of introduced animals from the islands of New Zealand, in Towns, D.R., Daugherty, C.H., and Atkinson, I.A.E., eds., Ecological restoration of New Zealand islands: Wellington, Conservation Science Publ. No. 2, New Zealand Department of Conservation, p. 137–146.
- Veitch, C.R., and Clout, M.N., 2002, Turning the tide: the eradication of invasive species: Gland, Switzerland, IUCN Invasive Species Specialist Group of the World Conservation Union (IUCN), 414 p.
- Vice, D.S., and Pitzler, M.E., 2002, Brown Treesnake control: economy of scales, in Clark, L., Hone, J., Shivik, J.A., Watkins, R.A., Vercauteren, K.C., and Yoder, J.K., eds., Human conflicts with wildlife: economic considerations: Fort Collins, Colo., Proceedings, Third National Wildlife Research Center Special Symposium, National Wildlife Research Center, p. 127–131.
- Vijayakumar, L., 1999, Individual identification of Indian and Reticulated Pythons based on blotch structure and arrangement: *Cobra*, v. 37, p. 10–16.
- Vinegar, A., 1973, The effects of temperature on the growth and development of embryos of the Indian Python, *Python molurus* (Reptilia: Serpentes: Boidae): *Copeia*, v. 1973, p. 171–173.
- Vinegar, A., Hutchison, V.H., and Dowling, H.G., 1970, Metabolism, energetics, and thermoregulation during brooding of snakes of the genus *Python* (Reptilia: Boidae): *Zoologica*, v. 55, p. 19–48.
- Waage, J.K., 1997, Controlling invasives: biology is best: *World Conservation*, v. 4/97–1/98, p. 23–25.
- Waage, J.K., and Mills, N.J., 1992, Biological control, in Crawley, M.J., ed., *Natural enemies: the population biology of predators, parasites and diseases*: Oxford, Blackwell Sci., p. 412–430.
- Wagner, E., 1976, Breeding the Burmese python, *Python molurus bivittatus* at Seattle Zoo: *International Zoo Yearbook*, v. 16, p. 83–85.
- Wall, F., 1903, A prodromus of the snakes hitherto recorded from China, Japan, and the Loo Choo Islands, with some notes: *Proceedings of the Zoological Society (London)*, v. 1903, p. 84–102.
- Wall, F., 1912, A popular treatise on the common Indian snakes: *Journal of the Bombay Natural History Society*, v. 21, p. 447–476.
- Wall, F., 1921, *Ophidia Taprobanica or the Snakes of Ceylon*: Colombo, Government Printer, 581 p.
- Wall, F., 1926, The Reticulate Python *Python reticulatus* (Schneider): *Journal of the Bombay Natural History Society*, v. 31, p. 84–90.
- Wall, F., and Evans, G.H., 1900, Occurrence of *Python molurus* in Burma: *Journal of the Bombay Natural History Society*, v. 13, p. 190–191.
- Waller, T., 2000, Sobre la localidad tipo de *Eunectes notaeus* Cope (Serpentes, Boidae): *Cuadernos de Herpetologia*, v. 14, p. 77–78.
- Waller, T., Buongermini Palumbo, E., and Micucci, P.A., 2001, *Eunectes notaeus* (Yellow Anaconda): Diet: *Herpetological Review*, v. 32, p. 47.
- Waller, T., and Micucci, P.A., 1993, Estado actual del conocimiento de la biología, comercio y conservación de las boas neotropicales: géneros *Boa* L. (1758) y *Eunectes*,

- Wagler (1830): TRAFFIC South America, Report prepared for the CITES Secretariat., 121 p.
- Waller, T., and Micucci, P.A., 2008, Anaconda conservation: A reply to Rivas: Iguana, v. 15, p. 51–53.
- Waller, T., Micucci, P.A., and Alvarenga, E., 2007, Conservation biology of the Yellow Anaconda (*Eunectes notaeus*) in northeastern Argentina, in Henderson, R.W., and Powell, R., eds., Biology of the boas and pythons: Eagle Mountain, Utah, Eagle Mountain Publishing, p. 340–362.
- Waller, T., Micucci, P.A., and Buongermini Palumbo, E., 1995, Distribucion y conservacion de la familia Boidae en el Paraguay: Autoridad Científica CITES del Paraguay, Secretaría CITES, TRAFFIC Sudamérica, p. 53.
- Walls, J.G., 1998a, The living boas; A complete guide to the boas of the world: Neptune City, N.J., T.F.H. Publ., 288 p.
- Walls, J.G., 1998b, The living pythons; A complete guide to the pythons of the world: Neptune City N.J., T.F.H. Publ. 256 p.
- Wasko, D.K., and Roberts, D.L., 2008, Boa constrictor (*Boa Constrictor*): Diet: Herpetological Review, v. 39, p. 466.
- Watkins-Colwell, G.J., and Leenders, T.A.A.M., 2003, Boa constrictor (*Boa Constrictor*): Maximum body size: Herpetological Review, v. 34, p. 61.
- Watson, D., 2004, The spatial and behavioural ecology of the Cayos Cochinos Boa constrictor: Southampton, England, U.K., University of Southampton, 51 p.
- Waye, H.L., 2007, Reproductive biology and behavior of the Brown Tree Snake (*Boiga irregularis*) on Guam: Corvallis, Oregon State Univ., Ph.D. dissertation, 161 p.
- Welch, K.R.G., 1994, Snakes of the world: a checklist, 2. Boas, Pythons, Shield-tails and Worm Snakes: Somerset, England, R and A Research and Information Ltd., 89 p.
- Whitaker, R., 1978, Common Indian snakes: a field guide: Delhi, India, Macmillan India, 154 p.
- Whitaker, R., 1993, Population status of the Indian Python (*Python molurus*) on the Indian subcontinent: Herpetological Natural History, v. 1, p. 87–89.
- Whitaker, R., and Captain, A., 2004, Snakes of India; the field guide: Chengalpattu, Tamil Nadu, India, Draco Books, 481 p.
- Whittier, J.M., and Crews, D., 1987, Seasonal reproduction: patterns and control, in Norris, D.O., and Jones, R.E., eds., Hormones and reproduction in fish, amphibians, and reptiles: New York, Plenum Press, p. 385–410.
- Whittier, J.M., Vanderduys, E., and O'Donoghue, P., 1997, A survey of the parasites and diseases of the brown tree snake in its native range: Report from Univ. of Queensland, unpaginated.
- Whitworth, J., 1974, Notes on the growth of an African python *Python sebae* and an Indian python *Python molurus* at the Cannon Aquarium and Vivarium, Manchester Museum: Intl Zoo Yearbook, v. 14, p. 140–141.
- Wiens, F., and Zitzmann, A., 1999, Predation on a wild Slow Loris (*Nycticebus coucang*) by a Reticulated Python (*Python reticulatus*): Folia Primatologica, v. 70, p. 362–364.
- Wiles, G.J., Bart, J., Beck, R.E., Jr., and Aguon, C.F., 2003, Impacts of the Brown Tree Snake: patterns of decline and species persistence in Guam's avifauna: Conservation Biology, v. 17, p. 1,350–1,360.

- Williams, J.D., and Scrocchi, G.J., 1994, Ofidios de agua dulce de la República Argentina., in Castellanos, Z.A., ed., Fauna de agua dulce de la República Argentina. Vol 42 (Reptilia) Fasc 3 (Ophidia: Lepidosauria), Museo La Plata, p. 1–55.
- Williamson, M., 2006, Explaining and predicting the success of invasive species during different stages of invasion: *Biological Invasions*, v. 8, p. 1,561–1,568.
- Williamson, M.A., 1967, Notes on the growth rate of *Python reticulatus* (Serpentes: Boidae): *Herpetologica*, v. 23, p. 130–132.
- Wilson, L.D., and Cruz Díaz, G.A., 1993, The herpetofauna of the Cayos Cochinos, Honduras: *Herpetological Natural History*, v. 1, no. 1, p. 13–23.
- Wilson, L.D., and Meyer, J.R., 1985, *The snakes of Honduras*, 2nd ed.: Milwaukee, Wis., Milwaukee Publ. Mus., 150 p.
- Witmer, G.W., Pitt, W.C., and Fagerstone, K.A., 2007, Managing vertebrate invasive species: proceedings of an international symposium: Fort Collins, Colo., USDA-APHIS Wildlife Services, National Wildlife Research Center, 493 p.
- Wodzicki, K., 1978, A review of existing control methods, in Dingwall, P.R., Atkinson, I.A.E., and Hay, C., eds., *The ecology and control of rodents in New Zealand nature reserves*: Wellington, New Zealand, New Zealand Department of Lands and Survey (Info. Ser. 4), p. 195–205.
- World Climate, 2007, World Climate: Available online at <http://www.worldclimate.com>, accessed Jun 2007–Dec 2008.
- Wright, B.S., 1960, Predation on big game in East Africa: *Journal of Wildlife Management*, v. 24, p. 1–15.
- Wunder, W., 1934, Nestbau und Brutpflege bei Reptilien: *Ergebnisse der biologie* (Berlin), v. 10, p. 1–36.
- Zhao, E., and Adler, K., 1993, *Herpetology of China*: Soc. Stud. Amphs. Repts., 505 p.
- Zhong, C., 1993, First records for *Ophisaurus harti* and *Python molurus bivittatus* from Jiangxi Province, China: *Asiatic Herpetological Research*, v. 5, p. 103–104.
- Ziegler, T., 2002, *Die Amphibien und Reptilien eines Tieflandfeuchtwald-Schutzgebietes in Vietnam*: Münster, Germany, Natur und Tier Verlag, 342 p.
- Ziegler, T., and Hermann, H.-W., 2000, Preliminary list of the herpetofauna of the Phong Nha-Ke Bang area in Quang Binh Province, Vietnam: *Biogeographica*, v. 76, p. 49–62.
- Zug, G.R., and Ernst, C.H., 2004, *Smithsonian answer book: snakes*: Washington, D.C., Smithsonian Books, 177 p.
- Zug, G.R., and Mitchell, J.C., 1995, Amphibians and reptiles of the Royal Chitwan National Park, Nepal: *Asiatic Herpetological Research*, v. 6, p. 172–180.
- Zug, G.R., Win, H., Thin, T., Min, T.Z., Lhon, W.Z., and Kyaw, K., 1998, Herpetofauna of the Chatthin Wildlife Sanctuary, north-central Myanmar with preliminary observations of their natural history: *Hamadryad*, v. 23, p. 111–120.
- Zweifel, R.G., and Norris, K.S., 1955, Contribution to the herpetology of Sonora, Mexico: Descriptions of new subspecies of snakes (*Micruroides euryxanthus* and *Lampropeltis getulus*) and miscellaneous collecting notes: *American Midland Naturalist*, v. 54, p. 230–249.

Appendix. Trade Volume of Giant Constrictor Snakes Imported to the United States.

Results reported here were extracted from records maintained by the Convention on International Trade in Endangered Wildlife (CITES). See chapter Two for additional discussion of these data, including caveats related to their reliability. CITES states that data after 2005 are incomplete, so data for 2006 and 2007 should not be considered definitive. Figures A.1, A.2, and A.3 are based on data from Table A.1.

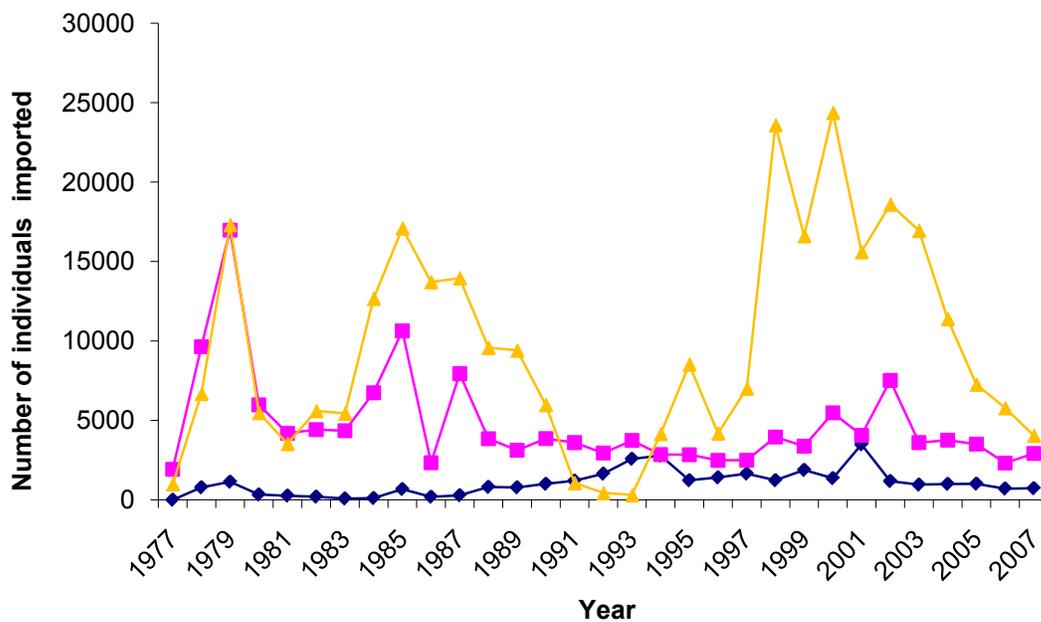


Figure A.1. Number of Indian Pythons (*P. molurus*; yellow), Reticulated Pythons (*B. reticulatus*; pink), and African Pythons (Northern (*P. sebae*) and Southern (*P. natalensis*) not distinguished in trade; blue) imported to the United States during the period 1977-2007.

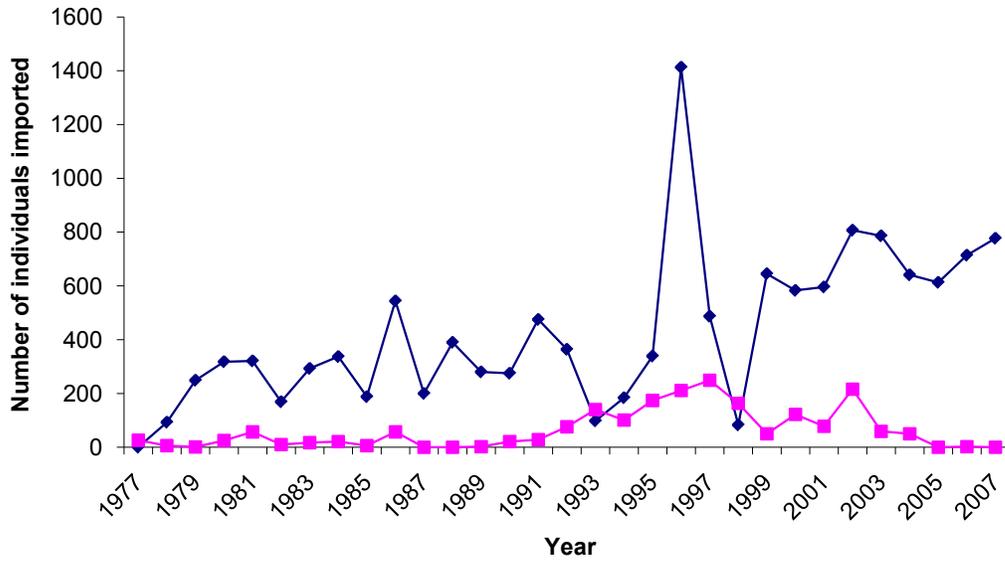


Figure A.2. Number of Green Anacondas (*E. murinus*; blue) and Yellow Anacondas (*E. notaeus*; pink) imported to the United States during the period 1977-2007.

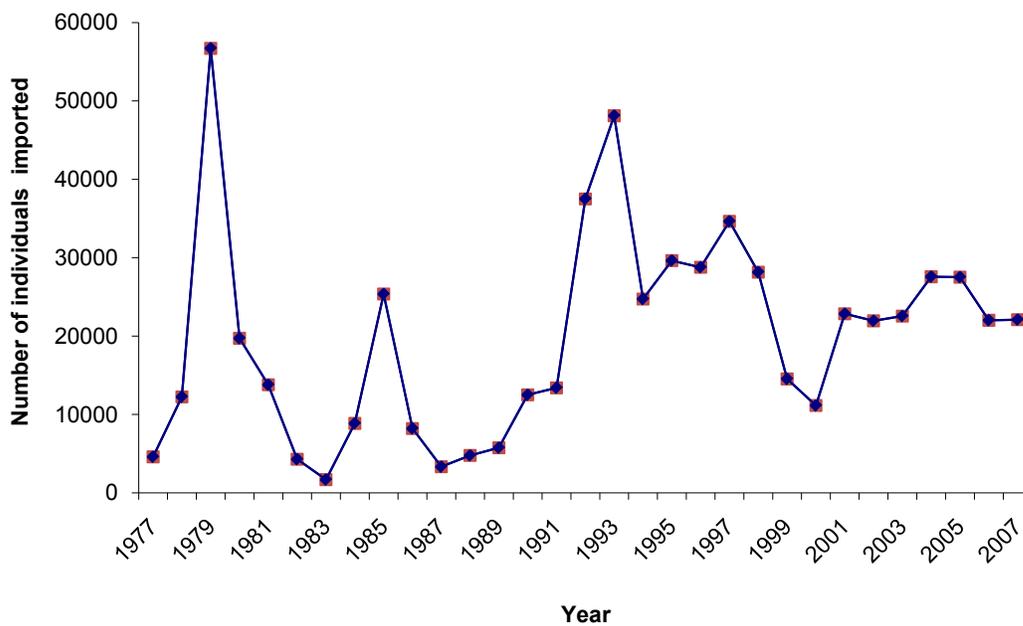


Figure A.3. Number of Boa Constrictors (*B. constrictor*; blue) imported to the United States during the period 1977-2007.

Table A.1. Numbers of individuals of six species of giant constrictor snakes imported to the United States during the period 1977-2007, as reported by CITES.

YEAR	<i>P. sebae</i>	<i>P. molurus</i>	<i>B. reticulatus</i>	<i>E. notaeus</i>	<i>E. murinus</i>	<i>B. constrictor</i>	TOTAL
1977	5	994	1926	26	0	4588	7539
1978	786	6683	9635	6	93	12242	29445
1979	1136	17309	16978	1	249	56707	92380
1980	335	5487	5983	25	318	19717	31865
1981	264	3536	4190	57	321	13786	22154
1982	200	5601	4425	10	169	4285	14690
1983	83	5443	4351	17	293	1683	11870
1984	111	12673	6744	21	337	8855	28741
1985	675	17102	10639	6	188	25362	53972
1986	191	13714	2340	57	544	8203	25049
1987	286	13962	7942	0	200	3326	25716
1988	813	9582	3851	0	390	4769	19405
1989	784	9412	3124	2	280	5750	19352
1990	1005	5982	3856	21	275	12503	23642
1991	1203	1065	3608	28	475	13391	19770
1992	1644	442	2948	76	364	37497	42971
1993	2579	308	3738	140	98	48107	54970
1994	2792	4161	2852	101	184	24724	34814
1995	1234	8530	2843	174	339	29626	42746
1996	1410	4192	2489	211	1413	28775	38490
1997	1651	7022	2498	249	487	34635	46542
1998	1233	23600	3958	163	83	28154	57191
1999	1881	16614	3381	50	645	14530	37101
2000	1364	24370	5479	122	583	11141	43059
2001	3488	15608	4068	78	596	22845	46683
2002	1181	18599	7519	216	807	21943	50265
2003	956	16948	3609	59	786	22549	44907
2004	1000	11395	3758	50	641	27569	44413
2005	1013	7266	3513	0	613	27512	39917
2006	706	5792	2321	2	714	22011	31546
2007	729	4051	2919	0	777	22087	30563
TOTAL	32738	297443	147485	1968	13262	618872	1111768

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