

Research Article

Supersize me: remains of three white-tailed deer (*Odocoileus virginianus*) in an invasive Burmese python (*Python molurus bivittatus*) in Florida

Scott M. Boback^{1*}, Ray W. Snow², Teresa Hsu³, Suzanne C. Peurach⁴, Carla J. Dove⁵ and Robert N. Reed⁶

¹Department of Biology, Dickinson College, Carlisle, Pennsylvania, USA

²Everglades National Park, National Park Service, Homestead, Florida, USA

³Department of Anthropology, Smithsonian Institution, Program in Human Ecology and Archaeobiology, Suitland, Maryland, USA

⁴United States Geological Survey, Patuxent Wildlife Research Center, Smithsonian Institution, Washington DC, USA

⁵Department of Vertebrate Zoology, Smithsonian Institution, Division of Birds, Washington DC, USA

⁶U.S. Geological Survey, Fort Collins Science Center, Fort Collins, Colorado, USA

*Corresponding author

E-mail addresses: bobacks@dickinson.edu (SMB), skip.snow.nps@gmail.com (RWS), hsuyt@si.edu (TH), peurachs@si.edu (SCP), dovec@si.edu (CJD), reedr@usgs.gov (RNR)

Received: 24 May 2016 / Accepted: 31 August 2016 / Published online: 21 September 2016

Handling editor: John Measey

Abstract

Snakes have become successful invaders in a wide variety of ecosystems worldwide. In southern Florida, USA, the Burmese python (*Python molurus bivittatus*) has become established across thousands of square kilometers including all of Everglades National Park (ENP). Both experimental and correlative data have supported a relationship between Burmese python predation and declines or extirpations of mid- to large-sized mammals in ENP. In June 2013 a large python (4.32 m snout-vent length, 48.3 kg) was captured and removed from the park. Subsequent necropsy revealed a massive amount of fecal matter (79 cm in length, 6.5 kg) within the snake's large intestine. A comparative examination of bone, teeth, and hooves extracted from the fecal contents revealed that this snake consumed three white-tailed deer (*Odocoileus virginianus*). This is the first report of an invasive Burmese python containing the remains of multiple white-tailed deer in its gut. Because the largest snakes native to southern Florida are not capable of consuming even mid-sized mammals, pythons likely represent a novel predatory threat to white-tailed deer in these habitats. This work highlights the potential impact of this large-bodied invasive snake and supports the need for more work on invasive predator-native prey relationships.

Key words: snake, predator, prey, invasion, mammal

Introduction

The Burmese python (*Python molurus bivittatus* Kuhl, 1820) is a large (up to 5.5 meters) snake native to Southeast Asia that has been popular in the North American and European pet trades for decades (Reed and Rodda 2009). An invasive population of this snake is now established in southern Florida, USA, producing viable clutches of eggs, and individuals of all size classes (e.g., adult, subadult, hatchling) have been documented (Snow et al. 2007b). Both correlative (Dorcas et al. 2012) and experimental (McCleery et al. 2015) studies have linked Burmese python predation to declines and extirpations of mid-sized mammals in the Greater

Everglades ecosystem. However, only correlative data have demonstrated a direct impact of Burmese pythons on large native mammals. Additional natural history observations of pythons and their prey are needed to clarify the impact of these exotic snakes on this unique natural area.

In Florida, free-ranging Burmese pythons have consumed a wide variety of birds, mammals, and one reptile, the American alligator (*Alligator mississippiensis* Daudin, 1802; Snow et al. 2007a; Rochford et al. 2010; Dove et al. 2001). Even large species of mammals and birds are vulnerable to predation by invasive pythons; bobcats (*Lynx rufus* Schreber, 1777), white-tailed deer (*Odocoileus virginianus* Zimmermann, 1780), and wood storks (*Mycteria americana*



Figure 1. Female Burmese python held by Bobby Hill (SFWMD). Photo was taken at the capture location just after the animal was euthanized.

Linnaeus, 1758) are all known to have been consumed by Burmese pythons in Everglades National Park (ENP; Snow et al. 2007a; Rochford et al. 2010; Dove et al. 2011). What is not known is the frequency (Snow et al. 2007a) and the sizes (and by extension the energy gain) of these large prey consumed by pythons. In this report we present detailed evidence demonstrating that a single Burmese python consumed three individual white-tailed deer. We use a hoof size-body weight relationship to estimate mass of each deer and then published data on hoof growth rates to reconstruct size and age of deer consumed.

Methods

On 3 June 2013, a large (4.32 m snout-vent length [4.78 m total length], 48.3 kg, 52.5 cm girth at midbody) female Burmese python was removed from northern ENP (25.69232° N, 80.67122° W; Figure 1). At the time of capture, the animal was partially exposed at the edge of the vegetation. The animal was euthanized at the capture site, and the carcass was transported to ENP Headquarters where it was stored at 2 °C. The animal was euthanized as

a part of lethal control by a management agency: South Florida Water Management District (SFWMD) and thus no permits were required.

On 5 June 2013, RWS performed a necropsy of the snake. Measurements and photographs were taken of external and internal morphology to document the condition of the python upon capture. A longitudinal incision was made running the length of the animal from snout to the vent. Fat bodies were removed and weighed. Developing follicles were characterized and measured using a millimeter ruler. The digestive tract was opened with another longitudinal incision, and all contents were removed for analysis. All fecal matter contained in the large intestine was weighed, washed with tap water in standard test sieves, and air-dried. All hard elements (e.g., bone, hooves) were extracted from hair by sorting and washing with tap water.

Results

Numerous dermal lesions were observed on the python, with most found on the ventral surface of the snake (Figure 2). Despite these external lesions, internally the snake appeared reproductively capable as the necropsy revealed abundant fat bodies (total

3.0 kg) and numerous pre-ovulatory/primary follicles (maximum diameter 5.7 mm) in the ovaries. The stomach was empty but the large intestine contained a large amount of hard fecal matter (6.5 kg [13% of the snake's body mass], 79 cm in length [18% of snake length], 42.5 cm girth at largest point [81% of maximal girth of snake]; Figure 3).

The fecal sample contained hair, bone fragments, hoof sheaths, and two teeth. Through comparisons with osteological specimens in the Archaeobiology and Mammalogy collections at the National Museum of Natural History, Smithsonian Institution, all skeletal and hoof remains were confirmed as white-tailed deer (*Odocoileus virginianus* and likely *O. v. seminolus* based on geographic location; Table 1). Comparison of the hair remains with reference specimens via light microscopy confirmed that the hair was also from white-tailed deer. To determine number of deer consumed, we grouped hoof sheaths and dewclaw sheaths based on size and color. The presence of twelve hooves and ten dewclaws confirmed that the snake had consumed at minimum three individual white-tailed deer (Figure 4).

Some of the remains allowed us to estimate age of deer that had been consumed by the python. Bone and bone fragments contain epiphyses that fuse at somewhat predictable ages, and we estimated age from some bone fragments using epiphyseal union tables (Purdue 1983; Table 1). Presence of deciduous teeth and tooth wear can also be used to age deer (Severinghaus 1949), although reliably aging older animals can be challenging due to variation in diet (see Gee et al. 2002). Nevertheless, the existence of a deciduous tooth (3rd premolar) that is present only in young fawns suggested the presence of an animal less than 2.5 months. The second tooth, a permanent 1st molar, suggested a second animal was greater than 12 months of age. Lastly, number and size of the hoof sheaths supported the conclusion that the python consumed one adult and two fawns. We used the predictable rate of postnatal hoof growth (Haugen and Speake 1958) to estimate age of the two youngest animals (Figure 5). Combining all these age estimate methods allowed us to confirm that the python consumed an adult deer greater than 12 months of age, a fawn between 24 and 30 days of age, and a fawn aged approximately 14 days.

We used the relationship between hoof sheath length and body weight for six *Odocoileus virginianus* of varying sizes (23–80 kg) collected from Alabama and Pennsylvania to estimate the body mass of each deer consumed by the python. From these limited data, we estimated that the three deer consumed by this python would have had live weights of approximately 45, 17, and 13 kg, respectively.



Figure 2. Burmese python carcass (A = full body; B = close up of posterior 1/3 of animal) just prior to necropsy showing skin lesions on ventral surface. Ruler is 15.5 cm.

Discussion

Previous work has documented Burmese pythons consuming white-tailed deer in ENP (e.g., Rochford et al. 2010); however, this is the first report of an invasive Burmese python ingesting multiple white-tailed deer. It is difficult to speculate on the frequency with which these deer were consumed especially considering published data on feeding frequency in free-ranging giant snakes are extremely scarce (but see Slip and Shine 1988 for data on carpet pythons, *Morelia spilota* Lacépède, 1804). Plus snakes are known to have long and variable fecal retention times (Lillywhite et al. 2002). However, because we know that two of the three deer consumed were fawns (estimated ages of both between 14 and 30 days old), and if we estimate those fawns were born on the median fawning date in ENP (22 February; Labisky et al. 1995), we can deduce that at least two of the three deer were consumed within the previous 87 days of the snake's capture on 3 June (14 day old fawn born on 22 Feb

Table 1. Material recovered from the large intestine of a Burmese python captured 03 June 2013 from ENP.

	Count	Material	Epiphyseal state	Identified as	Estimated Age	Notes
Teeth	1	Mandibular 3 rd deciduous premolar		<i>Odocoileus virginianus</i>	< 2.5 months ¹	Crown only
	1	Mandibular 1st permanent molar		<i>Odocoileus virginianus</i>	> 12 months ¹	Worn
Vertebrae	7	Vertebral centra		<i>Odocoileus virginianus</i>		
	9	Vertebral epiphyses		<i>Odocoileus virginianus</i>		
Appendages	1	Proximal humerus	unfused	<i>Odocoileus virginianus</i>	0–35 months ²	In 3 pieces
	1	Distal radius	unfused	<i>Odocoileus virginianus</i>	0–29 months ²	
	4	Carpals		<i>Odocoileus virginianus</i>	< 6 months	one right lateral, one left and one right radial, one 2nd/3rd carpal
	2	Distal metapodials	unfused	<i>Odocoileus virginianus</i>	0–29 months ²	
	18	Phalanges	mostly unfused	<i>Odocoileus virginianus</i>	0–12 months ²	4 proximal, 4 middle, 9 distal, 1 accessory
	1	Vestigial tarsal/metapodial		<i>Odocoileus virginianus</i>	adult ²	
	1	Sphenoid (base of skull)		<i>Odocoileus virginianus</i>		Fragment
Hoof sheaths	1	Hoof - digit III or IV		<i>Odocoileus virginianus</i>	adult ³	
	4	Dewclaw hooves - digits II and V		<i>Odocoileus virginianus</i>	adult ³	
	5	Hooves - digits III and IV		<i>Odocoileus virginianus</i>	24–30 days ⁴	
	2	Dewclaw hooves - digits II and V		<i>Odocoileus virginianus</i>		
	6	Hooves - digits III and IV		<i>Odocoileus virginianus</i>	14 days ⁴	
	4	Dewclaw hooves - digits II and V		<i>Odocoileus virginianus</i>		

¹ based on presence of germ teeth (i.e., absent from adults) and tooth wear

² based on epiphyseal union tables (Purdue 1983)

³ based on hoof size and coloration

⁴ based on postnatal hoof growth (Haugen and Speake 1958)

would have been consumed on 8 Mar and there are 87 days between 8 March and 3 June). We cannot speculate when this python ate the adult deer but the consumption of the two fawns and subsequent retention of fecal matter is well within the published maximum defecation interval (time elapsed between defecations) reported for captive *Python molurus* Linnaeus, 1758 (174 days; Lillywhite et al. 2002). Interestingly, the Burmese python that had previously been reported to consume a white-tailed deer fawn was captured on 22 March 2006 that is, 30 days after the median fawning date in ENP (Rochford et al. 2010).

Using our approximations for individual deer sizes, these three white-tailed deer represented 93%,

35%, and 27%, respectively, of the python's body mass. Interestingly, this particular python, although clearly an adult, was not particularly large relative to others collected from ENP (e.g., Krysko et al. 2012). Still, it is valuable to consider the biological significance of a single python consuming three deer within a period of several months. For instance, by knowing the caloric value of the combined deer and the energy efficiencies of a free-ranging python we might estimate the potential energy gain from these meals. Using captive Burmese pythons consuming rodent meals, researchers estimated an apparent assimilation efficiency of 84.7±0.4% (Cox and Secor 2007). That is roughly 85% of the ingested energy from a meal can be devoted to metabolism and

growth combined. Assuming the caloric value for deer is 7.9 kJ g^{-1} (estimated from skeletal muscle plus associated fat, skin, and hair of mule deer [*Odocoileus hemionus* Rafinesque, 1817]; Pritchard and Robbins 1990), the three deer consumed by this female python would represent a total of 592,500 kJ; 84.7% or 501,848 kJ of this would be available for python metabolism and growth (i.e., somatic growth, fat stores, and reproduction). Without an estimate of field metabolic rates (metabolism needed for all maintenance and activity) for free-ranging pythons we cannot know precisely how much of this ingested energy could be devoted to production. Nevertheless, this substantial amount of energy clearly contributed to the large amount of fat and developing follicles found in this snake that would translate to high growth rates and reproductive success for this female—both critical components for a successful invasion.

Although white-tailed deer are sympatric with large constricting snakes (e.g., boa constrictor, *Boa constrictor* Linnaeus, 1758) within Latin America, in southern Florida Burmese pythons likely represent a novel predatory threat to deer in ENP since snakes large enough to prey on medium- to large-sized mammals went extinct there at least 16 million years ago (Kluge 1988; Dorcas et al. 2012). Therefore specific predatory behaviors may equip pythons with a distinct advantage in procuring deer since deer may not recognize snake odors as a potential threat in Florida (Reed et al. 2012). Indeed Burmese pythons are quite capable of taking deer and other sizeable prey; a variety of medium to large ungulates have been known to be consumed by snakes in their native range including sambar (*Rusa unicolor* Kerr, 1792), chital (*Axis axis* Erxleben, 1777), hog deer (*Axis porcinus* Zimmermann, 1780), red muntjak (*Muntiacus muntjak* Zimmermann, 1780), Indian spotted chevrotain (*Moschiola meminna* Erxleben, 1777), and wild boar (*Sus scrofa* Linnaeus, 1758; Wall 1921; Whitaker and Captain 2004). Burmese python predation on white-tailed deer in ENP is concerning for a variety of reasons. Economically, white-tailed deer are an important game species that generates a large amount of revenue for the state through the sale of hunting licenses (U.S. Census Bureau 2011). Of equal or greater concern is the ecological impact of predation on a deer population that may be already suffering from low recruitment. In an extensive radiotelemetry study, only 9% (5 of 55) of radio-instrumented fawns survived to breeding age in ENP owing to high mortality from bobcats (Labisky et al. 1995). Additional work on white-tailed deer vital rates and recruitment is needed to fully establish the impact of exotic pythons on the deer population in ENP.

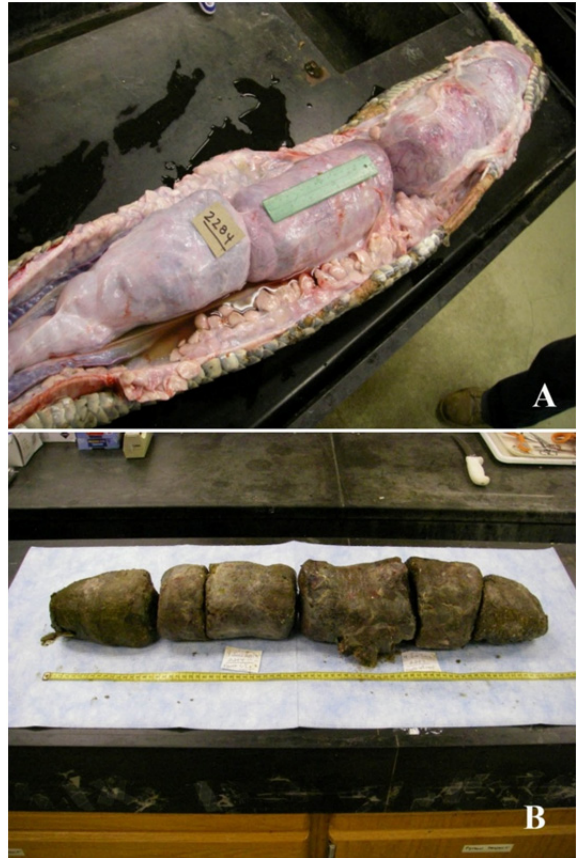


Figure 3. Burmese python large intestine (A = intact large intestine containing fecal matter) and fecal matter exposed (B).

Snakes exhibit traits which appear to make them particularly successful as invasive species. These traits include high reproductive potential, broad diets, low detection probabilities, and extremely low energetic requirements (Pough 1980; Christy et al. 2010; Reed et al. 2012). As a particularly telling example, brown treesnakes (*Boiga irregularis* Merrem, 1802) native to Australia and New Guinea, were introduced to Guam prior to the 1950's (Rodda et al. 1992) and contributed to the local or global extinction of at least ten bird species, but they were not implicated in these extinctions until several decades after their introduction (Savidge 1987). Burmese pythons established in southern Florida share a similar suite of characters, but they are also large-bodied—a trait that not only enables them to take large prey like white-tailed deer but may also be a primary driver in their invasion success (Reed et al. 2012). Correlative evidence suggests that white-tailed deer have declined in ENP by 94% since pythons became established (Dorcas et al. 2012). Because there have been multiple reports of pythons consuming deer in



Figure 4. White-tailed deer hooves ($n = 12$) and dewclaws ($n = 10$) recovered from Burmese python fecal material. Hooves are organized by individual: leftmost = adult, middle = large fawn, rightmost = small fawn.

ENP (Rochford et al. 2010; R.W. Snow, pers. comm., this report), and because individual detection probabilities for Burmese pythons are extremely low, the number of white-tailed deer consumed by pythons in ENP may be higher than previously realized.

Conclusions

We report the first instance of an invasive Burmese python (*P. m. bivittatus*) consuming multiple white-tailed deer in ENP. Viewed in the context of correlative (Dorcas et al. 2012) and experimental (McCleery et al. 2015) data linking Burmese pythons to declines of mammals in ENP, our report underscores the potential impact of an exotic snake predator on native prey populations—even those as large as white-tailed deer. We hope this report encourages additional work to develop methodologies to mitigate the impacts of this large-bodied invasive snake.

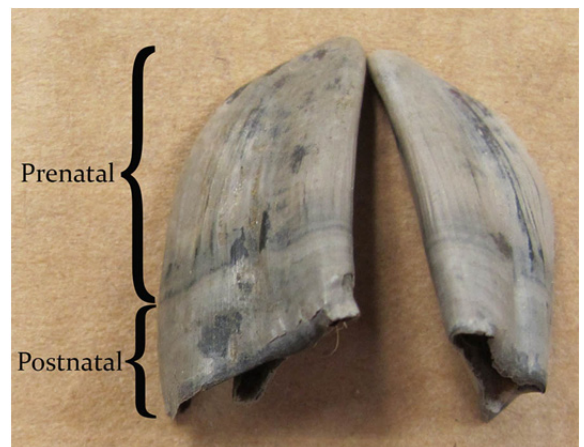


Figure 5. Close up of white-tailed deer hooves from a fawn (approximately 14 days old) recovered from Burmese python fecal material. Brackets delineate areas of prenatal and postnatal growth that were used to estimate age.

Acknowledgements

This work was made possible through funding provided by the U.S. National Park Service and the U.S. Geological Survey's Invasive Species Program. We acknowledge the contributions of Bobby Hill (SFWMD) who has personally removed more than 400 Burmese pythons from ENP and was captor of the python reported in this article. We thank H.E. Wingert, G.G. Sorrell, and D.V. Cuttie for donating deer legs. A.L. Gardner provided input and personal dewclaw specimens for comparison and aging purposes. The manuscript was improved by R.P. Reynolds, and two anonymous reviewers. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

References

- Christy MT, Yackel Adams AA, Rodda GH, Savidge JA, Tyrrell CL (2010) Modelling detection probabilities to evaluate management and control tools for an invasive species. *Journal of Applied Ecology* 47: 106–113, <http://dx.doi.org/10.1111/j.1365-2664.2009.01753.x>
- Cox CL, Secor SM (2007) Effects of meal size, clutch, and metabolism on the energy efficiencies of juvenile Burmese pythons, *Python molurus*. *Comparative Biochemistry and Physiology* 148: 861–868, <http://dx.doi.org/10.1016/j.cbpa.2007.08.029>
- Dorcas ME, Willson JD, Reed RN, Snow RW, Rochford MR, Miller MA, Meshaka WE, Andreadis PT, Mazzotti FJ, Romagosa CM, Hart KM (2012) Severe mammal declines coincide with proliferation of invasive Burmese pythons in Everglades National Park. *Proceedings of the National Academy of Sciences* 109: 2418–2422, <http://dx.doi.org/10.1073/pnas.1115226109>
- Dove CJ, Snow RW, Rochford MR, Mazzotti FJ (2011) Birds consumed by the invasive Burmese python (*Python molurus bivittatus*) in Everglades National Park, Florida, USA. *The Wilson Journal of Ornithology* 123: 126–131, <http://dx.doi.org/10.1676/10-092.1>
- Gee KL, Holman JH, Causey MK, Rossi AN, Armstrong JB (2002) Aging white-tailed deer by tooth replacement and wear: a critical evaluation of a time-honored technique. *Wildlife Society Bulletin* 30: 387–393
- Haugen AO, Speake DW (1958) Determining age of young fawn white-tailed deer. *Journal of Wildlife Management* 22: 319–321, <http://dx.doi.org/10.2307/3796471>
- Kluge AG (1988) Relationships of the Cenozoic boine snakes *Paraepicrates* and *Pseudoepicrates*. *Journal of Vertebrate Paleontology* 8: 229–230, <http://dx.doi.org/10.1080/02724634.1988.10011700>
- Krysko KL, Hart KM, Smith BJ, Selby TH, Cherkiss MS, Coutu NT, Reichart RM, Nunez LP, Mazzotti FJ, Snow RW (2012) Record length, mass, and clutch size in the nonindigenous Burmese python, *Python bivittatus* Kuhl 1820 (Squamata: Pythonidae), in Florida. *IRCF Reptiles and Amphibians: Conservation and Natural History* 19: 267–270
- Labisky RF, Boulay MC, Miller KE, Sargent RAJ, Zultowsky JM (1995) Population ecology of white-tailed deer in Big Cypress National Preserve and Everglades National Park. Final Report to USDI - National Park Service. Department of Wildlife Ecology and Conservation: University of Florida, 38 pp
- Lillywhite HB, de Delva P, Noonan BP (2002) Patterns of gut passage time and the chronic retention of fecal mass in viperid snakes. *Biology of the Vipers*. Boulder CO: Eagle Mountain Publishing, pp 497–506
- McCleery RA, Sovie A, Reed RN, Cunningham MW, Hunter ME, Hart KM (2015) Marsh rabbit mortalities tie pythons to the precipitous decline of mammals in the Everglades. *Proceedings of the Royal Society of London (B)* 282, <http://dx.doi.org/10.1098/rspb.2015.0120>
- Pough FH (1980) The advantages of ectothermy for tetrapods. *American Naturalist* 115: 92–112, <http://dx.doi.org/10.1086/283547>
- Pritchard GT, Robbins CT (1990) Digestive and metabolic efficiencies of grizzly and black bears. *Canadian Journal of Zoology* 68: 1645–1651, <http://dx.doi.org/10.1139/z90-244>
- Purdue JR (1983) Epiphyseal closure in white-tailed deer. *Journal of Wildlife Management* 47: 1207–1213, <http://dx.doi.org/10.2307/3808195>
- Reed RN, Rodda GH (2009) Giant constrictors: Biological and management profiles and an establishment risk assessment for nine large species of pythons, anacondas, and the boa constrictor. *US Geological Survey Open-File Report 2009-1202*
- Reed RN, Willson JD, Rodda GH, Dorcas ME (2012) Ecological correlates of invasion impact for Burmese pythons in Florida. *Integrative Zoology* 7: 254–270, <http://dx.doi.org/10.1111/j.1749-4877.2012.00304.x>
- Rochford MR, Krysko KL, Nifong J, Wilkins L, Snow RW, Cherkiss MS (2010) *Python molurus bivittatus* (Burmese python): Diet. *Herpetological Review* 41: 97
- Rodda GH, Fritts TH, Conry PJ (1992) Origin and population growth of the brown tree snake, *Boiga irregularis*, on Guam. *Pacific Science* 46: 46–57
- Savidge JA (1987) Extinction of an island forest avifauna by an introduced snake. *Ecology* 68: 660–668, <http://dx.doi.org/10.2307/1938471>
- Severinghaus CW (1949) Tooth development and wear as criteria of age in white-tailed deer. *Journal of Wildlife Management* 13: 195–216, <http://dx.doi.org/10.2307/3796089>
- Slip DJ, Shine R (1988) Feeding habits of the diamond python, *Morelia s. spilota*: ambush predation by a boid snake. *Journal of Herpetology* 22: 323–330, <http://dx.doi.org/10.2307/1564156>
- Snow RW, Brien ML, Cherkiss MS, Wilkins L, Mazzotti FJ (2007a) Dietary habits of the Burmese python, *Python molurus bivittatus*, in Everglades National Park, Florida. *The Herpetological Bulletin* 101: 5–7
- Snow RW, Krysko KL, Enge KM, Oberhofer L, Warren-Bradley A, Wilkins L (2007b) Introduced populations of *Boa constrictor* (Boidae) and *Python molurus bivittatus* (Pythonidae) in southern Florida. In: Henderson RW, Powell R (eds), *Biology of the Boas and Pythons*. Eagle Mountain, UT: Eagle Mountain Publishing, pp 416–438
- U. S. Census Bureau (2011) National Survey of Fishing, Hunting, and Wildlife-Associated Recreation. U.S. Department of Interior, U.S. Fish and Wildlife Service, and U.S. Department of Commerce, <http://www.census.gov/prod/2013pubs/fhw11-fl.pdf>
- Wall F (1921) *The Snakes of Ceylon*. Colombo, Ceylon: H.R. Cottle, Government Printer, 581 pp
- Whitaker R, Captain A (2004) *Snakes of India: The field guide*. Chennai, India: Draco Books, 479 pp