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Introduction of an Exotic Constricting Snake (*Boa constrictor*) and Its Establishment on St. Croix, U.S. Virgin Islands

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***Abstract.*—The introduction of boas from the pet trade to novel localities poses a threat to sub-tropical and tropical islands worldwide. The first constricting snake was found on St. Croix, U.S. Virgin Islands, in 2012. Despite efforts to work locally to remove snakes from the environment, we found increasing numbers of individuals each year, and we removed 88 boas from the wild on St. Croix through August 2018. We used spatial and genetic analyses to determine the range and origin of Boa Constrictors (*Boa constrictor*) on St. Croix, which is not native to St. Croix. We found that individuals were genetically identical with an origin in the Gulf of Mexico. We conclude that the boas are from a single source, or even a single founding female, originating in the pet trade. The boas have spread exponentially to occupy > 50% of the island since their introduction. We recommend strategies to eradicate non-native snakes on St. Croix including education, monitoring of native species, regulation, removal, and research.**

Key Words.—biological invasion; *Boa constrictor*; cytochrome b; islands; invasive species; phylogeography; predation

Introduction

Introductions of non-native amphibians and reptiles are increasing exponentially worldwide due to increased globalization (Kraus 2015; Capinha et al. 2017). International shipping containers, the global pet trade, and tourism are just some of the pathways that species can leave one region and enter a new region (Kraus 2008). The relatively warm, stable climate facilitates the establishment of many invasive species in the Caribbean; however, the Caribbean is both a source (e.g., Greenhouse Frog, *Eleutherodactylus planirostris*) and a receiver (e.g., South American Cane Toad, *Rhinella marina*) of invasive species (Powell et al. 2011). Many Caribbean countries have good records of established invasive species. For example, well-supported records exist of species that were established historically (e.g., St. Thomas 1960 for Coquí, *Eleutherodactylus coqui*) and recently (e.g., St. Croix 1995 for Puerto Rican Ameiva, *Pholidoscelis exsul*) in the Virgin Islands (Treglia et al. 2013). Fewer records exist of early detections of constricting snakes. Snakes are rapidly invading sub-tropical regions of North America and the Caribbean almost entirely through the release of pets by owners (Reed and Rodda 2009). A key challenge in the study of biodiversity has been to avoid introducing new species to new environments, yet species including constricting boas are common in the pet trade despite their propensity to become invasive in sub-tropical and tropical regions worldwide (Perring et al. 2015; Wiens and Hobbs 2015).

The constricting snakes available in the pet trade are commonly sold as juveniles, which are small and docile. The bite and constriction of juveniles does little to harm pet owners, but as boas grow larger, some owners no longer wish to invest in the substantial resources required to maintain a healthy constricting snake safely (Reed 2005). The release and escape of constricting snakes is the most likely invasion pathway for constricting snakes to enter sub-tropical areas of the U.S. (Reed and Rodda 2009). Boa Constrictors (*Boa constrictor*) from multiple regions of their native range have escaped, mixed, and established on the west coast of Puerto Rico since the early 1990s (Reynolds et al. 2013). No invasive constricting snake populations are known to occur across the remaining 100+ islands of the Puerto Rican archipelago (including U.S. Virgin Islands), although Florida and areas of the southeastern U.S. have populations of constricting snakes today (Reed and Rodda 2009). Elsewhere across the Caribbean, where Boa Constrictors are introduced, declines in native birds and reptiles have occurred (Martínez-Morales and Cuaron 1999). In Aruba, Boa Constrictors are established (Bushar et al. 2015), and boa predation on a range of native species has been observed (Quick et al. 2005). Changes to the ecosystem of Aruba, including an

order of magnitude increase in the abundance of reptile species preyed on by birds, has occurred since the boa invasion (Goessling et al. 2015).

In this study, we investigate sightings of Boa Constrictors on St. Croix, politically associated with the U.S. Virgin Islands (including St. Thomas and St. John of Puerto Rican archipelago). Despite shared geopolitical association, the biology of St. Croix is unique as a land bank island with endemic species and distinct conservation challenges (Pregill 1981; Platenberg 2007). Six of the seven endemic species of native reptiles on St. Croix are affected by the introduction of invasive species; only the endemic St. Croix Anole (*Anolis acutus*) appears unaffected by the introduction of invasive species (Platenberg 2007). Three extinctions (Saint Croix Racer, *Borikenophis sanctaecrucis*; Greater Saint Croix Skink, *Spondylurus magnacruzae*; Lesser Saint Croix Skink, *Capitellum parvicruzae*) are attributed to predation by a small Indian mongoose introduced from Myanmar to St. Croix in 1884 for biocontrol of rats foraging on sugar cane crops (Hoagland et al. 1989). The current extirpation and restriction of St. Croix Ground Lizards (*Pholidoscelis polops*) to offshore islands is similarly attributed to mongoose predation (Angeli et al. 2018). Beatty's Least Geckos (*Sphaerodactylus beattyi*) are restricted to the east end of the island because of competition from Big-scaled Least Geckos (*Sphaerodactylus macrolepis*) presumably introduced from the Puerto Rican archipelago (MacLean and Holt 1979). Native Virgin Islands Blindsnakes (*Antillotyphlops richardii*) are outcompeted by the globally invasive Flowerpot Blindsnakes (*Indotyphlops braminus*; Powell and Henderson 2012). Green Iguanas (*Iguana iguana*) introduced via the pet trade (López-Torres et al. 2012) and Puerto Rican Ground Lizards (*Ameiva exsul*) introduced in a shipment from Puerto Rico are established throughout St. Croix (Treglia et al. 2013). The release of large constricting snakes by pet owners in the western forests of St. Croix were reported to local authorities in 2012 (pers. obs.).

Our study is the first to investigate the reports of non-native constricting snakes on the island of St. Croix. We analyzed the local reports of Boa Constrictors, captured and retained a subset of the snakes to identify the species present, and mapped their geographic distribution on the island of St. Croix. We expected that the boas would occur most densely where they were first reported in the western forests of St. Croix, supporting the idea that the snake population could be traced back to the release of boa(s) from a single pet owner. We conducted a genetic analysis to determine the origin of the population on St. Croix. We tested the idea that snakes are established across a substantial area of the island by creating a map model to determine the known and most probable extent of snakes. We predicted that the population has established, and if so, the broader conclusion of the paper is that regulation of the pet trade needs to improve for Boa Constrictors, which quickly invade and easily establish in new environments.

Materials and Methods

Study site.—St. Croix (17°44'N, 64°43'W), U.S. Virgin Islands, is a 218 km^2 island that emerged as tectonic plates moved eastward and upward in the Cretaceous era 60 million y ago (Pregill 1981). The island is covered with roughly 30% subtropical moist forest and 70% dry tropical forest in various stages of secondary succession (Atkinson and Marín-Spiotta 2015). Mean annual precipitation is 1,060 mm and the temperature averages 26.5° C year-round. The clearing of 90% of the forest cover of the island coincided with a 200-y period of sugarcane cultivation lasting from the 1780s into the mid-1950s (Atkinson and Marín-Spiotta 2015). Rat predation on sugar cane triggered the introduction of mongoose to the island decimating native wildlife (Dodd 1978).

Non-native species on St. Croix.—Starting in the early 2000s, the Department of Planning and Natural Resources of the Division of Fish and Wildlife (DFW) of the U.S. Virgin Islands began to record reports of non-native species reported on St. Croix (pers. comm). None of the authors ever engaged in active searches for non-native species reported in this study. Rather reports were first observed by local citizens and reported to authorities starting in 2012. Increasing public concern about the effect of non-native snakes on the biota of the island escalated and local citizens started a web site (STX Snakes; www.stxsnakes.com) to publish information on boas in 2014. STX Snakes volunteers would alert local emergency responders to the presence of snakes and personnel of DFW responded to all calls related to non-native snakes. The authors responded by capturing snakes, visually inspecting morphological characters, and removing the individuals from the wild (Boback 2006; Wright 2012).

Range estimate.—Based on the confirmed reports, we created a range map of boas on St. Croix. We converted boa locality records to WGS-84 from multiple coordinate reference systems native to cell phones and handheld GPS using Google Maps. To plot the points, we uploaded a St. Croix coast outline (Gould et al. 2007) to QGIS 2.14.0-Essen in WGS-84 datum (QGIS Development Team. 2009. QGIS Geographic Information System. Open Source Foundation. Available from http://qgis.osgeo.org. [Accessed 15 March 2017]). We determined the extent and area of the boa observations by creating a minimum convex

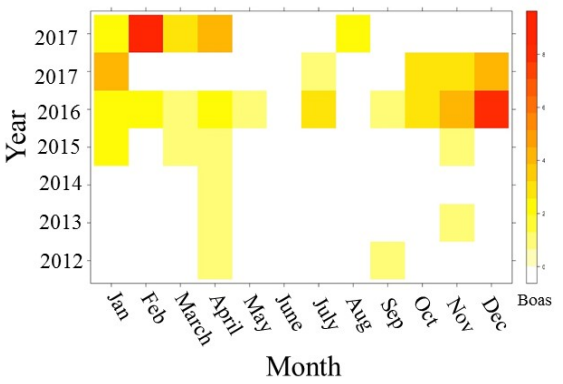

Figure 1. Monthly capture of non-native Boa constrictors (*Boa constrictor*) reported to the authors through August 2018. Each boa was confirmed by visual inspection.

polygon encompassing the areas around the points. Minimum convex polygons are commonly used to infer biologically meaningful estimates of species range (Burgman and Fox 2003). We calculated a best fit model of the rate of boa dispersal and fit a spatial interpolation using inverse distance weighting (QGIS core interpolation plug-in) across the island to estimate the maximum boa distribution. We used the area estimates from the minimum and maximum polygons to infer the range and potential range of boas on St. Croix.

Biological sampling.—In 2016 and 2017, we preserved boas for a permanent record of occurrence on St. Croix, which we stored at the Smithsonian Institution National Museum of Natural History (Table 1). We euthanized live animals with an injection of MS-222 (tricaine methanesulfonate) in the intraperitoneal cavity. We mixed the solution with 5 g of MS-222/liter H2O and buffered the solution to a pH of 7.0 with 10 g sodium bicarbonate. We used a dosage of 500 mg/kg by body weight following Conroy (2009). We preserved the animals with formalin, soaked the specimens in water, and stored each specimen in ethyl alcohol. We stored liver or other internal organ tissues in DMSO-EDTA at room temperature for no more than one month and transferred the tissues as soon as possible to a -80° C freezer. The tissue samples were digested for up to one month in 150 ul of AutoGen M2. To the digested solution, we added 150 ul M1 buffer with Proteinase K overnight. We extracted DNA in the AutoGen Prep 965f DNA extractor (AutoGen Inc., Holliston, Massachusetts, USA) using an animal tissue phenol-chloroform-isoamyl extraction and resuspended the DNA in AutoGen R9 buffer.

We sequenced the mtDNA gene cytochrome b (cyt b) using the following protocol. We amplified the DNA with the PCR primers L14910 (5' GACCTGTGATMTGAAAACC AYCGTTGT 3') and H16064 (5' CTTTGGTTTACAAGAACAATGCTTTA 3'; Burbrink et al. 2000) in 10 ul reactions, with 1 ul of DNA template, using 0.1 ul of Bioline Taq, 0.3 ul of primers (10 uM), 0.4 ul MgCl, 0.5 ul of dNTPs (10 uM) and 6.4 ul of H20 and were run with a 95° C hot start for 5 min, followed by 35 cycles of 95° C for 30 sec, 48° C annealing for 30 sec, and 72° C elongation for 1 min, with a final 72° C elongation for 5 min. The PCR products were purified with ExoSAP-ITTM enzyme and sequenced in both directions using PCR primers, 0.25 BigDye TM Cycle-sequence reactions and run on an ABI3730 (2011 Life Technologies) using the 950 chemistry run at the NMNH. Raw traces were aligned, trimmed, and edited in Geneious v 11.1.5 (Biomatters Ltd 2005–2016) and inspected for stop codons. Consensus sequences were aligned in using the Muscle plug-in in Geneious with other *Boa constrictor* sequences in GenBank (largely from Hynková et al. 2009, Suárez-Atilano et al. 2014, and Card et al. 2017). Specimens from GenBank with stop codons were omitted and ends were trimmed to maximize overlapping characters in the matrix. We conducted Maximum-likelihood analyses on the alignment in RAxML (v8.2.9, Stamatakis 2014) with the rapid bootstrap inferences (1,000 replicates) and subsequent thorough Maximum-likelihood search using the GTRGAMMA model.

Results

Boa records on St. Croix.—Each boa reported was confirmed by the authors and only included here with positive visual identification. Each boa reported here was found dead or euthanized by staff at DFW or by the authors. The first capture of a boa on the island of St. Croix was in 2010; in that year, just one individual was reported to DFW. That individual was a pet that a citizen reported to DFW as having escaped from its cage and it was found and returned. No boas were reported in 2011, but citizens reported two individual boas in 2012, two individual boas in 2013, and one individual boa in 2014. In 2015, local citizens reported and personnel of DFW captured five boas. The staff did not record reports of boas that resulted in no captures, and few reports were made from 2012–2015 without capture due to sustained search efforts by DFW to capture and assess all reports. In 2016, personnel of DFW captured 27 boas. By the end of 2017, 15 boas were captured by DFW (Fig. 1). By 31 August 2018, personnel of DFW had captured 22 boas. Most boas were caught from October to March, and no boas have ever been reported in June (Fig. 1). The reports and captures from 2012–2015 represent all boas, while we confirmed most but not all boas that citizens reported from 2016–2018. The size of most boas was 550–1,050 cm snout-vent length. Males and females have been found, but records do not indicate sex.

Table 1. Boa specimens (S) and tissues (T) deposited as vouchers at the Smithsonian Institution National Museum of Natural History (USNM), Washington, D.C., USA. We provide the locality (Latitude, Longitude) and field collection date (Year, Month) of all samples. The USNM numbers starting in 575- series refer to formalin-preserved specimens stored wet. The USNM Herp Tissue (HT) is available without the specimen or photograph, the USNM Herp Image (HI) is available as an image and tissue. We provide the GenBank Accession numbers for the boa cytochrome b sequences. All sequences were identical where they overlap and only differed by length obtained.

USNM	GenBank	Type	Latitude	Longitude	Year	Month
HT 143	MK330858	T	17.730147	-64.887576	2016	8
575068	MK330859	S,T	17.727122	-64.887103	2016	10
HI 2911	MK330860	T	17.717944	-64.871204	2016	10
575069	MK330861	S,T	17.714551	-64.873093	2016	10
575070	MK330862	S,T	17.753261	-64.881697	2016	6
575064		S,T	17.730657	-64.883197	2017	3
575065		S,T	17.724004	-64.881629	2017	3
575066		S,T	17.71821	-64.881978	2017	4
575067		S				

The area encompassing all captured boas was 61.6 km^2 as of 1 April 2017. We found that boas spread at a geometrically increasing rate in each year from 2012–2015. The spatial interpolation indicates that boas may range as far as 136.2 km^2 across St. Croix (Fig. 2).

We deposited eight tissue samples and seven boa specimens at the NMNH (Table 1). We collected five tissue samples from wild-caught individuals (Fig. 3). One snake was a roadkill sufficiently decayed such that we did not retain the animal but only took a photograph (USNM: HerpImage: 2911 add). We caught two animals live (USNM 575069–70), one animal was a roadkill (575068), and one animal was killed accidentally by an electric weed trimmer (USNM 575067). Three additional boas are in the Smithsonian National Museum of Natural History (USNM 575064–66)) as vouchers and permanent record of their presence on St. Croix.

We obtained sequence data for cyt b from five individuals. The base-pairs (bp) length ranged from 734–1,106 post quality trimming. Despite differing in length, the genetic sequences were identical; therefore, we used only the longest sequence (USNM 575069) in our alignment, which consisted of another 324 individuals from GenBank and was 1,062 bp in length. We deposited all five sequences in GenBank (Table 1). Our maximum-likelihood analysis recovered a similar overall topology to other studies, supporting the South and Central American clades, and the Pacific Coast clade ranging from western México from the Isthmus of Tehuantepec to Sonora (Fig. 4). The St. Croix haplotype was placed in the Central American clade (99% bootstrap support), in and among the Gulf of México clade of Suárez-Atilano et al. (2014).

Discussion

Exotic Boa Constrictor are established across 28.2–62.4% of the island of St. Croix from the far west to Salt River Bay. Because the island of St. Croix is isolated by distance (> 80 km) and a deep sea trench with strong currents from the northwestern islands of the Puerto Rican archipelago, the pet trade is the most likely source of these animals. If the origin of the snakes on St. Croix were the pet trade with multiple releases over time by multiple owners, genetic sequences would likely match a multitude of *Boa constrictor* populations common to the pet trade as in the Puerto Rico invasion

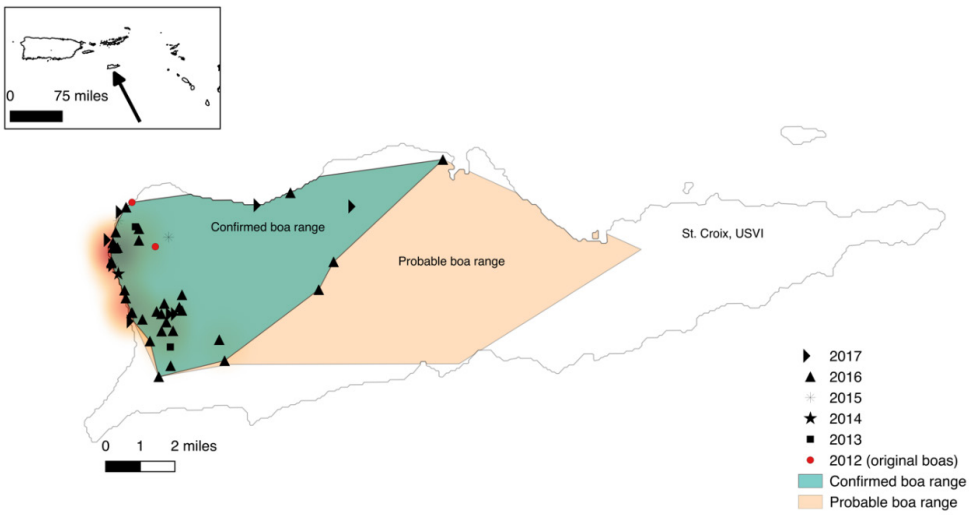

Figure 2 . Locations of Boa constrictors (*Boa constrictor*) encountered that were removed on St. Croix 2012–2017. The arrow in the inset Caribbean map points to the island of St. Croix, U.S. Virgin Islands. The coastline of St. Croix is overlaid with the confirmed (green) and probable (tan) boa ranges (see text for more details). The orange shading indicates areas where captures occur in the highest density.

Figure 3. Representative photographs of two Boa Constrictors (*Boa constrictor*) removed from St. Croix in November 2016. The first boa was found dead on the road (USNM 575068; A-C). A local citizen encountered the second boa on private property while engaged in routine yardwork (USNM: HerpImage: 2911; D-H). (Photographed by Nicole Angeli).

(Reynolds et al. 2013) or the populations in Cozumel (Vázquez-Domínguez et al. 2012). Because all the St. Croix individuals that are from different localities across many months shared an identical mitochondrial haplotype (for about 700–1,100 bp of cyt b), they are likely the result of a single introduction event, from a single source population, perhaps even from a single founding female. This is suggestive of a pet trade introduction. Our phylogenetic analysis places this haplotype in the Gulf of México clade of Suárez-Atilano et al. (2014), sister to an individual from the San Andrés Tuxtla, Veracruz, México (KJ621476), with moderate (71%) support. We note the lack of bootstrap support within the major clades of our study is consistent with other phylogenetic analyses of *Boa constrictor* populations, particularly when only cyt b is used (Hynková et al. 2009; Suárez-Atilano et al. 2014), but also when RADseq data are used (Card et al. 2016). Our results support the St. Croix population originating from the Gulf of México, Veracruz, perhaps from San Andrés Tuxtla. More intensive sampling and molecular data, such as microsatellite markers, would be needed to further pin-point the origin of this population (e.g. Vázquez-Domínguez et al. 2012).

The temperate, suitable climate for the boas and an abundance of domestic mammals on St. Croix facilitates further boa spread and establishment in the years to come. Cats, dogs, goats, rats, mice, deer, tortoises, and mongoose are free-ranging. Smaller livestock including pigs, sheep, calves, and chickens may be impacted. Sensitive habitat areas for birds, including freshwater streams, beaches, private lands, and salt ponds have boas present today. Private spaces harbored the majority of boas; however, in 2017, the record of a boa in the Salt River Bay National Historical Park and Ecological Preserve, designated as a national natural and cultural area, is the first instance of impacts on U.S. federally protected land on St. Croix.

On St. Croix, Boa Constrictors have been found hidden in small pipes, between wooden pallets, car engines, and rolled fencing material. The increasing captures of boas are thought to reflect the overall trend, rather than specific numbers of boas, as systematic surveys to determine the total latent abundance is outside the scope of this paper. No known native predators, for example Spectacled Caiman (*Caiman crocodilus*), Argentine Giant Tegu (*Salvator merianae*), or Southern Crested Caracara (*Caracara plancus*), exist on St. Croix. No methods for eradication exist. Research on methods for boa removal including early detection, predictive mapping, trapping, and exclusion barriers is on-going across other islands and ecosystems (Reed,

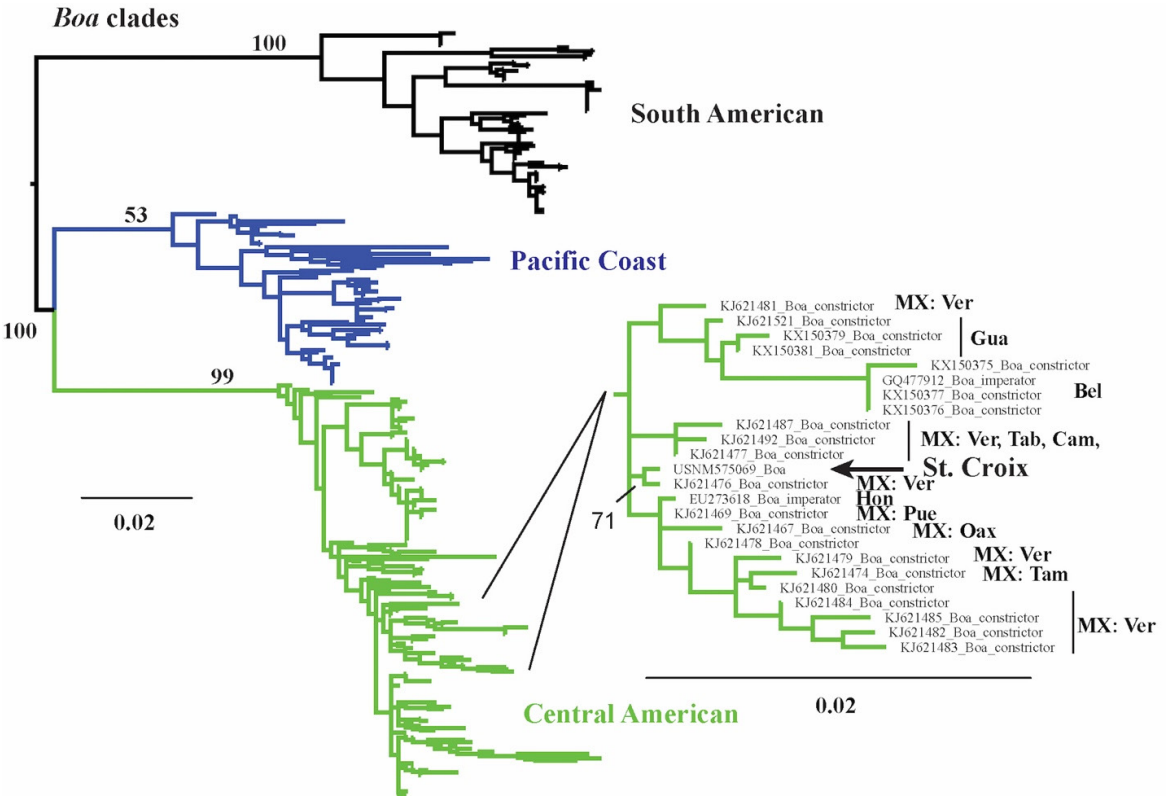

Figure 4. Maximum-likelihood phylogeny of Boa constrictor (*Boa constrictor*) based on 1062 bp (cyt b) and 325 taxa from GenBank, including the St. Croix haplotype. (Left) Overall tree and major clades within *Boa constrictor sensu lato*. (Right) Close-up of clade containing the St. Croix haplotype, with GenBank samples and their geographic localities (Bel = Belize; Gua = Guatemala; MX = México, Cam = Campeche, Oax = Oaxaca, Pue = Puebla, Tab = Tabasco, Tam = Tamaulipas, Ver = Veracruz (states in MX). Bootstrap support values are shown for relevant nodes > 50% (scale bars indicated maximum-likelihood distances).

R.N., and G.H. Rodda. 2008. A review of tools for snake control, and their potential applicability to control of *Boa constrictor* on Aruba. Wild Aruba. Available from http://www.wildaruba.org/Documents/Reed%20&%20Rodda%202008%20Wild%20Aruba%20mtg%20Review%20of%20snake%20control%2001A.pdf [Accessed 15 November 2017]). Few solutions, not even exclusion barriers, have been successfully tested for Boa Constrictors on Caribbean islands. The future response on St. Croix to the boa introduction, now past introduction and well-established, can be used for its opportunity to seek new methods of boa removal, pet trade education, and invasive species management in a small area. Until such time when techniques advance for boa eradication from the island, we have recommendations for St. Croix.

Recommendations.— Encourage the public to report boa sightings to local authorities. The government specifically restricts possession of territorially non-native species except by written consent (Virgin Islands Code [V.I.C.] 14 §192), yet citizens continue to advertise illegally retained boas for sale online. Public service announcements denouncing further capture, retention, breeding, and sale of wild individuals should be made on television, radio, print, and billboard media.

Use existing datasets to identify the effects of snakes on the island as done in other snake invasions (Wiles et al. 2003). All wildlife, native and non-native, will be affected by the presence of boas. Local bird watchers have collected over 30 y of sighting data on St. Croix in the online database eBird (www.ebird.org). The local animal welfare center has monthly intake records for free-roaming cats and dogs.

Remove all boas sighted from the wild. The best practices of the American Veterinary Medication Association, American Society of Ichthyologists and Herpetologists, and similarly accredited organizations recommend euthanasia by injection of MS-222 (tricaine methanesulfonate) into the intraperitoneal cavity of the animal (Leary et al. 2013). The solution can be made with 5 g MS-222/liter H_2O and buffered to a pH of 7.0 with 10 g sodium bicarbonate. The dosage should follow 500 mg/kg by snake body weight (Conroy et al. 2009). If not available, pithing may be performed, and the carcass discarded.

Enforce local restrictions for the unlawful importation and possession of non-native species. The government

restricts the importation or introduction of any animal non-native to the territory (12 V.I.C. §105.d), and specifically restricts importation and possession except by written consent of the government (14 V.I.C. §192). The authors are unaware of enforcement or prosecution related to unlawfully importing, breeding, and owning constricting snakes in the Virgin Islands.

Investigate the differences in this Caribbean introduction from the well-studied invasions of snakes across the Pacific Ocean and southern areas of the U.S. (Reed and Rodda 2009). Federal and local governments as well as invasive species experts at the University of the Virgin Islands and the University of Puerto Rico can study aspects of boa establishment and control on St. Croix and how its applicability from other localities within larger ecosystems (i.e., the Everglades in Florida, USA). Protect the native wildlife left on St. Croix. Establish perimeter traps and patrol ecologically sensitive areas during peak boa activity periods (December-February). The introduction and establishment of the boa is new, and many areas are still free of boas at this time.

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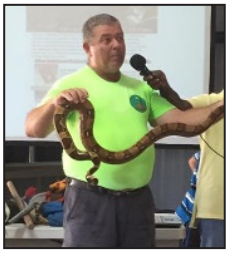

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