A Long-term Dietary Assessment of Invasive *Boa constrictor* on Aruba

Howard K. Reinert[1,6], Ashley E. Leto[1], Janis A. Tumaliuan[1], Sara Jackrel[2],
William I. Lutterschmidt[3], Lauretta M. Bushar[4], and R. Andrew Odum[5]

[1]Department of Biology, The College of New Jersey, Post Office Box 7718, Ewing, New Jersey 08628-0718, USA
[2]Division of Biological Sciences, Ecology, Behavior & Evolution Section, University of California San Diego,
9500 Gilman Drive. #0116, La Jolla, California 92093-0116, USA
[3]Department of Biological Sciences, Sam Houston State University, 1905 University Avenue, Huntsville, Texas 77341, USA
[4]Department of Biology, Arcadia University, 450 South Easton Road, Glenside, Pennsylvania 19038, USA
[5]Department of Herpetology, Toledo Zoological Society, Post Office Box 140130, Toledo, Ohio 43614-0801, USA
[6]Corresponding author, e-mail: hreinert@tcnj.edu

Abstract.—Invasive Boa Constrictors (*Boa constrictor*) have established a reproductive population on Aruba. High *B. constrictor* densities could stress prey populations on this small, faunally simplistic island. We examined diet, size, and condition of 501 *B. constrictor* at three periods over nearly 15 y: during early invasion, approaching the peak in encounters, and after 5 y of declining encounters. The 401 prey identified consisted of 32.9% mammals, 37.4% lizards, and 29.7% birds. Dietary proportion of these categories was consistent across sampling periods. Non-native prey were consumed in relatively high proportions. Despite a positive relationship between snake snout-vent length and prey mass, even the largest snakes consumed small prey. During the high encounter period, many snakes had empty digestive tracts, little abdominal fat, and low body mass, possibly due to a decline in prey availability; however, snakes from residential/agricultural areas had better body condition than those from natural areas. High population densities of the native Aruban Whiptail Lizard (*Cnemidophorus arubensis*) may provide a consistent food supply for *B. constrictor* in both natural and residential/agricultural areas, and domesticated prey near human habitation may subsidize the population in residential/agricultural areas. Improved body condition in the last sampling period suggests that the population is either stabilizing or poised for an increase. The endemic Aruba Island Rattlesnake (*Crotalus durissus unicolor*) and *B. constrictor* had similar, broad diets that overlapped heavily. Eradication of *B. constrictor* from Aruba is unlikely, but integration may be possible if the population can be stabilized at low densities. We recommend continued control efforts and systematic monitoring of prey populations.

Key Words.—Aruba; *Boa constrictor*; Caribbean; *Crotalus durissus unicolor*; diet; invasive species; predation

Introduction

Introduced species can pose a large threat to established ecosystems. Apex predators such as snakes typically represent a severe threat to native biota, as demonstrated by the Brown Treesnake (*Boiga irregularis*), which decimated the native vertebrate fauna of Guam (Savidge 1987; Fritts and Rodda 1998; Rodda et al. 1999). Likewise, the introduction of Burmese Pythons (*Python bivittatus*) to the Florida Everglades, USA, has negatively affected the native mammalian fauna (Snow et al. 2007a,b; Dorcas et al. 2011). Insular ecosystems are particularly vulnerable due to their low species redundancy, potential endemism, and susceptibility to extinction (Donlan et al. 2003; Cuarón et al. 2004; Donlan and Wilcox 2008). Understanding the dietary habits of an introduced species is crucial, as dietary habits direct trophic interactions and may influence habitat use as well as predator and prey distribution (Romero-Nájera et al. 2007; Pyšek and

Richardson 2010). Invasive species that are dietary generalists are of particular concern because they have the potential to impact a large number of prey species (Reed 2005; Reed and Rodda 2009).

The Boa Constrictor (*Boa constrictor*) is a geographically widespread boid, with four subspecies currently recognized throughout South America and the islands of Trinidad, Tobago, and Isla Margarita in the southern Caribbean (Reynolds and Henderson 2018). Its historic distribution, however, did not include the Dutch West Indian islands of Aruba, Bonaire, or Curaçao (Brongersma 1940, 1959; Schwartz and Henderson 1991; Bushar et al. 2015). Across its distribution, *B. constrictor* is a dietary generalist known to consume a wide range of prey items including birds, lizards, small mammals, and even larger mammals such as opossums, dogs, armadillos, and monkeys (Martins and Oliveira 1999; Pizzatto et al. 2009; Quick et al. 2005). Invasive *B. constrictor* are a threat because of their rapid maturation (3 y), long lifespan (40 y), and potential to

biennially produce large litters (50+) of well-developed offspring (Greene 1983; Reed and Rodda 2009).

The first specimens of *B. constrictor* were discovered on Aruba in 1999 (Bushar et al. 2015), and, despite eradication efforts, an island-wide population was established by 2005 (Quick et al. 2005). Aruba is a small, arid island with low faunal diversity (Hummelinck 1940; van Buurt 2006). The known and suspected influence of other introduced snake species on community structure (Rodda et al. 1999; Reed and Rodda 2009; Dorcas et al. 2011) provided the impetus for the current research effort. Of particular concern was the potential competitive interaction between *B. constrictor* and the endemic Aruba Island Rattlesnake (*Crotalus durissus unicolor*). A previous examination of the diet of *B. constrictor* on Aruba demonstrated its generalist dietary habits and suggested that *B. constrictor* may overlap with *C. d. unicolor* for food as well as space (Quick et al. 2005; Reinert et al. 2008). The current study examined the diet composition of *B. constrictor* over nearly 15 y to elucidate the broader implications of the invasion of this introduced predator on this small insular ecosystem.

Materials and Methods

We studied snakes on the 180 km² Dutch Caribbean island of Aruba, which lies in the southern Caribbean at 12.507445N, -69.957215W, approximately 29 km north of the coast of the Paraguaná peninsula of Venezuela. The elevation of the island ranges from sea level to 188 m. Aruba sits in the path of the easterly trade winds and has a consistent, warm and arid climate. Although wet and dry seasons are recognized, the relative difference in precipitation is minor. The vegetation of the island is dominated by desert and thorn-scrub communities (Fuenmayor et al. 2005).

Beginning in April 1999, sightings of *B. constrictor* were reported by local residents to officials of Arikok National Park and the Aruban Department of Agriculture, Husbandry, and Fisheries (Salvador Franken, pers. comm.). Reported snakes were collected and euthanized with an intracardiac injection of a sodium pentobarbital-based euthanasia solution administered by a licensed veterinarian from the Aruba Veterinaire Dienst as part of an effort to eradicate this invasive species (Pieter Barendsen, pers. comm.). This sampling of snakes was based largely upon chance encounters by island residents and included minimal directed or systematic sampling efforts. The rate of such chance encounters could be influenced by various temporal, climatic, or intrinsic physiological factors of the snakes themselves (Joppa et al. 2009; Durso et al. 2011; Gregory and Tuttle 2016). As a result, it should not necessarily be assumed that annual capture rates compiled in this manner (Fig. 1) accurately reflected the actual population density
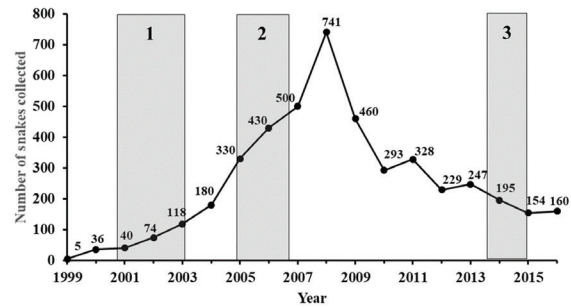

Figure 1. Total number of Boa Constrictors (*Boa constrictor*) collected and euthanized annually on Aruba and the three time periods when dietary samples were collected.

of *B. constrictor* on the island at any given time. To examine temporal changes in diet composition and body condition, we examined samples of snakes over three time periods: October 2000 to January 2003, January 2005 to July 2006, and November 2013 to January 2015 (Fig. 1). During each of these three time periods, we selected snakes captured within 24 h prior to euthanasia and having known locational information. We labeled each snake with the date and location of capture, then we bagged them in plastic and froze them for later necropsy. We later characterized the capture location as either a natural area (within or immediately adjacent to Arikok National Park) or a residential/agricultural area (in the immediate vicinity of houses and farms). The results of the first sampling period were originally summarized by Quick et al. (2005). We included these data in the current analysis. As suggested previously for population size, the snakes examined also may not precisely reflect the diet or condition of the general population during any given sampling period due to potential biases toward larger, more conspicuous snakes inherent in our sampling methodology.

During necropsy examination, we recorded the sex, mass (with and without intact consumed prey), and snout-vent length (SVL) of all sampled specimens. We removed and examined the stomach and lower gastro-intestinal tracts for prey contents. We identified any intact prey items at the time of dissection. We preserved partially digested, unidentifiable prey and feces in the alimentary canal in 70% ethanol and later examined the samples under a dissecting microscope (10–30× magnification) for feathers, scales, hair, teeth, beaks, claws, nails, bones, bone fragments, limbs, or other intact body parts. We examined mammal hair for macroscopic traits such as length, color, and banding pattern. We prepared wet-mount slides for compound light microscopic examination (40–400× magnification) of the medullar pigmentation of the hairs (Williams 1938). We made reverse impression slides of cuticle scale patterns by pressing hairs into partially dry, clear nail polish spread on glass microslides. We compared

Figure 2. Examples of the relative amount of fat bodies within the abdominal cavity of Boa Constrictors (*Boa constrictor*) on Aruba. Moderate fat (A) received a score of 2 and extensive fat (B) received a score of 3. (Photographs by William Lutterschmidt).

the characteristics from both wet-mount and reverse impression slides with reference hairs collected from potential prey on Aruba and with mammal hair keys (Mathiak 1938; Adorjan and Kolenosky 1969). We compared nails, claws, beaks, and scales with those from preserved specimens of birds, mammals, and lizards for qualities such as size and shape. We cleaned intact feathers and compared them with study specimens at the National Museum of Natural History (Washington D.C., USA) and the Academy of Natural Sciences of Drexel University (Philadelphia, Pennsylvania, USA). We identified feather remains through the examination of barb and nodal structure after they were prepared and mounted on microslides (Laybourne and Dove 1994). We identified prey to the lowest taxonomic level possible. We recorded the actual prey mass for all intact prey items found in the stomach. Because most prey items examined were either fully or partially digested, we also estimated average prey mass from samples of animals collected on the island (Bekker 1996; Quick et al. 2005) or from values reported in the literature (Brough 1983; del Hoyo et al. 1997; Dunning 2007). For non-intact prey having a potentially diverse size range (e.g., Green Iguana, *Iguana iguana*, and Cottontail Rabbit, *Sylvilagus floridanus*), we calculated the estimated size of the ingested prey based on the size of any intact remains (e.g., bones, claws, scales, hair).

Paired abdominal fat bodies (corpora adiposa) serve as the primary location of fat storage in snakes (Price 2017). We visually assessed the relative amount of abdominal fat and subjectively scored each snake based on the appearance of the fat bodies using the following scale: 0 = no fat bodies present within the abdominal cavity, 1 = small fat bodies present not obscuring other organs, 2 = moderately large fat bodies within the abdominal cavity that partially obscured other organs (Fig. 2), 3 = extensive fat bodies that filled the abdominal cavity, completely obscured other organs, and protruded upon incision of coelom (Fig. 2).

We used Chi-square Analyses to compare the frequency of occurrence of different prey items consumed, examine the differences among sampling periods, and compare diet samples of similar-sized *B. constrictor* and *C. d. unicolor*. We reported Yates Corrected Chi-square values for any analysis with only one degree of freedom. Prior to parametric statistical analyses, we examined the input data for normality using the Shapiro-Wilks test and for homoscedasticity of variances using Levene's Test, and data met assumptions. To analyze the relationship between total prey mass consumed and SVL, we used Pearson Product-moment Correlation. We used Two-way Analysis of Variance (ANOVA) and Two-way Analysis of Covariance (ANCOVA) followed by Tukey's HSD *a posteriori* tests (when appropriate) to examine the relationships between snake body mass, SVL, and body mass adjusted for SVL (adj. mass) between sexes and sampling periods for the snakes containing prey and between sexes and capture location type where snakes were collected in the 2005–2006 sampling period. We used One-way ANOVA to assess differences in precipitation and temperature among the sampling
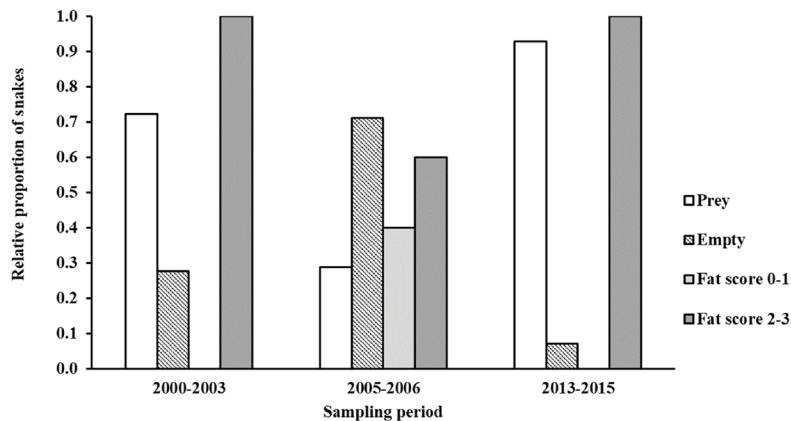
FIGURE 3. Comparative proportions of sampled Boa Constrictors (*Boa constrictor*) on Aruba that contained prey in their digestive tract and abdominal fat scores (0–1 = no to small fat bodies; 2–3 = moderately large to extensive fat bodies) over three sampling periods from 2000–2015.

periods. We compared the mean annual temperature and precipitation for the study period to the prior 30-y means using *t*-tests. We performed statistical analyses following Sokal and Rohlf (2012) and Zar (2010) using STATISTICA v13 (Dell Inc., Tulsa, Oklahoma, USA). We assessed dietary overlap of *B. constrictor* and *C. d. unicolor* with Morisita's Index (*C*) and diet breadth with the Shannon-Weiner Index (*H'* and *J'*) following Krebs (1999). The alpha level for significance for all statistical tests was 0.05.

RESULTS

Arikok National Park personnel, local residents, and our research group members collected and euthanized 4,520 *B. constrictor* on Aruba between April 1999 and December 2016 (Fig. 1). This nearly18-y period began with the discovery of the first snakes on the island. We examined the contents of the alimentary tract from a sample of 501 of the euthanized snakes during the three sampling periods (Fig. 1): 65 from 2000–2003; 295 from 2005–2006; and 141 from 2013–2015.

Of the 501 *B. constrictor* examined over the entire study period, 268 (53.5%) had prey remains in their alimentary tract. Of these, 177 snakes (66%) with prey contained a single item; the digestive tract of the remaining sample of 91 snakes (34%) contained up to five separate prey items. The frequencies of snakes containing prey and those with empty alimentary tracts varied markedly over the three sampling periods (χ^2 = 175.4, df = 2, *P* < 0.001). Of the 65 snakes examined during the early period of invasion, 47 (72.3%) contained prey remains, while the 295 snakes collected during the period of high encounters included only 87 (29.5%) containing prey items. The sample of 141 snakes collected after several years of declining

encounters included 134 (95.0%) that contained prey (Fig. 3). Similarly, all 350 snakes (100%) dissected in both the initial 2000–2003 and final 2013–2015 sampling periods had moderate to extensive abdominal fat content (fat score of 2–3 on a subjective scale from 0–3), while only 84 of the 141 snakes (60%) examined from 2005–2006 had moderate to extensive abdominal fat, and the differences were significant (χ^2 = 156.2, df =1, *P* < 0.001; Fig. 3).

We identified 401 prey items from the 268 snakes containing prey remains. Overall, three major prey groups (mammals, lizards, and birds) were consumed in relatively equal frequencies (χ^2 = 3.25, df = 2, *P* = 0.197; Table 1), and the general diet composition of *B. constrictor* did not change appreciably over the three sampling periods (χ^2 = 9.28, df = 4, *P* = 0.054; Table 1, Fig. 4). The endemic Aruban Whiptail Lizard (*Cnemidophorus arubensis*) comprised the single most frequent prey item in the diet of sampled *B. constrictor* at 22.4% of the prey items consumed; however, due to their relatively small size, *C. arubensis* only represented 2.4% of the diet by estimated mass. Although consumed
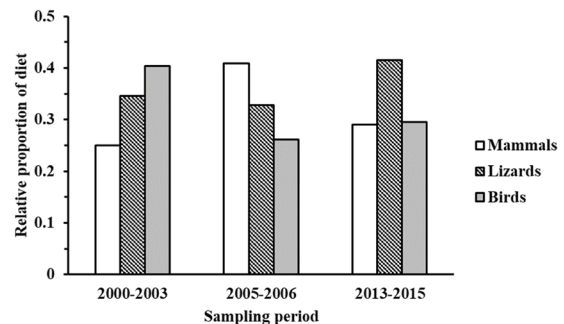

FIGURE 4. Comparative proportion of major prey groups in the diet of Boa Constrictors (*Boa constrictor*) on Aruba over three sampling periods from 2000 and 2015.

TABLE 1. Summary of prey identified from 268 Boa Constrictors (*Boa constrictor*) collected on Aruba 2000-2015. An asterisk (*) indicates a non-native species and three dashes (---) indicates values that could not be estimated. Taxa totals in bold.

Prey	2000–2003	2005–2006	2013–2015	Total	Percentage of sample	Average prey mass (g)	Percentage of sample (mass)
Mammals	**13**	**61**	**58**	**132**	**32.9**	---	**43.0**
Calomys hummelincki (Vesper Mouse)	0	6	5	11	2.7	8.5	0.2
*Canis familiaris** (Domestic Dog)	1	0	0	1	0.2	1850.0	3.2
*Felis catus** (Domestic Cat)	0	0	4	4	1.0	1766.0	12.6
*Mus musculus** (House Mouse)	0	16	20	36	9.0	18.5	1.2
*Rattus rattus** (Black Rat)	9	28	17	54	13.5	103.8	10.0
Sylvilagus flordinaus (Cottontail Rabbit)	3	11	2	16	4.0	556.0	15.8
Mammals (uncertain identity)	0	0	10	10	2.5	---	----
Lizards	**18**	**49**	**83**	**150**	**37.4**	---	**32.7**
Ameiva bifrontata (Cope's Ameiva)	10	9	3	22	5.5	32.3	1.3
Cnemidophorus arubensis (Aruban Whiptail)	6	30	54	90	22.4	14.7	2.3
Iguana iguana (Green Iguana)	2	10	20	32	8.0	511.0	29.1
Phyllodactylus julieni (Leaf-toed Gecko)	0	0	1	1	0.2	2.3	0.0
Thecadactylus rupicauda (Turnip-tailed Gecko)	0	0	1	1	0.2	10.0	0.0
Lizards (uncertain identity)	0	0	4	4	1.0	---	----
Birds	**21**	**39**	**59**	**119**	**29.7**	---	**24.3**
Amazona sp.* (Parrot)	0	0	1	1	0.2	163.0	0.2
Coereba flaveola (Bananaquit)	0	1	4	5	1.2	12.8	0.1
Colinus cristatus (Crested Bobwhite)	1	1	0	2	0.5	129.5	0.5
Columbina passerine (Ground Dove)	0	6	12	18	4.5	39.5	1.3
Eupsittula pertinax (Aruban Parakeet)	2	4	1	7	1.7	87.0	1.1
*Gallus gallus domesticus** (Chicken)	0	9	10	19	4.7	500.0	16.9
Leptotila verreauxi (White-tipped Dove)	0	0	1	1	0.2	155.0	0.3
Mimus gilvus (Tropical Mockingbird)	1	2	5	8	2.0	58.4	0.8
Molothrus bonariensis (Shiny Cowbird)	0	0	1	1	0.2	51.0	0.1
Myiarchus tyrannulus (Crested Flycatcher)	3	0	0	3	0.7	35.0	0.2
*Passer domesticus** (House Sparrow)	2	1	1	4	1.0	28.2	0.2
Patagioenas corensis (Bare-eyed Pigeon)	1	0	1	2	0.5	274.0	0.9
Setophaga striata (Blackpoll Warbler)	0	1	0	1	0.2	12.9	0.0
Tiaris bicolor (Black-faced Grassquit)	0	6	5	11	2.7	11.6	0.2
Zenaida auriculata (Eared Dove)	1	1	4	6	1.5	136.0	1.5
Passeriformes	5	0	0	5	1.2	---	---
Birds (uncertain identity)	5	7	13	25	6.2	---	---
Totals	**52**	**149**	**200**	**401**	**100**	---	**100**

at a lower frequency, *I. iguana* represented the greatest proportion of the diet by estimated mass over the entire sampling period (29.1%; Table 1). These large lizards were most frequently consumed by adult *B. constrictor* in excess of 120 cm SVL (Figs. 5, 6). In combination, non-indigenous species, including Black Rats (*Rattus rattus*), House Mice (*Mus musculus*), Domestic Cats (*Felis catus*), Domestic Dogs (*Canis familiaris*), House Sparrows (*Passer domesticus*), parrots (*Amazona* sp.), and Chickens (*Gallus gallus domesticus*), accounted for a large proportion of the overall diet (29.6% by frequency and 44.5% by estimated mass; Table 1).

The mass of ingested prey generally increased with SVL of sampled *B. constrictor* (r = 0.423, t = 7.61, df = 266, P < 0.001); however, even very large snakes did
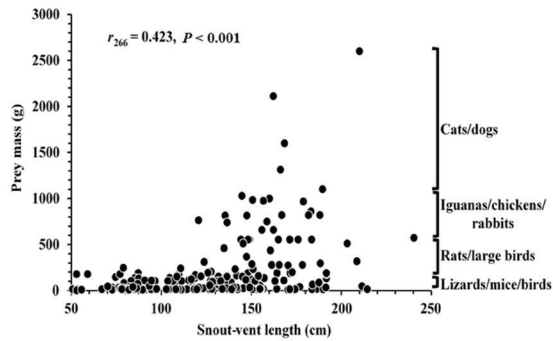
FIGURE 5. Relationship between the snout-vent length of Boa Constrictors (*Boa constrictor*) on Aruba and total prey mass consumed.

not exclude small prey items from their diet (Fig. 5). The largest snake in the 2005–2006 sample (a female, SVL = 240 cm, mass = 7,240 g) consumed both an 18.5 g *M. musculus* and a 556 g *S. floridanus*. At approximately 120 cm, snakes began to add larger prey such as *I. iguana*, *G. gallus domesticus*, *S. floridanus*, and *F. catus* to their diet (Figs. 5, 6). Overall, sampled *B. constrictor* contained prey averaging 14% of their body mass (standard error = 1.6%, n = 189). The largest single prey item identified in our sample was a 2,600 g *F. catus* eaten by a 3,650 g, 210 cm SVL female *B. constrictor*, which represented 71% of body mass of the snake (Fig. 6).

There were no differences between males and females that contained prey in the dietary analysis for SVL, mass, or adj. mass within each of the three sampling periods (SVL: $F_{1,262} = 0.231$, $P = 0.631$; mass: $F_{1,262} = 0.682$, $P = 0.410$; adj. mass: $F_{1,256} = 1.923$, $P = 0.148$; Table 2). There was also no interaction between sex and sampling period for any of these factors (SVL:

$F_{2,262} = 0.662$, $P = 0.517$; mass: $F_{2,262} = 0.489$, $P = 0.614$; adj. mass: $F_{2,256} = 1.131$, $P = 0.324$). Snout-vent length, mass, and adj. mass, however, did differ significantly among the three sampling periods (SVL: $F_{2,262} = 11.029$, $P < 0.001$; mass: $F_{2,262} = 4.381$, $P = 0.013$; adj. mass: $F_{2,256} = 6.282$, $P = 0.002$). Snakes that contained prey during the 2005-2006 sampling (n = 87) were significantly longer with greater body mass than those from either the 2000-2003 or the 2013-2015 sampling periods (Table 2). When snake mass was adjusted for SVL, however, the least-squares mean adj. mass of the 2005–2006 snakes was 271 g less for males and 302 g less for females than that of the 2000–2003 sampling and 129 g less for males and 141 g less for females than that of the 2013–2015 sampling (Table 2). The adj. mass of snakes was significantly lower in 2005–2006 than the mean adj. mass in the other two sampling periods (Table 2). Although the snakes of both sexes sampled in 2005–2006 were generally larger (greater SVL and unadjusted mass), they had lower mass relative to their SVL than in either the 2000–2003 or 2013–2015 samples (Table 2).

The initial (2000–2003) and final (2013–2015) samples of snakes containing prey came almost entirely from residential/agricultural areas of the island; however, during the 2005–2006 period, snakes containing prey were collected from both residential/agricultural (n = 62) and natural areas (n = 25) within or immediately adjacent to Arikok National Park. To determine whether the generally poorer body condition for snakes during this period was in some way skewed by an increased proportion of snakes sampled from natural areas, the analysis was repeated using only snakes from residential/agricultural areas. This revised analysis produced the same results. Snakes containing
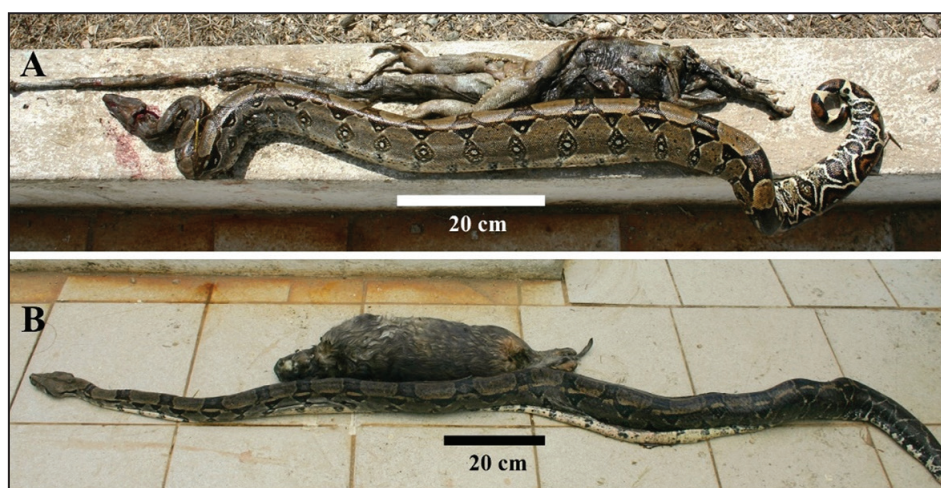

FIGURE 6. Large prey items of Boa Constrictors (*Boa constrictor*) on Aruba. (A) A 460 g, 35 cm snout-vent length (SVL), 110 cm total length Green Iguana (*Iguana iguana*) eaten by a 1,400 g, 135 cm SVL female snake. (B) A 2,600 g, 45 cm (body length) Domestic Cat (*Felis catus*) from a 3,650 g, 210 cm SVL male snake. Both items were swallowed headfirst, despite orientation of prey shown in B. (Photographs by Howard Reinert).

TABLE 2. Comparative means ± standard error (n) for snout-vent length (SVL), mass, and mass adjusted for SVL of Boa Constrictors (*Boa constrictor*) containing prey during three sampling periods on Aruba.

Variable	Sex	2000–2003	2005–2006	2013–2015
SVL (cm)	Female	91 ± 10.2 (26)	129 ± 4.3 (51)	116 ± 4.7 (83)
	Male	97 ± 11.2 (21)	126 ± 5.1 (36)	104 ± 6.0 (51)
Mass (g)	Female	800 ± 200.8 (26)	1,850 ± 168.4 (51)	1,518 ± 183.9 (83)
	Male	972 ± 239.0 (21)	1,565 ± 200.4 (36)	1,041 ± 234.7 (51)
Adj. mass (g)	Female	1,837 ± 232.6 (26)	1,534 ± 96.6 (51)	1,676 ± 104.4 (83)
	Male	1,498 ± 151.6 (21)	1,226 ± 70.3 (36)	1,355 ± 81.4 (51)

prey during the period approaching peak encounters had poorer body condition (lower mass at the same SVL) compared to the snakes sampled during the other two time periods (data not shown).

The relatively large numbers of snakes with complete SVL and mass data collected during the 2005–2006 sampling period from both residential/agricultural (n = 209) and natural areas (n = 80) allowed a comparison of the condition of all snakes (whether or not they contained prey) collected from these two different types of locations. There were no significant differences between males and females for SVL, mass, or adj. mass between natural areas and residential/agricultural areas (SVL: $F_{1,285}$ = 2.807, P = 0.095; mass: $F_{1,285}$ = 2.920, P = 0.088; adj. mass: $F_{1,281}$ = 0.308, P = 0.579). There was also no interaction between sex and location type for any of these factors (SVL: $F_{1,285}$ = 0.646, P = 0.422; mass: $F_{1,285}$ = 3.230, P = 0.073; adj. mass: $F_{1,281}$ = 3.534, P = 0.061). Snout-vent length, mass, and adj. mass, however, differed significantly between the two location types (SVL: $F_{1,285}$ = 5.521, P = 0.019; mass: $F_{1,285}$ = 19.34, P < 0.001; adj. mass: $F_{1,281}$ = 22.90, P < 0.001). Snakes collected from residential/agricultural locations averaged 10% longer SVL and 85% greater body mass than those from natural areas (Table 3). After adjusting

for differences in SVL, the relative body mass of snakes from residential areas still averaged 50% greater than snakes from natural areas (Table 3). Although the prior analysis indicated that the snakes collected during the 2005–2006 sampling period were in generally poorer body condition (lower fat scores and decreased mean adj. mass) than in the other sampling periods, within the 2005–2006 sampling cohort, the snakes from residential/ agricultural areas had better body condition than those from natural areas (Table 3).

Changes in the number of snakes collected or in the mass and condition of snakes in different sampling periods could not be clearly linked to differences or changes in the general climatic factors of annual average precipitation and temperature (Fig. 1, 7). Since 1999 when the first *B. constrictor* was discovered on the island, precipitation fluctuated widely around the prior 30-y average (1971–2000) of 409 mm with no consistent trend of increase or decrease (t = 1.56, df = 15, P = 0.140; Fig. 7). Consequently, the mean annual precipitation during each of the three diet sampling periods did not differ significantly ($F_{2,9}$ = 2.969, P = 0.102). The mean annual temperature, however, demonstrated a general upward trend (Fig. 7). The mean annual temperature from 2001–2016 was significantly higher at 28.5° C than

TABLE 3. Comparative means ± standard error (n) for snout-vent length (SVL), mass, and mass adjusted for SVL of Boa Constrictors (*Boa constrictor*) collected from residential/agricultural and natural areas on Aruba in 2005–2006.

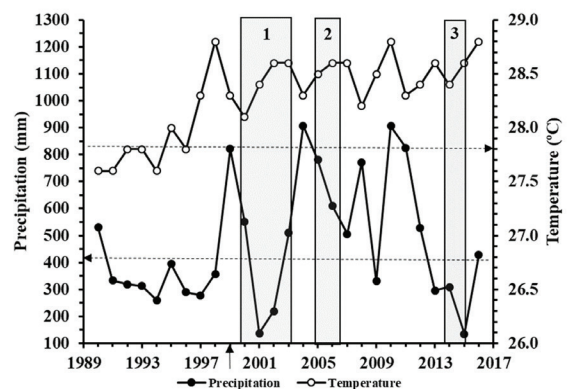| Variable	Sex	Residential/ agricultural areas	Natural areas
SVL (cm)	Female	127 ± 3.3 (113)	113 ± 5.5 (42)
	Male	116 ± 3.6 (96)	109 ± 5.8 (38)
Mass (g)	Female	1,949 ± 123.0 (113)	882 ± 201.7 (42)
	Male	1,345 ± 133.4 (96)	897 ± 212.1 (38)
Adj. mass (g)	Female	1,634 ± 58.0 (113)	967 ± 94.9 (42)
	Male	1,445 ± 61.9 (96)	1,119 ± 106.9 (38)

FIGURE 7. Average annual precipitation and temperature on Aruba during three diet sampling periods. Dashed lines are the average annual values for the period 1971 to 2000 and the arrow on the yearly axis indicates when the first Boa Constrictor (*Boa constrictor*) was captured on the island.

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the prior 30-y average of 27.8° C (t = 16.67, df = 15, P < 0.001). There was no detectable difference, however, in the mean annual temperatures during each of the three diet sampling periods ($F_{2,9}$ = 1.174, P = 0.352).

We received several reports of various animals being consumed by *B. constrictor* on the island that are not in the tabulated diet summary because they were not in the sampled snakes. The following observations are included here, however, because they were based on our own observations or they included supporting images. A radio-tracked female snake (BOA-38, SVL = 163 cm, mass = 1,900 g) was found dead approximately one day after it consumed a small Goat (*Capra hircus*) of unknown mass (pers. obs.). We received an image (https://www.boa-constrictors.com/sites/default/files/6_BoaAruba3.jpg) of an Aruban *B. constrictor* eating a Merlin (*Falco columbarius*; confirmed by Sergio Seipke, pers. comm.), which represented our only documentation of a raptor consumed by an Aruban *B. constrictor*.

A previous analysis of 33 prey items of *C. d. unicolor* found six taxa represented: 14 *C. arubensis*, eight *M. musculus*, four *S. floridanus*, two *R. rattus*, two Vesper Mice (*Calomys hummelincki*), and three small birds of uncertain identity (Reinert et al. 2008). All of these prey types were also found in the current samples examined from *B. constrictor* (Table 1). When 72 prey items from *B. constrictor* of similar size (< 94 cm SVL) were compared to that reported for *C. d. unicolor*, the similarity of their diets was large (C = 0.871). There was also no detectable difference in the frequency of consumption of the three major prey groups (mammals, lizards, birds) between these two snake species (χ^2 = 5.99, df = 2, P = 0.050). Diet breadth measures based on the same data from snakes with similar SVL indicated that *B. constrictor* (H' = 1.713, J' = 0.824) and *C. d. unicolor* (H' = 1.521, J' = 0.849) both had similar, broad, generalist diets (t = 1.30, df = 63, P = 0.198).

DISCUSSION

Our investigation of *B. constrictor* on Aruba supports prior observations of their diverse diet (Sironi et al. 2000; Quick et al. 2005; Pizzatto et al. 2009) and adds several new prey taxa. Additional prey species are constantly being added to the overall dietary list of this widespread, euryphagic snake (e.g., de Ogiori et al. 2016; Tavares de Sousa Machado et al. 2018; Santiago de Oliveira Meneses et al. 2019). With the exception of the seven bat species on the island (Bekker 1996), few vertebrates have escaped predation by *B. constrictor* on Aruba, but it is predictable that predation on these bats will eventually be observed (Thomas 1974; Arendt and Anthony 1986; Esberard and Vrcibradic 2007).

Our results documented a positive relationship between predator and prey size for Aruban *B. constrictor*. Maximum prey size consumed increased with snake size, as observed in various pythonids (Slip and Shine 1988; Shine 1991). Smaller or gape-limited snakes were restricted to smaller prey (Rodríguez-Robles and Greene 1999; Cundall and Greene 2000; King 2002). At approximately 120 cm SVL (about 1.0 kg mass), Aruban *B. constrictor* began to include larger prey items in their diets. Even large snakes continued to consume small prey, however, and in particular, small lizards figured prominently in the diet of snakes of all sizes (Ribeiro Sanches et al. 2018). In contrast, lizards were reportedly only consumed by immature *B. constrictor* in Brazil (Pizzatto et al. 2009). This difference may be a reflection of the high densities of lizards on Aruba, particularly *C. arubensis* (Goessling et al. 2015), and possibly the lower diversity of other prey species when compared to mainland Brazil. Consequently, Aruban *B. constrictor* illustrated the ontogenetic telescope diet model (Arnold 1993), where there is an increase in prey size with increasing snake size, but with no exclusion of smaller prey items from the diet. Similar broad prey inclusion has been observed in other ambush foraging snakes, such as the Diamond Python (*Morelia s. spilota*; Slip and Shine 1988) and tree snakes of the genus *Uromacer* (Henderson et al. 1987).

On average, *B. constrictor* consumed 14% of its body mass in a single feeding episode; however, we recorded an individual that consumed 71% of its body mass. Mainland Central American Boas (*Boa imperator*) in Belize consumed an average of 44% of their body mass in a single feeding episode while dwarf island forms consumed small passerine birds that averaged only 7.3% of their body mass based on a small sample of individuals (Boback 2005). Aruban *B. constrictor* is clearly an opportunist and a generalist in terms of both prey size and taxonomy (Glaudas et al. 2019).

Prey consumption appeared to be associated with encounter frequency of *B. constrictor*. The first sampling, when 72% of the snakes had prey in their digestive tract, was conducted during the early stages of invasion. At that time, snake encounters were infrequent, and we assume the population density of snakes was relatively low. The second sampling occurred when snake encounters were approaching their highest point, which we assume correlated (at least loosely) with a high population density, and only 29% of the individuals sampled had consumed prey. Likewise, the snakes sampled during the 2005–2006 period exhibited poorer body condition (lower mass at the same SVL and lower fat scores) than those sampled during both the 2000–2003 and 2013–2015 sampling periods. The paucity of snakes containing prey during the second sampling period may provide an explanation for the rapid decline in encounter rates following 2008. Although the chance

encounter rates upon which our samples were based may not precisely reflect population density, it appears possible that the population may have reached a density where many snakes became malnourished. This is further supported by the decreased amount of abdominal fat in snakes from the second sampling period. This could be interpreted as an invasive predator increasing to a point where it reduced its prey supply resulting in poor nutrition and a decline in its own population. Given the improved body condition of snakes in the third sampling period, *B. constrictor* may potentially be poised for a population increase, or, optimistically, the population could also move toward lower density stability.

Aruba is a small, isolated, desert island with a limited native fauna (Hummelinck 1940). The remaining natural areas of the island reflect these conditions, and suitably sized prey for larger *B. constrictor* are rarely observed (pers. obs.); however, in the vicinity of human habitation, there is a greater variety and higher density of both large and moderately large prey including *G. gallus domesticus* and *F. catus*, as well as *I. iguana* and *R. rattus* (pers. obs.). The larger size of *B. constrictor* collected from anthropogenically altered locations is likely a reflection of this enriched prey availability and may serve as an example of a subsidized snake population (Mishima et al. 1999; Rodda et al. 1999). This may be a significant factor in the success of the invasion of *B. constrictor* on Aruba as it apparently was for *B. irregularis* on Guam (Rodda et al. 1999).

This large invasive predator has likely placed increased pressure on many species on the faunally simplistic island ecosystem of Aruba. The reduced prey consumption and change in the body condition of *B. constrictor* during the period of high/increasing encounter rates appear as indirect evidence for a decline in prey density exacerbated by the very high predator population. *Boa constrictor* has been implicated in the perceived decline of the Burrowing Owl (*Athene cunicularia*), Aruban Parakeet (*Eupsittula pertinax*), and Crested Bobwhite (*Colinus cristatus*) on Aruba (Derix et al. 2013; Wells and Wells 2017). A 2011 bird count (Derix et al. 2013), as well as our own observations through 2018, found these three bird species to be present on Aruba, and, to our knowledge, *B. constrictor* has not caused the extirpation of any animal species on the island. There have been no apparent or suggested declines in lizards on the island. *Cnemidophorus arubensis* was the single most frequent prey of *B. constrictor*, but despite this predation pressure, populations of *C. arubensis* have increased since the introduction of *B. constrictor* (Goessling et al. 2015). The reasons for this increase remain unclear but may relate to a reduction of, or behavior change in, other lizard predators and/or competitors, particularly birds (Wright 1979; Calsbeek and Cox 2010).

The diet composition and breadth were similar and diet overlap was extensive between *B. constrictor* and *C. d. unicolor* of a similar size range. Well before the introduction of *B. constrictor*, *C. d. unicolor* was considered a rare species with a restricted distribution (U.S. Fish and Wildlife Service 1983; Reinert et al. 2002). The frequency of occurrence of *C. d. unicolor* appears to have remained stable since the introduction of *B. constrictor* to Aruba (pers. obs.). *Crotalus d. unicolor* is a dwarf member of the *C. durissus* complex that rarely exceeds 100 cm SVL. The distribution of *C. d. unicolor* is largely limited to areas of the island with low human density (Reinert et al. 2002). The rattlesnake is an ambush predator that subdues its prey with venom and forages terrestrially in thorn scrub for small lizards and small mammals (Reinert et al. 2008). Comparatively, *B. constrictor* occurs island wide (Bushar et al. 2015), subdues its prey by constriction, and forages both terrestrially and arboreally (pers. obs.) on an extensive variety of small and large prey. Differential microhabitat use, foraging strategies, and size may result in sufficient niche differentiation to promote coexistence between these two species (Stewart and Levin 1973). In fact, species of *Boa* coexist with other viperid species in insular ecosystems in the Caribbean, such as on Isla de Margarita (Fuenmayor et al. 2005), St. Lucia (Censky and Kaiser 1999), and Trinidad (Boos 2001). Also, the nearby arid Paraguaná Peninsula of Venezuela supports a diverse snake fauna including both *B. constrictor* and *C. d. cumanensis* (Barrio-Amoros et al. 2008). Consequently, the long-term coexistence of both *B. constrictor* and *C. d. unicolor* on Aruba appears highly plausible.

There have been several efforts to eradicate *B. constrictor* from Aruba. Between 1999 and 2016, 4,520 snakes were euthanized with the actual number killed likely being somewhat higher (Salvador Franken, pers. comm.). The decline in encounters that began in 2009 was no doubt at least partially attributable to this program; however, our analysis of diet and body condition suggests that overpopulation resulting in poor nutrition and subsequent mortality may have also been an important contributing factor. Organized hunts and a bounty program (10 AWG = 5.75 USD per snake) proved to be ineffective due to the cryptic behavior of *B. constrictor* and the inexperience of the participants (Andrew Revkin, unpubl. report; Diego Marquez, pers. comm.). A pilot effort to attract snakes to traps baited with live birds or chicken broth was ineffective likely due to the ambush predatory behavior of *B. constrictor* (Reed and Rodda 2009). Other suggestions for control, including the temporary release of Mongoose (*Herpestes auropunctatus*) and the introduction of viral inclusion body disease (IBD), were dismissed as ecologically untenable (Schumacher et al. 1994; Hays and Conant 2007).

The human population of Aruba has increased by over 25% since 1999, making it one of the most densely populated Caribbean islands with 623 people/km^2 (https://cbs.aw/wp/index.php/2013/03/07/aruban1foreign-population-by-age-and-sex-1998-2008/, https://cbs.aw/wp/index.php/2019/08/16/census-documentary-series/). Meanwhile, the number of tourists visiting the island nearly doubled to over one million visitors/year by 2016 (https://cbs.aw/wp/index.php/2016/01/22/da-1-aruba-tourism-authority-2/). From 1991 to 2010, the number of residential housing units on the island increased by 81.2%, and the number of automobiles on the island more than doubled (Derix 2013). Along with the increased human population, there has undoubtedly been an increase in both domestic and feral cats and dogs (Pieter Barendsen, pers. comm.), and their effect on the wildlife of Aruba may be substantial (Read and Bowen 2001; Loss et al. 2013; Loyd et al. 2013). Free-ranging Goats (*C. hircus*) have been degrading the island ecosystem for five centuries and even within Arikok National Park there are estimated to be over 40 Goats/km^2 (Veerbeek 2016). It is likely that the tremendous environmental influence of these factors contributes significantly to the general degradation of natural systems and the decline of many island species. With such pressures facing the native fauna, the addition of an invasive predator can only serve to exacerbate the problem of declining wildlife populations on the island.

We encourage monitoring and culling of the *B. constrictor* population through continuation of the established removal and euthanasia program. Regular, systematic removal of snakes from Arikok National Park may be especially helpful in reducing the predation pressure on native wildlife. We also encourage stringent biosecurity efforts to avoid both unintentional and intentional (pet trade) transport of *B. constrictor* to the neighboring islands of Bonaire and Curaçao. Boas (species unknown) have been reported sporadically from Curaçao in the past, but there has been no established population to date (van Buurt 2005). Periodic morphological examination of captured snakes could also provide useful and interesting comparative ecological information concerning potentially ongoing adaptation by *B. constrictor* to an insular environment (e.g., Boback 2006; Card et al. 2016). Past studies of *B. constrictor* (Quick et al. 2005; Bushar et al. 2015), *C. d. unicolor* (Reinert et al. 2002, 2008; Odum and Reinert 2015), mammals (Bekker 1996), and lizards (Goessling et al. 2015) have been done largely as separate, fragmented projects performed on a volunteer basis. To clearly assess environmental impacts, there is an urgent need for a centrally organized, adequately funded, comprehensive monitoring program of the wildlife species of Aruba, perhaps through the establishment of a biological survey program within the governmental framework.

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HOWARD K. REINERT is a Professor of Biology at The College of New Jersey, Ewing, USA. He received a B.S. from the Pennsylvania State University, State College, USA, a M.S. from Clarion University of Pennsylvania, Clarion, USA, where he studied Massasauga Rattlesnakes (*Sistrurus catenatus*), and a Ph.D. from Lehigh University, Bethlehem, Pennsylvania, USA, where he studied Northern Copperheads (*Agkistrodon contortrix mokesan*) and Timber Rattlesnakes (*Crotalus horridus*). He has been teaching and involving undergraduates in research since 1977. His research focus is on the ecology and conservation of snakes, and he has been studying the fauna of Aruba since 1992. (Photographed by Lauretta Bushar).

ASHLEY E. LETO is a graduate student in the Doctorate of Medicine (MD) program at Rutgers New Jersey Medical School in Newark, New Jersey, USA. She earned her B.S. in Biology from The College of New Jersey, Ewing, New Jersey, USA, where she studied the foraging ecology of Boa Constrictors (*Boa constrictor*) on the island of Aruba, as well as Red Cornsnake (*Pantherophis guttatus*) conservation. She remains passionate about her snake research but appreciates all amphibians and reptiles alike. (Photographed by Howard Reinert).

JANIS A. TUMALIUAN performed research with Howard Reinert from 2014 to 2017 while pursuing her undergraduate degree. She received a B.S. in Biology in 2017 from The College of New Jersey, Ewing, USA, a M.S. in Biomedical Sciences in 2019 from the Rutgers School of Graduate Studies Newark, New Jersey, USA, and is pursuing a M.D. degree. While her research at The College of New Jersey focused on snakes, she loves all reptiles and amphibians alike. (Photographed by Howard Reinert).

SARA JACKREL is an Assistant Professor of Ecology, Behavior & Evolution at University of California, San Diego, USA. She received her B.S. in Biology from The College of New Jersey, Ewing, USA, where she studied foraging behavior and habitat use in snakes. She received her Ph.D. in Ecology & Evolution from the University of Chicago, Illinois, USA, where she studied the drivers and consequences of intraspecific variation in plants on river ecosystems. Her current research interests involve the role of intraspecific variation, imparted by genetics, plasticity, and host associated microbes, on aquatic communities and ecosystems. (Photographer unknown).

WILLIAM I. LUTTERSCHMIDT is a Professor of Biology in the Department of Biological Sciences at Sam Houston State University, Huntsville, Texas, USA. His research interests focus mainly on the physiological and thermal ecology of ectothermic vertebrates and how physiological plasticity influences activity, behavior, and performance. William is the recipient of the University Excellence in Research Award from Sam Houston State University, Huntsville, Texas, USA, and serves as the editor of the Integrative Natural History Book Series published by the Texas A&M University Press. (Photographed by Howard Reinert).

LAURETTA M. BUSHAR is a Professor of Biology at Arcadia University, Glenside, Pennsylvania, USA. She received a B.A. in Biology and M.A. in Education from Lehigh University, Bethlehem, Pennsylvania, USA, and a Ph.D. in Biology from Bryn Mawr College, Bryn Mawr, Pennsylvania, USA. She conducts research on the ecology and genetic structure of threatened and endangered snake populations. (Photographed by Howard Reinert).

R. ANDREW ODUM served as the Curator of Herpetology at the Toledo Zoological Society, Toledo, Ohio, USA, from 1990 until his recent retirement. Prior to that he was a Conservation Biologist at the Houston Zoo, Houston, Texas, USA. He served as the Species Coordinator for the Aruba Island Rattlesnake Species Survival Plan of the Association of Zoos and Aquariums and has been performing research and conservation efforts on Aruba since 1982. (Photographed by Howard Reinert).