

ECOLOGY AND CONSERVATION OF AN EXPLOITED
INSULAR POPULATION OF *BOA CONSTRICTOR* (SQUAMATA: BOIDAE)
ON THE CAYOS COCHINOS, HONDURAS

ROBERT N. REED¹, SCOTT M. BOBACK², CHAD E. MONTGOMERY³, STEVEN GREEN⁴,
ZOE STEVENS⁵, AND DANIEL WATSON⁶



Robert N. Reed

(NEED CAPTION)

ABSTRACT.—The Cayos Cochinos, a group of small islands off the northern coast of Honduras, are home to an unusual dwarf form of *Boa constrictor*. This population was heavily impacted by collection for the live animal trade from 1979 to 1993, when a minimum of 5,000 boas was taken from the islands. An unknown level of illegal collection continues, as evidenced by recent arrests of poachers. Today, *B. constrictor* is found only on Cayo Cochino Grande and Cayo Cochino Pequeño. We conducted most of our research on the latter island, which is largely protected as a biological reserve. We captured 169 snakes during approximately four months of fieldwork in 2004 and 2005, and tracked seven females and one male via radiotelemetry. Females are longer and heavier than males. Although several large females had ingested large Honduran Spinytail Iguanas (*Ctenosaura melanosterna*), relatively few other prey items were found, indicating that small lizards or seasonally available migratory birds might be an important component of the annual energy budget for *B. constrictor*. In habitats with low thermal variability, *B. constrictor* rarely engages in behavioral thermoregulation. Multivariate analyses indicated that humans are biased towards seeing snakes in microhabitats that are used only occasionally by radiotelemetered snakes. Radiotelemetered individuals used arboreal microhabitats that tend to be higher in the canopy than those where snakes were captured, whereas all snakes used terrestrial microhabitats of high structural complexity compared to random locations. Both of these factors might serve to reduce their vulnerability to pulsed poaching episodes. A preliminary population size estimate for the Cayo Cochino Pequeño population is alarmingly low, and the long-term viability of the Cayo Cochino Grande population is even more questionable. Efforts to increase ecotourism on the Cayos Cochinos and to institute educational programs for local residents may help retard the poaching of *B. constrictor* and provide incentives for conservation.

INTRODUCTION

Boa constrictor is a large-bodied (to > 4 m total length) snake that is widely distributed in the Neotropics (Greene, 1983), ranging from the Sonoran Desert south of the border between the United States and Mexico to southern Argentina, and with many populations found on islands (Henderson et al., 1995; Porras, 1999). The species has been divided into multiple subspecies (McDiarmid et al., 1999), but these designations remain controversial (e.g., Wilson and Meyer, 1985). The ecology of *B. constrictor* remains poorly known, with the bulk of our knowledge of population-level biology coming from a few recent studies (Bertona and Chiaraviglio, 2003; Quick et al., 2005; Chiaraviglio and Bertona, this volume).

The densities of some populations of insular *B. constrictor* (and squamates in general; Rodda and Dean-Bradley, 2002) stand in stark contrast to those observed on the mainland. The typically low species diversity on small islands (MacArthur and Wilson, 1967) translates to low prey availability that often precludes viable populations of endothermic predators. The low metabolic rates of ectotherms, however, allow them to persist in times and places of low energy availability (Pough, 1983). Freed from most endothermic competitors and predators, insular *B. constrictor* can attain high densities (Boback, 2005). However, because small islands tend to lack large-bodied prey items, insular boas often are smaller than conspecifics on the mainland (Boback and Carpenter, this volume). Boa Constrictors, especially on small islands, also tend to exhibit markedly different color patterns than those on the mainland, possibly due to founder effects or natural selection responding to differing environmental pressures (Porras, 1999; S. Boback and L. Siefferman, unpublished).

Because of their small size, differing color patterns, and typically docile disposition, insular boas are in great demand in the live animal trade. Known by their island-specific names (e.g., Hog Island Boas, Corn Island Boas, Crawl Cay Boas, etc.), insular boas have been heavily exploited (Porras, 1999; Boback,

¹Department of Biology, Southern Utah University, 351 W. University Blvd., Cedar City, Utah 84720 USA. Present address: USGS Fort Collins Science Center, 2150 Centre Ave., Bldg. C, Fort Collins, Colorado 80526, USA. E-mail: robert_reed@usgs.gov

²Department of Biological Sciences, University of Alabama, 420 Biology Building, Tuscaloosa, Alabama 35487, USA. E-mail: sboback@ua.edu

³Department of Zoology, Southern Illinois University, Carbondale, Illinois 62901, USA.

⁴18 Durand Road, Earley, Reading, Berkshire, England RG6 5YR.

⁵15 The Brackens, Clayton, Newcastle under Lyme, Staffordshire, England ST5 4JL.

⁶13 Chancel Way, Marcham, Abingdon, Oxfordshire, England OX13 6QB.

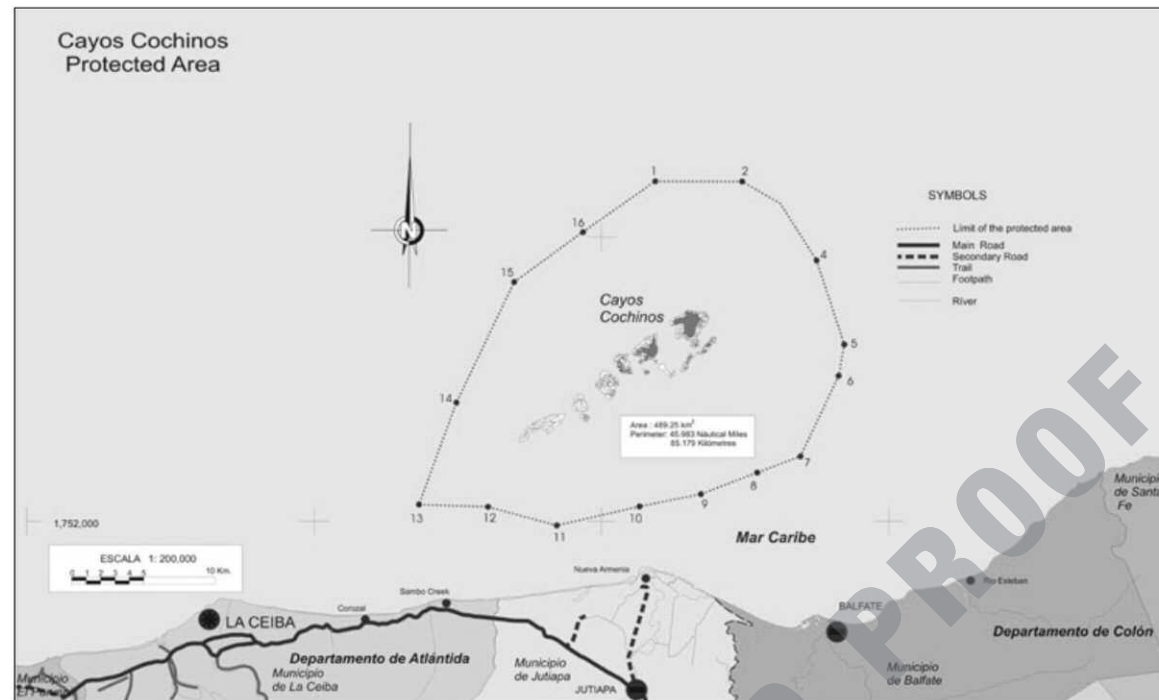


Fig. 1. General area map of the Cayos Cochinos, Departamento Islas de la Bahía (The Bay Islands), Honduras. Map courtesy of Operation Wallacea.

2005). Although some populations are now protected, collection (both legal and illegal) continues on many islands.

Herein we report on two field seasons of research on *B. constrictor* from the Cayos Cochinos Archipelago in Honduras. Snakes from the Cayos Cochinos typically are assigned to the subspecies *B. c. imperator*, which is widely distributed across Central America. Populations on the Cayos Cochinos are morphological variants found only on these islands. These snakes, known as Hog Island Boas, are prized for their pale pink dorsal coloration, small size, and docile temperament (Porrás, 1999; Russo, 2004). These populations were heavily exploited from 1979 to 1993. During a brief trip in 1988, Wilson and Cruz-Díaz (1993) found no boas on the islands, leading to speculation that these populations had been extirpated (Russo, 2004). In 2004, we were invited by Operation Wallacea (a nonprofit conservation group based in the United Kingdom) and the Honduran Coral Reef Foundation (HCRF) to initiate a long-term field study of *B. constrictor* in the Cayos Cochinos. Our ongoing goals are to examine the natural history (including population size, body size, movement, behavior, thermoregulation, and diet), population genetics, and level of human impact on these snakes in order to devise management plans to ensure the long-term viability of

their populations.

Study Site

The Cayos Cochinos are a group of small islands approximately 17 km north of the town of Nueva Armenia on the northern coast of Honduras and are part of the Departamento de Islas de la Bahía (the Bay Islands; McCranie et al., 2005; Fig. 1). The archipelago consists of two main islands and several smaller cays, with a total land area of 2.28 km² (Davidson, 1979). The largest of the two main islands, Cayo Cochino Grande, is approximately 1.55 km² in area, and the smaller of the two main islands, Cayo Cochino Pequeño, is approximately 0.64 km² (Davidson, 1979). Cayo Cochino Grande has a small population of Garifuna, also known as “Black Caribs,” who reside in the village of East End, as well as a small resort that caters to SCUBA divers. The only other permanent human presence in the Cayos Cochinos is the small village of Chachuate, located on a small cay southeast of Cayo Cochino Grande. Cayo Cochino Pequeño is uninhabited except for a small research station run by the Honduran Coral Reef Foundation (HCRF). We concentrated our research efforts on Cayo Cochino Pequeño, which measures 1.5 km from north to south and a maximum of 1.1 km from east to west, and reaches its highest elevation of 141 m at

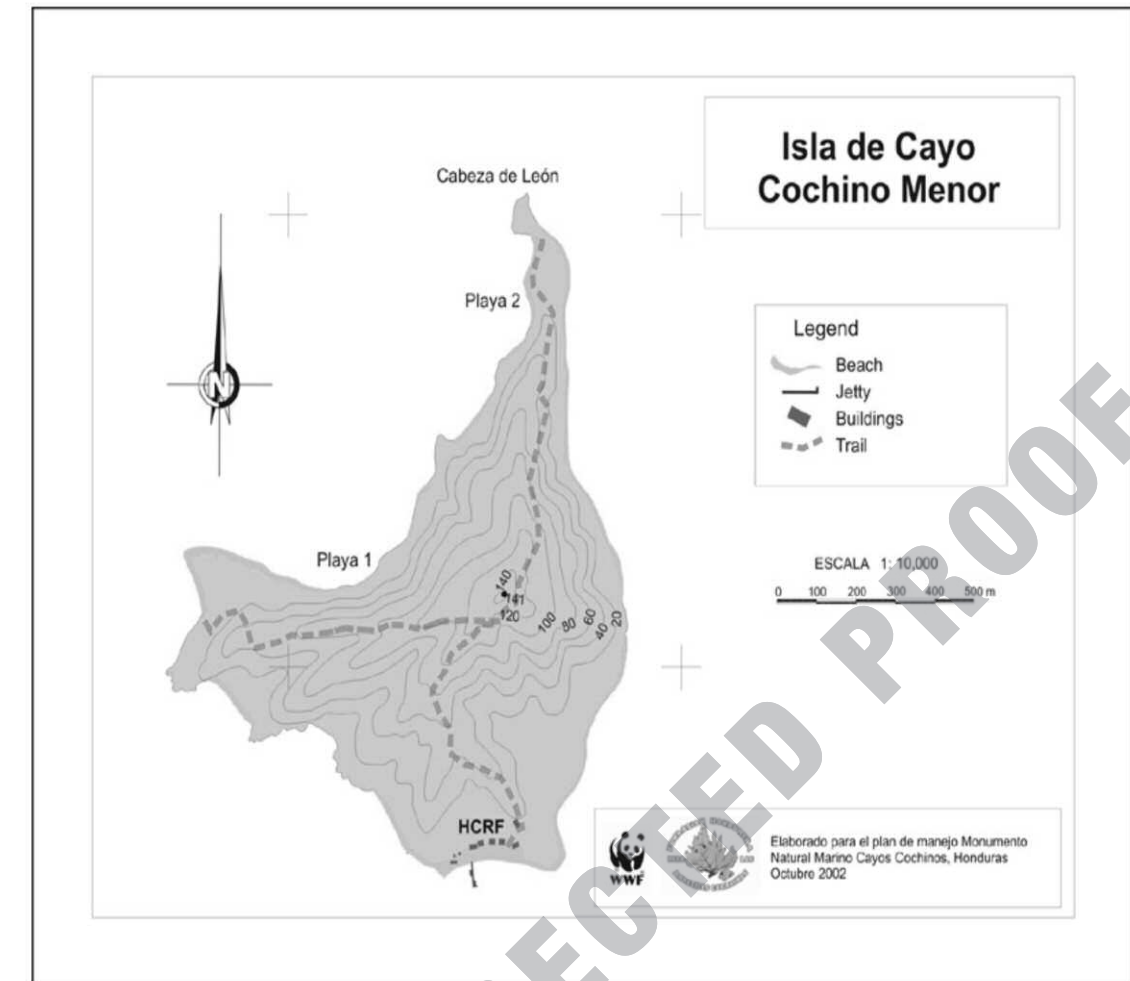


Fig. 2. Map of Cayo Cochino Pequeño, Cayos Cochinos, Honduras. Map courtesy of Honduran Coral Reef Foundation.

approximately the center of the island (Fig. 2). “Hill forest,” dominated mainly by tropical lowland oaks (*Quercus oleoides*), and “wind swept forest,” dominated by windswept lowland oaks, prostrate Sea Grapes (*Coccoloba uvifera*), or a mixture of the two, are the two primary habitats on the island (Wilson and Cruz Díaz, 1993). No non-volant mammals occur on the islands, other than a small number of Agoutis (*Dasyprocta punctata*). Only five species of resident landbirds have been recorded (Bermingham et al., 1998).

Exploitation of *Boa constrictor* on the Cayos Cochinos

The following narrative is based on information from the primary and popular literature, as well as interviews with Garifuna residents (including former snake collectors), HCRF personnel, Honduran Navy personnel, and members of the mainland Fiscali (the

rough equivalent of public defenders), who had dealt with a recent poaching case.

The history of poaching snakes from the Cayos Cochinos dates to the late 1970s. According to our sources, two Americans came to Nueva Armenia in 1979 and asked the local people to collect boas from the Cayos Cochinos. This timeline agrees approximately with that indicated by Porrás (1999). The capture and sale of *B. constrictor* from the Cayos Cochinos became a valuable source of income to many local people.

During the early 1980s, most residents of East End hunted boas as their main source of income, and residents of Chachuate and the mainland town of Nueva Armenia also participated. One former snake collector estimated that 60–70 people per day were involved in snake collecting, and that these activities persisted for several years. Another former collector related that 1,200 boas were taken by 14 collectors during a single



Robert N. Reed

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trip, and that a team of a dozen collectors could collect up to 300 boas per day. Porras (1999) stated that, "During the early 1980s, hundreds (if not thousands) of Hog Island Boas were exported from Honduras to the United States and Europe," but that imports dwindled by 1986, when populations were rumored to have been heavily depleted. Interestingly, the Fiscali and the Honduran Navy agree that collecting snakes on the Cayos Cochinos was always illegal, but that laws were not enforced due to the remoteness of the islands and a lack of a full-time government presence.

Organized collection of *B. constrictor* ceased in 1993, when the Honduran Coral Reef Foundation (HCRF) was established and the Cayos Cochinos was declared a national marine reserve. A small Honduran naval base was established in the village of East End, with a rotating crew of five men. The navy conducts daily patrols around the Cayos Cochinos, chiefly

enforcing fishing regulations, but occasionally searching boats for poached boas. While a management plan for the Cayos Cochinos was recently established (HCRF/WWF, 2004), it focuses primarily on marine resources in the protected area around the islands. The plan, however, acknowledges a lack of information on the ecological status of *B. constrictor*, and calls for increased research on its population status and efforts to replace the historical economy of exploitation with one based on ecotourism.

Our sources stated that from 5,000 to 15,000 boas were removed from the Cayos Cochinos between 1979 and 2004. The collection of 5,000 boas translates to >23 snakes per hectare from Cayo Cochino Pequeño and Cayo Cochino Grande collectively. During the early 1980s, *B. constrictor* was extirpated from all of the small cays surrounding the two main islands. The decrease in the number of snakes made it increasingly difficult for poachers to locate them. Mean snake body size also decreased as the population shrunk. Poachers generally acknowledge the fact that their actions depleted the population; however, the same poachers stated that recent trips to the Cayos Cochinos have yielded as many as 20 boas per person per day.

Although the collection of *B. constrictor* has undoubtedly decreased markedly since the 1980s, an unknown amount of poaching continues. In January 2004, two residents of the nearby mainland were apprehended by the Honduran Navy while leaving the Cayos Cochinos by boat. Their arrests were the product of eight months of intermittent surveillance by navy and HCRF personnel, reflecting the difficulty of catching poachers in possession of boas. The two men had 46 *B. constrictor* of various sizes (Fig. 3). One of the poachers informed us (about six months after his arrest and detainment) that an additional 32 boas had been left in bags on Cayo Cochino Grande; these snakes almost certainly perished. The two suspects were convicted of illegal removal of fauna from a marine reserve; one of them told us that he was fined 14,600 lempira (ca. US \$800), and that he would have to serve two years in prison after paying off the fine. These two arrests probably represent only a small proportion of continued poaching activities.

The Garifuna community on the Cayos Cochinos directs a fair amount of ill-will toward the HCRF, largely due to new regulations and the enforcement of pre-existing laws that prevent the exploitation of terrestrial and marine resources. Some residents are angry about the loss of income from capturing and

selling snakes, as well as lobsters, conchs, and commercial fish, while others express fear that large snakes will continue to grow and eventually become a threat to children. Additional outreach and education activities are necessary to involve the Garifuna community in current and future conservation efforts.

MATERIALS AND METHODS

We conducted fieldwork in 2004 and 2005, with multiple researchers visiting the islands during different (and sometimes overlapping) periods. Sampling periods spanned 03 July–07 September 2004, 31 May–08 June 2005, and 13 July–03 September 2005. Daily sampling efforts varied considerably depending on the number of volunteers provided by Operation Wallacea as field assistants. Typically, 1–3 experienced herpetologists and 0–10 relatively inexperienced volunteers were involved in daily sampling. We attempted to cover all areas of Cayo Cochino Pequeño. In 2004, the island was divided into 10 sections of roughly equal area, using GIS, and sampling efforts were fairly equal across each section (Green, 2005). In 2005, however, sampling efforts were concentrated in areas that had previously yielded the greatest numbers of *B. constrictor*.

We recorded data from all captured animals brought back to the lab, including snout-vent length

(SVL), tail length (TL; by stretching snakes along a measuring tape on a table), body mass (using an electronic balance accurate to ± 1 g), and gender (using hemipenial probes). All individuals were injected with a Passive Integrated Transponder (PIT) tag (11 x 3 mm), allowing for future identification (Camper and Dixon, 1988; Gibbons and Andrews, 2004). All processed snakes were released within 48 h at the site of capture.

We examined body size distributions for males and females from Cayo Cochino Pequeño, and tested for sexual size dimorphism (SSD) using non-parametric *t*-tests (Wilcoxon two-sample tests) on SVL and body mass. Additionally, we tested for differences in the relationship of body mass and SVL between sexes using an analysis of covariance (ANCOVA) on \log_{10} -transformed values, with SVL as the covariate and sex as a fixed effect. We tested for equality of slopes and, if the slopes were deemed equal, for differences in intercepts using adjusted means.

Body sizes of animals on Cayo Cochino Pequeño were compared to island and mainland *B. constrictor* from Belize (Boback, 2006), which were considered representative of mainland snakes. We performed a two-way ANCOVA on \log_{10} -transformed values of SVL and body mass by gender and location, and performed tests for equality of slopes and for adjusted means. A post-hoc matrix of least-squares differences was computed for all interactions of gender and location using a Tukey-Kramer adjustment for multiple comparisons.

Radiotelemetry

We surgically implanted intraperitoneal radiotransmitters (Holohil Systems Ltd., model SI-2T, 10 g, temperature-sensitive) into eight snakes in both 2004 and 2005 (Reinert and Cundall, 1982; Table 1). Transmitters weighed < 2.5% of snake body mass. Snakes were anesthetized with Isoflurane and closely monitored after surgery until they were fully active and alert. Snakes were released at the point of capture within 24 h of surgery, and subsequently were tracked daily using a Wildlife Materials TRX-1000S (Wildlife Materials, Inc., Carbondale, Illinois) receiver and a 2-element Yagi antenna.



Honduran Coral Reef Foundation

Fig. 3. Photograph from January 2004, showing some of the 46 *Boa constrictor* collected illegally from the Cayos Cochinos. The poachers were apprehended by the Honduran Navy as they left the Cayos Cochinos.

Table 1. Characteristics of radiotelemetered snakes during the 2004 and 2005 field seasons. Frequency = the frequency of the radiotransmitter in MHz, SVL = snout-vent length (cm), TL = total length (cm), Dates = period the snake was tracked, Days = number of days the snake was tracked.

Frequency	Sex	Mass	SVL	TL	Dates	Days
172.182	♀	505	109.0	121.5	09 July–29 Aug 2004	52
172.262	♀	565	109.0	121.5	07 July–29 Aug 2004	54
172.923	♀	495	105.5	117.2	07 July–29 Aug 2004	54
172.023	♂	430	98.5	115.0	14 July–29 Aug 2004	47
172.074	♀	682	103.2	116.0	15 July–02 Sept 2005	50
172.151	♀	738	104.5	117.2	15 July–02 Sept 2005	50
172.191	♀	837	107.0	121.1	15 July–02 Sept 2005	50
172.052	♀	4600	202.0	223.3	17 July–02 Sept 2005	48

Thermal Data

We recorded the ambient (shaded, 1 m above substrate) and substrate (1 cm below surface) temperatures to the nearest 1 °C immediately upon capturing a snake, as well as at each location of a telemetered snake. Internal body temperatures of telemetered snakes were determined by recording the pulse interval each time a snake was located, and extracting the temperature from a pre-determined calibration regression equation (specific to each radio transmitter) for the relationship between temperature and pulse rate.

Habitat Analysis

We recorded a suite of habitat variables (most following Reinert, 1984) at each initial capture location as well as at each location occupied by a radiotelemetered snake. We recorded data on 14 variables at each terrestrial site, and 10 variables at each arboreal site (Table 2). We also randomly sampled arboreal and terrestrial habitat data from 200 random sites (100 terrestrial, 100 arboreal) on Cayo Cochino Pequeño. To obtain random sites, we divided the island into 10 sections of roughly equal area (Stevens, 2005), determined the geometric center of each section, using GIS, and randomly assigned distances and directions (generated *a priori* in Microsoft Excel, Microsoft Corporation, Redmond, Washington) from this center until ten random sites were assigned to each section. Terrestrial habitat data were taken from each of these sites, and distances above ground were randomly assigned (determined as above) to these sites to identify locations from which we recorded arboreal habitat data.

We conducted principal components analyses (PCA), using the correlation matrix of the habitat variables, separately on terrestrial and arboreal datasets.

We used PC1 and PC2 in the analysis because SCREE plots showed a dramatic decrease in the explained variance for the other PC scores (Johnson, 1998). We analyzed differences in PC scores between initial capture locations, radiotelemetry locations, and random plots to examine habitat selection and observer bias in our results. We used radiotelemetry observations in the PCA if the location was new for an animal; in other words, if an animal moved to a new location and remained there for several consecutive days, we used this location once in the PCA. We considered all new telemetric locations across all telemetered snakes to be independent of each other, and treated them accordingly in the PCA.

All statistical tests were performed using SAS v. 9.0 or SPSS v. 13, with alpha set *a priori* at 0.05. Parametric tests were preferentially used unless data violated parametric assumptions, in which case non-parametric tests were performed. Dispersion around means is reported ± 1 SD unless otherwise indicated.

RESULTS

The 2004 field season produced 81 *Boa constrictors*, and the observed sex ratio was not significantly different from parity (36 ♂, 45 ♀, $\chi^2 = 1.0$, $P > 0.05$). The 2005 field season produced 105 snakes, again with an even sex ratio (53 ♂, 52 ♀, $\chi^2 = 0.009$, $P > 0.05$). These annual numbers do not include snakes recaptured during a single field season, but do include recaptures between years. Excluding recaptures, we captured 169 individuals. Overall, 46 snakes were captured in terrestrial locations (24 in 2004, 22 in 2005), and 150 in arboreal situations (60 in 2004, 90 in 2005); these numbers include recaptures with intervals > 15 days, as we considered these to be independent instances of habitat selection. Nearly all captures were from Cayo Cochino Pequeño, with six indi-

Table 2. Microhabitat variables and explanations of data collection methods. The two columns on the left describe variables collected from sites where snakes were captured in terrestrial locations, where radio-telemetered terrestrial snakes were located, and where random terrestrial plots were located. The two columns on the right describe variables collected from arboreal sites for all three of the above-mentioned groups.

TERRESTRIAL VARIABLES		ARBOREAL VARIABLES	
Microhabitat variable	Data collection	Microhabitat variable	Data collection
Rock	% rock substrate ¹ in 1 m ² around boa	D/A = dead or live tree	Visual determination
Vegetation	% vegetation ² in 1 m ² around boa	DBH = diameter at breast height	In meters
Log	% log substrate ³ in 1 m ² around boa	DG = distance above ground	In meters
Litter	% litter substrate ⁴ in 1 m ² around boa	DT = distance from trunk ⁵	In meters
WSD = woody stem density	No. woody stems in 1 m ² around boa	BD = branch diameter	In meters ⁶
WSH = woody stem height	Average stem height in 1 m ² around boa	BA = angle of branch	In degrees ⁷
MDR = mean distance to rock	In meters	WBD = woody branch density	No. branches in 1 m ³ around boa
MLR = mean length of rock	In meters	ABD = average branch diameter	In meters in 1 m ³ around boa
DNL = distance to nearest log	In meters	LD = percent leaf density	Visual estimation in 1 m ³
DINL = diameter of nearest log	In meters	CAN% ¹⁰ = percent canopy cover	Visual estimation
DNOV ⁸ = distance to nearest tree	In meters		
DBHOV ⁸ = dbh of nearest tree	In meters		
DNUN ⁹ = distance to nearest tree	In meters		
CAN% ¹⁰ = percent canopy cover	Visual estimation		
¹ gravel, dirt, cobble, or boulder	⁶ averaged if snake on >1 branch		
² grass, woody stem, or herbaceous	⁷ horizontal at 0°, straight up 90°, pointing down 270°		
³ twig, branch, tangle, or log	⁸ overstory tree		
⁴ deciduous, evergreen, or palm	⁹ understory tree		
⁵ or center of bush	¹⁰ above boa		

viduals captured from Cayo Cochino Grande during a number of sampling trips to that island. Those snakes were not included in subsequent analyses.

Population Size

Our sampling efforts were unequal between years of the study, in terms of both search effort (person-hours) and spatial sampling. Due to differences in search effort and a low number of recaptures, we were able to produce a crude estimate of population size by calculating a Lincoln-Peterson population size estimate. This calculation used 2004 as the initial sampling period and 2005 as the recapture period, resulting in a population size estimate of 632 ± 143 *Boa constrictor* on Cayo Cochino Pequeño.

Body Size

Females are significantly longer ($\bar{x} = 107.2 \pm 28$ cm, $\bar{x} = 92.43 \pm 12$ cm; $N = 194$, $Z = 4.92$, $P < 0.0001$) and more massive ($\bar{x} = 762.56 \pm 909$ g, $\bar{x} = 381.17 \pm 131$; $N = 193$, $Z = 4.95$, $P < 0.0001$) than males. The distribution of female SVLs is highly right-skewed, whereas that of males is more normally distributed (Fig. 4a). The distributions of female and

male body masses exhibited the same pattern with female mass showing even greater skewness than female SVL (Fig. 4b). Additionally, females have a significantly greater body mass at a given SVL relative to males (ANCOVA \log_{10} [mass] on sex, with \log_{10} [SVL] as the covariate ($N = 193$, $df = 3$, $F = 7.29$, $P = 0.008$, female slope = 2.99 ± 0.11 SE, male slope = 2.45 ± 0.15 SE; Fig. 5).

We compared our data to those for boas in both island and mainland populations from Belize (Boback, 2006). In contrast to insular boas from Belizean islands, which show a lack of sexual size dimorphism (SSD), snakes from Cayo Cochino Pequeño exhibit SSD with females being larger than males. The direction of the dimorphism is consistent with that for *B. constrictor* from the mainland of Belize (Boback, 2006). These data also were compared with those for *B. c. occidentalis* from Argentina (Fig. 6; Bertona and Chiaraviglio, 2003), which were similarly dimorphic. Males from Cayo Cochino Pequeño are shorter and lighter in body mass than those from Belize (all $P < 0.05$), and are shorter than males from other populations studied (Figs. 6, 7). Females from Cayo Cochino Pequeño are shorter and lighter in body mass than



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Typical oak forest (*Quercus oleoides*) habitat of Cayos Cochino Pequeño. One of the boas fitted with a radiotransmitter used the hollow log in the foreground and then moved to the bromeliad in the tree (center of image) where it remained for four days. Upon inspecting the bromeliad on the fourth day, we found a shed skin.

those from the mainland (all $P < 0.002$), but do not differ in size from either females or males from the Belizean islands or from mainland males. However, the three heaviest females from Cayo Cochino Pequeño had more than three times the body mass of the heaviest females from the Belizean islands (Boback, 2006). Additionally, a comparison of body shape revealed that males from the Belizean islands are relatively heavier than those from Cayo Cochino Pequeño (ANCOVA $\log_{10}[\text{mass}]$ on location with $\log_{10}[\text{SVL}]$ as the covariate: $N = 147$, $df = 3$, $F = 11.16$, P

$= 0.001$, Cayos slope = 2.45 ± 0.15 SE, Belize slope = 3.10 ± 0.12 SE; Fig. 7).

Diet

Of 216 captured *B. constrictor*, eight (4%) were in the process of consuming or obviously digesting prey. Four observations were of snakes consuming Honduran Spinytail Iguanas (*Ctenosaura melanosterna*), three of which have been reported elsewhere (Reed et al., 2006). The fourth observation was of a very large female (168 cm SVL, 16 cm TL, > 2 kg) that regurgitated a large *C. melanosterna* (156 cm total length, > 2 kg). This snake was released with no apparent ill effects. Two other observations were of average-sized (500–700 g) females found in the process of constricting and consuming Great-tailed Grackles (*Quiscalus mexicanus*). In both instances, the snakes had already grasped the birds by their heads and were in the process of constriction. One later regurgitated the grackle during processing. This 796-g female boa (123 cm SVL, 12.5 cm TL) had consumed a 158-g grackle. To minimize stress, the other snake that had consumed a grackle was not fully processed. Other instances included an unidentifiable prey item palpated from the gut of an adult male (100 cm SVL, 16 cm TL, 600 g with prey item) and an unidentified scat collected from a large female (179 cm SVL, 20.6 TL, 5500 g).

Thermoregulation

Based on 144 captures, ambient temperatures when snakes were captured ranged from 24.5 to 36.2 °C, with the greatest number of snakes (90 of 144) captured at temperatures from 29.0 to 30.9 °C. The mean ambient temperature at time of capture was 29.2 ± 1.9 °C.

Based on 182 records from seven telemetered adult female boas, body temperatures (T_b) ranged from 24.4 to 34.9 °C ($\bar{x} = 29.3 \pm 1.8$ °C). Ambient temperatures in 2004 (31.2 ± 2.5 °C) were significantly higher than ambient temperatures in 2005 (29.5 ± 1.5 °C;

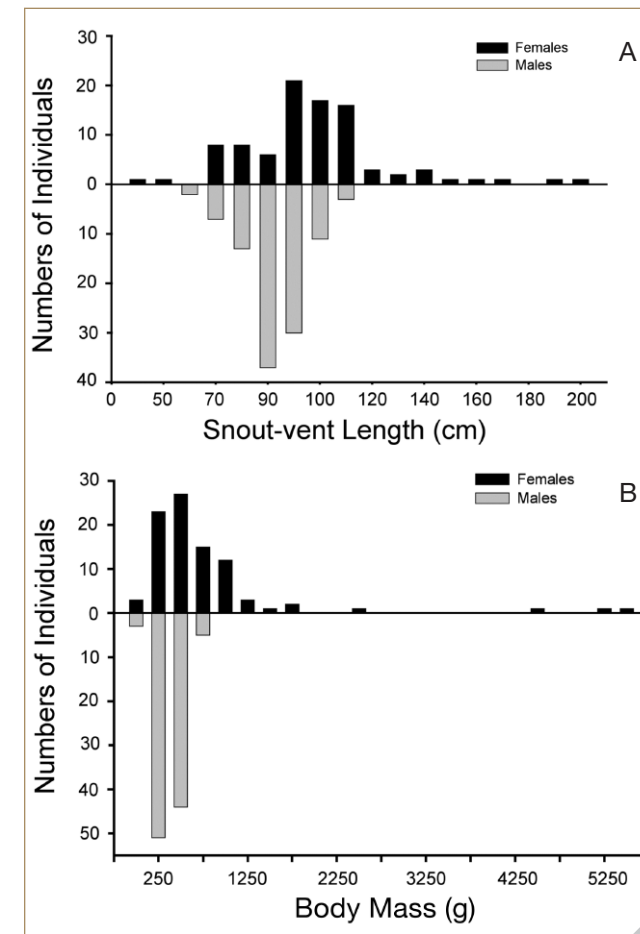


Fig. 4. Distribution of (a) snout-vent lengths (SVL, cm) and (b) body mass (g) among all *Boa constrictor* captured from the Cayos Cochinos, Honduras, during 2004–2005.

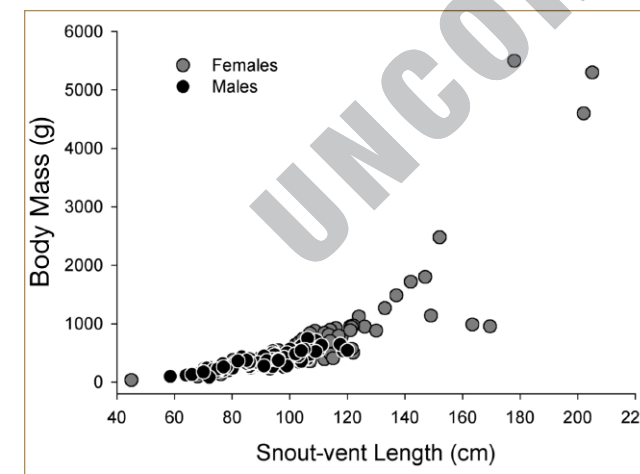


Fig. 5. Relationship between body mass (g) and snout-vent length (SVL, in cm) for all *Boa constrictor* captured from the Cayos Cochinos, Honduras, during 2004 and 2005.

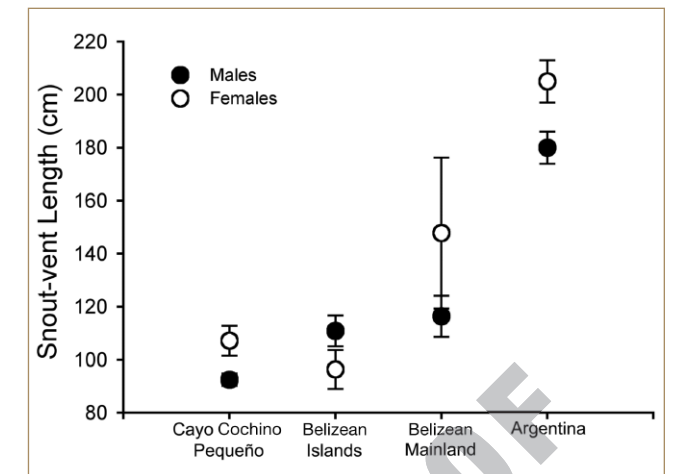


Fig. 6. Boxplot of snout-vent length (SVL) differences between male and female *Boa constrictor* for each of four populations. See text for further discussion of these populations.

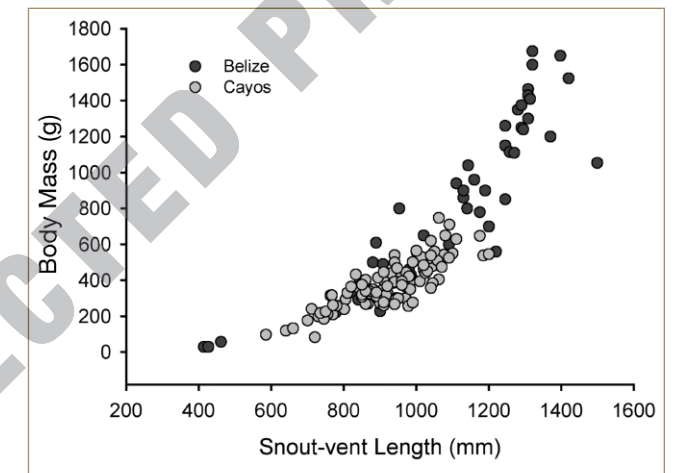


Fig. 7. Relationship between body mass (g) and snout-vent length (SVL, in cm) for male *Boa constrictor* captured from the Cayos Cochinos, Honduras during 2004–2005, as compared to those captured from an insular population during a previous study in Belize (Boback, 2006).

Wilcoxon two-sample test, $Z = 8.42$, $P < 0.0001$). On average, body temperatures were approximately 1.3 °C below ambient temperatures during both years.

Habitat Use

Considering data from initial captures, radiotelemetric locations, and random plots in arboreal sites, principal component 1 (PC1) explained 31.2% of the total variance in the data set, and principal component 2 (PC2) explained 18.4% of the total variance (49.6% of variance explained by PC1 and PC2 together). Only PC1 and PC2 had Eigenvalues greater than 1.0 for data from arboreal sites. The explanatory power of the

PCA was lower for terrestrial sites, as PC1 explained 19.4% of variance and PC2 explained 15.0% of variance (totaling 34.4% of variance). Five principal components resulting from terrestrial data had Eigenvalues greater than 1.0.

For arboreal locations, four variables had high (> |0.50|) loading scores in the component matrix for PC1: DG = 0.78, ABD = -0.61, CAN% = -0.56, and LD = 0.53. Three variables had high loading scores in the component matrix for arboreal PC2: LD = 0.60, WBD = 0.59, and DBH = -0.58. Analysis of variance revealed significant differences between PC1 scores among capture locations, telemetric locations, and random plots ($F = 198.29$, $df = 2$, $P < 0.001$, $r^2 = 0.57$; Fig. 8), with a Tukey HSD post-hoc test for multiple comparisons indicating significant differences between each pairwise combination of the three datasets. PC1 scores for random plots had the highest mean values ($\bar{x} = 0.91$), followed by scores for radio-tracked snakes locations ($\bar{x} = 0.28$), and lastly scores for capture locations ($\bar{x} = -0.78$).

Similarly, a second ANOVA revealed significant differences between PC2 scores among capture locations, tracking locations, and random plots, albeit with a low effect size ($F = 9.16$, $df = 2$, $P < 0.001$, $r^2 = 0.06$; Fig. 8). A Tukey HSD post-hoc test for multiple comparisons indicated significant pairwise differences between telemetric locations ($\bar{x} = 0.45$) and capture locations ($\bar{x} = -0.14$), as well as between telemetric and random locations ($\bar{x} = -0.11$). No differences between random and capture locations were significant.

For terrestrial locations, five variables had high loading scores in the component matrix for PC1: Rock % = 0.73, Leaf % = -0.67, DNOV = 0.53, DNUN = 0.49, and CAN % = -0.48. Four variables had high loading scores in the component matrix for terrestrial PC2: Veg % = 0.77, WSD = 0.55, MDR = 0.52, and Rock % = -0.52. No differences between PC1 scores among capture locations, telemetric locations, and random plots were significant (ANOVA, $F = 1.29$, $df = 2$, $P = 0.28$, $r^2 = 0.01$; Fig. 9). However, significant differences did occur between PC2 scores among these three data sets (ANOVA, $F = 3.13$, $df = 2$, $P = 0.05$, $r^2 = 0.03$; Fig. 9), with a Tukey HSD post-hoc test indicating significant pairwise differences between telemetric locations ($\bar{x} = 0.17$) and random plots ($\bar{x} = -0.17$).

These analyses revealed how *B. constrictor* uses available habitat and microhabitats where it is particularly visible to humans. For the arboreal data set, our

results indicated that random plots tended to be in microhabitats that were higher above ground, in areas with less canopy cover, smaller branches, and higher leaf densities as compared to capture sites and tracking locations. In turn, microhabitats that free-ranging snakes actually selected (as evidenced by telemetric locations) had intermediate values for the same traits, whereas capture sites had the lowest values. Telemetered snakes tended to occupy microhabitats with higher leaf and woody branch density and smaller diameter trees than did non-telemetered individuals.

DISCUSSION

Males from Cayo Cochino Pequeño exhibited an even body size distribution, whereas females exhibited a strongly right-skewed body size distribution. The skewness in female distribution appears to result from a handful of exceptionally long and heavy-bodied individuals. In fact, a gap existed in the distribution of female body masses. No females were collected between about 2.3 and 4.5 kg, but at least three females (and a fourth not included in these analyses due to scale failure) were found that exceeded 4.5 kg. We suggest that the paucity of females in this size range is due to either the distribution of prey sizes supported on Cayo Cochino Pequeño or the effects of collection for the live animal trade (see below).

Snakes from Cayo Cochino Pequeño exhibit female-biased SSD, which is consistent with the dimorphism reported for at least some mainland populations (Bertona and Chiaraviglio, 2003; Boback, 2006). Males and females from Cayo Cochino Pequeño are shorter and lighter than those from mainland Belize. However, females from Cayo Cochino Pequeño are similar in size to insular boas from Belize, whereas males from Cayo Cochino Pequeño are smaller. Using the formula of Lovich and Gibbons (1992), *Boa constrictor* from the Cayos Cochinos exhibited an SSD index of 0.16. Such female-biased SSD is typical of many species in the families Boidae and Pythonidae, and appears to reflect fecundity selection favoring large female body size (Shine, 1994). In those boa and python species that exhibit male-biased SSD, large male body size is typically found in populations with male-male combat (Shine, 1994; Pearson et al., 2002; Fearn et al., 2005). We observed no agonistic encounters between males on Cayo Cochino Pequeño, and we assume from the smaller sizes of males that combat does not occur in this population. However, the SSD index for *B. constrictor* on the Cayos Cochinos is calculated using mean body sizes

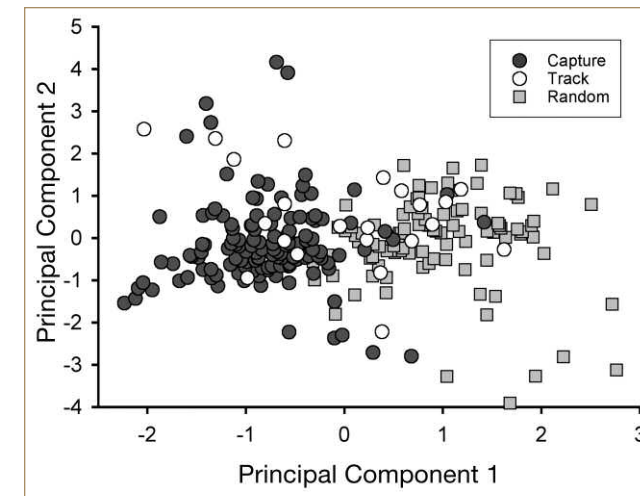


Fig. 8. Relationships between principal components 1 and 2 for arboreal locations. See text for description of how capture locations, tracking locations, and random plots were identified.

for each gender. If we instead calculate the SSD index for snakes from the Cayos Cochinos using the maximum observed body sizes for each gender, the resulting SSD index is 0.71. The difference between the two measures of SSD reflects the strong right skewness in body-size distribution of adult females.

Unlike observations from other populations of *B. constrictor* (Mole, 1924; Myres and Eells, 1968; Bertona and Chiaraviglio, 2003), we found no evidence of reproductive behavior (e.g., boas aggregated in the same refugium or sharing a microhabitat in close proximity) during the summer dry season, or observed anything that could be interpreted as courtship or mating behavior. Although we manually palpated most adult females, we did not detect ova or developing embryos. Only two individuals (a 37-g female found on 22 July 2005 and a 31-g female found on 31 August 2005) were obvious members of the young-of-the-year cohort, and we found no others that weighed < 85 g. Our assumption that the two smallest snakes are part of the 2005 cohort is supported by the fact that neonatal boas from insular populations in Belize average 34 g in body mass (Boback and Carpenter, this volume). Field and laboratory observations of reproduction in *B. constrictor* from islands off the coast of Belize leads us to suspect that mating occurs in February and March, with parturition from June through September (S. Boback, pers. observ.; Boback and Carpenter, this volume).

Throughout the range of *B. constrictor*, mainland populations exhibit a catholic diet that includes lizards, birds, and mammals (Greene, 1983; Boback et al., 2000; Sironi et al., 2000; Greene et al., 2003;

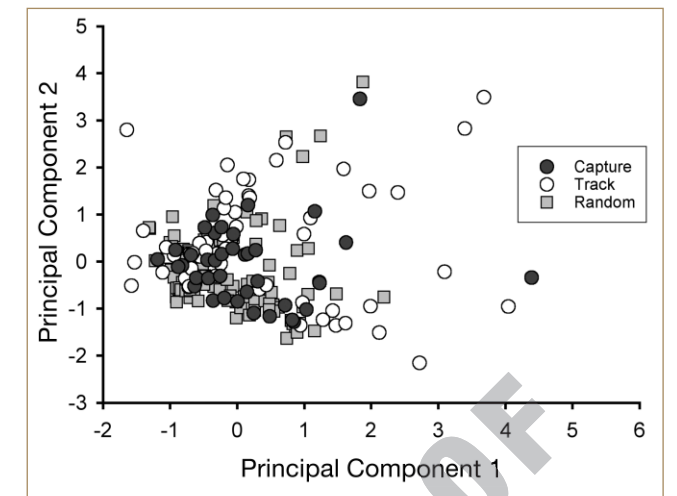


Fig. 9. Relationships between principal components 1 and 2 for terrestrial locations. See text for description of how capture locations, tracking locations, and random plots were identified.

Boback, 2004). In contrast, at least those populations on small islands tend to prey primarily on migratory birds and lizards (Gutsche, 2005; Boback, 2005; Boback, 2006; but see Quick et al., 2005 for dietary habits of an introduced population on Aruba that included mammals). On Cayo Cochino Pequeño, we found that boas ate adult *Ctenosaura melanosterna* and one resident bird species (*Quiscalus mexicanus*), both of which have been previously reported in the diet of *B. constrictor* (Greene et al., 2003; Gutsche, 2005). On Cayo Cochino Pequeño, a small population of Agoutis (*Dasyprocta punctata*) are the only small, non-volant mammals (Bermingham et al., 1998). Our observations of this species are restricted to a single sighting of a live individual and three apparently active burrows during >750 person-hours spent in the field. Migratory passerine birds are present in large numbers during fall and spring migrations between North America and Central America, with some migrants possibly overwintering on Cayo Cochino Pequeño (Bermingham et al., 1998). Although we have not detected migratory passerines in the stomachs of snakes on Cayo Cochino Pequeño, our surveys did not overlap with peak migration periods. Migratory passerines may represent a portion of the diet of *B. constrictor* on Cayo Cochino Pequeño, but these would represent relatively small meals. For instance, *B. constrictor* on West Snake Cay off the coast of Belize subsists on migratory Gray-breasted Martins (*Progne chalybea*) that average 7.3% of snake body mass (Boback, 2005). The two meals for which we could calculate relative meal size on Cayo Cochino Pequeño included a 19.8% bird meal (*Q.*

mexicanus) and a 78.6% *C. melanosterna* meal.

However, in contrast to Belizean islands that support two or three species of small lizards (*Anolis* [*Norops*] *sagrei*, *Phyllodactylus tuberculatus*, *Aristelliger georgeensis*), a number of resident prey species are potentially available to *B. constrictor* on Cayo Cochino Pequeño. These include three large lizards (*Basiliscus vittatus*, *C. melanosterna*, and *Iguana iguana*), five small lizards (*Phyllodactylus palmeus*, *Anolis allisoni*, *A. [Norops] lemuringus*, *Cnemidophorus lemniscatus*, and *Sphenomorphus cherriei*), one treefrog (*Smilisca baudinii*), and a few resident birds (*Q. mexicanus*, *Vireo magister*, *Columba leucocephala*, and *Chlorostilbon canivetii*). Although female snakes on Cayo Cochino Pequeño consume both *C. melanosterna* and resident birds, we have detected but one unknown prey item (a fecal sample) in a male. Despite the fact that we have not found any small lizards in the stomachs of males, two reasons support an assumption that lizards make up a substantial portion of their diet. First, preliminary abundance data obtained using line-transects in 2004 suggest that *A. [Norops] lemuringus* and *A. allisoni* are the most abundant potential prey species on the island (H. Shaw, unpublished). Second, our body-size patterns for Cayo Cochino Pequeño are in contrast to those of *B. constrictor* on Belizean islands that are known to rely on migratory passerine birds. Also in contrast to insular populations from Belize, snakes from Cayo Cochino Pequeño exhibit sexual size dimorphism with males being smaller. The abundance of small-bodied lizards and the relatively small size of insular males are consistent with the notion that male snakes rely heavily on lizard prey.

We found three adult females that appeared to be starving, two of which died within 36 h of capture. The two animals that died were among the eight longest snakes captured (note the three outliers in Fig. 5). We suspect the strong right-skew in the distribution of female body masses is a reflection of the ability of exceptionally large females to consume adult iguanas (*C. melanosterna* or *I. iguana*), and the availability of these two lizard species may be critical for supporting the largest females. This situation is similar to that observed in the Carpet Python (*Morelia spilota*) on islands off the western coast of Australia (Pearson et al., 2002), where the body-size distribution of available prey species is strongly bimodal. On the Cayos Cochinos, where male/male combat is unknown, little impetus exists for males to attain large body sizes or take advantage of large but rare prey species.

Conversely, fecundity selection acts to increase female body size, but few females are able to successfully locate and subdue large prey items and “make the jump” to specializing on large prey. We suspect that this scenario has influenced both the intersexual differences in body size and the extreme skew exhibited in female body size among *B. constrictor* on these islands.

The Cayos Cochinos are land-bridge islands that were connected to the mainland less than 5,000 years ago (Bermingham et al., 1998), and must have been home to many species of small rodents and non-volant insectivores before their isolation. Even considering the few species that would be predicted by species-area relationships for islands of this size (MacArthur and Wilson, 1967), the lack of small mammals is surprising. Native terrestrial mammals might have been eliminated by a hurricane or other catastrophic event, but the Antilles and Bay Islands, which are typically hit by the same hurricanes that affect the Cayos Cochinos, retain some small-bodied native mammals. We offer the possibility that small-bodied mammalian species were eliminated by *B. constrictor* subsequent to the islands’ isolation. If the extant population of *B. constrictor* is sustained largely by lizards and seasonal pulses of migratory birds, a large population could survive even in the face of declining populations of small mammals, and could slowly reduce those populations to the point of extinction. Small rodents dispersing to the islands from the mainland would similarly face a huge obstacle in establishing populations. Now that *B. constrictor* populations have declined, we suspect that rats or other human-commensals may be able to successfully colonize the Cayos Cochinos for the first time in several thousand years.

Snakes on Cayo Cochino Pequeño showed the same daily pattern in body temperature in both years of our study: steadily increasing their body temperature throughout the day and attaining maxima around 1600 h, just after ambient temperatures began to decrease. The daily body temperature profile may simply be a consequence of the low ambient temperature variability of tropical habitats and the relatively long equilibration time for heavy-bodied snakes (Grigg et al., 1979; Seebacher and Shine, 2004). Average ambient temperatures differed significantly between years, yet both exhibited patterns in which body temperature lagged behind ambient temperature by approximately 1.3 °C. The time constant appears to be responsible for this pattern, because snakes of similar size show similar daily thermal profiles that are

merely shifted up or down based on the T_a profile of that particular year. So, snakes on Cayo Cochino Pequeño are not thermoregulating behaviorally, but rather maintaining passively a relatively constant body temperature, which reflects low environmental temperature variability, large snake body mass, and subsequent long mass-dependent equilibration times (Seebacher and Shine, 2004). Previous studies on the thermal biology of *B. constrictor* showed daily body temperature ranges from 24.4 to 29.4 °C for an adult (11.3 kg) mainland individual, although a 1.7-°C daily fluctuation was more typical (Montgomery and Rand, 1978), and Brattstrom (1965) reported body temperatures of 26.0 °C and 34.0 °C in an adult and a juvenile *B. constrictor*, respectively.

Telemetered snakes were frequently not visible when they were high in the forest canopy (10–20 m above ground in extensive cover), and we did not record microhabitat variables when we could not see a snake. Consequently, the statistical difference on PC1 between random arboreal sites and arboreal telemetry locations probably would be at least partially negated if we had been able to collect data from non-visible boas. Similarly, because many of the non-visible telemetered boas were in large trees, the observation that captured boas were found in trees with larger diameters may be an artifact of the missing telemetry microhabitat data for non-visible snakes.

We do not consider microhabitat data from captured animals to be indicative of typical habitat selection, because snakes might be captured in microhabitats that are rarely used. Indeed, the difference between telemetered and captured arboreal boas along PC1 indicates that captured boas were found in microhabitats that are infrequently used by free-ranging snakes. Further, the arboreal data generally suggested that captures of *B. constrictor* on the Cayos Cochinos by humans are highly biased in favor of open microhabitats close to human eye level, with capture sites much closer to the ground than telemetry locations and random sites, and in areas with large trees and lower leaf and branch densities. We suspect that both opportunistic collectors and poachers purposefully looking for snakes share our bias towards capturing snakes in seldom-used microhabitats in which they are highly visible. If so, a single bout of collecting is likely to yield a small proportion of arboreal snakes in a given area. Ongoing collection efforts in the same region, however, will slowly reduce the population size, as boas eventually use these visible microhabitats and are captured. Because a small number of snakes is

visible at any one time, a single person collecting from the same habitat every day is likely to impact the population more negatively than a large group of collectors visiting at infrequent intervals, emphasizing the importance of reducing the frequency of snake poaching.

The results of the terrestrial PCA were somewhat less informative than those of the arboreal PCA, as random plot microhabitats largely overlapped telemetry locations and capture sites. However, our results indicated that terrestrial telemetry locations were in areas with fewer rocks but higher substrate vegetation and woody-stem density, when compared to random locations. Snakes appear to be selecting terrestrial habitats with high structural complexity, which possibly provide more shelter from predators or more effectively break up the outlines of snakes when approached by potential prey. Because visible rocks in the Cayos Cochinos tend to be large and dark in color, pale-colored individuals would stand out against rocks, and snakes may be avoiding rocky habitats for that reason.

Boa constrictor appears to utilize sites in deep canopy with little direct solar radiation, and individuals are very difficult to see in these locations. Only 31% of initial capture sites were in terrestrial microhabitats, whereas 48% of telemetry locations were in terrestrial microhabitats, providing further evidence of visual bias by humans when searching for snakes.

The conservation status of *B. constrictor* on the Cayos Cochinos remains uncertain, although population sizes have been reduced considerably by collecting. Our initial population size estimate for Cayo Cochino Pequeño (632 individuals) was alarmingly low, especially considering the estimated numbers that were exported from the island in some years. Our interviews yielded a minimum estimate of 5,000 (357/year) individuals removed from the island from 1979 to 1993. Therefore, our estimated population size on Cayo Cochino Pequeño is ~13% of the total harvest estimate and the number of snakes collected per year during that period. We also suspect that *B. constrictor* was formerly present on most of the outlying islands of the Cayos Cochinos, rather than being limited to Cayo Cochino Pequeño and Cayo Cochino Grande. Based on the above numbers and the number of small islands that probably supported boas before commercial exploitation began, these snakes were formerly much more abundant. The removal of approximately 77 boas by the arrested poachers in 2004 might have represented a significant portion of the total pop-

ulation on the Cayos Cochinos. Although 46 of those individuals reportedly were repatriated to the islands by HCRF personnel, the released snakes were split evenly between Cayo Cochino Pequeño and Cayo Cochino Grande without regard to island of origin.

We are especially concerned about the population status of *B. constrictor* on Cayo Cochino Grande, since this island has a permanent human settlement. The Honduran Navy limits its patrols to the marine areas around the islands, and we are aware of no terrestrial law enforcement. A number of men spend time in the interior of Cayo Cochino Grande cutting palm fronds for use in thatching roofs, and probably encounter snakes on a regular basis. Little monetary incentive exists for these men to abstain from collecting, especially if other people purchase and transport them to the mainland. We found few boas on this island during moderate sampling efforts in 2004 and 2005, and the population appears to be depressed relative to that on Cayo Cochino Pequeño. Although we have no population size estimate for Boa Constrictors on Cayo Cochino Grande, poaching levels probably have been unsustainable for quite some time. Particularly troubling are statements by former collectors and the arrested poachers that large snakes currently command the highest prices from buyers on the mainland. Opportunistic collectors may thus be more inclined to capture a large snake encountered in the forest, thus disproportionately impacting the population segment composed of adult females and contributing to the skew in the observed size distribution. Due to its relative freedom from human activities and to the presence of the HCRF field station, Cayo Cochino Pequeño likely holds the sole remaining Cayos Cochinos population of *B. constrictor* that is not declining. However, the small size of this population renders it especially vulnerable to stochastic events.

Any conservation plan for *B. constrictor* on the Cayos Cochinos must provide monetary benefits to local Garifuna stakeholders. Hiring local residents as field assistants could attract the most effective snake collectors, providing them with an alternative and legal form of income, while greatly increasing capture sample sizes for more rigorous population size estimates. Increasing the level of ecotourism on the island is a goal worth pursuing, especially if local residents are hired in every segment of the tourism industry. Former collectors could be employed as guides, providing more stable employment and reducing the incentive to collect snakes for outside income.

Conservation education should also be initiated for the local populace in order to instill a conservation ethic and correct negative myths and misunderstandings about *B. constrictor* and the role of the Honduran Coral Reef Foundation. We found that the majority of local residents are receptive to learning more about the unique Boa Constrictors in the Cayos Cochinos, and we are hopeful that the snake population will remain viable over the long term.

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