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Variation in Color and Color Change in Island and Mainland Boas (*Boa constrictor*)

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ABSTRACT.—**Physiological color change and geographic variation in coloration are well documented in several squamate lineages, having presumably evolved for cryptic, sexual signaling, and thermoregulatory functions. Only 11 snake species have demonstrated physiological color change, although anecdotal reports suggest it may be present in additional species. We describe color variation and physiological color change in island and mainland populations of *Boa constrictor* using full-spectrum reflectance spectrometry. We employed principal components analysis (PCA) summarizing the spectrometry data into two axes that describe the brightness (PC1) and chroma or relative intensity of particular wavelengths (PC2). Boas from island and mainland localities exhibited physiological color change, and this change occurred on a diel cycle. Boas from both locations were lighter at night and darker during the day. The magnitude of the color change differed between our two PC axes. Although change in brightness was similar for boas on the islands and the mainland, the change in chroma was greater in boas from the mainland. Color also varied seasonally; boas were lighter in color and reflected more long-wavelength light during the wet season than during the dry season in Belize. We suggest that a fundamental hormone cycle (melatonin/melanophore stimulating hormone, MSH) present in a wide variety of vertebrates, underlies the physiological color change in snakes. If this is true, color change may be more widespread than previously realized, and the perceptual bias of the human vision system may have caused researchers to discount its presence in snakes.**

Coloration is wondrously variable within many groups of animals and can presumably be explained by a balance between natural and sexual selection (Endler, 1978, 1983). Squamate reptiles are one such group exhibiting color variation among lineages, populations, and individuals. This diversity in color offers cryptic (Jackson et al., 1976; Pough, 1976; Medvin, 1990), thermoregulatory (Norris, 1967), and communicative (Madsen and Loman, 1987; Greenberg and Crews, 1990) functions.

In snakes, color and color pattern can vary among (geographic variation: e.g., Forsman and Aberg, 2008) and within populations (e.g., *Thamnophis sirtalis*: King, 1988; *Fordonia leucobalia*: Shine, 1991; *Bothriechis schlegelii*: Savage, 2002). Often, color polymorphism among populations is hypothesized to be an adaptation to match variable habitat color (Camin and Ehrlich 1958, King, 1987). Although some of the intraspecific color variation appears to have a genetic basis (e.g., Rosenblum et al., 2004), the reasons for many of the color polymorphisms in snakes remain unclear.

Color can also vary within individuals, and color change is well described in several squamate lineages. For example, species in the iguanian genera *Agama*, *Anolis*, and *Chamaeleo* are well known for their ability to rapidly adjust color (minutes to hours), exhibiting what is known as physiological color change (Pough et al., 2004; sometimes referred to as metachrosis, e.g., Rahn, 1941). Outside the Iguania, physiological color change appears less frequently within the squamate lineage. However, some diurnal geckonids (*Lygodactylus*, *Phelsuma*) undergo physiological color change in response to winning (bright) or losing (drab) an aggressive encounter (Kastle, 1964).

Physiological color change typically involves the movement of melanosomes (melanin-containing organelles) within dermal melanophores (melanin-containing cells). The movement of melanosomes into melanophore processes (superficial to other pigment containing cells) results in skin darkening, whereas the retraction of melanosomes to within the melanophore body (inferior to other pigment containing cells) results in skin lightening (Bagnara and Hadley, 1973).

In snakes, researchers have documented physiological color change in only 11 species (9 listed in Hedges et al., 1989; Shine, 1991; Boundy, 1994). Of these, most (8 of 11) are members of basal snake families (e.g., Boidae, Bolyeriidae, and Tropidophiidae) and are re-

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TABLE 1. Collection dates, location of origin, and morphometric data for individual Boa Constrictors used in this study.

Collection date	Location	SVL (mm)	Tail (mm)	Mass (g)
5/17/02	Crawl Cay	1,300	150.5	1,275
5/17/02	Crawl Cay	1,280	160.25	1,050
5/19/02	Lagoon Cay	760	90	247
5/19/02	Lagoon Cay	1,160	110.5	725
5/19/02	Lagoon Cay	1,110	120	660
5/25/02	West Snake Cay	1,060	120	750
5/25/02	West Snake Cay	1,180	130	1,275
5/22/02	Mainland	2,220	220.5	6,850
6/19/02	Mainland	2,230	240	7,700
6/26/02	Mainland	1,450	185	4,000

stricted to islands (7 of 11). Only three derived species (2 in Viperidae, 1 in Colubridae) have demonstrated physiological color change. However, unpublished reports suggest its occurrence in additional snake species (see Hedges et al., 1989).

In contrast to physiological color change, morphological color change is a slower process accomplished over a period of days to weeks and believed to involve an increased absolute number of melanosomes and melanophores (Bagnara and Hadley, 1973). Seasonal changes in color are thought to result from morphological color change for the function of enhancing the absorption of solar radiation during relatively cool periods (Waring, 1963). Seasonal color change has been described in five species of snakes including at least three elapids (Banks, 1981; Mirtschin and Davis, 1982; Shine, 1991), a viperid (Rehak, 1987), and a pythonid (Shine, 1991).

Boas (*Boa constrictor*) are ideal subjects for the investigation of color because this species shows tremendous variation in dorsal coloration across its range. Island populations of boas are particularly well known to possess strikingly different coloration in comparison to their mainland counterparts (Porras, 1999; Russo, 2004, 2007). On islands, boas are often lighter in color than those on the mainland and have been variously described as pink (Cayos Cochinos, Honduras), orange (Islas de Mais, Nicaragua), and gray (Crawl Cay, Belize). Pet-trade enthusiasts have reported that boas possess the ability to change color and have suggested that island boas posses a greater capacity for color change as compared to mainland boas (Russo, 2004, 2007). In fact, boas from Crawl Cay, Belize were marketed in the pet trade as ''chameleon boas'' because of their purported ability to change color (Porras, 1999). However, there has been no documentation of physiological color change in this species.

The goals of this study were to first test whether *B. constrictor* from Belize exhibited physiological color change. We then wished to determine whether the ability to change color differed between island and mainland populations. Finally, we examined whether physiological color change in boas varied seasonally.

MATERIALS AND METHODS

Husbandry.—We collected 10 female boas from Belize: three from the mainland and seven from three mangrove islands (Crawl Cay: $N = 2$, Lagoon Cay: $N = 3$, West Snake Cay: $N = 2$). Individual snakes varied in size (and possibly age) with mainland animals being much larger than island animals (Table 1). However, all mainland snakes and most island snakes produced litters in the lab and, thus, were sexually mature. General descriptions of habitats and biogeographic data for each of the islands are reported elsewhere (Boback, 2005), but overall, these were small (5–16 ha), low-lying, mangrove islands with relatively simple floral and faunal communities.

Three months prior to taking color measurements, boas were captured in Belize and exported to the United States and maintained in a laboratory at the Auburn University Natural History Learning Center in Auburn, Alabama. In the lab, boas were housed individually in plastic enclosures (1,220 × 610 × 610 mm; Boaphile Plastics, Cannon Falls, MN) lined with newsprint. Heat tape (30 × 30 cm, 17-watt Flexwatt: Calorique LTD, West Wareham, MA; approximately 42°C maximum temp) attached to the bottom end of each enclosure provided identical temperature gradients. Room temperature was maintained at 28°C (range 23.6–33.4°C) throughout the year. Large windows provided illumination. Boas were offered a diet of thawed and warmed *Gallus gallus* chicks or lab rats every two weeks, and large bowls of water were always available. The dates of feeding and ecdysis were recorded for all subjects.

Color Analysis.—Across its range, *B. constrictor* is extremely variable in color and pattern. In the region of Belize, individuals are usually assigned to the *imperator* subspecies and are characterized by a pattern of 22–30 dark (brown or black) dorsal saddles, bisected dorsolaterally by light streaks, on a lighter ground color usually varying from fawn-brown to gray (Fig. 1; Campbell, 1998; Stafford and Meyer, 2000; for photographs of range-wide color variation, see Russo, 2007). Dorsal saddles become a rust red color at roughly the vent and continue posteriorly. However, the intensi-

FIG. 1. Photographs showing color change within representative island (A, B) and mainland (C, D) boas (*Boa constrictor*) from Belize. Images on the left (A and C) were taken during the day, and the images on the right (B, D) are of the same two snakes taken during the night. Photos were taken immediately after removing snakes from their enclosures on 18 November 2003 using a Canon D300 digital camera with a Canon 22-55/f3.5-f4.5 lens under identical lighting conditions. Yellow arrows on snake C indicate locations where color measurements were taken: neck (between second and third dark dorsal blotches) and body (between 13th and 14th dark dorsal blotches). Note that the change in the island boa (A to B) appears greater relative to the change in the mainland boa (C to D) yet our data demonstrate that changes in brightness are similar between animals from the two environments.

ty of this red color varies across the species' range. The dorsal pattern (blotched-spotted category of Jackson et al., 1976) presumably serves to break up the snakes' outline, a feature that would be consistent with the idea that boas are primarily ambush predators (Greene, 1983). The color pattern is static throughout ontogeny with the exception that juvenile boas are usually more vivid (strongly contrasting pattern) than the adults, which tend to darken with age (Greene, 1983).

Boas were measured twice (i.e., day: 0800–1000 h; and night: 2000–2200 h) during each of 10 sampling periods. Measurement periods were distributed on average every 44 ± 6 days over the course of 13 months (17 October 2002 to 18 November 2003). Just prior to measuring color, we removed the snakes from their enclosures, placed them on a flat surface, and obtained body temperature (± 0.1°C) using a digital thermometer inserted 1 cm into the cloaca.

Reflectance measurements were taken with an Ocean Optics S2000 spectrometer (range 250–880 nm: Dunedin, FL) using a bifurcated micron fiber optic probe held at a 90° angle 5 mm from the skin surface. The probe was maintained at this fixed distance and angle by anchoring the probe within a 50 × 30 × 30 mm metal block. This block was held flush with the skin surface such that light from the probe always struck the snake at a 90° angle. A 2-mm measurement area was illuminated with both UV (deuterium bulb) and visible (tungsten-halogen bulb) light sources. The same probe measured reflectance. Reflectance data were generated relative to a white standard (Labsphere, Inc., North Sutton, NH). During preliminary tests, it was revealed

that the majority of color variation occurred in the regions between the dark dorsal saddles. Therefore, measurements were focused on this region. Reflectance was measured at two regions on the snake: a dorsal position between the second and third dark dorsal blotches/saddles (hereafter neck); and a dorsal position between the 13th and 14th dark dorsal blotches/saddles (hereafter body, Fig. 1). To obtain representative measures of color, we recorded and averaged three spectral measurements within each region during each sampling period. The three points were haphazardly selected, and we moved the probe at least 3 mm between each reading. OOIbase software (Ocean Optics, Dunedin, FL) was used to average 20 spectra that are instantaneously recorded at each of the three measurement locations. All recordings were taken under controlled laboratory and lighting conditions.

Color was expressed as percent reflectance per wavelength (i.e., spectral curves). Because the retinas of most bird and squamate species are sensitive to ultraviolet wavelengths (Chen et al., 1984; Fleishman et al., 1993; Sillman et al., 2001) analysis was restricted to wavelengths between 320 and 700 nm to complement the visual acuity of *B. constrictor* and their potential predators and prey. Each spectral curve consisted of 380 data points (% reflectance values from 321–700 nm at 1-nm intervals). We reduced spectral data by first calculating mean reflectance values for each 20-nm interval across the spectrum (e.g., mean 1 = 321–340 nm, mean 2 = 341–360 nm … mean 19 = 681–700 nm) and then performed principal components analysis (PCA, based on nonrotated correlation matrices) on these 19 variables (Endler, 1990). This method allowed for the objective reduction of a large amount of data into a few principal components that, by definition, are uncorrelated to each other (Tabachnick and Fidell, 2001, but for a critique of this method, see Endler and Mielke, 2005). Additionally, principal components are interpretable with commonly used measures of color. For instance, when PCA is run on spectral data, the first principal component (PC1) generally describes variation in brightness (lightness vs. darkness), whereas subsequent principal components would reflect variation in the intensity at particular wavelengths (i.e., chroma, Cuthill et al., 1999). This is confirmed by examining the factor loadings for the original variables on each component. For instance, if PC1 indeed represents variation in brightness, then the factor loadings for the original variables will all be positive and of a similar magnitude (Cuthill et al., 1999). If a remaining principal component (e.g., PC2) represents variation in relative amounts of short- versus long-wavelength light, then the factor loadings for original variables with short-wavelength reflections would be positive; those with long-wavelength reflections would be negative; and those near the middle would be near zero (Cuthill et al., 1999).

To determine whether the snakes' physiological state influenced our measures of color, a repeated-measures analysis of variance (ANOVA) was performed with individual repeated within both measurement period (approximately monthly) and time (day vs. night). Our dependent measures were brightness (PC1) and chroma (PC2), whereas our factors were the state of digestion (days since consuming meal), stage of ecdysis (days since last shed), and body temperature.

To compare color variation and physiological color change between island and mainland populations of boas, we ran a repeated-measures ANOVA using the MIXED procedure in SAS (vers. 9.1, 4th ed., Vols. 1–2, Statistical Analysis Systems Institute, Inc. Cary, NC, 1990) with individual repeated within both measurement period and time (day vs. night). Our dependent variables were brightness (PC1) and chroma (PC2), whereas our fixed-effects were location (island vs. mainland), time (day vs. night), season (wet [June through November] vs. dry [December through May]; Stafford and Meyer, 2000), location-by-time interaction, and location-by-season interaction.

All statistical procedures were performed using the SAS system (SAS, 1990, unpubl.); alpha was set at 0.05, and dispersion around means is indicated by ± SD unless otherwise noted. Analyses of color from our two selected body regions (neck and body) produced qualitatively similar results (data not shown). For simplicity, only the neck color analyses are reported.

Results

Upon running the principal components analysis, we found PC1 explained 86% of the variation in total reflectance, PC2 explained 10% of the variation in reflectance, and the remaining PCs explained less than 4% of the variation in reflectance. Because the first two principal components collectively explained 96% of the variation among subjects, and all remaining principal components had Eigen values less than 1, PC1 and PC2 were chosen as our indices of boa color. An examination of the factor loadings of the original variables on PC1 indicated all loadings were positive and of the same general magnitude; therefore, we refer to PC1 as ''brightness'' (hereafter brightness [PC1]; Table 2). Factor loadings on PC2 show that short wavelengths load positive, long wave-

TABLE 2. Factor loadings from principal components analysis (PCA) of color spectra. Variables = reflectance means of 20-nanometer intervals between 320 and 700 nanometers.

	Principal component axes	
Variables (nm)	1	2
321–340	0.736	0.425
341–360	0.838	0.483
361–380	0.880	0.459
381–400	0.907	0.408
401–420	0.929	0.334
421–440	0.950	0.264
441–460	0.963	0.208
461–480	0.976	0.151
481–500	0.983	0.078
501–520	0.992	−0.012
521–540	0.988	−0.084
541–560	0.986	−0.146
561–580	0.978	−0.202
581–600	0.965	−0.257
601–620	0.950	−0.310
621–640	0.931	−0.358
641–660	0.910	−0.400
661–680	0.886	−0.440
681–700	0.859	−0.478

lengths load negative, and those between 481 and 540 nm are about zero. Thus, we refer to PC2 as ''chroma'' (i.e., the relative intensity of light at particular wavelengths to the total reflectance, hereafter chroma [PC2]; Table 2).

The repeated-measures ANOVA revealed a significant effect of location on brightness (PC1). On average, boas from island locations were lighter compared to boas from the mainland (island PC1 mean = 0.22 ± 1.0, mainland PC1 mean = −0.51 ± 0.80; Table 3). Additionally, the mixed model indicated significant time effect revealing that island and mainland boas changed in brightness (PC1) between day and night measurements (Table 3). Boas from both island and mainland locations were lighter at night and darker during the day (Figs. 1, 2A). The interaction of location-by-time was not significant indicating that the diel change in brightness was of similar magnitude in boas from the two locations (Table 3; Fig. 2A).

With regard to chromatic variation, the repeated-measures ANOVA revealed a significant effect of time on chroma (PC2) indicating that island and mainland boas changed in chroma between day and night measurements (Table 3). The interaction of location-by-time was significant suggesting chromatic changes were dissimilar in boas from island and mainland locations. Mainland boas exhibited a greater change in chroma as compared to boas from the islands (Fig. 2B). Boas from mainland locations reflected more short-wavelength light (approximately 320–500 nm) during the day and relatively more long-wavelength light during the night. This difference is essentially a difference in spectral slope: steeper slope at night and shallower slope during the day (Fig. 3).

Boas exhibited seasonal variance in brightness (PC1). In the laboratory, boas were lighter during the wet season (mean PC1 = 0.29 ± 1.1) in comparison to the dry season (mean PC1 = −0.29 ± 0.85; Table 3). The interaction of location-by-season was not significant because the relative magnitude of the seasonal change in brightness was similar between boas from island and mainland locations (Table 3). Chroma also varied seasonally. Boas had lower chroma (PC2) scores and, thus, reflected more long-wavelength light (approximately 500–

TABLE 3. Results of mixed linear model testing for differences in brightness (PC1) and chroma (PC2) among boas from mangrove islands and the Belize mainland. Spectral data were obtained by measuring boa color during the day (0800–1000 h) and night (2000–2200 h; i.e., Time) on 10 sampling periods resulting in a total of 20 measurements per individual. These sampling periods were distributed approximately every 44 days spanning a calendar year (17 October 2002 to 18 November 2003). The spectral data were reduced using PCA resulting in two indices of color: brightness (PC1) and chroma (PC2). Seasonal effects were examined by classifying measures into corresponding dry (December through May) and wet (June through November) seasons in Belize. Significant *P*-values are indicated with an asterisk.

Dependent	Factor	df_{model}	df_{error}	*F*	*P*
Brightness (PC1)	Location	1	186	5.33	0.022*
	Time	1	186	6.03	0.015*
	Location × time	1	186	0.10	0.751
	Season	1	186	19.88	<0.001*
	Location × season	1	186	0.05	0.820
Chroma (PC2)	Location	1	186	3.64	0.058
	Time	1	186	45.69	<0.001*
	Location × time	1	186	7.14	0.008*
	Season	1	186	45.37	<0.001*
	Location × season	1	186	0.00	0.976

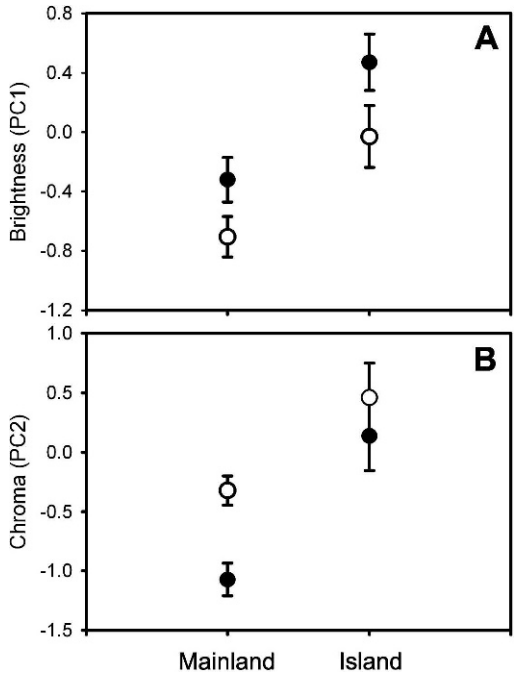

FIG. 2. Brightness (A) and chroma (B) variation and color change in *Boa constrictor* from island and mainland locations as illustrated by day (○) and night (●) PC scores (means ± SE). Data represent spectral measurements taken 10 times from the neck (between second and third dorsal blotches) of 10 female boas throughout a year. Higher PC1 scores indicate lighter individuals (reflecting more light across the spectrum), and lower PC1 scores indicate darker individuals (reflecting less light across the spectrum). Boas from islands are significantly lighter than boas from the mainland but change brightness by a similar amount. Regarding chromatic differences, greater PC2 scores indicate relatively greater reflectance in shorter wavelengths and relatively lower reflectance in longer wavelengths, whereas lower PC2 scores indicate relatively lower reflectance in shorter wavelengths and relatively greater reflectance in longer wavelengths. Compared to boas from the Belize mainland, boas from island environments reflect greater short-wavelength light and less long-wavelength light. Moreover, compared to boas from the Belize islands, boas from mainland environments change chroma greatly from day to night, whereas island boas change chroma very little.

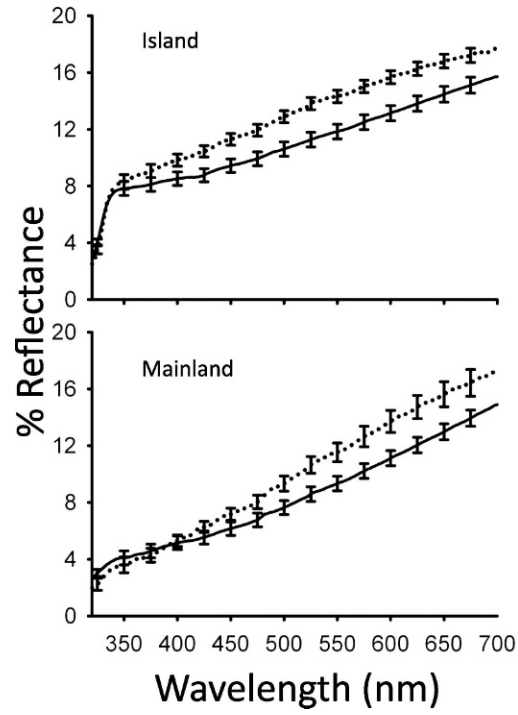

FIG. 3. Reflectance spectra (means ± SE at 25-nm intervals from 10 measurements spanning 13 months) of the skin of *Boa constrictor* from island and mainland locations in Belize taken during the day (solid line) and at night (dotted line). As compared to boas from the Belize mainland, boas from island environments reflect relatively more short-wavelength light but show a similar amount of color change between day and night measurements across the spectrum (note difference between solid and dotted lines). In contrast, boas from the Belize mainland show a greater change in long-wavelength light (500–700 nm) between day and night measures relative to changes in short-wavelength light (320–500 nm).

700 nm) during the Belize wet season (mean PC2 = −0.28 ± 1.0) when compared to the dry season (mean PC2 = 0.28 ± 0.87) in which boas reflected proportionally less long-wavelength light. The repeated-measures ANOVA for chroma (PC2) demonstrated no location-by-season interaction, thus indicating that the relative magnitude of the seasonal change in chroma was similar between boas from island and mainland locations.

DISCUSSION

Our results demonstrate that *B. constrictor* exhibits physiological color change, making it only the 12th species of snake in which this is known. Boas from island and mainland locations in Belize changed in brightness (lightness vs. darkness) between day and night measurements: boas were lighter at night and darker during the day. Boas also changed chroma between day and night but mainland snakes changed chroma to a greater extent than their island counterparts. Mainland boas reflected relatively more long-wavelength light at night and reflected relatively more short-wavelength light during the day. Additionally, brightness and chroma differed seasonally because boas were lighter and reflected relatively more long-wavelength light during the Belize wet season

than during the dry season. Although the popular literature reported that island boas possessed a greater capacity for color change (Porras, 1999), our results show that mainland boas change just as much in brightness and surpass island boas in their ability to change chroma. Now we explore possible explanations for variation in color and color change in boas and the implications of our findings.

Boas from the islands were lighter (had greater brightness (PC1) values) than boas from the adjacent mainland, and these differences could reflect thermoregulatory adaptations (Majerus, 1998). In ectotherms in general, lighter individuals have an advantage in hot environments where their color can reflect excessive solar radiation, whereas darker individuals have an advantage in cool environments because their color can facilitate absorption of solar radiation (e.g., Norris, 1967; Gibson and Falls, 1979; Sherbrooke, 1997). Although island boas appear to be lighter than their mainland counterparts, an opposite pattern has been shown in temperate colubrids. For instance, island populations of Gartersnakes (*Thamnophis sirtalis*) and Watersnakes (*Nerodia sipedon*) are darker in coloration compared to neighboring mainland populations (King, 1986, 2003), and it has been hypothesized that melanistic Gartersnakes are able to heat more rapidly in the cool island environments (Bittner et al., 2002). However, the diel change in color we observed in boas is inconsistent with a thermoregulatory hypothesis because snakes were darker during the day when presumably they would be most affected by solar radiation. Alternatively, the differences in brightness between boas from island and mainland locations could result from selective pressures to enhance crypsis in these environments. However, the conspicuousness of an organism is determined by the combination of a number of variables including the light reflected by the organism, ambient light, and background reflectance (Endler, 1990, 1993). To adequately test a crypsis hypothesis, we would need additional in situ data on ambient light and background reflectance.

We found changes in color to be consistent with a diel cycle, a feature common to most snake species documented to change color (e.g., *Tropidophis melanurus*, *Tropidophis feicki*, *Casarea dussumieri*; reviewed in Hedges et al., 1989). Also, Hedges et al. (1989) noted that color change was tightly correlated with snake activity; snakes were light at night when they were most active and dark during the day when they were least active. However, many groups of vertebrates exhibit a diel hormonal cycle involving melatonin, the pineal gland hormone responsible for circadian rhythms, and α-melanophore-stimulating hormone (α-MSH, Turner and Bagnara, 1971; Sherbrooke, 1988). This cycle can be influenced by a variety of factors including catecholamines (e.g., epinephrine/norepinephrine; Fujii and Oshima, 1986), gonadal hormones (Castrucci et al., 1997), and body temperature (Sherbrooke et al., 1994). Therefore, although multiple factors can contribute, skin darkening by day and lightening by night may be most parsimoniously explained by the presence of an intrinsic hormone cycle and that correlations between color change and activity are spurious because most snakes found to change color are also nocturnal.

In addition to the changes in brightness between day and night, our analyses showed that boas reflected proportionately more short-wavelength light during the day and proportionately more long-wavelength light during the night. However, mainland boas changed chroma to a greater extent than did island boas. The mechanism responsible for changes in chroma is not clear, but we suggest that it may be the same mechanism responsible for changes in brightness (migration of melanosomes within melanophores that are part of a dermal chromatophore unit; Bagnara et al., 1968; Bagnara and Hadley, 1973; Sherbrooke and Frost, 1989). For example, during daylight hours when snakes are darker, melanosomes dispersed into melanophore processes superficial to xanthophores and iridophores would absorb light and restrict it from reaching the pigments (e.g., pteridines and carotenoids) in this region that are responsible for reflecting long-wavelength light. During the night, melanosomes aggregate within the perinuclear region of the melanophores (inferior to xanthophores) causing snakes to be lighter while at the same time allowing more light to reach pigments reflecting long-wavelength light. Additional morphological and cytological data will be necessary to evaluate this idea.

Our data also revealed seasonal changes in coloration. In the lab, boas were lighter and reflected proportionally more long wavelengths during the wet season (June through November) in comparison to the dry season (December through May). The maintenance of the captive boas at relatively constant temperatures and humidity suggests that something other than temperature and humidity, such as change in photoperiod, is influencing their seasonal cycling. The difference in latitude between Auburn, Alabama (32.36.35N, 85.28.50W) and Belize (17.15.00N, 88.45.00W) resulted in a day length difference of approximately one hour longer during the summer solstice and one hour shorter during winter solstice. Longitude does not differ dramatically between the locations.

Therefore, although the absolute amount of light on any given day differed slightly (longer in summer or shorter in winter), the relative change in photoperiod was similar between Auburn, Alabama and Belize, Central America. Thus, we suspect our captive snakes responded to the change in photoperiod as if they were in Belize. This is consistent with the seasonal color change in *Pieris* butterflies and gonad development in Spotted Antbirds (*Hylophylax naevioides*), both of which can be induced by changes in photoperiod in the lab (Kingsolver and Wiernasz, 1991; Hau et al., 1998). Additionally, the reproductive cycle of our animals was synchronized with snakes in the field (captive females ovulated, copulated, and gave birth in the lab at times similar to free-ranging boas); thus, it is reasonable to surmise that the seasonal changes documented in the lab would be similar with those in free-ranging snakes.

The functional advantage of seasonal changes in color in boas is not clear. Seasonal changes in color have been documented in a number of snake species (Banks, 1981; Mirtschin and Davis, 1982; Shine, 1991). For some of these, a thermoregulatory advantage has been suggested because temperate snakes are generally darker during winter months when solar radiation (insolation) is low (Shine, 1991; Johnston, 1994). However, boas are tropical species and, thus, should be less constrained by seasonal fluctuations in temperature. Further, others have suggested color change is directly correlated with activity levels (e.g., McAlpine, 1983; Hedges et al., 1989); therefore, seasonal changes in color may be confounded by changes in activity. Data on activity patterns for free-ranging boas in Belize are unavailable, but elsewhere in their range (Argentina), boas are active year round (Chiaraviglio et al., 2003). Alternatively, seasonal changes in color may function to enhance crypsis because the light environment changes as a result of leaf phenology of tropical forest trees (Endler, 1993). During the Belize dry season (December through May), many Neotropical trees senesce and drop their leaves. In habitats dominated by these dry-season deciduous or senescing plants, ambient light environments (irradiance spectra) likely change significantly in comparison to the wet season when the plants are fully foliated (Endler, 1993; Thery, 2001). If seasonal changes in color are caused by crypsis, and if we assume loss of foliage results in increased radiance during the dry season, we might predict an advantage for lighter colored snakes during this time. Yet we found the opposite pattern because boas in the lab were darker during the Belize dry season. The lack of support for the crypsis hypothesis should be interpreted cautiously because, as mentioned previously, crypsis involves a complicated set of variables including but not limited to color, color pattern, ambient light, and background (Endler, 1978, 1993).

Our results demonstrate that boas from island and mainland locations were similar in some of our measures of color (the magnitude of the diel change in brightness and in the seasonal change in both brightness and chroma) but were different in others (overall brightness and in the magnitude of the diel change in chroma). We have invoked selection scenarios involving thermoregulatory or cryptic advantages to explain the differences in color and color change between the locations. However, it is important to note that we cannot exclude the possibility that these differences are the result of founder effects and subsequent genetic drift. Geological data indicates that all of these islands are relatively young in age (<8,000 yr old) and were formed approximately at the same time during recent sea level changes (Boback, 2006). We discount the possibility that these color differences are a result of phenotypic plasticity because we have observed, but not quantified, heritability of color through multiple litters born in the lab. Genetic distances (e.g., Keogh et al., 2005) as well as in situ performance measures (e.g., Slagsvold et al., 1995) will be necessary to disentangle selective versus nonselective explanations for these patterns.

Overall our findings suggest that physiological color change in snakes could be more common than previously thought. For instance, we noticed that the color change of the lighter island boas was much more striking to the human eye compared to the darker mainland boas; yet the spectral data clearly demonstrate that snakes from both localities changed brightness by a similar amount (compare Figs. 1 and 3). If color change is more conspicuous to humans in lighter snakes, and if island snakes, in general, are lighter than mainland forms, then published reports might be biased in favor of describing color change in island populations. Indeed, seven of the 11 snake species documented to exhibit physiological color change are restricted to islands (Hedges et al., 1989). Regardless, we argue that many more snake species may exhibit physiological color change (as suggested in Rahn, 1941; Hedges et al., 1989) and that this phenomenon may have gone unnoticed because of the visual bias of researchers. By using full-spectrum reflectance spectrometry, we can avoid this bias and may discover that color change is more widespread than previously thought.

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