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Evaluating Growth Rates of Captive, Wild, and Reintroduced Populations of the Imperiled Eastern Indigo Snake (*Drymarchon couperi*)

Houston C. Chandler[1,2,17], David Steen[3], Jack Blue[1], James E. Bogan[4], M. Rebecca Bolt[5], Tony Brady[6], David R. Breininger[7], Jorge Buening[6], Matt Elliott[8], James Godwin[9], Craig Guyer[10], Robert L. Hill[11], Michelle Hoffman[4], Natalie L. Hyslop[12], Christopher L. Jenkins[1], Chris Lechowicz[13], Matt Moore[8], Robert A. Moulis[1], Sara Piccolomini[10], Robert Redmond[1], Frankie H. Snow[14], Benjamin S. Stegenga[1], Dirk J. Stevenson[1,16], James Stiles[9,10], Sierra Stiles[10], Mark Wallace[1], Jimmy Waters[1], Michael Wines[9,10], and Javan M. Bauder[15]

[1] The Orianne Society, 11 Old Fruitstand Lane, Tiger, GA 30576, USA
[2] Department of Fish and Wildlife Conservation, Virginia Tech, 310 West Campus Drive, Blacksburg, VA 24061, USA
[3] Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission, 1105 SW Williston Road, Gainesville, FL 32601, USA
[4] Central Florida Zoo's Orianne Center for Indigo Conservation, 30931 Brantley Branch Road, Eustis, FL 32736, USA
[5] Bolt Outdoors, 4705 Seattle Street, Cocoa, FL 32927, USA
[6] Welaka National Fish Hatchery, 726 County Road 309, Welaka, FL 32193, USA
[7] Department of Biology, University of Central Florida, 4110 Libra Drive, Orlando, FL 32816, USA
[8] Georgia Department of Natural Resources, Wildlife Resources Division, 2067 US Highway 278 SE, Social Circle, GA 30025, USA
[9] Alabama Natural Heritage Program, Auburn University Museum of Natural History, Auburn University, 1090 South Donahue Drive, Auburn, AL 36849, USA
[10] Department of Biological Sciences, Auburn University, 331 Funchess Hall, Auburn, AL 36849, USA
[11] Zoo Atlanta, Herpetology Department, 800 Cherokee Avenue Southeast, Atlanta, GA 30315, USA
[12] Department of Biology, University of North Georgia, 3820 Mundy Mill Road, Oakwood, GA 30566, USA
[13] Sanibel-Captiva Conservation Foundation, 3333 Sanibel-Captiva Road, Sanibel, FL 33957, USA
[14] South Georgia State College, 100 West College Park Drive, Douglas, GA 31533, USA
[15] U.S. Geological Survey, Arizona Cooperative Fish and Wildlife Research Unit, University of Arizona, Tucson, AZ, USA

Abstract: Reintroduction of species at sites where populations have been extirpated has become a common technique in wildlife conservation. To track progress towards reintroduction success, effective postrelease monitoring is needed to document vital rates of individuals and the corresponding impact on population trajectories. We assessed growth and body size in Eastern Indigo Snakes (*Drymarchon couperi*) using a data set from multiple projects across the species' distribution, including free-ranging wild snakes, snakes reared in captive-breeding programs, and snakes released at two reintroduction sites. We used these data to fit a von Bertalanffy growth model in a Bayesian framework to quantify differences in growth among three broad categories of snakes (wild, captive, and reintroduced), while accounting for measurement error across various projects. We also compared changes in body mass of captive-born individuals from four captive rearing facilities. Asymptotic snout–vent length across all groups was 185 cm (95% credible interval = 177–194 cm) for males and 157 cm (95% credible interval = 153–161 cm) for females. Reintroduced snakes had a higher growth coefficient than either captive or wild snakes (e.g., captive females = 1.20 [1.06–1.35] d^{-1}; wild females = 1.22 [0.95–1.49] d^{-1}; reintroduced females = 1.62 [1.21–2.05] d^{-1}), indicating that current captive-breeding and rearing efforts for indigo snakes produce similar or faster growth trends compared to wild populations. Furthermore, daily changes in juvenile body weight relative to body size were similar in three of the four captive rearing facilities (mean for females at Orianne Center for Indigo Conservation = 0.57 [0.48–0.65]; Zoo Atlanta = 0.55 [0.37–0.72]; Welaka National Fish Hatchery = 0.55, [0.36–0.73]; Auburn University = 0.39 [0.21–0.58]). Long-term project success for indigo snake reintroductions will depend on continuing to implement best practices in an adaptive management framework.

Key words: Captive rearing; Conservation; Headstarting; Monitoring; von Bertalanffy growth model

In the midst of global biodiversity declines, including widespread population loss of even relatively common species (Gaston and Fuller 2007; Ceballos et al. 2017), managers have increasingly turned to translocations or reintroductions as pathways to restore populations to areas where they have been extirpated (Griffith et al. 1989; Fisher and Lindenmayer 2000; Resende et al. 2020). These programs commonly include some type of captive breeding component where individuals are bred in captivity and often raised to a relatively large body size (i.e., headstarting) before being released into the wild (Bowkett 2008; Griffiths and Pavajeau 2008). For projects with captive rearing and headstarting components, a quantitative assessment of individual growth rates, both in captivity and in the post-release environment, can be used to improve understanding of factors influencing growth and the effects of the headstarting period on growth rates over an individual's lifespan (Pérez-Buitrago et al. 2008; Sacerdote-Velat et al. 2014). Furthermore, assessments of individual growth can be integrated with estimates of other demographic parameters to form a post-release monitoring program, which can be used to guide reintroduction projects through an adaptive management framework (Ostermann et al. 2001; Muths and Dreitz 2008). For projects where low detectability and small population sizes limit the ability to calculate robust estimates of some demographic parameters (Tanadini and Schmidt 2011; Keiter et al. 2017), assessments of individual-level factors (e.g., growth, parasite load, or disease presence) that can be assessed with a relatively small number of recapture events can be used to better understand the ecology of reintroduced populations (Muths and Dreitz 2008; Merk et al. 2020; Viotto et al. 2020).

[16] Present address: Altamaha Environmental Consulting, Hinesville, GA 31313, USA
[17] Correspondence: e-mail, hchandler@oriannesociety.org

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Across a wide variety of taxonomic groups, individual body size and growth rate are fundamentally linked to a host of ecological and evolutionary processes (Case 1978; Andrews 1982; Peters 1986). In reptiles, juveniles typically experience rapid growth followed by slower growth as adults, but there are apparent differences in growth patterns both among individuals within a species and across higher taxonomic groups (Woodward et al. 2011; Congdon et al. 2013; Frýdlová et al. 2020). Intra- and inter-population differences in growth may be particularly relevant to snakes, whose relatively simple body form and gape-limited feeding have consequences for the types and quantity of prey they are able to consume (Lillywhite 2014). Larger snakes can consume larger and more diverse prey items and eat similarly sized prey items faster than their smaller counterparts (Shine 1991). In addition, snakes that consume more prey as juveniles experience elevated growth rates that can persist through much of their life (Madsen and Shine 2000). Multiple studies have shown positive relationships between snake body size, survival, and fecundity (Shine and Charnov 1992; Jenkins et al. 2009; Hyslop et al. 2012; Rose et al. 2018a). Although the size of snakes is limited by evolutionary constraints (Boback and Guyer 2003) and growth may be affected by site-specific features or annual variation in environmental conditions (Bronikowski 2000; Madsen and Shine 2001a; Jenkins et al. 2009), ecological theory suggests a fast growth rate conveys significant benefits to individuals that may ultimately translate to population-level processes.

Eastern Indigo Snakes (*Drymarchon couperi*, hereafter indigo snake) are listed as Threatened under the U.S. Endangered Species Act and are a large (>2.4 m) colubrid snake endemic to the southeastern United States, historically inhabiting parts of Georgia, Alabama, and Mississippi and all of Florida. However, indigo snakes have experienced range contractions and population declines driven by habitat loss, habitat degradation, and collection for the pet trade (Enge et al. 2013; U.S. Fish and Wildlife Service [USFWS] 2019). These declines were particularly severe in the western portion of the indigo snake's range in Mississippi, Alabama, and the Florida panhandle, and indigo snakes were functionally extirpated from this region by the 2000s (Enge et al. 2013). Population declines led to the initiation of indigo snake reintroduction efforts, but early attempts during the 1970s and 1980s were unsuccessful, likely because of an insufficient number of released snakes (538 individuals across 18 locations; Speake et al. 1987). As a result, indigo snake conservation partners initiated large-scale reintroduction efforts in the early 2000s as part of ongoing indigo snake recovery efforts (Stiles et al. 2013; Gitzen et al. 2016; USFWS 2019). Current reintroduction efforts are sustained using captive-bred individuals descended from wild-caught snakes and are focused on two sites: Conecuh National Forest in Alabama and Apalachicola Bluffs and Ravines Preserve in Florida. Postrelease monitoring studies have documented feeding (Steen et al. 2016) and reproduction (J. Godwin, personal observation) in these reintroduced populations. However, monitoring the status of these populations remains challenging because of low detection rates and high movement potential (Hyslop et al. 2012, 2014; Bauder et al. 2017).

In this study, we used length and weight data from free-ranging wild indigo snakes and captive-born indigo snakes, some of which were reintroduced to Alabama or Florida, to develop an individual growth model to explore factors influencing variation in body size and individual growth. We compiled body-size data from multiple studies and collaborators across the range of the indigo snake and from all facilities participating in indigo snake captive breeding and headstarting. Snakes, especially those reaching the size of adult indigo snakes, are difficult to measure, and the error associated with measuring snakes may present itself as individuals appearing to shrink between capture occasions (Madsen and Shine 2001b; Luiselli 2005). We therefore used a growth model that accounts for measurement error (Eaton and Link 2011), which also allowed us to explore variation in measurement error across data sources. Our study addressed four objectives. First, we tested whether individual growth trajectory varied among wild, captive, and reintroduced snakes. Second, we estimated the degree of measurement error separately among projects to test for differences in measurement techniques and to examine the impact of measurement error relative to mean snake size. Third, we tested for effects of the different captive rearing facilities on the rates of body mass change of headstarted individuals. Finally, we used the results of this study to provide considerations for future research needs associated with the ongoing indigo snake reintroduction program.

MATERIALS AND METHODS

Data Compilation

We compiled indigo snake length and weight data from available sources in Georgia, Florida, and Alabama, including wild snake populations, reintroduced populations, and snakes housed in captive facilities. In Georgia, wild snakes were measured during research and ongoing population monitoring projects across southern Georgia from 1998 to 2021 (e.g., Stevenson et al. 2003, 2009; Hyslop et al. 2009, 2014; Bauder et al. 2017). In Florida, we obtained data from a long-term monitoring project on Gulf Coast barrier islands in Lee County (2012–2021) and two radiotelemetry studies, one in Highlands County (2010–2013; Bauder et al. 2016, 2018) and the other in Brevard County (1998–2002; Breininger et al. 2011). We marked wild snakes with Passive Integrated Transponders (PIT tags) to identify individuals upon recapture. We also collected data from several captive facilities that either have been or currently are involved in ongoing indigo snake reintroduction efforts, including the Orianne Center for Indigo Conservation (OCIC; Lake County, Florida, 2013–2020), Auburn University (Lee County, Alabama, 2008–2011), Zoo Atlanta (Fulton County, Georgia, 2009–2017), and the Welaka National Fish Hatchery (WNFH; Putnam County, Florida, 2018–2021). Finally, we compiled measurements from snakes released and recaptured at the two reintroduction sites: Conecuh National Forest, Covington County, Alabama (source facilities: Auburn University, Zoo Atlanta, OCIC, and WNFH; release data = 2010–2020; recapture data = 2011–2021) and Apalachicola Bluffs and Ravines Preserve, Liberty County, Florida (source facilities: OCIC and WNFH; release data = 2017–2021; recapture data = 2018–2022). Additional details from all data sources are presented in the Appendix.

Snake Data and Processing

We measured body size data (snout–vent length [SVL], total length [TL], and/or mass) using a variety of methods across the various projects. We typically measured body length of wild snakes by positioning the snake adjacent to an outstretched

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Table 1.—Parameter estimates for measurement error when measuring the snout-vent length (SVL) of Eastern Indigo Snakes (*Drymarchon couperi*) across a variety of research projects. The multiple projects category includes snakes measured by different observers at different times (e.g., on Ft. Stewart and the adjacent Warnell Property). These individuals are not included in other categories. Sample size (n) represents the number of measurement occasions (1471 total individuals). All percent of mean SVL values include only actual SVL measurements and no predicted lengths.

					Percentile		% of mean SVL	
Project	State	Type	n	Mean	2.5	97.5	Male	Female
Apalachicola Bluffs and Ravines Preserve	Florida	Reintroduced	90	0.091	0.055	0.150	6.8	7.1
Brevard County[a]	Florida	Wild	129	0.055	0.042	0.073	—	—
Captive snakes	—	Captive	1299	0.027	0.024	0.029	3.9	4.0
Conecuh National Forest	Alabama	Reintroduced	111	0.058	0.046	0.073	4.5	5.0
Georgia Department of Natural Resources	Georgia	Wild	100	0.048	0.026	0.076	2.9	3.7
Highlands County	Florida	Wild	88	0.062	0.036	0.100	4.3	4.7
Lee County	Florida	Wild	66	0.053	0.034	0.079	3.4	3.8
Multiple projects	Georgia	Wild	134	0.038	0.031	0.047	2.3	2.7
Ft. Stewart	Georgia	Wild	487	0.039	0.034	0.045	2.4	2.7
The Orianne Society	Georgia	Wild	469	0.038	0.030	0.046	2.4	2.7
Warnell Property	Georgia	Wild	294	0.029	0.024	0.035	1.8	2.1

[a] All SVL measurements from the Brevard County study were predicted from total lengths using a linear regression model.

tape measure and slowly extending the body along the tape measure (typically using 1–3 observers), allowing the snake to relax portions of the body until a complete measurement was recorded. Some snakes were measured by extending a flexible tape measure down the snake's body. In some cases, measurements were repeated 2–3 times, and the average was taken to generate a final measurement. Some individuals involved in radiotelemetry studies were measured with a tape measure while fully relaxed under anesthesia for transmitter implantation or removal. In captivity, we measured hatchlings by stretching them along a tape measure, and we measured larger individuals using a squeeze box (Quinn and Jones 1974). We placed individuals in the squeeze box and then traced a line along their ventral side that was measured with a tape measure. We recorded mass in grams using Pesola spring scales, electronic balances, or triple beam balances and subtracted the mass of implanted radio transmitters when necessary. Finally, we determined sex using either secondary sexual characteristics (i.e., weakly keeled scales in males; Layne and Steiner 1996) or using a lubricated cloacal probe.

Prior to analyses, we refined our data set as follows. First, we removed all capture occasions where no size data were collected. Second, we checked for common transcription errors (e.g., SVL > TL) and either corrected mistakes or removed the capture occasion from the data set if the correct value could not be verified. Third, we removed all individuals recorded with an unknown sex. Fourth, we filtered data so that at least 1 d elapsed between measurements of wild individuals and at least 14 d elapsed between measurements of captive individuals. We used different growth intervals between these two data types to increase sample size in wild snakes for estimating measurement error, while limiting the number of intervals in captive snakes with little measurable growth. Finally, to explore variation in measurement error among studies, we assigned each snake a categorical identifier based on the study where it was measured (Table 1). We combined all captive snakes into a single category and most wild snakes were grouped according to their respective project's study area. However, several individuals in Georgia were captured as part of multiple projects, and we combined all such individuals into their own category. This resulted in 11 different categories that were used to model variation in measurement error (Table 1).

Individual Growth Analysis

We fit all models in our analyses within a Bayesian framework using JAGS (v4.3.0; Plummer 2003) called through R (v4.1.1; R Core Team 2021) with the package jagsUI (v1.5.2; Kellner 2021). We ran all models using 40,000 adaptive iterations and 40,000 burn-in iterations across three parallel Markov chains before sampling 100,000 iterations from the posterior distribution while retaining every 25th posterior sample. For all models, we visually assessed Markov chain convergence and mixing and ensured that Gelman–Rubin statistics ($\check{R}$) were <1.01 for all coefficient parameters (Brooks and Gelman 1998; Gelman and Hill 2006). For each model, we report means and 95% credible intervals (CRI; 2.5th and 97.5th percentiles) of each parameter posterior distribution.

We used SVL to fit a von Bertalanffy growth model (Fabens 1965), which has been shown to reflect the growth patterns of snakes recaptured during field studies appropriately (Shine and Charnov 1992; Shine and Iverson 1995; Blouin-Demers et al. 2002). We fit the von Bertalanffy model as follows:

$$L_t = L_{t-1} + (L_\infty - L_{t-1})(1 - e^{-k\Delta t}),$$

where L_∞ is the asymptotic length that individuals grow towards as they age, k is the growth coefficient that defines how quickly individuals approach L_∞, L_t is the length at time t, and Δt is the time interval between L_t and L_{t-1}. We calculated Δt as the time in days between measurement events and divided the number of days by 1000 to improve model convergence. We fit a parameterization of the von Bertalanffy growth model that also allowed us to account for and quantify measurement error across our data set (Eaton and Link 2011; Rose et al. 2018b). Briefly, this model treats the true SVL as an unobserved parameter and models both growth increments and measurement error (σ) through a stochastic gamma process (Eaton and Link 2011). This model also includes a parameter (λ) describing the ratio of the mean to the variance for the gamma distribution that is used to model the growth increments for each individual, thereby accounting for heterogeneity in individual growth rates, with low values of λ corresponding to high individual heterogeneity (Eaton and Link 2011).

We modeled L_∞ with a fixed effect of sex, given well-documented sexual size dimorphism present in adult indigo snakes (e.g., Stevenson et al. 2009). Although latitudinal variation in

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Table 2.—Parameters from three models describing body size and growth of Eastern Indigo Snakes (*Drymarchon couperi*). For each model, we report prior distributions and the mean and 95% CRI from their posterior distributions. The first model relates snake TL to SVL using data from all available individuals. The von Bertalanffy growth model estimates snake growth parameters while allowing estimated measurement error to vary randomly across different projects. This model includes parameters for asymptotic size (L_∞), growth coefficient (k), and individual variability in growth (λ). The third model compares daily changes in snake body weight standardized by body size (unitless values) across four captive facilities. Parameter values represent estimates for female snakes, while sex effects represent the difference between males and females. In the von Bertalanffy model values for k and λ represent values for captive snakes, and the wild and reintroduced effects represent the difference between estimates. In the body weight model, values represent estimates for the OCIC, with the other effects representing the difference between the various facility estimates. Coefficient parameters whose 95% CRI exclude zero are shown in bold. Prior distributions of *n* represent Gaussian distributions with mean and precision parameters.

				Percentile	
Model	Parameter	Prior	Mean	2.5	97.5
Linear model relating SVL to TL	Intercept	*n* (0, 0.1)	−0.79	−1.27	−0.30
	Slope (TL–SVL relationship)	***n* (0, 0.1)**	**0.84**	**0.84**	**0.85**
	Sex effect on slope	*n* (0, 0.1)	−0.09	−0.41	0.23
	SD of individual on slope	*Uniform* (1, 100)	2.36	2.22	2.50
von Bertalanffy growth model	Asymptotic size (L_∞)	*n* (1.85, 10) T(0)	1.57	1.53	1.61
	Sex effect on L_∞	***n* (0.2, 10)**	**0.28**	**0.24**	**0.33**
	Growth coefficient (k)	*n* (1, 10) T(0)	1.20	1.06	1.35
	Wild snake effect on k	*n* (0, 10)	0.02	−0.10	0.14
	Reintroduced snake effect on k	***n* (0, 10)**	**0.42**	**0.16**	**0.70**
	Sex effect on k	***n* (0, 10)**	**−0.17**	**−0.34**	**−0.02**
	Individual variability in growth (λ)	*Uniform* (0, 100)	24.67	19.11	31.23
	Wild snake effect on λ	***n* (0, 0.0001)**	**116.7**	**115.1**	**163.4**
	Reintroduced snake effect on λ	***n* (0, 0.0001)**	**116.2**	**31.82**	**242.3**
	Sex effect on λ	*n* (0, 0.0001)	2.47	−5.11	9.63
	Measurement error (σ_e)	*Beta* (1, 1)	0.04	0.01	0.06
	SD of survey type on σ_e	*Uniform* (0, 10)	0.03	0.01	0.08
Linear model relating facility to weight change	Intercept (OCIC effect)	*n* (0, 0.1)	0.57	0.48	0.65
	Auburn effect	***n* (0, 0.1)**	**−0.17**	**−0.27**	**−0.07**
	WNFH effect	*n* (0, 0.1)	−0.02	−0.13	0.08
	Zoo Atlanta effect	*n* (0, 0.1)	−0.02	−0.11	0.07
	Sex effect	*n* (0, 0.1)	0.01	−0.04	0.06
	SD of individual	*Uniform* (0, 10)	0.01	0.00	0.03

asymptotic body size among indigo snakes has been suggested (Allen and Neill 1952; Stevenson et al. 2009; Powell et al. 2016), we did not see qualitative evidence for this trend in our raw data and thus did not allow L_∞ to vary spatially. For both the k and λ parameters, we included fixed effects of sex and population type (wild, captive, or reintroduced). Because we were specifically interested in the growth trajectories of reintroduced snakes following their release, we excluded all captive (i.e., prerelease) measurements from these individuals. We also allowed measurement error (σ) to vary as a zero-mean Gaussian random effect across our 11 study categories. We did not include a random effect of individual in the von Bertalanffy model as this variation is accounted for with the gamma process. For all model parameters, we used either uninformative or weakly informative priors based on indigo snake ecology (see Table 2). We assessed the sensitivity of our posterior distributions to prior choice and found our inferences to be consistent across different reasonable formulations of weakly informative priors.

Because TL but not SVL was recorded on some capture occasions, we estimated SVL for these occasions using Gaussian generalized linear model of SVL as a function of TL. We included sex as a fixed effect and individual as a zero-mean Gaussian random effect to account for repeated measures of some individuals. We used uninformative priors for all parameters (Table 2) and used the predicted SVL estimates when fitting our von Bertalanffy model.

Finally, we compared the growth rates of juvenile snakes across four captive rearing facilities (OCIC, Zoo Atlanta, Auburn University, and WNFH) that raised juvenile indigo snakes (typically 1–2 yr) in preparation for release at reintroduction sites. For this analysis, we used mass because it was recorded for most individuals and measurement error was likely reduced. We truncated this data set to measurements recorded for snakes within the headstarting period and standardized all growth increments (change in mass over time) by the initial mass measurement of each snake. We used a Gaussian generalized linear mixed model to test for differences in change in mass among facilities and included individual as a zero-mean Gaussian random effect to account for the repeated measures on the same individual. We also included a fixed effect of snake sex and again used uninformative priors for all parameters (Table 2).

Results

We compiled a data set with 5073 occasions where an indigo snake had at least 1 length or weight measurement recorded, including data from 1503 individuals (1–26 measurement occasions per individual). The data set contained observations from wild snakes in Georgia ($n = 1668$) and Florida ($n = 349$), snakes that were measured as part of reintroduction projects ($n = 322$, includes measurements recorded at release), and snakes reared in captivity ($n = 2734$). Our filtering process resulted in 3267 measurement occasions (either SVL or TL) of 1471 individuals (Fig. 1). Mean SVL across all snakes was 116 ± 45 (SD) cm, and mean TL was 140 ± 52 (SD) cm. We found a strong positive relationship between SVL and TL, regardless of sex (Table 2; Fig. 2; Supplementary File 1, available online), and SVL typically accounted for approximately 80% of an individual's TL. We estimated SVLs on 252 occasions where only a TL measurement was available. This resulted in 2338 measurements from 542 individuals,

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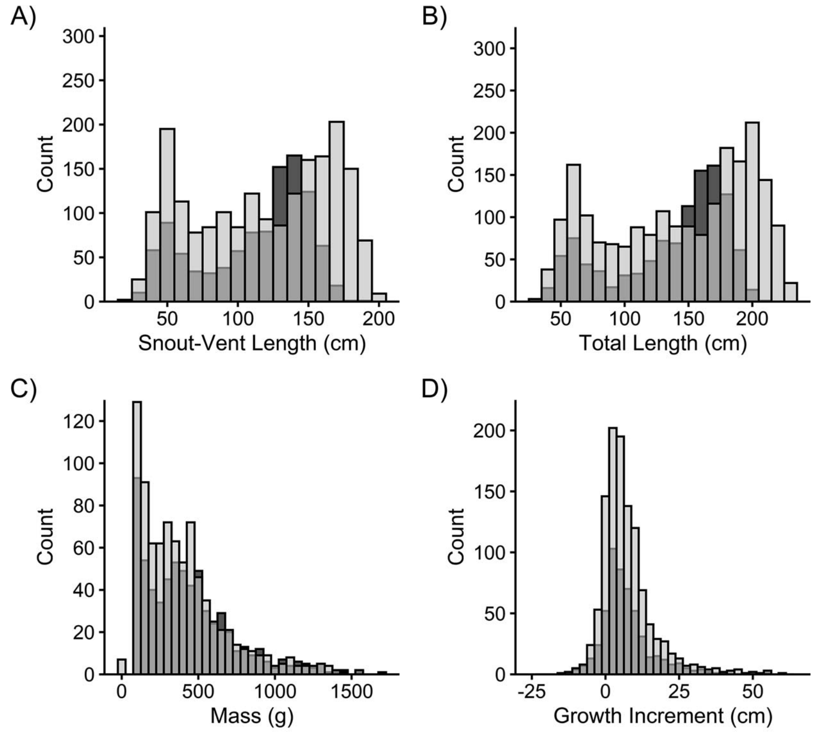

FIG. 1.—Distributions of size data for Eastern Indigo Snakes (*Drymarchon couperi*) across captive, reintroduced, and wild populations. SVL and TL (A, B) are reported for snakes of all sizes. Mass (C) is reported only for captive snakes during the headstarting period. Growth increments (D) represent the change in SVL between capture events for all snakes that were measured on multiple occasions. Note that overlap between the two sexes is shown in an intermediate color.

each with multiple SVL measurements, that were used to fit the von Bertalanffy growth model.

The von Bertalanffy model indicated an effect of sex on asymptotic SVL (sex effect on $L_\infty = 28$ cm; 95% CRI = 24–33 cm) and that male indigo snakes reach a longer asymptotic SVL ($L_\infty = 185$ cm; 95% CRI = 177–194 cm) when compared to female indigo snakes ($L_\infty = 157$ cm; 95% CRI = 153–161 cm; Table 2). There was also evidence of an effect of sex on growth

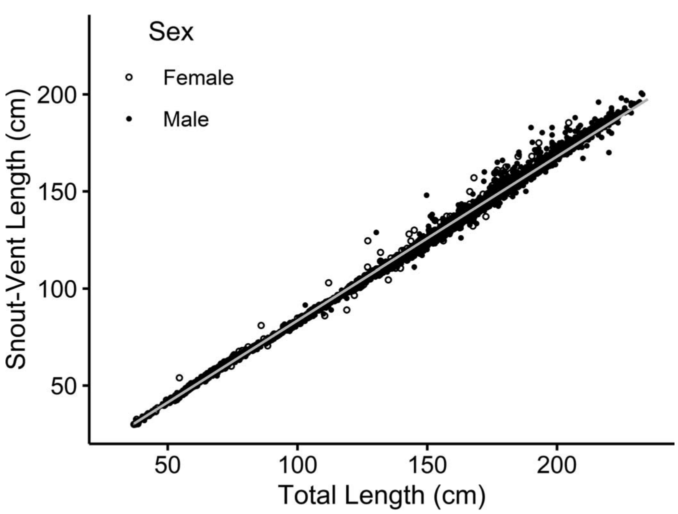

FIG. 2.—Relationship between TL and SVL of Eastern Indigo Snakes (*Drymarchon couperi*) across wild, captive, and reintroduced populations. The solid line represents the regression fit for male snakes, which was not significantly different from the regression line for female snakes.

coefficient (sex effect on $k = –0.17$ d^{-1}, 95% CRI = -0.34 to -0.02 d^{-1}), with male snakes taking longer than female snakes to approach their asymptotic size (e.g., k for captive females = 1.20 d^{-1}, 95% CRI = 1.06–1.35 d^{-1}; k for captive males = 1.02 d^{-1}, CRI = 0.72–1.34 d^{-1}). Reintroduced snakes tended to reach their asymptotic size more rapidly than either captive or wild individuals (reintroduced effect on $k = 0.42$ d^{-1}, 95% CRI = 0.16–0.70 d^{-1}). There was little evidence for differences in growth coefficient between captive or wild individuals (Table 2; Fig. 3). The effect of sex on individual heterogeneity in growth was larger than the effect of population type (wild, reintroduced, or captive), but the 95% CRI for the sex effect overlapped zero, whereas the 95% CRI for the effect of being a wild or reintroduced snake did not (Table 2). Individual heterogeneity in growth was higher (lower λ value) for captive snakes than for wild and reintroduced snakes (Table 2). Additional model details are presented in Supplementary File 1.

Both the raw data and our modeling results indicated that there was often substantial measurement error associated with measuring the length of indigo snakes. There were 194 instances of snakes with negative growth increments between capture occasions (approximately 9% of all increments using measured SVL). Growth increments using measured SVL ranged from -16 to 92 cm (7 $\pm$ 9 cm mean $\pm$ SD; Fig. 1D). The mean measurement error across all snakes was 4 cm (95% CRI = 1–6 cm), accounting for approximately 4.1% of the average female SVL and 3.9% of the average male SVL. Furthermore, measurement error was variable across projects, with mean error ranging from 3–9 cm (Table 1).

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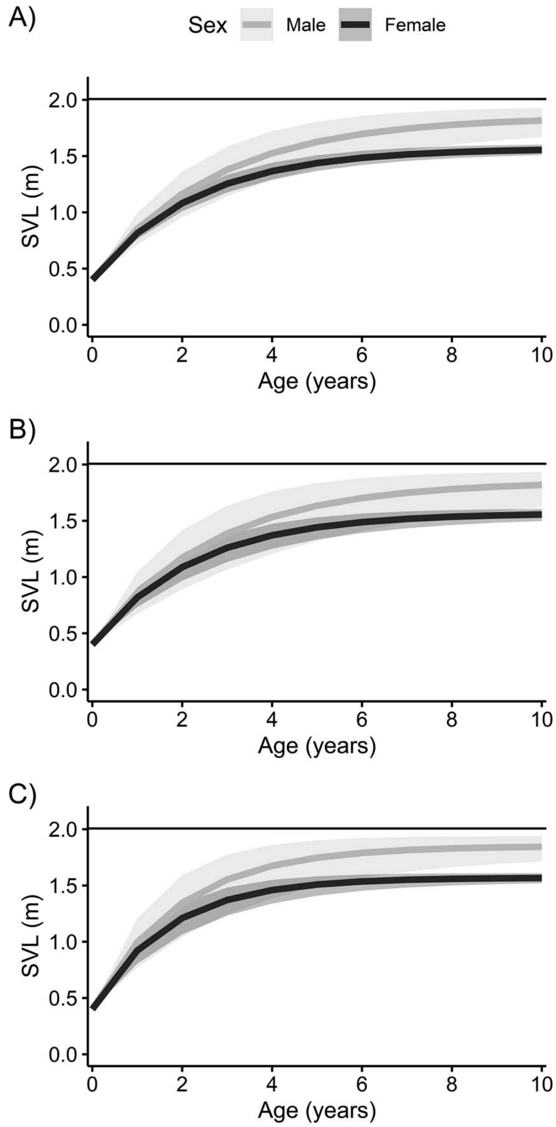

FIG. 3.—Growth curves based on the results of a von Bertalanffy growth model for Eastern Indigo Snake (*Drymarchon couperi*) SVL across wild (A), captive (B), and reintroduced (C) populations. Shaded regions equal 95% credible intervals, and curves were fit assuming a hatchling SVL of 40 cm based on data from captive individuals. The horizontal line represents the largest indigo snake recorded from wild populations in this study.

We used 2128 measurement occasions during the headstarting period to assess changes in snake mass (standardized by snake size) across captive rearing facilities. Indigo snake mass during the headstarting period ranged from 18.9–1692.5 g (mean = 303.7 g, SD = 291.7 g; Fig. 1C). We found that daily changes in body weight for juvenile snakes across four captive facilities were similar between male and female snakes (e.g., mean for females at the OCIC = 0.57, 95% CRI = 0.48–0.65; mean for males at the OCIC = 0.58, 95% CRI = 0.44–0.71). Furthermore, daily changes in weight relative to body size were similar in three of the four captive rearing facilities (mean for females at Zoo Atlanta = 0.55, 95% CRI = 0.37–0.72; WNFH = 0.55, 95% CRI = 0.36–0.73; Table 2; Fig. 4; Supplementary File 1). Snakes housed at Auburn University had the lowest daily change in body weight (mean for female snakes = 0.39, 95% CRI = 0.21–0.58; Table 2; Fig. 4).

DISCUSSION

In this study, we used indigo snake length and weight data from multiple studies and facilities to assess variability in growth across wild, reintroduced, and captive populations. There has been little effort to empirically evaluate growth for this imperiled species in either captive or free-ranging populations, and our analysis expands upon previous small-scale descriptions of indigo snake body size and growth (Layne and Steiner 1996; Stevenson et al. 2003, 2009; Wines et al. 2015). Stevenson et al. (2009) fit a von Bertalanffy growth model using data from 29 male, 16 female, and three hatchling indigo snakes from wild populations in southern Georgia (also used in our analyses), although their model did not incorporate individual heterogeneity or measurement error. Our results suggested that asymptotic size and the growth coefficient in wild snakes were larger than the values estimated by Stevenson et al. (2009; e.g., for male snakes $L_\infty = 1.85$ vs. 1.77 and $k = 1.05$ vs. 0.60). These differences can likely be attributed to our larger sample size, additional populations, greater variability in observed SVL, and our model parameterization accounting for more uncertainty (e.g., measurement error). Nevertheless, our inferences were broadly similar to those of Stevenson et al. (2009). For example, both our study and Stevenson et al. (2009) found that female snakes reached asymptotic SVL faster than male snakes and both sexes typically grow to approximately 50% of their asymptotic length in less than 2 yr. Our finding of strong male-biased sexual size dimorphism in SVL is also consistent with previously described trends in indigo snake body size (e.g., Layne and Steiner 1996; Stevenson et al. 2003).

We found that measurement error varied across projects that were included in our data set. Measurement error was lowest in captivity where snakes are either of smaller size or are measured using a squeeze box, which typically presents a more repeatable methodology for measuring snakes (Bertram and Larsen 2004). However, even though the absolute measurement error was smaller in captivity, it represented a higher percentage of the mean body size in that data set because of the high number of juvenile snakes. Across all projects, measurement error accounted for approximately 2.4–7.1% of the mean adult body size recorded in each study, which may have nontrivial consequences when using body size to explain variation in other aspects of indigo snake ecology (e.g., survival or fecundity). Measurement error may be substantial when measuring the length of large snakes even when they are measured repeatedly over short time periods (Cundall et al. 2016), and measurement error can cause individuals to appear to shrink over time (Madsen and Shine 2001b; Luiselli 2005). For ongoing projects, both in captivity and in the wild, it may be worth exploring alternative or additional techniques to reduce error in length measurements (Blouin-Demers 2003; Rivas et al. 2008; Astley et al. 2017).

Our results indicated that reintroduced snakes grew towards their asymptotic size faster than either captive or wild snakes (a difference of approximately 10% change in SVL per growth interval). This result was unexpected (e.g., Roe et al. 2010, 2015), and we offer some potential explanations that could account for this difference in growth coefficients. First, in comparison to snakes within extant, wild populations, reintroduced individuals may experience less intraspecific competition when released on sites without an established indigo snake population,

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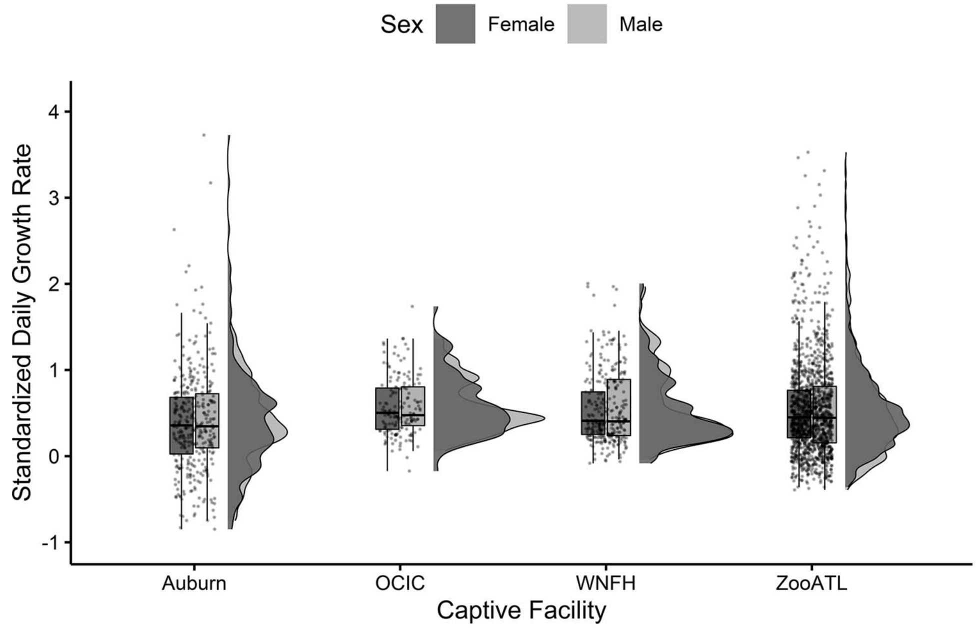

FIG. 4.—Distributions of daily change in body weight for headstarted Eastern Indigo Snakes (*D. couperi*) housed at four captive rearing facilities (Auburn, OCIC, WNFH, and Zoo Atlanta [ZooATL]). Values are unitless and represent the change in weight per day standardized by the initial weight during that growth increment.

potentially allowing them to acquire resources and grow faster (Wilbur 1977; Cushing and Li 1992). Second, faster growth at reintroduced sites could be related to lasting benefits from time spent in captivity because high growth rates mediated by resource availability experienced during the juvenile period can translate to high growth rates and larger sizes later in life (Cooch et al. 1991; Madsen and Shine 2000). Even though we did not detect a difference between captive and wild snakes, it is likely that the increased heterogeneity in captive snakes contributed to a lack of an overall positive effect of captivity (e.g., some snakes acclimate poorly to captivity). Third, trends in post-release growth could be further reinforced by biased recapture data that favor individuals who acclimate well to their post-release environment (if individuals that fared poorly were less likely to be recaptured or released initially). Regardless of the mechanisms involved, our results suggest that at least some reintroduced individuals experience growth rates higher than individuals in wild or captive settings. Finally, although we were unable to estimate asymptotic sizes for wild, captive, and reintroduced snakes separately, the limited data from reintroduced snakes indicated that some individuals were growing to comparable sizes several years postrelease (e.g., several reintroduced females with SVLs > 150 cm).

Indigo snake body size and growth rates likely have important consequences for the success of ongoing indigo snake reintroduction efforts (Folt et al. 2020). Indigo snake survival is higher at larger body sizes (Hyslop et al. 2012) and population modeling suggests releasing larger, headstarted indigo snakes (e.g., 2–3-year-olds vs. <2-year-olds; Folt et al. 2020) would result in lower extinction risk. Indigo snakes raised in captivity are typically provided with a prey base nutritionally different (e.g., higher fat content) than wild snakes (Dierenfeld et al. 2015). Additionally, wild indigo snakes prey extensively on other snakes (Stevenson et al. 2010), yet captive snakes are fed primarily nonsnake prey items (Goetz et al. 2018). Captive diets not only influence pre-release growth rates and body condition (Wines et al. 2015), but may influence foraging behavior, prey preferences, and growth of headstarted individuals after release. Fecundity also increases with body size in captive indigo snakes (Wines et al. 2015), suggesting that individuals with higher growth rates could have increased lifetime reproductive output.

We found evidence that indigo snakes headstarted at Auburn University (which occurred during the early years of the project) experienced slower increases in body mass relative to body size than snakes raised in other facilities. During this period, partners were actively evaluating best management practices for headstarting juvenile indigo snakes in captivity (Wines et al. 2015). Furthermore, all of these individuals were hatched from eggs laid by wild-caught females (Stiles et al. 2013) and may have acclimated poorly to captivity compared to individuals in more recent years that represent multiple generations of captive-born indigo snakes. Nevertheless, information on indigo snake husbandry gained during the early years of the project have since proved valuable for informing subsequent indigo snake captive breeding efforts at other facilities.

Despite the large data set used in this project, there are several important limitations to our data and analysis. First, although we assessed differences in measurement error across projects and broadly across population types, we lacked the data to examine growth rates at finer spatiotemporal or individual-level scales. There are likely significant spatiotemporal differences in wild indigo snake growth rates due to variation in growing season length and environmental factors (Wilbur and Collins 1973; Bronikowski 2000; Sogard 2011; Cadby et al. 2014; Rose et al. 2018b). Individual variation in growth could be influenced by a host of individual-level factors, including genetics, disease or parasite prevalence, home range characteristics, prey availability and the presence of competing species (Baltz et al. 1998; Lõhmus et al. 2010; Steen et al. 2013; Knafo et al. 2016; Bogan et al. 2020). Our data from Florida were relatively sparse; because little monitoring has been conducted in the state, we did not observe previously reported differences in

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asymptotic size across the species' range and our database did not include individuals near the maximum known size for indigo snakes in southern Florida (Allen and Neill 1952; Powell et al. 2016). Data limitations also prevented us from quantitatively assessing differences in juvenile growth between different population types (i.e., less than five juvenile indigo snakes were recaptured in the wild and only headstarted individuals were present at reintroduction sites), and our data set describing reintroduced snakes was relatively small overall. Finally, we note that there are differences in measurement error at finer scales than we were able to quantify (e.g., at the observer level).

There are few examples of snake reintroduction programs that would allow managers to identify best practices, and most existing efforts have occurred at small scales (Roe et al. 2010, 2015; Read et al. 2011; Sacerdote-Velat et al. 2014; Daltry et al. 2017). We offer several considerations, pertaining to snake growth and body size, for future research to inform ongoing indigo snake reintroduction efforts. First, the development of a standardized protocol for monitoring growth of snakes in captivity and at release sites upon recapture could help reduce the degree of measurement error and uncertainty associated with current data collection. Regularly recording the frequency and type of food provided could also be informative for evaluating the effects of such husbandry techniques on indigo snake growth rate, which in turn could help further maximize the growth rates of captive-born snakes (Wines et al. 2015). Second, creation of a centralized database would be useful for the ongoing reintroduction project to collect and store information about headstarted and released snakes in a standardized manner. Third, future research is needed to examine the factors influencing individual indigo snake growth rates at additional populations and consider the role of landscape and environmental factors in influencing growth rates. Indigo snakes have been the focus of one of the longest active reintroduction programs for snakes, but, given the failure of initial efforts to establish populations (Speake et al. 1987), continuing to refine best practices in both captive and wild settings will be an important aspect of long-term project success.

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SUPPLEMENTAL MATERIAL

Supplemental material associated with this article can be found online at https://doi.org/10.1655/Herpetologica-D-22-00041.s1.

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Appendix

Data Sources

Data sources included in a comprehensive database of Eastern Indigo Snake (*Drymarchon couperi*) length and weight data used to model variation in individual growth parameters. Some individuals were included in multiple data sets as they were recaptured as part of different projects (i.e., the total number of individuals was 1503).

Source	State	Type	Time span	Number of observations	Number of individuals
Apalachicola Bluffs and Ravines Preserve	Florida	Reintroduced	2017–2022	95	81
Auburn University	Alabama	Captive	2008–2011	518	32
Cape Canaveral	Florida	Wild	1998–2002	133	87
Conecuh National Forest	Alabama	Reintroduced	2010–2021	227	150
Ft. Stewart	Georgia	Wild	1998–2021	632	310
Georgia Department of Natural Resources	Georgia	Wild	2016–2021	117	96
Highlands County	Florida	Wild	2010–2013	149	81
Orianne Center for Indigo Conservation	Florida	Captive	2013–2020	346	64
Sanibel Islands	Florida	Wild	2012–2021	67	45
The Orianne Society	Georgia	Wild	2007–2021	522	374
Warnell Property	Georgia	Wild	2003–2021	397	187
Welaka National Fish Hatchery	Florida	Captive	2018–2021	369	69
Zoo Atlanta	Georgia	Captive	2009–2017	1,501	129

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