
AN EASTERN INDIGO SNAKE (*DRYMARCHON COUPERI*) MARK-RECAPTURE STUDY IN SOUTHEASTERN GEORGIA

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Abstract.—Recovery of the Eastern Indigo Snake (*Drymarchon couperi*) that is federally listed as threatened will require population monitoring throughout the species' range. From 1998 through 2006, we used mark-recapture methods to monitor *D. couperi* at Fort Stewart, Georgia, USA. We captured 93 individual *D. couperi* while surveying for snakes at Gopher Tortoise (*Gopherus polyphemus*) burrows, and we recaptured 40 (43%) of these snakes. Our observed adult male:adult female sex ratio was 2.1:1. Nineteen males and 13 females exhibited overwintering site fidelity by returning to the same sandhills in successive years. For snakes recaptured in consecutive years, mean monthly growth rates were 3.0–35.7 mm for 26 males and 2.5–22.1 mm for 11 females, with smaller snakes of both sexes exhibiting the most rapid growth rates. Size data from Fort Stewart and other sites in southeastern Georgia demonstrate that *D. couperi* exhibits male-biased sexual size dimorphism. Males attain asymptotic size (SVL = 1766 mm) in 7.27 years; females attain asymptotic size (SVL = 1441 mm) in 5.22 years. We estimated ages of 7–10+ years for several snakes recaptured 4–7 years after their initial capture(s). Because current population trends are poorly known, we encourage population monitoring at other sites where *D. couperi* can reliably be found by surveys at Gopher Tortoise burrows.

Key Words.—*Drymarchon couperi*, Eastern Indigo Snake, Gopher Tortoise, growth model, population monitoring, sexual size dimorphism, sex ratio, site fidelity

INTRODUCTION

Most snake species are not tractable to field studies due to their secretive and inconspicuous habits, extended periods of inactivity, low population densities, or extensive movements (Parker and Plummer 1987). However, mark-recapture studies of snakes may provide valuable information on survivorship, sex ratio, size and growth rates, and site fidelity (Fitch 1999; Bonnet et al. 2002; Stanford and King 2004). The Eastern Indigo Snake, *Drymarchon couperi*, (Fig. 1), federally listed as threatened under the U.S. Endangered Species Act in 1978 (U.S. Fish and Wildlife Service 1982), is the longest snake in North America (Conant and Collins, 1991, but see Devitt et al. 2007). In southeastern Georgia, adult *D. couperi* often return to the same

sandhill habitats (Fig. 2) in successive years to overwinter (Stevenson et al. 2003; Hyslop, N.L., J.M. Meyers, and R.J. Cooper. 2006. Movements, survival, and habitat use of the threatened Eastern Indigo Snake (*Drymarchon couperi*) in southeastern Georgia. Final report to Georgia Department of Natural Resources Nongame Wildlife and Natural Heritage Section. Social Circle, Athens, Georgia, USA. 88 p.). During the cooler months, adult *D. couperi* use Gopher Tortoise (*Gopherus polyphemus*) burrows for dens and frequently bask on the surface near tortoise burrow entrances (Diemer and Speake 1983; Stevenson et al. 2003; Hyslop et al. *op. cit.*). These life-history attributes allow for population monitoring using mark-recapture methods (Stevenson et al. 2003). Stevenson et al. (2003) summarized the first four years of a *D. couperi* mark-recapture study



FIGURE 1. A large adult male Eastern Indigo Snake (*Drymarchon couperi*). (Photographed by Dirk J. Stevenson)



FIGURE 2. Longleaf Pine (*Pinus palustris*) – Turkey Oak (*Quercus laevis*) sandhill habitat typical of our study sites. A burrow apron of a Gopher Tortoise (*Gopherus polyphemus*) is visible in the foreground (arrow). (Photographed by Dirk J. Stevenson)

conducted on Fort Stewart, Georgia; we extended this field study for an additional four years. Herein, we present results for the entirety of this 8-year study, providing additional data relating to *D. couperi* size and growth rates, sexual size dimorphism, overwintering site fidelity, and sex ratio.

MATERIALS AND METHODS

Data collection.—From 1998 through 2006, we monitored the *D. couperi* population on Fort Stewart, a large (113,064 ha) military installation located in the lower Coastal Plain of southeastern Georgia, USA. For the purposes of this paper, we define a *D. couperi* “subpopulation” as a discrete sandhill area known to support Gopher Tortoises and overwintering adult *D. couperi* that is at least 6.0 km from a similar site. Distances between six subpopulations in this study ranged from 6.5 to 27 km. We surveyed for *D. couperi* annually from mid-November through 31 March, a time when individuals have relatively small activity ranges and can predictably be found near tortoise burrows (Diemer and Speake 1983; Stevenson et al. 2003; Hyslop et al. *op. cit.*). We occasionally captured *D. couperi* at other times of the year incidental to other studies. Stevenson et al. (2003) provided additional details about our study areas. To permit positive identification of recaptures, we individually marked each snake that we captured by subcutaneously implanting a PIT (passive integrated transponder) tag on the side of the body ca. 20 scale rows anterior to the vent. We did not count a snake as a recapture unless ≥ 1 month separated captures.

We determined the sex of individuals using a lubricated cloacal probe. Male snakes with snout-vent lengths (SVL) > 1200 mm always possessed weak keels on 3–5 mid-dorsal scale rows; females lacked these keels (see Layne and Steiner 1984). We measured SVL and tail length (TAIL) to the nearest mm using a metal tape measure. We measured larger snakes by having two persons gently pull on opposite ends of the snake until it relaxed along its full length (Fitch 1987). In some cases, we measured fully relaxed snakes when they were under anesthesia prior to radiotransmitter surgery. We added SVL and TAIL to obtain total length (TL). We weighed snakes to the nearest 10 g using spring scales (Pesola AG, Baar, Switzerland). We processed *D. couperi* as described above and released them at their respective capture sites within 48 hours; we released radio-transmittered snakes ca. two weeks after transmitter implantation or removal surgery (Hyslop et al. *op. cit.*).

When presenting size data, we combined measurements from our Fort Stewart mark-recapture study with measurements of 36 snakes (16 males, 15 females, five undetermined) from other localities in southeastern Georgia that we found using the same methods as above, or that we found alive or dead on roads. Based on Speake et al. (1987) and Layne and Steiner (1996. Eastern Indigo Snake (*Drymarchon corais couperi*): Summary of research conducted on Archbold Biological Station. U.S. Fish and Wildlife Service Biological Report, Order No. 43910-6-0134, Jackson, Mississippi. 33 p.), we considered snakes with a SVL ≥ 1150 mm to be adults and snakes with a SVL = 1000–1149 mm to be subadults. When estimating snake ages,

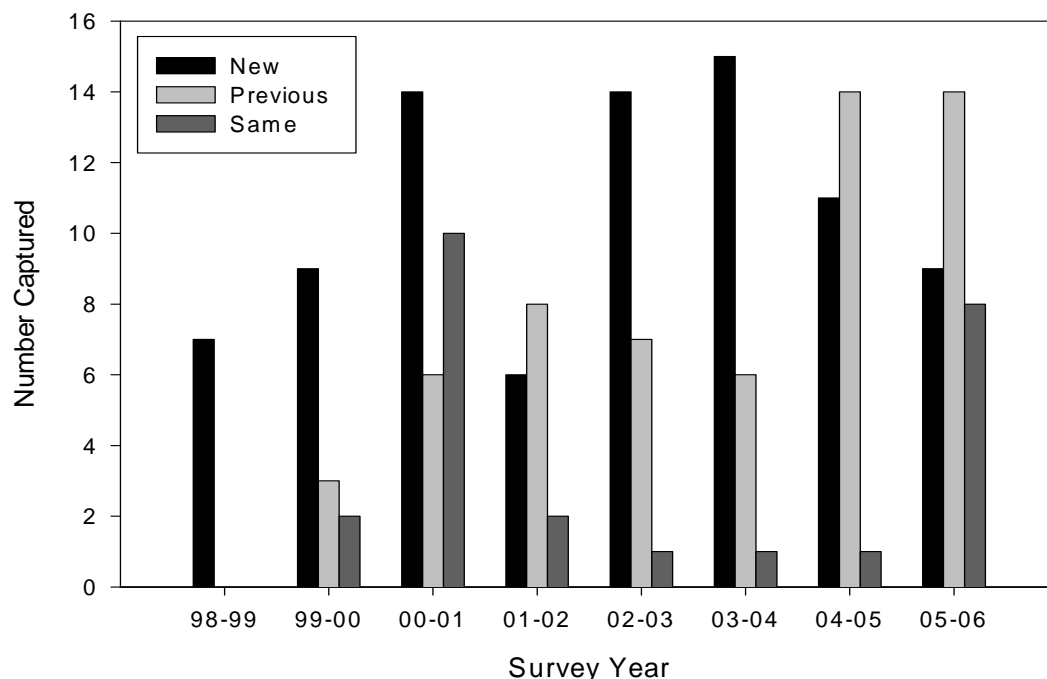


FIGURE 3. The yearly distribution of captures of *Drymarchon couperi* from Fort Stewart, Georgia, USA. Plotted are counts of new (unmarked) individuals, previous-year recaptures (snakes caught in an earlier year), and same-year recaptures from 1998 through 2006. A “snake year” begins on 1 November.

we assumed a hatch date of 1 September (Moulis 1976; U.S. Fish and Wildlife Service 1998). When plotting growth rate data of snakes captured more than once in a survey year, we used the latest capture date. Our growth rate data included five males and two females captured on a site contiguous with Fort Stewart, and 11 males and seven females implanted with radiotransmitters as part of a movements and habitat-use study (Hyslop et al. *op. cit.*). We used data for 10 of 12 radio-transmitted snakes for growth rate analyses (we deleted two females because their growth rates appeared atypically low compared to non-transmitted and transmitted females of similar lengths). Transmitter implantation and subsequent tracking may adversely affect snake growth (Rudolph et al. 1998; Weatherhead and Blouin-Demers 2004).

Statistical analyses.—We performed Student’s *t*-tests (*t*) using SigmaStat version 2.0 (Jandel Scientific, San Rafael, CA, USA) to compare the means of SVL and body mass between sexes after screening the data for violations of assumptions of normality and homogeneity of variance. We applied log transformations to body size variables to increase additivity and meet assumptions of homoscedasticity for parametric tests, but body mass data were not normally distributed, so we compared differences in median values between sexes using the Mann-Whitney rank sum test (*T*). We

determined absolute growth rates by dividing the increase in SVL in mm by the number of months (days/30.42) between captures. We only used individuals captured in consecutive survey years for growth rate analyses. After log transforming the data, we used Student’s *t*-tests to compare absolute growth rates of small (SVL = 950–1399 mm) and large (SVL ≥ 1400 mm) size classes of females, and small (SVL = 1000–1599 mm) and large (SVL ≥ 1600 mm) size classes of males. We used Chi-square tests (χ^2) for proportional comparisons (SigmaStat version 2.0) and a goodness of fit test (SAS version 9.1; SAS Institute, Inc., SAS/STAT®, Cary, NC, USA) to determine if observed sex ratios were different from 1:1. We recognized statistical significance at $P \leq 0.05$, and we report all means as \pm SE.

Size and growth.—We plotted the SVL of snakes captured by month and used clusters of winter captures (November–March) of relatively small snakes (≤ 1500 mm for males and ≤ 1400 mm for females) to assign them to three different year classes. Assuming a hatching date of 1 September, we calculated the ages of 14 males and five females that we initially captured when relatively small and recaptured at least once. We used this information to estimate the ages of other relatively small snakes that we captured only once, and added these to the dataset.

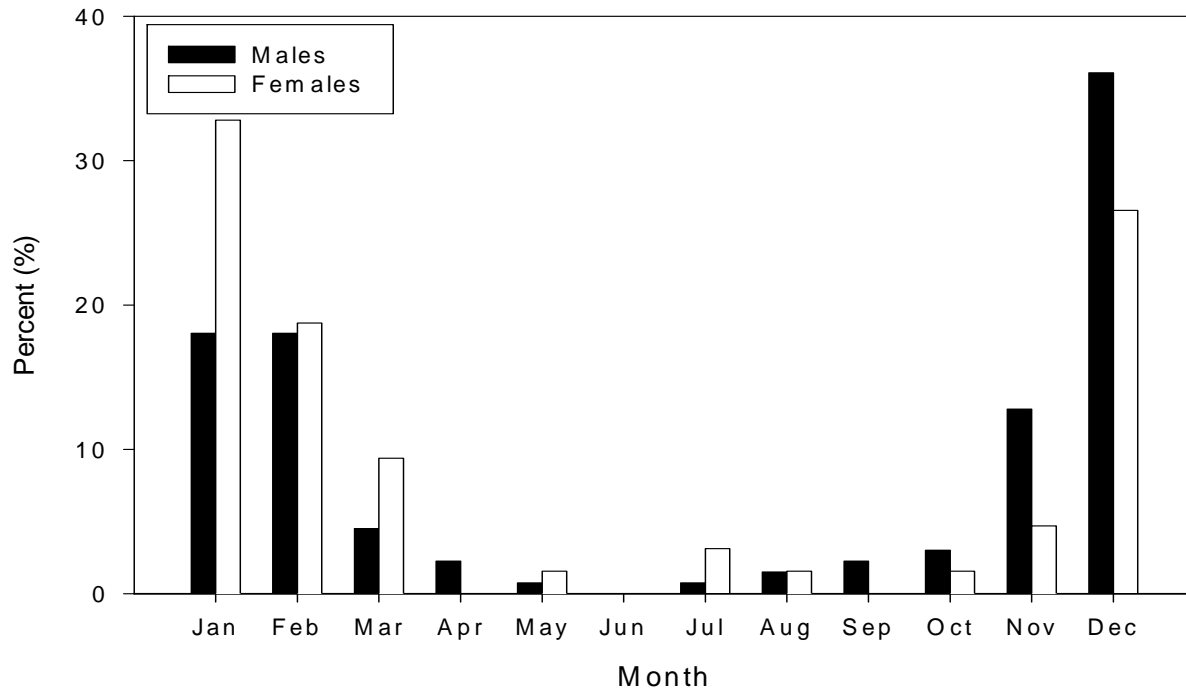


FIGURE 4. Monthly distribution of captures of 110 male and 54 female *Drymarchon couperi* from Fort Stewart, Georgia, USA.

Because our primary interest in the mass-SVL relation was in describing the relationship's form, we used the reduced (standardized) major axis method (RMA; Warton et al. 2006). We transformed these variables as $\ln(\text{mass}^{1/3})$ and $\ln(\text{SVL})$; if isometry applied, the expected RMA slope between these transformed variables would be 1.0. We performed estimation of the RMA and associated tests using SMATR software (Falster et al. 2006).

In addition to the question of the most appropriate line-fitting technique, we considered: (1) whether to estimate separate relations for males and females; (2) how to account for repeated measures of some individuals; and (3) whether to account for measurement error, which according to Warton et al. (2006), is not accommodated simply by using RMA. No software currently available can address all these issues directly while estimating RMA. We investigated these potential complications in several ways. First, we separated the data into subsets so that we estimated the RMA between $\ln(\text{mass}^{1/3})$ and $\ln(\text{SVL})$ by SMATR when each individual was represented only by its earliest recorded measurements of mass/SVL and its latest recorded measurements. We assessed commonalities of slope and elevation between males and females by likelihood ratio tests and Wald tests, respectively (Warton et al. 2006). Second, using SAS/STAT[®] PROC GLIMMIX ver. 9.1 we applied a "mixed" linear model to the entire data set

with $\ln(\text{mass}^{1/3})$ as response and $\ln(\text{SVL})$, sex, and the interaction of $\ln(\text{SVL})$ and sex as fixed predictor effects; we considered repeated measures on individuals as between-individual and within-individual random effects. We assessed homogeneity of the slopes between males and females, differences in elevation by sex, and random effects of repeated measures on individuals by type III F tests and by the AIC_c criterion (Burnham and Anderson 2002). We judged measurement error from differences in SVL and mass when we repeated measurements on individuals after ≤ 30 days and ≤ 60 days.

For those individual snakes with estimated ages, we applied Von Bertalanffy growth models using SAS/STAT[®] PROC NLIN following examples in Khattree and Naik (1995, p. 243). The basic model was:

$$\text{size} = a*(1-\exp(-g*(\text{age}-t)))$$

where size is mass or SVL, *a* is the size asymptote, *g* is the rate at which the asymptote is achieved (or "curvature parameter"), and *t* is the "initial condition parameter" (the "hypothetical age at which size is 0"). We assessed heterogeneity of models between males and females by likelihood ratio tests, and we assessed the influence of repeated measures of individuals by the AIC_c criterion after adding random effects to the Von Bertalanffy models using SAS/STAT[®] PROC

TABLE 1. Survivorship/age estimates of *Drymarchon couperi* marked and recaptured on Fort Stewart, Georgia, USA (date of birth is assumed to be 1 September).

Sex	Initial Capture			Last Capture		
	Date	SVL (mm)	Est. Age (yr)	Date	SVL (mm)	Est. Age (yr)
+	1/27/99	965	1.41	3/10/02	1384	4.53
+	2/19/04	1016	1.48	12/04/05	1333	3.26
+	2/13/05	1149	1.46	12/02/05	1345	2.26
+	1/22/99	1422	3.39	12/23/05	1575	10.33
+	1/03/00	1461	4.34	2/15/06	1594	10.46
+	1/14/01	1486	4.37	2/23/06	1626	9.48
+	12/17/02	1505	5.29	3/30/05	1600	7.58
+	1/27/99	1067	1.41	2/20/01	1511	3.48
O ₃	12/09/03	1148	1.26	2/11/05	1461	2.45
O ₃	11/30/00	1232	1.25	2/29/04	1720	4.50
O ₃	1/22/99	1321	2.40	2/15/06	1873	9.42
O ₃	1/28/02	1346	2.42	3/18/05	1740	5.80
O ₃	11/08/02	1400	2.19	1/30/06	1727	5.42
O ₃	12/16/02	1461	2.30	3/30/05	1715	4.58
O ₃	11/26/03	1465	2.24	2/24/06	1702	4.49
O ₃	1/03/00	1575	3.34	12/04/05	1861	9.26
O ₃	12/05/99	1600	3.27	11/16/03	1820	7.22

NLMIXED. We calculated r^2 with adjustments for sample size and number of estimated parameters (r^2_1 in Kvalseth 1985).

RESULTS

Fort Stewart mark-recapture data.—From 1998 through 2006, we captured and marked 93 *D. couperi* (63 males, 29 females, one undetermined), and recaptured 43% of these snakes a total of 71 times (Fig. 3). We recaptured 26 males 47 times, and we recaptured 14 females 24 times. We found four males and two females outside of our annual winter survey period. We captured and marked 72 *D. couperi* (47 males, 24 females, one undetermined) in the winter survey period during the first seven years of this study. We recaptured 33 (45.8%) of these 72 snakes in at least one additional survey year, including 20 males (42.6% of all males) and 13 females (54.2% of all females). We recaptured 12 males and five females in 3–5 different survey years. Except for three males and one female, we initially marked all of these snakes as adults ($n = 75$) or large subadults ($n = 13$). The number of captures for an individual ranged from 1 to 6, and capture intervals spanned from one month to 7.1 years. We recaptured five males and three females, which we initially marked as adults, 4–7 years later.

Recapture rates did not differ between sexes for snakes captured only in previous survey years ($\chi^2 = 0.271$, $df = 1$, $P = 0.60$) or within the same survey year ($\chi^2 = 0.191$, $df = 1$, $P = 0.66$). Of the 72 *D. couperi* marked during the first seven years of the study, 19 males and 13 females exhibited overwintering site fidelity, returning to the same sandhill where previously captured. Nine males and five females returned to the same sandhill to overwinter in 3–5 different years.

From November through March, we recorded 92.7% ($n = 110$) of all male captures and 92.2% ($n = 54$) of all female captures (Fig. 4), but the proportion of males and females collected in each of these five months differed ($\chi^2 = 11.5$, $df = 4$, $P = 0.02$). We found more males than females early in the winter survey period. In November–December, we captured 53.6% of males and 31.5% of females, whereas in January–March, we captured 64.8% of females and 39.1% of males (Fig. 4). Excluding juveniles, our observed male:female sex ratio was 2.1:1, which was significantly different than 1:1 ($\chi^2 = 11.4$, $df = 1$, $P < 0.001$).

We found most *D. couperi* (86% of all captures) within 5–15 m of tortoise burrows. We often captured snakes during return visits to tortoise burrows where we had observed fresh shed skins or tracks of large snakes. After emerging from tortoise burrows, *D. couperi* often move a short distance before coiling in a sun-lit area to bask. Coiled or otherwise, immobile snakes are remarkably cryptic when partly concealed by Saw Palmetto (*Serenoa repens*) fronds, Wiregrass (*Aristida stricta*), fallen branches, or clumps of runner oaks (*Quercus minima*, *Q. pumila*). We observed most snakes on the surface at temperatures between 15.5° and 22.2°C. On sunny mornings after cold nights, however, we found snakes basking near tortoise burrows at air temperatures of 7.2 °C. Although we found two young-of-year (YOY) *D. couperi* in sandhills close to where adult snakes overwintered, we did not find winter surveys of tortoise burrows to be effective at detecting smaller size classes. One YOY snake used a juvenile tortoise burrow as a refuge, and the other used a small tunnel associated with an old, collapsed burrow of a Nine-banded Armadillo (*Dasypus novemcinctus*). The only other snake species regularly encountered (i.e., ≥ 5 observations) at tortoise burrows during our winter surveys were the Eastern Coachwhip (*Masticophis*

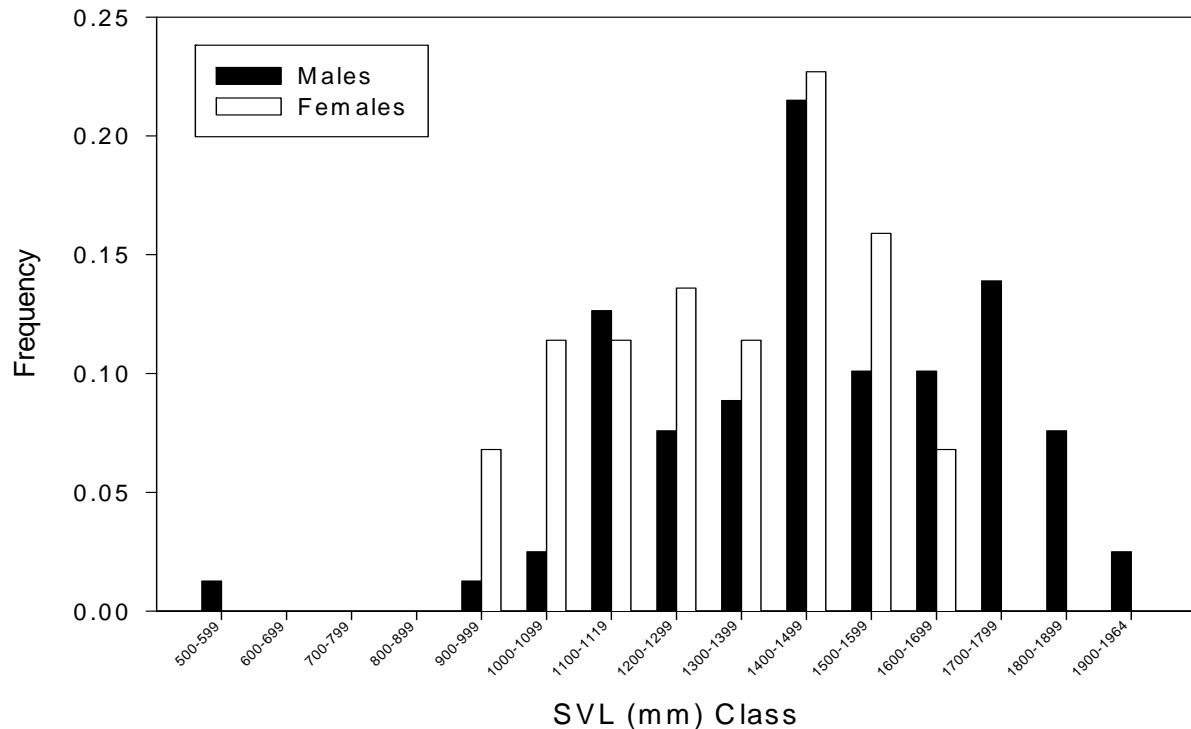


FIGURE 5. Size distribution (SVL) of 79 male and 44 female *Drymarchon couperi* from southeastern Georgia, USA.

flagellum flagellum) and Eastern Diamondback Rattlesnake (*Crotalus adamanteus*); all 16 *C. adamanteus* we observed were adults.

Size and Growth.—When initially captured, 79 males were 584–1956 mm SVL, and 44 females were 920–1695 mm SVL (Fig. 5). We did not determine the sex of three small, wild-caught snakes (SVL = 584–780 mm) and three captive-hatched snakes (SVL = 350–390 mm). The mean SVL of males (1477 ± 29.2 mm) was significantly greater ($t = 3.25$, $df = 121$, $P = 0.002$) than that of females (1329 ± 31.0 mm). Only 6.8% of females but 34.2% of males were ≥ 1600 mm SVL (Fig. 5). When initially captured, 77 males were 90.2–4420 g, and 41 females were 310–3260 g (Fig. 6). The mean mass of males (1929.5 ± 114.7 g) was significantly greater ($T_{41,77} = 1945.5$, $P = 0.005$) than that of females (1390.5 ± 109.1 g). Only 4.8% of females but 31.2% of males were ≥ 2400 g (Fig. 6).

For snakes recaptured in consecutive survey years (i.e., 9–16 months between captures), we determined mean monthly growth rates of 3.0–35.7 mm for 26 males and 2.48–22.1 mm for 11 females. Twelve males in the small size class had a mean absolute growth rate (17.0 ± 3.03 mm) that was significantly higher ($t = 3.65$, $df = 23$, $P = 0.001$) than that of 13 males in the large size class (6.78 ± 0.845 mm). Three females in the small size class

had a mean absolute growth rate (17.0 ± 4.13 mm) that was significantly higher ($t = 4.99$, $df = 9$, $P = 0.0008$) than that of eight females in the large size class (3.92 ± 0.754 mm). Absolute growth rates of small males and small females did not differ ($t = 0.284$, $df = 13$, $P = 0.78$), but large males grew significantly faster than large females ($t = 2.88$, $df = 19$, $P = 0.01$).

Growth rates of males (Fig. 7) and females (Fig. 8) captured in different survey years indicate that smaller snakes grew more rapidly than larger snakes, with growth rates declining with increasing SVL for both males and females. Although both sexes approached their asymptotic lengths at similar rates, growth rates of adult males did not decrease until ca. 1750–1850 mm SVL (Fig. 7), whereas growth rates of adult females slowed or ceased at SVL = 1450–1550 mm (Fig. 8).

When we plotted lengths of snakes captured by month, we observed clusters of winter captures at 960–1200 mm SVL for males and 960–1150 mm SVL for females, which likely represented snakes in their second winter. Numerous winter captures of males 1350–1500 mm SVL and females 1250–1350 mm SVL were presumably snakes in their third winter. By their fourth winter, males were 1500–1650 mm SVL and females 1350–1450 mm SVL. Due to overlap in SVL at larger sizes, it becomes difficult to estimate ages of males after their fourth winter and females after their third winter.

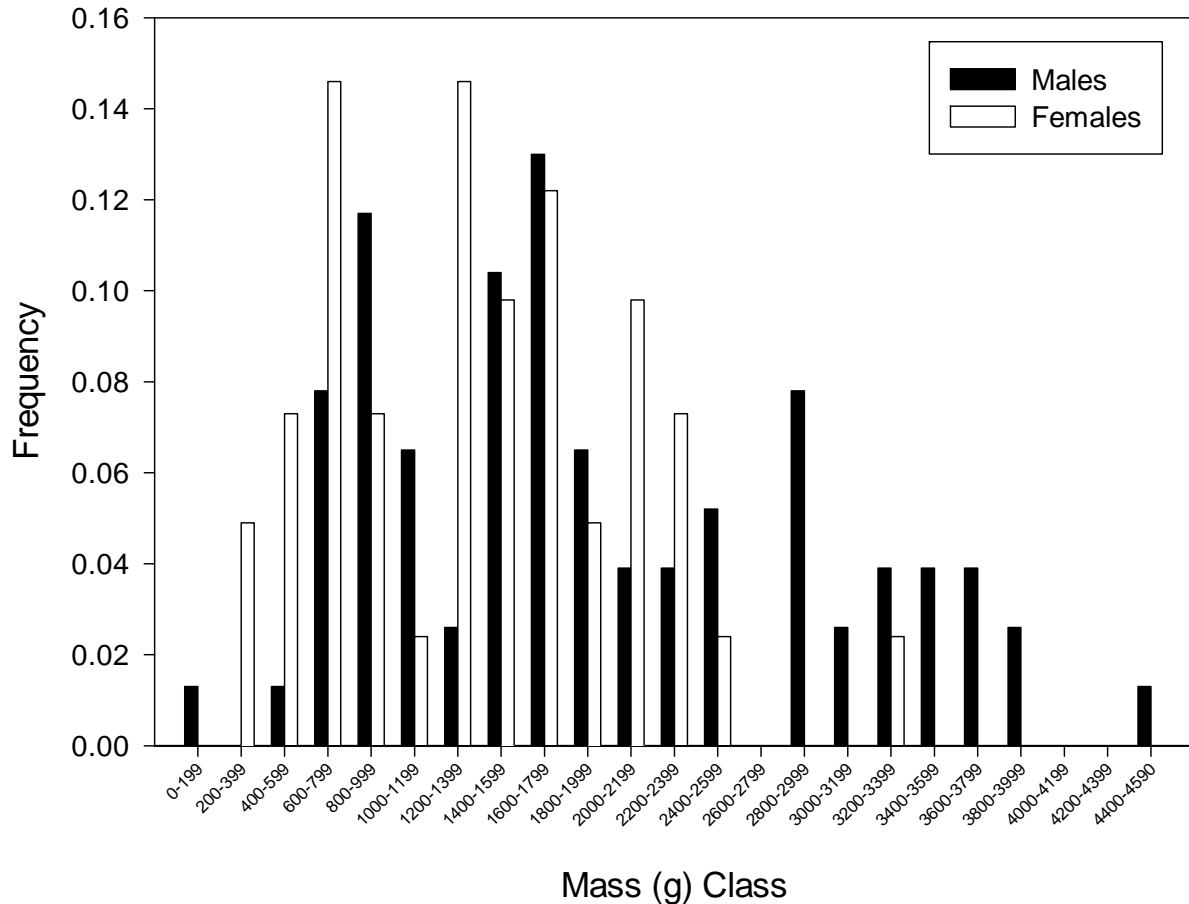


FIGURE 6. Size distribution (mass) of 77 male and 41 female *Drymarchon couperi* from southeastern Georgia.

Estimating age based upon size class, we estimated ages of 7–10+ years for three males and four females that we initially marked as adults and recaptured 4–7 years later (Table 1).

The differences between SMATR estimates of male and female RMA slopes and intercepts were small and nonsignificant, regardless whether we limited observations to just the first or last record for an individual. This conformed to the visual impression from plotting the data. We obtained similar results from the linear models produced with PROC GLIMMIX; there was no evidence that the slope or intercept should be estimated separately between the sexes, and there was negligible change when we included random effect of repeated measurements on individuals. The number of measurements on known individuals varied from 1 to 6; mean = 1.8; median and mode = 1. The AIC_c criterion favored the model without random individual effects.

We plotted all data collected for $\ln(\text{mass}^{1/3})$ vs. $\ln(\text{SVL})$ (Fig. 9). We did not include data for the three

hatchlings of unknown sex that weighed < 50 g in the fit because we would have needed a curvilinear model, even with log scales. The RMA fit was ($r^2 = 0.951$, 95% CI for slope = 1.049 - 1.115, 95% CI for intercept = $[-5.654] - (-5.168)$), $n = 205$):

$$\ln(\text{mass}^{1/3}) = -5.411 + 1.082 \cdot \ln(\text{SVL}).$$

This suggests slight hyperallometry in the average mass-length relationship for post-hatchling indigo snakes.

Khattree and Naik's (1995) sequential method indicated that the Von Bertalanffy growth curves were significantly heterogeneous for males and females. We measured five females and 18 males with estimated ages at least twice. Adding a random effect via PROC NLMIXED for repeated measures did not improve the sex-specific model fits by the AIC_c criterion. Hence, we determined models while ignoring the pseudoreplication from resampling of some individuals. We included data for the three hatchlings of unknown sex in both the male

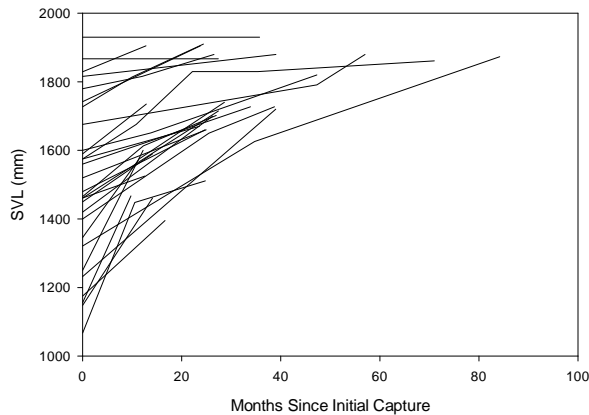


FIGURE 7. Growth data based on snout-vent length (SVL) for 29 male *Drymarchon couperi* from southeastern Georgia, USA. The SVL we measured at first captured is plotted at zero months.

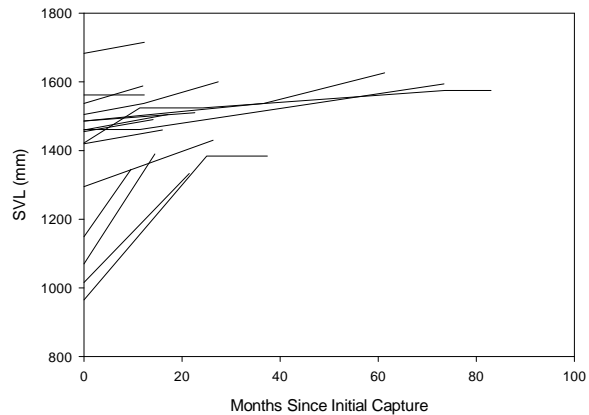


FIGURE 8. Growth data based on snout-vent length (SVL) for 16 female *Drymarchon couperi* from southeastern Georgia, USA. The SVL we measured at first captured is plotted at zero months.

and female model estimates. For males, the fitted models were ($n = 74$, $r^2_{adj} = 0.94$):

$$SVL = 1766*(1-\exp(-0.5970*(age-(-0.4401))))$$

For females, the fitted models were ($n = 32$, $r^2_{adj} = 0.73$):

$$SVL = 1441*(1-\exp(-0.8254*(age-(-0.3552))))$$

The r^2_{adj} should also be considered approximate because we resampled some individuals.

We estimated growth curves with 95% prediction intervals for SVL (Fig. 10). Lines beyond the range of observed data are extrapolations. Fitted lines and prediction intervals were similar if we limited data to the first or last time that we observed an individual.

Inverses of the above Von Bertalanffy equations provide age estimates in years for a given SVL, which for males is:

$$age = (1/(-0.5970))*\ln(1-(SVL/1766))+(-0.4401)$$

The equation for females is:

$$age = (1/(-0.8254))*\ln(1-(SVL/1441))+(-0.3552)$$

We cannot use these equations with an SVL equal to or exceeding the estimated asymptote because the argument of the logarithm would be ≤ 0 . The asymptotic SVL is 1766 mm for males and 1441 mm for females. Using the inverse Von Bertalanffy equations, we calculated the estimated ages at which a given percentage of asymptotic SVL would be reached. The estimated ages at which males reach 50%, 75%, 90%, 95%, and 99% of asymptotic length are 0.72, 1.88, 3.42, 4.58, and 7.27 years, respectively. The estimated ages of females measuring 50%, 75%, 90%, 95%, and 99% of

asymptotic length are 0.48, 1.32, 2.43, 3.27, and 5.22 years, respectively.

DISCUSSION

In southern Florida, Layne and Steiner (*op. cit.*) recaptured only 15.7 % of 236 *D. couperi* marked over a 27-year period, but they opportunistically encountered most of their snakes. In contrast, we recaptured 43.0% of 93 marked *D. couperi* over an 8-year period, primarily by revisiting the same sandhill sites during the winter survey period. Stevenson et al. (2003) and Hyslop et al. (*op. cit.*) reported that adult *D. couperi* often exhibit overwintering site fidelity by returning to the same sandhills, commonly using some of the same tortoise burrows for refugia in successive years. Speake (1993) also recaptured snakes at the same tortoise burrows as in previous winters, and he mentioned that *D. couperi* exhibited a “homing instinct.”

Our size data reinforce earlier statements that *D. couperi* exhibits male-biased sexual size dimorphism (Layne and Steiner *op. cit.*; Stevenson et al. 2003). Males may be larger than females because they grow faster, live longer, reach sexual maturity at a different age or size, or a combination of these factors (Blouin-Demers et al. 2002). Males are usually larger in those snake species exhibiting male-male combat, resulting from an increase in the extent of growth in adult males (Shine 1994). Our field observations and location data from radio-transmitted snakes (Hyslop et al. *op. cit.*) indicate that mate-searching by males and interactions between adult males are a prominent part of *D. couperi* reproduction. We frequently located from one to several adult males in or near a refuge (typically a tortoise burrow) containing an adult female during November–January, which coincides with the peak of the breeding season (Speake et al. 1987; O’Connor 1991). We

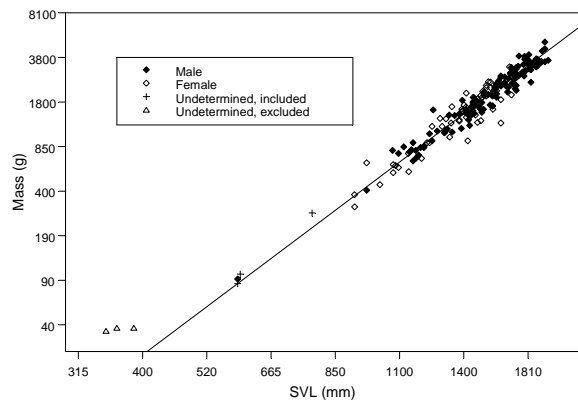


FIGURE 9. Logarithmic plot of SVL vs. $\text{mass}^{1/3}$ for 79 male (123 measurements) and 44 female (65 measurements) *Drymarchon couperi* from southeastern Georgia, USA. The slope and intercept of the line did not differ between sexes, so the data were combined. The tick labels are approximate and arithmetic, but the scale units are based on natural logarithms.

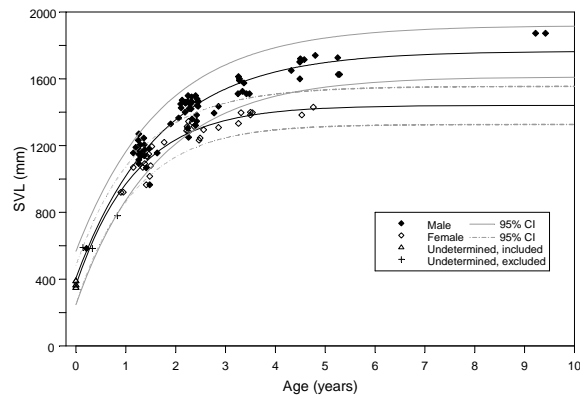


FIGURE 10. Estimated growth curves with 95% prediction intervals for 44 male and 25 female *Drymarchon couperi* from southeastern Georgia, USA. All snakes (including recaptures) initially captured at ≤ 1500 mm SVL for males or ≤ 1400 mm SVL for females are plotted. Date of birth for all snakes is assumed to be 1 September, and lines beyond the range of observed data are extrapolations.

observed adult males with fresh bite wounds on their necks, likely the result of combat encounters with other males (Allen and Neill 1952), and male combat in our study population during this period (Stevenson 2003; Dirk Stevenson, pers. obs.).

At Fort Stewart, we observed an adult *D. couperi* male:female sex ratio of 2.1:1. A multi-year *D. couperi* population survey conducted at a site near Fort Stewart (using the same survey methods employed in our study) also documented an adult sex ratio $> 2:1$ ($n = 65$; R. Redmond, pers. comm.). In a sample of 145 known-sex individuals > 800 mm TL from south-central Florida, the adult sex ratio was 1.54:1, whereas the sex ratio of 36 juveniles (< 800 mm TL) did not differ from 1:1 (Layne and Steiner 1996). Our observed adult sex ratio did not differ significantly ($\chi^2 = 0.0916$, $df = 1$, $P = 0.34$) from the adult sex ratio found by Layne and Steiner (*op. cit.*). For colubrid snakes, sex ratios at birth are generally 1:1 (Parker and Plummer 1987), and this is likely the case for *D. couperi* (Moulis 1976; Layne and Steiner *op. cit.*). Skewed sex ratios observed in later age groups, assuming equality at hatching, may result from sexual differences in mortality, activity patterns, immigration/emigration, or sampling biases (Parker and Plummer 1987). Captures of male snakes could predominate in our sample due to increased surface activity associated with reproduction, more sedentary or reclusive behavior by females, or sexual differences in habitat preferences. However, we doubt these are possible explanations for our observed sex ratio because males and females had similar recapture rates, and an intensive radiotelemetry study carried out on our study area did not detect major differences between the sexes in habitat use or in time spent on the surface during our winter survey period (Hyslop et al. *op. cit.*). We

attribute the observed male-biased adult sex ratio of *D. couperi* to differential survival of males and females. Female survival may be lower due to energetic costs associated with reproduction, higher predation rates, higher overwinter mortality, or a combination of factors. In the Rat Snake (*Elaphe obsoleta* [*Pantherophis obsoletus*]), another colubrid snake with male combat and male-biased sexual size dimorphism, males grow faster and survive slightly better than females, because survival improves with size (Blouin-Demers et al. 2002).

Based on criteria presented by Parker and Plummer (1987), *D. couperi* is properly classified as a late-maturing colubrid snake. Characteristics of *D. couperi* include delayed maturity (i.e., females mature at ≥ 2 years of age; Speake et al. 1987; Layne and Steiner *op. cit.*), high adult survivorship (Stevenson et al. 2003; Breininger et al. 2004; this study), high longevity (Bowler 1977; this study), low to medium fecundity with small annual clutches (Moulis 1976; Speake et al. 1987; Moler 1992), low juvenile survivorship, rapid growth of males compared to females (Layne and Steiner *op. cit.*; this study), male-biased sexual size dimorphism (Layne and Steiner *op. cit.*; Stevenson et al. 2003; this study), male combat (Moler 1992; Stevenson 2003), and a high ratio of mature to immature individuals (untested, but supported by this study). Maximum longevity and population structure for a late-maturing snake species is such that a significant proportion of the population is older than four years (Parker and Plummer 1987). The slower growth rate of females suggests that costs of reproduction (i.e., a significant proportion of resources allocated to vitellogenesis) may influence their growth, resulting in the observed sexual size dimorphism (Bonnet et al. 2002).

Our results for estimating size of animals in their 2nd year were very similar to those of Layne and Steiner (1996). Due to asymptotic growth curves, it is difficult to estimate age from size after the 4th winter. However, applying the growth-age curve with our mark-recapture data, we estimated that the oldest *D. couperi* recaptured were at least 7–10 years old. Maximum longevity for *D. couperi* in captivity exceeds 25 years (Bowler 1977).

Our largest male was 1956 mm SVL (2286 mm TL), whereas the maximum reported length for the species is 2629 mm TL (Conant and Collins 1991). Allen and Neill (1952) commented on the tremendous size (2440–2590 mm TL) attained by a number of wild *D. couperi* from the Everglades and Cape Sable region of southern Florida, and mentioned that specimens > 2286 mm TL are seldom found elsewhere within the species' range. However, only a few males in contemporary literature exceeded > 2286 mm TL, with the longest measuring 2516 mm TL (Steiner, T.M., O.L. Bass, Jr., and J.A. Kushlan. 1983. Status of the Eastern Indigo Snake in southern Florida national parks and vicinity. South Florida Research Center Report SFRC-83/01. Everglades National Park, Homestead, Florida. 25 p.; Layne and Steiner *op. cit.*).

A bias in most snake studies is a lack of adequate sampling of juveniles (Parker and Plummer 1987), leading to missing information on juvenile recruitment, growth, and survival. This was certainly true for our study, as we seldom found juvenile *D. couperi*. We recommend that future researchers determine habits, survivorship, and growth rates of juveniles, along with investigating the life expectancy and causes of mortality of females, and the age and size at sexual maturity for both sexes.

Our Fort Stewart mark-recapture study took place on a large, protected, and intensively managed landscape that apparently supports a robust *D. couperi* population. We captured and marked 93 snakes here in 1998–2006, and investigators conducting a *D. couperi* study at a site contiguous with Fort Stewart marked 65 *D. couperi* (mostly adults) in 2002–2007 (Robert Redmond, pers. comm.). On average, we captured one *D. couperi* per five person-hours during the mid-November through 31 March survey period; once, we found seven individuals in one day. Remarkably, four investigators working at the aforementioned site contiguous with Fort Stewart captured 18 *D. couperi* (11 of which were previously marked [i.e., PIT-tagged] snakes) near tortoise burrows on a single date in December (Robert Redmond, pers. comm.).

Of salient importance to the *D. couperi* population inhabiting Fort Stewart is an active habitat management program that uses prescribed fire to manage sandy upland pine habitats. Since 1992, Fort Stewart land managers have annually prescribe-burned an average of ca. 42,000 ha, including ca. 16,000 ha during the

growing season (David Pope, pers. comm.). Most of the military installation is prescribe-burned every 2–4 years, which maintains or improves habitat integrity of native Longleaf Pine (*Pinus palustris*)–Wiregrass upland habitats (pine flatwoods and sandhills), enhancing habitat quality for *G. polyphemus* and *D. couperi* (Auffenberg and Franz 1982; Landers and Speake 1980; Carlile 1995). The Fort Stewart *D. couperi* population also benefits from most of the base being unfragmented by paved roads or development. As a result, large (20–60 ha), intact sandhills, which are vital winter habitat and known nesting habitat (Speake et al. 1978; Williamson, G.K., and R.A. Moulis. 1979. Survey of reptiles and amphibians on Fort Stewart and Hunter Army Airfield. Report to U.S. Army, contract DACA 21-77-c-0155, Fort Stewart, Georgia, USA. 338 p.; Smith 1987), are contiguous with extensive wetlands and other poorly drained habitats that are important foraging areas (Speake et al. 1978; Hyslop et al. *op. cit.*).

Adult *D. couperi* have very large home ranges that may encompass over a thousand hectares, and individuals often travel between upland and wetland habitats (Speake et al. 1978; Hyslop et al. *op. cit.*; Dodd and Barichivich 2007), making this species potentially vulnerable to habitat fragmentation (Breininger et al. 2004; Hyslop et al. *op. cit.*). In fact, simulation models suggest that the likelihood of populations of large snakes persisting within a given area decreases as “edge” increases relative to protected habitat (Breininger et al. 2004). Maintenance of viable populations of *D. couperi* and other large species of snakes in the southeastern United States likely requires protecting large, contiguous sections of unfragmented habitat (Dodd and Barichivich 2007).

Reliable survey methods for *D. couperi* are known only for sites where the species uses tortoise burrows during the winter (Stevenson et al. 2003). Adequate techniques may not exist for other portions of the range (Breininger et al. 2004). Our study further demonstrates that adult and large subadult snakes can be captured, and recaptured, between years, allowing successful monitoring of *D. couperi* populations where the species overwinters in tortoise burrows. In an effort to increase capture success, we recommend that future *D. couperi* surveyors utilize single-opening funnel traps (Lips 1991) placed selectively (i.e., at burrows with snake tracks) at the mouths of tortoise burrows during the cooler months (November–March). Unfortunately, recent population trend data are largely lacking for both Georgia and Florida populations of *D. couperi* (U.S. Fish and Wildlife Service 1998; Stevenson, D.J. 2006. Distribution and status of the Eastern Indigo Snake in Georgia. Unpublished Report to the Georgia Department of Natural Resources Nongame Endangered Wildlife Program. Forsyth, Georgia, USA). We strongly

encourage population monitoring of *D. couperi* at other sites throughout its range.

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