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Survival and population growth of a long-lived threatened snake species, *Drymarchon couperi* (Eastern Indigo Snake)

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Abstract Demographic data provide a basis for understanding the life history and ecology of species, factors which are vital for informing conservation efforts; however, little is known regarding the population ecology of most snake species, including the threatened Eastern Indigo Snake (*Drymarchon couperi*). We used 11 years (1999–2009) of capture-mark-recapture (CMR) and 2.5 years (2003–2005) of radiotelemetry data from southeastern Georgia, USA, in a CMR modeling framework to estimate apparent survival, capture and transition probabilities, and evaluate factors influencing these parameters. The model-averaged estimate of overall apparent annual survival probability was 0.700 ($\pm$0.030 SE) and is comparable to that obtained from known fate analysis (radiotelemetry) at the same site. Body size positively influenced survival, regardless of sex. Capture probability differed seasonally by sex, suggesting lower capture probability for females in fall and males in winter. There was no evidence for effect of precipitation or site-specific differences in survival. Model averaged estimate of annual adult survival estimated using multistate CMR models was 0.738 ± 0.030 and 0.515 ± 0.189 for subadults. We estimated population growth rate (λ) and elasticity (proportional sensitivity) of λ to vital rates using a stage-structured matrix population model. Population growth rate ranged from 0.96 to 1.03 depending on the value of the probability of transitioning from subadult to adult stage. The λ was proportionally most sensitive to changes in adult survival rate, followed by subadult survival. Our results suggest that protecting adult snakes and their habitats would result in the highest likelihood of long-term population stability and growth.

Keywords AIC · Capture-mark-recapture (CMR) models · Elasticity analysis · Multistate CMR models · Sensitivity analysis · Stage-based matrix population model

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Introduction

Detailed and reliable demographic data provide a basis for understanding the life history and ecology of a species, factors which are vital for informing conservation efforts (Dodd 1987, 1993; Stanford and King 2004). Demographic analyses also allow the determination of influential life history variables on population growth, and the pattern of these influences. These data, however, are often difficult to obtain for certain taxa, including most snake species (Parker and Plummer 1987). This is in part because of the lack of interest historically in the group (Dodd 1993), their secretive and cryptic nature (Fitch 1987), long periods of inactivity, and often relatively low densities (Parker and Plummer 1987). Snakes, however, may constitute important components of ecosystems, in terms of local biomass, and as predators (Godley 1980; Fitch 1999).

Drymarchon couperi (Eastern Indigo Snake), federally listed as threatened since 1978 (United States Fish and Wildlife Service 1978), has been the focus of recent research and conservation efforts across its range in the southeastern United States. A large, up to 2.63 m (Conant and Collins 1998), nonvenomous colubrid, *D. couperi* is a diurnal, active-foraging species that preys on a wide array of vertebrates, especially other snakes (Stevenson et al. 2010). Breeding occurs from October to March (Groves 1960; Speake et al. 1978; Steiner et al. 1983), a period when the snakes are primarily associated with sandhill habitats. Gestation lasts 100–150 days (Smith 1987; O'Connor 1991) and a single clutch of 4–12 relatively large eggs (37–89 g) is laid in May and June (Moulis 1976; Steiner et al. 1983; Moler 1985; Speake et al. 1987) which hatch after approximately 3 months (Groves 1960; Smith 1987). *Drymarchon couperi* exhibits male-biased sexual size dimorphism, annual reproduction, and a delayed age at sexual maturity [(3–4 years) Speake et al. 1978; Stevenson et al. 2009]. Throughout much of its range, the species is closely associated with xeric sand ridge communities (sandhills), especially during the fall-winter breeding season where *D. couperi* is often found in association with the burrows of *Gopherus polyphemus* [(Gopher Tortoise) Speake et al. 1978; Landers and Speake 1980; Speake and McGlincy 1981]. Tortoise burrows are used as protection from environmental extremes, fire, and predators (Speake et al. 1978; Landers and Speake 1980; Speake and McGlincy 1981; Hyslop et al. 2009a). Additionally, foraging, nesting, ecdysis and potentially mating may occur in or near the burrows (Landers and Speake 1980; Stevenson et al. 2009; Hyslop et al. 2009a). Intact longleaf pine (*Pinus palustris*) and wiregrass (*Aristida stricta*) sandhills used by *D. couperi* have experienced precipitous declines, with less than 3% of their pre-European colonization area remaining (Landers et al. 1995; Frost 2006). Conservation and restoration of these varied habitats requires detailed knowledge of the ecology of multiple species reliant on these systems.

Despite the conservation importance of *D. couperi*, multiple radiotelemetry studies (Speake et al. 1978; Moler 1985; Smith 1987; Breininger et al. 2004; Dodd and Barichivich 2007; Hyslop 2007; Hyslop et al. 2009a), and mark-recapture efforts (Layne and Steiner 1996; Stevenson et al. 2003), little is known regarding demographic parameters or population trends of *D. couperi* (Breininger et al. 2004) primarily because of difficulties in obtaining adequate sample sizes. Since Federal listing of *D. couperi*, there is evidence of ongoing declines which are largely attributable to declining tortoise populations and habitat alteration caused primarily by development, fire suppression, commercial forestry practices, and agriculture (United States Fish and Wildlife Service 1978, 2008; Stevenson 2006). Here, we use 11-year capture-mark-recapture

(CMR) and 2.5 years of radiotelemetry data collected in southeastern Georgia in a CMR modeling approach to estimate demographic parameters and to evaluate factors influencing these parameters. Our specific objectives were to: (1) estimate adult and subadult apparent survival and transition probability for *D. couperi* at two adjacent study sites in southeastern Georgia; (2) test hypotheses regarding the influence of intrinsic (sex, body size, year, season) and extrinsic factors (precipitation, site of capture) on demographic parameters; and (3) estimate population growth rate, and evaluate the proportional sensitivity of population growth rate to demographic parameters.

Methods

Study area

Data for this study were collected by surveying annually for snakes at tortoise burrows on xeric sandhills at Fort Stewart Military Instillation (FSMI; 113,064 ha total area) and adjacent private lands located in the Coastal Plain of southeastern Georgia, USA. Because of differences in land use and habitat management histories, xeric sandhill communities on both Fort Stewart and private land study sites varied with respect to vegetation, and included: intact, mature longleaf pine–turkey oak–wiregrass habitat; young (5–15 years) to medium (16–40 years) age slash (*Pinus elliottii*) or loblolly (*Pinus taeda*) pine plantations; recently restored (i.e., formerly in slash or loblolly pine plantations that were clearcut) longleaf pine–wiregrass habitats. Fire-maintained (i.e., open-canopied) and fire-suppressed (i.e., more close-canopied) examples of both the first and second types above were present on both Fort Stewart and private land sites. Xeric sandhills at both sites were interspersed with mesic pine flatwoods, mixed pine–oak forests, bottomland hardwood habitats, and wetlands (including isolated depressional wetlands, blackwater creek swamps, seepage-influenced bay swamps, and impoundments; Wharton 1978). Recent (1990–present) habitat management practices at the Fort Stewart sites (i.e., prescribed burns, selective thinning, longleaf pine planting, wiregrass seeding, and control of xerophytic oaks via herbicide application) have promoted or enhanced open-canopied longleaf pine habitats. Management activities on private land included some of the same methods as Fort Stewart, but many areas were fire-suppressed and not actively managed, or managed for timber production, primarily loblolly pine and slash pine, and game species [i.e., *Odocoileus virginianus* (white-tailed deer), *Meleagris gallopavo* (wild turkey), and *Colinus virginianus* (northern bobwhite)].

Although both study sites consisted of multiple isolated sandhills where snake surveys were conducted, for the

purpose of analysis, we consider the areas within the study sites contiguous due to the ability of the snakes to travel between these discrete areas (Hyslop 2007). Further details of habitats and land use are available elsewhere (Stevenson et al. 2003, 2009; Hyslop 2007).

Data collection

Systematic CMR studies of *D. couperi* were conducted annually from 1999 to 2009 over 11 consecutive field seasons at both Fort Stewart and private lands from October through March (Stevenson et al. 2009) at eight sandhills (6 on FSMI; 2 on private lands) that ranged in size from 15 to 307 ha ($\bar{x} = 136$ ha). The survey period corresponded to the period when snakes showed their lowest average movement distance per day (except October), smallest seasonal home ranges, and highest use of sandhill habitats and tortoise burrows annually (Diemer and Speake 1983; Hyslop 2007; Hyslop et al. 2009a), allowing for more reliable capture of individuals than during warmer months. CMR data were collected by two research groups, one on Fort Stewart from 1999 to 2009 (Stevenson et al. 2003, 2009) and the other on private lands from 2003 to 2009 (M. Wallace, personal communication). In addition, a radiotelemetry study was conducted from 2003 to 2005 at both study sites ($n = 32$ individuals; Hyslop et al. 2009a). CMR surveys were conducted between 5 and 50 days per year and snakes were primarily captured by hand. Large snake traps along drift fences were also installed at both sites from 2003 to 2004, resulting in five subadult and one adult *D. couperi* capture (Hyslop et al. 2009b). At capture, snakes were sexed, weighed, measured [snout-vent length (SVL)], and marked with a passive integrated transponder (PIT) for individual identification (Stevenson et al. 2003, 2009). Snakes were typically processed on-site, or in the laboratory before being released (maximum 24–72 h later) at site of capture. Further details regarding field methods are available in Stevenson et al. (2009).

Estimation of, and factors influencing, demographic parameters

For CMR analysis, captures were delineated into two, 3-month sampling occasions: October through December and January through March, roughly equivalent to fall and winter, respectively. The two sampling occasions were followed by a 6 month period when snakes were not actively sampled because of annual dispersal from and reduced use of upland sandhill habitats where the snakes overwintered (Hyslop 2007; Hyslop et al. 2009a). Years were delineated from 1 June of year t to 31 May of year $t + 1$ (hereafter, "sampling year").

To estimate demographic parameters and factors influencing these parameters, we first used Cormack–Jolly–Seber (CJS; Cormack 1964; Jolly 1965; Seber 1965) models to estimate overall apparent survival (ϕ) and to examine hypotheses regarding effects of factors on survival and capture probability (ρ). Secondly, we used multistate CMR to obtain estimate of subadult and adult survival along with transition probability from subadult to adult stage. Sample size limitations precluded hypothesis testing using the multistate modeling approach.

We first tested for the influence of monitoring method (telemetry or CMR) on snake survival using CJS, but found no evidence that apparent survival differed between snakes monitored by different methods. Since the number of snakes monitored by telemetry was small ($n = 32$) and no differences were detected in survival, we pooled snakes for further analysis. We also tested for effects of standardized body size and compared this to effects of unstandardized body size using CJS models. The slope parameter (β) for both models was positive and estimated 95% CIs did not span zero; however, the model including the effect of unstandardized body size was 1.5 times more likely than the model including standardized body size. We therefore retained unstandardized body size for further modeling efforts.

The data were insufficient to support a fully time-dependent CJS model; we therefore constructed the most parameterized model with ≤ 2 inestimable parameters for bootstrap goodness of fit testing (Shine and Bonnet 2009) using Program MARK (500 iterations; White and Burnham 1999). This model included an additive effect of time (year) and grouping variable (sex) for survival; and an interactive effect of year and sex for capture probability. The estimated $\hat{c}$ was 0.822, indicating no lack of fit or overdispersion of data; thus, no quasilikelihood or variance inflation factor correction was necessary.

We examined a priori hypotheses regarding the influence of year, season, sex, and body size (SVL). We predicted that apparent survival would be positively influenced by body size, with larger individuals experiencing higher survival, regardless of sex, because of size and experience-related advantages. Patterns found in snake survival suggest generally that larger adults have a higher survival probability than smaller adults (Jayne and Bennett 1990; Blouin-Demers et al. 2002). We also expected that survival would vary seasonally, with lower probability of survival in winter compared to fall, in part because of lower temperatures and also because snakes in winter were commonly observed with lower body mass and varying degrees of infection by a vesicular skin disease (T.M. Norton, unpublished data). We predicted that survival would be lower for females because of increased energetic needs for reproduction, increased exposure during

gestation (Shine and Bonnet 2009; Hyslop et al. 2009a), and because the species exhibits male-biased sexual size dimorphism (Layne and Steiner 1996; Stevenson et al. 2009) potentially leading to size-based survival advantages. Although we did not have a biological reason to suspect changes in overall apparent survival over the course of the study, we did consider that experience-based improvement in snake detection by observers could positively influence capture probability over time. We used an information-theoretic approach, based on Akaike Information Criterion corrected for small sample size (AIC_c), for model comparison and statistical inferences concerning the effects of covariates on apparent survival and capture probabilities (Akaike 1973; Burnham and Anderson 2002; Williams et al. 2002).

To examine effects of extrinsic factors on survival we examined the effects of measures of precipitation and site of capture on survival using the top CJS model as the base model for testing. There were several years with total annual rainfall that deviated substantially from the previous 24-year average coinciding with a protracted drought experienced in southeastern Georgia. From 1985 to 2009 average annual rainfall, as calculated per sampling year, was 119.4 cm ($\pm$5.39 SE). Between 1999 and 2009, four sampling years had significantly lower rainfall totals than the average for the proceeding 24 years (dry; $\bar{x} = 81.3$ cm/ sampling year $\pm$ 6.75). We expected lower survival in sampling years characterized by dry conditions or years following dry conditions because of expected effects on prey availability (e.g., snakes, amphibians, small mammals; Stevenson et al. 2010).

For all models, capture probability for the telemetry group was constrained to 1 because of the reliability of resighting these individuals. The unequal sampling regime (i.e., 2, 3-month sampling occasions separated by 1, 6-month period) was incorporated into model design. We calculated model-averaged estimates of survival and capture probability to account for uncertainty in model selection using reduced model sets with the parameter of interest (Burnham and Anderson 2002). We implemented CJS models in Program MARK v. 6.1 (White and Burnham 1999) using RMark interface v. 1.9.1 (Laake and Rexstad 2007). Results are average $\pm$ SE.

Estimation of population growth rate (λ) and sensitivity of λ to demographic parameters

We used a female only, post-breeding census stage-structured matrix population model (Caswell 2001) for demographic analyses. We used a 1-year projection interval and three stages based on the life history of the species (Fig. 1). The first stage represented hatchlings (ca. 0–3 months of age) and juveniles (ca. 4–12 months) and stage duration
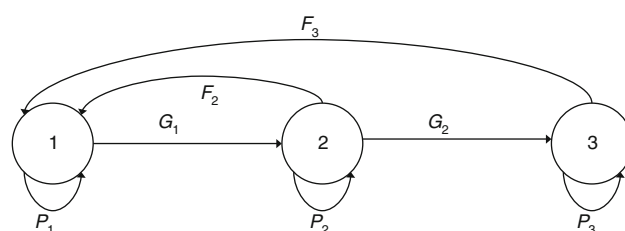
Fig. 1 Life cycle graph for female *Drymarchon couperi*. *Numbers* represent stages in the life cycle: *1* first year, *2* subadult [$\leq$120 cm snout-vent length (SVL)]; *3* adult (>120 cm SVL). *Arrows* indicate the probability of surviving and remaining in the same stage (P), probability of surviving and growing to next stage (G), and fertility (F)

was constrained to 1 year. We combined hatchlings and juveniles into one stage because of the paucity of information on these stages. Stage two included non-breeding subadults $\leq$120 cm SVL likely in their second and third years. Stage three represented adult females >120 cm SVL. The population projection matrix ($\mathbf{A}$) took the form:

$$\mathbf{A} = \begin{bmatrix} 0 & P_2\psi_2 m_3 & P_3 m_3 \\ P_h P_j & P_2(1 - \psi_2) & 0 \\ 0 & P_2\psi_2 & P_3 \end{bmatrix}$$

where ψ_i is the transition probability from stage i to stage $i + 1$ conditional on survival, P_i is the survival rate of stage i, and m_i is the fecundity of stage i. Survival for stage one was estimated as the product of hatchling survival (P_h/3 months) and juvenile survival (P_j/9 months; $P_1 = P_h \times P_j$; Table 1).

We used multistate CMR analysis (Brownie et al. 1993; Nichols and Kendall 1995; Williams et al. 2002) to estimate P_2 (apparent survival probability for subadults), P_3 (apparent survival probability for adults), and Ψ (probability of transitioning from subadult to adult state, conditional on survival). *Drymarchon couperi* reach maturation at approximately 110 cm SVL regardless of sex (Speake et al. 1978; Layne and Steiner 1996; Stevenson et al. 2009). Because of some uncertainty in this value and the low sample size of subadults, we used 120 cm to delineate subadults from adults. Sampling occasions and data structure were similar to that used for CJS analysis. We allowed apparent survival probability to be state-specific, and fixed capture probability to vary by sex and season as in the top ranked CJS model. We set transition probabilities from adult to subadult state to 0 and from adult to adult state to 1. The multistate CMR analyses were implemented in Program MARK v. 6.1 (White and Burnham 1999) using RMark interface v. 1.9.1 (Laake and Rexstad 2007).

Data on reproductive parameters of free-ranging *D. couperi*, however, are sparse. Therefore, we used data summarized from studies of captive snakes, field observations, and published accounts (Smith 1987; Speake et al.

Table 1 Average vital rates and transition probabilities (±SE where available) for *Drymarchon couperi* used in deterministic matrix population model

Rate	Estimate (SE)	Lower	Upper
Hatchling survival[a] (P_h)	0.49	0.05	0.90
Juvenile survival[b] (P_j)	0.59	0.05	0.90
Subadult survival[c] (P_s)	0.52 (0.20)	0.16	0.85
Adult survival[c] (P_a)	0.74 (0.03)	0.52	0.89
Clutch size	4.75	3.00	6.00
Nest survival	0.75	0.25	0.95
Hatching rate	0.75	0.25	0.95
Breeding probability	0.75	0.50	0.95
Transition from stage 1–2 (ψ_1)	1.00	1.00	1.00
Transition from stage 2–3 (ψ_2)	0.99 (0.01)	0.50	1.00

Upper and lower values were used in simulations. Subadult and adult survival and transition from stage two to three were estimated from multistate CMR analysis presented here (standard errors in parentheses). Hatchling and juvenile survival were estimated from a telemetry study on free-ranging, captive reared individuals (Smith 1987). Clutch size and hatching rate were estimated from captive breeding efforts where wild females were brought to captivity and laid eggs. We estimated breeding probability from field observations and information from captive programs suggesting annual breeding is likely in the species. See text for further details

[a] Hatchling survival over 3 month period

[b] Juvenile survival over 9 month period

[c] Annual survival

1987; Breininger et al. 2004; Stevenson et al. 2009) to provide reasonable starting estimates of reproductive parameters. *Drymarchon couperi* is oviparous; wild females lay a single clutch of 4–12 relatively large eggs ($\bar{x} = 9$) from April to June which hatch after approximately 3 months (Moulis 1976; Steiner et al. 1983; Moler 1985; Speake et al. 1987; F. Antonio, personal communication; J. Godwin, personal communication). Sexual maturity may be reached in 2–4 years (Speake et al. 1987; Stevenson et al. 2009; F. Antonio, personal communication) and females are potentially capable of annual reproduction (Speake et al. 1987; Hyslop et al. 2009c). Longevity estimates from wild populations are >10 years (Stevenson et al. 2009), with >25 years reported in captive individuals (Bowler 1977; J. Godwin, personal communication).

Hatchling and juvenile survival estimates were derived from a telemetry study on captive-reared hatchling and juvenile *D. couperi* (Smith 1987). Although stage two individuals were pre-reproductive, some of the individuals survived and grew to stage three during the projection interval; thus, fertility rate for stage two was calculated as $P_2\psi_2 m_3$. We estimated the fertility of stage three as the product of survival and fecundity rates for this stage. Fecundity was estimated as the product of average clutch

size divided by 2 (assuming a 1:1 hatchling sex ratio; Moulis 1976; Parker and Plummer 1987), nest survival, hatching rate, and probability that a female would breed in a given year (breeding probability). We found no data on hatching rate (proportion of eggs that successfully hatch) or nest survival (probability that a nest survives until hatching) in natural habitats; thus, we used a range of values for these parameters based on our knowledge of snake ecology and data from captive breeding programs. Hatching rate and clutch size were estimated from several captive breeding programs where gravid snakes were taken from the wild and eggs were reared in captivity (Speake et al. 1987; J. Godwin, personal communication; R. Redmond, personal communication). For hatching rate, we reduced our estimate by 0.1 from that reported to provide a more conservative estimate for wild individuals. Estimated values of demographic parameters are presented in Table 1.

Most subadult snakes in our sample were likely 1.25–2.5 years in age when initially marked and in their second or third winters. This relative lack of smaller subadults in the sample likely biased our estimate of ψ_2 high. Therefore, we ran models with a range of ψ_2 values between 0.5 and 0.99 for comparative purposes.

We estimated the asymptotic population growth rate (λ) as the dominant eigenvalue of the population projection matrix (Caswell 2001). Elasticity, or proportional sensitivity, of λ (de Kroon et al. 2000) to entries of the population projection matrix and to lower-level vital rates (i.e., hatchling survival, clutch size, breeding probability) was calculated using methods described in detail by Caswell (2001). Because we did not have estimates of variance for all demographic parameters, we were unable to calculate variance for λ in a reasonable manner. We used Matlab (version 7.9.0, Mathworks, Inc., Natick, MA, USA) for all matrix model calculations.

Results

From October 1999 to March 2009, there were 278 captures of 132 individuals (94 males, 38 females; 2.5:1 sex ratio) at Fort Stewart. On the private lands, there were 159 captures of 92 individuals (61 Males, 31 females; 2:1 sex ratio) between January 2003 and March 2009 (Fig. 2; M. Wallace, personal communication). Average female SVL was 139.9 cm (±1.91) and 155.9 cm (±2.14) for males. The data set included 33 subadults ranging from 50 to 120 cm SVL, and 191 adults ranging from 121 to 197 cm. There were 123 individuals with only one capture (including 24 subadults); however, there was little biological evidence to suggest that snakes caught only once were necessarily transient. From the CMR and telemetry data, there were only four instances (all males) of a snake
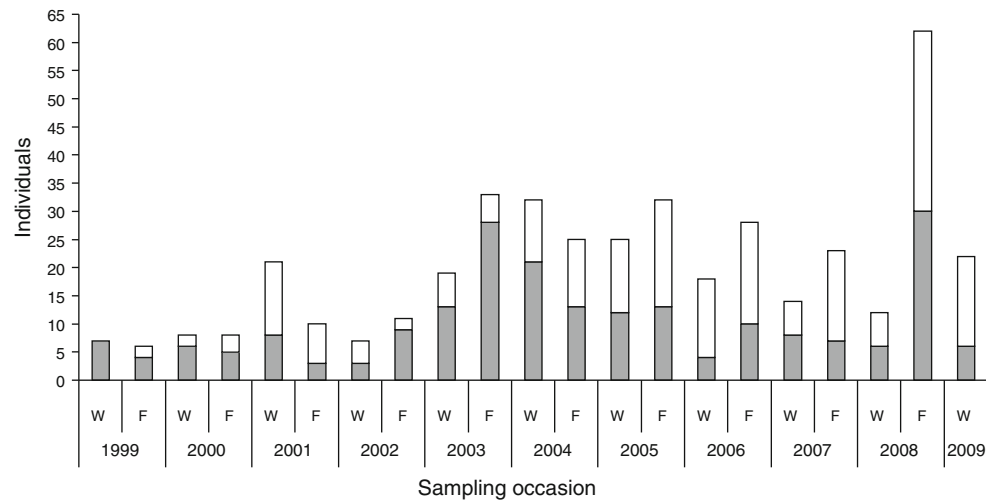
Fig. 2 Individual new captures (*filled*) and recaptures (*open*) in winter (*W*; January–March) and fall (*F*; October–December) sampling occasions for *Drymarchon couperi*, 1999–2009, Georgia

Table 2 Subset of Cormack–Jolly–Seber model results examining effects of season (fall: October–November; winter: January–March), sex, body size (SVL), and sampling year on apparent survival (ϕ) and capture probability (ρ) for *Drymarchon couperi*, 1999–2009 in Georgia

Model number	Model[a]	Number of parameters	AIC$_c$ weight	ΔAIC$_c$	Deviance
1.	ϕ (size) ρ (season × sex)	6	0.819	0.00	871.96
2.	ϕ (size × sex) ρ (season × sex)	8	0.118	3.86	871.68
3.	ϕ (size) ρ (season)	4	0.016	7.88	883.96
4.	ϕ (size) ρ (season + sex)	5	0.007	9.58	883.60
5.	ϕ (year + sex) ρ (size)	13	0.006	9.73	866.90
6.	ϕ (.) ρ (size × sex)	5	0.005	10.19	884.21
7.	ϕ (sex) ρ (size × sex)	6	0.004	10.73	882.70
8.	ϕ (.) ρ (size)	3	0.004	10.86	888.90
9.	ϕ (size) ρ (size)	4	0.004	10.89	886.90
10.	ϕ (size) ρ (size × sex)	6	0.004	10.90	882.80

Top ten models are show here. Effects of years of low precipitation (dry) and site of capture (site) are shown in Appendix I (ESM)

[a] An "×" indicates interaction and "+" indicates an additive effect. A period (.) indicates constant value of the parameter

originally observed over-wintering in one area being observed in another area >2 km away.

Estimation of, and factors influencing, demographic parameters

The model-averaged estimate of probability of apparent survival over 3-month sampling occasions was 0.915 ± 0.010; and 0.700 ± 0.030 annually. The most parsimonious CJS model (model 1; Table 2) examining effects of time, sex, and body size indicated that apparent survival was positively influenced by body size ($\beta = 0.0214 \pm 0.0054$; Fig. 3) and included an interaction of season and sex for capture probability (model 1, Table 2). This top ranked model was 6.9 times more likely than the next approximating model (model 2, Table 2) which

included an interactive effect of size and sex on survival and interactive effect of season and sex on capture probability. Sample size limitations precluded testing for interactive effects for survival, except for interaction of size and sex. There was no evidence for seasonal variation (3 month survival; $\phi_{\text{fall}} = 0.966 \pm 0.031$, $\phi_{\text{winter}} = 0.913 \pm 0.014$) or sex-specific differences (3 month $\phi_{\text{male}} = 0.930 \pm 0.011$, $\phi_{\text{female}} = 0.914 \pm 0.018$) in survival. Capture probability varied seasonally between sexes, with higher detection of males in fall ($\rho_{\text{fall}} = 0.30 \pm 0.038$; $\rho_{\text{winter}} = 0.13 \pm 0.021$) and of females in winter ($\rho_{\text{fall}} = 0.16 \pm 0.044$; $\rho_{\text{winter}} = 0.23 \pm 0.047$).

We tested for the effect of rainfall and site of capture on survival using model 1 in Table 2 as the base model. Although estimated survival was slightly higher at Fort Stewart (3 month $\phi_{\text{Fort Stewart}} = 0.932 \pm 0.010$, ϕ_{Private}
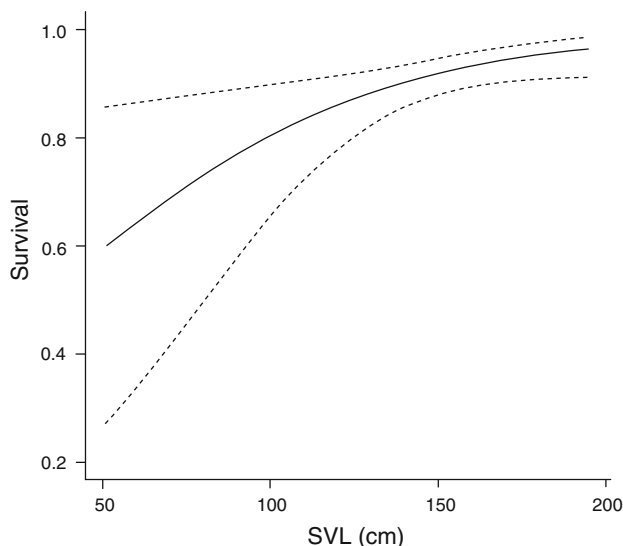
Fig. 3 Relationship between 3-month model-averaged apparent survival rates and body size [snout-vent length (SVL)] for *Drymarchon couperi*, 1999–2009 in Georgia based on modeled estimates of parameters for models that included body size as a covariate

lands $= 0.908 \pm 0.018$), the site-specificity of survival was not supported by data [Appendix I in Electronic Supplementary Material (ESM)]. Additionally, although estimated survival during low rainfall years was slightly higher than in other years, evidence for this effect was also weak (3 month $\phi_{dry} = 0.946 \pm 0.019$, $\phi_{other} = 0.910 \pm 0.012$; Appendix I in ESM).

Based on multistate CMR analysis, probability of apparent annual survival was 0.738 ± 0.030 for adults and 0.515 ± 0.189 for subadults. Estimated transition probability from subadult to adult stage was 0.818 ± 0.156 for the 3-month sampling period and 0.998 ± 0.002 annually.

Estimation of population growth rate and sensitivity to demographic parameters

Population growth rate was 1.031 based on parameter values presented in Table 1. The estimates of growth rate varied considerably depending on values of demographic parameters used. Elasticity matrix suggested that λ was proportionally most sensitive to changes in adult survival (elasticity 0.402) followed by that in first year survival (0.220). Elasticity analysis involving lower-level parameters also indicated that λ was proportionately most sensitive to changes in adult survival (0.559) followed by that in subadult survival (0.221; Fig. 4). We also examined elasticities over the range of values of demographic parameters presented in Table 1. We found that regardless of magnitude, reductions in all parameter values resulted in increased importance of adult survival to λ. Contrary to this, increases in parameter values resulted in increased

elasticity values for first year and subadult survival as well as for reproductive parameters.

We found $\lambda = 0.956$ when $\psi_2 = 0.50$, a likely estimate of ψ_2 if individuals stayed in stage two for 2 years on average. Lambda was <1.0 when ψ_2 was less than approximately 0.75, regardless of the parameter value within the range considered (Fig. 5). At values of hatching and juvenile survival <0.4, increases in survival rates had greater effect on λ, especially when $\psi_2 > 0.8$ (Fig. 5a, b). Changes in subadult and adult survival rates compared to changes to ψ_2 showed little effect on λ (Fig. 5c, d). Simulated reductions in ψ_2 led to a reduction in lower-level elasticity of λ to both hatchling and juvenile survival and reproductive parameters contrasted with increases in elasticities of adult and subadult survival (Fig. 4).

Uncertainty in hatchling, juvenile, and subadult survival compared to adult survival rates suggested $\lambda < 1.0$ with 3 month hatchling survival <0.40, 9 month juvenile survival <0.50, and annual subadult survival <0.45. Simulations also suggested that increasing hatchling, juvenile, or subadult survival rate by 0.10 increased λ by approximately 0.05 (Fig. 5).

Changes in estimated values of reproductive parameters also influenced λ. There was an approximate 0.05 change in λ with each unit (1 egg) change in clutch size. The smallest change in λ in relation to a reproductive parameter was seen with breeding probability. Changes in hatching and nest survival suggested an approximate 0.04 change in λ for each 0.10 change in either parameter, with $\lambda < 1$ when estimated parameter values were <0.5.

Discussion

Estimation of, and factors influencing, demographic parameters

Estimates of annual survival from this study (0.700 ± 0.030) were comparable to estimates from known fate analysis on a radiotelemetry study conducted at the same sites, which reported annual survival probability as 0.89 (± 0.074; $n = 25$ individuals) in 2003 and 0.72 (± 0.088; $n = 27$) in 2004 (Hyslop et al. 2009c). The CMR-based estimates reported here are slightly lower than those reported for the known fate telemetry study, at least in part, because CMR-based analyses cannot distinguish between mortality and permanent emigration (i.e., dispersal), which can negatively bias survival estimates. In a review of snake survival, Parker and Plummer (1987) reported annual survival of 0.70 for late-maturing temperate colubrids (5 species) and 0.77 for late-maturing temperate viperids (4 species).
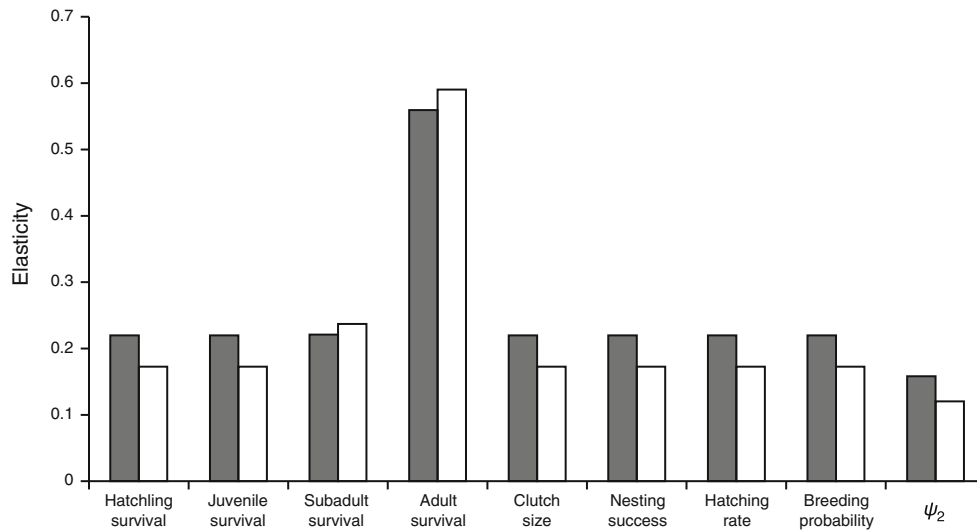
Fig. 4 Elasticity of λ to changes in lower-level vital rates for two values of ψ_2: $\psi_2 = 0.99$ (*filled*) and $\psi_2 = 0.50$ (*open*) for *Drymarchon couperi*. Parameter values are presented in Table 1

Fig. 5 Effects on asymptotic population growth rate (λ) from changes in transition probability from stage two to three (ψ_2) for *Drymarchon couperi* in relation to changes in hatchling (**a**), juvenile (**b**), subadult (**c**), and adult (**d**) survival. An *asterisk* indicates the estimated value of that parameter. All other parameters were held as presented in Table 1
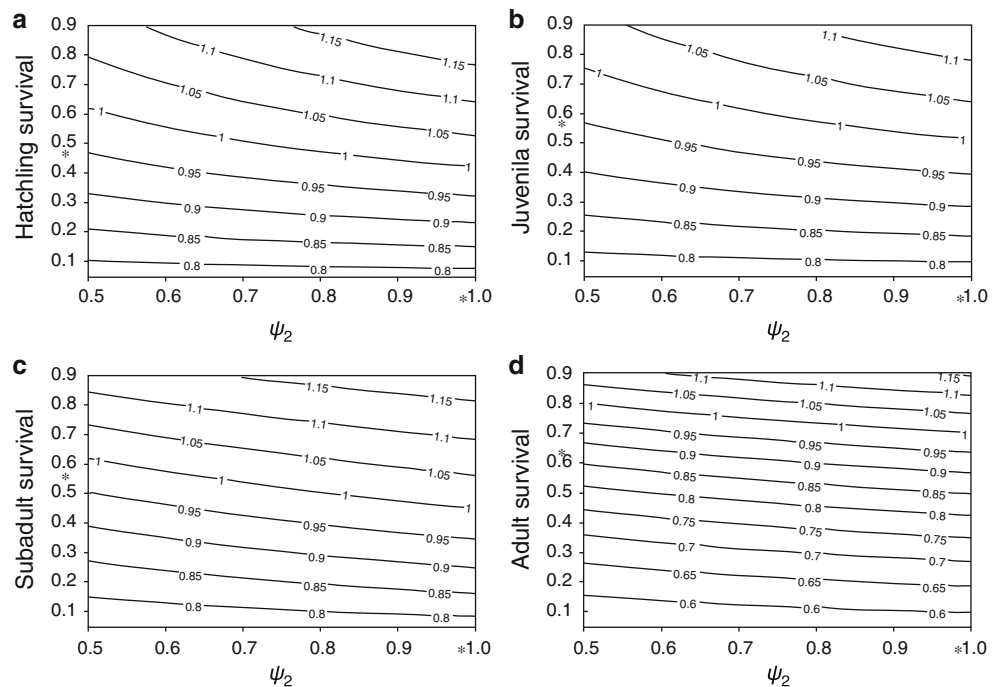
There was no evidence for sex-specific differences in survival given our data and model set; these findings are consistent with previously reported results (Hyslop et al. 2009c). We expected survival to be lower for females because of potentially higher costs associated with reproduction than found in males (Shine and Bonnet 2009). If reproductive factors are assumed to influence survival in females, as seen with some other snakes (Bonnet et al. 1999; Shine and Bonnet 2009), then these effects may have been obscured if reproductive costs were balanced because of greater movement distance, on average, of males (Hyslop 2007) which may decrease survival by increasing interactions with predators, humans, and roads (Bonnet et al. 1999). We also found no evidence for temporal variation in survival or capture probability as indicated by no evidence for the effect of year. This result is likely due in part to sample size limitations resulting in lack of estimability of all parameters in time-dependent models.

Larger adult *D. couperi* likely have fewer potential predators than smaller individuals; thus, body size may be expected to positively influence survival. Consistent with this expectation, we found that body size positively

influenced survival, regardless of sex (model 1; Table 2). This pattern has also been found with other snake species (Jayne and Bennett 1990; Blouin-Demers et al. 2002). However, patterns of influence of body size on survival in snakes are not well established and have been found to favor larger or smaller individuals depending on the species and environmental conditions (Forsman 1993; Hyslop et al. 2009c). Previous results (Hyslop et al. 2009c) suggested negative effect of size, standardized by sex, as the strongest predictor of adult *D. couperi* survival, indicating that larger snakes within each sex were more susceptible to mortality than smaller ones. Contrary to this, results from the current study suggest that body size, standardized by sex or not, positively affected survival. A potential explanation for this discrepancy may relate to sample size limitations of the telemetry study, as suggested in Hyslop et al. (2009c).

Modeling results indicated a seasonal shift in capture probability that differentially affected sexes, suggesting lower capture probability for females in fall and males in winter (see Stevenson et al. 2009), a pattern likely affected by intersexual differences in behaviors. In fall, male *D. couperi* have been found to move more frequently and further than females (Hyslop 2007), thus making them potentially more available for capture. In winter, females had slightly higher movement frequency than males and exhibited the greatest difference in use of underground shelters between males and females of any season (Hyslop 2007), with females using underground shelters less compared to males; thus, females may have been more available for capture during winter.

Estimation of adult apparent survival from multistate models was comparable to overall survival estimates from CJS models. Survival estimates of subadults were lower than that of adults. The probability of transition from subadult to adult stage was close to 1 and likely reflected the relatively high percentage of larger subadults in our sample. State specific survival estimates for *D. couperi* have not been reported before and thus these estimates represent the first report of subadult survival in the species. However, the accuracy of our estimates is limited by the relatively small sample size and recapture rate.

An additional potential problem in our analyses included violation of the CMR assumption of instantaneous sampling periods with no mortality. Because of the sparseness of the data, we used 3-month periods as the sampling occasion (O'Brien et al. 2005). Another potential bias prompted by the low sample size involved assuming equal survival for fall and winter within a sampling year when years were compared. Although we do not have data on permanent emigration in this population, CMR and telemetry data indicate only four instances of a snake originally caught during fall/winter breeding in one area being caught in another area >2 km away, including one adult male snake that moved 22 km (Stevenson and Hyslop 2010). Thus, the frequency of dispersal in adult snakes may be limited in this population. Despite these potential limitations, we believe the estimates of overall as well as state-specific survival reported in this study are reasonable and representative of *D. couperi* at our study sites.

Estimation of population growth rate and sensitivity to demographic parameters

Population growth rate ranged between approximately 0.96 and 1.03, depending on the value of ψ_2 assumed. We used a range of values for ψ_2 because of the known directional bias, although of unknown magnitude, in this parameter. Overall, λ was proportionally more sensitive to changes in survival rates, especially of adults, than other parameters, a pattern that held for all combinations of demographic parameters used. Increases in parameter values, however, resulted in higher elasticities for first year and subadult survival as well as reproductive parameters. These patterns of elasticities were expected as population growth rates of long-lived species tend to be more sensitive to changes in adult survival (Oli and Dobson 2003).

There are few reports of population growth rates in snakes (Webb et al. 2002; Altwegg et al. 2005) and fewer still for species native to North America (Whiting et al. 2008). Studies investigating population ecology of a Viperid (Altwegg et al. 2005) and a long-lived Elapid (average generation time of 10.4 years) (Webb et al. 2002) also found λ to be more sensitive to changes in adult survival rates, but this pattern did not hold for a shorter-lived Elapid (average generation time of 5.9 years) also studied (Webb et al. 2002).

Data on population ecology of snakes are limited (Parker and Plummer 1987; Whiting et al. 1997), and our data likewise were less than ideal which may have influenced results of our matrix model analysis. Uncertainty in estimates of λ may arise from uncertainty in adult and subadult survival estimates, which included death and permanent emigration but not immigration, potentially biasing the estimates low. In a review of studies reporting first year survival of early-maturing North American snakes, Whiting et al. (2008) estimated average annual survival at 0.24. *Drymarchon couperi* is considered a late-maturing colubrid (Stevenson et al. 2009); however, our estimates of first year survival of approximately 0.29 is similar to that estimated for early-maturing colubrids in their first year. This may suggest that our estimate for first year survival is low, especially since it is based on limited data, or that survival differences in late and early maturing colubrids are not as pronounced as seen in adults ($\overline{x}_{\text{late-maturing adult}} = 0.703$; $\overline{x}_{\text{early-maturing adult}} = 0.493$; Parker and Plummer 1987).

Regarding degree of certainly in our estimates of reproductive parameters, we had relatively high confidence in our estimate of clutch size because it was largely generated from reports of females that were wild-caught as gravid to lay eggs in captivity. Our estimate of nest and hatching success had the least support from empirical field data and information from captive programs could not be reliably used because of a lack of correlation to natural conditions. Unfortunately, it is unclear how hatching rates reported for captive breeding efforts relate to those in the wild. If captive conditions reflect ideal natural conditions, then captive hatching success may reflect an upper most value for this parameter; however, differences in breeding programs may result in lower hatching success than the range of values found naturally. Uncertainties in values of some demographic parameters could have potentially influenced estimates of population growth rate and elasticities. Thus, our results of matrix model analyses should be interpreted with caution.

Future monitoring efforts should be designed to improve estimates of hatchling, juvenile, and subadult survival, to which λ was proportionally most sensitive, as well as more robust estimates of ψ_2. In addition, future modeling efforts may consider up to five life history stages, including hatchling, juvenile, subadult, adult, and larger adults. There is some evidence that larger adult females may have greater reproductive output in terms of number of eggs laid per clutch (Smith 1987; J. Godwin, personal communication). It is also important to focus future efforts on generating field-based estimates of reproductive parameters, especially given the lack of data from natural populations regarding these parameters.

Conservation implications

Estimation of demographic parameters such as survival rates in free-ranging animal populations can aid in decisions regarding allocation of resources by informing large-scale modeling efforts such as population viability analysis and extinction threshold modeling (e.g., Fahrig 2001; Breininger et al. 2004; Rhodes et al. 2008). The results of the analyses presented here are an important first step. However, because of uncertainty regarding many of the estimated parameters in the matrix population model, our results should be interpreted with caution. Nonetheless, the results of sensitivity and uncertainty analyses to identify parameters that have the largest effect on λ should help future conservation and research efforts.

The growth rate of our study population was proportionately most sensitive to changes in adult survival which is likely influenced by over-wintering habitat (xeric sandhills with tortoise burrows) and also to a significant extent by adjacent habitats, particularly lowland and wetland habitats which snakes have been found to use extensively in warmer months, especially for foraging (Hyslop 2007). Fort Stewart and many adjacent private lands may represent relatively ideal conditions for *D. couperi* because of the paucity of paved roads, extremely large area, the presence of high-quality, fire-managed longleaf pine–wiregrass habitats that support sizeable tortoise populations, and extensive wetland habitats interspersed with sandhill uplands. Therefore, estimates of demographic parameters from the Fort Stewart and private lands population may be particularly valuable as a benchmark with which to compare estimates from other populations.

Estimates of population growth rate and elasticity of growth rates to demographic variable are important for conservation and management decisions (Caswell 2001; Williams et al. 2002; Stahl and Oli 2006), but these were not previously available for *D. couperi*. Our results indicated survival of adult snakes as the most influential on λ. Although not unexpected for a long-lived species, this result has important conservation implications regarding the allocation of resources for the protection of adults and transitioning subadults in a population. As discussed in Stevenson et al. (2009) and Hyslop (2007), this might be best accomplished by continuance or adoption of upland restoration and management focused on fostering open-canopied habitat supporting *G. polyphemus* populations and maintaining connectivity between these sites and adjacent wetland habitats (Hyslop et al. 2009a).

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