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SURVIVAL OF RADIO-IMPLANTED *DRYMARCHON COUPERI* (EASTERN INDIGO SNAKE) IN RELATION TO BODY SIZE AND SEX

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Abstract: *Drymarchon couperi* (eastern indigo snake) has experienced population declines across its range primarily as a result of extensive habitat loss, fragmentation, and degradation. Conservation efforts for *D. couperi* have been hindered, in part, because of informational gaps regarding the species, including a lack of data on population ecology and estimates of demographic parameters such as survival. We conducted a 2-year radiotelemetry study of *D. couperi* on Fort Stewart Military Reservation and adjacent private lands located in southeastern Georgia to assess individual characteristics associated with probability of survival. We used known-fate modeling to estimate survival, and an information-theoretic approach, based on a priori hypotheses, to examine intraspecific differences in survival probabilities relative to individual covariates (sex, size, size standardized by sex, and overwintering location). Annual survival in 2003 and 2004 was 0.89 (95% CI = 0.73–0.97, n = 25) and 0.72 (95% CI = 0.52–0.86; n = 27), respectively. Results indicated that body size, standardized by sex, was the most important covariate determining survival of adult *D. couperi*, suggesting lower survival for larger individuals within each sex. We are uncertain of the mechanisms underlying this result, but possibilities may include greater resource needs for larger individuals within each sex, necessitating larger or more frequent movements, or a population with older individuals. Our results may also have been influenced by analysis limitations because of sample size, other sources of individual variation, or environmental conditions.

Key words: Drymarchon couperi; Eastern Indigo Snake; Georgia; Mortality; Radio-implanted; Radiotelemetry; Sex; Size; Survival

Estimates of survival for wildlife populations are essential to our understanding of population dynamics and for conservation efforts drawing from the results of population modeling (Williams et al., 2002). For some species, factors that influence survival are not well understood, thus limiting application of these estimates to conservation efforts (Martin, 1995). These deficiencies in our understanding of survival are particularly evident for many snake species (Parker and Plummer, 1987), for which the ability to locate and recapture individuals for survival analysis is often hindered by the cryptic nature and long periods of inactivity characteristic of many species. In addition, many snake species occur at naturally or artificially low densities, which can further inhibit the ability to estimate demographic parameters accurately (Parker and Plummer, 1987).

Drymarchon couperi (eastern indigo snake), a federally threatened species of the southeastern coastal plain of the United States (United States Fish and Wildlife Service, 1978), is illustrative of a species that is difficult to survey (Hyslop et al., 2009; Stevenson et al., 2003) and largely lacks data related to population ecology, including estimates of demographic parameters such as survival. Population declines at the time of federal listing were caused primarily by commercial collection coupled with extensive habitat loss (USFWS, 1978). Federal protection largely curtailed commercial take, presumably reducing its impact on natural populations (Lawler, 1977). However, habitat loss, fragmentation, and degradation remain primary threats to *D. couperi* populations (USFWS, 1978, 1999), with additional sources of mortality including highway fatalities, wanton killings, pesticide and other chemical exposure, and illegal take (Lawler, 1977; USFWS, 1978).

Upland habitats in the southeastern coastal plain were primarily dominated by longleaf pine (*Pinus palustris*) and wiregrass (*Aristida*

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stricta) communities prior to European settlement; however, because of development and other land uses, less than two percent of these forests remain (Landers et al., 1995). In the northern portion of the range, in southern Georgia and northern Florida, the species is affiliated with these uplands and associated *Gopherus polyphemus* (gopher tortoise) populations, where *D. couperi* uses tortoise burrows presumably for protection from environmental extremes and predation (Landers and Speake, 1980; Speake and McGlincy, 1981). Commensal use of tortoise burrows, and use of other underground shelters, is especially pronounced from late fall through early spring when both males and females are often located in upland habitats (Hyslop, 2007). In spring, males move from their overwintering upland habitats to other upland habitats and wetlands, whereas females remain in the overwintering uplands during gestation where they may be observed basking near *G. polyphemus* burrows (Hyslop, 2007). Breeding occurs from October through February in Georgia (Speake et al., 1987), with oviposition in late spring (Groves, 1960; Speake et al., 1987). *Drymarchon couperi* is a potentially long-lived species, with maximum reported captive longevity of 25 yr and 11 mo (Bowler, 1977; Shaw, 1959), although estimates from free-ranging individuals are lacking. In the winter in Georgia, *D. couperi* exhibit the smallest movement distances and frequency of the year, including extended periods of inactivity (Hyslop, 2007; Speake et al., 1978). In warmer months, movements are extensive for both sexes; however, on average males occupy home ranges approximately five times larger than those of females (Hyslop, 2007).

Methods commonly used to estimate probability of survival in snakes include mark-recapture and radiotelemetry. Mark-recapture studies of snakes often suffer from low recapture rates because of difficulties in reliably locating individuals, which can potentially influence survival estimates (Parker and Plummer, 1987; Turner, 1977). Radiotelemetry, although often more time intensive and expensive, allows for relatively consistent monitoring of individuals. This approach can improve survival estimates and ability to estimate influence of individual covariates on survival; however, sample size limitations and complications from radio implantation procedures may confound survival estimates from telemetry efforts (White and Garrott, 1990).

We initiated this study to estimate survival probabilities and to examine correlates of intraspecific survival for *D. couperi* radiolocated during 30 mo in Georgia. We estimated monthly and annual survival using known-fate modeling and examined effects of individual covariates on survival probabilities. We generated a priori hypotheses for influences of various factors on survival based on *D. couperi* natural history information and previous research on snake survival (Bronikowski and Arnold, 1999; Parker and Plummer, 1987). We predicted that intraspecific probability of survival would be related to body size, with larger individuals experiencing higher survival, regardless of sex, because of size and experience-related advantages. We also expected that survival would vary temporally, with lower probability of survival in late winter and early spring when snakes may be observed with lower mass and varying degrees of infection by a vesicular skin disease (N. L. Hyslop, personal observation; T. M. Norton, unpublished data). During the spring and summer, we predicted that survival would be lower for females than males because of increased energetic needs for reproduction and incubation. Alternatively, we expected survival to be lower for males because of their propensity to move over larger distances (Hyslop, 2007) and therefore be at greater risk from humans, predators, and other hazards, especially roads (Bonnet et al., 1999). These effects, however, may be obscured if males, being generally larger in size, retain higher survival. Habitat type and variation in land use may also influence survival because of differences in the spatial arrangement of resources needed for long-term survival.

Materials and Methods

Study Area

We conducted a radiotelemetry study of *D. couperi* on Fort Stewart Military Reservation and adjacent private lands located in the coastal plain of southeastern Georgia. Study sites at Fort Stewart, calculated by delineating a rectangle around all snake locations, covered approximately 8000 ha of its total 111,600 ha (Stevenson et al., 2003). Private lands adjacent to Fort Stewart were contiguous and covered approximately 6000 ha. Details of habitats and land use are available elsewhere for Fort Stewart (Hyslop et al., in press; Stevenson et al., 2003) and private land sites (Hyslop et al., in press).

Telemetry

We captured snakes by hand on xeric upland sandhill habitats with *G. polyphemus* populations (Stevenson et al., 2003) on Fort Stewart and private land during late fall to early spring, 2002–2004. We initially selected adult snakes for radio implantation as they were encountered, then more selectively based on sex and site of capture to ensure the study areas and sexes were represented as evenly as possible. We captured and implanted 20 snakes (7 female, 13 male) with transmitters from December 2002 to April 2003 and 12 additional snakes (6 female, 6 male) from October 2003 to March 2004. We used 16-g temperature-sensitive radiotransmitters from December 2002 to November 2003 ($n = 24$) (AI-2T, 36 mo, 15×37 mm; Holohil Systems, Ltd., Ontario, Canada), and 9-g transmitters from December 2003 to March 2004 ($n = 8$) (SI-2T, 18 mo, 11×33 mm), because of reduced battery life requirements in the second year of the study.

Implantation of radiotransmitters in snakes during winter may lead to increased mortality (Rudolph et al., 1998); however, in Georgia, late fall and winter searches near *G. polyphemus* burrows are one of the few methods available for locating *D. couperi* (Diemer and Speake, 1981; Stevenson et al., 2003). Therefore, we worked to develop surgical and care protocols that reduced risks to the animals from handling and implantation procedures. Prior to surgery, we acclimated snakes to higher temperatures for 1 to 2 days (21–27 C thermogradient). Implantation procedures followed Reinert and Cundall (1982), with minor modifications. Snakes were placed in a clear plastic tube, induced with isoflurane, and subsequently intubated with an uncuffed endotracheal tube. Snakes were maintained on isoflurane and manually ventilated throughout the procedure. Heart rate was monitored using an ultrasonic Doppler probe placed over the heart. A water-circulating heating pad was used to keep the snakes warm during the surgical procedure and during initial recovery. We prepared snakes for surgery using standard sterile techniques. Transmitters were gas sterilized and surgically implanted (by T. M. Norton) in the coelomic cavity, approximately two-thirds from the anterior. The antenna was threaded subcutaneously anterior to the transmitter using sterilized copper tubing, which was removed from the body through a small incision in the skin at the anterior end of the tube. The coelomic wall and muscle were not sutured, while the skin was closed using a simple interrupted suture pattern with 4.0 polydioxone monofilament absorbable suture material.

While anesthetized, individuals were also weighed, measured (snout–vent [SVL] and tail length), and sexed by cloacal probing. To assess the health status of each snake, a physical exam, complete blood count, and plasma biochemical panel were performed. Each snake received ceftazidime (Fortaz) at 20 mg/kg intramuscularly every 72 h for a minimum of 3 treatments to prevent secondary bacterial infections. Snakes were held individually, in large-snake enclosures, for 10–16 days post-operatively at elevated temperatures (21–27 C thermogradient) for recovery. We provided snakes an acclimation period of 1 to 2 days prior to release in cooler temperatures to reflect daytime conditions when captured (15–21 C thermogradient; Hyslop et al., 2009). We released snakes at their point of capture during late morning on days with forecasted maximum temperatures >15.5 C and overnight lows >4 C. Radiotelemetry began approximately 24 h after release. We located snakes 2 to 3 times per week by foot and vehicle using homing techniques (Mech, 1983). In spring 2004, we used ultrasound and/or radiographs on 9 of 10 females in the study at that time to assess reproductive condition.

Survival Analysis

We used known-fate modeling in program MARK v. 4.3 (White and Burnham, 1999) to estimate survival and its relationship to individual covariates for radio-implanted *D. couperi* (Kaplan and Meier, 1958; Pollock et al., 1989). Radiotelemetry data collection for home range estimation ended in December 2004; however, we continued to track snakes monthly through June 2005, which provided survival data from January 2003 to June 2005. We divided the data into 30, 1-month periods for analysis, retaining the individual as the sampling unit.

Candidate models tested for effect of time of year, sex, size, and over-wintering site on survival. Our global model, from which more specific hypotheses were derived, predicted that differences in survival were influenced by movement/habitat use patterns, sex, and size of individuals. We included four individual covariates in analysis: sex, overwintering site (Site; dummy variable coded for overwintering on private lands versus Fort Stewart), SVL at capture (Size), and SVL scaled by sex (Size, standardized). Because *D. couperi* exhibits male-biased sexual size dimorphism (Layne and Steiner, 1996; Stevenson et al., 2003), we standardized size by sex using residuals of size versus sex regression and used these residuals as a covariate in our survival models. Individual covariates were standardized and logit link functions were used for all models.

Home range size of *D. couperi* tracked in this study was related to size and sex (Hyslop, 2007); therefore, we did not include this measure as an individual covariate in survival modeling. We used an information-theoretic approach, Akaike's Information Criterion (Akaike, 1973), corrected for small sample sizes (AICc; Hurvich and Tsai, 1989), to assess candidate models and select the best approximating confidence set of models for inference (90% confidence set; Burnham and Anderson, 2002).

Results

Radiotelemetry

We obtained survival data for 32 snakes implanted with radiotransmitters. Male SVL averaged 158 cm (range 120–191); average weight at capture was 2.2 kg (range 0.7–4.3). Females averaged 138 cm SVL (range 110–156) and 1.5 kg (range 0.6–2.3). All females examined for reproductive condition in spring 2004 (n = 9) showed signs of initial egg formation (non-shelled eggs observed). Complications associated with transmitters were found in two implanted snakes. Both cases included the transmitter antenna protruding from the skin, leading to localized infections around the base of the antennae and transmitter. Transmitters were surgically removed in both snakes. One died later from infection (in captivity) and the other was released after a short recovery from surgery; both were removed from the study (censored) at time of recapture.

Of 20 snakes implanted December 2002–April 2003, we analytically censored 11 (6 female, 4 male) because of mortality (n = 8), transmitter complication (n = 2), and depleted transmitter battery (n = 1). We also censored 3 (1 female, 2 male) of 12 snakes implanted between October 2003–March 2004 because of mortality (n = 2) and unknown fate (n = 1). There was no correlation of health status at the time of transmitter implantation with subsequent mortality. Of 10 in-field mortalities recorded, eight were from the 20 snakes implanted in the first year with 16-g transmitters, one was from four snakes implanted in the second year with 16-g transmitters, and one was from the eight snakes implanted in the second year with the 9-g transmitter. Because only one snake with the 9-g transmitter died during the study, we could not include this factor in the survival models. Instead, we calculated the mean proportion of possible tracking days that snakes were tracked for the two transmitter types, with the individual retained as sampling unit. For 16-g transmitters, the average was 0.84 of potential tracking days (0.74–0.94, 95% CI); the 9-g transmitters average was 0.91 (0.73–1.0, 95% CI).

In one mortality case, a wide-ranging male was killed by a vehicle on an unpaved road. A female implanted in the first year was found dead on the surface <50 m from the overwintering site. Necropsy (T. M. Norton) revealed a vertebral fracture containing keratin (skin) fragments and further analysis suggested this snake likely died from a penetrating wound, consistent with puncture from a talon. Three individuals died within a

TABLE 1.—Date of capture, sex, size, mass (at capture), and radiotelemetry details for mortalities of *Drymarchon couperi* radiolocated 2003–2005, Georgia. Status refers to details of death, if known, or state of remains found. Individuals found on the surface with unknown cause of death were partially coiled near underground shelters they had recently been using, with no apparent signs of external trauma. Both snakes presumed underground with unknown cause of death were in *Gopherus polyphemus* burrows.

Capture date	Sex	SVL (cm)	Total length (cm)	Mass (kg)	Site[1]	Days monitored	Removed from study	Status
9 Jan 2003	F	151	177	1.94	FS	628	28 Sep 2004	Unknown, on surface
21 Jan 2003	F	142	168	1.54	FS	402	27 Feb 2004	Wound, talon
2 Feb 2003	F	146	173	1.64	FS	508	24 Jun 2004	Wound, unknown
24 Feb 2003	M	191	226	4.26	FS	202	14 Sep 2003	Transmitter only
25 Feb 2003	F	124	150	1.20	FS	355	15 Feb 2004	Unknown, underground
26 Feb 2003	M	152	182	1.60	PL	795	1 May 2005	Unknown, on surface
9 Mar 2003	M	178	210	2.78	PL	222	17 Oct 2003	Vehicle impact
11 Apr 2003	F	152	181	1.90	PL	375	20 Apr 2004	Unknown, on surface
16 Nov 2003	M	182	217	3.58	FS	105	29 Feb 2004	Unknown, underground
28 Nov 2003	F	145	175	1.70	PL	108	15 Mar 2004	Transmitter only

[1] Fort Stewart (FS) or private lands (PL).

12-day period in February 2004. Two were presumed dead in *G. polyphemus* burrows and the other was found dead coiled on the surface with no observable external trauma. Of all mortalities recorded, 3 occurred in winter, 3 in spring, 2 in summer, and 2 in fall (Table 1).

Survival Analysis

The model-averaged estimate of monthly survival (95% CI) for snakes tracked January 2003–June 2005 was 0.98 (0.97–1.00). Annual survival probability was 0.89 (0.74–0.97, n = 25) in 2003 and 0.72 (0.52–0.86; n = 27) in 2004. The model-averaged estimate of probability of survival for radio-implanted snakes was 0.61 (0.40–0.82) from January 2003 to June 2005. Only one candidate model was included in the 90% model confidence set evaluating survival probabilities (Table 2). This model (weight ω_i = 0.44) included size as standardized by sex. Survival model-averaged parameter estimates indicated a strong negative relationship of size standardized by sex, suggesting lower probability of survival with increasing size within each sex. No other variables had predictive power (Table 3). We failed to detect a predictive relationship for time of year on survival; all models that included time or changes with time had little or no support (Table 2).

DISCUSSION

Mean annual survival rates in this study were similar to those previously reported for late-maturing, temperate snakes. In a review

TABLE 2.—Evaluation of candidate models for differences in annual survival of radio-implanted *Drymarchon couperi*, January 2003–June 2005, Georgia. Size (standardized) was the only model that fit within 90% confidence set. All models included an intercept term.

Model[1]	K	AICc	ΔAICc	ω_i	Model likelihood
Size (standardized)	2	98.79	0.000	0.436	1.000
Size (standardized), Site	3	100.61	1.817	0.175	0.402
Sex	2	101.31	2.516	0.124	0.284
Intercept	1	101.56	2.765	0.109	0.250
Size	2	102.53	3.739	0.067	0.154
Sex, Site	3	103.27	4.477	0.046	0.106
Site	2	103.56	4.764	0.040	0.092
Sex (time)	29	133.90	36.60	0.000	0.000
Time	30	137.69	38.90	0.000	0.000
Site (time)	28	138.38	39.59	0.000	0.000
Size (standardized; time)	30	140.15	41.35	0.000	0.000

[1] Model parameters: Sex (female), Size (snout-vent length), Site (on private lands), Size (standardized; snout-vent length standardized by sex).

TABLE 3.—Importance of size (standardized by sex) on probability of survival for radio-implanted *Drymarchon couperi*, January 2003–June 2005, Georgia. Values are model-averaged parameter estimates, unconditional standard errors, and confidence intervals for individual covariate effects on annual survival.

		95% Confidence interval	
Parameter[1]	Beta	Lower	Upper
Intercept	3.835	1.860	5.811
Size (standardized)	−0.880	−1.721	−0.038
Site	0.148	−0.372	0.667
Sex	−0.070	−0.448	0.317
Size	−0.030	−0.292	0.238

[1] Model parameters: Sex (female), Size (snout-vent length), Site (on private lands), Size (standardized; snout-vent length standardized by sex).

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).

Our results suggested a 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. This result was unexpected because patterns found in other studies of snake survival generally suggest that larger adults have a higher survival probability than smaller adults (Blouin-Demers et al., 2002; Jayne and Bennett, 1990). However, similar patterns of survival have been found in marine iguanas (*Amblyrhynchus cristatus*), where survival was highest for intermediate-sized individuals and lowest for sub-adults and largest-sized individuals (Laurie and Brown, 1990). Our results may be attributable to several factors including resource needs or age of larger individuals; however, we cannot comment on sub-adult survival; exclude potential influences of sample size on our modeling results; or that other factors, such as additional individual variation, environmental conditions, and effects of transmitters (Weatherhead and Blouin-Demers, 2004) may also have influenced adult *D. couperi* survival.

Modeling of individual covariates affecting home range size (Hyslop, 2007) and survival in the population we studied produced contrasting results. Home range size was influenced most by sex. Males maintained larger home ranges than females, regardless of their body size, indicating a biological difference influencing home range size between males and females, potentially influenced by selection of mates or searching for resources (Hyslop, 2007). We expected survival probability to decrease with increasing movements because of the potential for increased interactions with predators and humans; however, home range modeling indicated that larger individuals within each sex did not show larger movements (Hyslop, 2007).

Although there is a lack of evidence relating larger home ranges to larger individuals within each sex (Hyslop, 2007), larger, more frequent movements may have important survival implications for *D. couperi* populations in more fragmented habitat. For example, our study sites lacked paved roads within areas used by snakes; however, road mortality in areas with higher densities of paved roads can reduce survival rates (Andrews and Gibbons, 2005; Bonnet et al., 1999; Rudolph and Burgdorf, 1997). We incidentally observed four *D. couperi*, not in our radiotelemetry study, killed by vehicles on paved roads surrounding our study sites in addition to the radio-implanted snake killed at the site by a vehicle on an unpaved road. In a recent telemetry study in central Florida, vehicles caused approximately 40% of in-field mortality (R. Bolt, Dynamac Corporation, Kennedy Space Center, Florida, personal communication). Therefore, our survival results may not represent typical relationships observed between movement and survival because of high overall habitat quality and lack of paved roads at our study site.

We found disproportionately higher mortality in female snakes, given the sex ratio of tracked snakes (13 female: 19 male); however, modeling did not indicate an effect of sex on survival. Nine of ten females examined in spring 2004 had eggs in early stages of development, suggesting that annual reproduction in *D. couperi* may occur. Speake et al. (1987) reported that all but one of 21 female *D. couperi* captured during 10 consecutive springs was gravid. Physiological stresses, related to gestation and migration to reach appropriate egg-laying habitats, have been implicated with higher female mortality (Parker and Plummer, 1987). However, females radiotracked in Georgia did not make larger than average movements prior to late spring; instead they primarily remained on sandhill habitats where they overwintered (Hyslop, 2007).

An assumption of survival analysis is that capture and radio-implantation procedures do not influence survival of the individual (Winterstein et al., 2001). To address this concern, we only implanted adult snakes, monitored snake health throughout the study, and used the smallest transmitters possible, given battery-life requirements. No radio-tracked snake perished within three months of surgery, suggesting that capture, surgery, and transmitters did not have immediate negative effects on survival. There was no difference between proportions of potential days tracked for those individuals with the 16-g versus the 9-g transmitters; however, the small sample size limits conclusions regarding the effect of transmitters on survival. Smaller individuals within each sex, however, had higher survival probabilities, leaving the possibility that transmitter size was not a major contributing factor in mortality in this study.

Survival in natural environments may fluctuate annually in snakes, as may the relationship between body size and survival (Forsman, 1993). Our annual survival rates did not differ between years; however, temporal data are insufficient to conclude that survival rates are stable in the population we studied. Results suggesting lower survival with larger individuals within each sex may be indicative of a population in which some individuals survive long enough to senesce or succumb to factors experienced at larger sizes. Our results may be representative of survival probabilities in relatively intact habitat and present a direction for future studies focusing on sources of mortality in wild *D. couperi* populations in less ideal habitats.

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