

THE EFFECT OF BODY SIZE ON COTTONMOUTH (*AGKISTRODON PISCIVORUS*) SURVIVAL, RECAPTURE PROBABILITY, AND BEHAVIOR IN AN ALABAMA SWAMP

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Abstract.—In an effort to improve knowledge of Cottonmouth (*Agkistrodon piscivorus*) life history and behavior, we conducted a capture-mark-recapture study in Tuskegee National Forest, Alabama over four years to examine the influence of body size on survival, recapture probabilities, and behavior; as well as monitor change in the population's body-size distribution over time. Our estimate of annual Cottonmouth survival (0.79) is among the highest reported for all snakes. Although we did not detect an effect of body size on survival, the probability of recapturing individuals increased with body size up to a snout-vent-length of 82 cm, after which it remained approximately constant. Relative to large snakes, small snakes were more likely to be found in a resting coil and less likely to move away from researchers, suggesting that our lower probability of recapturing small snakes was not due to behavioral avoidance of researchers but perhaps dispersal patterns or microhabitat use. Furthermore, the observed frequency of snakes ≤ 30 cm in length increased each year, indicative of an increase in recruitment over time. Our findings provide new information about Cottonmouth life history, and we suggest future paths of research that could further enhance knowledge of Cottonmouth demography and population dynamics.

Key Words.—*Agkistrodon piscivorus*; behavior; capture-mark-recapture; Cottonmouth; life history; survival; snake

INTRODUCTION

Life-history traits of animals with indeterminate growth, like snakes, often vary with body size, which closely correlates with age (Blueweiss et al. 1978; Dunham and Miles 1985). For example, small and immature snakes typically spend more time foraging, which subjects them to greater predation risk and possibly lower survivorship (e.g., Shine 1996; Bronikowski and Arnold 1999; Webb et al. 2003). Determining how body size affects survival provides insight into life-history evolution (Stearns 1992) and can improve models used for population viability and ecological risk assessment (Burgman et al. 1993). Thus, conservation efforts require accurate estimates of survivorship, and relationships between survival and factors like body size (Bury 2006; McCallum and McCallum 2006).

Most biologists use 'return rates' to estimate snake survival (see citations within Shine and Charnov 1992; Shine and Schwartzkopf 1992). Estimates of survival based on return rates introduce bias because they confound the probability of survival with the probability of recapturing live individuals (Martin et al. 1995). To alleviate this bias, recent studies have used capture-mark-recapture methods to estimate probabilities of snake survival conditional on simultaneous estimates of recapture probability (e.g., Forsman 1993; Flatt et al. 1997; Diller and Wallace 2002; Stanford and King 2004; Lind et al. 2005). Many view the recapture probability as a nuisance parameter that is necessary for attaining accurate estimates of survival. However, it can provide important insight into biologically meaningful parameters (e.g., Viallefont et al. 1995; Dufour and Clark 2002). For example, size-related recapture probability could reflect whether body size is related to age-based emigration from the study area, a behavioral



FIGURE 1. Cottonmouth (*Agkistrodon piscivorus*) from Macon County, Alabama, USA. (Photographed by Roger Birkhead).

response to humans, or both (Lourdais et al. 2002; Rodda et al. 2002). To disentangle these potential drivers of size-related recapture probabilities, observations of behavior immediately before capture can be used to isolate size-related behavioral responses of snakes to humans. In addition, these sorts of observations can provide useful information about the behavioral ecology of snakes (e.g., Shine et al. 2002; Roth and Johnson 2004).

Body size is also highly correlated with life-history traits such as fecundity, and because of this, changes in the distribution of body-size classes in a population can have important effects on population dynamics that are often overlooked (Caswell 2001). Relative to a population in its stable size distribution, a sudden shift towards small individuals that display low fecundity and survivorship will depress short-term rates of population growth. In comparison, a population skewed toward large individuals with high fecundity and survival will exhibit a much higher rate of population growth (Koons et al. 2005). Thus, to develop population models for guiding conservation and management, ecologists need to estimate the effect of body size on demographic parameters, as well as changes in the population's distribution of body size over time.

Several long-term studies on the semi-aquatic Cottonmouth (*Agkistrodon piscivorus*; Fig. 1) exist (Burkett 1966; Wharton 1966; Blem and Blem 1995; Ford 2002; Roth and Johnson 2004), but none account for recapture probabilities. Consequently, we cannot

assess the reliability of existing survival estimates. Our objectives here are to utilize a 4-year capture-mark-recapture study of Eastern Cottonmouths (*A. p. piscivorus*) to: (1) provide the first maximum-likelihood estimates of Cottonmouth survival conditional on recapture probability; (2) examine the influence of body size on survival and recapture probabilities; (3) examine snake behavior in relation to body size; and (4) describe the distribution of body size in our population over time.

MATERIALS AND METHODS

Study site.—In May of 2001, we initiated a capture-mark-recapture study of Cottonmouths at a beaver swamp in Tuskegee National Forest (TNF), Macon County, Alabama, USA (32° 29' 19" N, 85° 35' 39" W). This location is within the zone of potential intergradation of all three Cottonmouth subspecies (Eastern *A. p. piscivorus*, Florida *A. p. conanti*, and Western *A. p. leucostoma*; Conant and Collins 1991). The study site lies in the southeastern Coastal Plain of Alabama in a hydric area of regenerating mixed pine and hardwood forest. We focused on one intermittently active beaver swamp ~ 2 ha in size. Shallow areas had such dominant vegetation as Sugarcane Plume Grass (*Eriarthus giganteus*), Alder (*Alnus serrulata*), Red Maple (*Acer rubrum*), Camphor-Weed (*Pluchea camphorata*), Bur-Weed (*Sparganium americanum*), and Waterpod (*Hydrolea* sp.). Spatter-Dock (*Nuphar lutea*) and Pondweed (*Potamogeton* sp.) dominated the deeper areas.

Field methods.—From 2001 to 2004, we conducted capture-mark-recapture surveys approximately every two weeks during the most active period for snakes each year (nine sampling occasions in May – September 2001, 17 in March – August 2002, 17 in March – September 2003, and 14 in March – September 2004). Between 2–8 investigators conducted nocturnal surveys by walking/wading along parallel transects that followed the perimeter of the swamp. We alternated starting points for each sampling period. Furthermore, we defined the non-survey season as the period of time between the end of surveying in year t and the beginning of surveys in year $t + 1$.

Snakes were captured using Pilstrom-style tongs and placed in a transport device (Birkhead et al. 2004). After capture, we transported snakes to the Craig Guyer laboratory at Auburn University (< 15 km away), and housed them in a climate-controlled room until processing the following morning. In the lab, we recorded snout-vent length (SVL, nearest 1 mm), tail length (nearest 1 mm), mass (nearest 1 g), sex, and several other variables for use in other studies. We measured length and mass by aligning the snake along a

TABLE 1. A list of hypothesized models for weekly survival (ϕ) and recapture probabilities (ρ) for Cottonmouths (*Agistrodon piscivorus*) at Tuskegee National Forest, Alabama as a function of snout-vent-length (SVL), a quadratic model of snout-vent-length (SVL-Q), year, season (see Materials and Methods for definitions), sex, and the (null) hypothesis that weekly survival, recapture probability, or both were constant across all time periods and all individuals. Based on Akaike's Information Criterion (AIC_c) and Akaike weight (ω_m), the best approximating model is denoted in bold. The symbol Δ_m is the difference between AIC_c of model m and that of the top-ranking model. Akaike weight is the likelihood of model m given the data, relative to other hypothesized models (Akaike weights sum to 1), and K is the number of parameters in the model. The Global model contained the effects of year, season, sex, and a categorical body size variable for both weekly survival and recapture probability.

| Explanatory Variables | | | | | | |
|-----------------------|-------------|---------------------|----------------|-------------|-------------|----------|
| Model | ϕ | ρ | AIC_c | Δ_m | ω_m | K |
| 1 | Global | Global | 1699.07 | 17.07 | < 0.01 | 12 |
| 2 | null | null | 1728.00 | 46.00 | < 0.01 | 2 |
| 3 | null | season | 1728.24 | 46.24 | < 0.01 | 3 |
| 4 | null | year | 1707.61 | 25.62 | < 0.01 | 3 |
| 5 | null | sex | 1729.96 | 47.96 | < 0.01 | 3 |
| 6 | null | SVL | 1703.77 | 21.78 | < 0.01 | 3 |
| 7 | null | SVL-Q | 1697.72 | 15.72 | < 0.01 | 4 |
| 8 | null | SVL-Q + year | 1682.00 | 0.00 | 0.67 | 5 |
| 9 | season | null | 1730.02 | 48.02 | < 0.01 | 3 |
| 10 | year | null | 1729.84 | 47.85 | < 0.01 | 3 |
| 11 | sex | null | 1729.05 | 47.06 | < 0.01 | 3 |
| 12 | SVL | null | 1718.37 | 36.37 | < 0.01 | 3 |
| 13 | SVL-Q | null | 1716.96 | 34.96 | < 0.01 | 4 |
| 14 | SVL | SVL-Q + year | 1684.04 | 2.04 | 0.24 | 6 |
| 15 | SVL-Q | SVL-Q + year | 1685.96 | 3.97 | 0.09 | 7 |

fixed measuring tape and using a digital scale, respectively (Fisher-Scientific EMD 5000, Pittsburg, Pennsylvania, USA, 5000 g capacity). Sex was determined by probing for the presence of retracted hemipenes. To individually identify each snake, we injected a passive integrated transponder (PIT) tag subcutaneously approximately 5 cm anterior to the vent along the junction of the dorsal and ventral scales, and sealed the injection site with cyanoacrylate glue (Krazy Glue, Columbus, Ohio, USA). We also gave each snake a sub-caudal cohort scale-clip to indicate initial year of capture and to provide a tissue sample. Only one instance of PIT tag loss was observed in the first year of the study. In addition, we recaptured one individual approximately one month after initial implantation and the PIT tag was partially protruding from the injection site. Subsequent to this instance, we injected PIT tags toward the posterior, and never observed another tag loss throughout the remainder of the study. We returned all snakes to their point of capture < 24 h after capture.

Survival analysis.—To estimate survival and recapture probabilities for Cottonmouths on our study area, we used an extension of the Cormack-Jolly-Seber (CJS) estimator for populations open to migration (Cormack 1964; Jolly 1965; Seber 1965; Pollock et al. 1990). We used version 4.3 of program MARK to conduct the analysis (White and Burnham 1999). Unless otherwise stated, we defined survival probability (ϕ_i) as the probability that a snake alive in week i survived and did not permanently emigrate from the study area in

week $i + 1$. We defined recapture probability (ρ_i) as the probability of capturing a marked snake alive in week i that did not permanently emigrate in week i . We chose to estimate survival and recapture probabilities on a weekly time scale because our shortest intervals between sampling occasions were ~ 1 week. Although intervals between sampling were often > 1 week (see field methods), we scaled estimates of survival and recapture probabilities for longer time intervals to shorter periods of time by taking the x^{th} root of the relevant probability, where x is the number of weeks between sampling (x need not be a whole number). This allowed us to present results on a consistent, comparable time scale. (For a thorough explanation of capture-mark-recapture survival analysis see Lebreton et al. 1992; Williams et al. 2002; Mazerolle et al. 2007).

To address our objectives, we focused on estimating the effect of body size on Cottonmouth survival and recapture probabilities. We also accounted for possible temporal variation and sex differences in these probabilities to isolate the effect of body size. In previous analyses, we found that annual differences in weekly survival or recapture probability were best parameterized as different in 2001 relative to 2002–2004 (i.e., better than parameterizations allowing for differences in each of the four years, temporal trends among years, etc.). Furthermore, within-year differences in weekly survival or recapture probability were best captured by allowing a probability to differ between the survey and non-survey seasons (i.e., better than

TABLE 2. List of hypothesized models for Cottonmouth (*Agkistrodon piscivorus*) behavior immediately before capture at Tuskegee National Forest, Alabama, USA as a function of snout-vent-length (SVL), a quadratic model of snout-vent-length (SVL-Q), yearA (years treated as a continuous covariate), yearB (years treated as they were in the survival and recapture analysis [see Materials and Methods for definitions]), yearC (years treated as a factor), season (season treated as 2 categories), sex, and the (null) hypothesis that behavior was constant across all time periods and all individuals. Based on Akaike's Information Criterion (AIC_c) and Akaike weight (ω_m), the best approximating model is denoted in bold.

The symbol Δ_m is the difference between AIC_c of model m and that of the top-ranking model. Akaike weight is the likelihood of model m given the data, relative to other hypothesized models (Akaike weights sum to 1), and K is the number of parameters in the model.

| | Model | AIC_c | Δ_m | ω_m | K |
|----------|---------------|---------------|-------------|-------------|----------|
| 1 | null | 676.70 | 10.24 | 0.00 | 2 |
| 2 | SVL | 666.49 | 0.02 | 0.26 | 3 |
| 3 | yearA | 675.84 | 9.38 | 0.00 | 3 |
| 4 | yearB | 678.72 | 12.25 | 0.00 | 3 |
| 5 | yearC | 677.11 | 10.64 | 0.00 | 5 |
| 6 | season | 676.77 | 10.30 | 0.00 | 3 |
| 7 | sex | 676.82 | 10.35 | 0.00 | 3 |
| 8 | SVL-Q | 666.47 | 0.00 | 0.27 | 4 |
| 9 | SVL + yearA | 666.54 | 0.08 | 0.26 | 4 |
| 10 | SVL-Q + yearA | 667.05 | 0.59 | 0.20 | 5 |

parameterizations allowing for finer-scale differences during the survey seasons). We call these parameterizations of temporal variation in survival or recapture probability the 'year' and 'season' explanatory variables, respectively.

To determine whether our data met the assumptions of the CJS estimator, we first developed a 'global' model containing all main effects (year, season, sex, and a categorical variable for body size) for both weekly survival and recapture probability. We did not consider interaction terms because of our modest sample size of captures and recaptures ($n = 391$). We then used the parametric bootstrap routine ($n = 1000$ simulations) in program MARK to evaluate goodness-of-fit of the global model. As suggested by White et al. (2001), we used a categorical variable for body size in the global model because goodness-of-fit tests do not yet allow for continuous explanatory variables. With the resulting bootstrap output, we estimated the probability of observing a model deviance as great, or greater, than that observed for the global model. We then estimated the variance inflation factor (\hat{c}) as the quotient of the observed deviance for the global model and the mean deviance computed from the bootstrap simulations. When data are over-dispersed, \hat{c} is > 1 (Burnham and Anderson 1998).

Upon determining fit of the global model, we developed a suite of simpler models nested within the global model (Table 1). In this suite, we parameterized SVL as a continuously linear or quadratic (i.e., allowing curvature in relationships) explanatory variable to gain more detailed insight into the potential effects of body size on survival and recapture probabilities. To evaluate the statistical support for our candidate models containing different combinations of the explanatory variables for survival and recapture probability, we used Akaike's Information Criterion adjusted for sample size

(AIC_c) and Akaike weights (ω_m ; Akaike 1973). We considered the best approximating model to be that with the lowest AIC_c value and highest Akaike weight (for discussion on the application of AIC methods in Herpetology, see Mazerolle 2006).

We captured a moderately large number of individuals once and never recaptured them again ($n = 115$), indicating the possibility that some individuals may spend only a short amount of time on the study site en route to another location (i.e., transient). Because CJS survival represents the probability of surviving and not permanently emigrating, transient individuals in a dataset have an apparent survival probability of zero, which can lead to overall estimates of survival that are biased low for residents of a local population. Rather than subjectively discarding individuals with the previously mentioned capture histories from the data set, we parameterized survival during the interval immediately following first capture separately from subsequent intervals to isolate and control for a possible effect of transients on survival (Pradel et al. 1995; 1997; Sandercock 2006). We then tested for the importance of such an effect by incorporating this parameterization into our top-ranking model to see if it improved AIC_c by ≥ 2 units (Burnham and Anderson 1998).

In all models, we linked weekly survival and recapture probability to the linear model with explanatory variables using the logit-link function. Each coefficient $\hat{\beta}_j$ describes the relationship between an explanatory variable (e.g., SVL) and the response parameter of interest (e.g., survival) on the logit scale. We estimated $\hat{\beta}_j$ for individual-based explanatory variables using standardized data. The statistical precision of each $\hat{\beta}_j$ appearing in our top-ranking models was assessed

TABLE 3. List of hypothesized models for Cottonmouth (*Agistrodon piscivorus*) snout-vent-length (SVL; for captured individuals) at Tuskegee National Forest, Alabama, USA as a function of yearA (years treated as a continuous covariate), yearB (years treated as they were in the survival and recapture analysis [see Materials and Methods for definitions]), yearC (years treated as a factor), season (season treated as 2 categories), sex, and the (null) hypothesis that behavior was constant across all time periods and all individuals. Based on Akaike's Information Criterion (AIC_c) and Akaike weight (ω_m), the best approximating model is denoted in bold. The symbol Δ_m is the difference between AIC_c of model m and that of the top-ranking model. Akaike weight is the likelihood of model m given the data, relative to other hypothesized models (Akaike weights sum to 1), and K is the number of parameters in the model.

| | Model | AIC _c | Δ_m | ω_m | K |
|---|-----------------------------|------------------|-------------|-------------|----------|
| 1 | null | 58840.41 | 1717.49 | 0.00 | 1 |
| 2 | yearA | 57243.01 | 120.09 | 0.00 | 2 |
| 3 | yearB | 57947.46 | 824.54 | 0.00 | 2 |
| 4 | yearC | 57227.90 | 104.98 | 0.00 | 4 |
| 5 | season | 58758.88 | 1635.96 | 0.00 | 2 |
| 6 | sex | 58795.60 | 1672.68 | 0.00 | 2 |
| 7 | yearC + sex | 57126.15 | 3.23 | 0.17 | 5 |
| 8 | yearC + season | 57227.60 | 104.68 | 0.00 | 5 |
| 9 | yearC + sex + season | 57122.92 | 0.00 | 0.83 | 6 |

according to the degree to which 95% confidence intervals for each $\hat{\beta}_j$ overlapped zero (Graybill and Iyer 1994). For comparison with other studies, we computed annual survival probabilities by raising weekly survival probabilities to appropriate powers. Accordingly, we estimated the variance of annual survival using the delta method (Seber 1982).

Behavioral analysis.—Immediately before capture, we noted the behavior of each snake, which we classified into three categories: resting coil, outstretched, and moving. We believed that these behaviors could be treated on an ordinal scale in response to our presence, with ‘resting coil’ (i.e., a loose coil without any defensive displays such as gaping, vibrating tail, or strikes; Glaudas and Winne 2007) representing the least active response to our presence and ‘moving’ representing the most active response. Using these categories, we conducted an ordinal logistic regression (McCullagh 1980) using the Design package in R 2.5.0 (R Development Core Team 2007) to examine how body size, year, season, and sex were related to Cottonmouth behavior immediately before capture (see list of hypothesized models in Table 2). We classified ‘season’ into two categories: an early survey season that began when the first snake was encountered each year (mean start date: 23 March) and ended on 31 May (approximate median of survey dates), and a late survey season that began on 1 June and continued until the end of our research activities each year (mean end date: 12 September). We used the AIC methods described above to evaluate the amount of support in our data for each hypothesized model. To account for repeated measurements, we adjusted measures of variance, and then used 95% confidence intervals to assess the precision of estimated covariate effects on Cottonmouth behavior. To evaluate the predictive power of our best

approximating model, we used the area under the receiver-operating-characteristic (ROC) curve, which ranges from zero to one and measures the ability of a model to discriminate among events (here, behavioral categories) given the covariate values (Hosmer and Lemeshow 2000).

Distribution of body size.—In the analysis of body size, we retained one measure of SVL per individual per season (early and late survey seasons) per year. Multiple measurements on the few individuals that were recaptured within a season were always within 1 cm of each other, and thus we retained the first measurement. We used general linear models in R 2.5.0 (R Development Core Team 2007) and histograms to examine how the mean and distribution of body size varied across years, seasons, and sex categories in our marked sample. The AIC methods described above were used to evaluate the amount of support in our data for each hypothesized general linear model (see Table 3). To account for repeated measurements on individuals across seasons and years, we adjusted measures of variance, and then used 95% confidence intervals to assess the precision of estimated covariate effects on mean Cottonmouth body size.

RESULTS

Survival and recapture probabilities.—We encountered snakes during 51 of 55 visits to the swamp (414 total person-hours). Surveys in which no snakes were encountered all preceded the start of the survey period used in analyses. We averaged 3.6 observers per night (range: 2–8 observers). The earliest start time was 1958, the latest was 2204, and our average survey duration was 116 min (range: 73–209 min). From 2001 to 2004, we attained 391 observations (effective sample size) on 198 marked Cottonmouths for estimating

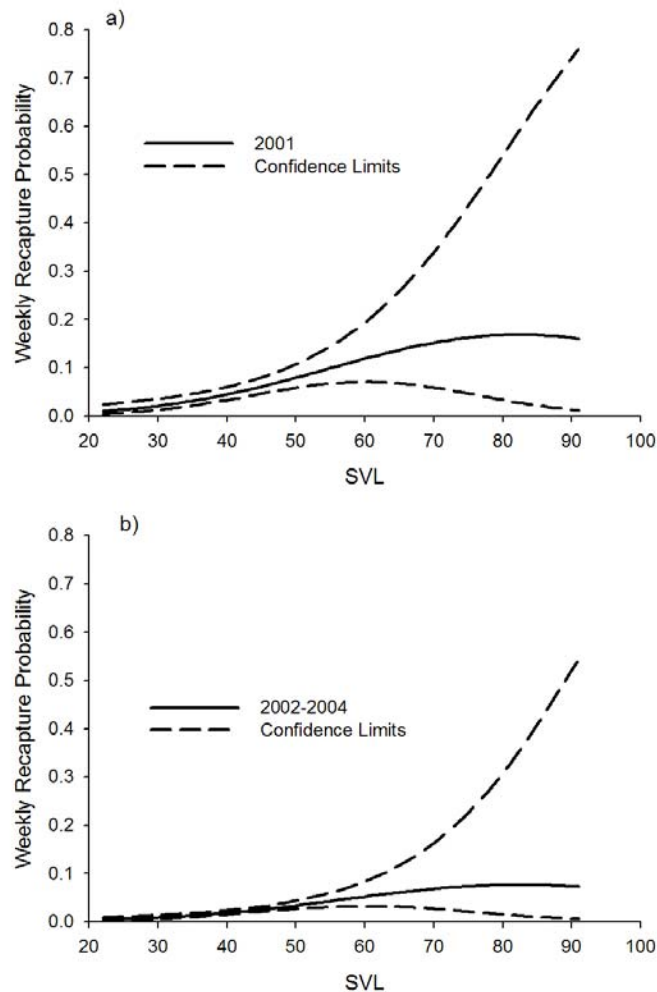


FIGURE 2. Weekly recapture probabilities for Cottonmouths (*Agkistrodon piscivorus*) at Tuskegee National Forest, Alabama, USA as a function of snout-vent-length (SVL, measured in cm) in a) 2001, and b) the years 2002 to 2004.

weekly survival and recapture probability. The global model fit the data ($P = 0.99$), and we found no evidence for extra-binomial variation ($\hat{c} = 0.82$).

Among our original list of hypothesized models (Table I), the best approximating model did not indicate any effect of year, season, sex, or body size on survival. However, it did indicate a curved increase in recapture probability with body size and that recapture probability was higher in 2001 than during 2002 to 2004 (Model 8). Adding a ‘transient effect’ to this model improved AIC_c by 4.22 units ($AIC_c = 1677.78$), indicating a strong effect of transient individuals on survival during the interval immediately following first capture. Further exploratory

analysis indicated an effect of SVL on survival during the interval immediately following first capture, but not thereafter ($AIC_c = 1669.22$, a further improvement of 8.56 units).

Basing inference upon the latter, best performing model, our estimate of survival for the first week following capture was 0.944 (95% CI: 0.858 to 0.980; evaluated at mean SVL) and the effect of body size was negative (for standardized SVL $\hat{\beta}_{\text{intercept}} = 2.83$, 95% CI: 1.80 to 3.87; $\hat{\beta}_{\text{SVL}} = -1.34$, 95% CI: -2.18 to -0.50). Survival during subsequent weeks was constant across the range of SVL and much higher (0.995, 95% CI:

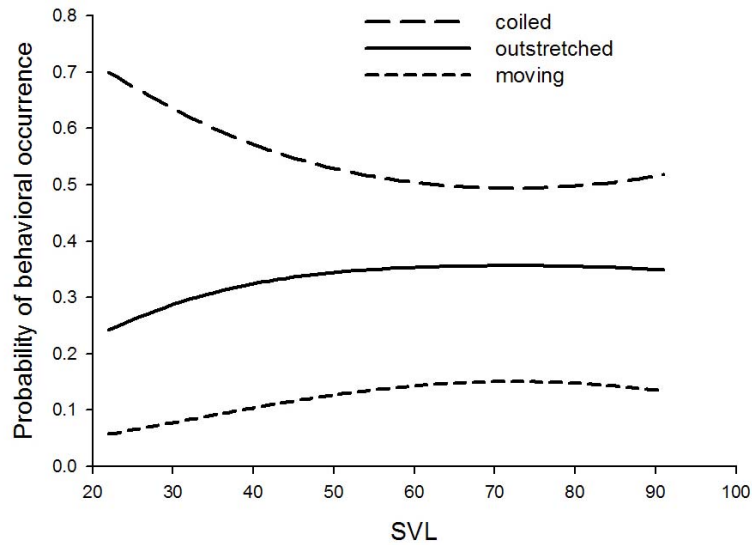


FIGURE 3. The probability of locating Cottonmouths in a resting coil, outstretched, or moving position immediately before capture at Tuskegee National Forest, Alabama in relation to snout-vent-length (SVL, measured in cm).

0.992 to 0.997). Because our data did not indicate an effect of season on weekly survival probability, we estimated annual survival for the resident population by raising weekly survival to the 52nd power (i.e., annual survival = weekly survival⁵² = 0.79, 95% CI: 0.69 to 0.88).

Weekly recapture probability was higher in 2001 than during 2002 to 2004, but in all years, recapture probability increased with body size up until SVL = 82 cm, after which it decreased slightly (Fig. 2). Wide confidence intervals for recapture probability at the larger end of the SVL range indicate that the latter decrease in recapture probability was imprecisely estimated (Fig. 2). Thus, recapture probabilities for snakes with SVL > 82 cm were likely similar to the maximum of 0.168 in 2001 and 0.077 during 2002 to 2004.

Cottonmouth behavior.—Based upon our top performing model of behavior, we found that the probability of locating a Cottonmouth in a resting coil before capture was generally higher than it being outstretched ($\hat{\beta}_{\text{intercept, outstretched}} = -2.68$, 95% CI: -2.82 to -2.54) or moving ($\hat{\beta}_{\text{intercept, moving}} = -4.40$, 95% CI: -4.53 to -4.25). Yet, the quadratic effect of body size on Cottonmouth behavior ($\hat{\beta}_{\text{SVL}} = 0.098$, 95% CI: 0.092 to 0.10; $\hat{\beta}_{\text{SVL}^2} = -0.00068$, 95% CI: -0.00073 to -0.00062; area under ROC curve = 0.58) indicated that the probability of a snake being in a resting coil decreased with body size, whereas the probabilities of a snake being outstretched or moving increased with body size

(Fig. 3). The year effects in models 9 and 10 (Table 2) indicated a slight decrease in outstretched and moving behavior over the course of the study (net change in probability ≈ 0.05) and a slight increase in resting coil behavior (change in probability ≈ 0.05), but these effects were imprecisely estimated (confidence intervals overlapped zero). As a result, models 9 and 10 received less support than more parsimonious ones containing only the effect of body size (Table 2).

Distribution of body size.—Across all captured individuals, mean SVL was 52.13 cm over the course of our study (SE = 1.03, range: 22.1 – 91 cm). Our best model of body size indicated that mean SVL varied among years, seasons, and sex categories (Table 3). Mean SVL of captured individuals consistently decreased across years ($\hat{\beta}_{\text{intercept}} = 57.97$, 95% CI: 57.73 to 58.21; $\hat{\beta}_{2002} = -1.40$, 95% CI: -1.56 to -1.24; $\hat{\beta}_{2003} = -3.71$, 95% CI: -3.90 to -3.51; $\hat{\beta}_{2004} = -5.80$, 95% CI: -6.02 to -5.59) because the distribution of SVL shifted toward a higher frequency of small individuals over time (Fig. 4). Similarly, because the sample of individuals captured during late survey seasons consisted of a slightly greater frequency of small individuals (≤ 30 cm) and lower frequency of large individuals (> 60 cm; Fig. 5), mean SVL was slightly lower in late survey seasons ($\hat{\beta}_{\text{late}} = -0.26$, 95% CI: -0.40 to -0.12) relative to early survey seasons. Lastly, males were slightly

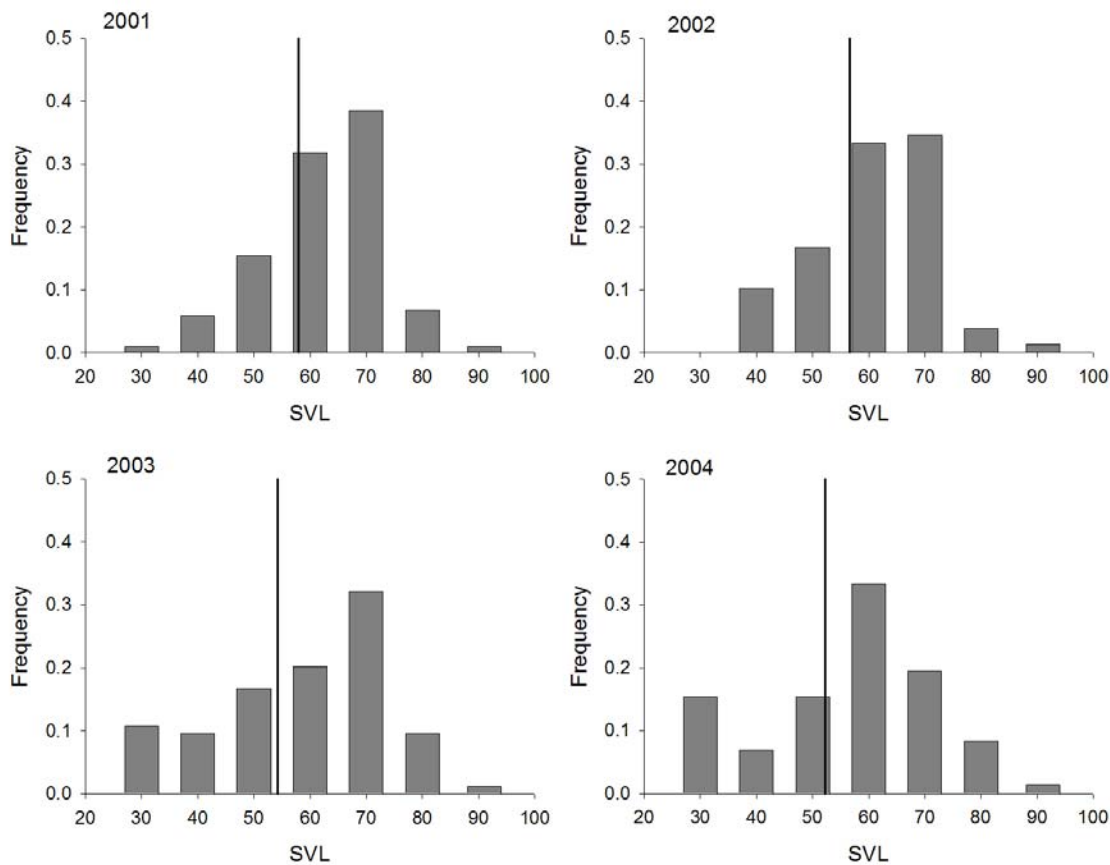


FIGURE 4. Changes in the mean (vertical line) and distribution of snout-vent-length (SVL, measured in cm) of Cottonmouths (*Agkistrodon piscivorus*) across study years at Tuskegee National Forest, Alabama.

larger ($\hat{\beta}_{\text{male}} = 1.25$, 95% CI: 0.99 to 1.51) than females, and the distribution of male SVL was more evenly distributed across the range of SVLs observed in our captured sample (Fig. 6).

DISCUSSION

The need for unbiased statistical estimates of survival has long been recognized by snake biologists (Turner 1977; Parker and Plummer 1987; Dunham et al. 1988; Pike et al. 2008). Here, for the first time, we present capture-mark-recapture estimates of Cottonmouth survival that are conditional on simultaneous estimates of recapture probability. Our estimate of Cottonmouth annual survival (0.79) is near the upper range of Ford's (2002) return rates for the western subspecies (0.30 to 1.0; maximum $n = 13$), greater than those for the closely-related Copperhead (*Agkistrodon contortrix*; 0.70 and 0.71), and is near the upper range of all return-rate estimates for snakes (0.35 to 0.85; Shine and Charnov

1992; Shine and Schwartzkopf 1992). Brown et al. (2007) also used capture-mark-recapture methods, and attained estimates of sub-adult and adult survival (0.822 to 0.999) for Timber Rattlesnakes (*Crotalus horridus*) that are the highest ever reported for snakes. Hence, capture-mark-recapture estimates of survival suggest that venomous snake species may have higher annual probabilities of survival than previously reported.

There are undoubtedly many herpetological capture-mark-recapture studies like ours in which the recapture probability is far too low to attain a realistic return-rate estimate of survival (Turner 1977; Dunham et al. 1988; Martin et al. 1995). For example, annual return rates during our study were < 0.01 , much lower than our estimate of survival conditioned on recapture probability (0.79). Failure to statistically account for transient individuals would have led to under-estimation of survival as well (resulting in a 0.72 annual survival probability). The use of modern capture-mark-recapture methods, however, allowed us to make full use of our data and alleviate these sources of bias.

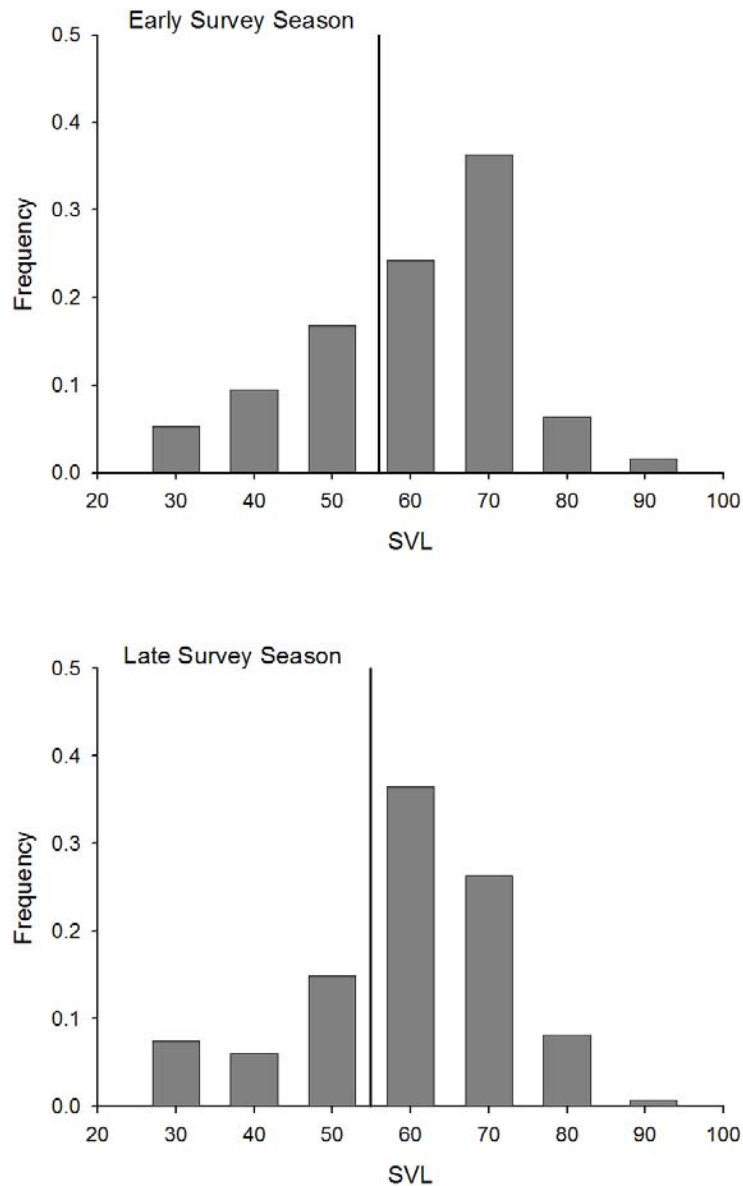


FIGURE 5. The mean (vertical line) and distribution of snout-vent-length (SVL, measured in cm) of Cottonmouths (*Agistrodon piscivorus*) in the early survey seasons relative to late survey seasons at Tuskegee National Forest, Alabama (see Materials and Methods for definitions of survey seasons).

Nevertheless, we were not able to detect effects of year, season, sex, or body size on survival. It is possible that survival was truly independent of these variables; however, we may not have followed the marked sample over a long enough period of time, or did not catch a large enough sample to detect such effects. Low recapture probabilities may have also affected our ability

to detect year, season, sex, and body-size effects on survival. Although low recapture probabilities do not bias estimates of survival, they can lead to reduced precision in survival estimates, in turn making it more difficult to statistically identify variables related to survival (Williams et al. 2002).

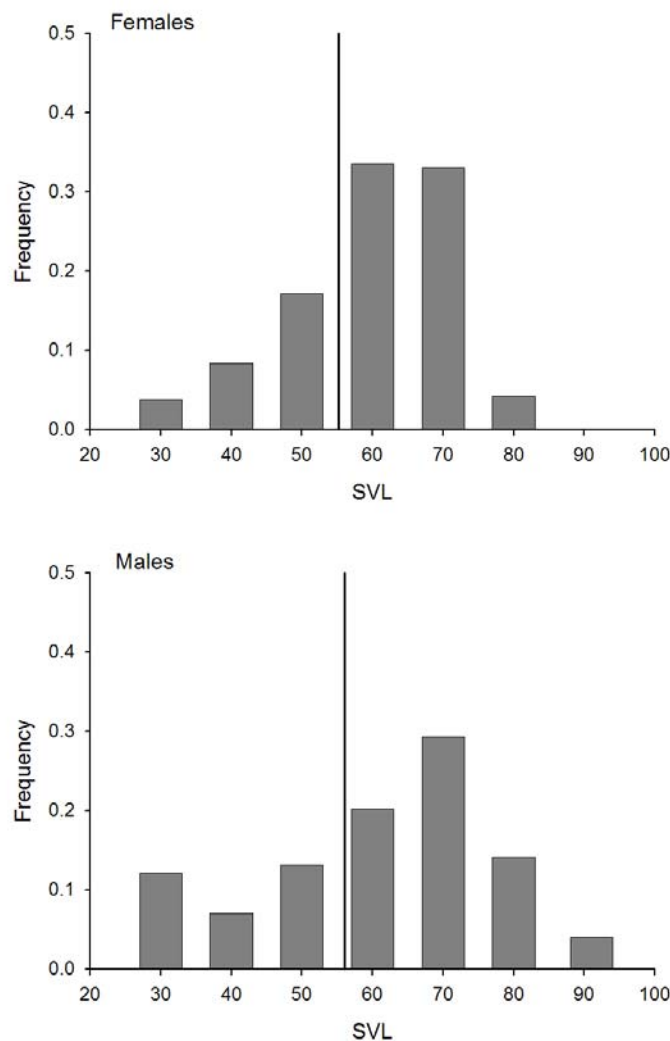


FIGURE 6. The mean (vertical line) and distribution of female snout-vent-length (SVL, measured in cm) of Cottonmouths (*Agkistrodon piscivorus*) relative to males at Tuskegee National Forest, Alabama, USA.

Failure to recapture live animals that use a study area can occur because of individuals temporarily dispersing off the study area or because of behavior that affects the ability of researchers to capture individuals (Williams et al. 2002). Reported relationships between snake body size and behavior towards researchers are mixed. For example, large adult snakes are said to be better capable of defense, making them less likely to retreat from humans (Shine et al. 2002; Roth and Johnson 2004). Glaudas et al. (2006) report that large adult Cottonmouths habituate to non-harmful predatory stimuli (defensive behavior decreased over time when

exposed to stimuli on a daily basis), whereas neonates do not. Gibbons and Dorcas (2002), on the other hand, found no relationship between Cottonmouth SVL and their defensive response toward humans. In contradiction to these findings, we found that the probability of a Cottonmouth moving away from researchers increased with body size, whereas the probability of locating a snake in a resting coil was negatively related to body size. Thus, if behavioral avoidance of researchers had affected recapture probability we would have found a negative relationship between recapture probability and SVL. We observed

just the opposite, suggesting that the positive relationship between recapture probability and SVL was driven by other factors. For example, small snakes may have temporarily dispersed from the study area at a higher rate than large snakes, perhaps in order to avoid cannibalization by conspecifics (Mitchell 1986). Alternatively, thermal requirements and greater susceptibility to predators may have forced small snakes to use habitats that make them more difficult to detect and recapture relative to large snakes (Lourdais et al. 2002). Also, large snakes might simply have been more visible among the habitat background making them easier to detect and capture than small snakes (Whitaker and Shine 1999; Sun et al. 2001). To identify which of the aforementioned factors affect recapture probabilities, a study would have to be conducted over a broader spatial extent than ours (see e.g., Roth 2005).

We also discovered that recapture probabilities declined after the initial year of study. Over time we qualitatively observed changes in vegetative growth associated with more complete drying of the beaver pond in and around the study swamp that could have made it more difficult to recapture snakes. We did not consistently measure important variables such as water level and vegetation cover, and could not formally examine how these factors may have influenced our probability of recapturing snakes.

Most Cottonmouth studies focus on the mean and distribution of SVL among adult snakes (Hill and Beaupre 2008). We focused on the mean and distribution of SVL across adults and juveniles such that we could learn more about the influence of changes in the population size structure on recapture probability, behavior, and demographic processes, such as recruitment. As is typical in venomous snakes (Shine 1993), males were larger than females. However, because we pooled data across juveniles and adults, our mean sex-specific estimates were smaller than those reported in other Cottonmouth studies (Hill and Beaupre 2008). In late survey seasons, we captured a greater frequency of Cottonmouths ≤ 30 cm in length relative to early survey seasons, perhaps because parturition occurred during the late survey season on our study area (snakes brought into the lab gave birth in late summer and early fall to neonates averaging 21 cm in SVL; unpubl. data). Furthermore, the frequency of small snakes in our sample of captured individuals increased each year. If the sample of captured individuals was indicative of the true SVL distribution in the population, this would suggest an increase in recruitment rates over time via reproduction or immigration because apparent survival was constant across the observed range of SVL. However, to confidently make inference about changes in the size-distribution of a population, size-specific recapture probabilities should be estimated precisely and accounted for in analyses of a population's size

distribution (Sun et al. 2001; Bonnet et al. 2003; Conn and Diefenbach 2007; Mazerolle et al. 2007). Nonetheless, the frequency of small individuals in the sample of captured and recaptured individuals increased over time. Because small individuals were more difficult to recapture, it is therefore not surprising that our estimates of recapture probability decreased after the first year of study (according to our best model without interaction terms).

In hindsight, it would have been advantageous to use several methods of trapping (e.g., nocturnal visual surveys along with drift fences and box traps) to ensure higher recapture probabilities (e.g., Rodda et al. 1992, 1999) and better chances of detecting variables that affect survival. Future studies should try to sample intensively at particular times of the year and in multiple locations, which would allow for explicit estimation of dispersal, recruitment, and population growth rates using 'multi-state' and 'robust design' capture-mark-recapture estimators (e.g., Kendall et al. 1995, 1997; Nichols and Kendall 1995; Aubry et al. 2009).

Nevertheless, we are the first to report Cottonmouth survival probabilities that are not confounded with probabilities of recapture (e.g., return rates). By conducting a capture-mark-recapture analysis, we found that (1) Cottonmouth survival was quite high; (2) recapture probabilities increased with SVL; (3) small snakes were more likely to be in a resting coil and not fleeing from human researchers; and (4) an increasing frequency of small snakes were encountered over the course of the study, suggesting an increase in local recruitment or immigration that could help sustain the population. Lastly, it seems that the distribution of body size in a Cottonmouth population can change rapidly. Information such as this could be used in long-term studies to assess the influence of an unstable distribution of body size (akin to unstable age distribution) on population dynamics for the purposes of designing conservation and management plans (Koons et al. 2005).

Acknowledgments.—We thank the following for assistance in the field and lab: Kristin Bakkegard, Kyle Barrett, Richard Beauman, Nickolas Bieser, Michelle Boback, Lesley de Souza, Matthew Grilliot, Craig Guyer, Shannon Hoss, Valerie Johnson, Daniel Moen, Deanne Moosman, Paul Moosman, John Peterson, Sam Raia, Robert Reed, Abigail Sorenson, Geoffrey Sorrell, John Steffen, John Styrsky, James Uertz, William Underwood, and Jeremy White. RDB thanks James B. Grand for introducing him to survival analysis. The manuscript benefited from the comments of Gordon Rodda, Natalie Hyslop, Whit Gibbons, Travis Folk, Craig Guyer, and Sean Graham. Thanks to Thomas E. Haines of Tuskegee National Forest for permission to conduct research (Special Use Permit TUS700705).

Research took place under guidelines approved by Auburn University IACUC # 2002-0220.

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