

REPRODUCTION IN THE WESTERN COTTONMOUTH, *AGKISTRODON PISCIVORUS LEUCOSTOMA*, IN A FLOODPLAIN FOREST

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**ABSTRACT**—Reproductive data on the western cottonmouth, *Agkistrodon piscivorus leucostoma*, are scarce, generally incomplete, and usually based on pooled years for a given area. Current paradigms suggest that reproductive output in snakes can be influenced by local resource availability so temporal variation is important to document. Pregnant female western cottonmouths were collected for 3 consecutive years (2000–2002) from a lowland hardwood forest in northeastern Texas. This bottomland is exposed to flood pulses during winter that produce variable, but often large, amounts of prey for semi-aquatic snakes. Data recorded from 27 females indicated no difference in their snout-vent lengths (SVL) or masses among years. Of all reproductive traits, only clutch mass was correlated to female SVL and only in 1 year. Clutch mass and relative clutch mass varied temporally, suggesting reproductive output was influenced by prey availability. However, clutch size and mean offspring mass (that together comprise clutch mass) were both consistent among years. There was variation in mean offspring SVL and mass among females, and a negative correlation of both offspring characteristics to clutch size. These results suggest that the reproductive output of individual females might be responding to variation in prey availability in different ways (i.e., some by varying offspring number and others by modifying offspring size). Testing this hypothesis will require monitoring individual females for multiple years.

**RESUMEN**—Datos de la reproducción de la víbora mocasin de boca de algodón, *Agkistrodon piscivorus leucostoma* son escasos, generalmente incompletos, y usualmente basados en varios años agrupados de un área específica. Paradigmas actuales sugieren que el esfuerzo reproductivo de serpientes puede ser influenciado por la disponibilidad de recursos locales, por lo que es importante la documentación de la variación temporal de esos recursos. Hembras gravidas de la víbora fueron colectadas por tres años consecutivos (2000–2002) en un bosque deciduo de tierra baja del noreste de Texas. Durante el invierno esta área está expuesta a repetidas inundaciones que producen variable, pero a menudo, grandes cantidades de presas disponibles para serpientes semiacuáticas. Los datos obtenidos de 27 hembras no indicaron una diferencia en la longitud hocico-cloaca (LHC) o en el peso entre los años. De todas las características reproductivas, únicamente el peso de la camada estuvo correlacionado con el LHC de la hembra y por sólo un año. El peso de la camada (PC) y el peso relativo de la camada variaron temporalmente, sugiriendo que el esfuerzo reproductivo estuvo influenciado por la disponibilidad de presas. Sin embargo, el tamaño de la camada y el peso promedio de las crías (que juntos constituyen el PC) fueron consistentes durante los años de estudio. Hubo una variación en el LHC promedio de las crías y el peso de las hembras, y una correlación negativa entre las dos características de las crías con el tamaño de la camada. Estos resultados sugieren que el esfuerzo reproductivo de hembras individuales podría responder a la variación en la disponibilidad de presas de modos diferentes (por ejemplo, algunas hembras varían el número de crías mientras que otras modifican el tamaño de ellas). Probar esta hipótesis requerirá un monitoreo individual de hembras durante varios años.

The western cottonmouth, *Agkistrodon piscivorus leucostoma*, is an abundant snake in most of its range; however, reproductive data for it are relatively rare (Fitch, 1985; Gloyd and Co-

nant, 1990; Ford et al., 1990). One long-term recapture study in northeastern Texas indicated western cottonmouths have relatively few large offspring that have high first-year surviv-

al. However, these data were for only 8 clutches pooled from several years (Ford, 2002) and reproductive traits of snakes are known to be influenced by year-to-year variation in prey availability (Bonnet et al., 2000, 2001; Seigel and Ford, 2001).

In floodplain forests, amphibian and fish densities are strongly related to periodicity in flood pulses (Finger and Stewart, 1987; Turner et al., 1994). In hardwood lowlands of northeastern Texas, semi-aquatic snakes, including the cottonmouth, feed on trapped fish and larval amphibians in ephemeral pools that develop in the spring and summer after winter floods (Doles, 2000; Yacelga, 2002). Western cottonmouths also ambush other snakes, adult frogs and small mammals that come to the edge of the water (Ford, pers. observ.). The intake of prey for these snakes varies dramatically relative to yearly rainfall and the timing of drying of the pools (Dole, 2000; Yacelga, 2002; Ford, pers. observ.). The ecological study on western cottonmouths by Ford (2002) was in a small spring-fed pond with little year-to-year fluctuation in water levels. Multi-year reproductive data on western cottonmouths from a stochastic bottomland site will not only provide comparative data from another location, but should also give some insight into the phenotypic plasticity of the reproductive traits of this snake.

Tests of the impact of energy intake on reproduction have been conducted both in the field and laboratory with North American colubrids (Ford and Seigel, 1989*a*, 1989*b*; Seigel and Ford, 1991; Gregory and Skebo, 1998), vipers in the Old World (Andren and Nilson, 1983; Bonnet et al., 2001; Li-xin et al., 2002; Lourdais et al., 2002; Luiselli and Zuffi, 2002), and pythons in Australia (Shine and Madsen, 1997; Madsen and Shine, 1999). The basic paradigm is that an amount of energy is first allocated to the reproductive event and then partitioned into number and size of offspring (Lande, 1982; Charnov, 1989). The optimal strategy for a species or population is thought to be related to their adaptation to local conditions (Seigel and Ford, 2001), but this should also be affected by fluctuating environments (Schaffer, 1974). However, multi-year reproductive data are still inadequate for establishing general influences of the environment on patterns of trade-offs for snakes. Additional re-

productive data on species from stochastic environments, such as floodplain forests, will be particularly important to obtain.

**METHODS—Study Species and Area**—The western cottonmouth is an abundant species in the Old Sabine Bottom Wildlife Management Area (OSBWMA), a 2,300-ha bottomland hardwood forest in Smith County on the southern side of the Sabine River in northeastern Texas managed by the Texas Parks and Wildlife Department (Doles, 2000; Lancaster and Ford, 2003). Pregnant cottonmouths are easily found there on the open mud banks of drying pools and can be collected just prior to parturition.

**Data Collection and Analysis**—Adult pregnant female western cottonmouths were captured from 15 July to 15 August in 2000, 2001, and 2002. Most females delivered by late August, so the length of time in captivity, known to affect reproductive traits in snakes (Farr and Gregory, 1991), was minimized. During 2001 and 2002, meristic data on non-pregnant females also were collected. Pregnant females were taken to the Ophidian Research Colony laboratory at the University of Texas at Tyler and kept in individual cages in a room at 28°C with a 12L:12D photoperiod. Water was provided ad libitum, and a mouse was offered to each snake once every other week. Snakes were weighed to the nearest 1 g every 2 weeks until parturition, and females did not noticeably change mass in the short time maintained in captivity. Parturition date, post-parturient mass, snout-vent length (SVL) and total length (TL) were recorded for each female, as was clutch size (live and stillborn offspring). Each offspring was measured to the nearest 0.1 cm SVL and TL, weighed to the nearest 0.1 g, and sexed by eversion of the hemipenes. After data collection, females and offspring were tagged with Passive Integrated Transponders (PIT tags) and released at the capture location of the female.

All data were examined for normality, and analyses were conducted using Statview and SuperAnova (SAS Institute Inc., 1999). A model II analysis of variance was used to test among female variation in offspring SVL and body mass (Sokal and Rohlf, 1995). Means and *SD* for offspring SVL, TL, and body mass were calculated for both sexes of each clutch. However, data for the sexes combined were used in analyses. Means and *SD* for SVL, post-parturient mass, clutch size, clutch mass (mean offspring mass times clutch size), and relative clutch mass (RCM: clutch mass/post-parturient mass) were calculated for females for each year. Linear regressions of clutch size, clutch mass, mean offspring SVL, and mean offspring mass against female SVL were conducted for each year and also for the entire data set. Because only clutch mass was correlated to female SVL, one-way analyses of variance were used to examine year

TABLE 1—Reproductive traits of 27 western cottonmouths, *Agkistrodon piscivorus leucostoma*, from the Old Sabine Bottom Wildlife Management Area, northeastern Texas, during August (Aug) and September (Sep). Means  $\pm$  1 SD. *F* and *P* values are for year-to-year comparisons of data from reproductive females. See text for analysis of relative clutch mass (RCM). SVL = snout-vent length, PP = postparturient.

Date born	Status	Number of clutches	Female SVL (cm)	PP mass (g)	Clutch size	Clutch mass (g)	RCM (%)
2 Aug to 29 Aug 2002	Reproductive	5	57.3 $\pm$ 2.54	188.6 $\pm$ 26.69	4.8 $\pm$ 0.84	66.4 $\pm$ 5.45	35.9 $\pm$ 6.50
	Nonreproductive	3	60.0 $\pm$ 6.08	238.6 $\pm$ 27.62			
22 Aug to 9 Sep 2001	Reproductive	8	59.3 $\pm$ 4.77	223.5 $\pm$ 52.45	4.3 $\pm$ 0.71	59.9 $\pm$ 6.94	27.8 $\pm$ 5.90
	Nonreproductive	5	58.0 $\pm$ 5.96	242.6 $\pm$ 67.90			
14 Aug to 1 Sep 2000	Reproductive	6	57.6 $\pm$ 1.50	217.8 $\pm$ 19.53	4.2 $\pm$ 0.98	54.7 $\pm$ 2.56	25.2 $\pm$ 1.70
<i>F</i>			0.617	1.331	0.925	6.142	11.159
<i>P</i>			0.552	0.292	0.417	0.0105	0.001

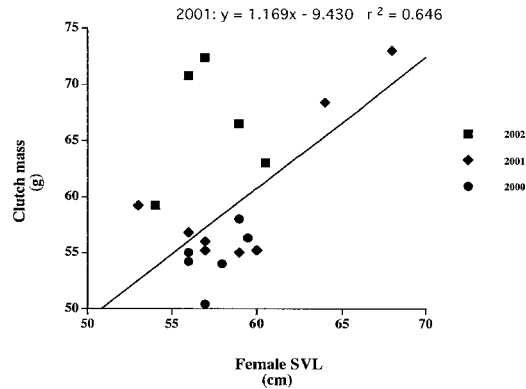


FIG. 1—Clutch masses of 19 female western cottonmouths, *Agkistrodon piscivorus leucostoma*, from the Old Sabine Bottom Wildlife Management Area, northeastern Texas. Correlations to female snout-vent lengths were significant only in 2001, which is the regression line shown. Clutch masses were significantly higher in 2000 than the other 2 years.

to year variation of all traits except clutch mass and RCM. Fisher PLSD was used to compare years a posteriori. Yearly variation in clutch mass was analyzed with ANCOVA with SVL as the covariate, and RCM was compared using ANCOVA with female mass as the covariate (see Ford and Seigel, 1989b). Interaction terms (year\*SVL and year\*mass) were nonsignificant and were removed from each analysis. The proportion of non-pregnant females was calculated in 2001 and 2002 (no data were available in 2000), and an ANOVA was used to compare their SVLs and masses to those of the postparturient females.

RESULTS—We collected 27 adult female western cottonmouths at OSBWMA. Nineteen of those snakes produced offspring (Table 1). The 8 non-pregnant females were not different in SVL from pregnant females ( $F = 0.94$ ,  $P = 0.76$ ). Parturition dates ranged from 14 August to 13 September. Of all reproductive traits, only clutch mass was correlated to female SVL ( $F = 4.30$ ,  $P = 0.05$ ; Fig. 1). When conducted for each year, clutch mass was significantly correlated to female length only in year 2001 ( $F = 7.10$ ,  $P = 0.003$ ), although it was marginal in both 2000 and 2002 (respectively;  $F = 6.69$ ,  $P = 0.06$ ;  $F = 6.33$ ,  $P = 0.10$ ). Females were similar in length each year and averaged about 58 cm SVL (Table 1), and although females in 2002 averaged only 188.6 g postpartum, this was not significantly lower than either 2000 or 2001 (Table 1). Mean clutch size was consistent

TABLE 2—Mean offspring traits of 19 female western cottonmouths, *Agkistrodon piscivorus leucostoma*, from the Old Sabine Bottom Wildlife Management Area, northeastern Texas. Mean (of clutch means)  $\pm 1$  SD. SVL = snout-vent length, TL = total length. Overall ranges of individual offspring are given in the parentheses below each mean.

Year	Sex	<i>n</i>	SVL (cm)	TL (cm)	Mass (g)
2002	M	7	20.8 $\pm$ 0.52 (19.9–21.3)	24.9 $\pm$ 0.60 (24.1–25.6)	13.2 $\pm$ 1.04 (11.8–14.6)
	F	15	20.4 $\pm$ 1.39 (16.5–22.3)	24.5 $\pm$ 1.05 (23.1–26.5)	14.2 $\pm$ 3.00 (11.1–20.4)
2001	M	13	21.1 $\pm$ 0.71 (20.1–22.2)	25.4 $\pm$ 0.81 (24.3–26.8)	16.1 $\pm$ 4.03 (13.1–26.9)
	F	17	20.6 $\pm$ 0.68 (19.8–21.7)	24.6 $\pm$ 0.74 (23.7–25.8)	13.8 $\pm$ 2.18 (11.7–18.1)
2000	M	9	20.9 $\pm$ 1.46 (18.0–22.5)	25.2 $\pm$ 1.65 (22.0–27.0)	13.6 $\pm$ 2.25 (9.6–16.5)
	F	11	20.4 $\pm$ 1.18 (18.5–22.0)	24.3 $\pm$ 1.36 (22.0–26.0)	13.6 $\pm$ 2.18 (10.1–17.8)

among years (Table 1) and did not differ from that reported in Ford (2002) ( $F = 1.17$ ,  $P = 0.34$ ). Mean clutch mass ranged from 54.7 to 66.4 g. Females in 2000 had significantly higher clutch masses than in either other year (2000 vs 2002,  $P = 0.003$ ; 2000 vs 2001,  $P = 0.05$ ; Table 1, Fig. 1). RCM varied from a mean of 25.2 to 35.9%, with 2002 being significantly higher than either other year (2002 vs 2000,  $P = 0.002$ ; 2002 vs 2001,  $P = 0.04$ ; Table 1). Two females pregnant in 2001 were not pregnant when recaptured in 2002.

Seventy-two offspring (29 males) were born

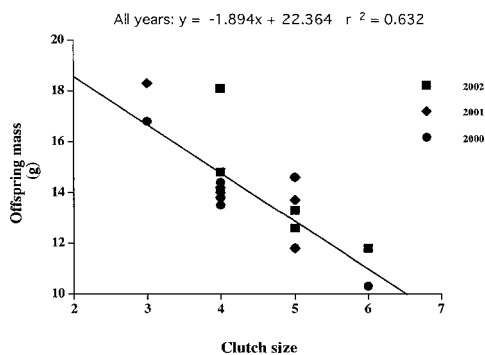


FIG. 2—Mean offspring masses correlated to clutch size for 19 female western cottonmouths, *Agkistrodon piscivorus leucostoma*, from the Old Sabine Bottom Wildlife Management Area, northeastern Texas. The regression line for all data is shown. However, by year, only 2002 showed significant correlation, whereas 2000 and 2001 were marginal.

(Table 2). This was not different from a 50/50 sex ratio (Pearson's Chi-square = 2.72,  $P = 0.098$ ). No year-to-year variation was evident in their morphological traits (SVL:  $F = 0.001$ ,  $P = 0.999$ ; mass:  $F = 0.083$ ,  $P = 0.920$ ). Mean offspring SVL varied among all females, exhibiting a range from 18.7 to 21.8 cm ( $F = 6.507$ ,  $P < 0.0001$ ; among group variance component = 52.3%), and mean offspring mass varied from 10.3 to 18.3 g ( $F = 6.931$ ,  $P < 0.0001$ ; among group variance component = 54.1%). For all years combined, mean offspring size was negatively correlated to clutch size (SVL:  $F = 10.98$ ,  $P = 0.004$ ; mass:  $F = 4.299$ ,  $P = 0.05$ ; Fig. 2), but by year, only in 2000 for SVL ( $F = 10.97$ ,  $P = 0.016$ ) and in 2001 for offspring mass ( $F = 17.96$ ,  $P = 0.013$ ).

DISCUSSION—Ford (2002) included some reproductive data for western cottonmouths near a small spring-fed pond that are useful for comparison to our study. His site (Sheff's Wood; a Nature Conservancy preserve) is only a few kilometers from OSBWMA. At OSBWMA, parturition dates for western cottonmouths were consistent among years and slightly earlier than recorded at Sheff's Wood (Ford, 2002) but in line with the literature for the subspecies (Gloyd and Conant, 1990). Slightly over 60% of the western cottonmouths collected at OSBWMA were pregnant (Table 1), suggesting that a biannual cycle is typical, but some females might gain enough energy

to reproduce in consecutive years. Both Kofron (1979) and Blem (1981) indicated some populations of western cottonmouths probably reproduce annually, but Ford (2002) found that less than 50% of western cottonmouths were pregnant each year. However, he did document 1 female reproducing in successive years. The only 2 recaptured females in our study that were pregnant in 2001 were not reproductive in 2002. The fact that non-pregnant females were not significantly heavier than post-parturient females suggests those non-reproductive females might not have regained sufficient mass from prior reproductive events to reproduce in the current year. However, see Bonnet and Naulleau (1996) and Bonnet et al. (2002) for discussions of problems in determining reproductive frequency in snakes.

Clutch size was consistent among years for western cottonmouths at OSBWMA and not significantly different than at Sheff's Wood (Ford, 2002). At OSBWMA, clutch size was not correlated to female SVL. However, the range of female SVL was small and more data from longer females might change this relationship, but it should be noted the 2 largest females did not have the highest clutch sizes. This lack of correlation contrasts with most other snakes (Ford and Seigel, 1989b) and for western cottonmouths in other locations (Ford, 2002; B. Greene, pers. comm.). Also, the alternative energetic tradeoff that longer females have larger offspring was not noted. Because clutch mass was correlated to female size (Fig. 1), we suggest there might be different strategies among females such that some larger females increase the number of young they have and others increase offspring size. There was significant among-female variation in offspring SVL and mass, and such alternate strategies would tend to mask the correlation of either offspring size or number to female SVL. The negative correlation of offspring size and clutch size (Fig. 2) supports this idea because longer females with larger offspring will be less able to increase number than would females producing small young. Examining variance in reproductive traits of different size females could test this hypothesis; however, the low sample of larger females prevents that with this data set.

We assume the variation in mean clutch masses among years in this study mirrors occurrence of temporal differences in prey intake.

We had anticipated that environmental stochasticity at OSBWMA would be reflected in changes in offspring size rather than number, because the relatively large offspring of this species would constrain adding more offspring in years with additional energy availability (Nussbaum, 1981). Recalling that clutch mass is clutch size times offspring mass, the lack of yearly variation in either offspring size or clutch size was confusing. As mentioned above, mean offspring SVLs and masses were highly variable among females, and the same rationale (i.e., multiple strategies for females masking the effect of yearly variation in prey availability) might explain the results here.

Prey availability in this floodplain is highly stochastic, and though it might seem that the reproductive characteristics of the cottonmouths were not responding to this variability, we feel that the yearly difference in clutch mass is evidence to the contrary. The variation in mean offspring SVL and mass among females and the overall negative correlation of offspring size and clutch size support our hypothesis that female western cottonmouths might have multiple strategies for responding to variable prey availability. Long-term studies at this site on this species, concentrating on the responses of individual females in different years, would be worthwhile.

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