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Body Size, Growth, and Reproduction in a Population of Western Cottonmouths (*Agkistrodon piscivorus leucostoma*) in the Ozark Mountains of Northwest Arkansas

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Life histories of a species often vary geographically, and comparative studies of populations in different habitats are useful for understanding how environmental variation influences life history. Such studies are currently lacking for most snake species despite their growing importance as model organisms for life history studies. We present life history data for a population of Western Cottonmouths (*Agkistrodon piscivorus leucostoma*) inhabiting a ''riffle–pool'' creek system (Rocky Grove) located in the Ozark Mountains in northwest Arkansas and compare our results with those available for other populations. One hundred forty-two individual snakes were captured 283 times from August 1996 through September 2003. Mean snout–vent length (SVL) of adult Rocky Grove *A. piscivorus* (males 60.8 ± 2.68 cm, $n = 47$, females 54.9 ± 1.74 cm, $n = 47$) was among the smallest reported for any population of *A. piscivorus*. Rocky Grove *A. piscivorus* also exhibited low degree of sexual size dimorphism (SSD) compared to other localities, and mean female SVL was 90.3% that of males. Growth rates were the slowest reported for any temperate zone pitviper (males 0.151 ± 0.053 cm/month, $n = 46$, females 0.178 ± 0.06 cm/month, $n = 66$). Limited data also indicate low reproductive output for this population in terms of frequency of reproduction and litter size. Female reproduction averaged less than biennial as evidenced by consistently low proportion of pregnant to non-pregnant females (18.4%) and reproductive histories of individual female snakes. Litter size averaged 4.1 ± 0.63 ($n = 10$). Mating at Rocky Grove occurs in late summer but may also occur in spring. *Agkistrodon piscivorus* at this study site may be limited in energy acquisition rates relative to the conspecifics in other parts of the range.

BODY size, growth rate, age at first reproduction, frequency of reproduction, and litter size are life history characters that affect the population biology of all organisms (Stearns, 1992). Body size and growth rate are particularly important because of their relation to reproductive output, longevity, age at first reproduction, competitive ability, susceptibility to predation, food habits, and whole organism energy budgets (Dunham et al., 1989; Bronikowski, 2001; Boback and Guyer, 2003). Because availability of prey and other resources may vary between years, studies of growth rates in long-lived animals should be conducted over an adequate time period (>five years) to assess annual variation in growth (Parker and Plummer, 1987; Madsen and Shine, 2001; Diller and Wallace, 2002).

Life histories vary among populations (Gibbons et al., 1981; Grant and Dunham, 1990; Beaupre, 1995), and both genetic and environmental factors contribute to variation in life histories (Stearns, 1980; Ford and Seigel, 1989; Sinervo and Adolph, 1994). Intraspecific comparisons of geographically separated populations are a productive way to study the relationship between life history characters and the environment (Macartney and Gregory, 1988; Shine, 2003). Comparative life history studies will increase our knowledge of why organisms exhibit certain life history traits and how these traits affect their abundance and distribution.

Snakes are often considered difficult to study (Toft, 1985; Parker and Plummer, 1987; Vitt, 1987; but see Shine, 2003), and our understanding of their life histories lags behind that of other taxa. Due to various attributes, pitvipers have become increasingly important model organisms in ecology, physiology, and evolution (Beaupre and Duvall, 1998; Beaupre, 2002). Pitvipers often have large body size, are locally abundant, and are behaviorally easy to follow and observe in the field using radio telemetry. Pitvipers are relatively long lived, and variation in resource abundance among years often results in annual variation in growth rates and other life history traits (Bonnet et al., 2001; Ford et al., 2004).

As a wide-ranging temperate zone pitviper, *Agkistrodon piscivorus* is a good model organism for studies of geographic variation in life history (Ford, 2002). It is locally abundant throughout the southeastern United States, from northern Virginia south to the Florida Keys, west to central Texas, and north into eastern Oklahoma, southern Missouri, and southern Illinois (Gloyd and Conant, 1990). Three subspecies are recognized: the Eastern Cottonmouth (*A. p. piscivorus*) in the northeastern part of its range, the Florida Cottonmouth (*A. p. conanti*) in Florida, and the Western Cottonmouth (*A. p. leucostoma*) west of the Mississippi River (Gloyd and Conant, 1990). *Agkistrodon piscivorus* are generally lowland species but occupy a variety of habitats, including swamps, lakes and ponds, rivers, estuaries, and streams (Burkett, 1966; Blem, 1981; Gloyd and Conant, 1990). The upper elevational limit of *A. piscivorus* is 700 meters (Burkett, 1966). *Agkistrodon piscivorus* often occur in high densities and are easily captured making the species

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amenable for mark–recapture studies. Adults are also large enough to allow for implantation of radio transmitters.

Herein we present a life history (body size, sexual size dimorphism [SSD], growth rates, and reproductive output) analysis of a population of Western Cottonmouths (*Agkistrodon piscivorus leucostoma*) at a location called Rocky Grove in the Ozark Mountains of northwest Arkansas. Results of this study are then compared with available data from other *A. piscivorus* populations across the species range. Rocky Grove differs from the lowland environs (swamps and estuaries) considered more typical of the species. Previous studies of *A. piscivorus* life history have been conducted in lowland areas (Blem and Blem, 1995; Scott et al., 1995; Ford, 2002). Rocky Grove is in the northern part of the range of *A. piscivorus* and near its upper elevational limit, thus environmental temperatures are lower than those of populations at lower elevations. *Agkistrodon piscivorus* habitat in Rocky Grove is subject to seasonal high flow, and drought and prey availability is probably seasonally variable. Our data provide an important contrast to life history data for *A. piscivorus* in other parts of the range.

MATERIALS AND METHODS

Rocky Grove study area.—*Agkistrodon piscivorus leucostoma* was studied in a system of small mountain creeks in the Ozark Mountains of northwestern Arkansas at an elevation of approximately 550 m. The Rocky Grove study area is located 50 miles east of Fayetteville, Arkansas at approximately 35°52′N, 93°30′W and comprises the confluence of three creeks which flow over a predominantly bedrock substrate often adjacent to steep bluffs. The creeks are typical "riffle–pool" systems with water level varying seasonally and yearly depending upon rainfall (Brown and Matthews, 1995). By late summer the creek beds are usually mostly dry with only small pools of water remaining in the bedrock.

Mark–recapture.—A mark–recapture study was conducted from August 1996 to September 2003. No sampling was conducted in 2002. Visual surveys for *A. piscivorus* were usually conducted at night by walking the creeks and looking into rock crevices with a flashlight. During the warm summer nights of July, August, and September, *A. piscivorus* was easily observed and captured on bedrock in the drying creek bottoms. Snakes were also captured at communal dens in spring and fall. Sampling was usually done in an *ad hoc* fashion by one or two people with effort allocated each year as follows: 1996—10 days from 1 August to 3 October; 1997—27 days from 19 April to 20 October; 1998—53 days from 1 April to 8 November; 1999—14 days from 3 April to 9 October; 2000—51 days from April 5 to November 10; 2001—66 days from 2 April to 7 October; 2003—five days from 26 March to 18 September. Intensive searches of the entire study area were conducted by four people on 30 July, 13 and 29 August, 2001 and 17 August, 2003.

After capture, snakes were transported to a nearby field station for processing, and later returned to the capture location. Snakes were weighed (± 0.1 grams) using a triple beam balance and measured (± 1–2 mm) for snout–vent length (SVL), total length (TL), head width (HW), and head length (HL) using a squeeze box (Quinn and Jones, 1974). Snakes were sexed by hemipenial probing. Passive integrated transponders (AVID Identification Systems, Inc., Norco, CA) were used to uniquely mark individuals (Camper and Dixon, 1986). *Agkistrodon piscivorus* is viviparous and female snakes were palpated to determine reproductive state, and to count follicles or developing embryos. In late summer and early autumn follicles could be distinguished from embryos based on size, turgidity, and position in the animal. Embryos are located more posterior in the lower oviduct whereas vittellogenic follicles are more anterior in the ovary.

Growth rates were determined for snakes with a minimum three-month interval between captures. The five-month inactive season (15 October to 15 April) was subtracted from the total time between captures for determination of growth rates assuming no growth during low temperature hibernation (Beaupre et al., 1998; Brito and Rebelo, 2003). Bonnet et al. (2002) found no change in body mass or SVL during hibernation in *Vipera aspis*. *Agkistrodon piscivorus conanti* on Cedar Keys, Florida showed periods of no growth during periods of little to no food availability (Wharton, 1966). A separate growth rate was determined for each period between captures for those snakes that were captured more than twice.

Five pregnant female *A. piscivorus* (two in 2001 and three in 2003), collected in August and September, were held in captivity until parturition to obtain data on number and size of offspring and date of birth. Captive snakes were maintained at 28°C with 12L:12D light cycle. Litter size was calculated using either the number of enlarged follicles or developing embryos counted during palpation of pregnant snakes, or the number of viable or stillborn offspring per female snake that gave birth in the laboratory (Ford and Seigel, 1989). Average litter size estimates include data from both sources. The proportion of pregnant to non-pregnant female *A. piscivorus* captured each year was estimated. Scat production by captive pregnant females was noted to determine if they had been feeding.

Statistical analyses.—Snakes ≥ 45 cm SVL were considered adults after Burkett (1966). Data on minimum size at reproduction in female *A. piscivorus* from Rocky Grove (48.0 cm) corroborated that finding. A Wilcoxon Two-Sample Test was used to compare SVL and mass between the sexes for adults because one or both of the data sets (male or female) were not normally distributed. Neonate weight and SVL were compared by *t*-tests. Only measurements from the first capture were used for individuals that were recaptured. We quantified the degree of SSD using the SSD Index of Gibbons and Lovich (1990). Original size data (SVL and weight) of *A. piscivorus* from Zaidan (2001) were obtained and compared to those from our study using Wilcoxon Two-Sample Tests (for male SVL and weight and female weight). Female SVL data were compared by a *t*-test because they were normally distributed in both samples. Zaidan's snakes were captured within 50 miles of our study area but at lower elevations.

We used Pearson's Chi-Squared Tests for Goodness of Fit to determine if sex ratios of snakes captured in each year and at birth differed from 1:1. Total number of male and female snakes caught each year was used in the analysis, but recaptures from within that year were not included.

A simple parametric linear regression was used to describe the relationship between initial SVL and growth rate for each sex based on an *a priori* assumption that males and females may have different growth rates. The influence of sex (independent variable) and initial SVL (covariate) on growth rate was analyzed using the MIXED procedure in SAS

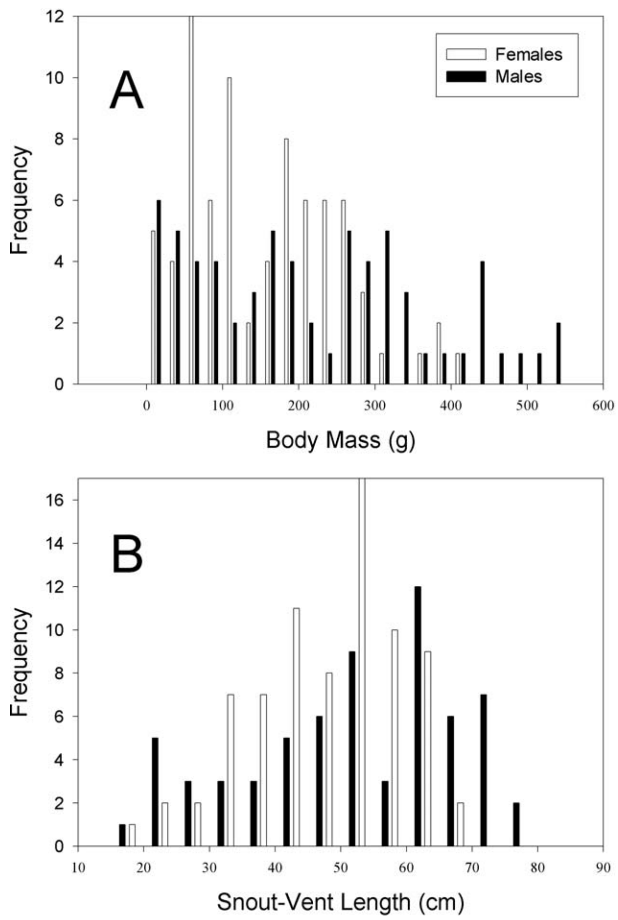

Fig. 1. Size distributions of male (n = 65) and female (n = 77) *Agkistrodon piscivorus* at first capture. (A) Mass. (B) SVL.

because growth rate measurements were repeated over time on many of the snakes (Statistical Analysis Systems Institute, Cary, NC, 2001). The interaction of sex and SVL was also included in the analysis as a test for homogeneity of slopes.

All statistical analyses were conducted using SAS version 8.2 for Windows (Statistical Analysis Systems Institute, Cary, NC, 2001). Response variables were tested for normality using a Shapiro–Wilks Test and data sets with $P \leq 0.1$ were considered to be non-normal. A Type I error of 0.05 was applied for all other statistical tests. Averages are reported ± 2 SE unless otherwise noted.

RESULTS

Body size and sexual size dimorphism.—A total of 142 individual *A. piscivorus* was captured and 94 were adults (≥45 cm SVL). There were 141 recaptures for a total of 283 captures. Adult females (n = 47) averaged 218.7 ± 22.2 g in weight, 54.9 ± 1.7 cm in SVL, and 64.0 ± 2.0 cm TL, while adult males (n = 47) averaged 284.5 ± 35.6 g in weight, 60.8 ± 2.8 cm in SVL, and 72.4 ± 2.9 cm in TL (Table 1). Data on male weight and SVL, and female weight were not normally distributed (W = 0.95, P = 0.04; W = 0.95, P = 0.05; W = 0.94, P = 0.024, respectively). Female SVL data were normal (W = 0.97, P = 0.34). Wilcoxon Two-Sample Tests indicated that adult males were significantly larger than adult females in weight (Z = 2.95, P = 0.003, Fig. 1) and SVL (Z = 3.33, P < 0.001, Fig. 1). The SSD Index for adult snakes from Rocky Grove is −0.90 based on SVL.

Zaidan's data on male weight and SVL and female weight were not normally distributed (W = 0.95, P = 0.07; W = 0.93, P = 0.01; W = 0.88, P = 0.002, respectively), but female SVL data were normal (W = 0.97, P = 0.34). Male (n = 38) and female (n = 34) *A. piscivorus* from Zaidan (2001) were significantly larger than those from Rocky Grove in both weight (males Z = 4.59, P < 0.0001; females Z = 3.0, P = 0.002) and SVL (males Z = 3.96, P < 0.0001; females t = −2.04, P = 0.045).

Sex ratio.—The proportion of male to female captures (juveniles and adults) was 7:12 in 1996, 10:7 in 1997, 14:16 in 1998, 4:6 in 1999, 28:33 in 2000, 35:44 in 2001, and 15:21 in 2003. These proportions were not significantly different from 1:1 based on a χ^2 test (P > 0.10 in all cases) despite the fact that there were slightly more males captured than females in all years except 1997.

Growth rates.—Sixty-four snakes were recaptured at least once with a minimum three-month period between captures. Multiple recaptures were obtained for some of these snakes, and a total of 112 growth rate estimates were obtained (Fig. 2). The number of recaptures per individual ranged from one to seven. Average growth rates for males and females are shown in Table 2. Growth rates ranged from −0.13 to 1.04 cm/month. Results of the mixed model analysis of repeated measures procedure indicate a significant effect of sex (F = 4.18, P = 0.043) and SVL (F = 87.46, P < 0.0001) on growth rates. The test for homogeneity of slopes was significant (F = 7.86, P = 0.006), indicating that the influence of SVL on growth was dependent on sex. Growth rates were negatively correlated with initial SVL in both sexes (Table 2). Males and females under 55 cm SVL had similar growth rates (Table 2). Females larger than 55 cm SVL grew very little, while males over 55 cm SVL continued to grow (Table 2, Fig. 2).

Reproduction.—Average SVL of pregnant female *A. piscivorus* in Rocky Grove was 58.0 ± 2.6 cm (range 48.0–65.1, n = 16). Litter size was determined by palpation in five pregnant females caught on 15 July (three) and 10 August (one) 2000 and 29 August 2001 (one). Five additional females collected later in the season were held in the laboratory until parturition. Data on litter size, size of offspring, and parturition dates are presented in Table 1. Average total clutch mass (TCM) from the five laboratory pregnant snakes was 52.1 ± 11.0 g (range 39.8 to 68.8 g). In one of the laboratory born clutches of five offspring, all were stillborn but fully formed. Another clutch of three had one stillborn neonate that was also fully formed but had a deformed (bent) vertebral column, and we did not determine SVL for this snake. Neither average mass nor SVL differed by sex in neonates (t_{mass} = −0.92, P = 0.37, t_{SVL} = 0.30, P = 0.77). Sex ratio at birth (ten males to nine females) did not differ significantly from 1:1 (χ^2 = 0.053, df = 1, P > 0.50).

The proportion of pregnant to non-pregnant females was 57.1% (four of seven) in 1996, 19.2% (five of 26) in 2000, 11.8% (four of 34) in 2001, and 15% (three of 20) in 2003. Insufficient captures were made during the 1997, 1998, and 1999 active season to provide insight into proportions of pregnant to non-pregnant females. Total percentage of pregnant females for all years combined was 18.4%.

Two adult female snakes were pregnant one year, not pregnant the following year, and pregnant again the next

Table 1. Review of Data on Adult Body Size and Reproduction for *Agkistrodon piscivorus* from Localities across the Range. Size data are means ± 2SE. SSD = Sexual Size Dimorphism Index after Gibbons and Lovich (1990). Subspecies is given after the Site name: Apl = *A. p. leucostoma*, App = *A. p. piscivorus*, Apc = *A. p. conanti*. Litter Size estimates include range in parentheses when available. Error terms were converted to 2SE from original reference. ?—Type of error term not specified in original reference. *—error estimate not provided in original reference. np—indicates data are from non-pregnant females only. NWAR—northwest Arkansas, HVA—Hopewell, Virginia, SEVA—southeast Virginia, NENC—northeast North Carolina, SC—South Carolina, KY—Kentucky, NET—northeast Texas.

Site	SVL (cm)		Mass (g)		SSD	Litter size	Neonate SVL (cm)	Nenonate mass (g)	Parturition dates	Reference
	Female	Male	Female	Male						
NWAR (Apl)	54.9 ± 1.7 *n* = 47	60.8 ± 2.8 *n* = 47	218.7 ± 22.2 *n* = 47	284.5 ± 35.6 *n* = 47	−0.90	4.1 ± 0.62 (3–5), *n* = 10	20.3 ± 0.70 (17.9–22.6), *n* = 20	13.0 ± 1.2 (8.8–17.9), *n* = 19	10–28 Sept. *n* = 5	Present study
NWAR (Apl)	57.9 ± 2.9 *n* = 33	71.6 ± 5.7 *n* = 39	299.1 ± 11.2 *n* = 33	547.2 ± 8.4 *n* = 39	−0.81					Zaidan (2001)
HVA (App)			402.6 ± 57.4 *n* = 14 nr	857.2 ± 121.2 *n* = 68 nr		7.68 ± 3.54 *n* = 24	21.1 * *n* = 80	17.3 * *n* = 80		Blem (1981)
HVA (App)	70.4 ± 3.5 *n* = 56	83.1 ± 3.8 *n* = 80			−0.85	7.6 ± 0.58 (4–12), *n* = 44	21.2 ± 0.25 (18.4–24.3), *n* = 93	16.9 ± 0.20 (11.5–24.1), *n* = 93	23 Aug.–3 Oct. *n* = 19	Blem and Blem (1995)
SEVA (App)	54.8 ± 5.7 *n* = 18	63.0 ± 8.9 *n* = 36			−0.87					Blem and Blem (1995)
NENC (App)	55.2 ± 4.9 *n* = 7	65.2 ± 1.3 *n* = 15			−0.85					Blem and Blem (1995)
NC (App)						7.4 ± 1.1 (5–l1), *n* = 15	26.1 (24.3–28.9), *n* = 11		Late Sept. to Aug.	Palmer and Braswell (1995)
SC (App)	69.7 ± 2.7 *n* = 49 (np)	76.7 ± 1.1 *n* = 93			−0.91	6.0 ± 0.4? (3–10), *n* = 30				Scott et al. (1995)
NET (Apl)						5.0 ± 0.82 *n* = 8	20.7 ± 0.60 *n* = 8	14.9 ± 1.7 *n* = 8	25 Aug.–7 Sept.	Ford (2002)
NET (Apl)	58.4* *n* = 27		226.8* *n* = 27			4.4* *n* = 19	(18.8–21.8)* *n* = 19	(10.3–18.3)* *n* = 19	14 Aug.–13 Sept.	Ford et al. (2004)
Florida (Apc)	102.8^{max}	152.4^{max}	1816^{max}	3660^{max}	−0.68	6.5 ± 0.76 (3–11), *n* = 31			Aug.–Sept.	Allen and Swindell (1948)
Cedar Keys, Florida (Apc)						5.5 ± 0.52 (3–8), *n* = 24	33.2_{TL}* (32.4–35.0), *n* = 19	30.9* (26.5–34.8), *n* = 19	6–9 Sept.	Wharton (1966)
KY (Apl)	Both sexes about 70.0 (26.0–99.3), *n* = 167				4.7* (2–10), *n* = 10	26.0* *n* = 3			3 Sept.	Barbour (1956)

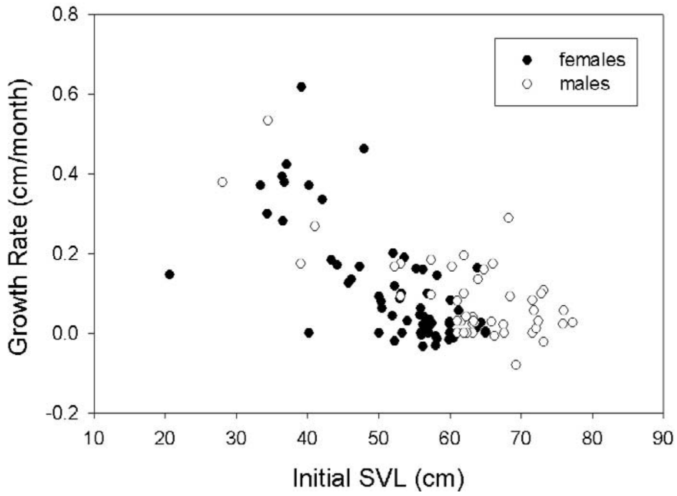

Fig. 2. Growth rate as a function of initial SVL in recaptured male and female *Agkistrodon piscivorus* at Rocky Grove.

year. One snake was pregnant in two consecutive years (2000 and 2001). The observation in 2000 was made on 15 July, and it is unlikely that vitellogenic follicles would be large enough at that time to be confused with embryos (Seigel and Ford, 1987). The 2001 observation was based on a laboratory birth. Eleven females were non-reproductive for at least two years in a row and one adult female was non-reproductive for four consecutive years. Seven of 15 pregnant females produced stools while in captivity. Parturition dates for the four litters in the laboratory were 10, 15, and 21 (two litters) September (Table 1). For the fifth litter one neonate was stillborn on 28 September, and four more were stillborn on 2 October (Table 1).

Mating and association.—Copulation was observed once on 16 August 1998. The two snakes were floating in the water at the edge of the creek under an earthen bank among tangled tree roots. The snakes had their bodies outstretched away from one another. The female snake was undergoing ecdysis. Snakes were considered to be engaged in ''bisexual pairing'' when two snakes of opposite sex were located in close proximity (≤0.5 m) to one another. Bisexual pairing in late summer was observed on ten occasions: 16 August 1998; 22 August and 3 September 2000; 30 July and 3, 12, 13, 15, 17 August and 11 September 2001. Courtship behavior (chin rubbing) was observed during the 3 September 2000 observation. Bisexual pairings in spring were observed on four occasions: 24 April and 3 May 1998; 20 April 2000; and 11 April 2001. One of the spring observations of bisexual pairing was made near a hibernaculum upon emergence from the den and may have resulted from aggregation of the snakes at the communal den and not from reproductive activity. Male–male agonistic behavior was not observed.

DISCUSSION

Body size.—Average body size of Rocky Grove *A. piscivorus* is among the smallest reported for the species (Table 1). Interestingly, Rocky Grove snakes were even statistically smaller than conspecifics from lower elevations at localities within 50 km of our study area (Zaidan, 2001). Zaidan's data come from a number of different locations in northwest Arkansas, not just a single population. Gloyd and Conant (1990) reported that *A. p. leucostoma* is the smallest of the three subspecies, with the maximum recorded size being 157.5 cm total length for a snake from Mississippi.

Despite the small average size of the snakes at Rocky Grove, the minimum size at maturity appears to be similar to that of other populations of this subspecies. The smallest vitellogenic female *A. piscivorus* observed during our study was 48.0 cm SVL, which is similar to the smallest pregnant *A. p. leucostoma* in a Texas population (45 cm SVL, Burkett, 1966). However, the smallest pregnant *A. p. leucostoma* from another Texas population was 54 cm SVL (Ford, 2002). Minimum SVL of sexually mature female *A. p. piscivorus* in a Virginia population was reported to be 73.2 cm SVL (Blem, 1981); however, a later publication on the same population reports a minimum pregnant female size of 61.9 cm SVL (Blem and Blem, 1995). Male *A. p. conanti* in an island population reached maturity at 65.0 cm TL, and females matured at 80.0 cm TL (Wharton, 1966).

Sexual size dimorphism.—*Agkistrodon piscivorus* at Rocky Grove was sexually dimorphic in both SVL and mass (Fig. 1, Table 1) a phenomenon which has been documented in *A. piscivorus* across its range (Burkett, 1966; Gloyd and Conant, 1990; Blem and Blem, 1995). Larger size in males has often been explained from an evolutionary standpoint

Table 2. Predictive Equations for Estimating Growth Rate of Male and Female Rocky Grove *Agkistrodon piscivorus* Based on Initial SVL. Only the average growth rate is shown when regressions are non-significant ($P > 0.05$).

Size range	Male growth rate (cm/month)	Female growth rate (cm/month)
>55 cm SVL	average = 0.109 ± 0.48 $n = 39$	average = 0.051 ± 0.03 $n = 34$
<55 cm SVL	1.032 − 0.015 SVL $P = 0.006$ $r^2 = 0.802$ $n = 7$ average = 0.381 ± 0.16	1.29 − 0.022 SVL $P = 0.002$ $r^2 = 0.366$ $n = 32$ average = 0.313 ± 0.10
All sizes	0.810−0.0105 SVL $P < 0.0001$ $r^2 = 0.38$ average = 0.151 ± 0.053 $n = 46$	1.195−0.019 SVL $P < 0.0001$ $r^2 = 0.51$ average = 0.178 ± 0.060 $n = 66$

as an adaptation for enhancing competitive ability in male–male combats for mate acquisition (Shine, 1978, 1993, 1994). *Agkistrodon piscivorus* is known to engage in male–male combat (Zaidan et al., 2003), and large size in males may be an adaptation to enhance competitive ability in combat (Shine, 1993, 1994). The explanation of large size enhancing combat ability for males may explain why there is selection for large size among males but does not explain why females should be smaller relative to males.

An understanding of the proximate causes of SSD is also of interest and may help in the formulation of ultimate explanations (Shine, 1994; Beaupre et al., 1998). Low growth was observed in female Rocky Grove *A. piscivorus* after they reached their approximate average size of reproduction (58 cm), while males continue to grow into adulthood (Table 2, Fig. 2), which is consistent with the hypothesis that sexual size dimorphism in this population results from females allocating energy into reproduction rather than growth after reaching reproductive size. A similar pattern has been observed in *Crotalus atrox* in Arizona (Beaupre et al., 1998). We had no way of aging *A. piscivorus* so this explanation is based on size class data only.

Agkistrodon piscivorus at Rocky Grove appear to have a lesser degree of sexual size dimorphism than that of other *A. piscivorus* populations. Adult *A. piscivorus* at Rocky Grove had an SSD Index of −0.90 based on SVL, while Zaidan (2001) reports an SSD Index of −0.81 for the snakes in his study (Table 1). A review of the literature on body size in *A. piscivorus* shows geographic variation in the degree of SSD (Table 1). Statistical comparisons of degree of SSD are not possible without the original data, but *A. piscivorus* at Rocky Grove had the lowest degree of SSD of any other population studied except one in South Carolina (Scott et al., 1995). Geographic variation in the degree of SSD has also been observed for other snake taxa (Schwaner and Sarre, 1990; Forsman, 1991; Pearson et al., 2002). Intraspecific geographic variation in body size and degree of sexual size dimorphism has been attributed to variation in prey availability and, specifically, prey size (Schwaner and Sarre, 1985; Shine, 1987). It is not clear if larger body size is an adaptation to facilitate the ingestion of larger prey (genetic) or a phenotypically plastic response to food availability and its influence on energy intake (Shine, 1987; Schwaner and Sarre, 1990). Individual based computer simulation models of pitvipers indicate that the degree of SSD should increase in populations in environments with greater prey abundance (Beaupre, 2002).

Rocky Grove *A. piscivorus* are likely to be food limited at times. Prey availability appears to be seasonally and annually variable, related to rainfall, and unpredictable. Rocky Grove *A. piscivorus* probably forage most successfully in late summer when little rain falls, creek water levels are low, and small fish (including *Semotilius atromaculatus*), trapped in pools in the bedrock, are abundant and make easy prey (Hill, 2004). We witnessed *A. piscivorus* gorging themselves on fish in the early fall. The snakes are probably less successful at foraging when water levels are high and creeks are flowing or when water levels have remained low for long periods of time and fish trapped in bedrock pools die of hyperthermia or anoxia. *Agkistrodon piscivorus piscivorus* in a South Carolina swamp also appeared to rely upon unpredictable, low water levels for successful foraging (Scott et al., 1995), and this population also had a low degree of SSD. Prey abundance is likely to be an important factor influencing geographic variation in SSD, and this question should be addressed in future research.

Sex ratio.—The result of equal sex ratios, both in adults and at birth, in *A. piscivorus* at Rocky Grove was also obtained for *A. p. leucostoma* in northeast Texas (Ford, 2002) and *A. p. piscivorus* in northern Virginia (Blem and Blem, 1995). However, adult *A. p. piscivorus* in Virginia had a significantly male biased sex ratio (Blem, 1981). Sex ratios of snakes at birth are usually 1:1 (Parker and Plummer, 1987). Sex ratios in adult snakes often appear to deviate from 1:1, but this may be an artifact of sampling bias due to sexual variation in behavior, activity, or habitat use (Parker and Plummer, 1987).

Growth rates.—Average growth rates of *A. piscivorus* at Rocky Grove (0.151 cm/month for males and 0.178 cm/month for females) are low relative to those of other populations of *A. piscivorus* and other pitvipers in general. *Agkistrodon p. leucostoma* in northeastern Texas grew at approximately 1.4 cm/month on average (Ford, 2002). *Agkistrodon piscivorus* in Virgina grew from approximately 1.3 to 1.6 cm/month during their first 41 months of life (Blem and Blem, 1995). These rates exceed even the maximum growth rate for Rocky Grove snakes (1.04 cm/month). Burkett (1966) reported growth rates averaging about 0.72 cm/month for three *A. piscivorus*, from an unspecified locality, during their first 143 days of life. *Agkistrodon piscivorus conanti* on Cedar Key, Florida grow approximately 1.46 cm/month in their first year of life and 1.3 cm/month in their second year (Wharton, 1966). The rattlesnakes (genera *Sisturus* and *Crotalus*) appear to be the sister group of the *Agkistrodon* (Gutberlet and Harvey, 2002; Parkinson et al., 2002) and comparisons of *A. piscivorus* life histories with those of rattlesnakes are of interest. *Crotalus atrox* in Arizona had maximal growth rates of 3 to 4 cm/month (Beaupre et al., 1998). Average growth rates of Rocky Grove *A. piscivorus* were similar to those for male *C. atrox* over 80 cm SVL (0.17 cm/month). But male *C. atrox* in this size range grew at a relatively slower rate than smaller individuals. *Crotalus oreganus oreganus* in Idaho had mean growth rates of 2.6 cm/month for females and 2.9 cm/month for males (Diller and Wallace, 2002). Values from Diller and Wallace (2002) were converted from cm/year to cm/month allowing an active season of seven months per year to make their units comparable to those of this study.

Reproduction.—Litter sizes for the small sample of *A. piscivorus* at Rocky Grove (average = 4.1, range 3–5) were similar to, but smaller than, those reported for *A. piscivorus* at other localities (Table 1). Size of neonates was similar to that found for many other populations (Table 1). Neonates from two separate Texas populations were similar in size to those in our study (Ford, 2002; Ford et al., 2004). A sample of *A. p. leucostoma* from across the geographic range had slightly smaller neonates than those observed in our study (Burkett, 1966). Neonate *A. p. conanti* on Sea Horse Key, Florida were much larger than any other *A. piscivorus* population, probably due to the large body size of adult females at this locality (Wharton, 1966). Total Clutch Mass of Rocky Grove *A. piscivorus* was similar to, but slightly lower than, that reported by Ford et al. (2004) from a Texas population. Estimates of reproductive output based on small sample sizes may be biased (Bonnet et al., 2003), and thus our results should be considered tentative. Fitch (1985) predicts that clutch size should increase with elevation and latitude. Our limited data on clutch size are inconsistent with Fitch's prediction but are insufficient to address the hypothesis that clutch size increases with elevation and latitude.

Frequency of reproduction in *A. piscivorus* at Rocky Grove appears to be variable and less than biennial on average. Reproductive histories of individual adult female *A. piscivorus* at Rocky Grove indicate that many snakes reproduced on a less than biennial basis. Twelve individuals were not pregnant for two or more consecutive years. The total percentage of pregnant females (18.4%) is also extremely low and is consistent with a less than biennial frequency of reproduction; however, this finding is based on a low sample size. The proportion of pregnant to non-pregnant females within a sample from a population has been used to infer frequency of reproduction with percentages of 50% or lower indicating biennial reproduction (Gibbons, 1972; Scott et al., 1995; Ford, 2002). This approach to estimating frequency of reproduction might be misleading if data from only one or two years are used because reproductive output in snakes shows annual variation and is related to prey abundance each year (Seigel and Ford, 1987; Diller and Wallace, 2002; Ford et al., 2004). Annual variation in prey availability might result in synchrony of reproduction in snakes. Determination of female reproductive state by palpation can potentially be misleading because it may not possible to distinguish between secondary vitellogenic follicles and embryos (Seigel and Ford, 1987). Four years of data on percentage of pregnant to non-pregnant females are presented in this study, and all indicate a low frequency of reproduction. It is unlikely that all four of these years had uncharacteristically low prey availability, and we feel confident in our assessment of the reproductive state of the female snakes reported herein. If we had mistaken secondary vitellogenic follicles for embryos this would over estimate the percentage of pregnant females. The average percentage of pregnant females from the present study (18.4%) is the lowest reported for any *A. piscivorus* population. Frequency of reproduction in *A. piscivorus* is geographically variable. Seventy percent of adult females from one Texas population were pregnant (Ford et al., 2004). Less than 50% of adult female *A. p. leucostoma* in northeast Texas were pregnant (Ford, 2002), while 42% were pregnant in another study of the subspecies (Burkett, 1966). Proportion of pregnant to non-pregnant adult female *A. p. piscivorus* ranged from 50% in one year to 24% in a South Carolina population (Scott et al., 1995). Eighty-three percent of adult female *A. p. piscivorus* from a Virginia location were gravid (n = 29, Blem, 1981). *Agkistrodon piscivorus conanti* in Florida showed a biennial frequency of reproduction (Wharton, 1966). In Virginia and Louisiana, *A. piscivorus* appear to reproduce annually (Kofron, 1979; Blem, 1981; Blem and Blem, 1995). Many temperate zone pitvipers exhibit biennial frequency of reproduction, although this is almost certainly dependent upon resource availability and may vary among years (Gibbons, 1972; Beaupre, 2002; Diller and Wallace, 2002). Frequency of reproduction ranged from annual to triennial in a population of *C. oreganus oreganus* in Idaho, and proportion of reproductive females was correlated to prey density the prior year (Diller and Wallace, 2002).

Mating.—Ten observations of bisexual pairing and one observation of actual copulation in late summer confirm a late summer mating period in this population. Four observations of bisexual pairing in April and May suggest Rocky Grove *A. piscivorus* may also mate in the spring. Bisexual pairing is one of the criteria used for determining timing of mating in snakes (Schuett, 1992; Aldridge and Duvall, 2002; Zaidan et al., 2003).

Previous knowledge on timing of mating in *A. piscivorus* comes primarily from indirect observations such as bisexual pairing, male–male agonistic behavior, or hormonal cycles, and only one observation of actual copulation has been published. Several observations of reproductive behavior in *A. p. leucostoma* support a late summer mating period similar to that observed at Rocky Grove. Combat, presumably between two males, was observed in *A. p. leucostoma* in Missouri on 4 September (Perry, 1978). In northwest Arkansas bisexual pairing and male–male agonistic behavior occurred in late summer and early Autumn and coincided with peaks in plasma testosterone in males (Zaidan et al., 2003). Martin (1984) observed courtship and male–male agonistic behavior on 30 September in St. Martin Parish, Louisiana, but actual coition was not observed. Other reports indicate mating may occur at other times of the year. Ramsey (1948) observed two *A. p. leucostoma* in Texas in combat on 20 June. A pair of *A. p. leucostoma* was observed in copulation on 10 March near New Orleans, Louisiana (Beyer, 1898). Male *A. p. leucostoma* in Alabama showed peaks in both spermiogenic activity and plasma testosterone levels in July and August (Johnson et al., 1982). Snakes from this Alabama population apparently can mate upon emergence from hibernation and any time thereafter, but copulation was not observed in the field (Johnson et al., 1982). Gloyd and Conant (1990:240) suggest that mating probably occurs when females ovulate in early spring in *A. p. leucostoma*. Wharton (1969) observed bisexual pairings of *A. p. conanti* on Sea Horse Key in every month of the year but January, and considered this evidence that mating occurs almost year round in that population. Determination of timing of mating without observing actual copulation may lead to erroneous conclusions, and further studies on sexual activity and hormone cycles in *A. piscivorus* are needed. Clearly timing of mating varies geographically in *A. piscivorus*. Geographic variation in the time of sexual activity in snakes has also been documented in *Crotalus horridus* (Aldridge and Brown, 1995) and *Crotalus oreganus oreganus* (Aldridge and Duvall, 2002).

It is interesting to note that no male–male combat was observed in Rocky Grove *A. piscivorus* despite extensive time spent in the field observing these snakes. Lack of observed male combat may indicate additional behavioral variation in the mating system of the Rocky Grove population compared to others.

Feeding by pregnant females.—The observation that pregnant females produced stools while in captivity may suggest that these animals were feeding; however, capture may have induced defecation of feces retained from meals ingested prior to pregnancy in these snakes (Lillywhite et al., 2002). Pregnant female *A. piscivorus* were also observed in a foraging posture, providing further evidence that these snakes may feed while pregnant (Hill, 2004). Zaidan et al. (2003) suggested that female *A. piscivorus* in northwest Arkansas do not feed when pregnant. Lack of feeding in pregnant females was also observed in *Crotalus horridus* (Keenlyne, 1972; Reinert and et al., 1984). It is often assumed that pregnant female pitvipers do not feed, but little data exist in the literature on this subject.

Summary.—Several facts indicate that *A. piscivorus* at Rocky Grove is limited in energy acquisition rates. Body size and degree of SSD of Rocky Grove snakes are among the lowest reported for the species anywhere in the range. Reproductive output also appears low based on our limited data. Rocky Grove *A. piscivorus* also have growth rates that are low relative to other *A. piscivorus* populations and temperate zone pitvipers in general. The limitation in energy acquisition rates is probably due to low or seasonally variable prey abundance.

Environmental temperature can limit activity time and thus energy acquisition rates in terrestrial ectotherms (Dunham et al., 1989; Beaupre, 1995). Limitation of activity time due to high environmental temperatures is unlikely for *A. piscivorus* in Rocky Grove. Wills and Beaupre (2000) studied operative and body temperature distributions in *C. horridus* at a location similar to Rocky Grove in northwest Arkansas. They found no evidence for thermal constraints on surface activity due to high environmental temperatures. Low environmental temperatures could possibly limit activity especially in spring and fall. A mechanistic explanation of the reduced body size and reproductive output in Rocky Grove *A. piscivorus* would require a more detailed study of their energy budget and thermal environment, and comparative work with other populations.

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