ing we cannot separate the two alternative mechanisms of predator escape.

The overall low predation rate (9.5%) by largemouth bass in experimental ponds suggests that bass are unlikely to be a major predator of hatchling *Trachemys scripta.* The fact that no live turtles were eaten reinforces this conclusion. Additionally, a study of the stomach contents of largemouth bass in a South Carolina reservoir with an abundance of *T. scripta* and other numerous species (Gibbons, 1970; Gibbons et al., 1981), revealed that no turtles were eaten (n = 765 bass dissected; Bennett and Gibbons, 1972). Bass may be occasional predators on hatchling turtles but the evidence strongly suggests that turtles are not a primary food source. Other large aquatic predators (e.g., juvenile alligators), however, may be important in shaping the population dynamics and life history of aquatic turtles through age- or size-specific mortality.

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WINTER BREEDING OF *CRYPTOBRANCHUS ALLEGANIENSIS BISHOPI* IN ARKANSAS.—Breeding occurs in late summer or early fall throughout the range of the eastern hellbender, *Cryptobranchus alleganiensis alleganiensis,* and in at least one of the four populations of the Ozark hellbender, *C. a. bishopi* (Nickerson and Mays, 1973). However, Baker (1963) found that the testes of *C. a. bishopi* collected in the Spring River, Arkansas, contained spermatozoa from mid-Aug. to early Dec. Further, Peterson (1985) captured seven gravid females in Dec. in the Spring River; two males were captured that were expelling seminal fluid. Therefore, the objective of this study was to determine whether the hellbender population in the Spring River has a unique breeding season. Also, we compared the seasonal changes in mass of gonads of Spring River hellbenders with changes in reproductive organs of the *C. a. alleganiensis* population in the Niangua River, Missouri, which breeds in late summer or early fall (Dundee and Dundee, 1965; Taber et al., 1975; Peterson, 1988).

Methods.—Hellbenders were collected 1–3 times monthly from Sept. 1979–Oct. 1980 in the Niangua River in Laclede County, Missouri, and from Oct. 1985–Sept. 1986 in the Spring River in Fulton County, Arkansas. We made a final

TABLE 1. TOTAL LENGTH (MM), BODY MASS (G), AND MASS OF BOTH GONADS (G) OF MATURE HELLBENDERS. CV = Coefficient of variation.

			Total length	Body mass		Gonad mass	
Population	Sex	n	Range	Range	CV	Range	CV
Niangua R.	M	45	344–579	275–1624	40.2%	1.8–30.6	91.8%
	F	73	390–569	432–1237	28.3%	6.9–114.5	80.3%
Spring R.	M	31	421–558	445–1190	20.5%	1.4–31.8	70.7%
	F	31	439–611	615–1956	29.2%	11.7–148.3	68.3%

trip to the Spring River on 31 Jan. 1987 to search for any indication of breeding. Hellbenders were captured by hand or with a dip net beneath overturned rocks or logs during daylight. Iced specimens were overanesthetized in a tricaine solution within 24 h of capture. We measured TL to the nearest 1 mm and body mass (BM) to the nearest 1 g. Ovaries, oviducts, and testes of Niangua hellbenders were placed in an alcohol-formalin-acetic acid fixative for 24 h and stored in 70% ethanol before mass was determined to the nearest 0.1 g. Reproductive organs of Spring River hellbenders were measured before preservation immediately after death.

Percentages of BM represented by the gonads (GSI) were calculated for each salamander. Packard and Boardman (1988) criticized the use of ratios to scale data that vary allometrically with body size. They suggested employing linear regression and analysis of covariance (ANCOVA) to reduce the variation in a physiological variable associated with body size. DeVlaming et al. (1982) also recommended the use of ANCOVA to determine which gonadal mass-body size model is most suitable for a gonadal index. However, ratios are adequate for scaling data when the coefficient of variation for the denominator variable is small relative to the coefficient of variation for the numerator variable (Anderson and Lydic, 1977). Also, Sokal and Rohlf (1981) do not recommend the use of least squares regression and ANCOVA unless the independent variable is measured without error or target values of the independent variable are set.

Diameters of 20 oocytes of the largest size class from one ovary were measured to the nearest 0.5 mm. All means are presented ±1 SE.

Maximum-minimum thermometers were fastened under water near the bank of both streams from fall 1980 to fall 1981. Water temperature ranges were recorded monthly.

Results.—Males in the Niangua River (Table 1) could be identified externally from late July into Dec. by swelling around the cloaca. In Spring River males, swelling was most evident from late July–Feb.; slight swelling was present the remainder of the year. Males in the Spring River expelled seminal fluid copiously on 13 Jan. 1986 and in small quantities on 31 Jan. 1987.

Male GSI values decreased rapidly after breeding in Sept. in the Niangua River and remained low until spring (Fig. 1). Increase in mean GSI values of Niangua males occurred mostly between early May (0.47 ± 0.06%, n = 4) and Aug. (2.95 ± 0.46%, n = 4). Testes of Spring River hellbenders also decreased rapidly in size after breeding (Fig. 2). As they regressed, the testes often consisted of two or more small lobes. The mean GSI value was least during March (0.42 ± 0.07%, n = 3). It was greatest during Aug. (3.10 ± 0.02%, n = 2) and Dec. (3.07 ± 0.70%, n = 3).

Kruskal-Wallis tests indicated that the ratio of testicular mass to BM differed significantly among seasons (four 3 mo periods) in both the Niangua ($H = 29.2, P < 0.001$) and Spring River populations ($H = 19.8, P < 0.001$). A nonparametric, multiple comparison procedure (Dunn, 1964; Zar, 1984) indicated a significant difference in the relative testicular mass of Niangua males during July–Sept. (the period prior to breeding) and all other 3 mo periods (Table 2). However, the relative testicular mass of Spring River males during Oct. to early Jan. (prior to breeding) did not differ significantly from the relative testicular mass during July–Sept.

Two Niangua females with eggs in their body cavities and oviducts were collected on 25 Sept. 1980. Fifteen eggs were observed entangled in algae. In the Spring River, one female collected on 4 Jan. 1986 had a few ova in the coelom and oviducts. Six eggs were observed entangled in vegetation on 13 Jan. in the Spring River. On

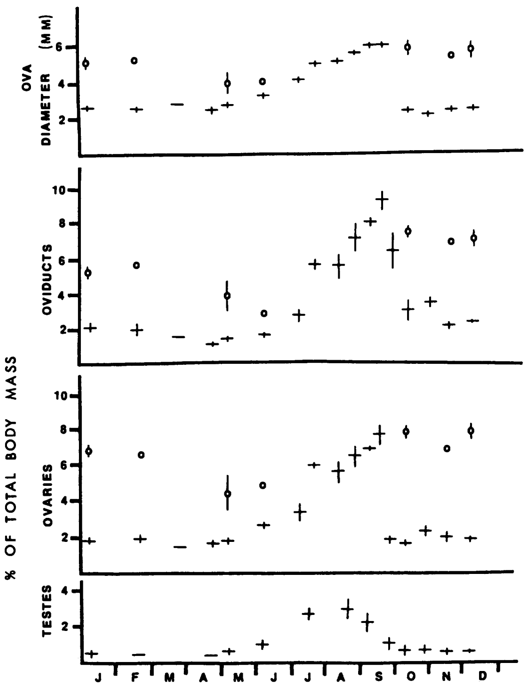

Fig. 1. Mean (±1 SE) diameter of ova and mean relative mass of oviducts, ovaries, and testes of Niangua River hellbenders. Circles represent females that did not oviposit during previous breeding season.

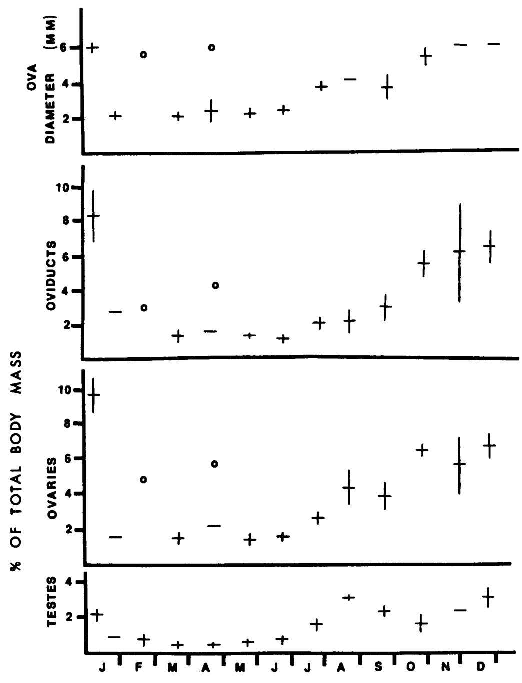

Fig. 2. Mean (±1 SE) diameter of ova and mean relative mass of oviducts, ovaries, and testes of Spring River hellbenders. Circles represent females that did not oviposit during previous breeding season.

25 Jan. 1986, three egg clutches were found in open water. Eggs were collected from each clutch but failed to develop. On 20 Feb., a clutch of embryos was found about 20 d old based on the developmental stages of Smith (1912b). On 31 Jan. 1987, a single clutch of eggs was found in the Spring River.

Ovaries represented a maximum mean percentage of BM of Niangua females on 17 Sept. (7.82 ± 0.49%, n = 9), just prior to ovulation. By 10 Dec., the mean GSI had decreased to 1.93 ± 0.09% (n = 4), excluding the females that had retained their clutch. The GSI was lowest in early spring, but increased greatly between early May and Sept. In the Spring River, the mean GSI was greatest in early Jan. (9.79 ± 1.02%, n = 2), also just prior to ovulation. A female captured on 25 Jan. had oviposited; the GSI was 1.62%. The mean GSI had decreased by March to 1.46 ± 0.91% (n = 4). Relative mass of ovaries remained low through spring. Increase occurred mostly in late summer. However, until Dec., diameters of ova were less than the 6 mm size attained by ova of females just prior to ovulation in Pennsylvania (Smith, 1912a) and in the Niangua River.

Kruskal-Wallis tests also indicated that the ratio of ovarian mass to BM differed significantly among 3 mo periods in the Niangua (H = 41.9, $P < 0.001$) and Spring River populations (H = 19.9, $P < 0.001$). A significant difference was found in the magnitude of relative ovarian mass of Niangua females during July–Sept. and all other 3 mo periods. However, the relative ovarian mass of Spring River females during Oct.–early Jan. did not differ significantly from the relative ovarian mass during July–Sept.

Seasonal changes in relative mass of oviducts exhibited the same pattern as ovaries. Loss of oviductal mass occurred immediately after oviposition in Niangua females due to secretion of the gelatinous material that covered each egg. Oviducts continued to regress after oviposition. Enlargement occurred during late spring and summer. In the Spring River, relative oviductal mass increased greatly during autumn. After oviposition in Jan., relative mass of oviducts remained low during spring and summer.

TABLE 2. PAIRWISE COMPARISONS OF RATIOS OF GONAD MASS TO BODY MASS BETWEEN 3 MO PERIODS FOR BOTH SEXES. Spring River comparisons above diagonal. Niangua River comparisons below diagonal.

	Jan.–March		April–June		July–Sept.		Oct.–Dec.[a]	
	M	F	M	F	M	F	M	F
Jan.–March			ns	ns	*	ns	*	*
April–June	ns	ns			*	ns	*	*
July–Sept.	*	*	*	*			ns	ns
Oct.–Dec.	ns	ns	ns	ns	*	*		

* Significant at an experimentwise error rate of $\alpha = 0.05$.
[a] Includes two male and two female hellbenders caught in early Jan. (before spawning) in the Spring River.

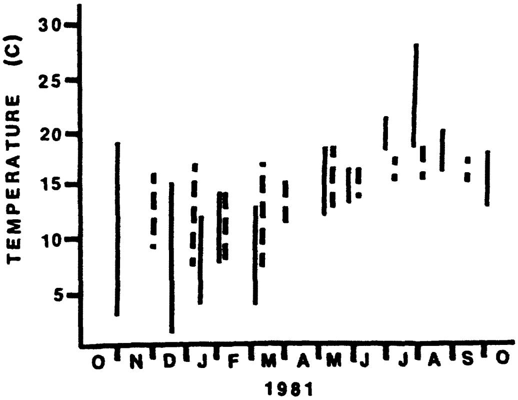

Fig. 3. Maximum and minimum temperatures between readings in the Niangua River (solid lines) and Spring River (dashed lines).

Although ova were produced annually by all females, 13 of 40 females collected between 9 Oct. and 5 June in the Niangua River had not oviposited during the previous breeding period. The two females collected on 9 Oct. that had not spawned had viable mature oocytes based on histological examination; however, the other 11 females had atretic oocytes (Ingersol, 1982). Two of 12 females collected between Feb. and July in the Spring River retained ova. One (captured on 20 Feb.) had many oocytes that were enlarged and nearly translucent. These females (from both rivers) did not appear physically impaired. Also the maturing oocytes for the next breeding season had a mean diameter similar to that of females that had spawned. Each female was producing a clutch for the coming breeding season despite protracted atresia of the previous clutch.

The monthly water temperature range of the Spring River was often narrower than that of the Niangua River (Fig. 3). Also the Spring River was generally cooler in summer and warmer in winter. However, the minimum temperature in the Niangua River during Sept. (1981), when *C. a. alleganiensis* begin breeding, was not lower than the minimum temperature in Nov. (1980) in the Spring River, more than a month before breeding occurs there.

Discussion.—*Cryptobranchus a. alleganiensis* breed between late Aug. and early Oct. in Pennsylvania (Smith, 1912a), West Virginia (Green, 1933), New York (Bishop, 1941), Tennessee (Huheey and Stupka, 1967), Alabama (Mount, 1975), and Indiana (Kern, 1986). Peterson (1985) also found that *C. a. alleganiensis* breed in Sept. in the Big Piney and Gasconade rivers in Missouri. Dundee and Dundee (1965) reported collecting an egg mass on 3 Sept. 1954 and two gravid females on 14 Nov. 1954 in the Niangua River. Thus they inferred that breeding occurred over a period of 2 mo. However, they did not indicate whether they found females that were not gravid on the latter date. Possibly these two females had ova that were atretic because one female collected on 15 Nov. in this study had ova that superficially appeared normal but were shown to be atretic (Ingersol, 1982). Smith (1912a) also captured a few females after the breeding season in Pennsylvania with an entire clutch of eggs that appeared to be degenerating.

Dundee and Dundee (1965) reported that *C. a. bishopi* from the Spring River had maturing ova that were 5 mm in diameter in late Aug. but that peak size of ova was attained in Oct. They suggested that *C. a. bishopi* populations oviposit 2 mo later than *C. a. alleganiensis*, although no complete separation of the breeding season occurs. However, eggs of *C. a. bishopi* have been found in the North Fork River from 13 Sept.–8 Oct. (Nickerson and Mays, 1973; Nickerson and Tohulka, 1986), similar to the spawning time of *C. a. alleganiensis*. Further, Dundee and Dundee (1965) reported examining only 14 *C. a. bishopi*. Of these 14, two were from the Eleven Point River, and none was from the Current River, the other two *C. a. bishopi* populations. Although we have no information about the breeding time of *C. a. bishopi* in the Current River, we have obtained a few embryos from the Eleven Point River in late Nov. Thus the winter breeding in the Spring River is possibly unique among populations of both subspecies.

Dundee and Dundee (1965) hypothesized that the stenothermal conditions of the Spring River resulted in a later breeding season there. The warmer minimum temperatures in the Spring River during fall and early winter could be contributing to the later breeding season. Mean ovum diameter was not a maximum until Dec., and mean GSI values of females increased continually through fall and early winter. However, relative gonadal mass during Oct.–early Jan. in the Spring River population did not differ significantly from the relative gonadal mass during July–Sept. for either sex. This may be due in part to the small monthly sample sizes affecting the power of the multiple contrasts procedure. But at least male Spring River hellbenders may be ready to breed in early fall, since Baker (1963) found that testes contained spermatozoa from mid-Aug. to Dec. Experimental studies are needed to examine what environmental cues are necessary to initiate breeding.

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