



## **Fecundity in the Hellbender, *Cryptobranchus alleganiensis***

Milton S. Topping; Chris A. Ingersol

*Copeia*, Vol. 1981, No. 4. (Dec. 29, 1981), pp. 873-876.

Stable URL:

<http://links.jstor.org/sici?sici=0045-8511%281981%29%3A1981%3A4%3C873%3AFITHCA%3E2.0.CO%3B2-0>

*Copeia* is currently published by American Society of Ichthyologists and Herpetologists.

---

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/asih.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

---

The JSTOR Archive is a trusted digital repository providing for long-term preservation and access to leading academic journals and scholarly literature from around the world. The Archive is supported by libraries, scholarly societies, publishers, and foundations. It is an initiative of JSTOR, a not-for-profit organization with a mission to help the scholarly community take advantage of advances in technology. For more information regarding JSTOR, please contact [support@jstor.org](mailto:support@jstor.org).

TABLE 2. AVERAGE PERCENTAGE OF STRATIFICATION (0% = SURFACE, 100% = BOTTOM) ON THE TWO OBSERVATION NIGHTS FOR EACH OF THREE SIZES OF EACH SPECIES (OF *Ambystoma*) AT FIVE TIMES DURING THE NIGHT.

Time	Small	Medium	Large
<i>A. maculatum</i>			
1800	36-42	50-46	88-94
2100	32-44	58-38	97-97
2400	18-42	56-51	95-98
0300	32-42	63-52	100-97
0600	100-42	66-46	100-96
<i>A. opacum</i>			
1800		75-57	84-84
2100		52-52	56-76
2400		62-56	53-77
0300		62-60	81-100
0600		100-100	100-100
<i>A. talpoideum</i>			
1800	41-45	26-36	41-45
2100	45-45	27-32	42-45
2400	57-45	20-24	45-45
0300	60-60	41-33	57-44
0600	100-100	44-45	100-100

diversity of the prey populations relative to those in other areas.

Our data indicate that different species and/or stages can exhibit different stratification behaviors, at least under the stated conditions; factors mentioned earlier may alter the patterns. Even so, distinct strata of stages or species were not observed, and the high variation within a given group negated statistical separation of the data. Percentages of stratification depths did not change with absolute water depth. The uniformity of diets does not indicate that these behaviors are effective in reducing food competition. Although it appears that the larvae feed to some degree at all times, the increased feeding rate at dusk (Anderson and Graham, 1967), indicates that the intensity of feeding behavior is elevated by reduced light intensity even though the salamanders and plankton are always in contact. This is further supported by the lack of increase in the number of benthic macroinvertebrates per gut during the day. Thus, it seems the larvae must stratify to remain in contact with the greatest concentration of the most abundant but smallest prey at a time when feeding is behaviorally most intense. Ex-

act interpretation of seeming differences in stratification depths will have to wait on further data involving monospecific populations and other pertinent factors.

*Acknowledgments.*—J. P. Kelly, M. T. Christensen and M. A. Stevens aided in data collection. Ray R. Vaughn, Deputy Regional Director (Atlanta, Georgia) of the Fish and Wildlife Service, and Travis H. McDaniel, Manager of Noxubee National Wildlife Refuge, kindly provided necessary permits and other assistance.

#### LITERATURE CITED

- ANDERSON, J. D., AND R. E. GRAHAM. 1967. Vertical migration and stratification of larval *Ambystoma*. *Copeia* 1967:371-374.
- ANDERSON, J. E., AND G. K. WILLIAMSON. 1974. Nocturnal stratification in the larvae of the mole salamander, *Ambystoma talpoideum*. *Herpetologica* 30:28-29.
- HASSINGER, D. D., AND J. D. ANDERSON. 1970. The effect of lunar eclipse on nocturnal stratification of larval *Ambystoma opacum*. *Copeia* 1970:178-179.
- , AND G. H. DALRYMPLE. 1970. The early life history and ecology of *Ambystoma tigrinum* and *Ambystoma opacum* in New Jersey. *Amer. Midl. Nat.* 84:474-495.
- LAFRENTZ, K. 1930. Beitrage zur Herpetologie Mexikos. I. Untersuchungen uber die Lebensgeschichte mexikanischer *Ambystoma*-Arten. *Abh. Berlin Mus. Naturwiss.* 6:91-127.
- WORTHINGTON, R. D. 1968. Observations on the relative sizes of three species of salamander larvae in a Maryland pond. *Herpetologica* 24:242-246.
- . 1969. Additional observations on sympatric species of salamander larvae in a Maryland pond. *Herpetologica* 25:227-229.
- LYN C. BRANCH AND RONALD ALTIG, *Department of Biological Sciences, Mississippi State University, Mississippi State, Mississippi 39762*. Accepted 8 Sept. 1980.

*Cop.*, 1981(4), pp. 873-876  
© 1981 by the American Society of  
Ichthyologists and Herpetologists

**FECUNDITY IN THE HELLBENDER, *CRYPTOBRANCHUS ALLEGANIENSIS*.**—The hellbender, *Cryptobranchus alleganiensis*, is a large, long-lived salamander which inhabits many clear cool streams of the central and eastern United States. The species contains two

TABLE 1. NUMBER OF MATURE EGGS IN EACH OVARY OF *Cryptobranchus a. alleganiensis* AND *C. a. bishopi*.

<i>C. a. alleganiensis</i>				<i>C. a. bishopi</i>			
Total length (mm)	First ovary	Second ovary	Difference	Total length (mm)	First ovary	Second ovary	Difference
408	87	82	5	525	297	225	72
432	128	111	17	503	426	369	57
432	142	114	28	464	260	247	13
442	139	113	26	467	204	202	2
465	195	175	20	408	139	111	28
472	233	183	50	541	243	221	22
505	261	211	50	461	199	191	8
517	268	240	28	463	243	172	71
525	341	304	37	394	147	123	24

subspecies, *C. a. alleganiensis* and *Cryptobranchus a. bishopi*, both of which occur in Missouri. The former is distributed throughout the range of the species, whereas the latter is restricted to the North Fork of the White River in south-central Missouri and to the Black River system in southeastern Missouri and northeastern Arkansas. In Missouri, the subspecies are geographically isolated with *C. a. alleganiensis* occurring in northward flowing tributaries of the Missouri River in the Ozark Uplands physiographic region.

In general, adult *C. a. alleganiensis* are larger and weigh more than adult *C. a. bishopi*, although there is substantial size variation between populations of the subspecies (Peterson, 1979, Nickerson and Mays, 1973). In Missouri, female *C. a. alleganiensis* are reported to reach sexual maturity at 380 mm total length and breed from Sept. until Nov. (Taber et al., 1975), while female *C. a. bishopi* are reported to reach sexual maturity at about 385 mm total length and to breed from Sept. until Oct. (Nickerson and Mays, 1973). Smith (1907) reported that an average sized female *C. a. alleganiensis* will lay about 450 eggs, while Nickerson and Mays (1973) reported that three female *C. a. bishopi* maintained in the laboratory laid an average of 270 eggs. Nickerson and Mays (1973) agreed with Smith (1907) that larger, and presumably older, females will lay more eggs. Our study was undertaken to determine fecundity in populations of the two subspecies in which age and growth had been determined (Taber et al., 1975; Peterson, 1979).

*C. a. alleganiensis* were collected from the Niangua River, Laclede Co., Missouri and *C. a. bishopi* from the North Fork of the White River,

Ozark Co., Missouri during September 1979. All females >380 mm total length were gravid. Individuals were weighed ( $\pm 1$  g) and their total lengths measured ( $\pm 1$  mm) in the laboratory. Ovaries and oviducts were removed and preserved in alcohol-formalin-acetic acid fixative. After a minimum of 24 h to permit tissue infiltration, the ovaries were dissected free of the oviducts, weighed ( $\pm 0.0001$  g) and the apparently mature eggs (i.e., >3.5 mm diameter) counted. Additional *C. a. alleganiensis* were collected at approximately monthly intervals after September 1979 by one of us (CAI) to study gametogenesis and these were used to deduce the number of eggs retained or resorbed.

One ovary was usually heavier than the other in both subspecies, so the eggs from each ovary were counted separately when possible. Analysis of those data (Table 1) using a paired t-test indicated that one ovary systematically contained more eggs than the other in both *C. a. alleganiensis* ( $t = 5.87$ ,  $df = 8$ ,  $P < 0.001$ ) and *C. a. bishopi* ( $t = 3.69$ ,  $df = 8$ ,  $0.01 > P > 0.005$ ). The side of the animal from which each ovary was taken was not recorded, thus we do not know if the ovary from one side systematically contains more eggs than the other.

The relationships for each subspecies between the number of mature eggs and total length were analyzed using Model II regression (Sokal and Rohlf, 1969) (Fig. 1). Although Model I analysis yielded virtually identical results, Model II was selected because the error in measurement of total length is sometimes large. Although scatter about the regression for *C. a. bishopi* ( $r^2 = 0.53$ ) was greater than for *C. a. alleganiensis* ( $r^2 = 0.99$ ), both showed a significant positive linear relationship. The num-

ber of mature eggs in *C. a. alleganiensis* can be predicted using

$$\text{Number of Mature Eggs} = 3.495 \text{ Total Length (mm)} - 1,260.34$$

and the number of mature eggs in *C. a. bishopi* by

$$\text{Number of Mature Eggs} = 2.685 \text{ Total Length (mm)} - 810.01.$$

The slopes of the two regressions did not differ significantly ( $t = 0.11$ ,  $df = 15$ ), but the y-intercept of *C. a. bishopi* was significantly larger than for *C. a. alleganiensis* ( $t = 12.59$ ,  $df = 15$ ,  $P < 0.001$ ).

Data from *C. a. alleganiensis* collected after September 1979 suggest that not all gravid females lay their eggs during the same season. Of the 27 females collected during Oct. 1979 to Feb. 1980, 8 collected after 15 Nov. 1979 were apparently gravid. The relationship between the number of mature eggs retained and total length of those eight females is similar to that obtained prior to egg laying (Fig. 1). The tendency to retain eggs was not restricted to any particular size class.

Spent female *C. a. alleganiensis* collected after September 1979 still contained some apparently mature ova. Although the scatter was greater ( $r^2 = 0.52$ ) than for females prior to egg laying, a significant positive linear relationship still existed between the number of mature eggs remaining in the ovary (to be resorbed?) and total length. The relationship was

$$\text{Number of Mature Eggs Remaining} = 0.470 \text{ Total Length (mm)} - 119.45.$$

Fecundity, or the number of mature eggs laid by a female, was obtained by subtracting the equation for the number of mature eggs remaining, from the equation used to predict the number of mature eggs contained. The resulting equation was

$$\text{Fecundity} = 3.025 \text{ Total Length (mm)} - 1,140.89.$$

Minimum sizes of sexually mature females of *C. a. alleganiensis* (390 mm) and *C. a. bishopi* (394 mm) collected in this study agree with those reported by Taber et al. (1975) and Nickerson and Mays (1973). Application of age-length relationships derived by Taber et al. (1975) for *C. a. alleganiensis* and Peterson (1979) for *C. a. bishopi* suggested that *C. a. bish-*

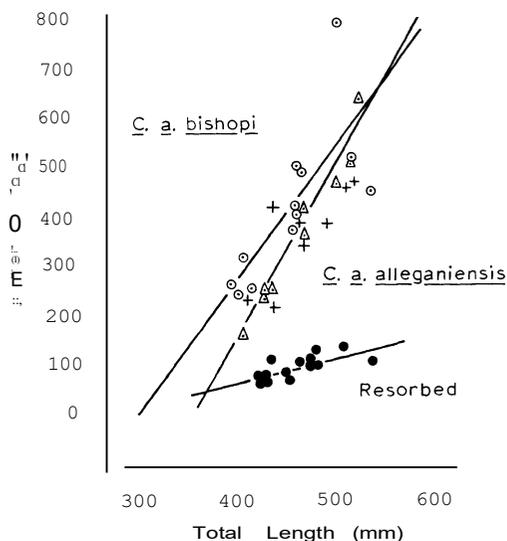


Fig. 1. Relationship between number of mature eggs and total length in *Cryptobranchus a. alleganiensis* triangles ( $N = 9$ ) and *C. a. bishopi* circles ( $N = 12$ ), and between number of eggs resorbed and total length in *C. a. alleganiensis* dots ( $N = 14$ ). The number of mature eggs retained by *C. a. alleganiensis* collected after the breeding is indicated by plus sign.

*opi* is slightly older at sexual maturity (8-9 years) than is *C. a. alleganiensis* (7-8 years).

Difference in the number of mature eggs in *C. a. alleganiensis* prior to egg laying versus the number of eggs which remain afterward indicates that about 76% of the eggs are laid and the remainder are resorbed. If the frequency of gravid females obtained between Oct. 1979 and Feb. 1980 is representative of the population, then only about 50% of the apparently mature eggs present during any given year will be laid. Nevertheless, the reproductive potential for *C. a. alleganiensis* is still large. Egg retention and resorption in *C. a. bishopi* were not studied but, given the similarity between the total number of eggs and total length in the two subspecies and the genetic uniformity present throughout the range of the species (Merkle et al., 1977), a generally similar pattern might be expected.

Presence of a significantly larger y-intercept and statistically identical slope for the relationship between number of mature eggs for *C. a. bishopi* in comparison to *C. a. alleganiensis* suggests that a mature female *C. a. bishopi* of equal length should produce more eggs and perhaps be more fecund. Thus, it is possible that a pop-

ulation of smaller average sized *C. a. bishopi* might possess the same reproductive potential as a population of larger sized *C. a. alleganiensis* with an identical number and age distribution.

*Acknowledgments.*-R. F. Wilkinson, Jr., D. Moll and Charles Coatney helped in the field. Max A. Nickerson and Chris L. Peterson reviewed the manuscript.

#### LITERATURE CITED

- MERKLE, D. A., S. I. GUTTMAN AND M.A. NICKERSON. 1977. Genetic uniformity throughout the range of the hellbender, *Cryptobranchus alleganiensis*. *Copeia* 1977:549-553.
- NICKERSON, M.A., AND C. E. MAYS. 1973. The hellbenders: North American "giant salamanders." Milwaukee Public Museum. Publ. Biol. Geol. No. 1.
- PETERSON, C. L. 1979. Age and growth of the Ozark hellbender. Unpubl. Master's Thesis. Southwest Missouri State University, Springfield.
- SMITH, B. G. 1907. The life history and habits of *Cryptobranchus alleganiensis*. *Biol. Bull.* 13:5-39.
- SoKAL, R.R., AND F.J. ROHLF. 1969. *Biometry*. Freeman, San Francisco.
- TABER, C. A., R. F. WILKINSON, Jr. AND M. S. TOPPING. 1975. Age and growth of hellbenders in the Niangua River, Missouri. *Copeia* 1975:633-639.
- MILTON S. TOPPING AND CHRIS A. INGERSOL, *Department of Life Sciences, Southwest Missouri State University, Springfield, Missouri 65802.* Accepted 24 Sept. 1980.

*Copeia*, 1981(4), pp. 876-879  
© 1981 by the American Society of  
Ichthyologists and Herpetologists

GEOGRAPHIC VARIATION OF PROTEINS AND CALL IN *RANA PIP/ENS* FROM THE NORTHCENTRAL UNITED STATES.-The northern leopard frog, *Rana pipiens*, is found across much of the northern one-third of the United States. East of the Rocky Mountains, the southern margin of its range adjoins that of the southern leopard frog, *R. sphenoccephala* (*R. utricularia*) in the east and the plains leopard frog, *R. blairi* in the central United States. Although the species are largely allopatric, the ranges of adjacent forms may frequently overlap and occasional hybrid frogs may be found within these areas of sympatry (Pace, 1974; Brown and

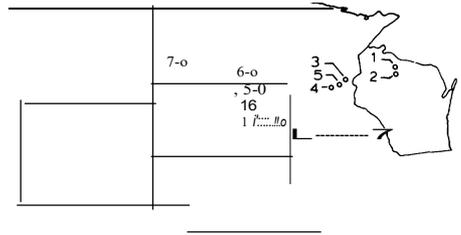


Fig. 1. Map of collecting sites.

Brown, 1972; Axtell, 1976; Dunlap and Kruse, 1976; Lynch, 1978).

Cope (1889) recognized two subspecies of leopard frogs (*R. virescens* = *R. pipiens*) in the northern United States; *R. virescens virescens* in the east and *R. v. brachycephala* west of the Great Plains (type locality = Yellowstone River). Although a number of investigators were unable to distinguish between the putative subspecies on the basis of the morphological criteria proposed by Cope (Kellogg, 1932; Trapido and Clausen, 1938; Moore, 1944), Kauffeld (1937) considered Cope's subspecies to be distinct enough to warrant their recognition as separate species. The fourth edition of the Check List of North American Amphibians and Reptiles (Stejneger and Barbour, 1939) followed Kauffeld in assigning specific rank, but in the sixth edition (Schmidt, 1953) they are recognized but again reduced to subspecific rank. In a review of the status of these northern populations, Wright and Wright (1949) are uncertain of the validity of *R. p. brachycephala* and suggest that if it exists, it is western with the interface between the two forms bisecting the states of Minnesota and Iowa.

Thus, the question of the degree of east-west differentiation of *R. pipiens* is still unanswered and interpretations based on traditional morphological data are open to disagreement. Consequently, the present study was undertaken in an effort to resolve the problem by examining the patterns of protein variation across a transect from the Yellowstone River in Montana into northern Wisconsin and comparing mating calls from populations at each end of the transect.

*Materials and methods.*-The locations of the collection sites (Fig. 1) and the number of specimens in each sample follow. Wisconsin: 1) 0.4 km S Hicks Landing, Sailor Creek Flowage,