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Examination of Long-Term Growth of *Cryptobranchus alleganiensis* Predicted by Linear Regression Methods

Author s : Chris L. Peterson, Milton S. Topping, Robert F. Wilkinson, Jr., Charles A. Taber

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tion. This could provide a priming of the MCP circuits under natural conditions.

The drug regimen used previously to induce MCP in progesterone-primed, non-ovulating toads included vasotocin or mesotocin as well as PG, but it was not determined whether the peptide was really essential (Schmidt, 1984). The present study shows that MCP can be induced without exogenous peptide. It remains to be determined whether these peptides have some degree of facilitatory action.

The icv application of PG in progesterone-primed toads seems to be a reliable method for inducing MCP. This confirms that MCP can be induced pharmacologically, in the absence of ovulation (Schmidt, 1984). (Under natural conditions, MCP occurs only in gravid females.) The ability to induce MCP pharmacologically in non-ovulating female anurans, in the laboratory, and at the convenience of the investigator, should facilitate neurophysiological, neuroendocrinological, ethological, and evolutionary studies of anuran acoustic behavior.

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EXAMINATION OF LONG-TERM GROWTH OF *CRYPTOBRANCHUS ALLEGANIENSIS* PREDICTED BY LINEAR REGRESSION METHODS.—Analysis of life history patterns of a species depends on accurate assignment of age to individuals or cohorts. Aging methods which have been used on amphibians include examination of skeletal annuli (Peabody, 1961), counting testicular lobes (Organ, 1961), detection of discrete size classes (Hairston, 1983), and mark-recapture studies (Taber et al., 1975; Tilley, 1980; Peterson et al., 1983).

Life history studies of the hellbender, *Cryptobranchus alleganiensis alleganiensis* were made in 1971–73 by Taber et al. (1975) in the Niangua River, Missouri, and analogous studies of the Ozark hellbender, *Cryptobranchus alleganiensis bishopi* were made by Peterson et al. (1983) in 1977–78 in the North Fork River. Both subspecies of hellbenders were heat branded for mark and recapture studies, their mean monthly growth rates calculated as a function of total length (TL), and their ages deduced from the successive addition of mean monthly growth increments to length at transformation.

Based on the ages and growth rates of the two subspecies, Taber et al. (1975) and Peterson et al. (1983) deduced that 1) both subspecies live more than 25 years in their natural habitats, 2) there is no evidence supporting differential growth rates for the sexes, 3) growth is greater and more variable in *C. a. alleganiensis*, 4) females have higher age-specific survivorship in both subspecies and 5) individuals less than 5 years old are uncommon in both subspecies. However, variation in individual growth of both subspecies, together with decreasing growth at larger sizes, results in overlap of lengths in successive age classes of individuals greater than 430 mm TL and can result in biased estimates of age frequency (Westrheim and Ricker, 1978). In addition, juveniles were relatively less common in the recapture samples than in the

populations sampled (Taber et al., 1975; Peterson et al., 1983), which could result in overestimation of age based on the age-growth models. Consequently, interpretation of the age-specific aspects of the life history of *C. alleganiensis* is dependent on the accuracy of the growth-age models employed.

If there are errors in the independent variable, least squares regression (LS) provides biased, inconsistent estimators for the relationship between mean monthly growth (Y) and TL (X). Least squares regression will provide a functional relationship only if target values of X are set or if severe assumptions can be imposed on the problem, such as the properties of the distribution of measurement error and the covariance of the measurement error and random error term (Neter and Wasserman, 1974). However, the LS equation is still suitable for prediction (Bartlett, 1949). Ricker (1973) has suggested that when both variables are subject to natural variability and measurement error, the functional relationship between the two variables is best described by the geometric mean functional regression (GM), Wald's functional regression, or the Nair-Bartlett functional regression (N-B) with the N-B method being superior to Wald's method only if sample size is large.

From 1971 until 1973, 1,132 *C. a. alleganiensis* were marked and 306 recaptured, while 744 *C. a. bishopi* were marked and 180 recaptured from 1977 until 1978. Enough of the previously marked individuals of both subspecies were recaptured in 1980 to evaluate the various regression models as predictors of long-term individual growth.

*Methods.*—In Sept. 1980, 18 *C. a. alleganiensis* marked by Taber et al. (1975) and Wiggs (1977) in the Niangua River during 1971–74 and 26 *C. a. bishopi* marked by Peterson et al. (1983) in the North Fork River during 1977–78 were recaptured and measured to determine long-term growth. Additionally, 3 hellbenders marked by Taber et al. (1975) in the Niangua were recaptured by Max A. Nickerson in 1976 and were included in the analyses. Recaptured, marked individuals were anesthetized with tricaine and their TLs measured ( $\pm 1$  mm). Observed TLs were then compared to TLs predicted by GM, N-B and LS regressions computed from growth data collected by Taber et al. (1975) and Peterson et al. (1983). The equations for *C. a. alleganiensis* were

$$\Delta TL_{(mm)}/\text{month} = 6.3474 - 0.0122 TL_{(mm)} \\ \dots \text{(LS)}$$

$$\Delta TL_{(mm)}/\text{month} = 9.2048 - 0.0193 TL_{(mm)} \\ \dots \text{(GM)}$$

$$\Delta TL_{(mm)}/\text{month} = 6.5372 - 0.0122 TL_{(mm)} \\ \dots \text{(N-B)}$$

while the equations for *C. a. bishopi* were

$$\Delta TL_{(mm)}/\text{month} = 8.5715 - 0.0192 TL_{(mm)} \\ \dots \text{(LS)}$$

$$\Delta TL_{(mm)}/\text{month} = 9.3289 - 0.0214 TL_{(mm)} \\ \dots \text{(GM)}$$

$$\Delta TL_{(mm)}/\text{month} = 6.9375 - 0.0148 TL_{(mm)} \\ \dots \text{(N-B)}.$$

Initial TL of each identified individual was used as the independent variable, and mean monthly growth was calculated as the dependent variable. This growth increment was then added to the initial TL to form a new TL, and new monthly growth increments were calculated repetitively for the period between initial (as described previously) and final capture (1980).

Duplicate measurements of TL of 31 anesthetized hellbenders collected from the North Fork by the same observers, technique and equipment were made during 1979 to check variability in measurement error. No reference was made to initial measurements when duplicate measurements were made approximately one hour later. These data were used to assess the importance of measurement error in the regression estimates.

Variation and bias in estimation of growth using the three models for both subspecies were evaluated using Hartley's test and one-way ANOVA, respectively. Accuracy of the three models in predicting growth was examined with chi-square tests:

$$\sum [(\text{observed final TL} \\ - \text{predicted TL})^2 / \text{predicted TL}].$$

*Results and discussion.*—Measurements and growth predicted from each equation for *C. a. alleganiensis* and *C. a. bishopi* are given in Tables 1, 2, respectively. Hartley's method indicated homoscedasticity between the final observed TLs and those predicted by the regression models, and the ANOVA indicated no significant difference between the methods for either *C. a. alleganiensis* ( $H_{1,21} = 1.55$  and  $F_{[5,80]} = 1.83$ ) or *C. a. bishopi* ( $H_{1,26} = 2.45$  and  $F_{[3,100]} = 0.04$ ). However, the predicted and observed TLs for *C. a. alleganiensis* did differ sig-

TABLE 1. COMPARISON OF THE OBSERVED FINAL TLS WITH TLS PREDICTED WITH LS, GM, AND N-B MODELS FOR *C. a. alleganiensis*.

Brand	Sex	Observed TL (mm)		Growth (months)	Predicted TL (mm)			Deviation (mm)		
		Initial	Final		LS	GM	N-B	LS	GM	N-B
126	M	244	435	104	455	444	454	-20	-11	-19
1208	F	270	469	81	437	434	437	32	35	32
2306*	—	285	410	24	348	357	349	62	53	61
596	F	295	459	100	466	451	465	-7	8	-6
315	F	308	451	107	476	456	475	-25	-5	-24
1719	F	318	435	74	449	439	448	-14	-4	-13
677	F	332	499	98	476	455	475	23	44	24
1109	F	356	477	86	475	454	473	2	23	4
1904	F	398	537	73	481	458	480	56	79	57
1783	F	405	437	74	485	460	483	-48	-23	-46
009	F	411	466	108	506	469	503	-40	-3	-37
1785	F	420	483	74	491	463	489	-8	10	-6
1229	F	426	468	83	499	467	496	-31	1	-28
1905*	—	427	434	27	458	447	458	-24	-13	-24
1755	F	443	463	73	500	469	498	-37	-6	-35
1979*	—	444	485	25	469	457	468	16	28	17
763	M	447	445	97	512	472	509	-67	-27	-64
1214	F	452	500	83	508	472	506	-8	28	-6
1845	F	460	490	73	508	473	505	-18	17	-15
700	F	533	529	97	539	485	535	-10	44	-6
681	F	586	591	97	556	493	551	35	98	40
Mean								-6.2	18.4	-4.5
Standard error								7.3	7.1	7.2

\* Recaptured and measured by Max A. Nickerson in 1976.

nificantly for the LS ( $\chi^2_{1201} = 49.79$ ), GM ( $\chi^2_{1201} = 61.53$ ), and N-B ( $\chi^2_{1201} = 48.04$ ) models. Although the LS and GM regressions seem to underestimate the growth of large individuals, the observed TLLs of *C. a. bishopi* and the predicted TLLs did not differ significantly for any model: LS ( $\chi^2_{1251} = 22.91$ ), GM ( $\chi^2_{1251} = 25.40$ ), N-B ( $\chi^2_{1251} = 22.62$ ).

Variability about the regressions due to measurement error was evaluated using the duplicated measurements of 31 *C. a. bishopi* and compared to the total variance about the N-B regression line as described by Ricker (1973). The greatest discrepancy in TL measurements was 25 mm, the least 0 mm. The mean absolute deviation was 1.3 mm (SE = 1.4 mm). For the predicted growth using the N-B equation and the two TL measurement for each hellbender, the greatest discrepancy was 3.0 mm/month. The absolute mean deviation of the 31 pairs of predicted growth was 0.02 mm/month (SE = 0.02 mm/month). The observational variance between the first and second measurements of TL ( $\Sigma (X_1 - X_2)^2/2n = 27.903$ ) represents 0.011% of the residual mean square of TL as a

function of monthly growth ( $s^2_{xy} = 251,286.06$ ), while the variance between the first and second estimates of mean monthly growth ( $\Sigma (Y_1 - Y_2)^2/2n = 0.006$ ) represents 0.0047% of the residual mean square of monthly growth as a function of TL ( $s^2_{yx} = 127.77$ ).

Because there is variability in growth of individuals and a straight line is used to describe growth at all sizes beyond the larval stage, the deviations between the final observed TLLs and the expected TLLs are surprisingly small for North Fork hellbenders (Table 2). Agreement between the observed and predicted TLLs for the N-B model provides credibility for the age-length curve generated for Ozark hellbenders from the N-B regression between mean monthly growth and TL (Peterson et al., 1983). Further, agreement between the observed and predicted TLLs suggests that food availability and seasonal temperatures had not changed greatly in the habitat during the interval. However, more to the point is that the TLLs predicted by the LS and the GM models also do not differ significantly from the observed TLLs; and while the models fail to predict the observed TLLs as

TABLE 2. COMPARISON OF THE OBSERVED FINAL TLS WITH TLS PREDICTED WITH LS, GM, AND N-B MODELS FOR *C. a. bishopi*.

Brand	Sex	Observed TL (mm)		Growth (months)	Predicted TL (mm)			Deviation (mm)		
		Initial	Final		LS	GM	N-B	LS	GM	N-B
83	M	240	308	22	312	314	304	-4	-6	4
517	—	244	307	27	326	329	318	-19	-22	-11
84	M	248	322	22	317	319	310	5	3	12
645	F	263	345	26	336	337	329	9	16	16
408	F	271	415	35	357	359	351	58	56	64
530	F	279	331	27	347	348	342	-16	-17	-11
1019	M	282	325	22	339	340	334	-14	-15	-9
503	F	283	357	27	350	351	345	7	6	12
439	F	304	380	35	374	374	371	6	6	3
687	F	305	343	26	361	361	358	-18	-18	-15
1023	F	316	361	22	361	361	359	0	0	2
103	M	330	393	40	392	391	392	1	2	1
420	M	363	410	35	404	402	406	6	8	4
351	M	365	395	39	408	405	411	-13	-10	-16
686	F	372	389	26	401	399	403	-12	-10	-14
629	F	377	403	26	405	402	406	-2	1	-3
179	F	400	398	40	425	421	431	-27	-23	-33
1020	F	402	402	22	417	415	421	-15	-13	-19
550	F	411	434	27	425	422	430	9	12	4
289	F	413	440	39	431	426	438	9	14	2
492	F	418	433	27	430	426	435	3	7	-2
552	F	424	436	27	433	429	439	3	7	-3
127	F	429	474	40	438	433	447	36	41	27
285	F	439	449	39	443	437	452	6	12	-3
135	F	448	475	40	447	441	457	28	34	18
647	F	454	475	26	451	446	459	24	29	16
Mean								2.7	4.3	1.8
Standard error								3.7	3.8	3.6

well for *C. a. alleganiensis*, they do predict Tls without significant bias. The deviations in Table 1 are not as large as might be expected considering the number of months of growth; one individual was captured nine years earlier during the first day of marking. Certainly the growth models are useful for describing growth of hellbenders from the North Fork and predict growth of hellbenders from the Niangua without bias.

Finally, Ricker (1973) has suggested that the larger the natural component of variability is in contrast to measurement error, the better, relatively, the GM regression should be in estimating the true functional regression. However, our findings suggest that, given the variability in the age-growth relationships of both *C. a. alleganiensis* and *C. a. bishopi*, there are no detectable differences between predictions based on the three kinds of regressions (LS, GM, N-B),

despite the evidence that only a small fraction of the total variance from the regression lines is due to measurement error. While the distinction between regressions permitting measurement error in both variables versus those permitting error in only the dependent variable is of theoretical significance and can be of practical importance, in this instance it is not.

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**MOUTH GAPING AND HEAD SHAKING BY PRAIRIE RATTLESNAKES ARE ASSOCIATED WITH VOMERONASAL ORGAN OLFACTION.**—Mouth gaping, often called yawning due to its resemblance to the mammalian behavior, is commonly observed during feeding behavior of rattlesnakes and has been interpreted as “vacuum activity” (Dullemeijer, 1961), and as a mechanism for stretching or realigning the jaw (Klauber, 1972). We have recently presented evidence (Graves and Duvall, 1983) that this behavior occurs with greater frequency when prairie rattlesnakes (*Crotalus*

*viridis viridis*) are exposed to conspecific chemical cues than when exposed to control odors. We suggested that mouth gaping may somehow facilitate vomeronasal organ (VNO) olfaction, probably mechanically or via increased blood-flow, based on the above indirect evidence. The experiment described here was designed to test directly the hypothesis that mouth gaping is associated with VNO olfaction.

Additionally, head shaking, a behavior not previously described which consists of two or three rapid jerks of the head horizontally, was investigated. We have also observed head shaking by prairie rattlesnakes exposed to conspecific chemical cues, and, therefore, we hypothesize that this action may be associated with VNO olfaction as well.

**Methods.**—Subjects were 16 prairie rattlesnakes captured in southern Wyoming which had been in captivity for at least one year. All had been housed communally in a 122 × 79 × 95 cm wooden cage with a plexiglass floor and wire screen top. The floor was covered with newspaper, water was provided ad libitum, a 12L:12D photoperiod and heat were supplied by one 150 watt light bulb, and snakes were fed live white lab mice.

Prior to the experiment, half of the subject's VNO ducts were sealed by suturing together the ridges of skin bordering the fenestra vomeronasalis in the manner described by Kubie and Halpern (1979). These procedures render subjects “avomic” (i.e., unable to detect chemical cues with the VNO; Graves and Duvall, 1985; Kubie and Halpern, 1979). Sham procedures were performed on the other eight subjects. The latter consisted of placing one suture in the skin on each side of the fenestra vomeronasalis. All VNO closures and sham procedures were performed with subjects under Brevitol Sodium anesthesia (Wang et al., 1977) at a dosage of 15 mg/kg body weight. All subjects were allowed two to three days to recover from the surgery and were tested only once.

Each trial consisted of placing one subject in a clean glass aquarium measuring 60 × 30 × 31 cm. Chiszar et al. (1978) have shown that such exposure of rattlesnakes to a novel environment induces high levels of exploratory behavior including tongue-VNO system chemosensory investigation. Each subject was then observed during the 10 min test trial via a video tape camera and monitor. Mouth gapes, head shakes and tongue flicks were quantified.