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Movement and Catchability of the Hellbender, *Cryptobranchus alleganiensis*

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ABSTRACT.—Between 5 September and 7 November 1985, 21 samples were made for hellbenders in a 100 m section of the Niangua River, Missouri. Fifty-one adult males and 59 adult females were marked. Mean number of recaptures per individual was 3.0 for males and 4.8 for females. Heterogeneity of capture was strongly indicated, probably due to the tendency of some individuals to occupy the same cover consistently. This resulted in an average minimum estimate by the Jolly-Seber method of 25 males and 27 females on the 2600 m² site. Both immigration and emigration were observed. Five to 11% of hellbenders on the site during a three-day interval may have been transients. Mean net movement upstream or downstream of 21 males and 42 females was not significantly different from 0 m/day.

According to Caughley (1977), mark-recapture models are not particularly robust to even small deviations from their assumptions, and the greatest source of error is unequal catchability. Further, he stated that unequal catchability is more the rule than the exception and that it has been established for populations of many vertebrates. Thus it is imperative to determine if the random sampling assumption has been violated so that population estimates can be properly interpreted. Pollock (1982) described two general types of alternatives that may be acting in a population to produce unequal catchability: (1) heterogeneity—the probability of capture in any sample is an inherent property of the animal and may vary over the population; and (2) trap response—learning may result in trap-shy or trap-happy animals.

Mark-recapture models have been used in previous studies of hellbenders (Nickerson and Mays, 1973*a*; Peterson et al., 1983; Peterson, 1985) to estimate population size where hellbenders were captured by turning rocks throughout the study site. Peterson (1985) hypothesized that a problem may exist because some hellbenders seek shelter in inaccessible crevices under bedrock or under boulders too large to be moved so that they are less catchable than hellbenders that occupy rocks which are turnable and easily accessible. It is unknown whether the same individuals consistently choose such sites, however. This is important to know because the estimate of population size would not be affected if individuals with a high chance of being caught in one sample did not necessarily have a similarly high chance in another. Thus heterogeneity might not be a problem. If there is a correlation between individual catchabilities on different days, however, then a larger variation in catchability results in greater bias (Begon, 1979).

One of the goals of this study was to determine whether hellbenders tend to occupy the same shelter consistently. Subsidiary goals were to determine whether the population could be considered closed even over a few days and whether emigration and immigration are permanent. Also, in mark-recapture population studies, the position of marked individuals in the population after sampling should not be different from that which would be expected if they had never been caught (Begon, 1979). Thus I wanted to determine what might be the effect on the distribution of hellbenders released at a single location on the site as had been done by Peterson et al. (1983) and Peterson (1985).

Another major objective was to obtain a measure of dispersal. Although dispersal is an essential part of the life cycle of most organisms, produces gene flow, and affects community composition, it is seldom measured in a population study (Krebs, 1985). Peterson (1985) hypothesized that emigration was an important component in local population composition because Jolly-Seber estimates of the probability that an individual would not die nor emigrate over a three-year period in four populations were much lower than the survivorship indicated in life tables of the same populations.

Study Area and Methods

A 100 m section of the Niangua River about 1 km north of Bennett Spring State Park, Laclede County, Missouri, was divided into 5 m sections along the bank. The stream is 20–30 m wide, and the area of the site was 2600 m^2. Large rocks and crevices in bedrock provided shelter for hellbenders, particularly in the downstream 70 m. The upper 30 m had few large rocks, but hellbenders were found in crevices and cracks under smooth bedrock and a few slabs that had broken away from the bedrock. Except for an occasional boulder, gravel substrate 10 to 15 m wide along one shore did not provide diurnal habitat for postlarval hellbenders. The depth was nowhere more than 1.7 m and mostly less than 1 m.

Hellbenders were captured by hand during the day by turning rocks, reaching into crevices, and occasionally breaking bedrock by hand or with a crowbar. A swim mask was worn to aid visibility. Twenty-one samples were made between 5 September and 7 November 1985. The total length (TL) of hellbenders not captured previously was measured to the nearest cm and mass to the nearest g. They were heat-branded (Clark, 1971) on the venter with a three-digit number. Males were identified by enlarged cloacal glands, females by the absence of swelling about the cloaca. If captured in the downstream 50 m, the newly marked hellbenders were released 30 m from the downstream border of the site. If captured in the upper 50 m, they were released 80 m from the downstream end. All recaptured animals were replaced under the rock or in the crevice where they were captured. A few hellbenders had to be replaced several times before they again accepted the cover. For recaptures, the distance upstream along the bank from the downstream end of the site was recorded. Distances between 5 m marks were estimated to the nearest m. An attempt was made to return all rocks to their original position, regardless of whether they sheltered a hellbender.

Segments of 20 m immediately downstream of the site and 35 m upstream of the site (also divided into 5 m sections) were checked sporadically for marked animals. Unmarked hellbenders outside the 100 m study site were branded and returned to their capture rock without any initial displacement.

Net movement of recaptured animals (from the initial capture location for animals caught outside the study site and from the first recapture location for hellbenders caught within the site) was calculated by addition of distances measured along the bank between successive captures. Downstream movements were given a negative sign.

On 6 October, all hellbenders caught wtihin the 100 m study site (whether marked previously or not) were simultaneously released 50 m upstream from the downsteram boundary. The rocks where they were captured were marked with uniquely painted stones. The intercapture distance as measured parallel to the bank, disregarding whether upstream or downstream, between 6 and 7 October was used to determine whether the distribution of animals was affected by the displacement. For the salamanders displaced on 6 October, only the movements before or after that date were used in the analysis of net movement unless they returned to the original location on 7 October.

On 9 October, each crevice or rock where a hellbender was captured was marked with a painted rock. During the following 6 samples, these identified shelters were always examined to determine how many times a hellbender would use the same cover. At the end of the sixth sample (sample 20), all hellbenders captured on the study site were translocated 1 km upstream to begin a homing study, but continued flooding after 7 November prevented the investigation.

Caughley (1977) stated that if the study period is short enough to ensure that natural mortality is minimal, then capture data for all sample periods can be used in a test of equal catchability or random sampling. He also stated that if catchability is constant the distribution of frequencies of capture will form a zero-truncated binomial distribution that approximates a zero-truncated Poisson distribution when the number of sampling periods is large relative to the mean number of times an animal is captured. A truncated Poisson distribution (Caughley, 1977) was fitted to the observed capture frequencies of hellbenders, and the fit was tested by a chi-square test to determine if capture heterogeneity was indicated.

The Jolly-Seber method as described by Begon (1979) was used to estimate population size (N_i), the probability that an individual present on day i will be present on day i + 1 (P_i), and the additions to the population between samples (B_i).

Results

Population Composition and Catchabilty.—Fifty-one adult males (mean mass = 620 g, SE = 24) and 59 adult females (mean mass = 779 g, SE = 28) were captured on the study site: a sex ratio not significantly different ($\chi^2 = 0.446$, $P > 0.5$) from 1:1. Based on TL (Taber et al., 1975), no juveniles were observed. For the 21 samples, the average percentage of females was 63.5 (SE = 2.8). An average of 16.2 (SE = 0.9) females and 9.7 (SE = 1.1) males was caught per sample. Males were more numerous only in two samples. On 18 September, 49 hellbenders were captured, 19 more than in any other sample; 28 of them were males. Many were not under shelters, unlike all other samples. On 7 November, 11 of 15 hellbenders were males; 9 of the males and 2 females were captured by breaking bedrock. Of the 11 captured under bedrock, 4 were unmarked, and 3 had not been seen for a month. No significant difference ($\chi^2 = 10.171$, df = 19, $P > 0.9$) in catchability of the sexes was indicated, however, employing the test described by Begon (1979).

In the 20 recapture periods, the average percentage of the male sample that had previously been marked was 78.4 (SE = 5.6). Recaptures comprised an average of 84.7% (SE = 4.2) of the female samples. Nineteen males were captured 3 to 17 times (14 six or more times); 34 females were captured 3 to 19 times (23 six or more times). The mean number of recaptures per individual for the 51 males was 3.0 (SE = 0.6); for the 59 females, it was 4.8 (SE = 0.7). The capture frequencies for both sexes were significantly different ($P < 0.005$) from that based on a zero-truncated Poisson distribution, strongly indicating that catchability was not constant throughout the population.

The number of individuals marked and released on the study site on sample 20 (5 November) and recaptured was zero for both sexes because of the translocation of hellbenders on that date. Therefore population size could not be estimated for sample 20 (Table 1). Also, the Jolly-Seber model does not provide size estimates for the first or last sample (7 November). The average estimates of P_i are for a three-day period, the average time between samples. Thus it is estimated that 5% of the males and 7% of the females ($1 - \bar{P}_i$) emigrated during a three-day interval. If P_i that exceed 1.0 are truncated, then the estimates are 11% for males and 8% for females.

Movement.—From 16 September to 21 October, 7 hellbenders were branded between 3 and 34 m upstream of the study site and 7 between 3 and 20 m downstream of the site. Of these 14, 2 from downstream and 1 from upstream were captured later within the study site. Two of the 3 were caught subsequently outside the study site, so immigration was not necessarily permanent. Of the 107 hellbenders caught initially within the study site, 7 animals were caught later from 2 to 12 m downstream of the study site, and 6 were captured from 1 to 34 m upstream of the site. One animal was caught 10 m downstream from the site on the third day of sampling. This was the first time sampling was done outside the study area, and it demonstrates that the population was not closed for even a few days. Five of the 13 hellbenders that left the site were subsequently recaptured within the 100 m study area.

If the data are normally distributed, then for both sexes the 90% confidence limits

TABLE 1. Estimates of population size (N_i), probability that an individual present on sample i will not emigrate or die before sample i + 1 (P_i), and the additions to the population from sample i to sample i + 1 (B_i) for both sexes of *Cryptobranchus alleganiensis.*

	N_i		SE_N		P_i		SE_P		B_i	
Date	M	F	M	F	M	F	M	F	M	F
5 Sept.	—	—	—	—	0.857	0.900	0.000	0.000	—	—
7 Sept.	15.0	31.5	11.1	12.2	1.000	1.035	0.000	0.091	3.0	−9.0
9 Sept.	18.0	23.6	13.4	3.4	1.171	0.882	0.186	0.039	1.0	5.4
11 Sept.	22.1	26.2	5.5	2.4	0.821	1.038	0.158	0.048	11.2	4.3
13 Sept.	29.3	31.5	12.0	2.3	0.924	1.032	0.148	0.125	−2.5	3.5
16 Sept.	24.6	36.0	5.3	4.7	0.982	0.894	0.169	0.182	28.3	23.3
18 Sept.	52.4	55.5	11.8	13.2	0.713	0.604	0.104	0.088	−8.5	−6.0
24 Sept.	28.9	27.5	3.9	2.4	0.758	0.980	0.110	0.110	1.4	3.9
26 Sept.	23.3	30.9	2.7	3.8	0.945	0.785	0.100	0.076	0.9	−0.1
1 Oct.	22.9	24.1	2.3	1.5	0.960	1.002	0.098	0.083	−0.9	0.9
3 Oct.	21.1	25.1	1.6	2.1	0.939	0.812	0.094	0.058	3.6	3.4
6 Oct.	23.4	23.8	2.6	1.2	0.917	1.013	0.054	0.028	−1.4	−0.8
7 Oct.	20.0	23.3	0.0	0.6	1.056	0.955	0.081	0.035	0.0	−0.1
9 Oct.	21.1	22.2	1.6	0.6	0.939	0.961	0.094	0.040	3.6	0.1
15 Oct.	23.4	21.4	2.6	0.7	1.132	0.898	0.202	0.038	0.7	0.0
21 Oct.	27.2	19.2	5.1	0.5	0.756	0.938	0.145	0.025	−1.2	2.1
25 Oct.	19.4	20.1	2.0	0.5	1.801	1.013	0.932	0.028	0.1	−0.2
27 Oct.	35.0	20.2	17.7	0.6	0.446	0.920	0.235	0.054	0.0	0.0
2 Nov.	15.6	19.9	2.2	1.2	—	—	—	—	—	—
$\bar{x}$	24.6	26.8			0.951	0.926			2.3	1.8
$SE_{\bar{x}}$	2.0	2.0			0.063	0.026			1.9	1.6

for the mean of net movement per day include zero (Table 2 and Fig. 1). A Mann-Whitney *U*-test indicated no significant difference ($t_s = 0.30, P > 0.5$) in net movement per day between males and females. No significant difference ($t_s = 1.05$, $P > 0.2$) was indicated in net movement per day between hellbenders of 38 to 45 cm TL and those of 46 to 55 cm TL. The hellbenders in the smaller size group would be about 7 to 13 years old (Taber et al., 1975). The mean distance along the bank, disregarding whether upstream or downstream, between successive captures per individual varied from 0.0–42.5 m for males and 0.0–15.5 m for females. Sixty-seven percent of the males and 88% of the females had mean intercapture distances of less than 10 m.

Of the 30 hellbenders released in the middle of the study site at 1600 h on 6 October, 10 males and 17 females were recaptured the next day. Three males and 7 females had returned to the same rock where they had been captured on 6 October. The average intercapture distance (between transections) for the two days was 8.8 m (SE 2.8, range 0–40) for the males and 6.8 m (SE 3.1, range 0–51) for the females. Eighty percent of the males and 82% of the females had an intercapture distance of less than 10 m for the two days. No significant correlation (r = 0.237, $P > 0.2$) was found between distance displaced on 6 October and the intercapture distance between 6 and 7 October.

On 9 October, 35 individuals were captured between 10 m downstream of the study site and 35 m upstream. During the following six samples through 5 November, 6 of the 35 were captured six times, 6 five times, 2 four times, 1 three times, and 8 once under the same rocks as 9 October. Seven were not recaptured under their shelter of that date. Four individuals returned to the marked rock after being absent on one or more samples. The others were present only on consecutive samples. One male, because of the uniqueness of position of its rock, was known to be sheltered by the same cover on 16 of 17 consecutive samples, and one female was found under the largest turnable rock on 11 consecutive samples. Three other females recaptured 9–14 times were never recaptured more than 1 m upstream or downstream of their initial recaptures.

Discussion

Population Composition and Catchability.—Hillis and Bellis (1971) found few juveniles in their movement study. Peterson (1985) also found very few juveniles in two Ozark streams, but in a third stream 25% of the animals were juveniles. Taber et al. (1975) and Peterson et al. (1983) reported that the populations they studied were dominated by adults, but a considerable number of juveniles was captured. The former study was of the Niangua population about 10 km downstream from this study.

Taber et al. (1975) reported that the survivorship of adult female hellbenders was higher than that of adult males, which might suggest that females were more numerous in the population. This was supported by the Niangua male to female sex ratio of 1:1.6 reported by Wiggs (1977) with a ratio of 1:4 for hellbenders 15+ years of age. Wiggs (1976), however, found a 1:1 ratio, and Nickerson and Mays (1973*b*) reported a 1.3:1 ratio for the Niangua River. The results of this study indicate that the determination of sex ratio may depend on the timing of samples; one sex may be more evident on certain days. According to Smith (1912), the sex ratio of hellbenders collected in northwestern Pennsylvania varied with the time of year and also from place to place within the stream. He particularly made a distinction between the breeding season and nonbreeding season and between breeding grounds and localities unsuitable for breeding. Males were in general more numerous on the breeding grounds throughout the year and in sole occupancy of nests after spawning; they were less numerous in areas unsuitable for breeding (where there existed swift current, only rocks barely large enough to serve as cover, or quiet pools). Females increased in numbers on the breeding grounds only just before and during the breeding season (Smith, 1912).

It is not surprising that capture heterogeneity was indicated. The tendency for at least some hellbenders to occupy the same cover for many days, as found in this study,

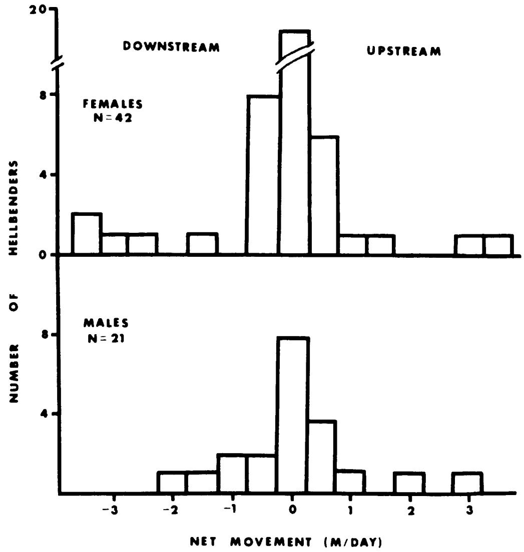

FIG. 1. Net movement of male and female *Cryptobranchus alleganiensis* from site of initial capture, or from first recapture site for animals experimentally displaced.

would make hellbenders that choose large but turnable rocks more likely to be captured on many samples than those that hide in extensive holes in the bedrock, under an immovable boulder, or in deep, swift sections of the river. Peterson (1985) did not detect a significant deviation from random sampling by Leslie's (1958) test in two populations for which there were adequate data; however, a significant difference in catchability of the sexes and of age classes was found in one population. Leslie's (1958) test is incapable of distinguishing whether such subgroups are equally catchable (Roff, 1973). Additionally in this study, the emigration of some individuals was not permanent, possibly because their area of activity overlapped the boundary of the study site. This adds to the problem of sampling because hellbender habitat is probably never discrete nor uniformly distributed. Finally, the marking of rocks could have enhanced the unequal catchability by making it essentially impossible to miss flipping certain rocks and thus finding certain hellbenders, even though an attempt was made to search the entire site on each sample.

Population size will be underestimated

TABLE 2. Movement of male (N = 21) and female (N = 42) *Cryptobranchus alleganiensis*. All measurements parallel to the stream bank; downstream movement indicated by minus sign.

	Sex	Mean	SE	Range
Number of recaptures/individual	M	6.8	0.8	2–14
	F	7.5	0.7	2–18
Days between first and last recaptures/individual	M	33	3	7–59
	F	29	3	2–59
Net movement/individual (m/day)	M	0.06	0.23	−2.11–2.88
	F	−0.14	0.20	−3.88–3.41
Distance between maximum upstream and downstream captures/individual (m)	M	25	6	0–85
	F	17	3	0–66

if the equal catchability assumption is violated (Begon, 1979). Thus the best that can be said for the population size estimates in Table 1 is that they may represent a minimum boundary of the number of hellbenders on the site. This is possibly true for estimates in previous studies in which I have been involved; however, there was no attempt to reposition rocks, and intervals between samples were much longer than in this study. It would be useful to determine if movement changes over a longer period. The standard error values must also be viewed cautiously because they are correlated with the population estimates (Manly, 1971). Thus, underestimates result in confidence limits that are too narrow.

Estimates of P_i, in contrast, will not be affected by unequal catchability (Begon, 1979). Carothers (1979) reported that even with a statistically significant indication of unequal catchability, the bias in P_i estimates may be lower than that due to sampling variation and thus of little practical significance. Therefore the estimates of P_i should still be reasonable except for sampling variation (evident in estimates that exceed 1.0). As only adults were involved, it is very unlikely that the estimates reflect any mortality, considering the length of the study period and the survivorship of adults (Taber et al., 1975; Peterson et al., 1983; Peterson, 1985). Thus the estimates represent the proportion of the population not emigrating between samples. It is assumed that immigration was approximately equal to emigration. Estimates of B_i suggest that there were very few immigrants between samples, except during the third week in September, near the height of the breeding season in the Niangua River (Ingersol, 1982). However, the calculation of B_i is directly influenced by N_i which is probably underestimated. This is why standard errors of B_i were not tabulated.

Wiggs (1977) noted 67 movements of 100 to 3500 m by nondisplaced hellbenders, but he reported that there was a 93% probability that a recaptured animal would be on the site (100 m sites) of initial capture. The estimates in this study of the percentage of the population that were transients are similar; however, emigration may have been increased merely because of the continued disturbance from sampling. Further, emigration was not necessarily permanent. Such part-time residents of the site may have resulted in underestimates of P_i. Moreover, because estimates were for a period including the breeding season, when individuals may be most active, the number of transients may be lower during much of the year. This is supported by the 18 September sample when more hellbenders were captured than on any other sample. However, rather than being immigrants, many of these animals may have been residents that simply had left inaccessible hiding places on the site, as suggested by the capture of some individuals under bedrock on 7 November that had not been seen for a month. Both Wiggs (1977) and Peterson (1985) reported finding unmarked hellbenders during each sample, even though sites were worked many times.

Again, it was unknown whether the animals were always present or were immigrants.

Movement.—Fidelity to a circumscribed area has been suggested for hellbenders over a short period in previous movement studies. Hillis and Bellis (1971) estimated an average circular home range size of 346 m^2 and a median home range of 113 m^2 based on daytime captures during one summer. Only 13 animals were caught more than three times, however, with a maximum of five times. Coatney (1982) estimated a mean elliptical home range size of 90 m^2 by monitoring nocturnal activity with telemetry equipment for two weeks. Some hellbenders have also exhibited faithfulness to a site for months (Nickerson, 1980) and years (Peterson et al., 1985). In this study, a majority of both sexes and size groups showed little tendency to move systematically upstream or downstream and thus exhibited an affinity for a certain portion of the stream (Fig. 1). This was also indicated in the intercapture distance between 6 and 7 October. A third of the animals displaced returned to the shelters where they were captured. Further, the percentage of hellbenders with a mean intercapture distance (for the entire study period) of less than 10 m was essentially the same as the percentage of individuals with an intercapture distance of less than 10 m captured on 6 and 7 October. Therefore the distribution of animals was probably not much affected in previous studies (Peterson et al., 1983; Peterson, 1985) by release of salamanders together at one location of the study site, especially as periods between samples were seldom less than two weeks. Wiggs (1977) also found that some translocated hellbenders returned to the rocks where captured, one after a displacement of 900 m.

Activity areas could not be estimated because only distance along the bank was measured. Lateral movement was observed, but the width of suitable diurnal habitat was mostly less than 15 m. A few individuals were not observed to move upstream or downstream even though captured numerous times, but this does not mean that they were not active at night. Coatney (1982) stated that hellbenders tend to return to a "home rock" at dawn after being active during the night, although activity does not occur on all nights.

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LITERATURE CITED

BEGON, M. 1979. Investigating animal abundance: capture-recapture for biologists. Edward Arnold Publ., London. 97 pp.

CAROTHERS, A. D. 1979. Quantifying unequal catchability and its effect on survival estimates in an actual population. J. Anim. Ecol. 48:863–869.

CAUGHLEY, G. 1977. Analysis of vertebrate populations. John Wiley and Sons, New York. 234 pp.

CLARK, D. R., JR. 1971. Branding as a marking technique for amphibians and reptiles. Copeia 1971: 148–151.

COATNEY, C. E., JR. 1982. Home range and nocturnal activity of the Ozark hellbender. M.S. Thesis. Southwest Missouri State Univ. Springfield. 55 pp.

HILLIS, R. E., AND E. D. BELLIS. 1971. Some aspects of the ecology of the hellbender, *Cryptobranchus alleganiensis alleganiensis*, in a Pennsylvania stream. J. Herpetol. 5:121–126.

INGERSOL, C. A. 1982. Seasonal reproductive changes in *Cryptobranchus alleganiensis*. M.S. Thesis. Southwest Missouri State Univ. Springfield. 72 pp.

KREBS, C. J. 1985. Ecology: the experimental analysis of distribution and abundance. 3rd ed. Harper and Row, New York. 800 pp.

LESLIE, P. H. 1958. Statistical appendix. J. Anim. Ecol. 27:84–86.

MANLY, B. F. J. 1971. A simulation study of Jolly's method for analysing capture-recapture data. Biometrics 27:415–424.

NICKERSON, M. A. 1980. Return of captive Ozark hellbenders, *Cryptobranchus alleganiensis bishopi*, to site of capture. Copeia 1980:536–537.

———, AND C. E. MAYS. 1973*a*. A study of the Ozark hellbender, *Cryptobranchus alleganiensis bishopi*. Ecology 54:1164–1165.

———, AND ———. 1973*b*. The hellbenders: North American "giant salamanders." Milwaukee Publ. Mus., Publ. Biol. Geol. 1:1–106.

PETERSON, C. L. 1985. Comparative demography of four populations of the hellbender, *Cryptobranchus alleganiensis*, in the Ozarks. Ph.D. Dissertation. Univ. Missouri. Columbia. 158 pp.

———, M. S. TOPPING, R. F. WILKINSON, JR., AND C. A. TABER. 1985. An examination of long-term growth of *Cryptobranchus alleganiensis* predicted by linear regression methods. Copeia 1985:492–496.

———, R. F. WILKINSON, JR., M. S. TOPPING, AND D. E. METTER. 1983. Age and growth of the Ozark hellbender (*Cryptobranchus alleganiensis bishopi*). Copeia 1983:225–231.

POLLOCK, K. H. 1982. A capture-recapture design robust to unequal probability of capture. J. Wildl. Management 46:752–757.

ROFF, D. A. 1973. An examination of some statistical tests used in the analysis of mark-recapture data. Oecologia 12:35–54.

SMITH, B. G. 1912. The embryology of *Cryptobranchus allegheniensis*, including comparisons with some other vertebrates. I. Introduction; the history of the egg before cleavage. J. Morphol. 23:61-157.

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.

WIGGS, J. N. 1976. Food habits, starvation, and growth in the hellbender, *Cryptobranchus alleganiensis*. M.S. Thesis. Southwest Missouri State Univ. Springfield. 32 pp.

WIGGS, R. L. 1977. Movement and homing in the hellbender, *Cryptobranchus alleganiensis*, in the Niangua River, Missouri. M.S. Thesis, Southwest Missouri State Univ. Springfield. 45 pp.

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A. D. Carothers
The Journal of Animal Ecology, Vol. 48, No. 3. (Oct., 1979), pp. 863-869.
Stable URL:
http://links.jstor.org/sici?sici=0021-8790%28197910%2948%3A3%3C863%3AQUCAIE%3E2.0.CO%3B2-3

Branding as a Marking Technique for Amphibians and Reptiles
Donald R. Clark, Jr.
Copeia, Vol. 1971, No. 1. (Mar. 8, 1971), pp. 148-151.
Stable URL:
http://links.jstor.org/sici?sici=0045-8511%2819710308%293%3A1971%3A1%3C148%3ABAAMTF%3E2.0.CO%3B2-L

Some Aspects of the Ecology of the Hellbender, Cryptobranchus alleganiensis alleganiensis, in a Pennsylvania Stream
Robert E. Hillis; Edward D. Bellis
Journal of Herpetology, Vol. 5, No. 3/4. (Dec. 15, 1971), pp. 121-126.
Stable URL:
http://links.jstor.org/sici?sici=0022-1511%2819711215%295%3A3%2F4%3C121%3ASAOTEO%3E2.0.CO%3B2-H

http://www.jstor.org

LINKED CITATIONS

A Simulation Study of Jolly's Method for Analysing Capture-Recapture Data
B. F. J. Manly
Biometrics, Vol. 27, No. 2. (Jun., 1971), pp. 415-424.
Stable URL:
http://links.jstor.org/sici?sici=0006-341X%28197106%2927%3A2%3C415%3AASSOJM%3E2.0.CO%3B2-7

Return of Captive Ozark Hellbenders, Cryptobranchus alleganiensis bishopi, to Site of Capture
Max A. Nickerson
Copeia, Vol. 1980, No. 3. (Sep. 6, 1980), pp. 536-537.
Stable URL:
http://links.jstor.org/sici?sici=0045-8511%2819800906%293%3A1980%3A3%3C536%3AROCOHC%3E2.0.CO%3B2-0

A Study of the Ozark Hellbender Cryptobranchus Alleganiensis Bishopi
Max A. Nickerson; Charles E. Mays
Ecology, Vol. 54, No. 5. (Sep., 1973), pp. 1164-1165.
Stable URL:
http://links.jstor.org/sici?sici=0012-9658%28197309%2954%3A5%3C1164%3AASOTOH%3E2.0.CO%3B2-R

Examination of Long-Term Growth of Cryptobranchus alleganiensis Predicted by Linear Regression Methods
Chris L. Peterson; Milton S. Topping; Robert F. Wilkinson, Jr.; Charles A. Taber
Copeia, Vol. 1985, No. 2. (May 3, 1985), pp. 492-496.
Stable URL:
http://links.jstor.org/sici?sici=0045-8511%2819850503%293%3A1985%3A2%3C492%3AEOLGOC%3E2.0.CO%3B2-A

Age and Growth of the Ozark Hellbender (Cryptobranchus alleganiensis bishopi)
Chris L. Peterson; Robert F. Wilkinson, Jr.; Milton S. Topping; Dean E. Metter
Copeia, Vol. 1983, No. 1. (Feb. 10, 1983), pp. 225-231.
Stable URL:
http://links.jstor.org/sici?sici=0045-8511%2819830210%293%3A1983%3A1%3C225%3AAAGOTO%3E2.0.CO%3B2-5

Age and Growth of Hellbenders in the Niangua River, Missouri
Charles A. Taber; R. F. Wilkinson, Jr.; Milton S. Topping
Copeia, Vol. 1975, No. 4. (Dec. 31, 1975), pp. 633-639.
Stable URL:
http://links.jstor.org/sici?sici=0045-8511%2819751231%293%3A1975%3A4%3C633%3AAAGOHI%3E2.0.CO%3B2-H