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Population Status of the Eastern Hellbender (*Cryptobranchus alleganiensis alleganiensis*) in Indiana

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Abstract.—Studies that assess current and historical population densities accurately provide valuable information for management of wildlife species, particularly those in need of immediate conservation concern. The Eastern Hellbender (*Cryptobranchus alleganiensis alleganiensis*) has experienced drastic declines throughout its range during the previous few decades. This study documents its continued decline over the past 25 years in the last known remaining population in southern Indiana. We conducted mark–recapture surveys from June 2008 to October 2008 and July 2009 to September 2009 at 35 sites. Despite a considerable increase in effort over previous surveys, we documented fewer total captures and extremely low population densities. Density was estimated at 0.06 individuals/100 m^2, and catch per unit effort was 0.05 individuals/person hour throughout the entire study area. This represents not only a significant decline in numbers from the historical study, but also is well below that reported for populations throughout the species' range. Sex ratios were skewed significantly toward males (2.6 males : 1 female). No subadults or larvae were found, and only two nests were located. This population consists almost exclusively of large, older-age class individuals that show limited signs of reproduction.

The giant salamanders of the family Cryptobranchidae are represented in the United States by the Eastern Hellbender (*Cryptobranchus alleganiensis alleganiensis*) and the Ozark Hellbender (*Cryptobranchus alleganiensis bishopi*). They range throughout much of the Midwest and eastern portions of the country (Petranka, 1998). Both subspecies occupy higher trophic levels and serve many important roles in lotic ecosystems (Hillis and Bellis, 1971; Nickerson and Mays, 1973b). They have been reported to maintain high population densities and represent a considerable amount of the biomass in a given area (Nickerson and Mays, 1973b; Humphries and Pauley, 2005). Hellbenders are believed to influence aquatic invertebrate community dynamics through predation on crayfish (Humphries and Pauley, 2005). Recently, hellbender populations have experienced precipitous declines throughout their range, including areas that historically contained large, stable populations exhibiting no explicit signs of decline (Kern, 1984; Mayasich et al., 2003; Wheeler et al., 2003; Foster et al., 2009). Purported reasons for these declines include habitat alteration (Nickerson and Mays, 1973b), poor water quality (Briggler et al., 2007), direct persecution or illegal collection (Nickerson and Briggler, 2007), and possibly outbreaks of the amphibian chytrid fungus (*Batrachochytrium dendrobatidis*; Briggler et al., 2008). In the Midwest, hellbender declines have been especially severe. Populations in Ohio and Missouri continue to decline, whereas hellbenders have been extirpated in Illinois and reduced to a single river drainage in Indiana (Peterson, 1985; Wheeler et al., 2003). Reports of these widespread population declines coupled with the species' important ecological roles within aquatic systems has resulted in a series of new population assessments across much of the hellbender's geographic range.

Recent estimates of hellbender population density vary considerably, often by as much as an order of magnitude (Hillis and Bellis, 1971; Nickerson et al., 2002; Mayashich et al., 2003; Wheeler et al., 2003; Humphries and Pauley, 2005; Table 1). Many studies have reported densities ranging from 1–6 individuals/100 m^2, whereas some report much lower densities (Peterson et al., 1988). Also, considerable variation in population densities occurs between sites. Humphries and Pauley (2005) reported an average population density of 0.8 individuals/100 m^2 in their study site but also documented densities as high as 1.2 individuals/100 m^2 in one section. Hillis and Bellis (1971) found similar variation in population densities within rivers in Pennsylvania. Sex ratios within populations vary, but typically can be found near parity (Smith, 1907; Kern, 1984). Although estimates of current population densities are important, studies that compare current and historical population densities are particularly insightful to establish both the rate and extent of population declines. Unfortunately, only a small subset of studies has been able to capitalize on these data (Table 1). Indiana is one of only a few states in which a series of population surveys have been conducted throughout the last 15–20 years. Remarkably, many of the sample sites and sampling methods are consistent between studies and, thus, have created an opportunity to empirically evaluate population declines.

Historically, hellbenders in Indiana have been found throughout both the Ohio and Wabash River drainages. Hellbender populations are now known to persist in only a small portion of the Ohio River drainage in southern Indiana. Kern (1984) surveyed the Ohio River drainages throughout southern Indiana but found that hellbenders were restricted to the Blue River. Kern (1984) surveyed 12 sites and captured 130 individuals, including two juveniles. At one site, 68 hellbenders were captured, and density was estimated to be 20.2 6 7.7 hellbenders/100 m^2. More recent surveys (Indiana Department of Natural Resources, unpubl. data) over the last decade have documented continued population declines. Herein, we used mark–recapture to estimate abundance for Indiana hellbenders and compare these estimates to results from historical studies, determine relative body size and condition, and evaluate habitat use throughout the study area.

Materials and Methods

Study Area.—The Blue River watershed is located in southern Indiana and intersects two of Indiana's natural regions originating in the Mitchell Karst Plain Section of the Highland Rim and crossing into the Escarpment Section of the Shawnee Hills. The Blue River winds through a complex of agriculture, forest, and rocky cliffs until converging with the Ohio River. It is comprised of long stretches of deep pools with interspersed riffle and run habitats. Average summer (23 May to 25 September) depths are fairly shallow (37.15 cm 6 20.53), and summer water temperatures average 21.17uC 6 1.78. Yearly water temperatures range from 0.02uC in the winter to 25.94uC in the summer but maintain relatively high dissolved oxygen levels (10.15 6 2.14 mg/L) throughout (Burgmeier et al., unpubl. data). The average spring–summer turbidity level was

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TABLE 1. Previous studies reporting population densities or relative abundances for hellbender populations.

Author	Date	Density	Historic density	Relative abundance	Location
Bothner and Gottlieb[a]	1991	0.32–3.73/100 m^2, (5.75–58.82/100 m^2)[b]	–	–	NY
Burgmeier et al.	This study	0.06/100 m^2	See Kern, 1984	0.05 ind/h	IN
Foster et al.[a]	2009	0–1.07/100 m^2, (0–20/100 m^2)[b]	See Bother and Gottlieb, 1991	–	NY
Hillis and Bellis[a]	1971	0.99/100 m^2	–	–	PA
Humphries and Pauley	2005	0.8–1.2/100 m^2	–	–	WV
Humphries	2007	–	–	7.4 ind/h	NC
Kern[c]	1984	20.2 6 7.7/100 m^2	–	–	IN
Nickerson and Mays[a]	1973a	10/80–100 m^2	–	–	MO
Nickerson et al.	2002	–	–	0.25–0.65 ind/h	TN
Peterson et al.	1988	1–6/100 m^2	–	–	MO
Wheeler et al.	2003	3.3 6 0.77 (16)–10 6 2.52 (4)[d]	6.2 6 1.05 (35)–54.9 6 10.20 (17)	–	MO

[a] Standardized from original data to fit table. Extrapolated from reported area (m^2) to 100 m^2.
[b] Original ecological density reported in study (in parentheses).
[c] Density estimated at only one site.
[d] Expressed as the number of hellbenders captured per day. Numbers in parentheses indicates the number of sampling days.

9.31 NTU 6 15.48 (Burgmeier et al., unpubl. data). Substrate varies with some areas characterized by predominately bedrock bottom, whereas others consists of gravel and cobble. Regardless of substrate type, many areas maintain a thin layer of silt. Boulder-sized (-256 mm diameter) limestone slabs suitable for hellbender refugia are spread throughout the river (Burgmeier et al., in press).

Site Selection.—Sample sites were chosen through an iterative process. First, the entire study area was floated and characterized according to flow type, substrate composition, and boulder size (Garmin 72, Garmin, Olathe, KS). A map was then constructed from habitat data gathered from the canoe survey using ArcGIS 9.2 (ESRI, Redlands, CA). The Hawth's Tools Extension (Beyer, 2004) was used to join our data to base layer data in the United States Geological Service's National Hydrography Dataset (USGS, 2007). Sample sites were selected based on a set of criteria consisting of three categories: flow type, substrate, and boulder size. Each parameter contained subcategories, which were assigned a value based on their suitability as habitat. A selection was run to choose sites based on a set of predetermined habitat suitability characteristics (Table 2). Based on their potential quality as hellbender habitat, the resulting selections were divided into four categories: primary, secondary, tertiary, and unsuitable. Thirty-five sites were selected. Twenty-five sites were selected from the primary and secondary categories using the iterative process described above. The 10 remaining sites were historical Indiana Department of Natural Resources sampling sites. IDNR sites were chosen in 1996 by IDNR personnel based on their suitability as habitat and their ease of access. Furthermore, IDNR sites are surveyed annually and are known to be areas of recent hellbender activity. An additional seven sites were surveyed multiple times as part of another study but were not included in the mark–recapture estimates. Our sampling efforts were focused on areas with riffles and runs (although some pools were also sampled), gravel or cobble substrate containing abundant boulder-sized slab rock cover, and an average depth less than 1 m.

TABLE 2. A description and ranking of criteria used to select sample sites in our study area. Habitat was ranked from Primary (best) to Unacceptable (worst). Flow: 1 5 Pool, 2 5 Riffle, 3 5 Riffle/run complex. Substrate: 1 5 Bedrock, 2 5 Silt, 3 5 Sand, 4 5 Gravel, 5 5 Cobble. Boulders Size: 1 5 Small (256–512 mm), 2 5 Medium (512–1,024 mm), 3 5 Large (1,024–4,096 mm).

	Selection criteria		
Site classification	Flow	Substrate	Boulders[a]
Primary	3	4	2
Secondary	2 or 3	4	1
Tertiary	1	3 or 4	1
Unacceptable	–	2	0

[a] Indicates the most frequently represented category.

Capture and Handling.—Hellbenders were collected from September 2007, June to October 2008, and July to September 2009. Each of the 35 mark–recapture sites was surveyed five times with three surveys conducted in 2008 and two in 2009. All sites were surveyed at least once during the breeding season. To obtain accurate population estimates using open population mark–recapture models, it is recommended that at least three, but preferably more, sampling occasions are conducted (Donnelly and Guyer, 1994; Elzinga et al., 2001). Additional surveys not included in our mark–recapture estimate were conducted at seven other sites for exploratory purposes, bringing the total number of sites to 42. Most surveys were conducted in teams of at least four people. Hellbenders were captured by hand or net after flipping all possible boulder-sized rocks within the stream; no leverage devices were used. Underwater goggles were worn to aid in visibility when needed. Stream flow conditions were evaluated before surveying to ensure conditions were within suitable ranges for effective surveys (depth ,1 m). Captured individuals were placed ventral side up in a custom ''bender board'' squeeze box to prevent struggling (Burgmeier et al., 2010). Gender, total length (cm), snout–vent length (cm), and weight (g) were recorded for all individuals. Gender was determined via cloacal swelling during the breeding season (approximately mid-August through late September). Outside of the breeding season, individuals cannot be sexed based on external morphological characters; therefore, we collected blood sam- ples from all individuals for positive gender identification using laboratory analyses. We used a phosphoprotein assay on blood serum to identify vitellogenin (VTG) presence (female) or absence (male) to properly identify unsexed individuals (Burgmeier, 2010). Both methods were used when available. All hellbenders were scanned with Biomark FS2001F-ISO and AVID Multiscan 125 PIT tag readers. If no chip was found, a Biomark 134.2 kHz tag was implanted in the tail approximately 8 cm posterior to the hind leg. Habitat measurements were taken at all capture locations and include coordinates (UTM), water temperature (uC), water depth (cm), distance to shore (m), distance to nearest shelter (cm), number of shelter rocks (-20 cm diameter) within 6-m radius, weather (sunny, partly cloudy, cloudy, raining), substrate (bedrock, silt, sand, gravel, cobble), flow type (pool, riffle, run), and rock length (cm),
width (cm), and depth (cm).

Data Analysis.—Absolute abundance for the Blue River watershed was calculated using the POPAN parameterization of the Jolly-Seber Model (Begon, 1979) in Program MARK. Akaike's Information Criterion (AIC) values were used to select the best available model (Akaike, 1973). From this

TABLE 3. Known densities and site classifications for all 42 sites surveyed during our study.

Site	Class	Area (100 m^2)	Ind	Density (Ind/100 m^2)
1[a]	Exploratory	11.56	4	0.35
2[a]	Exploratory	36.02	0	0.00
3[a]	Exploratory	63.56	0	0.00
4[a]	Exploratory	18.49	0	0.00
5[a]	Exploratory	20.61	0	0.00
6[b]	Exploratory	N/A	1	N/A
7[b]	Exploratory	N/A	1	N/A
8	IDNR	67.02	14	0.21
9	IDNR	34.28	6	0.18
10	IDNR	114.21	10	0.09
11	IDNR	89.17	5	0.06
12	IDNR	44.68	2	0.04
13	IDNR	70.49	3	0.04
14	IDNR	50.27	2	0.04
15	IDNR	75.31	2	0.03
16	IDNR	62.40	1	0.02
17	IDNR	48.15	0	0.00
18	Primary	54.70	3	0.05
19	Primary	37.56	2	0.05
20	Primary	115.37	1	0.01
21	Primary	38.33	0	0.00
22	Primary	67.60	0	0.00
23	Primary	46.42	0	0.00
24	Primary	26.19	0	0.00
25	Secondary	67.80	12	0.18
26	Secondary	23.88	3	0.13
27	Secondary	34.28	3	0.09
28	Secondary	11.56	1	0.09
29	Secondary	15.60	1	0.06
30	Secondary	37.17	2	0.05
31	Secondary	39.29	2	0.05
32	Secondary	23.30	1	0.04
33	Secondary	71.45	3	0.04
34	Secondary	64.91	2	0.03
35	Secondary	55.08	1	0.02
36	Secondary	29.28	0	0.00
37	Secondary	44.68	0	0.00
38	Secondary	24.85	0	0.00
39	Secondary	58.55	0	0.00
40	Secondary	74.73	0	0.00
41	Secondary	64.14		0.00
42	Secondary	20.80	0	0.00

[a] Sites not included in mark–recapture estimate, but included toward known density estimate.
[b] Two sites surveyed, but not included in estimates because of lack of survey effort and spatial data.

estimate, we calculated absolute density (the estimated number of individuals per 100 m^2). Known density (the number of known individuals/per 100 m^2) was calculated as well using information from the 35 mark–recapture sample sites and five additional sample sites. Absolute density provides an estimate of the population density, whereas known density provides a known minimum density estimate for the population. The estimates should be considered applicable only to our 35 and 40 sample sites respectively. Catch per unit effort (CPUE) was estimated as the number of hellbenders captured per sampling hour. All surveys were timed and the number of surveyors recorded. We estimated biomass for both the absolute and known densities as the mean individual mass multiplied by the density. Size classes were arranged in 5-cm intervals as per Nickerson et al. (2002). A Chi-square goodness-of-fit test was used to determine whether sex ratio differed from parity. Student's *t*-test and nonparametric Mann-Whitney *U*-tests were used to compare morphological and habitat use differences between genders.

RESULTS

A total of 1,514 sampling hours were spent surveying approximately 203,366 m^2 of river. A total of 70 individual hellbenders were captured and marked during the five mark–recapture surveys. Twenty-one individuals were recaptured at least once, but only seven were recaptured twice or more. Our recapture rate was 30% based on the 21 recaptures. When the seven exploratory sites are included (for a total of 42 sites), the total number of hellbenders captured increased from 70 to 88. Hellbenders were captured at 26 of the 42 sites (62%). The majority of sites (74%) resulted in two or fewer captured individuals, whereas the remaining 26% had three or more captured individuals per site. All individuals captured throughout the study were adults. During exploratory surveys, two nests were discovered within 25 m of each other, and both were guarded by males. Eggs were fertilized and estimated to be in Harrison stage 17 (Harrison, 1969). No other nests were found during the study.

Using data from 35 sampling sites and five capture occasions, we produced a population estimate of 114 (95% CI 5 94–152) hellbenders for the study sites. AIC values were lowest for the constant capture and survival with time-dependent probability of entry model. The absolute density estimate was 0.06 individuals/100 m^2, whereas the known density for the entire 40-site study area was slightly lower at 0.04 individuals/100 m^2 (*N* 5 86). Two exploratory sites were not included in this estimate because of a lack of accurate site dimensions resulting in the exclusion of two captured individuals and the reduction in sample size from 88 to 86. The highest known density recorded at an individual site was

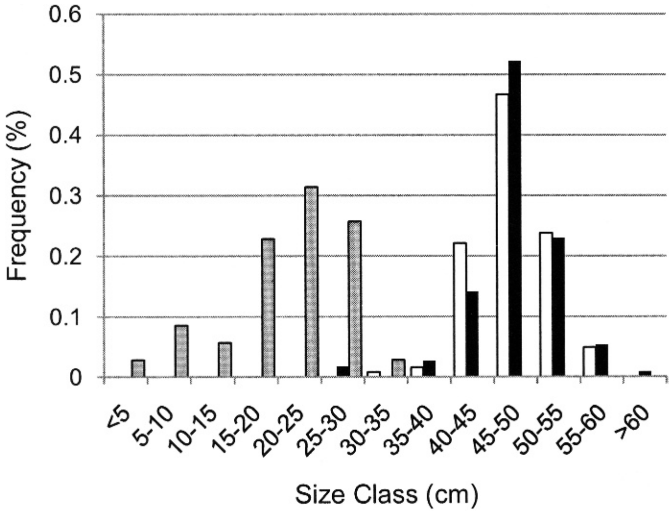

FIG. 1. Illustrates the differences in size class distribution present between a ''stable'' population of hellbenders found in Georgia and a geriatric, nonproductive population found in Indiana. The historic distribution for Indiana is included to illustrate the relative lack of younger age classes entering the population over the past several decades. Present study (white bars); historical Kern 1984 Indiana surveys (black bars); SDU, unpubl. 2009 Georgia survey (gray bars).

0.35 individuals/100 m^2 (Table 3). Catch per unit effort was 0.05 individuals/sampling hour. Biomass estimated from the absolute density was 3.51 kg/ha but decreased slightly to 2.70 kg/ha when calculated using the known density. Seventy-eight hellbenders could be assigned a gender using a combination of external morphology and blood chemistry analysis. Sex ratios were 2.6 : 1 (56 males and 22 females) and significantly skewed toward males (χ^2 5 14.82, *P* , 0.05).

Size classes were skewed toward large (and presumably old) adults (Fig. 1). The mean total and snout–vent lengths for the population were 47.58 6 4.10 cm and 32.01 6 2.86 cm, respectively. Mean total weight was 627.16 6 162.78 g. Females were significantly larger for total length, snout–vent length, and weight (Table 4). Most captured individuals appeared healthy with two notable exceptions. Two males, each located at different sites and captured two months apart, appeared grossly malnourished with visible bones down their trunk and tail. However, other individuals captured at these sites appeared healthy (*N* 5 2). All individuals were tested for the amphibian chytrid fungus (Burgmeier et al., in press).

Hellbenders were found primarily on gravel substrates (69.30%) and to a lesser extent, silt (14.91%). Sand, bedrock, and cobble were rarely used. Most individuals were located in runs (72.03%), with riffles and pools being used similarly at 13.56% and 14.41%, respectively. Shelter size ranged from 1,598.4 cm^2 to 26,784 cm^2, with a mean size of 10,303.46 6 5,662.89 cm^2. There were no significant differences in shelter use between males and females (*U* 5 21.35, *P* 5 0.18). Mean distance to the nearest shelter was 12.00 6 18.53 cm, whereas mean distance to shore was 4.53 m 6 2.54. Hellbender shelter rocks were surrounded by a mean of 57 6 39.98 suitable alternative shelters (- 20 cm) within a 6-m radius.

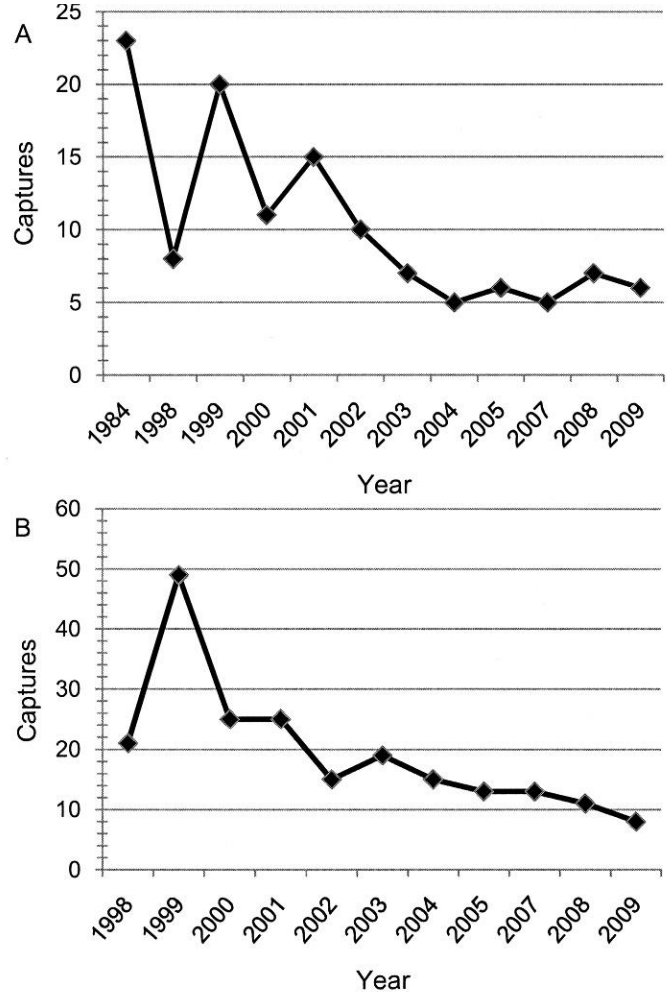

FIG. 2. (A) Annual captures at five sites surveyed by Kern (1984), IDNR (1998–2007), and our study (2008–2009). (B) Annual captures during the annual 11-site IDNR hellbender survey. Years 2008 and 2009 reflect the number of captures during our study at the same 11 sites. No survey was conducted in 2006 because of high water levels. The sampling efforts for the final three years was approximately double that of previous years.

DISCUSSION

Hellbenders have experienced significant declines in Indiana since the most recent extensive survey was performed in the mid-1980s (Kern, 1984). Indeed, population monitoring by the IDNR has documented noticeable declines within several commonly searched sites (Fig. 2), and local anglers frequently offer anecdotes concerning the perceptible lack of encounters while fishing. Despite a substantial increase in sampling effort (42 sites vs. 12) over Kern's (1984) historical survey, the current surveys resulted in far fewer individual captures.

Eight of the 12 sites surveyed in the previous study were included, at least in part, in the current survey sites, and in all but one case resulted in fewer captures (Fig. 3). A similar pattern was observed when comparing our survey results to

TABLE 4. A comparison between morphological measurements from Kern (1984) and the present study.

	Kern, 1984 Total (Mean 6 SD)	Total (Mean 6 SD)	Male (Mean 6 SD)	Female (Mean 6 SD)	*P*-value[a]
TL (cm)	48.18 6 4.76	47.58 6 4.10	46.63 6 2.95	49.39 6 5.75	0.017
SVL (cm)	32.00 6 3.31	32.01 6 2.86	31.15 6 1.91	33.82 6 3.92	0.001
Weight (g)	685.90 6 216.3	627.16 6 162.78	589.58 6 126.76	681.26 6 193.15	0.019

[a] *P*-value represents comparison between males and females during our study only.

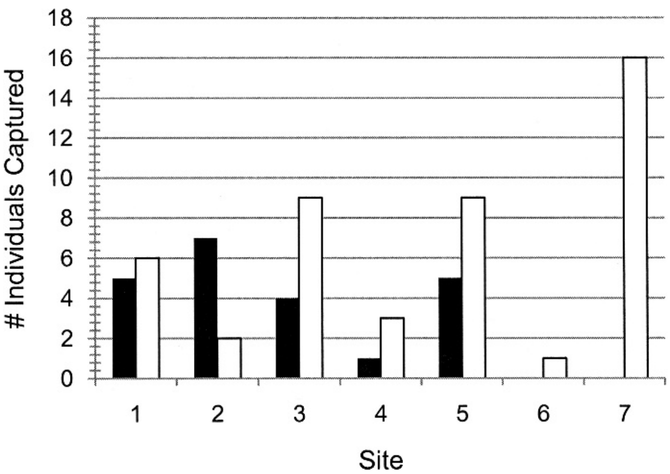

FIG. 3. A comparison of hellbender captures between seven sites surveyed historically by Kern (1984) and during the present study. Site 5 is a combination of two Kern sites as they fit into one of ours. Present study (black bars), Kern, 1984 (white bars).

more recent IDNR surveys. Two IDNR sites included in our surveys annually yielded 5–10 individuals per sampling occasion yet during our study these sites were intensively searched up to seven times during summer and early fall from 2007–2009 and resulted in only 2–3 individuals per site. Repeated sampling disturbance has been proposed as a potential cause of hellbenders emigrating out of particular sites; however, recent telemetry data on this population suggest repeated surveys do not significantly affect long-term individual movements (Burgmeier et al., in press). Also, declining numbers of hellbenders have resulted in animals becoming patchily distributed throughout the river. Well over half of all individuals came from only seven sites. This could have tremendous implications on gene flow and resulting genetic structure within this population as an individual's ability to find a potential mate decreases.

There has been little recruitment in this population over the past two decades (Kern, 1984; IDNR, unpubl. data; this study). In the current study, we were unable to locate larvae or subadults at any of the 42 sites. As a result, the population was skewed toward large adults. Although we recognize the sampling bias toward larger size classes when using the rock-lifting technique, a portion of the nongilled subadults present in a stable population should have been captured using the same methods as adults (Peterson et al., 1983; Nickerson and Krysko, 2003; Foster et al., 2008; NGB, pers. obs.). Indeed, as part of another study, the authors sampled hellbender populations in Georgia and found gilled larvae and nongilled subadults using rock flipping. Adult-biased populations are not uncommon, but younger age classes can still typically be found when present, albeit in far fewer numbers than adults (Nickerson et al., 2003; Foster et al., 2009). Thus, the lack of subadults in this study was likely representative of their absence rather than sampling bias. However, future surveys targeting subadult age classes will be conducted following a protocol similar to that described in Foster et al. (2009).

Two nests were detected in close proximity to each other during our surveys, but no larvae were found in a monitoring survey conducted the following summer. Future larval surveys will be targeted at this area to determine reproductive success. Few other nests have been reported during the previous decade in the Blue River, and those that have been documented were observed at sites known to maintain the highest densities within our study area (Z. Walker, pers. comm.). Although these sites were included in our study, we detected no indication of current reproduction.

The mark–recapture estimates from this study clearly indicate that hellbender numbers are declining in Indiana. However, our population estimate is not directly comparable to most other studies because we used an open-population model. An open population model was necessary for the Blue River population because both death and emigration were documented at several locations as part of another study using radio telemetry (Burgmeier et al., in press). The length of time between successive surveys (more than three weeks) also precluded the use of a closed-population model. Stable hellbender populations have typically been reported at densities of 0.8–6 individuals per 100 m^2 (Hillis and Bellis, 1971; Peterson et al., 1988; Humphries and Pauley, 2005). At 0.04 individuals/100 m^2, the density estimate for our study sites is an order of magnitude lower than other reported populations (Table 1). Our estimates of catch per unit effort were considerably lower than other populations as well (Peterson et al., 1988; Humphries and Pauley, 2005). Even populations considered ''low density'' reported considerably higher catches per unit effort (0.25–0.65 individuals/hour; Nickerson et al., 2002). Surveys in this study were typically conducted by four or five individuals, which are comparable to other surveys; thus, it is unlikely that our lower CPUE was caused by different levels of effort compared to other studies.

Hellbenders do not appear to make up a significant portion of biomass in the Blue River. In fact, the biomass estimates are much lower than previously reported, despite larger average body sizes in this study. This is most likely a result of the low densities found in the Blue River drainage. The sex ratio of the population was biased toward males but within the range reported for other populations. Smith (1907) reported a skewed ratio of up to 3 : 1 males to females in the Allegheny River in Pennsylvania, and Pfingsten (1989) found an even greater skew of 3.4 : 1. Conversely, both female-biased and 1 : 1 ratios have been reported from other populations (Nickerson and Mays, 1973b; Peterson, 1987; Bothner and Gottlieb, 1991; Table 1). In Indiana, Kern (1984) reported a nearly even sex ratio of 1.03 : 1 males to females for the entire study area and 0.74 : 1 males to females at a known nesting site containing a large number of individuals. Under most situations, a male-biased sex ratio would not be considered problematic; however, with a low-density population, it could have drastic effects on the individual fitness of remaining individuals. Depending on the distribution of individuals, breeding opportunities could be hampered by the lack potential mates (Scribner et al., 1997; Gibbs, 1998; Jehle et al., 2001).

Reports of sexual size dimorphism for Eastern Hellbenders are inconsistent (Nickerson and Mays, 1973b; Taber et al., 1975; Mayasich et al., 2003; Humphries and Pauley, 2005). In the current study, females were significantly larger than males for all three standard measurements. The sexual dimorphisms we observed could be a by-product of life-history patterns (e.g., gravid females are older than males) or by interspecific sex differences (e.g., females have longer SVL to store more ova). We cannot distinguish between these (or other) hypotheses with the existing data sets, although it is notable that our results are largely consistent with those reported in Kern (1984). Most hellbenders in the population appeared healthy and active, and only two noticeably underweight individuals were located within two sites where other healthy individuals have been found. However, it is worth noting though that the two sites were within 2.4 km of each other and might be subject to similar environmental conditions. A mostly healthy population indicates suitable resources are present to support current population levels. Likewise, it provides some support for the idea that the exogenous environmental stressors examined are not currently affecting the population's physical fitness. However, it does not preclude these factors as potential past causes of declines nor does it provide a biological endpoint for other potential consequences of these factors such as reproductive fitness.

Hellbender use of gravel substrates and large, flat rocks is widely documented (Hillis and Bellis, 1971; Blais, 1996; Humphries and Pauley, 2005; Burgmeier et al., unpubl. data). Our findings are concordant with this pattern and indicate hellbenders use gravel disproportionately to other available types. This is possibly attributable to the increased abundance of macroinvertebrates at these same areas; however, more extensive research in this aspect of hellbender ecology would be needed to further elucidate habitat preferences. Distance to nearest shelter, distance to shore, and the number of suitable shelter rocks within a 6-m radius were all similar to numbers reported in a radio-telemetry study of the same population (Burgmeier et al., in press). These findings suggest that hellbenders choose areas with abundant cover and are rarely more than a body's length from an alternative shelter. Moreover, the abundance of available shelters would suggest that the lack of suitable shelters is not a likely cause for decline.

Hellbender numbers in Indiana have declined steadily over the past two decades. Our results reveal that the current population structure consists of a predominately geriatric, low density population with little to no recruitment over the past two decades. Although the low densities reported herein are likely a contributing factor to these declines, other causes are not readily apparent from this data set. Studies evaluating the current levels of genetic variation, habitat quality, and overall animal health are needed to fully assess the contributing factors to hellbender declines in the Blue River drainage of Indiana.

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