



# A quantitative field study of paternal care in Ozark hellbenders, North America's giant salamanders

Rachel A. Settle<sup>1</sup> · Jeffrey T. Briggler<sup>2</sup> · Alicia Mathis<sup>1</sup> 

Received: 14 December 2017 / Accepted: 22 June 2018 / Published online: 11 July 2018  
© Japan Ethological Society and Springer Japan KK, part of Springer Nature 2018

## Abstract

Paternal care is relatively uncommon in tetrapods but appears to be the rule in the large aquatic salamanders of the primitive family Cryptobranchidae (North America: hellbenders, genus *Cryptobranchus*; Asia: giant salamanders, genus *Andrias*). For the Ozark hellbender, *C. alleganiensis bishopi*, a federally endangered subspecies, anecdotal observations of paternal care have been reported, but no quantitative assessments have been made. We quantified behavior of a guarding male hellbender from video footage collected over 6 weeks in 2008 from a naturally occurring nest. We quantified behavior of the guarding male to help develop hypotheses about costs and benefits of paternal care. Overall, there were high frequencies of tail fanning of the eggs and rocking behaviors (rhythmic, lateral back-and-forth movements of the body), which increase aeration of the nest. The male rarely left the nest unguarded and spent over half of the recorded time at the nest exposed at the nest entrance. Potential egg predators observed included centrarchid, cyprinid, ictalurid, and percid fishes, with centrarchids being the most common and exhibiting the most interest in the nest. The frequency of foraging by the male was low ( $n=8$  strikes at identifiable prey), with a 37% success rate. The male was observed to consume seven of his eggs. Our data represent the first systematic analysis of paternal care of Ozark hellbenders and elucidate some of the costs (low foraging success, potential energetic costs of tail fanning and rocking) and benefits (aeration of eggs, protection from egg predators) of paternal care.

**Keywords** Paternal care · Nest guarding · Reproduction · Cryptobranchidae · Salamander

## Introduction

Although fairly common in fishes (Gross 2005), care of offspring by the male parent is relatively rare in tetrapods. Maternal care is common in salamanders, but paternal care has only been definitively observed in primitive aquatic species of the families Cryptobranchidae and Sirenidae (Nussbaum 2003; Reinhard et al. 2013). Detailed observations of parental care in natural habitats are rare due to the secretive nature of salamanders, with nests typically hidden under

rocks, in mats of vegetation, in burrows, or under (or within) rotting logs (Petranka 1998). Therefore, information for most species is mostly anecdotal.

All extant salamander species within the family Cryptobranchidae (*Andrias japonicus*, *A. davidianus*, *Cryptobranchus alleganiensis*) engage in paternal care of their offspring (Smith 1907; Tago 1927; Nussbaum 1985). Cryptobranchids are collectively known as the giant salamanders, with the genus *Cryptobranchus* being the largest salamander in North America and the Asian *Andrias* being the largest salamander in the world. All species of Cryptobranchidae are listed on the IUCN Red List, and *C. a. bishopi* is listed as federally endangered by the United States. Recent video recordings of two male *A. japonicus* guarding nests (one natural, one artificial) revealed that, in addition to guarding, males invested considerable time in bouts of tail fanning and agitating the eggs and also ate diseased or dead eggs (Okada et al. 2015; Takahashi et al. 2017). The only member of this family to occur outside of Asia is the hellbender, *Cryptobranchus alleganiensis*, which occurs in parts of the eastern United States. Anecdotal field observations of paternal care by hellbenders

**Electronic supplementary material** The online version of this article (<https://doi.org/10.1007/s10164-018-0553-0>) contains supplementary material, which is available to authorized users.

✉ Alicia Mathis  
aliciamathis@missouristate.edu

<sup>1</sup> Department of Biology, Missouri State University, Springfield, MO 65897, USA

<sup>2</sup> Missouri Department of Conservation, Jefferson City, MO 65201, USA

suggested that males protect the eggs from predators (Smith 1907; Bishop 1941). However, in at least some cases males have been reported to consume their own eggs (Unger and Williams 2017). No systematic observations of paternal care have been reported for hellbenders, either in captivity or from natural habitats.

Asian giant salamanders and hellbenders have been separated for approximately 70 million years (Browne et al. 2012), allowing substantial time for divergence in morphology, ecology and behavior; however, many similarities remain. A detailed review of the ecology and behavior of the two extant genera is provided by Browne et al. (2014; see references therein), and we summarize the major points of comparison presented in their review here. The most striking differences are that of size, lifespan and age, with *A. japonicus* reaching a maximum of 150 cm in total length, becoming sexually mature at about 8 years, with a longevity of 60+ years, and *C. a. bishopi* usually reaching only about 50 cm, maturing at 4–6 years, with a lifespan of 30+ years. Egg sizes and size at metamorphosis are slightly larger for giant salamanders than for hellbenders, potentially making maintaining adequate aeration more of a challenge for *A. japonicus*. Both genera occur in cool temperate zones and occupy oligotrophic, rocky streams, usually with fast/moderate flow, although there is some habitat variation among populations. Both genera are mostly nocturnal, although diurnal activity has been reported in some populations of *Cryptobranchus*. Both are cannibalistic (particularly oophagic), and are euryphagic, with *Andrias* tending to eat more vertebrates (fish, frogs, water shrews) along with crabs and aquatic insects, and *Cryptobranchus* diets tending to be dominated by invertebrates (insects, snails, worms, and, particularly, crayfish) along with fish and tadpoles. Dietary differences could result in differences between the two species in access to prey during nest guarding. Both genera show seasonal reproduction, with males defending spawning sites, courting and mating with multiple females, and guarding the eggs and larvae. Spawning sites may differ somewhat in ways that could affect temperature and aeration, with male *Andrias* frequently occupying burrows in river banks and *Cryptobranchus* more typically defending spawning sites in hollows under rocks and cavities in bedrock.

This study provides the first systematic data on paternal care collected from a hellbender nest. Qualitatively, our goals were to determine the occurrence, prevalence, and persistence of behaviors that likely are associated with costs and benefits of parental care (e.g., Royle et al. 2012). Quantitatively, for the nest in this study, we determined: (1) the percentage of time that the male spent at the nest versus away from the nest, (2) the percentage of time that the male spent at the nest entrance versus inside the nest, (3) whether and how frequently hellbenders exhibited the behaviors of tail-fanning and rocking, which were described for

guarding male *A. japonicus* (Okada et al. 2015; Takahashi et al. 2017), (4) whether the hellbender foraged while at the nest entrance, and, if so, the identity of the prey, including its own eggs, and (5) the identity of fish species (potential prey or egg predators) that were visible near the nest and their behavior with respect to the nest. In addition to providing insights into the likely costs and benefits of paternal care in this species, this study also allows for qualitative comparisons of paternal care in its closest living confamilial, *A. japonicus*.

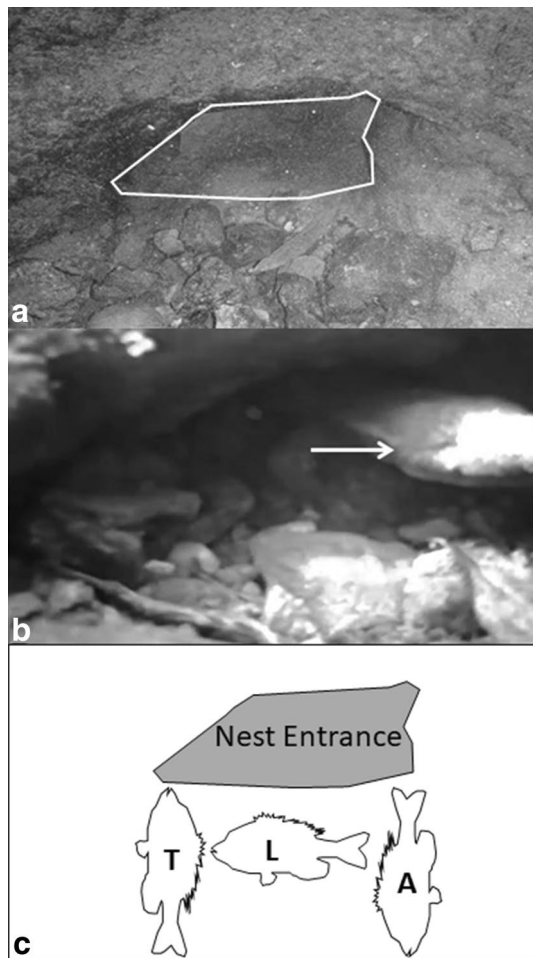
## Materials and methods

### Nest site and video set-up

The nest (cavity = 18 cm wide) was located within a bedrock crevice in the North Fork of the White River (Ozark County, Missouri, USA), and oriented perpendicular to stream flow (Fig. 1a, b). To protect the nest site from potential disturbance, specific location information will not be disclosed. The nest contained a fertilized clutch of eggs (estimate: 2–5 days old) guarded by a single male (mass = 310 g, total length = 40 cm, snout-vent length = 26.5 cm). We did not attempt to count the eggs or measure the egg mass because doing so would require substantial disturbance of the nest. We recorded nest activity using an infrared underwater video camera (2007 model of Aqua-Vu imaging system; approximately 28 cm from nest entrance). To decrease the possibility of vandalism or other disturbance, we locked the VCR recorder in a camouflaged metal container that was hidden several meters up the bank, and buried the cord in gravel. A field team from the Missouri Department of Conservation changed tapes and batteries, generally every 1–2 days, with occasional longer gaps.

### Video data

We collected video data between 8 October and 15 November during the 2008 breeding season, using 24-, 40-, or 64-h recording modes ( $n = 14$  tapes; Table 1). Total length of the tapes varied ( $\bar{x} \pm SD = 5.4 \pm 2.21$  h; range = 2.2–8.2 h) depending on recording mode and the battery life of the camera. Variation of recording modes was due to practical considerations of when a member of the field team was available to replace the spent tape and recharge the battery. Faster recording modes allowed for collection of the most data per videotape but resulted in lower quality images. Visibility on some of the tapes was also limited due to insufficient light or obstruction of the lens by floating debris; the percentage of viewable footage per tape ranged from 0 to virtually 100% ( $\bar{x} \pm SD = 53.60 \pm 30.98\%$ ).



**Fig. 1** **a** Nest located within a bedrock crevice, with the nest entrance (approximately 18 cm wide and 8 cm tall; width of larger cobble, approximately 1.5–8.5 cm) outlined in white; **b** Video screenshot of the nest's entrance with the hellbender's head (arrow) protruding from the nest; **c** orientations of fish to the nest as either toward (*T*), lateral (*L*), or away (*A*) from the nest entrance

## Data collection

We recorded the time that the male spent either at the nest or away from the nest and calculated the percent time spent in nest occupancy as the time spent at the nest divided by the total observable footage for each tape. Measurements of the duration away from the nest began when the hellbender swam completely out of the frame and ended when he re-entered the frame. If the hellbender was at the nest, we measured the time at the nest entrance and calculated the percent time at the nest entrance (Fig. 1b) by dividing the cumulative time at the nest entrance by the total duration spent at the nest for each video.

We recorded the following hellbender behavioral variables: occurrence of (1) strikes at prey, (2) tail-fanning, and (3) rocking, and observations of fishes (either potential egg

predators or hellbender prey) near the nest entrance. For each “strike at prey”, we recorded: (1) the type of potential prey item (crayfish or fish, with species identified where possible), and (2) whether the strike was successful.

We measured the duration of the hellbender tail-fanning and rocking for each video. Tail-fanning was movement of the tail in a rhythmic, lateral motion over fertilized eggs (Browne et al. 2014; Okada et al. 2015). Rocking was side to side motion of the hellbender's body when he was otherwise stationary within the nest (Okada et al. 2015). For each tape, we calculated the percent time spent in each behavior as the total time observed in the behavior divided by the viewable footage (see Table 1) of that tape.

For each fish that entered the frame, we identified the family and species when possible. We categorized the orientation of each fish as toward the nest (*T*), away from the nest (*A*), or lateral to the nest (*L*) (Fig. 1c). To minimize the possibility of repeatedly recording the presence of the same individual, we did not record the presence of any other fish of the same species for 2 min; individuals did not appear to remain around the nest for longer than 2 min (personal observations). When a fish oriented in more than one direction during the 2-min window, only the initial direction was used for the statistical analysis.

## Data analyses

The occurrence of tail-fanning, rocking, and nest guarding behaviors were variable over time, and data are depicted graphically to illustrate patterns. Percent time spent at the nest entrance appeared to decline linearly, and so we analyzed these data with a Spearman's correlation rank test (RStudio v. 0.98.1091). A chi-square test (Minitab v. 16.1.0) was used to determine whether the frequency of orientations (toward, lateral, away) differed between the two fish taxa.

## Ethical note

The video data were collected with the approval of the Missouri Department of Conservation. Observations of a single male hellbender minimized potential negative effects on this endangered species. The most likely effect of disturbance, abandonment of the nest by the guarding male, did not occur.

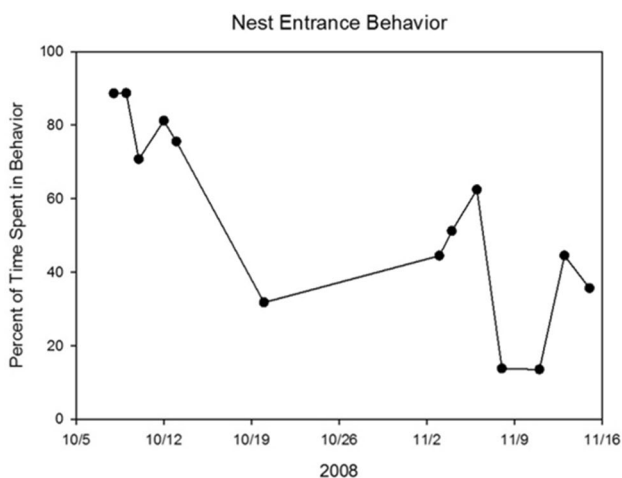
## Results

### Nest occupancy and entrance behavior

Overall, the male occupied the nest for approximately 98.4% of the 41.7 h of observable footage. Over the span of 38 days, the hellbender was recorded leaving the nest 11 times, with the nest left unguarded for an average of 270 s

**Table 1** Characteristics of the 14 videotapes analyzed in this study. The date range refers to the dates the tapes were inserted and removed. Length is the total length of each recorded video. Recording mode specifies the recording setting for each video. Viewable footage refers to the recorded time that included unobstructed footage that allowed for data collection

Video number	Date range (2008)	Length h:min:s	Recording mode (h)	Viewable footage h:min:s
1	8 Oct–9 Oct	5:20:13	24	5:14:19
2	9 Oct–10 Oct	8:11:39	24	8:11:21
3	10 Oct–12 Oct	8:10:16	40	8:05:14
4	12 Oct–13 Oct	7:28:39	24	3:43:49
5	13 Oct–14 Oct	6:23:12	40	3:49:30
6	17 Oct–20 Oct	7:51:35	64	0:00:00
7	20 Oct–3 Nov	2:26:39	40	1:22:54
8	3 Nov–4 Nov	3:51:14	40	1:13:20
9	4 Nov–6 Nov	2:40:40	40	1:09:09
10	6 Nov–8 Nov	5:37:39	64	4:37:59
11	8 Nov–11 Nov	3:45:55	64	1:27:22
12	11 Nov–13 Nov	5:40:59	64	1:11:05
13	13 Nov–14 Nov	2:11:39	64	0:45:30
14	15 Nov–16 Nov	2:18:37	64	0:49:15



**Fig. 2** Percent of observed nest-occupancy time that the male hellbender was visible at the nest entrance between 5 October and 16 November 2008

(SD = 294.85, range 61–1111 s) per trip. At the beginning of the recording period, the hellbender spent approximately 90% of the video exposed at the front of the nest, but this percentage declined to about 20–40% by the end of the study ( $r_s = -0.780$ ,  $P < 0.003$ , Fig. 2). There also was a significant positive correlation between the number of fish observations per video and the amount of time the hellbender spent at the entrance in each video ( $r_s = 0.709$ ,  $P < 0.007$ , Fig. 3). Overall, the hellbender spent 55% of his time at the nest entrance.

### Hellbender behavior: tail fanning, rocking, and strikes at prey

Overall, tail fanning (supplementary information, S1) was generally more frequent than rocking (Fig. 4). Tail fanning occupied at least 40% of the time observed at the nest entrance on 5/13 tapes whereas rocking peaked at about 20%. Both behaviors were highly variable, with some of the variability likely due to relatively short periods of viewable footage (Table 1) available on some tapes.

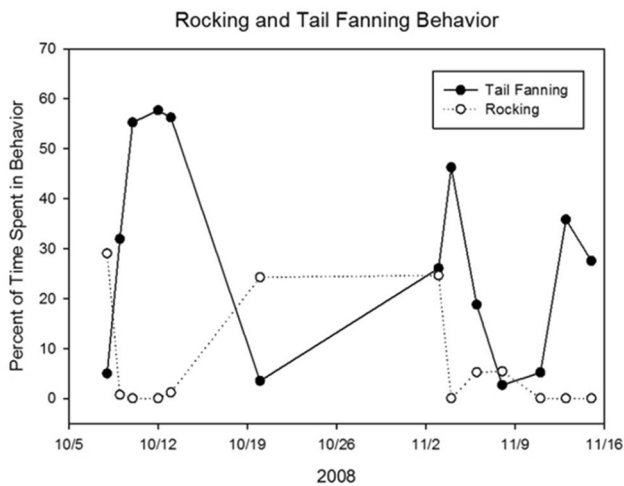
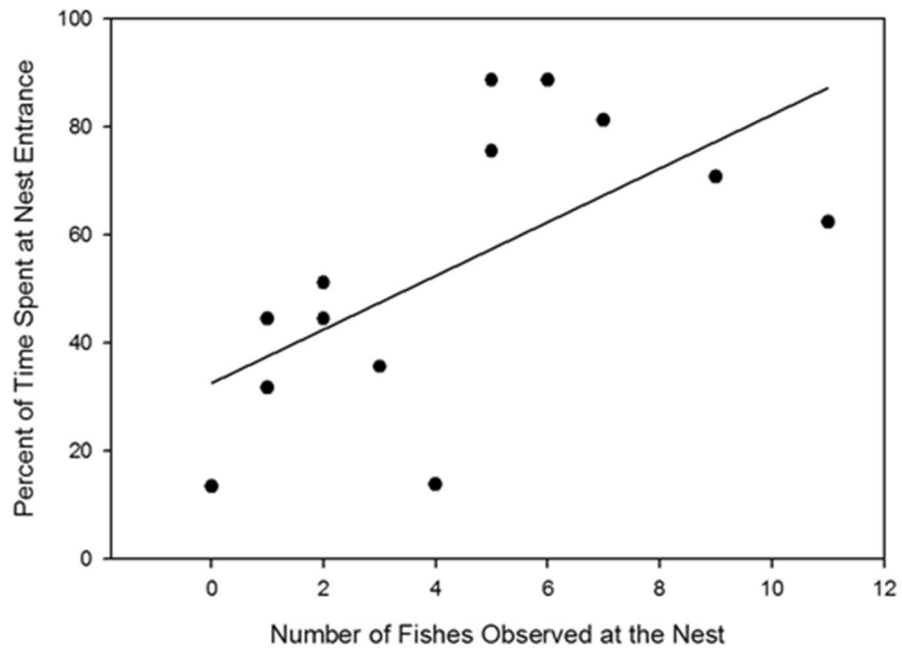
A total of 10 strikes at prey were observed. For two unidentified prey items, we could not determine whether the strikes were successful. For the remaining eight prey items, the success rate of the hellbender foraging at the nest was 37.5%, with the only three successful strikes at fishes of the family Cyprinidae. The unsuccessful bites were directed toward crayfish (4) and small cyprinid fishes (1). The hellbender consumed seven of his eggs (supplementary information, S2), either singly or in pairs, within view of the camera during videos 2, 3, and 4.

### Fish presence and behavior

The first sighting of fishes began early in the first video and continued sporadically over the course of the study. Because our observations occurred 2–5 days after fertilization, it is unlikely that fishes were attracted by recent spawning activity. The total number of fishes observed was 56 (Table 2), with 68% of the observations being of the family Centrarchidae. Identified centrarchid species included *Lepomis megalotis*, *Pomoxis nigromaculatus*, *L. macrochirus* and *Micropterus* sp. (both *M. dolomieu* and *M. salmoides* have been observed at this site during this time period according

**Fig. 3** Percent of time spent at the nest entrance as a function of the number of fishes observed at the nest

**Correlation Analysis of Nest Entrance Behavior and Fish Observations**



**Fig. 4** The proportion of observable time that a male hellbender spent rocking and tail fanning between 5 October and 16 November 2008

to records from the Missouri Department of Conservation). The next most common family was Cyprinidae (23%). Because of their small size and the low image-quality of the videos, species of cyprinids were difficult to identify; some appeared to be striped shiners (*Luxilus chrysocephalus*). The two observations of ictalurids were catfish (likely bullhead catfish, *Ameiurus* sp., based on MDC fish census data). Observed percids were two log perch (Percina caprodes) and one darter (Etheostoma sp.).

Fishes were oriented toward the nest in 37 of the 56 observations, with the remainder being almost evenly split

**Table 2** Number of fish from four families observed at the nest over the course of the study, and their respective orientations with respect to the nest. Because of low cell sizes for non centrarchids, statistical analysis was for centrarchid vs. non centrarchid ( $\chi^2_{2,56} = 13.14$ ,  $P = 0.001$ )

Family	Orientation		
	Toward	Lateral	Away
Centrarchidae	31	3	4
Non centrarchid			
Cyprinidae	6	3	4
Percidae	0	2	1
Ictaluridae	0	2	0

between lateral and away orientations (Table 2). Because of the small number of expected values per cell, we combined all non-centrarchids into one group for statistical analysis. Centrarchids were significantly more likely to be oriented toward the nest than non-centrarchids ( $\chi^2_{2,56} = 13.136$ ,  $P = 0.001$ ). One centrarchid was observed to consume a single egg that had slowly drifted from the nest near the end of video 4.

**Discussion**

The research presented here is a case study and by definition does not yield estimates of the range of variation that is present in the population. As such, inferences from our

quantitative findings for one individual should be made with caution. However, the data have the advantage of being collected from a natural nest in a natural habitat over a period of approximately 5 weeks (approximately 45–84% of brooding period, based on the estimate of 45–84 days for brooding by Peterson 1988). These data provide the first long-term quantitative study of nest guarding for hellbenders.

Nest occupancy by the male during the observation period was remarkably high. The hellbender rarely left the nest unguarded, with the average time spent away from the nest being less than 5 min (maximum of 18.5 min). Okada et al. (2015) also found strong nest fidelity by guarding males of *A. japonicus* (range of 1.3–125 min/day away from the nest).

The proportion of the time at the nest that the male spent with his head at the front of the nest varied throughout the season, with the highest percentage (about 90%) at the beginning of the season, declining to about 20–40% over the next 5 weeks. The threat of egg predation by other hellbenders appears to be particularly high during and shortly after the oviposition period when eggs trailing from the females' cloacae or floating in the water may draw attention to the nests (e.g., Smith 1907; Peterson 1988). Although we did not observe other hellbenders approaching the nest, which may reflect the relatively low densities of hellbenders (e.g., Wheeler et al. 2003), we infer that one function of the male's position at the nest opening is vigilance against potential conspecific egg predators.

Presence at the nest opening was positively correlated with the presence of fishes, which could be due to either vigilance against nest predators, or attraction to potential prey (see below). Takahashi et al. (2017) observed minnows at an abandoned *A. japonicus* nest but not at a nest that was guarded by the male, supporting a role of protection of the eggs from potential egg predators. Defense against egg predators has also been reported for terrestrial female plethodontid salamanders (Trauth et al. 2006; Forester 1978, 1979). It is likely that guarding against egg predators is a common benefit of brooding in salamanders.

The male hellbender was an opportunistic forager while at the nest entrance, and supplemental foraging possibly could have occurred during the male's trips away from the nest. Only about a third of eight observed strikes were successful. Observations of foraging success for hellbenders in natural conditions are rare, but Dunn (2016) observed one eastern hellbender at a fish spawning site making 19 strikes at fishes, with only two strikes successful. In our study, all of the strikes were directed toward either crayfish or cyprinid fishes, which are potential prey (e.g., diets reviewed in Nickerson and Mays 1973; Peterson 1985; Peterson et al. 1989). Although, crayfish (*Orconectus* sp.) are generally cited as the primary prey type (Smith 1907; Swanson 1948; Nickerson and Mays 1973), no strikes at crayfish were successful.

Crayfish are predators of salamander eggs (e.g., Gamradt and Kats 1996), and so strikes at crayfish may be a result of nest defense rather than foraging per se. As has been reported for some other salamander species (e.g., Krzysik 1980), we hypothesize that lost feeding opportunities may be a cost of nest guarding in hellbenders.

We observed seven instances of egg predation by the guarding male. Filial cannibalism by hellbenders in nature has been confirmed via genetic analyses (Unger and Williams 2017), and is likely a frequent occurrence (Nickerson and Mays 1973). Smith (1907) hypothesized that male hellbenders consume their own eggs because of their value as food. However, in some other species of salamanders (e.g., Tilley 1972; Forester 1979), including *A. japonicus* (Okada et al. 2015), egg consumption by guarding individuals has been observed to be removal of fungal-infected (nonviable) eggs from the nest, a behavior that Okada et al. (2015) termed hygienic filial cannibalism. This behavior may contribute to hatching success by decreasing the likelihood of fungal infections spreading to healthy, non-contaminated eggs (Forester 1979). We could not determine the condition of the eggs that were consumed because of the low quality of the videotape images and so are unable to test this hypothesis in our study.

Tail fanning was performed at relatively high frequencies, about 60% of the time that the male was at the nest entrance. For guarding males of *A. japonicus* (Okada et al. 2015; Takahashi et al. 2017), the percent time tail fanning was lower at both a naturally occurring (maximum about 5%) and an artificial (maximum about 53%) nest than for hellbenders in this study (Okada et al. 2015). Tail fanning (Okada et al. 2015) and rocking (Harlan and Wilkinson 1981) are performed at higher rates when oxygen concentrations are low, suggesting that these behaviors function to increase dissolved oxygen (DO) levels to the eggs. Low DO levels have been linked to poor survival of fish embryos (Hale et al. 2003) and Takahashi et al. (2017) suggested that low DO levels contributed to the abandonment of the artificial nest by the guarding male.

Rocking by the hellbender occurred for substantial periods of up to about 25% of the time that the male was at the nest entrance. Rocking was not performed at all at the artificial *A. japonicus* nest (Okada et al. 2015), and was somewhat less frequent at their natural nest (up to 14% of the time) than for our hellbender nest. Rocking behavior increases in frequency in low-oxygen conditions and helps to maintain blood oxygen tensions (Harlan and Wilkinson 1981). Bishop (1941) suggested that rocking may also facilitate aeration of egg masses. Although not as common as tail fanning, rocking during egg incubation has been reported for at least one fish (Smith-Grayton and Keenleyside 1978). Okada et al. (2015) did not consider rocking to be a part of parental investment (Trivers 1972) for *A. japonicus* because

this behavior is also performed in the absence of eggs. However, rocking could be categorized as parental investment if rates of rocking were higher in the presence of eggs than when eggs are absent. Whether the embryos benefit from rocking behavior, and, if so, whether the behavior would meet Trivers' criteria for classification as parental investment requires further study. Males also had the option of swimming to the surface for supplemental air breathing, which potentially could have occurred during absences from the nest. An egg-guarding male *A. japonicus* performed supplemental surface breathing, but in that case the male did not have to leave the nest for air breathing because the water where the nest was located was shallow (Okada et al. 2015).

Egg agitation, which was frequent for *A. japonicus* (Okada et al. 2015), could provide additional DO to the developing embryos and enhance the hatching success. We recommend the excellent video images of this behavior provided in the supplemental material of Okada et al. (2015). We did not see egg agitation at the hellbender nest, although the position of the camera limited our view of the eggs; it is also possible that tail fanning may have served as de facto agitation if the tail physically disturbed the eggs. Artificial egg agitation was initiated in rearing developing eggs at the Ron Goellner Center for Hellbender Conservation (Saint Louis Zoo, Saint Louis, Missouri, USA) in the absence of a guarding male, and hatching success increased substantially (Chawna Schuette, pers. comm.).

Over half of the fishes observed were centrarchids, which were frequently oriented toward the nest, indicating a higher level of interest in the nest than the other fish species. Some centrarchids are known to engage in nest-raiding behavior (Pflieger 1997), so their primary role may be as potential egg predators. Diet studies generally do not list centrarchids as prey (e.g., Nickerson and Mays 1973; Petranka 1998). For the remaining fish taxa (Cyprinidae, Ictaluridae, Percidae) there were no consistent orientation patterns with respect to the nest. The vulnerability of these smaller fishes to predation from the defending male may have deterred them from showing strong interest in the nest.

Understanding the evolution of paternal care in hellbenders requires a knowledge of costs and benefits of brooding behaviors. We provide the following hypotheses. Guarding males benefit from increased survival of eggs via decreased predation from other hellbenders (e.g., Smith 1907) and predatory fishes (this study) and from removal of pathogenic or dead eggs from the nest (e.g., Forester 1979). In addition, consumption of some eggs throughout the guarding period (this study) could provide some nutrition to the male. Costs of paternal care include the acquisition and defense of the spawning site (e.g., Hopkins and DuRant 2011; Miller and Miller 2005), the low rate of foraging success during the egg guarding period (this study), and the energy expenditure necessary to sustain high rates of tail fanning and rocking

(this study). The dramatic population declines of Ozark hellbenders (e.g., 75–85% in Missouri: Wheeler et al. 2003) could substantially impact the costs and benefits associated with egg guarding in hellbenders, but specific predictions require additional data on shifting costs and benefits for both males and females.

**Acknowledgements** We thank the reviewers for their helpful comments. We are grateful to Cathy Bodinof and her field crew for changing batteries and VCR tapes during the video collection process. Research funding was provided by the Graduate College and the Biology Department at Missouri State University and the Missouri Department of Conservation.

## Compliance with ethical standards

**Conflict of interest** The authors declare that there is no conflict of interest.

## References

- Bishop SC (1941) The salamanders of New York. N Y State Mus Bull 243:1–365
- Browne RK, Li H, Wang Z, Hime PM, McMillan A, Wu M, Diaz R, Hongxing Z, McGinnity D, Briggler JT (2012) The giant salamanders (Cryptobranchidae): Part A. Palaeontology, phylogeny, genetics, and morphology. Amphib Reptil Conserv 5:17–29
- Browne RK, Li H, Wang Z, Okada S, Hime P, McMillan A, Wu M, Diaz R, McGinnity D, Briggler JT (2014) The giant salamanders (Cryptobranchidae): Part B. Biogeography, ecology and reproduction. Amphib Reptil Conserv 5:30–50
- Dunn CG (2016) Documentation of *Cryptobranchus alleganiensis alleganiensis* (eastern hellbender) predation on nest-associate stream fishes. Northeast Nat 23:N8–N11
- Forester DC (1978) Laboratory encounters between attending *Desmognathus ochropaeus* (Amphibia, Urodela, Plethodontidae) females and potential predators. J Herpetol 12:537–541
- Forester DC (1979) The adaptiveness of parental care in *Desmognathus ochropaeus*. Copeia 1979:332–341
- Gamradt SC, Kats LB (1996) Effect of introduced crayfish and mosquitofish on California newts. Conserv Biol 10:1155–1162
- Gross MR (2005) The evolution of parental care. Q Rev Biol 80:27–45
- Hale RE, Mary CMS, Lindström K (2003) Parental responses to changes in costs and benefits along an environmental gradient. Environ Biol Fish 67:107–116
- Harlan RA, Wilkinson RF (1981) The effects of progressive hypoxia and rocking activity on blood oxygen tension for hellbenders, *Cryptobranchus alleganiensis*. J Herpetol 15:383–388
- Hopkins WA, DuRant SE (2011) Innate immunity and stress physiology of eastern hellbenders from two stream reaches with differing habitat quality. Gen Comp Endocrinol 174:2107–2115
- Krzysik AJ (1980) Trophic aspects of brooding behavior in *Desmognathus fuscus*. J Herpetol 14:426–428
- Miller BT, Miller JL (2005) Prevalence of physical abnormalities in eastern hellbender (*Cryptobranchus alleganiensis alleganiensis*) populations of middle Tennessee. Southeast Nat 4:513–520
- Nickerson MA, Mays CE (1973) The hellbenders: North American “giant salamanders”. Milwaukee Publ Mus Spec Publ Biol Geol 1:1–106
- Nussbaum RA (1985) The evolution of parental care in salamanders. Misc Publ Mus Zool Univ Michigan 169:1–50

- Nussbaum RA (2003) Parental care. In: Sever DM (ed) Reproductive biology and phylogeny of Urodela. Science Publishers, Enfield, pp 527–612
- Okada S, Fukuda Y, Takahashi MK (2015) Paternal care behaviors of Japanese giant salamander *Andrias japonicus* in natural populations. *J Ethol* 33:1–7
- Peterson CL (1985) Comparative demography of four populations of the hellbender, *Cryptobranchus alleganiensis*, in the Ozarks. PhD dissertation, University of Missouri, Columbia
- Peterson CL (1988) Breeding activities of the hellbender in Missouri. *Herpetol Rev* 19:28–29
- Peterson CL, Reed JW, Wilkinson RF (1989) Seasonal food habits of *Cryptobranchus alleganiensis* (Caudata: Cryptobranchidae). *Southwest Nat* 34:438–441
- Petranka JW (1998) Salamanders of the United States and Canada. Smithsonian Institution Press, Washington, DC
- Pflieger WL (1997) The fishes of Missouri, revised edition. Missouri Department of Conservation, Jefferson City
- Reinhard S, Sebastian S, Kupfer A (2013) External fertilization and paternal care in the paedomorphic salamander *Siren intermedia* Barnes, 1826 (Urodela: Sirenidae). *Zool Anz* 253:1–5
- Royle N, Smiseth PT, Kölliker M (eds) (2012) The evolution of parental care. Oxford University Press, Oxford
- Smith BG (1907) The life history and habits of *Cryptobranchus allegheniensis*. *Biol Bull* 13:5–39
- Smith-Grayton PK, Keenleyside MHA (1978) Male-female parental roles in *Heterotilapia multispinosa* (Pisces: Cichlidae). *Anim Behav* 26:520–526
- Swanson PL (1948) Note on the amphibians of Vernango County, Pennsylvania. *Am Midl Nat* 40:362–371
- Tago K (1927) Notes on the habits and life history of *Megalobatrachus japonicus*. *Cong Int Zool Budapest* 1927:828–838
- Takahashi MK, Okada S, Fukuda Y (2017) From embryos to larvae: seven-month-long paternal care by male Japanese giant salamander. *J Zool* 302:24–31. <https://doi.org/10.1111/jzo.12433>
- Tilley SG (1972) Aspects of parental care and embryonic development in *Desmognathus ochrophaeus*. *Copeia* 1972:532–540
- Trauth SE, McCallum ML, Jordan RR, Saugey DA (2006) Brooding postures and nest site fidelity in the western slimy salamander, *Plethodon albagula* (Caudata: Plethodontidae) from an abandoned mine shaft in Arkansas. *Herpetol Nat Hist* 9:141–149
- Trivers RL (1972) Parental investment and sexual selection. In: Campbell B (ed) Sexual selection and the descent of man 1871–1971. Aldine, Chicago, pp 136–179
- Unger SD, Williams RN (2017) Genetic confirmation of filial cannibalism in North America's giant salamander, the eastern hellbender *Cryptobranchus alleganiensis alleganiensis*. *Ethol Ecol Evol*. <https://doi.org/10.1080/03949370.2017.1342696>
- Wheeler BA, Prosen E, Mathis A, Wilkinson RF (2003) Population declines of a long-lived salamander: a 20+ year study of hellbenders, *Cryptobranchus alleganiensis*. *Biol Conserv* 109:151–156