Ecology and Diversity

SCIEPublish

Review

Will Cognitively Challenging Headstarted Amphibians with Ecologically Appropriate Stimuli Lead to Greater Repatriation Success?

Michael J. Lannoo [1], Vicky Poole [2], Tim Herman [3], Robert Hill [4], Allan P. Pessier [5], Ruth Marcec-Greaves [6], Mark Vassallo [7], David Vardukyan [7], Michael Andrus [7], Wynona Shellabarger [7], Brad Barr [7], Claire Lannoye-Hall [7], Nathan J. Engbrecht [8] and Rochelle M. Stiles [9],*

[1] Indiana University School of Medicine—ISU, Terre Haute, IN 47809, USA; mlannoo@iu.edu (M.J.L.)
[2] Fort Worth Zoo, Fort Worth, TX 76110, USA; vpoole@fortworthzoo.org (V.P.)
[3] Indoor Ecosystems, Whitehouse, OH 43571, USA; taherman@gmail.com (T.H.)
[4] Zoo Atlanta, Atlanta, GA 30315, USA; rhill@zooatlanta.org (R.H.)
[5] College of Veterinary Medicine, Washington State University, Pullman, WA 99164, USA; apessier@wsu.edu (A.P.P.)
[6] Lincoln Children's Zoo, Lincoln, NE 68502, USA; rmarcec-greaves@lincolnzoo.org (R.M.-G.)
[7] Detroit Zoological Society, Royal Oak, MI 48067, USA; mvassallo@dzs.org (M.V.); dvardukyan@dzs.org (D.V.); mandrus@dzs.org (M.A.); wshellabarger@dzs.org (W.S.); bbarr@dzs.org (B.B.); clannoyehall@dzs.org (C.L.-H.)
[8] Indiana Department of Natural Resources, Bloomington, IN 47401, USA; nengbrecht@dnr.in.gov (N.J.E.)
[9] San Francisco Zoological Society, San Francisco, CA 94132, USA

* Corresponding author. E-mail: rochelles@sfzoo.org (R.M.S.)

Received: 14 May 2026; Revised: 12 June 2026; Accepted: 18 June 2026; Available online: 26 June 2026

ABSTRACT: The frequent failure of headstarting programs suggests we are overlooking important factors in amphibian reintroduction science. Since many repatriation efforts are in vain, such programs can become difficult to justify from a cost-benefit perspective (chronic failure also takes its toll on staff morale), ultimately working against the goals of conservation programs. The question of how to properly prepare amphibian larvae or juveniles for reintroduction and persistence in the landscape is of utmost importance. Here, we offer a previously unconsidered perspective that is predicated on the idea that amphibians, being vertebrates, have forebrain-based cognitive capabilities aligned along the nucleus accumbens-based *reward* system and the amygdaloid nuclei-based *fear* system. Experiences uploaded by the ventromedial pallium as memories are thought to be tagged as accumbens-based 'good' or amygdala-based 'bad', and stored as (relatively) long-term memories; as such, amphibians are said to be salient creatures. The necessarily nurturing nature of zoo husbandry protocols naturally works against young amphibians acquiring ecologically realistic life lessons, especially when these forebrain reward and fear circuits are developing. For example, in zoos, food provisioning eliminates the reward associated with searching for and then finding food, and the emphasis on survival in captivity means headstarted animals released into the wild have no opportunity to experience fear. Such under-stimulated reward/fear circuits poorly prepare headstarted animals for life in the wild. It follows that kindling this circuitry as it develops with ecologically relevant stimuli will better prepare animals for life following release into the wild. To the extent that realistic headstarting protocols call for sacrificing a few animals to enhance the experiences of the remaining many, they will no doubt be resisted by institutions. But we have two choices here: keep doing things the way we have been doing and expect different outcomes, or experiment with new ideas based on a broader understanding of these animals—ideas such as these we are now proposing—to improve the success of repatriation efforts.

Keywords: Reintroduction; Captive-rearing; Conservation; Release; Predator training; Survival; Zoo; Aquarium

1. Introduction

Members of the vertebrate class Amphibia appear especially vulnerable to environmental challenges posed by the Anthropocene, in large part because they can neither flee far nor fast from the many forms of environmental degradation currently affecting Earth’s tropical, temperate, and subpolar ecosystems [1–4]. Further, most amphibians have complex life histories and therefore must rely on both high-quality aquatic *and* terrestrial ecosystems to complete their life cycles, which, using Boolean logic [5], has an innately higher probability of failure than when survival is dependent on the quality of a single habitat type (but see [6]). For these reasons, and because amphibians form critical links in the trophic structure affecting reptiles, birds, and mammals, amphibian conservation has become a global priority.

One goal of modern amphibian conservation efforts has been to reverse declines by re-establishing extirpated populations after ecosystems have been restored or recovered [7–10]. However, the survival of animals following release into the wild has been generally poor, and in too many cases, these efforts have failed to meet their goal of re-establishing populations [8,11–13]. There have been many proposed causes for these failures, which include unsuitable habitat at the release site causing death or dispersal, animals being preyed upon immediately, genetic issues ranging from drift to bottlenecks, translocation shock, and disease [7–9,11,12,14–17]. Our purpose here is not to revisit these causes but rather to introduce an additional factor that, similar to genetic issues, is externally unobservable but may explain the failure of repatriation efforts when such failures cannot be attributed to other causes. Our idea comes from the fact that amphibians are vertebrates and therefore have cognitive functions that develop during certain critical periods when neuronal circuits form. We propose that, in the absence of appropriate ecological stimulation during these critical periods, animals may not develop the necessary cognitive tools needed to successfully meet the post-release demands of a novel and threatening environment. In essence, we challenge the assumption that healthy captive headstarted animals will always innately adjust and thrive after release. To address this issue, we propose re-imagining how we raise headstarted animals. In short, we suggest that providing them with ecologically realistic and challenging situations as their forebrains develop fear and reward circuits should better prepare them for life in the wild and increase post-release survivorship.

2. The Role of Zoos in Headstarting Programs

The animals seeding repatriation (definition following [9]) efforts often come from captive-rearing and release (*i.e.*, headstarting) programs, which are typically centered in zoos and aquariums [11,18]; but see [19]. For the purposes of the present discussion, amphibian headstarting involves collecting eggs from clutches laid in the wild, transporting them to a rearing facility, hatching them, and raising the larvae under controlled conditions with the goal of increasing survivorship during early, vulnerable life-history stages [20]. While there has been considerable success in raising healthy headstarted animals for reintroduction programs (*i.e.*, if these animals remained in captivity, they would live for years, possibly a decade or more), as mentioned above, the survival of animals once released into the wild has been generally poor and/or underreported, and may be further obscured by publication bias that overrepresents successful outcomes [20,21].

3. Identifying Reasons for Headstarting Failures

Because repatriated amphibians can be difficult to monitor, it is rare that the reasons for their failure to establish are known. When causes are known, they tend to be based on ecological or genetic factors. A few examples illustrate this point. Predation can rapidly eliminate released cohorts, such as Cane Toads (*Rhinella marina*) consuming newly metamorphosed *Peltophryne* juveniles or gartersnakes preying on juvenile Yosemite Toads (*Anaxyrus canorus*; *pers. comm.* T. May). Habitat degradation may also drive failure; for instance, stream siltation can destroy the rock crevices that Eastern Hellbenders (*Cryptobranchus alleganiensis*) require for cover and nesting sites, while the introduction of predaceous fish can also wipe out Hellbender cohorts [22]. Large-scale disturbances, such as wildfire (reviewed by [23]), and genetic limitations may further constrain population recovery. Other factors include low survival of developmentally malformed tadpoles [24] or newly metamorphosed frogs. Disease represents another well-documented driver of repatriation failures: in Sierra Nevada and Mountain Yellow-legged Frogs (*Rana sierrae, Rana muscosa*), individuals sourced from *Batrachochytrium dendrobatidis*-naïve populations can succumb to chytridiomycosis following release (*unpubl. data,* L. Jacobs; *unpubl. data,* San Francisco Zoo and partners). Again, these are not the situations we will be considering here. Instead, we focus on instances where headstarted animals are released into habitats without obvious dangers or deficits yet are not successful, or where headstarted animals are introduced into a depleted population yet do not successfully supplement that population.

What can we do to increase the survivorship of headstarted amphibians released into the wild? As we emphasize to caretakers participating in the long-running Amphibian Taxon Advisory Group Amphibian Management School, the survivorship and wellbeing of individuals in captivity are tied to recreating critical elements of a species' natural history (see also [8,11,25,26]). This is especially true of headstarted animals destined for release into the wild. For example, compared with diurnal releases (convenient for humans), nocturnal releases (more aligned with natural amphibian activity patterns and misaligned with common amphibian predators) often increase survivorship [8,27]. Similarly, placement of individuals into predator-avoidant microhabitats (*i.e.*, soft releases) buys time for newly released animals to acclimate and become oriented to their surroundings [13,15,20,28–30].

The problem with raising headstarted animals in captivity is that modern zoo husbandry techniques typically emphasize raising healthy, stress-free animals by meeting an animal's every need, including offering an adequate and balanced diet, ensuring optimum ranges of temperature and ideal water composition, reducing exposure to harmful chemicals such as chlorine and phosphorus, isolating animals from pathogens, minimizing intraspecific aggression, and excluding predators [18,26].

This approach works well when raising animals for display or education. But when headstarting animals for release in nature, providing for every need without requiring animals to work towards meeting these needs, for example, by searching for high-quality food, discovering optimal physical and chemical conditions, interacting with aggressive conspecifics, and learning to avoid predators, likely has consequences for animals destined to be released into the wild and asked to fend for themselves. Further, even when calls to provide an enriched environment are heeded, such efforts are rarely tied to any real-world situations [11,12]. Here we suggest that offering ecologically realistic challenges and choices to headstarted larvae should better prepare them for release into nature. Unlike other workers who have offered a similar suggestion [8,11,12,31], we base our assertion on the idea that headstarted animals must be appropriately stimulated when developing the nervous system circuitry that will underlie all their future behavior (see also [32,33]).

4. Amphibian Cognition and Its Development

Amphibian survival following stress-free headstarting would approximate wild survival if Tinbergen and Ewert's views of amphibians as anoetic (non-thinking) animals were true [34–36]. Tinbergen [34] believed amphibians were "simple reflex machines" (see also [37]). Similarly, Ewert [35,36] felt that in amphibians, key stimuli (innate releasing mechanisms) activated fixed patterns of behavioral responses (*i.e.*, reflexes), much like a key fitting a lock [38–40]. That is, once sensory receptors have identified an object and a location, a pre-programmed circuit in the midbrain tectum is "dialed up" (the metaphor here is a rotary telephone, reflecting the technology of the day). Further, Ewert [35,36] felt individual tectal locations existed for all possible stimulations and positions, meaning an amphibian's response to any situation is genetically, reflexively programmed into their nervous system circuitry.

If Tinbergen [34] and Ewert's [36] perspective is correct, amphibians are unable to learn, and they could be raised as if they were plants. But we now know amphibians have cognitive abilities [41]. They form associations and memories, the basis of learning. For example: (a) European Spadefoot (*Pelobates cultripes*) tadpoles learn to associate non-threatening stimuli with conspecific alarm cues and subsequently consider these benign stimuli threatening [42]; (b) experiences change the temperament of *Rana arvalis* tadpoles [43]; (c) repetition of a stimulus results in Wood Frog (*Rana sylvatica*) tadpoles remembering it longer [44]; (d) calling American Bullfrog (*Rana catesbeiana*) males learn to recognize (*i.e.*, remember) and ignore the calls of adjacent males [45]; and (e) as Red-backed Salamanders (*Plethodon cinereus*) become more familiar with a novel prey species they become more efficient foragers on that species [46].

Amphibians are also masters at remembering and navigating landscapes, and will use different senses and strategies to locate sites important to them [47–50]. For example, during navigation: (a) adult Marsh Frogs (*Pelophylax ridibundus*) use magnetic fields [51]; (b) adult Terrestrial Toads (*Rhinella arenarum*) use geometric and feature cues [52–54]; and (c) adult Green and Black Poison Dart Frogs (*Dendrobates auratus*) use a cognitive map [55].

Further, amphibians are aware of their environment. For example, after prescribed burns eliminate their vegetative cover, adult Crawfish Frogs (*Rana areolata*) spend more time in their burrows compared to frogs in intact ecosystems, a behavior Engbrecht and Lannoo [56] interpret as minimizing exposure to potential predators (if true, such anticipation is a cognitive ability Tinbergen [34] and Ewert [36] would dismiss as an amphibian impossibility).

Amphibians are also socially aware. For example, Wood Frog (*Rana sylvatica*) tadpoles learn to avoid predators by watching the reactions of other Wood Frog tadpoles [57]. And, consistent with the observations of Bee et al. [45], mentioned above, breeding American Bullfrogs are highly attuned to social situations. Young (small) males must decide whether to (a) join a breeding chorus (lek), where they have a higher probability of mating but face competition and perhaps injury from larger males (high risk/high reward), or (b) become a satellite male, remaining on the periphery where they might ambush and mate with a female moving towards the lek (low risk/low reward). Further, when females are ready to breed, they locate the lek of large males and assess the number and location of peripheral satellite males. If there are few satellite males, females approach the lek on the water surface. If there are numerous satellite males, females dive underwater and surface in or near the lek to avoid being amplexed by smaller, perhaps less fit, males, which could mean wasting an entire year's reproductive effort (*pers. comm.* R. Howard) [41,58].

Amphibians are likewise self-aware. In their encounters with Eastern Gartersnakes (*Thamnophis sirtalis*), Crawfish Frog adults must assess their body size relative to the snake's size to determine whether the snake is a potential predator (gartersnakes will prey on young Crawfish Frogs), a potential prey (Crawfish Frog adults are big enough to ingest a young gartersnake), or presents no danger or opportunity (these two species occasionally share burrows; [41]).

Finally, amphibian cognitive skills vary across species. Burmeister [59] compared Green and Black Poison Dart Frogs (*Dendrobates auratus*) with Túngara Frogs (*Engystomops pustulosus*) and found the more complex ecological and social environments of Poison Dart Frogs correlated with higher levels of gene expression tied to neurogenesis, synaptic plasticity, and cellular activity. This is an important concept not only when headstarting animals but also when considering the timing of their release (see below).

As with all cognitive abilities there are age-specific times—termed critical periods, sensitive periods, or developmental windows—in young vertebrates when the brain is particularly receptive to ecological and social stimuli [60–67]. Critical periods arise during the development of sensory, associative, and motor circuits responsible for detecting and responding to particular stimuli. Exposure to appropriate stimuli during these developmental windows influences the number and strength of maturing synaptic connections in central nervous system circuits (e.g., [68]). If these synapses fail to form, axons retract, and the parent neurons, having no function and being energetically expensive, undergo programmed death, a process called apoptosis (e.g., [69]). A non-stimulated circuit that loses a high number of neurons to apoptotic death will not function normally. As Ohmer et al. [70] note, a tadpole's environment has lasting effects on its juvenile and adult behavior.

5. The Senses Driving Critical Periods

Tadpoles in the wild are naturally exposed to relevant stimuli during these critical periods and therefore typically form an appropriate number of functional synapses (if they didn't, they would behave abnormally and be rapidly selected against). Examples of relevant stimuli include light, detected by photoreceptors in the eyes, the pineal gland, and by melanophores in the tail; sound, detected by hair cells in the inner ear; water displacements, detected by hair cells arranged in epidermal lateral line organs; and ambient temperature, assessed by receptors and free nerve endings in the epidermis [71]. Tadpoles also sense a variety of organic and inorganic molecules using an array of four chemosensory systems: the principal and accessory olfactory systems, taste, and specialized epidermal chemosensory cells called stiftchenzellen ('spike cells') [72]. Olfaction is generally regarded as distant smell, taste is oral smell (produced most robustly by macerated food), and chemosensation, as assessed by stiftchenzellen is thought to encompass 'vague' smell [71,72].

With the exception of olfaction, information from each of these senses courses through the brainstem and is filtered and tuned before reaching the forebrain telencephalon; olfactory cues project directly into the telencephalon. Based on neuroanatomy, Striedter and Northcutt [73] suggest anurans have an olfactory dominated telencephalon. Ethologists and physiologists agree [74–76]. Petranka [76] found *Bufo americanus* tadpoles are attracted to 'rich' food patches and avoid areas containing alarm substances (schreckstoff). When tested on whether attractive food or schreckstoff was the stronger stimulus, bufonid tadpoles did not choose between them but rather exhibited an intermediate response [76]. Other examples of tadpoles relying on olfactory cues include the observation that bufonid tadpoles learn the odor of their invertebrate prey [77], and while hylid tadpoles use kairomones to detect the presence of a predator [78], ranid and bufonid tadpoles use schreckstoff to detect the act of predation [79–83]. Ranid tadpoles exposed to schreckstoff increase their corticosterone production within the neuroendocrine stress axis, overseen by the hypothalamus [84].

Olfaction is also important in other situations. Bufonid tadpoles use chemical cues to recognize kin [85], rhacophorid tadpoles are attracted to chemical cues associated with females depositing trophic eggs (unfertilized eggs laid to provide nutrition for tadpoles in impoverished environments such as epiphytic bromeliad tanks) [47,86,87], and older Cane Toad tadpoles chemically suppress viability in younger conspecific tadpoles [88].

Vision is also an important sense in tadpoles, especially for detecting overhead predators ([36]; see also [89]). Herons and egrets hunt along wetland shorelines searching for tadpoles in shallow water.

Tadpoles use visual cues, especially motion, to escape this form of predation. Further, recent experimental work demonstrates the importance of integrating multiple sensory modalities in shaping antipredator responses. Hammond et al. [90] combined visual and olfactory cues to expose headstarted Mountain Yellow-legged Frog (*Rana muscosa*) tadpoles and metamorphosed frogs to a gartersnake (physically separated but both visible and chemically detectable). Predator-exposed tadpoles exhibited altered morphology, slower development (an approximately 14 d delay), reduced movement, and weighed less than controls. Predator training also improved post-release survival, although this training did not carry over across metamorphosis and had to be reinforced in later life history stages.

Every tadpole sensory system except lateral line mechanoreception persists (with modifications) through metamorphosis and carries over into adulthood [71]. Memories acquired from stimulating these sensory systems during the tadpole stage are likely uploaded by the telencephalic ventromedial pallium and remembered as positive (reward) or negative (threat) experiences mediated by the nucleus accumbens or amygdala, respectively [41,58,59,65,73,91,92]. This circuitry is as far as we will go in ascribing higher-order cognitive processes to amphibians. For example, we are uncomfortable with the idea that amphibians have emotions [93], although, when assigning ‘good’ or ‘bad’ tags to memories, we agree that amphibians have salience. We are now also uncomfortable with using the term ‘personality’ to identify an amphibian’s position on the Shy-Bold Continuum and prefer to use ‘temperament’ instead [29]. Such human-based vocabulary implies shared neurological causes between human and amphibian behavior when we know human neocortex, especially the prefrontal cortex, is a cognitive gamechanger.

Tadpole brain anatomy remains understudied. There is, for example, no ‘go to’ atlas of the tadpole brain that one can refer to as a baseline neuroanatomical reference. Further, when early neuroembryologists studied tadpole brains, it was with the assumption that the anuran central nervous system formed linearly from embryo through larval stage to adulthood [94,95]. That is, early workers treated frog neuroembryology as if an amphibian were just another terrestrial vertebrate, with brains growing along a single developmental vector towards adulthood. A more modern and realistic perspective incorporates the fact that amphibians have a biphasic life history and that both tadpole and adult life history stages, while constrained by being phases of the same organism, can to a great degree develop and evolve separately in response to functional/ecological demands [96–101]. This is the basis of ‘Starrett’s Rule’, which states that the plainest of adult frogs often have the most bizarre tadpoles, while the strangest adults typically have the most mundane tadpoles [97,102]. The few studies on tadpole brain growth show that most of the development of the hindbrain medulla occurs prior to metamorphosis [103] and that at metamorphosis, the forebrain diencephalon widens and the telencephalon elongates as new neurons are added [104]. Absent high-resolution information on tadpole brains and their development, the best proof for the presence of critical periods during amphibian development remains behavioral evidence.

Given the presence of critical periods and the fact that most anuran tadpoles and adults are very different animals, the retention of tadpole memories *per se* may be less important to a post-metamorphic frog than the role experiences play in developing the forebrain reward and threat circuits. A headstarted tadpole that has never searched for food has never been rewarded for seeking and finding food. If circuits mediated by the nucleus accumbens require rewards following effort to properly develop, such headstarted tadpoles may not create the circuitry necessary to motivate feeding in post-metamorphic juveniles or adults. Similarly, a headstarted tadpole that never knows fear may miss the developmental window for the establishment of robust fear circuits mediated by the nucleus accumbens. Absent such circuitry, post-metamorphic frogs may not be able to elicit a fear response adequate to the reality of living in an environment that is, as Tennyson noted, “red in tooth and claw” [105].

In addition to the possibility of neural risk/reward circuits failing to develop properly, headstarting situations can reverse an animal’s reaction to natural risk/reward stimuli (see also [11]. Ewert [36] summarized European Toad responses to other animals as:

small and moving = prey: *approach*;

large and looming = predator: *flee*.

In a reversal of "Ewert's Rule", headstarted animals can quickly learn to associate food (reward) with large, looming objects (*i.e.*, people). In this scenario, rather than stimulating amygdaloid fear circuits, large, looming objects stimulate nucleus accumbens reward circuits. In the wild, a headstarted amphibian that approaches a predator, thinking it will be fed, is rarely given the opportunity to make this mistake twice.

6. The Failure of Vertebrate Headstarting Programs Is Not Restricted to Amphibians

The reduced fitness of headstarted vertebrates released into the wild is not limited to amphibians; this problem occurs in all vertebrate classes. For example, it has been observed in captive-raised salmon from wild stocks [106–108], gamebirds [109], and to a lesser extent, mammals [110], including European Otters (*Lutra lutra*) [111], Scandinavian Roe Deer (*Capreolus capreolus*) [112], and Black-footed Ferrets (*Mustella nigripes*) [113]. This suggests a common cause or set of causes related to the lack or exposure to or experience with situations encountered once captive-reared animals are released into nature.

7. Providing Appropriate Scenarios Simulating Natural Conditions to Headstarted Amphibians

We are not the first to recognize that environmental enrichment can stimulate cognition in amphibians. Burghardt [93] chastised zookeepers for not enriching the lives of their captive amphibians and reptiles. His solution centered on the concept of "controlled deprivation," meaning he understood that even the best captive environments do not completely reflect natural ecosystems; therefore, it becomes important to provide a subset of the natural world that offers the most enriching experiences. In emphasizing such enrichment, however, Burghardt [93] did not distinguish between artificial and natural enhancement. We believe this difference is important.

With the concept of developing the neural circuitry during critical periods in mind, we propose offering headstarted tadpoles a range of ecologically realistic situations, as follows:

(1) Periodically expose tadpoles to wetland water from the landscape where they will be released. This not only introduces them to natural food and predator odors, but swimming in such water may help build natural microbiotic gut flora, which in turn influences neurodevelopment and behavioral responses through the microbiota-gut-brain (MGB) axis [114]. (Note: wetland water can serve as a vector for pathogens, including ranaviruses and *Batrachochytrium dendrobatidis* [*Bd*]; programs should mitigate this risk and consult with veterinary and regulatory partners.)

(2) Offer different quality food options and allow tadpoles to choose. This should stimulate the nucleus accumbens reward circuits as they develop. Because tadpoles naturally graze throughout the water column, they distribute food across benthic, midwater, and surface zones. Further, offer these food items at different times of the day and night; in nature, prey rarely present themselves on a regular schedule.

(3) Periodically introduce natural aquatic predators (invertebrates such as giant water bugs, predaceous diving beetles, and dragonfly naiads [115,116]; vertebrates such as salamander larvae) and allow them to prey on a few tadpoles [117–120]. This will introduce kairomones and schreckstoff into the tadpoles' environment and should stimulate telencephalic amygdaloid fear circuits as they are developing. Indeed, predator-induced phenotypes, likely mediated by hormonal and autonomic cues originating from the forebrain hypothalamus, are commonly observed in hylid tadpoles [121–123].

If the introduction of live predators is not feasible, exposure to predator-associated sensory cues may still promote learning, as demonstrated using combined visual and olfactory cues in headstarted Mountain Yellow-legged Frogs [90]. Indeed, the Indiana Hellbender Recovery Team, based at Purdue, is exposing a subset of their headstarted larvae to schreckstoff and will be monitoring post-release survivorship in exposed and unexposed animals (Unpublished Final Report for Grant T7R27 submitted to the Indiana Department of Natural Resources in 2023; see also [30]).

An early idea among zookeepers was that briefly introducing predators to captive animals decreased lethargy, which they felt somehow decreased stress [11,124,125]. While we question this positive relationship between lethargy and stress, we know predator-induced stress (*i.e.*, fear) increases corticosterone production within the neuroendocrine stress axis, which involves the amygdaloid nuclei [84].

(4) Randomly fly large objects [119] over rearing tanks as recommended by Hayes et al. [11], and while doing so, introduce schreckstoff. This pairing of visual and chemical cues will condition tadpoles to avoid large, moving objects overhead.

(5) In temperate species, vary water temperatures across the range of tadpole tolerances [126]. In nature, when cold fronts roll through, tadpoles of spring breeding guild species can temporarily find their wetlands iced over [127]. In addition to reflecting natural environmental variability, temperature fluctuations can confer physiological benefits and, in some species, may be necessary for normal development (e.g., Foothill Yellow-legged Frog [*Rana boylii*], *pers. comm.* S. Kupferberg and D. Minier). Beyond physiology, temperature variability may also influence behavior and cognition; Oborová et al. [66] found that temperature extremes heightened exploratory behavior in Alpine Newts (*Ichthyosaura alpestris*), and exploration is a cognitive function.

(6) Vary dissolved oxygen (DO) levels for tadpoles that possess developed lungs. Shallow wetlands containing macrophytes exhibit a daily cycle of DO variation, as these submerged plants photosynthesize in daylight and respire at night [127]. In these wetlands, DO levels are highest in late afternoon/early evening, often reaching supersaturated levels, and lowest at sunrise, when a combination of both plant and animal respiration creates hypoxic, and sometimes anoxic, conditions. Tadpoles with lungs and access to the water surface have little difficulty with low DO levels; they will gulp air and fill their lungs with atmospheric oxygen. In addition to reflecting natural environmental variability, an animal's response to DO fluctuations might confer physiological benefits necessary for normal development. Even if this cannot be proven at this time, what is inarguable is amphibians raised under natural conditions exhibit levels of survivorship and recruitment sufficient to maintain populations or establish new populations, while animals raised artificially, in captivity, rarely manage this [8]. Given this reality, our contention is the nearer captive-rearing programs come to mimicking the physical, chemical, and biological challenges animals find in nature, including DO extremes, the more likely they will be successful in the wild.

(7) Vary water levels to mimic evaporative losses and rainfall gains. Seasonal and semi-permanent wetlands are dynamic, variable systems that present challenges to developing amphibian brains that in turn influence the development of forebrain risk/reward circuits. In many temperate systems, single-season tadpoles experience progressive drying during mid- to late summer, often accompanied by increasing temperatures. In some species, these drought conditions can serve as a developmental cue; experimentally simulating these conditions—by reducing water levels while increasing temperature—can accelerate or trigger metamorphosis. For example, in Sierra Nevada Yellow-legged Frogs (*Rana sierrae*), drought simulation can successfully encourage metamorphosis in tadpoles that may otherwise require multiple years to complete larval development (*unpubl. data*, San Francisco Zoo and partners). More broadly, variation in temperature and hydrology influences growth and development in ranids.

(8) The best solution to successfully headstarting may be to release tadpoles into their target wetlands as soon as possible [9]. Gosner Stage 25 tadpoles should be large enough to escape most vertebrate gape-limited predators, and swim fast enough to outpace most invertebrate predators. This suggestion is especially relevant for species like Túngara Frogs that appear to truncate forebrain neurogenesis [59]. In contrast, species that exhibit an extended period of neurogenesis, such as Poison Dart Frogs [59], might have the neuronal plasticity to adapt more quickly once released into the wild. Such an extended

period of neurogenesis might also be found in juveniles of species that naturally never have the opportunity to react to an environment before finding themselves in one, such as direct developing species in the genera *Plethodon* and *Eleutherodactylus* [128] and live bearers in the genus *Nectophrynoides* [129].

(9) Finally, what works for one species may fail in another, even when these species are closely related [130]. For example, Midland Chorus Frog (*Pseudacris triseriata*) tadpoles focus on feeding, while closely related and often syntopic Spring Peeper (*P. crucifer*) tadpoles focus on avoiding predators [117]. Relyea [131] exposed tadpoles of six anuran species to five different predator species and found that each tadpole species exhibited different responses to the same predator species. The morphological, behavioral, and ecological diversity encompassed by amphibians is staggering. Anuran amphibians alone comprise 57 families encompassing ~7843 species [4]. Each frog species must have some feature—molecular, morphological, physiological, or behavioral—that makes it unique. Anuran novelty includes aquatic, terrestrial, arboreal, or subterranean lifestyles; locomotory capabilities that include swimming, walking, jumping, and gliding; internal or external fertilization; egg masses that are laid aquatically, terrestrially, or arboreally; parental care that consists of maternal provisioning, egg carrying, tadpole transport, and egg incubation; generalist or specialist approaches to feeding; pigmentation patterns that emphasize camouflage, are aposematic, or vary to match the background; calling synchronously or asynchronously; philopatry; toxicity; cocoon building; and water conservation measures that use behavior (microsite selection) or behavioral physiology (e.g., waxy lipid secretions the frog spreads over its body) [132–134].

This adult variation is compounded by differences in tadpole morphology, behavior, and ecology, which also varies widely. For example, Orton [96] describes four basic types of tadpoles (see also [100]) while Amin and colleagues [135] have proposed an additional Type V based on the tadpoles of *Lepidobatrachu*s *laevis*.

Given this variation in anuran morphology, ecology, and behavior, anuran brains must be considerably more variable than neuroanatomists working under a 'scala natura' approach were willing to acknowledge, although thankfully (we are reminded of the quote: "Funeral by funeral, theory advances", attributed to Max Planck) this perspective is changing [58,136–139]. Brain variation in the telencephalon suggests cognitive variation (see [33,59]. As Bräuer et al. [140] emphasize, there is not 'one cognition'.

Many of these recommended actions might be accomplished at most institutions, though they may require some updating of existing protocols, securing additional funding, and collaborating with ethologists and field biologists. In some cases, facilities may be resistant to adopting these changes unless they are requested or required by governing bodies (e.g., USFWS, state agencies). Most actions require approval by Institutional Animal Care and Use Committees (IACUCs) and permitting divisions of state and federal agencies.

While varying environmental parameters and diet should not seriously challenge husbandry protocols, introducing predators and allowing limited mortality may encounter serious resistance. This will vary by institution, as AZA-accredited facilities are not monolithic. Proposals that include sacrificing animals for the greater good will require strong justification and supporting evidence, including potentially a directive from the managing body of the program. Another option would be to "farm out" headstarted animals to conservation or university partners, following proper IACUC protocols or research committee reviews, thereby allowing flexibility to try "novel" concepts, such as challenging tadpoles to survive in a more natural setting to better prepare them for life in the wild.

8. Standard Framework

Rather than have the above recommendations come across as hardline prescriptions, we suggest considering each one of them as hypotheses to be tested as part of a larger repatriation research program coordinated across zoos. The goal is not to replace existing protocols. Rather, it is to evaluate the efficacy of different enrichment protocols in improving post-release survival and to allow institutions to develop best practices for captive populations marked for headstart. To aid this evaluation, we suggest standardizing a simple experimental structure that applies across scenarios both before and after release, which is categorized as follows:

- Treatment *vs.* Control Groups: Divide animals into at least two groups: one experiencing the proposed ecological stimulus (treatment), and one reared under standard husbandry conditions (control).
- Standardized Pre-release Assessments: Where feasible, evaluate behavioral or physiological responses prior to release. These may include foraging latency or efficiency, response to predator-associated cues (e.g., reduced activity or refuge use), exploratory behavior, growth, development, or body condition. These measures serve as indicators of whether the treatments are influencing behavior in the theorized direction.
- Post-release Monitoring: Mark and identify individuals by treatment group and track short-term survival, site retention, dispersal patterns, and habitat use. This data will reflect whether pre-release differences translate into improved survival in the wild.
- Comparative Evaluation: Evaluate effectiveness by comparing treatment and control groups across both pre- and post-release metrics.

9. Applying This Framework to Specific Testable Scenarios

To test scenario 1, institutions could expose one group of animals to wetland water, another to filtered water. Before releasing these animals into the wild, analyze gut microbial communities and compare between the two groups (and perhaps with wild counterparts from the wetland water source). Mark animals according to treatment and record survivorship during follow-up surveys.

To test scenario 2, feed one set of larvae different food items on variable feeding schedules with a non-uniform food presentation, feed another group with the standard practice of ubiquitous food inundation on a repeating schedule, and monitor growth while animals are in captivity. Prior to release, mark animals according to treatment and record survivorship during follow-up surveys.

If studies like this are done for each of the above scenarios, and post-release survivorship is enhanced, it would be wise to develop a set of husbandry guidelines (with variations and caveats) for headstarted animals that are distinct from the currently established husbandry guidelines for animals that will remain in captivity (e.g., [141]). Individually, these experiments may yield modest or contextually dependent results. However, if multiple institutions adopt similar frameworks and track a shared set of outcome metrics, collective data could clarify which interventions are most effective. In this way, the scenarios proposed here are not intended as fixed protocols, but as a foundation for a coordinated research effort to refine amphibian headstarting practices.

10. Conclusions

Zoos and aquariums play a critical role in headstarting amphibians for release into the wild with the goal of either re-establishing extirpated populations or augmenting depleted populations. While a few successes have been realized, and are rightfully celebrated, most of these efforts have been disappointing. There are many reasons for these failures, but in most cases the cause(s) remain unknown. This can be particularly frustrating when outwardly healthy amphibians are released into apparently intact landscapes containing critical ecosystems (e.g., wetlands for breeding, uplands for feeding, and overwintering sites). To address this problem, we propose incorporating our knowledge of vertebrate brain development into amphibian headstarting protocols. That is, we suggest that while current headstarting protocols designed to provide for every animal need and comfort succeed in raising healthy animals for exhibit or education, they fail to stimulate forebrain fear and reward circuits as they develop, and therefore fail to provide post-release animals with neuronal circuits ready to meet the challenges and uncertainties faced by living life in the wild. To facilitate these modifications, we propose exposing headstarted animals to: variations in food availability and quantity; predators or their chemical cues; and variations in water quality and quantity. Further, we recognize the stunning amount of variation that exists among the more than 8000 species of amphibians, and understand this means that protocols demonstrated to work in one species may fail in others, even among closely related species.

Acknowledgments

The authors constitute the current faculty and adjuncts of the Association of Zoos and Aquariums' (AZA's) Amphibian Management School (https://www.aza.org/calendar/event/5595301), which meets biennially at the Detroit Zoological Society's National Amphibian Conservation Center (https://detroitzooblog.org/tag/national-amphibian-conservation-center/). Over the past decade, instructors informally discussed how to enhance the survivorship of captive-reared animals released into the wild. During the 2026 course these discussions intensified and became focused, resulting in the creation of this manuscript. Our perspectives towards amphibian headstarting and the framework we suggest for implementing them are our professional opinions and do not represent any policies or standards established by the AZA. If we have seen farther, it is because we are standing on the shoulders of giants. Bob Johnson, Joe Mendelson, Jenny Pramuk, Ron Gagliardo, Andy Odum, Diane Barber, and Shelly Grow are either former AZA Amphibian School instructors or colleagues who have contributed to the amphibian conservation mission of North American zoos and aquariums. We thank them for their decades-long inspiration, dedication, and friendship.

Author Contributions

Conceptualization, M.J.L., V.P., T.H., R.H., M.V., D.V., N.J.E., R.M.S.; Methodology, M.J.L., V.P., T.H., R.H., A.P.P., R.M.-G., M.V., D.V., M.A., W.S., B.B., C.L.-H., R.M.S.; Writing—Original Draft Preparation, M.J.L., V.P., T.H., R.H., M.V., D.V., N.J.E., R.M.S.; Writing—Review & Editing, V.P., T.H., R.H., M.V., D.V., N.J.E., R.M.S.

Ethics Statement

This article does not present research with ethical considerations and permits.

Informed Consent Statement

Not applicable.

Data Availability Statement

All other data produced in this study are provided in this manuscript.

Funding

This research received no external funding.

Declaration of Competing Interest

The authors declare they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

References

1. Stuart SN, Chanson JC, Cox NA, Young BE, Rodrigues AL, Fischman DL, et al. Status and trends of amphibian declines and extinctions worldwide. *Science* **2004**, *306*, 1783–1786. DOI:10.1126/science.1103538
2. Mendelson JR, III, Lips KR, Gagliardo RW, Rabb GB, Collins JP, Diffendorfer JE, et al. Confronting amphibian declines and extinctions. *Science* **2006**, *313*, 48. DOI:10.1126/science.1128396
3. Luedtke JA, Chanson J, Neam K, Hobin L, Maciel AO, Catenazzi A, et al. Ongoing declines for the world's amphibians in the face of emerging threats. *Nature* **2023**, *622*, 308–314. DOI:10.1038/s41586-023-06578-4
4. AmphibiaWeb. Amphibian Declines. Available online: https://amphibiaweb.org/declines/ (accessed on 10 March 2026).
5. Zohuri B, Moghaddam M. What is Boolean Logic and how it works. In *Business Resilience System (BRS): Driven Through Boolean, Fuzzy Logics and Cloud Computation*; Springer: Cham, Switzerland, 2007. DOI:10.1007/978-3-319-53417-6_6
6. Brooks GC, Kindsvater HK. Early development drives variation in amphibian vulnerability to global change. *Front. Ecol. Evol*. **2022**, *10*, 813414. DOI:10.3389/fevo.2022.813414
7. Burke RL. Relocations, repatriations, and translocations of amphibians and reptiles: Taking a broader view. *Herpetologica* **1991**, *47*, 350–357. Available online: https://www.jstor.org/stable/3892627 (accessed on 10 March 2026).
8. Dodd CK, Seigel RA. Relocation, repatriation, and translocation of amphibians and reptiles: Are they conservation strategies that work? *Herpetologica* **1991**, *47*, 336–350. Available online: https://www.jstor.org/stable/3892626 (accessed on 17 March 2026).
9. Reinert HK. Translocation as a conservation strategy for amphibians and reptiles: Some comments, concerns, and observations. *Herpetologica* **1991**, *47*, 357–363. Available online: https://www.jstor.org/stable/3892628 (accessed on 21 March 2026).
10. Bogisich A, Candia AK, Cantrell J, Collins C, Reichling SB, Poo S. Dusky Gopher Frog (*Lithobates sevosus*) repatriation at a reintroduction site through zoo-led captive-release efforts. *Zoo Biol*. **2025**, *44*, 230–236. DOI:10.1002/zoo.21889
11. Hayes MP, Jennings MR, Mellen JD. Beyond mammals: Environmental enrichment for amphibians and reptiles. In *Second Nature: Environmental Enrichment for Captive Animals*; Smithsonian Institution Press: Washington, DC, USA, 1998; pp. 205–235.
12. Griffiths RA, Pavajeau L. Captive breeding, reintroduction, and the conservation of amphibians. *Conserv. Biol*. **2007**, *22*, 852–861. DOI:10.1111/j.1523-1739.2008.00967.x
13. Germano JM, Bishop PJ. Suitability of amphibians and reptiles for translocation. *Conserv. Biol.* **2009**, *23*, 7–15. DOI:10.1111/j.1523-1739.2008.01123.x
14. Parker KA, Dickens MJ, Clarke RH, Lovegrove TG. The theory and practice of catching, moving and releasing animals. In *Reintroduction Biology: Integrating Science and Management*; Blackwell Publishing Ltd.: Oxford, UK, 2012; pp. 105–137.
15. Polasik JS, Murphy MA, Abbott T, Vincent K. Factors limiting early life stage survival and growth during endangered Wyoming toad reintroductions. *J. Wildl. Manag.* **2015**, *80*, 540–552. DOI:10.1002/jwmg.1031
16. McCallen EB, Kraus BT, Burgmeier NG, Fei S, Williams RN. Movement and habitat use of Eastern Hellbenders (*Cryptobranchus alleganiensis*) following population augmentation. *Herpetologica* **2018**, *74*, 283–293. DOI:10.1655/Herpetologica-D-17-00044.1
17. US Fish and Wildlife Service. *Revised Recovery Plan for the Houston Toad (Anaxyrus [=Bufo] houstonensis)*; US Fish and Wildlife Service: Albuquerque, NM, USA, 2022.
18. Pramuk JB, Gagliardo R. General amphibian husbandry. In *Amphibian Husbandry Resource Guide*; Association of Zoos & Aquariums: Baltimore, MD, USA, 2012; pp. 5–59.
19. Brichieri-Colombi TA, Lloyd NA, McPherson JM, Moehrenschlager A. Limited contributions of released animals from zoos to North American conservation translocations. *Conserv. Biol*. **2019**, *33*, 33–39. DOI:10.1111/cobi.13160
20. Linhoff LJ, Soorae PS, Harding G, Donnelly MA, Germano JM, Hunter DA, et al. (Eds.) *IUCN Guidelines for Amphibian Reintroductions and Other Conservation Translocations*, 1st ed.; IUCN: Gland, Switzerland, 2021.
21. Miller KA, Bell TP, Germano JM. Understanding publication bias in reintroduction biology by assessing translocations of New Zealand herpetofauna. *Conserv. Biol.* **2014**, *28*, 1045–1056. DOI:10.1111/cobi.12254
22. Burgmeier NG, Unger SD, Meyer JL, Sutton TM, Williams RN. Health and habitat quality assessment for the eastern hellbender (*Cryptobranchus alleganiensis alleganiensis*) in Indiana, USA. *J. Wildl. Dis*. **2011**, *47*, 836–488. DOI:10.7589/0090-3558-47.4.836
23. Pilliod DS, Bury RB, Hyde EJ, Pearl CA, Corn PS. Fire and amphibians in North America. *For. Ecol. Manag.* **2003**, *178*, 163–181. DOI:10.1016/S0378-1127(03)00060-4
24. Lannoo MJ. *Malformed Frogs*; University of California Press: Berkeley, CA, USA, 2008.

25. Johnson BR. Conservation of threatened amphibians: the integration of captive breeding and field research. In *Proceedings of the Conference on Captive Propagation and Husbandry of Reptiles and Amphibians*; Special Publication 6; Northern California Herpetological Society: Davis, CA, USA, 1991; pp. 33–38.
26. Amphibian Taxon Advisory Group. *Amphibian Management School*; Amphibian Taxon Advisory Group: Silver Spring, MD, USA, 2017.
27. Griffith B, Scott JM, Carpenter JW, Reed C. Translocation as a species conservation tool: Status and strategy. *Science* **1989**, *245*, 477–480. DOI:10.1126/science.245.4917.477
28. Linhoff LJ, Donnelly MA. Assessing release strategies for reintroductions of endangered Wyoming Toads. *Wildl. Soc. Bull.* **2022**, *46*, e1341. DOI:10.1002/wsb.1341
29. Engbrecht NJ, Stiles RM, Lannoo MJ, Shults, LH. A review of the ecology, behavior, and cognitive capabilities of Crawfish Frogs (*Rana areolata*) with the goal of restoring extirpated populations. *Discov. Ecol.* **2026**, *2*, 10. DOI:10.1007/s44396-026-00028-x
30. Williams RN, Burgmeier NG. Comparing the effects of environmental enrichment, seasonality, and soft-release on site retention and survivorship of captive-reared Eastern Hellbenders (*Cryptobranchus allegeniansis*). *Herpetologica*, **2022**, *78*, 225–234. DOI:10.1655/Herpetologica-D-21-00014
31. McKeown S. The ecosystem approach: New survival strategies for managing and displaying reptiles and amphibians in zoos. In *Proceedings of the Eighth Symposium on Captive Propagation and Husbandry of Reptiles and Amphibians*; California Herpetological Society: Davis, CA, USA, 1985; pp. 1–5.
32. Mettke-Hofmann C. Cognitive ecology: Ecological factors, lifestyles, and cognition. *Wiley Interdiscip. Rev. Cogn. Sci.* **2014**, *5*, 345–360. DOI:10.1002/wcs.1289
33. Moss CF, Shettleworth SJ. *Neuroethological Studies of Cognitive and Perceptual Processes*; Taylor and Francis: New York, NY, USA, 2019.
34. Tinbergen N. *The Study of Instinct*; Oxford University Press: Oxford, UK, 1953.
35. Ewert J-P. Neural mechanisms of prey-catching and avoidance behavior in toads (*Bufo bufo* L.). *Brain Behav. Evol.* **1970**, *3*, 36–56. DOI:10.1159/000125462
36. Ewert JP. The visual system of the toad: Behavioral and physiological studies on a pattern recognition system. In *The Amphibian Visual System*; Academic Press: New York, NY, USA, 1976; pp. 142–202.
37. Roth G. *The Long Evolution of Brains and Minds*; Springer: Berlin/Heidelberg, Germany, 2013.
38. von Uexküll VJ. *Umwelt und Innenweltder Tiere*; Springer: Berlin/Heidelberg, Germany, 1909; p. 259.
39. Lorenz K. Vergleichende Verhaltensforschung. *Zool. Anz. Suppl. Bd.* **1939**, *12*, 69–102. Available online: http://www.klha.at/papers/1939-VerglVerhaltensforschung.pdf (accessed on 21 March 2026).
40. Marler PR, Hamilton WJ. *Mechanisms of Animal Behavior*; John Wiley and Sons: New York, NY, USA, 1966.
41. Lannoo MJ, Stiles RM. The use of cognition by amphibians confronting environmental change: Examples from the behavioral ecology of Crawfish Frogs (*Rana areolata*). *Animals* **2025**, *15*, 736. DOI:10.3390/ani15050736
42. Polo-Cavia N, Gomez-Mestre I. Learned recognition of introduced predators determines survival of tadpole prey. *Funct. Ecol.* **2014**, *28*, 432–439. DOI:10.1111/1365-2435.12175
43. Plaskonka B, Zaborowska A, Mikulski A, Pietrzak B. Predation risk experienced by tadpoles shapes personalities before but not after metamorphosis. *Ecol. Evol.* **2024**, *14*, e70532. DOI:10.1002/ece3.70532
44. Chivers DP, Ferrari MCO. Tadpole antipredator responses change over time: What is the role of learning and generalization? *Behav. Ecol.* **2013**, *24*, 1114–1121. DOI:10.1093/beheco/art038
45. Bee MA, Marshall VT, Humfield SC, Gerhardt HC. The role of learning in the formation of frog choruses. *Integr. Comp. Biol.* **2002**, *42*, 1193.
46. Gibbons ME, Ferguson AM, Lee DR. Both learning and heritability affect foraging behaviour of Red-backed Salamanders, *Plethodon cinereus*. *Anim. Behav.* **2005**, *69*, 721–732. DOI:10.1016/j.anbehav.2004.06.021
47. Lehtinen RM, Lannoo MJ, Wassersug RJ. *Phytotelm-Breeding Anurans: Past, Present And Future Research*; Miscellaneous Publications; Museum of Zoology, University of Michigan: Ann Arbor, MI, USA, 2004; pp. 1–9.
48. Sinsch U. Orientation behaviour of toads (*Bufo bufo*) displaced from the breeding site. *J. Comp. Physiol A.* **1987**, *161*, 715–727. DOI:10.1007/bf00605013
49. Schulte LM. Feeding or avoiding? Facultative egg feeding in a Peruvian poison frog (*Ranitomeya variabilis*). *Ethol. Ecol. Evol.* **2014**, *26*, 58–68. DOI:10.1080/03949370.2013.850453
50. Pašukonis A, Trenkwalder K, Ringler M, Ringler E, Mangione R, Steininger J, et al. The significance of spatial memory for water finding in a tadpole-transporting frog. *Anim. Behav.* **2016**, *116*, 89–98. DOI:10.1016/j.anbehav.2016.02.023
51. Shakhparonov VV, Ogurtsov SV. Marsh Frogs, *Pelophylax ridibundus,* determine migratory direction by magnetic field. *J. Comp. Physiol. A* **2017**, *203*, 35–45. DOI:10.1007/s00359-016-1132-x

52. Sotelo MI, Bingman VP, Muzio RN. Goal orientation by geometric and feature cues: spatial learning in the terrestrial toad *Rhinella arenarum*. *Anim. Cogn*. **2015**, *18*, 315–323. DOI:10.1007/s10071-014-0802-8
53. Sotelo MI, Bingman VP, Muzio RN. Slope-based and geometric encoding of a goal location by the terrestrial toad *Rhinella arenarum*. *J. Comp. Psychol*. **2017**, *131*, 362–369. DOI:10.1037/com0000084
54. Sotelo MI, Florencia Daneri M, Bingman P, Muzio RN. Amphibian spatial cognition, medial pallium and other supporting telencephalic structures. *Neurosci. Behav. Rev*. **2024**, *163*, 105739. DOI:10.1016/j.neubiorev.2024.105739
55. Liu Y, Day LB, Summers K, Burmeister SS. A cognitive map in a Poison Frog. *J. Exp. Biol*. **2019**, *222*, jeb197467. DOI:10.1242/jeb.197467
56. Engbrecht NJ, Lannoo MJ. Crawfish Frog behavioral differences in postburned and vegetated grasslands. *Fire Ecol*. **2012**, *8*, 63–76. DOI:10.4996/fireecology.0801063
57. Chivers DP, Ferrari MCO. Social learning of predators by tadpoles: Does food restriction alter the efficacy of tutors as information sources? *Anim. Behav*. **2014**, *89*, 93–97. DOI:10.1016/j.anbehav.2013.12.018
58. Lannoo MJ, Stiles RM. Do adult frogs remember their lives as tadpoles and behave accordingly? A consideration of memory and personality in anuran amphibians. *Diversity* **2025**, *17*, 506. DOI:10.3390/d17080506
59. Burmeister SS. Ecology, cognition, and the hippocampus: A tale of two frogs. *Brain Behav. Evol.* **2022**, *97*, 211–224. DOI:10.1159/000522108
60. Sebastian CE, Pfau K, Horn ER. An age-dependent sensitivity of the roll-induced vestibuloocular reflex to hypergravity exposure of several days in an amphibian (*Xenopus laevis*). *Acta Astronaut.* **1998**, *42*, 419–430. DOI:10.1016/S0094-5765(98)00136-2
61. Andersen SL. Trajectories of brain development: point of vulnerability or window of opportunity? *Neurosci. Biobehav. Rev*. **2003**, *27*, 3–18. DOI:10.1016/s0149-7634(03)00005-8
62. Hensch TK. Critical period regulation. *Annu Rev Neurosci.* **2004**, *27*, 549–579. DOI:10.1146/annurev.neuro.27.070203.144327
63. Knudsen EI. Sensitive periods in the development of the brain and behavior. *J. Cogn. Neurosci*. **2004**, *16*, 1412–1425. DOI:10.1162/0898929042304796
64. Mueller CA. Critical windows in animal development: Interactions between environment, phenotype, and time. In *Development and Environment*; Springer: Cham, Switzerland, 2018, DOI:10.1007/978-3-319-75935-7_3
65. Burmeister SS. Brain-behavior relationships of cognition in vertebrates: Lessons from amphibians. Chapter 3. *Adv. Study Behav*. **2022**, *54*, 109–127. DOI:10.1016/bs.asb.2022.01.004
66. Oborová V, Šugerková M, Gvoždik L. Sensitivity of amphibian embryos to timing and magnitude of present and future thermal extremes. *J. Exp. Zool. A. Ecol. Integr. Physiol.* **2023**, *341*, 377–388. DOI:10.1002/jez.2791
67. Walasek N, Panchanathan K, Frankenhuis W. The evolution of sensitive periods beyond early ontogeny: Bringing theory and data. *Funct. Ecol*. **2025**, *39*, 2962–2973. DOI:10.111/1365–2435.14615
68. Roberts A, Li W-C, Soffe SR. How neurons generate behavior in a hatching amphibian tadpole: an outline. *Front. Behav. Neurosci.* **2010**, *4*, 1–11. DOI:10.3389/fnbeh.2010.00016
69. Ishizuya-Oka A, Hasebe T, Shi YB. Apoptosis in amphibian organs during metamorphosis. *Apoptosis* **2010**, *15*, 350–364. DOI:10.1007/s10495-009-0422-y
70. Ohmer MEB, Hammond TT, Switzer S, Wantman T, Bednark JG, Paciotta E, et al. Developmental environment has lasting effects on amphibian post-metamorphic behavior and thermal physiology. *J. Exp. Biol*. **2023**, *226*, jeb244883. DOI:10.1242/jeb.244883
71. Lannoo MJ. Integration: Nervous and sensory systems. In *Tadpoles: The Biology of Anuran Larvae*; University of Chicago Press: Chicago, IL, USA, 1999; pp. 149–169.
72. Whitear M. Identification of the epidermal 'Stiftchenzellen' of frog tadpoles by electron microscopy. *Cell Tissue Res*. **1976**, *175*, 391–402. DOI:10.1007/BF00218717
73. Striedter GF, Northcutt RG. *Brains Through Time: A Natural History of Vertebrates*; Oxford University Press: Oxford, UK, 2020.
74. Nunes AL, Richter-Boix A, Laurila A, Rebelo R. Do anuran larvae respond behaviourally to chemical cues from an invasive crayfish predator? A community-wide study. *Oecologia* **2013**, *171*, 115–127. DOI:10.1007/s00442-012-2389-6
75. Scribano G, Balestrieri A, Gazzola A, Pellitteri-Rosa D. Strong behavioural defensive responses of endemic *Rana latastei* tadpoles induced by a native predator's odour. *Ethology* **2020**, *126*, 922–930. DOI:10.1111/eth.13072
76. Petranka JW. Response of toad tadpoles to conflicting chemical stimuli: Predator avoidance versus "optimal" foraging. *Herpetologica* **1989**, *45*, 283–292. DOI:10.2307/1445978
77. Dole JW, Rose BB, Tachiki KH. Western Toads (*Bufo boreas*) learn odor of prey insects. *Herpetologica* **1981**, *37*, 63–68. Available online: https://www.jstor.org/stable/3891797 (accessed on 15 March 2026).

78. Petranka JW, Kats LB, Sih A. Predator-prey interactions among fish and larval amphibians: Use of chemical cues to detect predatory fish. *Anim. Behav*. **1987**, *35*, 420–425. DOI:10.1016/S0003-3472(87)80266-X
79. Hews DK. Alarm response in larval western toads, *Bufo boreas*: Release of larval chemicals by a natural predator and its effect on predator capture efficiency. *Anim. Behav*. **1988**, *36*, 125–133. DOI:10.1016/s0003-3472(88)80255-0
80. Hagman M, Shine R. Tadpoles of invasive cane toads (*Bufo marinus*) do not respond behaviourally to chemical cues from tadpoles of four species of Australian frogs. *Aust. J. Zool*. **2008**, *56*, 211–213. DOI:10.1071/ZO08005
81. Hagman M, Shine R. Factors influencing responses to alarm pheromone by larvae of invasive cane toads, *Bufo marinus*. *J. Chem. Ecol*. **2009**, *35*, 265–271. DOI:10.1007/s10886-009-9592-x
82. Wilson DJ, Lefcort H. The effect of predator diet on the alarm response of Red-legged Frog, *Rana aurora*, tadpoles. *Anim. Behav*. **1993**, *46*, 1017–1019. DOI:10.1006/anbe.1993.1285
83. Fraker ME, Hu F, Cuddapah V, McCollum SA, Relyea RA, Hempel J, et al. Characterization of an alarm pheromone secreted by amphibian tadpoles that induces behavioral inhibition and suppression of the neuroendocrine stress axis. *Horm Behav*. **2009**, *55*, 520–529. DOI:10.1016/j.yhbeh.2009.01.007
84. Maher JM, Werner EE, Denver RJ. Stress hormones mediate predator-induced phenotypic plasticity in amphibian tadpoles. *Proc. Biol. Sci.* **2013**, *280*, 20123075. DOI:10.1098/rspb.2012.3075
85. Waldman B. Olfactory basis of kin recognition in toad tadpoles. *J. Comp. Physiol*. **1985**, *156*, 565–577. DOI:10.1007/BF00619107
86. Lannoo MJ, Townsend DS, Wassersug RJ. Larval life in the leaves: Arboreal tadpole types, with special attention to the morphology, ecology, and behavior of the oophagous *Osteopilus brunneus* (Hylidae) larva. *Fieldiana (Zool.) Ser.* **1987**, *38*, 1–31. DOI:10.5962/bhl.title.2932
87. Kam Y-C, Yang H-W. Female-offspring communication in a Taiwanese tree frog, *Chirixalus eiffingeri (Anura: Rhacophoridae)*. *Anim. Behav*. **2002**, *64*, 881–886. DOI:10.1006/anbe.2002.2004
88. McCann S, Crossland M, Greenlees M, Shine R. Field trial of chemical suppression of embryonic Cane Toads (*Rhinella marina*) by older conspecifics. *Ecol. Evol.* **2020**, *10*, 10177–10185. DOI:10.1002/ece3.6678
89. Espanha J, Vasconcelos M, Eterovick P. The role of tadpole coloration against visually oriented predators. *Behav. Ecol. Sociobiol.* **2016**, *70*, 255–267. DOI:10.1007/s00265-015-2044-4
90. Hammond TT, Jacobs LE, Curtis MJ, Trotman EM, Swaisgood RR, Shier DM. Early life experience with predators impacts development, behavior, and post-translocation outcomes in an endangered amphibian. *Anim. Conserv.* **2023**, *27*, 23–36. DOI:10.1111/acv.12880
91. Herrick CJ. The morphology of the forebrain in Amphibia and Reptilia. *J. Comp. Neurol. Psychol.* **1910**, *20*, 413–547. DOI:10.1002/cne.920200502
92. Papini MR, Muzio RN, Segura ET. Instrumental learning in toads (*Bufo arenarum*): Reinforcer magnitude and medial pallium. *Brain Behav. Evol*. **1995**, *46*, 61–71. DOI:10.1159/000113259
93. Burghardt GM. Environmental enrichment and cognitive complexity in reptiles and amphibians: Concepts, review, and implications for captive populations. *Appl. Anim. Behav. Sci*. **2013**, *147*, 286–298. DOI:10.1016/j.applanim.2013.04.013
94. Rugh R. *The Frog: Reproduction and Development*; The Blakiston Company: Toronto, ON, Canada, 1951.
95. Keating MJ, Kennard C. Binocular visual neurons in the frog thalamus. *J. Physiol*. **1976**, *258*, 69–70.
96. Orton GL. The systematics of vertebrate larvae. *Syst. Zool*. **1953**, *2*, 63–75. DOI:10.2307/sysbio/2.2.63
97. Wassersug RJ, Heyer WR. *A Survey of Internal Oral Features of Leptodactyloid Larvae (Amphibia: Anura)*; Smithsonian Contribution to Zoology Number 457; Smithsonian Institution Press: Washington, DC, USA, 1988; p. 99.
98. Altig R, Johnson GF. Guilds of anuran larvae: Relationships among developmental modes, morphologies, and habitats. *Herpetol. Monogr*. **1989**, *3*, 81–109. DOI:10.2307/1466987
99. McDiarmid RW, Altig R. Research: Materials and techniques. In *Tadpoles: The Biology of Anuran Larvae*; University of Chicago Press: Chicago, IL, USA, 1999. pp. 7–23.
100. Roelants K, Haas A, Bossuyt F. Anuran radiations and the evolution of tadpole morphospace. *Proc. Nat. Acad. Sci. USA* **2011**, *108*, 8731–8736. DOI:10.1073/pnas.1100633108
101. Fabrezi M, Quinzio S, Goldberg J, de Sá RO. The development of *Dermatonotus muelleri* (Anura: Microhylidae: Gastrophryninae). *J. Herpetol*. **2012**, *46*, 363–380. DOI:10.1670/11-194
102. Savage JM. The tadpole of the Costa Rican Fringe-limbed Treefrog, *Hyla fimbrimembra*. *Proc. Biol. Soc. Wash*. **1981**, *93*, 1177–1183. Available online: https://pascalfrancis.inist.fr/vibad/index.php?action=getRecordDetail&idt=PASCAL8110215126 (accessed on 20 March 2026).
103. Pesetsky I. The role of the thyroid in the development of Mauthner's neuron in anurans. *Gen. Comp. Endocrinol*. **1966**, *2*, 229–235. DOI:10.1016/0016-6480(62)90007-2

104. Allen BM. Brain development in anuran larvae after thyroid or pituitary removal. *Endocrinology* **1924**, *8*, 639–615. DOI:10.1210/endo-8-5-639
105. Tennyson AHH. *In Memorium*; Edward Moxon, Dover Street: London, UK, 1850; pp. 1–216. Available online: https://web.english.upenn.edu/~cavitch/pdf-library/Tennyson_In_Memoriam_1850_Moxon_edition.pdf (accessed on 30 March 2026).
106. Berejikian BA. The effects of hatchery and wild ancestry and experience on the ability of steelhead trout fry (*Oncorhynchus mykiss*) to avoid a benthic predator. *Can. J. Fish. Aquat. Sci.* **1995**, *52*, 2476–2482. DOI:10.1139/f95-838
107. Ford MJ. Selection in captivity during supportive breeding may reduce fitness in the wild. *Conserv. Biol*. **2002**, *16*, 815–825. DOI:10.1046/j.1523-1739.2002.00257.x
108. Araki H, Berejikian BA, Ford MJ, Blouin MS. Fitness of hatchery-reared salmonids in the wild. *Evol. Appl.* **2008**, *1*, 342–355. DOI:10.1111/j.1752-4571.2008.00026.x
109. Musil DD, Connelly JW. Survival and reproduction of pen-reared vs translocated wild pheasants *Phasianus colchicus*. *Wildl. Biol*. **2009**, *15*, 80–88. DOI:10.2981/07-049
110. Jule KR, Leaver LA, Lea SEG. The effects of captive experience on reintroduction survival in carnivores: a review and analysis. *Biol. Conserv*. **2008**, *141*, 355–363. DOI:10.1016/j.biocon.2007.11.007
111. Sjöåsen T. Survivorship of captive-bred and wild-caught reintroduced European Otters *Lutra lutra* in Sweden. *Biol. Conserv*. **1996**, *76*, 161–165. DOI:10.1016/0006-3207(95)00097-6
112. Pandini W, Cesaris C. Home range and habitat use of Roe Deer (*Capreolus capreolus*) reared in captivity and released in the wild. *Hystrix* **1997**, *9*, 45–50. Available online: http://www.italian-journal-of-mammalogy.it/pdf-77689-13883?filename=Home%20range%20and%20habitat.pdf (accessed on 15 March 2026).
113. Poessel SA, Brek SW, Biggins DE, Livieri TM, Crooks KR, Angeloni L. Landscape features influence postrelease predation on endangered Black-footed Ferrets. *J. Mammal*. **2011**, *92*, 732–741. DOI:10.1644/10-MAMM-S-061.1
114. Emerson KJ, Woodley SK. Something in the water: aquatic microbial communities influence the larval amphibians gut microbiota, neurodevelopment and behavior. *Proc. R. Soc. B* **2024**, *291*, 20232850. DOI:10.1098/rspb.2023.2850
115. Lawler P. Behavioral responses to predators and predation risk in four species of larval anurans. *Anim. Behav*. **1989**, *38*, 1039–1047. DOI:10.1016/S0003-3472(89)80142-3
116. Kahn JA, Roberts A. The neuromuscular basis of rhythmic struggling movements in embryos of *Xenopus laevis*. *J. Exp. Biol*. **1982**, *99*, 197–205. DOI:10.1242/jeb.99.1.197
117. Smith DC, Van Buskirk J. Phenotypic design, plasticity, and ecological performance in two tadpole species. *Am. Nat.* **2005**, *145*, 211–233. DOI:10.1086/285737
118. Kraaijeveld-Smit FJL, Griffiths RA, Moore RD, Beebee TJC. Captive breeding and the fitness of reintroduced species: A test of the responses to predators in a threatened amphibian. *J. Appl. Ecol*. **2006**, *43*, 360–365. DOI:10.1111/j.1365-2664.2006.01137.x
119. Ferrari MCO, Chivers DP. Temporal variability, threat sensitivity and conflicting information about the nature of risk: Understanding the dynamics of tadpole antipredator behaviour. *Anim. Behav.* **2009**, *78*, 11–16. DOI:10.1016/j.anbehav.2009.03.016
120. Ferrari MCO, Wisenden BD, Chivers DP. Chemical ecology of predator-prey interactions in aquatic ecosystems: A review and prospectus. *Can. J. Zool.* **2010**, *88*. DOI:10.1139/Z10-029
121. Van Buskirk J, McCollum SA. Functional mechanisms of an inducible defence in tadpoles: morphology and behaviour influence mortality risk from predation. *J. Evol. Biol.* **2000**, *13*, 336–347. DOI.10.1046/j.1420-9101.2000.00173.x
122. Richardson JL. Novel features of an inducible defense system in larval tree frogs (*Hyla chrysoscelis*). *Ecology* **2006**, *87*, 780–787. DOI.10.1890/05-0536
123. Hettyey A, Tóth Z, Thonhauser KE, Frommen JG, Penn DJ, Van Buskirk J. The relative importance of prey-borne and predator-borne chemical cues for inducible antipredator responses in tadpoles. *Oecologia* **2015**, *179*, 699–710. DOI:10.1007/s00442-015-3382-7
124. Chamove AS, Moodie EM. Are alarming events good for captive monkeys? *Appl. Anim. Behav. Sci.* **1990**, 27, 169–176. DOI:10.1016/0168-1591(90)90016-7
125. Moodie EM, Chamove AS. Brief threatening events beneficial for captive tamarins? *Zoo Biol.* **1990**, *9*, 275–286. DOI:10.1002/zoo.1430090403
126. Hoff KvS, Blaustein AR, McDiarmid RW, Altig R. Behavior: interactions and their consequences. In *Tadpoles: The Biology of Anuran Larvae*; University of Chicago Press: Chicago, IL, USA, 1999; pp. 215–239.
127. Lannoo MJ. Complementary occupancy of semi-permanent wetlands by Tiger Salamander (*Ambystoma tigrinum*) larvae and fishes as indicated by zooplankton size and color: How respiratory physiology explains community ecology. *Ichthyol. Herpetol.* **2021**, *109*, 1060–1067. DOI:10.1643/h2021083

128. Lannoo MJ. (Ed.) *Amphibian Declines: The Conservation Status of United States Species*; University of California Press: Berkeley, CA, USA, 2005.
129. Thrane C, Lyakurwa JV, Liedtke HC, Menegon M, Petzold A, Loader SP, et al. Museomics and integrative taxonomy reveal three new species of glandular viviparous tree toads (*Nectophrynoides*) in Tanzania's Eastern Arc Mountains (Anura: Bufonidae). *Vertebr. Zool.* **2025**, *75*, 459–485. DOI.10.3897/vz.75.e167008
130. Fabrezi M, Quinzio SI, Goldberg J, Cruz JC, Pereyra, MC, Wassersug RJ. Developmental changes and novelties in ceratophryid frogs. *Evodevo* **2016**, *7*, 5. DOI:10.1186/s13227-016-0043-9
131. Relyea RA. Morphological and behavioral plasticity of larval anurans in response to different predators. *Ecology* **2001**, *82*, 523–540. DOI.10.1890/0012-9658(2001)082[0523:MABPOL]2.0.CO;2
132. Duellman WE, Trueb L. *Biology of Amphibians*; Johns Hopkins University Press: Baltimore, MD, USA, 1994.
133. Wells KD. *The Ecology and Behavior of Amphibians*; University of Chicago Press: Chicago, IL, USA, 2007.
134. Halliday T. *The Book of Frogs: A Life-size Guide to Six Hundred Species from Around the World*; University of Chicago Press: Chicago, IL, USA, 2015.
135. Amin NM, Womble M, Ledon-Rettig C, Hull M, Dickinson A, Nascone-Yoder N. Budgett's frog (*Lepidobatrachus laevis*): New amphibian embryo for developmental biology. *Dev. Biol*. **2015**, *405*, 291–303. DOI:10.1016/j.ydbio.2015.06.007
136. Northcutt RG, Gans C. [Review of] Frog Neurobiology: A Handbook. Edited by R. Llinás & W. Precht. *Q. Rev. Biol*. **1977**, *52*, 450. DOI:10.1086/410263
137. Taylor GM, Nol E, Boire D. Brain regions and encephalization in anurans: Adaptation or stability? *Brain Behav. Evol*. **1995**, *45*, 96–109. DOI:10.1159/000113543
138. Liao WB, Lou SL, Zeng Y, Merilä J. Evolution of anuran brains: Disentangling ecological and phylogenetic sources of variation. *J. Evol. Biol*. **2015**, *28*, 1986–1996. DOI:10.1111/jeb.12714
139. Manzano AS, Herrel A, Fabre A-C, Abdala V. Variation in brain anatomy in frogs and its possible bearing on locomotor ecology. *J. Anat*. **2017**, *231*, 38–58. DOI:10.1111/joa.12613
140. Bräuer J, Hanus D, Pika S, Gray R, Uomini N. Old and new approaches to animal cognition: There is not 'one cognition'. *J. Intell*. **2020**, *8*, 28. DOI:10.3390/jintelligence8030028
141. Poole VA, Grow S. *Amphibian Husbandry Resource Guide*; Association of Zoos & Aquariums: Baltimore, MD, USA, 2012.