REVIEW

The importance of enrichment for advancing amphibian welfare and conservation goals: A review of a neglected topic

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Abstract.—**Enrichment, broadly the provision of stimuli to improve the welfare of captive animals, is known to be important in husbandry practice and in the success of** *ex situ* **conservation and reintroduction programs. Practical evidence of the importance of enrichment exists for a number of taxa, yet amphibians are poorly represented. There is no reason to assume** *a priori* **that amphibians would not benefit from enrichment and, given their increasing prominence in captive programs, their requirements in captivity beyond basic husbandry should be the focus of more intense study. We review the existing body of research on enrichment for amphibians, as well as that for fish and reptiles, which may be regarded as behaviorally and neurologically broadly similar to amphibians. We also briefly discuss mechanisms by which enrichment might affect amphibian fitness and, therefore, reintroduction success. Our review supports the contention that there may be important consequences of enrichment for both captive welfare and** *ex situ* **conservation success in amphibians and that amphibian enrichment effects may be highly variable taxonomically. In the face of increasing numbers of captive amphibian species and the importance of** *ex situ* **populations in ensuring their species level persistence, enrichment for amphibians may be an increasingly important research area.**

Key words. Behavior, conservation, environmental enrichment, re-introduction, welfare, *ex situ*, fish, reptiles

Introduction

A wide range of amphibian species is currently maintained in captivity. Some species are used as models in laboratory research, including the ubiquitous *Xenopus laevis* and the dendrobatid frogs used to study skin peptides (reviewed by Daly 1998) and caecilians used in biomechanics research (e.g., Summers and O'Reilly 1997) and leaf frogs involved in conservation research (Ogilvy et al. 2012a, b). Several species are farmed (in addition to the many collected from the wild) for food or other products and others are maintained by private individuals as hobby or pet animals (Gascon et al. 2005). In addition, the *ex situ* conservation response to the on-going global amphibian extinction crisis (e.g., Gagliardo et al. 2008; Lee et al. 2006; Norris 2007) has drawn much publicity to the growing number of amphibians maintained for conservation breeding and education in zoos and similar institutions. This increase in captive amphibians (both

in actual numbers and species held) and their mounting conservation importance, has highlighted the need for a more thorough understanding of amphibian captive husbandry (Gascon et al. 2005), particularly for species that have no history in captivity and for those that are intended for release into the wild (Gagliardo et al. 2008; Gascon et al. 2005).

For many other taxa, the importance of enrichment has been identified for not only the welfare, or the physical and psychological wellbeing, of individual animals in captivity or those destined for release, but also for the overall/long-term success of reintroduction projects (Crane and Mathis 2010; Shepherdson et al. 1998; Young 2003). However, the implications of past work on the value of enrichment schemes for captive species currently has limited scope because enrichment has neither explicitly used nor well researched in amphibians (de Azevedo et al. 2007; Burghardt 2013). The objective of this paper is to draw attention to this lack of knowledge

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Table 1. Studies of enrichment in amphibians.

Species	Origin	Type of enrichment investigated	Findings	Notes	Reference
Xenopus laevis	Unknown	Shelter provision	No effect on growth rate. Frogs provided with shelter reluctant to leave it, even when provided with food.	Small sample size; unknown origins and genetics (see Chum et al. 2013)	Hilken et al. (1995)
Xenopus laevis	Laboratory bred	Shelter provision	Frogs use any shelter provided, but prefer plastic tubes to plants, rocks and wood. Frogs prefer tanks with shelter to tanks with no shelter. Frogs showed increased activity and reduced panic in tanks with shelter.	—	Brown and Nixon (2004)
Xenopus laevis	Laboratory bred	Shelter provision	Provision of plastic tubes reduced aggressive encounters, wounds and/or cannibalisation events.	—	Toreilles and Green (2007)
Xenopus laevis	Laboratory bred	Shelter provision	No effect on growth rates. Reluctant to leave shelter.	—	Gouchie et al. (2008)
Xenopus laevis	Laboratory bred	Shelter provision	No effect on growth rates or body condition (fat bodies). Higher propensity to clump together without shelter.	—	Archard (2012)
Xenopus laevis	Laboratory bred tadpoles	1. Surface area size 2. Water depth 3. Aquatic partitioning/ maze	1. Reduced surface area increased air-breathing behavior 2. Shallow water reduced growth rates and caused abnormal floating behavior (tadpoles could not surface to breath properly) 3. Tadpoles avoided narrower passages (2 cm) and preferred wider ones (4 cm)	Enrichments are not ecologically relevant to this species; this work may have limited implications for captive husbandry	Calich and Wassersug (2012)
Xenopus laevis	Laboratory bred females	1. Shelter provision 2. Conspecific provision (always with shelter)	1. Refuge provision reduced daytime activity and animals used shelter when provided 2. Addition of conspecific further reduced daytime activity in increased refuge use. No aggression observed and refuges were shared	—	Archard (2013)
Lithobates catesbeianus	Farmed/wild-caught	Environmental complexity (ramps, perches and caves)	Improved general welfare (general aspect and condition of animals)	High density laboratory condition	Bang and Mack (1998)
Lithobates catesbeianus	Farmed/wild-caught	Shelter provision	Reduction in mortality and improvement in condition	High density laboratory condition	Hedge and Saunders (2002)
Dendrobates tinctorius *D. azureus* *D. auratus* *D. leucomelas* Mainly reported as aggregate data across species	Zoo bred	1. Feeding enrichment (control vs. insect dispenser vs. broadcast feed/aphid stem) 2. Enclosure switch	1. Some effects on behavior (mainly activity) 2. Effect on activity levels (enclosure switch lead to higher activity levels)	Very small sample sizes. Issues with experimental design, including few replicates and unexplained measures	Hurme et al. (2003)
Oophaga pumilio	Zoo bred	Feeding enrichment (feeding dish control vs. feeding dish with leaf cover to allow insects to disperse)	Increased foraging duration, increased duration between prey capture events and reduced rapid feeding	—	Campbell-Palmer et al. (2006)

Table 1. Studies of enrichment in amphibians (continued).

Species	Origin	Type of enrichment investigated	Findings	Notes	Reference
Mannophryne trinitatis	Wild collected as tadpoles	1. Shelter provision 2. Substrate type	1. Strong, positive effect on growth rates. No effect on behavior (weak effect on time spent jumping) 2. Preferred shallow water	Substrate preference predicted by habitat	Walsh and Downie (2005)
Physalaemus pustulosus	Wild collected as spawn		1. No/weak effect on growth or behavior 2. Preferred dig-able (sand or gravel) substrate		
Leptodactylus fuscus					
Agalychnis callidryas	Laboratory bred juveniles and adults	Shelter provision	Frogs prefer planted to non-planted enclosures. This preference increases when animals are deprived of plants before choice test. Froglets reared with plants grow faster and are in better condition than those reared without. Frogs reared with plants have more diverse and more abundant cutaneous bacterial communities.	—	Michaels et al. (2014b)
Cryptobranchus alleganiensis	Wild collected as eggs (head-starting program)	Pre-release anti-predator training	Hellbenders were able to learn to exhibit a fright response to trout scent after classical conditioning; control animals showed no such improvement.	—	Crane and Mathis (2010)

and to call for more research in order to better understand the importance of enrichment for this taxon. We will explore the meaning of enrichment for amphibians, review the body of existing research (Table 1), and discuss the neglect of this field as well as how and why enrichment may be important as a focus for both amphibian conservation and welfare research activity. Finally, we will suggest a potential structure and goals for future research in this area (Table 2).

Concepts of enrichment

Enrichment for captive animals has been defined in various ways, but in general, is any intervention designed to improve animal welfare beyond the basic requirements for survival, usually taking the form of modifications to enclosures or husbandry protocols. Well known examples include the provision of bamboo stems filled with grubs for captive Aye-aye (*Daubentonia madagascariensis*) (Quinn and Wilson 2004), running wheels for captive rodents (Hutchinson et al. 2005) and the spraying of unfamiliar scents on parts of the enclosures for big cats; e.g., Szokalski et al. 2012 in tigers (*Panthera tigris*).

Enrichment is often sub-divided into environmental, behavioral, and social categories. Shepherdson (1998) defined environmental enrichment as any intervention that provides "the environmental stimuli necessary for optimal psychological and physiological well-being." This is distinct from behavioral enrichment, which is designed to elicit or allow the expression of specific behav-

iors or behavioral repertoires (Shepherdson 1994). Social enrichment, the provision of access to other individuals (usually, but not always, conspecifics) to cater for social interaction needs (including both environmental and behavioral components), has also been identified as important for a number of taxa (Berejikian et al. 2001; Lantermann 1993; Miranda de la Lama and Mattiello 2010; Polverino et al. 2012; Saxby et al. 2010; Sloman et al. 2011; reviewed by Hayes et al. 1998 and Young 2003; see below).

Enrichment can influence behavioral repertoires and stress levels beyond addressing stereotypical behavior and physical health problems (reviewed by Young 2003) and can affect physical brain structure in species as diverse as mice (*Mus musculus*) and crickets (*Acheta domestica*) (Lomassese et al. 2000; van Praag et al. 2000). These findings have led to a current view of enrichment, which recognizes the importance of all three categories for the psychological as well as the physical welfare of captive animals (Dawkins 2006; Young 2003).

The three forms of enrichment can be used to improve conservation success by training animals with the aim of improving survivorship upon release; e.g., anti-predator training in the black footed ferret (*Mustela nigripes*; Dobson and Lyles 2000). Although some forms of training may be beneficial, the use of enrichment may result in conflict between maximizing individual welfare in captivity and equipping animals destined for release with the most appropriate survival skills (Caro and Sherman 2013; Harrington et al. 2013), and both objectives should

Table 2. Key areas of species biology knowledge required for effective enrichment research, potential tools for assessing enrichment needs and effects and areas of amphibian captive husbandry for which enrichment may be important.

Key areas of amphibian biology, to be integrated into enrichment research			Potential measures of welfare and fitness		Potential areas of captive husbandry for enrichment research focus

Cognition	Learned and hard-wired behavioral components	*Inter- and Intra- individual, phenotypic and genetic variation*	Catalogue existing issues in captive amphibians and their husbandry	*Comparisons against wild populations, where appropriate*	Enclosure design
					• Size
					• Complexity
					  - Permanent (furniture and decor)
					  - Temporal (novel objects, timed misting)
					• Refuges
					• Lighting
					  - Wavelength
					  - Photoperiod
					  - Intensity

	Perception of environment		Behavior and behavioral assays		
Behavior	Natural behavioral repertoires and activity levels of species		Foraging success		Environmental parameters • Gradients • Fluctuation (seasonal and diel)
	Foraging strategies and dietary composition		Growth and development		
	Reproductive behavior • Breeding strategies • Mate choice • Competition for mates/breeding sites		Body condition		Threat stimuli • Predation • Competition • Environmental stressors (e.g., drying ponds)
	Migration and home ranges		Hormones • Stress • Reproductive		Encouraging specific behavioral responses
	Antipredator behavior		Micro- and macro-biotas associated with animals • Beneficial communities (mainly skin and gut) • Parasite and pathogen loads		Nutrition and food presentation • Nutritional content • Temporal variation • Variation in food types (different species of prey animal or algae) • Total abundance
	"Personality" vs behavioral plasticity		Pathologies • Behavioral • Physical (disease, malformation and pathogen susceptibility)		
Interactions	Intra- and inter-specific		Reproductive success		Social enrichment • Presence of conspecifics and non-conspecifics • Stability of social groups • Territory creation and maintenance • Mate choice • Human habituation
	As predators, prey and competitors				
Genetics and evolution	Heritability of traits		Survivorship		
	Potential for selection				

be considered for conservation breeding populations. The ferrets trained for release, for example, although not physically harmed, would have been psychologically distressed by being pursued by muzzled dogs as is a prerequisite of successful aversive training. This topic will continue to be controversial, as it is impossible to objectively resolve the relative importance of individual welfare and the persistence of a species as a whole, or whether the compromise of one is worth the assurance of the other. However, it is important to consider the individual welfare gains of such training post release. Pre-release anti-predator training may compromise welfare of animals in captivity, but may result in a larger welfare gain, when animals avoid predators in the wild.

Burghardt (1996) suggested that the term "controlled deprivation" might be more appropriate than "enrichment." This term acknowledges that it is impossible to provide in captivity the level of stimulation gained by animals in the wild, but rather management strategies should seek to strategically provide stimulation in such a way as to control the effects of general deprivation. The term "enrichment" may suggest a positive increase in

stimulation due to management strategies, when in fact it is not. While "controlled deprivation" is perhaps more honest, the vast majority of work continues to use the term "enrichment." We will therefore continue to do so, but with the caveat that such strategies enrich the life of captive animals compared with captive life devoid of any stimulation, rather than compared with what they might receive in the wild.

The conceptual framework of enrichment has largely focused on birds and mammals, and it may be problematic to apply it consistently when assessing enrichment for amphibians, particularly because the distinction between environmental and behavioral enrichment is blurred. Amphibian behaviors are often linked to specific physiological functions, such as basking, hunting or burrowing, or to reproduction, so we will not differentiate between these two enrichment types. Additionally, the highly specific environmental requirements of captive amphibians mean that many aspects of amphibian husbandry, such as UVB provision (Antwis and Browne 2009) and nutrition (e.g., Antwis et al. 2014; Li et al. 2009; Ogilvy et al. 2012a, b), impact both basic requirements and enrichment as described by Shepherdson (1998). The relative lack of empirical work in this field further hinders differentiation between different enrichment categories. We opt to exclude aspects of husbandry that offer benefits only to "physiological well-being," in order to allow a focus on true enrichment that transcends basic husbandry. Within this category, there is a distinction between enrichment solutions that simply provide animals with things that they have evolved to psychologically rely upon and those that offer specific learning opportunities. The provision of shelter may fall into the former category, for example, while training amphibians to avoid predators may be included in the latter. Both may be important to consider, although learning-oriented enrichment may be of greater significance to animals intended for release.

The neglect of amphibian enrichment research

Within the conservation and animal welfare literature there is a lack of research on amphibians and reptiles compared with the other tetrapod vertebrates (de Azavedo et al. 2007; Bonnet et al. 2002; Griffiths and Pavajeau 2008; Griffiths and Dos Santos 2012) and the body of published work in the area of enrichment for amphibians is limited (Table 1).

Amphibians, like all ectotherms, have historically been perceived as animals that cannot suffer, or do not feel pain, at least to the same degree as mammals and birds (Gross 2003). This bias has meant that the use of anaesthetics and analgesics during amphibian veterinary care and surgical procedures in the laboratory and field is relatively recent (Machin 1999). Although arguments have been made to suggest that amphibians (and fish) do not exhibit consciousness or emotion, while the amniotes do to varying degrees (reviewed by Cabanac, et al.

2009), this is by no means conclusive. The identification of pain pathways shared between amphibians and other amniotes (Stevens 2004) suggests an ability to experience pain, even if in a different and more restricted sense than in amniote taxa. This argument notwithstanding, the capacity to suffer in the presence of pain does not influence the importance of enrichment for conservation purposes.

Additionally, amphibian behavioral motivations, the reasons animals exhibit a particular behavior, are more difficult for humans to intuit than those of mammals and, to a lesser extent, birds, both of which may engage in behaviors more easily recognized by humans. Along with a lack of available, amphibian-specific measures of welfare, the difficulty in instinctively understanding amphibian behavioral motivations may have reduced interest in enrichment for this group as there may be fewer easily noticed welfare problems. Furthermore, the reliance of many amphibian species on highly specific environmental conditions often necessitates more complex and often "naturalistic" environments than would be required to maintain and breed mammals or birds, or even many reptiles. Consequently obvious symptoms of extreme deprivation may be less apparent, unlike in other taxa that may survive and reproduce in confined and bare enclosures, the more complex environmental requirements of some amphibians may be more difficult to disentangle from their basic husbandry. The rapidity with which many amphibians physiologically succumb to poor environmental conditions (Wright and Whitaker 2001) may not allow the development of any potential behavioral abnormalities before an animal dies. Moreover, the reduced activity in many contexts and lower metabolic capacity of many amphibians may reduce or mask the appearance of active behavioral stereotypes in some taxa. Additionally, increased stress hormone levels have been associated with a downregulation of behaviors, including reproduction (Moore and Miller 1984; Moore and Zoeller 1985; Chrousos 1997; Moore and Jessop 2003) and foraging (Crespi and Denver 2005; Carr et al. 2002), in some amphibians and so the effects of poor enrichment may, in some cases, manifest as absences of normal behavior instead deviant or new behaviors.

The relatively innate, "hard-wired" behavior of amphibians is often used to support the idea that enrichment, and consequently research investigating it, is not an important consideration, particularly in *ex situ* conservation (Bloxam and Tonge 1995; Griffiths and Pavajeau 2008). Some forms of enrichment involve learning (e.g., antipredator behavior learning; Dobson and Lyles 2000), whereas others may simply allow the manifestation of behaviors without a learning component. Although amphibians may not rely on captive conditions to develop normal behavioral repertoires as mammals or birds, their behaviors can be complex (reviewed by Burghardt 2013) and the role of learning is more important (reviewed by Bee et al. 2012; Wells 2007) than was previously thought.

Research on enrichment in amphibians, reptiles and fish

Measuring the impact of enrichment on amphibians

Objective measures of amphibian welfare have not been well developed or validated, beyond major issues such as cannibalism and bite trauma (Toreilles and Green 2007). Stereotypical behaviors in amphibians are poorly defined or understood (there is no mention of behavioral problems in Wright and Whitaker's (2001) otherwise comprehensive amphibian medicine and captive husbandry volume), and are usually only recognized in the form of gross trauma. It is likely that abnormal and stereotypical behaviors frequently used to assess welfare in mammals and birds may not be applicable to amphibians. Moreover, a number of commonly used measures are subject to *a priori* assumptions about their interpretation and, although they may seem reasonable, good rationales for the use and interpretation of characters as measures of welfare are rarely given. Activity levels have been used (Archard 2013; Campbell-Palmer et al. 2006; Hurme et al. 2003), but the conclusion that particular effects (e.g., increased foraging time or reduced daytime activity) translate to improved welfare remain largely untested assumptions. Similarly, authors generally interpret faster growth rates and larger fat bodies as indicators of better welfare, as well as being indicative of the production of more robust individuals. Dawkins' (1983; 1990) "consumer demand" methodology to assess animal needs has not been applied to amphibians, although choice chambers have been used to assess preferences (Michaels et al. 2014b; Walsh and Downie 2005). In reptiles, trade-offs between palatable food and cold temperatures have been used to assess the "consumer value" of a food reward to green iguana (*Iguana iguana*; Balasko and Cabanc 1998) and this methodology could be applied to amphibians.

Corticosteroid or "stress" hormone levels have been used to assess welfare in amphibians (Coddington and Cree 1995; Narayan et al. 2010, 2011a, b; Narayan and Hero 2011; Paolucci et al. 1990; Zerani et al. 1991), but beyond easily interpreted contexts such as capture, transport, and toe clipping, they can be problematic. In particular, a lack of baseline data across different contexts for most species makes interpretation, in terms of welfare, of isolated samples difficult. "Stress" is best viewed in its evolutionary, physiological, genetic, ecological, and behavioral contexts (Boonstra 2013) and increased levels are associated with and necessary for normal behaviors including reproduction (Moore and Jessop 2003; Narayan et al. 2010), immune responses (Rollins-Smith 2001), and adaptive plasticity (Denver 1997). "Stress" and "distress" are very different states, with only the latter having negative impacts on animal fitness and welfare, and these must be considered separately (Linklater and Gedir 2011). However, non-endocrine, unambiguous measures of welfare must be developed in order to prop-

erly distinguish between stress, which may be normally physiologically elevated in certain contexts, and distress in amphibians. Measurements of suites, instead of isolated, characters (e.g., Michaels et al. 2014b) will help to build a more easily interpreted picture of the effects of enrichment. Assessment of symbiotic or mutualistic bacterial communities on the physiologically active skin of amphibians may provide a new measure of welfare. These communities are sensitive to facets of enclosure design that can also be shown to impact other "traditional" measures of welfare and fitness including growth rates, body condition, behavior, and reproductive output (Antwis et al. 2014; Michaels et al. 2014b) as well as corticosteroid levels following challenges (R. Antwis, unpublished data). Although these communities do not allow distinction between stress and distress, they provide an additional line of enquiry in this area. Given the important impact of microbial communities on disease resistance (Bletz et al. 2013), this field can provide strong links between enrichment and the likelihood of reintroduction success.

Importantly, any evidence must be interpreted in the context of the focal species (Michaels et al. 2014a). Increased activity levels, for example, are more likely to be beneficial in actively hunting species than in ambush predators that do not typically engage in extended locomotion. Comparison between wild and captive conspecifics may provide guide "targets" for developmental and physiological measures, such as body condition, as well as a means to establish natural behavioral repertoires.

Existing enrichment research in amphibians

We identified 14 primary research articles on amphibian enrichment, summarized in Table 1, all but one (Crane and Mathis' (2010) hellbender training study; see below) of which were concerned primarily with improving individual welfare of captive animals, as opposed to improving breeding or release success. In some cases, the impact of enrichment has not been investigated beyond a subjective assessment of "appreciation" by people and practicality (e.g., Hanley 1993; Kirkland and Poole 2002) and such work has not been included in this count. Burghardt (2013) reviewed evidence for the effects of enrichment in both reptiles and amphibians, but did not include some of the studies discussed here. Furthermore, the focus of his review was on cognition and its implications for the understanding of enrichment for reptiles and amphibians, as well as a consideration of evidence for consciousness, play, and emotion in these groups. There was no discussion of pre-release training or the role of enrichment in conservation for amphibians.

Shelter provision is the most investigated form of enrichment for amphibians, including the common model organism *Xenopus laevis* (reviewed by Chum et al. 2013; Tinsley 2010; see Table 1), and in five other species (*Physalaemus pustulosus*, *Leptodactylus fuscus*, *Man-*

nophryne trinitatis, *Agalychnis callidryas*, and *Lithobates catesbeianus*; Table 1). Although shelter provision undoubtedly has physiological benefits for amphibians (Michaels et al. 2014b; Walsh and Downie 2005), behavioral tests (see Table 1) have suggested a psychological element to the effects of shelter provision, implying that it falls within our definition of enrichment for amphibians. However, more comprehensive investigations of this are warranted.

The conclusions of this literature are somewhat mixed, particularly for *Xenopus* but in general support the importance of shelter provision for frogs studied (Archard 2013; Chum et al. 2013; Bang and Mack 1998; Hedge and Saunders 2002; Michaels et al. 2014b; Tinsley 2010; Walsh and Downie 2005; Table 1). In non-*Xenopus* species, multiple measures of welfare and fitness all show improvements in the presence of enrichment. In *Xenopus*, changes in behavior do not seem to be reflected in growth rates or body condition, nor are these negatively affected by enrichment. These differences between taxa in response to the same type of enrichment (shelter provision) are indicative of the limited degree to which findings from one species can be applied to others, and the need for the development of species-specific measures of welfare. They also highlight the importance of measuring a number of variables in response to enrichment.

Two studies investigate enrichment through environmental complexity beyond shelter provision. Bang and Mack (1998) showed that increased general environmental complexity in the form of ramps, perches, and caves positively affected the welfare of captive bullfrogs (*Lithobates catesbeianus*; Table 1), although it is unclear if this extended beyond the effects of shelter alone (Hedge and Saunders 2002). Calich and Wassersug (2012) found impacts of water depth, surface-area size and aquatic partitioning on the behavior of *X. laevis* tadpoles, but the enclosure modifications were not ecologically relevant to this open-water species (Tinsley and Kobel 1996) and the findings are perhaps of limited use in developing husbandry protocols.

Food-delivery enrichment affects behavior and activity levels in dendrobatid frogs (Campbell-Palmer et al. 2006; Hurme et al. 2003), whereas introduction of frogs to novel environments also increased activity levels (Hurme et al. 2003). Archard (2013) investigated the effect of social enrichment, through the provision of conspecifics, in an enclosure containing a refuge, as well as the effect of shelter *per se* (see above). The author found that *X. laevis* exhibited reduced daytime activity, beyond the reduction seen when refugia are provided, when conspecifics are present in tanks with shelter. This result was interpreted as an improvement in welfare, but such and interpretation may be viewed as ambiguous, particularly in a species known to show a degree of territoriality in the wild (Tinsley and Kobel 1996).

One study has investigated the use of enrichment to train hellbenders (*Cryptobranchus alleganiensis*) for release into the wild. Crane and Mathis (2010) used a combination of trout-scented water and conspecific distress secretions to train hellbender larvae in head-starting programs to avoid predation by predatory trout. This pre-release training may be classed as a form of enrichment for these salamanders, encouraging them to express normal anti-predator behavior, but manipulating this to improve future survival in the face of invasive alien predators. Several classes of amphibian behavior have now been shown to include learned components, including predator avoidance (Crane and Mathis 2010 in *Cryptobranchus alleganiensis*; Epp and Gabor 2008 in *Eurycea nana*; Ferrari and Chivers 2008 in several species of anuran larvae), territoriality (Dawson and Ryan 2009; 2012 in *Physalaemus pustulosus*), foraging (Sontag et al. 2006 in anuran larvae) and other aspects of social behavior (Bee et al. 2012; Wells 2007). Moreover, complexity and cognition, whereby behavioral processes exceed simple responses to stimuli, have been detected in a range of amphibian behaviors, including spatial learning and homing (Brattstrom, 1990; Shoop 1965) and individual recognition (Gauthier and Miaud 2003). Amphibians are also capable of visual discrimination learning, identifying objects based on visual characteristics, (Jenkin and Laberge 2010) and even rudimentary quantity learning, showing the capacity to compare quantities, (Krusche et al. 2010; Uller et al. 2003). Although these findings have implications for all areas of enrichment for amphibians, they suggest that enrichment in captivity might have particular applications in pre-release training. However, applying this increased knowledge of amphibian learning and behavioral complexity to enrichment has not been empirically tested (apart from the aforementioned hellbender study). Furthermore, in the context of predation the ethics of any compromise between welfare and long-term reintroduction success must be carefully considered (Caro and Sherman 2013; Harrington et al. 2013).

Some of the research investigating enrichment for amphibians is problematic in terms of sample size and experimental design. Hurme et al. (2003) could not detect significance in some effects due to extremely limited sample size. Walsh and Downie (2005) used a sample size suitable for statistical analysis, but in their cover provision experiments, fossorial or semi-fossorial anuran species (*Leptodactylus fuscus* and *Physalaemus pustulosus*) were provided with a soft substrate in enclosures both with and without cover. As the authors admit, it is likely that the effects of cover provision in these species were weaker in comparison with the non-fossorial third study species (*Mannophryne trinitatis*) due to this soft substrate acting as "cover" for the frogs, which could simply burrow in order to hide.

Enrichment research in amphibians is subject to strong taxonomic bias in addition to bias towards shelter provision. Half of the articles (seven of 15, Table 1) used *X. laevis* as a study species, while of the other species used, six of eleven were dendrobatoid frogs and only one

caudate was represented (Table 1). To our best knowledge, there has been, to date, no explicit research on enrichment for caecilians (Gymnophiona). However, one biomechanics study (Ducey et al. 1993) may be relevant to caecilian enrichment, as it demonstrates that caecilians of four fossorial species (*Ichthyophis kohtaoensis*, *Dermophis mexicanus*, *Gymnopis syntrema*, and *Schistometopum thomense*) preferred and were most capable of digging in uncompacted soil, and that they use existing burrows rather than constructing new ones if given the choice. This concurs with field studies, which have generally found terrestrial caecilians in looser, more friable soil and leaf-litter in established burrow systems (Kupfer et al. 2005; Malonza and Measey 2005; Measey 2004; Oomen et al. 2000; Habidata.co.uk).

Comparison with fish and reptile literature

For amphibians, given the narrowness of enrichment types investigated and the limited range of focal species (both taxonomically and ecologically), it is difficult to extrapolate current evidence to other amphibians and to other enrichment types. In order to predict the importance of enrichment for amphibians, therefore, we examined evidence from the two vertebrate taxa most similar to amphibians: reptiles and fish. Despite the fact that mammals and birds are better studied (de Azevedo et al. 2007), reptiles and fish are generally more similar to amphibians in neurological complexity, cognitive ability, physiology, and ecology. The literature for fish is much larger than for amphibians and that for reptiles is both larger and includes a wider range of enrichment types (de Azevedo et al. 2007). We do not suggest that these groups are identical in their needs, but until advances in amphibian enrichment research are forthcoming, inference from these taxa may be important to consider. Furthermore, methodologies used to assess enrichment in reptiles and fish may easily transfer to the study of amphibians.

Research on fish has focused largely on the commercial improvement of fisheries, the improvement of fitness in animals intended for release to the wild, and to a lesser degree on the welfare of fish species commonly used in biomedical research. Enrichment through environmental complexity generally improves cognitive and learning ability in fish (Brown and Braithwaite 2005 in *Brachyraphis episcope*; reviewed by Strand et al. 2010), reduce stress and stress-related behavior and metabolic activity (Batzina and Karakatsouli 2012 in *Sparus auratus*; Finstad et al. 2007 in *Salmo salar*; Millidine et al. 2006 in *S. salar*; Zimmerman et al. 2012 in *Gadus morhua*), increases behavioral plasticity (Berejikian et al. 2001 in *Onychorhyncus mykiss*), increases territory holding power (Nijmen and Heuts 2000 in a variety of species) and improves foraging, risk assessment, and predator-avoidance behavior (Braithwaite and Salvanes 2005 in *G. morhua*; Brown et al. 1998 in *O. mykiss*; Brown et al. 2003 in *S. salar*; Lee and Berejikian 2008

in *O. mykiss*; Roberts et al. 2011 in *S. salar*). Moberg et al. (2011) found increased timidity of *G. morhua* reared in enriched hatchery conditions once exposed to a novel arena, possibly due to less developed coping strategies in animals reared with shelter. This body of evidence should stimulate interest in similar phenomena linked to environmental complexity in amphibians, which could have important implications for the success of release or reintroduction projects. It seems that innate, "hard-wired" fish behavior can be enhanced and honed by enrichment in the form of exposure to simulated predator disturbance (Berejikian et al. 2003 in *O. tshawytscha*) or by social learning (Vilhunen et al. 2005 in *Salvelinus alpinus*; reviewed by Brown and Laland 2001). The similarity to the limited literature on comparable phenomena in amphibians (Crane and Mathis 2010; Epp and Gabor 2008; Ferrari and Chivers 2008; Sontag et al. 2006) suggests that there is much to learn about the application of amphibian learning to captive husbandry and pre-release training.

Enrichment in fish farms also improves growth rates, similar to the effects of shelter provision in amphibian species (Archard 2013; Chum et al. 2013; Tinsley 2010; Walsh and Downie 2005), increases potential stocking densities and reduces aggression (Batzina and Karakatsouli 2012; Finstad et al. 2007), as does enrichment in amphibians (*X. laevis*; Toreilles and Green 2007). The impacts of enrichment may be trans-generational; Evans et al. (2014) found that adult farmed salmon (*S. salar*) in enclosures enriched by exposure to wild conditions while in captivity produced offspring with a two-fold increase in survivorship compared with fish maintained under standard farm conditions. Given the normal use of pre-release training only in the individuals to be exposed to predation (Crane and Mathis 2010), it may be important to investigate trans-generational effects of enrichment in amphibians.

A few studies have focused on individual welfare in laboratory and aquarium fish species, but as for amphibians these have mainly investigated cover provision. This work has, surprisingly, found little benefit to providing enrichment in laboratory aquaria, in the form of cover/environmental complexity, with fish often showing no differences in growth rates or stress-hormone levels (Brydges and Braithwaite 2009 in *Gasterosteus aculeatus*; Wilkes et al. 2012 in *Danio rerio*), although these are perhaps not comprehensive measures of welfare. Kistler et al. (2011), however, found a preference for structured, rather than barren, environments in both *D. rerio* and the barb *Puntius oligolepis*. These contradictory results may partly be due to the highly constrained nature of enrichment solutions within strictly controlled laboratory conditions. The glass rods provided as enrichment for zebrafish by Wilkes et al. (2012) may not have been sufficient to generate a beneficial effect, whereas the plants and hides provided in the preference study of Kistler et al. (2011) may have been complex enough to generate a detectable behavioral response in the same species.

Furthermore, as neither study analyzed both behavioral and developmental/endocrine data, it is possible that any improvement to welfare did not translate to all measures.

Saxby et al. (2010) and Sloman et al. (2011) found evidence for welfare and behavioral benefits of social enrichment in terms of both increased group size and mixed species assemblages in a variety of fish species commonly kept in home aquaria. Similarly, schooling and mixed species assemblages are common in anuran tadpoles in the wild and may have implications for learning (Ferrari and Chivers 2008; Sontag et al. 2006); the application of this for conservation breeding may be important to consider.

Reptiles have been better studied than amphibians in terms of enrichment research (de Azevedo 2007; Hayes et al. 1998) and attempts have been made in reptiles to identify and define stereotypical behavior and to suggest aetiologies (Bels 1989; Hayes et al. 1998; Warwick 1990). This literature is more focused on individual welfare of captive animals than is the fish literature and has involved zoo animals, as opposed to farms. Small sample sizes and anecdotal reports are a common problem in the reptile enrichment literature and much of it includes reasoned suggestions for enrichment, rather than empirical evidence of its efficacy (Burghardt 2013; Hayes et al. 1998). For this reason, enrichment solutions are, in general, more suitable for short-term use by a small group of animals, in contrast to the types of larger-scale enrichment often investigated in fish.

Captive conditions alter and reverse wild patterns of antipredator behavior of reptiles (Hennig and Dunlap 1978; Hennig 1979, both in *Anolis carolinensis*) and strike-induced chemosensory searching ("scent-trailing;" Marmie et al. 1990 in *Crotalus enyo*). The provision of a complex environment in captivity improves cognitive behavior (Almli and Burghardt 2006 in *Elaphe obsoleta*) and reduces stress hormone levels and stress-related escape behavior (Case et al. 2005 in *Terrapene carolina*). Blue-tongue skinks (*Tiliqua scincoides*) show alterations to activity patterns and exhibit reduced weight gain and obesity when provided with larger enclosures and the opportunity to hunt for insect prey (Phillips et al. 2011). Complex environments are also actively sought out by reptiles (Case et al. 2005 in *T. carolina*), while individuals of cryptic species may also seek out and prefer appropriately colored refugia (Garrett and Smith 1994 in *Morelia viridis*), as do wild amphibians (Pacific treefrogs, *Pseudacris regilla*; Morey 1990). Furthermore, although sometimes controversial (Burghardt 2005), some reptiles have been reported to engage in divertive, play behavior when provided with novel objects (Burghardt et al. 1966 and Burghardt 2005 in *Trionyx triunguis*; Hill 1946, Murphy 2002 and Burghardt 2005 in *Varanus komodoensis*; Lazell and Spitzer 1977 in *Alligator mississippiensis*). Animals have also exhibited a reduction in self-mutilation (Burghardt et al. 1996) and engaged in normal behavioral repertoires instead of apathy or ste-

reotyping when provided with such enrichment (Therrien et al. 2007 in *Caretta caretta* and *Chelonia mydas*). Also, monitors (*Varanus albigularis* and *V. rudicollis*) and anoles (*Anolis evermanni*) were capable of rapidly learning to solve cognitively demanding tasks (Gaalema 2011; Leal and Powell 2012; Manrod et al. 2008).

In contrast, Marmie et al. (1990) found no differences between groups of rattlesnakes (*Crotalus enyo*) raised in large or small enclosures, and wild conspecifics, in their ability to explore novel environments. Likewise, Rosier and Langkilde (2011) found no differences in *Sceloporus undulatus* behavior, stress hormone levels, survivorship and growth when a complex environment (climbing space) was provided. However, the small size and relative simplicity of the enclosures utilized in these cases may not have provided the degree of complexity required to provide effective enrichment for these animals: there has been some discussion of the validity of experimental design (see Burghardt 2013 for a summary of this exchange).

Finally, a few studies in reptiles examined the relationship between enrichment and survival in reintroduced animals, with encouraging results. Cook et al. (1978) reported the use of enrichment in the form of pre-release desert survival training of captive desert tortoises (*Gopherus agassizii*) in California and suggested that this approach improved survival from 0% in earlier release trials to 70% in trained tortoises. Although pre-release enrichment and training may have improved release success, rehabilitation centers also treated tortoises for a host of diseases that do not seem to have been addressed in earlier reintroduction attempts (the documentation is unclear), so the true impact of training is difficult to ascertain. Price-Rees et al. (2013) reported a similar training effort in blue-tongue skinks (*Tiliqua scincoides intermedia*), where aversive training was used to prevent lizards from eating lethally toxic cane toads (*Rhinella marina*), with large improvements in survivorship compared with control skinks. These findings reinforce the need for further investigation into the role of enrichment in pre-release training for amphibians. They also highlight the potential for such slightly aversive training to significantly improve both the welfare of individuals released into the wild and the success of conservation initiatives.

What impacts might enrichment have for captive amphibians?

Impacts on welfare

Enrichment has been demonstrated to reduce mortality and injury in some amphibians and to improve growth rates and body condition in others (Table 1). Furthermore, the majority of amphibian diseases found in captive populations and regularly treated by specialist veterinarians are related to improper husbandry (Wright and

Whitaker 2001). Obesity, metabolic bone disease (MBD) and related nutritional disorders are common problems in captivity (Gagliardo et al. 2008; Lee et al. 2006; Wright and Whitaker 2001). Enrichment designed to increase the effort required to forage for food (alongside a balanced diet; Li et al. 2009) increased activity levels (Campbell-Palmer et al. 2006) and, for actively foraging species (see below), should re-balance energy budgets while allowing animals to satiate their hunger, as has been demonstrated in skinks (Phillips et al. 2011) and cats (Clarke et al. 2005). Likewise, enrichment to encourage basking behavior in appropriate species (e.g., *Pelophylax lessonae*, which spend considerable portions of the day in the wild basking in sunlight; Michaels and Preziosi 2013), alongside the provision of Ultraviolet B radiation in suitable doses and gradients, is likely to be important in facilitating calcium uptake from the gut in many species, thus avoiding clinical and subclinical Metabolic Bone Disease (MBD) (Antwis and Browne 2009; Verschooren et al. 2011). Alongside basic facilitation via perches and basking sites, the provision of shelter and environmental complexity may alleviate perceived predation pressure and encourage basking behavior.

Beyond effects on the health and physical welfare of captive amphibians, enrichment may also have implications for psychological welfare. Enrichment may improve the cognitive engagement and capacity of amphibians, as has been shown in both reptiles and fish, as well as allowing animals to avoid perceived predation pressure (Michaels et al. 2014b). Further work is needed, however, to address these issues and to establish how enrichment may influence psychological well-being.

Implications for conservation

Enrichment may improve the success of reintroduction and head-starting programs in amphibian conservation. Evidence from amphibians, reptiles and fish strongly suggests that enrichment can influence a suite of characteristics, from growth rates to anti-predator behavior, which may influence the success of reintroductions. Furthermore, the potential for trans-generational effects warrants investigation in captivity. The provision of enrichment may influence survival and reproduction and consequently the genetic changes that occur over multiple generations, generating animals adapted to a captive environment (Frankham 2008). Genetic adaptation to captivity, or domestication, occurs due to differences between the wild and captive environment via genetic drift, founder effects, the unintentional selection for animals suited to the captive environment rather than the wild habitat into which they will eventually be released, or a combination these forces (Frankham 2008). Evidence for this phenomenon has been found in a wide range of breeding programs (reviewed Witzenberger and Hochkirch 2011) may be evident in a single generation (Christie et al. 2012). Amphibians are no exception, and adap-

tation to captivity has been detected in this group. For example, lack of exposure to predator cues and predation pressure resulted in loss of anti-predator behavior in the tadpoles of *Alytes muletensis* after 8−12 generations in captivity in association with a reduction in genetic diversity (Kraaijeveld-Smit et al. 2006). Although many captive breeding programs run studbooks to preserve genetic diversity and avoid genetic adaptation to captivity, these may fail due to unrealistic model assumptions (Witzenberger and Hochkirch 2011). In amphibian studbooks, tadpoles do not tend to be included as individuals and so populations may suffer non-random mortality before allele frequency changes can be prevented. The high fecundity of many amphibians means that most larvae cannot be raised to adulthood and necessary culls often remove tadpoles or metamorphs perceived to be weaker or smaller (C. Michaels, per. observ.). The use of enrichment to sort behaviorally fit and less fit animals, for example in response to predator cues, may be a more valid basis for culls than, for example, body size, although this idea is inevitably a source of ethical controversy (Caro and Sherman 2013; Harrington et al. 2013). Appropriately applied enrichment may also prevent more domesticated animals from gaining reproductive advantages in captivity. For example, animals that are unable to hunt effectively, but are capable of producing large numbers of young and readily reproduce in captivity may contribute disproportionately to programs unless animals are forced to forage more naturally for prey. Similarly, the use of enrichment may allow less domesticated animals to thrive in captivity, where they may be lost from breeding programs if housed without appropriate stimulation.

Finally, non-genetic inherited traits ("maternal" or "parental" effects) are becoming increasingly recognized as important in evolutionary terms. The genetic or environmental background of parents can influence offspring phenotype regardless of the genetic correlation between parents and offspring (Marshall and Uller 2007; Mousseau and Fox 1998). Epigenetic effects may improve or reduce offspring fitness, depending on the system and circumstances and can influence a wide range of characters in most plant and animal taxa (Franklin and Mansuy 2010; Marshall and Uller 2007; Mousseau and Dingle 1991; Mousseau and Fox 1998; Roach and Wulff 1987). Epigenetic effects have been reported in a number of amphibian taxa (including Kaplan 1987; Kaplan and Philips 2006; Pakkasmaa et al. 2003; Parichy and Kaplan 1992; Räsänen et al. 2003) and are of increasing importance in the consideration of animal behavior and welfare (reviewed Jensen 2014). They may be linked to the degree of enrichment in the captive environment, although this has not been studied in amphibians. McCormick (2006), for example, found that crowding in a number of marine fish species resulted in decreased fitness, regardless of their genotype, of offspring, independent of genotype, even when offspring were raised under identical, spacious conditions. Similarly, Evans et al. (2014)

demonstrated trans-generational effects of enrichment in salmon bred for conservation, such that enriching parental enclosures improved post-release survivorship in offspring. Enrichment for captive amphibians therefore has the potential to influence the fitness of future generations through both epigenetic and genetic effects. Importantly, the phenotype (and therefore chance of survival in the wild) of an individual is determined by the interaction between genes and the environment (including both direct and epigenetic/parental components), both of which can be partially determined by the enrichment strategies employed in captivity.

As these effects cannot be controlled through studbooks, it may be of great importance to provide a degree of enrichment that does not encourage epigenetic changes in captive amphibians.

Future directions for research

Being at the early stage of enrichment research in amphibians means that little is known of its impact on welfare and fitness or which types of enrichment may be important. Amphibian captive welfare and methods suitable for measuring it are poorly understood or underdeveloped in comparison with other taxa. Given the urgency to provide answers for *ex situ* conservation projects (Gascon et al. 2005) it is important to develop enrichment research goals and priorities. Table 2 outlines a potential structure for enrichment research in amphibians. Most areas of amphibian husbandry are strongly constrained by the natural history of the species in question (Michaels et al. 2014a) and needs and responses to captive stimuli vary greatly among taxa and sometimes between populations (e.g., Tidwell et al. 2013). A more thorough understanding of the biology of focal species can aid in the design of meaningful enrichment and experiments. Consequently, we recommend that researchers first develop a good understanding of the biology of focal species before attempting to develop and evaluate enrichment activities. Based on this knowledge, experimental methods and measures of welfare can be developed and areas both already identified as important in amphibians, and those highlighted by work in fish and reptiles, can be investigated. It is important to develop objective measures of welfare, including identification of stereotypical or abnormal behaviors in captive amphibians. Ideally, researchers should aim to use as many different measures of welfare and fitness as possible in order to develop the best possible picture of the effects of enrichment. Comparisons between wild and captive conspecifics may also help with this process, particularly where enrichment is intended to improve the suitability of animals for release. Objective measures of welfare may also aid in addressing conflicts between training required for improved reintroduction success and ensuring that animals are not distressed while in human care.

Collaboration between research institutions, which have the experimental expertise to carry out meaningful research, and zoological collections, which have access to animals and species-specific knowledge may expedite research. With these tools, research could better determine the need for and impact of enrichment for both individual captive welfare and long-term conservation success in amphibians. Such knowledge could help to successfully and humanely maintain these animals in captivity and to successfully release them into the wild.

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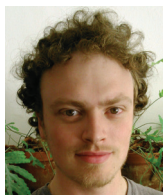
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