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REVIEW PAPER

Amphibians and conservation breeding programmes: do all threatened amphibians belong on the ark?

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Abstract Amphibians are facing an extinction crisis, and conservation breeding programmes are a tool used to prevent imminent species extinctions. Compared to mammals and birds, amphibians are considered ideal candidates for these programmes due to their small body size and low space requirements, high fecundity, applicability of reproductive technologies, short generation time, lack of parental care, hard wired behaviour, low maintenance requirements, relative cost effectiveness of such programmes, the success of several amphibian conservation breeding programmes and because captive husbandry capacity exists. Superficially, these reasons appear sound and conservation breeding has improved the conservation status of several amphibian species, however it is impossible to make generalisations about the biology or geo-political context of an entire class. Many threatened amphibian species fail to meet criteria that are commonly cited as reasons why amphibians are suitable for conservation breeding programmes. There are also limitations associated with maintaining populations of amphibians in the zoo and private sectors, and these could potentially undermine the success of conservation breeding programmes and reintroductions. We recommend that species that have been assessed as high priorities for ex situ conservation action are subsequently individually reassessed to determine their suitability for inclusion in conservation breeding programmes. The limitations and risks of maintaining ex situ populations of amphibians need to be considered from the outset and, where possible, mitigated. This should improve programme success rates and ensure that the limited funds dedicated to ex situ amphibian conservation are allocated to projects which have the greatest chance of success.

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The amphibian crisis

Contemporary amphibian declines have been precipitous, global, and sometimes enigmatic; no other group of vertebrates that has been completely assessed is currently faced with a higher level of endangerment (Alford and Richards 1999; Stuart et al. 2004). At least 30 % of all described amphibian species are currently threatened with extinction (Zippel and Mendelson 2008). Additionally, many amphibian faunas are poorly known and the threat status in some regions may therefore be underestimated (Iskandar and Erdelen 2006; Foufopoulos and Richards 2007; Rowley et al. 2010).

The factors driving global amphibian population declines are diverse, often synergistic, predominantly anthropogenic and intrinsically linked to uncontrolled human population growth (Gascon et al. 2007). While threats such as over-exploitation, habitat degradation, pollution and invasive species can potentially be ameliorated, many others, including climate change and several emerging infectious diseases (see review in Woodhams et al. 2011), are not reversible within the foreseeable future (Smith and Sutherland 2014).

Incidences of enigmatic declines are positively associated with species living in the tropics at high elevation in riparian habitats and negatively associated with species living at low altitudes in lentic habitats (Stuart et al. 2004). Evidence suggests that rapid enigmatic declines are linked to the emergence of chytridiomycosis as areas characterised by these declines overlap with areas of the highest environmental suitability for the chytrid fungus (Lötters et al. 2009). Amphibian chytrid fungi are non host specific, and infect all extant orders of Amphibia (Gower et al. 2013). Ranavirus is another emerging amphibian pathogen and has been documented to cause mass mortalities of both wild and captive amphibians (Miller et al. 2008; Gray et al. 2009). Attempts to mitigate these diseases in nature have been largely unsuccessful to date (see references within Smith and Sutherland 2014).

Why conserve amphibians?

A number of reasons have been proposed as to why amphibians should be conserved. Amphibians have an economic value; they are used for food, medicines, research and are increasingly popular as pets (Collins and Crump 2009; Tapley et al. 2011), Frogs are an important food item for many people (Gonwou and Rödel 2008), and there is a substantial international trade in frog meat. Between 1996 and 2006 it was estimated that between 8,000,000 to 12,000,000 kg of frogs' legs were imported globally (Warkentin et al. 2009; Gratwicke et al. 2010). Some species are of scientific or medical importance; secretions from amphibians have been documented to contain painkillers as well as antimicrobial peptides (Badio and Daly 1994; Fleming et al. 2009; Azevedo Calderon et al. 2011). Amphibians provide ecosystem services and the loss of one or more species can reduce the quality of the services within an ecosystem as amphibians play a crucial role in nutrient cycling and energy flow in aquatic and terrestrial ecosystems (Collins and Crump 2009). The removal of amphibians from, or reduction in numbers of amphibians in, a system can have dire consequences; over collection of frogs for the international meat trade resulted in an increase in agricultural pests in India (Altherr et al. 2011).

There are also aesthetic and cultural reasons for conserving amphibians. Humans strive to connect with nature and appreciate the beauty of nature and the uniqueness of each species (Wilson 1984). In many cultures amphibians are significant as they symbolise fertility and new beginnings as well as resurrection (Collins and Crump 2009), and amphibians are still represented in popular contemporary culture.

There are ethical arguments too; the majority of people would concur that each species has the right to exist and has its own intrinsic value regardless of its value to humans (Collins and Crump 2009). This ethical argument is powerful as it is central to the majority of belief systems and religions (Groom et al. 2006).

Amphibian conservation breeding programmes

In 2005, the IUCN/SSC Amphibian Conservation Summit produced the Amphibian Conservation Action Plan (ACAP) as an urgent call for globally coordinated conservation action to address amphibian declines. Several organisations were subsequently formed to co-ordinate amphibian conservation on a global scale, including the Amphibian Ark (AArk) and the Amphibian Specialist Group (ASG).

The Amphibian Survival Alliance (ASA) was established in 2011 as an umbrella organisation for amphibian conservation practitioners, and works closely with AArk and the ASG. The ASA prioritised the establishment of ex situ rescue populations of threatened amphibians in zoos and other institutions (Bishop et al. 2012). These programmes aim to maintain genetically representative populations in captivity while threat processes in the wild are being addressed, and subsequently provide animals for population supplementation, reintroduction, or translocation programmes (Zippel et al. 2011). In light of climate change and emerging infectious disease, protecting large swathes of habitat in order to protect species may not be enough to ensure the survival of many species (Redford et al. 2012; Minteer and Collins 2013; Pritchard et al. 2013). The majority of landscapes are becoming ever more human dominated, and the difference between managed and wild systems is increasingly indistinct (Minteer and Collins 2013). Conservation biologists now recognise that in situ and ex situ techniques are complimentary and the distinction between the two is increasingly blurred or even obsolete (Redford et al. 2012; Pritchard et al. 2013). Conservation practitioners are increasingly integrating both in situ and ex situ methods in order to conserve biodiversity, with ex situ populations functioning as metapopulations through conservation management and direct field interventions (Scheele et al. 2014). Ultimately though, ex situ programmes are the last line of defence for populations disappearing too quickly or facing threats too severe or complicated to conserve through in situ action alone.

AArk identifies the most appropriate conservation actions for threatened species through regional needs-based assessments and its programme initiation tool, and provides training and best practice guidelines for ex situ managers (Zippel et al. 2011). The likely suitability of the species for a conservation breeding programme (CBP) is not explicitly considered during the assessment process. There is also an issue around the 'uptake' of prioritised species; of the 186 CBPs for threatened amphibian species that AArk is aware of, only 67 are for species assessed as requiring rescue programmes (K. Johnson pers. com.). To what extent, if any, the issue of species suitability for a CBP contributes to this is unknown.

Conservation breeding programmes are an attractive option for amphibian conservation practitioners because they are exciting, provide good publicity and practitioners believe they are contributing to conservation (Norris 2007; Bowkett 2009). This belief is certainly not baseless as CBPs played a major role in 17 of the 68 instances where the IUCN threat level assigned to a species had improved by 2010, including two of the four amphibian species whose IUCN threat level had been downgraded (Hoffmann et al. 2010). In a review of the effectiveness of captive breeding and reintroduction programmes for amphibians, Griffiths and Pavajeau (2008) found that 12 out of 14 species that were part of CBPs bred successfully post-release, with seven species meeting the ultimate goal of establishing self-sustaining populations in the wild.

Although CBPs have been integral to the successful conservation of several threatened amphibian species, the 50 % success rate documented by Griffiths and Pavajeau (2008) indicates that there is room for substantial improvement. Amphibians are disproportionately diverse and threatened in the tropics (Stuart et al. 2008) and many species from these regions have not been maintained in captivity before. Moreover, the majority of species held in CBPs being monitored by AArk have not reproduced beyond the F1 generation despite more than a decade of ex situ efforts in some cases (Michaels et al. 2014a). Overall, little has been achieved relative to the scale of the problem despite all of the capacity building and prioritisation efforts that have been conducted around the world in recent years. It is important to note that many programmes have started within the last 10 years, however, and it can take several years to establish a programme and develop successful captive husbandry techniques before releases can occur, followed by years of rigorous post-release monitoring before a programme can ultimately be judged as successful or unsuccessful. In some situation the threats in the wild may not have been mitigated and releases may not be possible. Despite this, we believe that we are at the point where we can, and should, critically evaluate how decisions regarding the establishment of amphibian CBPs are being made and, if necessary, look at ways of improving the decision-making process in order to maximise the chances of ultimate success.

Are all amphibians suitable candidates for CBPs?

Amphibians have been considered ideal candidates for CBPs for a number of reasons, including general attributes of amphibians such as small body size and associated low space requirements, high fecundity, applicability of reproductive technologies, short generation time, lack of parental care, hard wired behaviour, low maintenance requirements, the cost effectiveness of such programmes when compared with programmes for other vertebrates, the success of several amphibian CBPs and reintroductions and because capacity exists in the private and zoo sectors (Bloxam and Tonge 1995; Balmford et al. 1996; Griffiths and Pavajeau 2008; Browne et al. 2011; Smith and Sutherland 2014). However, these are generalisations and many threatened amphibian species do not meet one or more of these criteria; this potentially affects their suitability as candidates for CBPs. Even when a species appears suited to a CBP, there may still be significant problems associated with the establishment of a successful ex situ initiative, including insufficient resources and geo-political issues.

Small size and low space requirements

Whilst most amphibians are relatively small and often require significantly less space than similar programmes for many birds and mammals, a number of threatened species attain large sizes and/or have large space requirements. Large amphibians could be inherently at risk as they will likely be the target of hunters (Malhotra et al. 2007; Rowley et al. 2010; Chan et al. 2014). Hunting is a reversible threat, and heavily persecuted large species could therefore be a priority focus of CBPs. These species require large facilities to maintain adequate numbers of stock and are not suited to the standard amphibian conservation breeding facility (e.g. Browne et al. 2007; Gagliardo et al. 2008). The investment required to create facilities large enough to hold viable populations of amphibians has been cited as a limiting factor even for small species (Barber and Poole 2014; Cikanek et al. 2014).

Additionally, many amphibians are territorial (Hermanns et al. 2002) and territorial amphibians may need more space than would be expected. Many small amphibians require relatively large enclosures for their size. Some species are capable of jumping long distances (James and Wilson 2008) and may experience poor health and welfare if maintained in restricted spaces. Physical trauma is common in confined frogs with this kind of locomotory ability (Wright and Whitaker 2001). Others, including many bufonids, require large spaces over which migrations can be simulated in order for successful natural reproduction to take place (C. Michaels, pers. obs.).

High fecundity and short generation time

It is overly simplistic to state that amphibians produce large clutches and that populations can grow rapidly over relatively short periods of time. Whilst many species do exhibit these characteristics, clutch size is highly variable amongst species, ranging from a single egg to more than 45,000 (Duellman and Trueb 1994; Estrada and Hedges 2006). Small species and species with specialised reproductive modes tend to produce smaller clutches (Duellman and Trueb 1994), and fecundity is lower in caecilians than in anurans and caudates (Duellman and Trueb 1994). The species most in need of CBPs may be those with reduced fecundity; low fecundity is associated with increased likelihood of experiencing chytrid related declines (Bielby et al. 2008), although not all declining species have small clutches (Crump 2005). High fecundity in itself may also be of limited use unless coupled with an appropriate founder base, resources to successfully maintain a rapidly expanding captive population and population management to ensure on-going genetic viability. Unfortunately, studbooks are often absent, poorly managed or subject to false assumptions that render them flawed (Witzenberger and Hochkirch 2011), hence the management strategies required to control population size while preserving genetic diversity in highly fecund species may be lacking.

Many amphibians have generation times that are much shorter than those of birds and mammals, with some anurans maturing in as little as 6 months. Short generation times are characteristic of anurans in lowland tropical environments, i.e. those not commonly associated with enigmatic decline. Many amphibians may not breed until they are at least 5 years of age (Duellman and Trueb 1994), and for some species estimated generation lengths are up to 15 years (Liang et al. 2004). Generation length typically increases with altitude and latitude and is typically longer in salamanders than in anurans. As amphibian declines are positively associated with high elevation species living in streams, CBPs that focus on species with longer generation times will not exhibit the rapid build-up of captive populations suggested by Bloxam and Tonge (1995); over time these programmes may require more substantial investment. In other respects, these species may make better candidates for CBPs than short-lived species with rapid generation times, as longer generation lengths reduce the risk of genetic adaptation to captivity (Frankham 2008).

Hard wired behaviour

Amphibians are often considered hard wired both physiologically and behaviourally (Griffiths and Pavajeau 2008). Although limited research has been undertaken in this area, Crane and Mathis (2011) demonstrated successful pre-release training of salamanders, whereby larvae were taught to display appropriate anti-predator behaviour towards introduced rainbow trout. Moreover, learning has been shown to play a part in a range of behaviours across a number of amphibian species. These include foraging (Sontag et al. 2006), predator avoidance (Epp and Gabor 2008; Ferrari and Chivers 2008), territoriality (Dawson and Ryan 2012), maze learning (Brattstrom 1990) and visual discrimination (Jenkin and Laberge 2010). In some cases, social learning has been detected between species in mixed schools of tadpoles (Ferrari and Chivers 2008). This is not to say that amphibian behaviours are as learning-dependent as those of birds or mammals, but neither can they be said to be predominantly hard-wired. Learned components of behaviours may prove vital in preparing stock for successful release and may also, as demonstrated by Crane and Mathis (2011), represent opportunities to ameliorate the effects of threats in the wild. The additional resources required to cater to learned behaviours in amphibians must therefore be considered when planning CBPs (Michaels et al. 2014b).

Because learned behaviours appear to be more important for amphibians than previously thought, exposure to predators, competitors, parasitism and starvation prior to release may be important to ensure reintroduction success. As with other vertebrate taxa, this may directly trade off against the need to ensure high welfare standards for captive animals.

Easy to maintain and breed

Many threatened species have not been maintained in captivity prior to the decision to establish a CBP; determining appropriate husbandry and breeding techniques is therefore crucial to programme success. It has become apparent, however, that amphibians have complex and varied husbandry requirements and are not necessarily easy to maintain and breed (Browne et al. 2006; Antwis and Browne 2009; Verschooren et al. 2011; Ogilvy et al. 2012; Dugas et al. 2013; Antwis et al. 2014; Michaels et al. 2014a, c). Many species have failed to thrive (Norris 2007; Gagliardo et al. 2008) or breed in captivity (Birkett et al. 1999), while others have not bred reliably or in sufficient numbers to maintain genetically viable populations (Coloma and Almeida-Reinoso 2012). In an analysis of the efficacy of amphibian CBPs, just 55 % produced tadpoles, metamorphs or juveniles (Smith and Sutherland 2014). Tropical species in particular have proven difficult to maintain and breed in captivity, due to high levels of endemism (Collen et al. 2008) combined with a tendency towards high levels of environmental specificity and little or no husbandry experience or field data (Michaels et al. 2014a).

Poor captive breeding success may be related to inadequate nutrition, sub optimal health, failure to provide the correct environmental regime, habitat attributes and/or breeding triggers, difficulty in spawning and/or low survival rates from egg to early juvenile stages (Browne and Zippel 2007; Kouba et al. 2009). This is further complicated by the complex life cycles exhibited by many amphibian species, as different stages can have very different requirements. Most anuran larvae have never been reared in captivity and information on how to rear larvae is lacking in peer reviewed literature (Pryor 2014). Given the potential for husbandry to significantly affect fitness related characters in tadpoles (Martins et al. 2013; Michaels and Preziosi 2015), this can be a serious impediment to programme success.

In some cases, appropriate husbandry and breeding techniques for threatened species can be inferred from similar species or related taxa (Preece 1998). However, many amphibian species have unique dietary, microclimate, water quality and behavioural requirements or species-specific breeding triggers (Michaels et al. 2014a; Browne et al. 2007), and successfully breeding and rearing a closely related species does not guarantee success with the target species (K. Bradfield, pers. obs.). Providing these species with the appropriate captive conditions often involves a "trial and error" approach; this can substantially increase the time and resources required to determine whether the species is a suitable candidate for a CBP. Although this approach is being replaced with a more efficient evidence-based experimental approach (Michaels et al. 2014c, d; Tapley et al. 2014a), the resources required to develop suitable husbandry protocols may still be considerable.

Nutritional problems have been cited as a major barrier to the implementation of amphibian CBPs in general (Gagliardo et al. 2008; Antwis and Browne 2009; Pryor 2014; Tapley et al. 2015). The nutritional requirements of most amphibians are unknown, and will change with life stage for species with complex life cycles (Densmore and Green 2007). Even when the diet is known, it is often impossible to replicate in captivity, as captive diets are limited by the commercial availability of food species and the ability to establish breeding colonies of appropriate species, as well as difficulties in providing prey species themselves with suitable diets. This could have significant repercussions for CBPs. For example, five lineages of frogs are currently known to sequester alkaloids from their wild diets; alkaloids act as defences against predators and micro-organisms (Rodríguez et al. 2010). One such alkaloid, batrachotoxin, reduces over time in captive *Phyllobates terribilis* that were collected from the wild, and is totally lacking in captive bred frogs (Daly et al. 1980).

Recent research on carotenoids further illustrates the complexities of amphibian nutritional requirements and their potential importance to CBPs. Carotenoid supplementation has been shown to positively affect fecundity, larval development and skin pigmentation (Ogilvy and Preziosi 2011; Ogilvy et al. 2012; Dugas et al. 2013). Pigmentation is an important indicator of fitness in sexual communication and/or as an aposematic signal to potential predators (Robertson and Robertson 2008; Maan and Cummings 2012); captive bred animals that lack these signals may therefore be more vulnerable to predators or unable to effectively communicate with conspecifics after release. Carotenoid availability also affects the composition of bacterial colonies associated with amphibian skin (Antwis et al. 2014). Diverse bacterial colonies may offer protection against pathogens (Antwis et al. 2014), but captive environments can significantly alter the bacterial skin floras implicated in disease resistance (Loudon et al. 2013; Antwis et al. 2014; Michaels et al. 2014d); captive bred animals may therefore lack this protection.

Despite all of the potential issues, there have recently been several notable successes maintaining and breeding 'difficult' species (Gagliardo et al. 2010; Gawor et al. 2012; Igawa et al. 2013) and species whose wild habitats are difficult to recreate in captivity (Preininger et al. 2012). These successes are encouraging, but developing appropriate captive breeding protocols is not necessarily enough. As the ultimate goal of CBPs is to establish self-sustaining wild populations and/or successfully supplement existing populations, animals produced by CBPs must also be capable of surviving and breeding in the wild. CBPs should aim to replicate wild environments and conditions as closely as possible, as this will minimise the risk of producing animals not suited to wild conditions. Captive management should therefore be informed by field data and knowledge of the biology of the species (Michaels and Preziosi 2013; Michaels et al. 2014a). Replicating wild conditions also has the benefit of improving captive breeding success (Godfrey and Sanders 2004). When individuals are collected from one site to establish a CBP but captive bred individuals will be released at another site, efforts should be made to ensure that environmental conditions at the release site do not differ significantly from those at the collection site. If conditions vary significantly between sites, individuals should ideally be reared in conditions that replicate those of the release site. The moor frog (*Rana arvalis*), for example, exhibits a high degree of local adaptation to varying pH levels in breeding ponds across its large range (Räsänen et al. 2003a). The cost of mismatched adaptive traits and environmental pH is high (Andrén et al. 1989), therefore any conservation breeding initiative for this species would need to ensure that source and recipient habitats have similar pH values, or exploit the rapid evolutionary rate of this trait (Andrén et al. 1989; Räsänen et al. 2003a, b; Merilä et al. 2004) to allow captive populations to track changes in their eventual release sites. However, as little is currently known about the micro-climates utilised by most amphibian species in the wild (Michaels et al. 2014a), captive programmes may unwittingly produce captive bred stock that are not adapted to conditions at their release sites.

Whilst these issues are not unique to amphibians they are compounded by the paucity of research relevant to amphibian CBPs (Anderson et al. 2008; Browne et al. 2011), as most research has focused on mammals and birds (Anderson et al. 2008).

Applicability of reproductive technologies

The recent increase in the number of amphibian CBPs for species that have not previously been held in captivity and for which there is little knowledge of reproductive mechanisms has resulted in a "captive breeding crisis" (Kouba et al. 2009). Reproductive dysfunctions are common and are usually the result of poor nutrition, stress or the absence of environmental stimuli; while the first two causes can usually be corrected, the third is much more difficult to rectify (Kouba et al. 2012). Assisted Reproductive Techniques (ART) may reduce or eliminate common problems by ensuring that founder animals are not lost before they have reproduced, the maximum amount of genetic diversity is maintained in the captive population, and, when captive environments differ from wild ones, it is not only individuals that are either suited to the captive environment or will invest resources in mating in sub-optimal conditions that breed successfully. ART can also facilitate multiple paternity of clutches, the transfer of sperm between facilities rather than adults (Kouba et al. 2009), and selection for disease resistance (Clulow et al. 2012). Several CBPs already use ART; e.g. fertile clutches of the Extinct in the Wild *Anaxyrus baxteri* have only been produced using hormone treatment (Browne et al. 2006).

ART are not necessarily a quick fix; although hormone efficacy may be predicted by phylogeny (Silla and Roberts 2012), protocols are species-specific and can be difficult to determine for one or both sexes (Browne et al. 2008; Mann et al. 2010). Inappropriate hormone dosages can have adverse effects, even death (Michael et al. 2004). ART can allow husbandry practitioners to appear to achieve programme goals whilst masking underlying husbandry issues that prevent animals from breeding naturally. If individuals bred in captivity have reduced fitness or are of compromised health status, their survival post-release may be reduced and the chances of programme success decreased. ART also remove sexual selection, which could adversely affect CBP success given that sexual selection may increase offspring health and survival (Wedekind 2002). ART should therefore not be viewed as a panacea to overcome the limitations of captive husbandry (Maruska 1986), and additional research into the effects of ART on CBP success, as well as into the husbandry practices required to stimulate natural breeding, is required.

Cost effectiveness

Amphibian CBPs often do not require the same level of resourcing as programmes for mammalian and avian taxa due to relatively small space and low keeper time requirements. The biphasic life cycles of many species do, however, mean that additional costs will be incurred due to the need to provide specialist aquatic life support systems and associated monitoring equipment to ensure that water parameters are optimal and remain stable.

Hosting an amphibian CBP may be cost effective relative to other taxa, especially large bodied species (Balmford et al. 1996), but the cost of a properly established and managed amphibian CBP can still be substantial and, given the lower profile of most amphibian conservation projects, it may be difficult to raise sufficient funds. Moreover, the perceived cost effectiveness and publicity potential of amphibian CBPs may make them attractive to small institutions with limited capacity (Browne et al. 2011), but such institutions may lack veterinary and keeping capacity, as well as appropriate financial support, and be inherently unsuitable to host CBPs. A CBP also requires a considerable and often long-term commitment. Captive populations of the Kihansi spray toad (*Nectophrynoides asperginis*) were established at Bronx and Toledo Zoos in 2000 (Rija et al. 2011), but the first reintroductions did not occur until 2012; it is still not secure in the wild and the CBP continues 15 years later. In the Panama Amphibian Rescue and Conservation Project, 20 species were brought into captivity between 2001 and 2005 for reintroduction at an appropriate time in the future (Gagliardo et al. 2008); to date there have been no reintroductions. As the threats for many species are not currently reversible (and CBPs often focus on these species in particular), the necessary commitment may be indefinite and beyond the means of many organisations.

This is not to say that a CBP should not be established if sufficient funds for at least 10 years or more cannot be secured up front. Indeed, it can be very difficult to secure long-term funding before the potential value of a CBP to the conservation of the species is clear. A number of programmes have started with a relatively small commitment of funds initially, but have been able to generate the required funds to continue after demonstrating that the captive programme can contribute to conservation efforts (e.g. *Geocrinia* froglet programmes at Perth Zoo; K. Bradfield, pers. obs.). In cases where suitable, threat-free habitat is available and captive bred animals can be released into the wild in the short term, even a small number of releases may make a substantial contribution to the recovery of the species. In cases where release to the wild is the goal but this cannot occur in the short term due to the nature of the threats facing the species, keeping the species in captivity for only two or three years has no conservation value. It is therefore very important to acknowledge the longer-term and possibly indefinite duration of the CBP from the start, and ensure that sufficient funding in the medium to long term is at least a possibility. In these cases, it is also very important that efforts are made to secure the necessary longer term funding as soon as it is clear that the CBP is viable (e.g. F1 individuals have produced fertile eggs). If substantial funding cannot be secured at this point, the programme should be reassessed.

Conservation breeding and reintroductions can be successful

Griffiths and Pavajeau (2008) reviewed the success of amphibian captive breeding and head starting programmes; of the programmes that could be assessed, 62 % were highly successful, 24 % were partially successful and 14 % exhibited low success. In comparison, a review of the effectiveness of captive breeding and reintroductions for birds found that birds bred or showed normal behaviours in 30 % of programmes (Williams et al. 2012). While these figures suggest a relatively good level of success for amphibian CBPs, almost half of programmes reviewed focussed on wide ranging, temperate species that are tolerant of anthropogenically altered habitats and for which established husbandry protocols already existed. The majority of amphibian biodiversity and the largest proportion of species at risk of extinction are, however, found in the tropics; unfortunately there has been limited success to date with CBPs for tropical species (Michaels et al. 2014a). Knowledge of the captive husbandry requirements of tropical species is increasing, so success rates may improve in future.

Additionally, most of the programmes reviewed by Griffiths and Pavajeau (2008) dealt with species suffering local declines in parts of their range due to anthropogenic habitat loss or alteration. Given that the threats facing many species of global conservation interest are enigmatic or currently irreversible (e.g. disease) and occur across the entire distributional range, reintroduction will not be as straightforward with these species. The success rate documented by Griffiths and Pavajeau (2008) therefore cannot be used as an indication of the likelihood of success for many of the species most in need of conservation action.

Capacity exists in the zoo, aquarium and private sectors

In 2008, Zippel et al. determined that the maximum global capacity for viable conservation populations of threatened amphibian species was only 50 (Zippel and Mendelson 2008). While 101 species are currently listed by AArk as held in captivity for rescue or supplementation of wild populations and another 23 are listed as held for research relevant to conservation (note that the potential for long-term viability of each is not documented), the most recent estimate of the number of amphibian species in need of captive assurance colonies was 943 (Zippel et al. 2011). Even more alarmingly, this limited capacity does not exist in the countries where the majority of amphibian declines are taking place (Gagliardo et al. 2008; Edmonds et al. 2012). Initiatives in these countries are hindered by a lack of funds, a lack of trained personnel and a lack of organisation, i.e. a lack of capacity (Van Der Spuy and Krebs 2008).

Maintaining amphibians outside of their geographic range or in facilities with either non-sympatric species or sympatric species of unknown origin may expose individuals in CBPs to novel pathogens (Pessier and Mendelson 2010; Zippel et al. 2011). These could then be transferred to other species present at release sites, with potentially serious negative consequences (Cunningham et al. 2003). Chytridiomycosis was detected in *A. muletensis* on Mallorca, and the source was traced back to a captive breeding facility which had sent captive bred stock to the island for reintroduction (Walker et al. 2008). Although this was prior to the discovery of amphibian chytrid and no measures were in place to prevent disease transmission between species in the captive facility at that time, the risk exists any time a species is housed outside its geographic range and/or at an institution that also houses amphibian species from outside its range. Current recommended biosecurity measures serve to minimise the risk of animals acquiring novel pathogens but do not eliminate it, and the risk increases as the length of time a species is maintained in captivity increases. This is compounded by the fact that reliable ante-mortem screening techniques for many pathogens of concern (e.g. ranaviruses) are not currently available (St-Amour and Lesbarrères 2007). Conversely, native amphibians could be exposed to foreign pathogens from exotic species held in CBPs (Robertson and Robertson 2008). The risks of maintaining amphibians outside of their geographic distribution are therefore disproportionate to the potential gain, and the current recommendation is that rescue colonies are maintained as close to their natural range as possible (Gagliardo et al. 2008; Zippel et al. 2011). Maintaining amphibians within their current or former distributional range also facilitates the recreation of natural environmental cycles which may lead to greater breeding success, is often cost effective and instils pride and confidence in range country stake holders (Gagliardo et al. 2008; Edmonds et al. 2012). However, political instability and conflict may preclude the establishment of CBPs within the former distributional range of a species. For example, while 92 % of Haiti's diverse and largely endemic amphibian fauna is threatened, political instability in Haiti means that developing facilities in country is not feasible at present. In such situations, the risks associated with establishing out-of-range facilities must be weighed very carefully against the 'value' of the species, likely success of a CBP, and the potential to carry out the in situ work necessary to ensure suitable protected habitat is likely to be available to release animals into in future. Table 1 summarises the potential advantages and disadvantages of establishing CBPs within the geographic range of the species.

Existing ex situ capacity is often cited when justifying why CBPs are a suitable conservation option for amphibians, however this justification requires careful evaluation. There are a variety of potential institutions where CBPs can be hosted, the positive and negatives of each of these are summarised in Table 2.

The benefits of collaboration amongst different types of institutions and/or individuals are considerable. Together, these can provide specific knowledge, husbandry and species management skills, resources, research facilities and methods, long-term and short-term funding, and a direct use for animals not needed for the CBP (for exhibit or for research). Collaboration is key and partnerships between institutions/individuals can compensate for each of the disadvantages outlined in Tables 1 and 2.

Other considerations

Genetic and phenotypic adaptation to captivity

Animals in CBPs may adapt to captivity within one generation as a result of environmental effects on phenotypic traits. A number of aspects of the captive environment affect the fitness of amphibians (e.g. Ogilvy et al. 2012; Dugas et al. 2013; Antwis et al. 2014; Michaels et al. 2014c, d) and have the potential to negatively affect the success of both future captive reproduction and re-introduction attempts.

A species may become progressively more genetically adapted to captivity even when a comprehensive genetic management plan is in place (Snyder et al. 1996) as a result of different selection pressures acting in different environments. The high sensitivity and rapid environmentally linked mortality of young larvae, in particular, to their environment can lead to selection mediated mortality that can be very difficult to mitigate. Genetic adaptation to captivity increases exponentially with the number of generations bred in captivity (Frankham 2008), and so may be particularly rapid in species that exhibit the supposedly advantageous characteristic of short generation length. Loss of genetic diversity and adaptation to captive environments may reduce the ability of individuals produced in CBPs to respond to their natural environments. Tadpoles of *A. muletensis*, for example, maintained in captivity for more than eight generations exhibited a loss of genetic variation

Table 1 Potential advantages and disadvantages of hosting CBPs in situ

Advantage	Disadvantage
CBPs established within the geographic range of the target species	
Can be cost effective	Lack of capacity in some range states (husbandry and veterinary) including personnel and diagnostic capabilities May not be cost effective to develop dedicated facilities within range if there are already suitable facilities or zoos/aquariums with capacity within the same geographic region Even with significant investment it is unlikely that all range states will be able to develop dedicated facilities for CBPs due to a number of factors including political instability, high levels of risk associated with accessing and staffing facilities, etc. Potential difficulty in sourcing and maintaining specialist equipment (e.g. appropriate UV-B emitting lamps and life support systems) Facilities, infrastructure and resources may exist in range state but not within the geographic range of the species in question. Geographic range areas may be remote and so more prone to crime, instability, corruption, poor maintenance, difficulty acquiring necessary equipment and staff shortages
Programme may generate more interest if it involved a local species particularly if the species is culturally significant	May not generate interest and funds
Instil pride and confidence for in country stakeholders	Pride and confidence may not be enough to ensure that a CBP is established/viable in the long-term
Allows institutions already possessing amphibian husbandry capacity to focus on any threatened local species	Not all institutions with amphibian husbandry capacity have local native species that require CBPs Considerable investment has been made in developing CBPs outside geographic range of the target species; institutions/partners involved in such programmes may be unwilling to transfer them
Reducing the number of out-of-range colonies decreases the risk posed by these colonies to native amphibians in the host institutions locality/country Reduced risk of transfer of novel pathogens between individuals in CBP and wild amphibians in surrounding area	Proximity to in situ threats, such as disease
Easier to synchronise amphibians in facilities within their range with natural environmental parameters If there is a potential husbandry issue, CBP personnel can acquire relevant environmental data from the field with relative ease	Synchrony with external environment may still be problematic if amphibians are to be housed in dedicated indoor facilities in order to minimise disease risk

Table 1 continued

Advantage	Disadvantage
Increased possibility of meeting the nutritional requirements of amphibians in the CBP as live food may be harvested from the field (if appropriate; disease risk may prevent this) and/or founding stock for new breeding facilities may be collected from the field (again, if appropriate)	Only a small number of prey species may be suitable for mass production If feeder colonies are established using native species and commercially bred feeder invertebrates are not readily available, the collapse of feeder colonies could have serious repercussions
The CBP is fully integrated with other project components including public outreach and field work. This facilitates improved communication between all stakeholders involved in the conservation effort	
Environmentally friendly (e.g. smaller carbon footprint, waste water may not need to be disinfected with chemicals that may be harmful to the environment)	

and an associated decrease in an anti-predator defensive trait (Kraaijeveld-Smit et al. 2006).

Replicating all aspects of natural environments would avoid adaptation to artificial captive environments, but achieving this is very difficult for some aspects and impossible for others. Strategies to minimise genetic adaptation to captivity are therefore required. Minimising the number of generations that a species is kept in captivity, by reducing the length of time a species is held in captivity, increasing generation length or using cryopreservation, is the most effective (Frankham 2008; Williams and Hoffman 2009). Cryopreservation cannot be widely used at present as unique protocols need to be developed for each species (Williams and Hoffman 2009). Given that amphibians of many species can live and remain reproductively active for in excess of 10 years in captivity (Duellman and Trueb 1994) and the largest species of amphibian (i.e. ones that are often threatened by reversible threats such as hunting) are the longest lived (Guarino et al. 2014), increasing generational length is potentially a very useful strategy. However, the average lifespan in captivity is unknown for many species, and attempts to delay reproduction could result in the failure of CBPs due to unexpected senescence. Even for species whose generational length can be increased substantially, it still may not be sufficient to avoid adverse effects of genetic adaptation to captivity if the species needs to be kept in captivity for an extended period. Moreover, fecundity and offspring quality vary with age in a variety of animal species (e.g. Kern et al. 2001; Robertson and Rendell 2001). While animals may still be able to reproduce later in life, CBP co-ordinators may need to compromise between increased generation length and effects on fecundity and offspring quality.

Periodic importations from a wild population to augment the captive population also slows genetic adaptation to captivity (Frankham and Loebel 1992); modelling can be used to determine the appropriate number of individuals and frequency of imports. The quarantine space implications of importing new founders needs to be considered, and the ability to remove individuals from the wild in future may be limited or non-existent for species of greatest conservation concern. A programme fundamentally dependent on wild populations for its long term viability cannot be considered a true safety-net for a species.

Table 2 Potential advantages and disadvantages of different hosting institutions for CBPs

Advantage	Disadvantage
CBPs established in zoos and aquaria	
Staff usually maintain high standards of husbandry and have strong networks of experienced colleagues that can provide relevant advice	Potentially serious biosecurity issues; many zoos and aquariums hold large phylogenetically and geographically diverse collections acquired from a variety of sources and often at high densities. Risk of exposure to novel pathogens is therefore often high, although dedicated facilities, equipment and staff that are separate from 'general' collection species facilities, equipment and staff minimise this risk. Smaller institutions may not have the resources necessary to establish and maintain the required biosecurity measures, however
Usually good facilities, often able to establish high security facilities when necessary	Zoo finances are often directly linked to the national economy and this could potentially undermine long term commitment to CBPs due to their cost (for programs being partially or fully funded by the institution itself)
	The costs associated with establishing and running dedicated facilities with dedicated staff can be considerably higher in the countries where zoo and aquarium capacity is currently concentrated than in range states
Usually good access to veterinary care/on site veterinary care	Institutions without sufficient internal capacity may commit to CBPs due to the push for zoos and aquariums to become involved in ex situ initiatives for amphibians and their apparent suitability for them
Usually well regulated and have access to a wealth of professional experience and tried and tested husbandry and breeding guidelines	Not all zoos and aquaria are members of regional standard setting organisations (e.g. EAZA, BIAZA, AZA, ZAA), although this can be overcome by requiring that participants in CBPs are accredited members of their regional association where one exists
Potential to conduct/contribute to conservation-related research	Potential ethical issues associated with breeding animals for particular research projects (e.g. disease trials)
Good for capacity building	Potentially high staff turn over; at least partially offset by larger work force
Good for education and awareness raising	
Staff experienced in managing populations, members of regional associations also have access to management guidelines and professional support as required	Currently, the majority of captive populations of both common and threatened amphibians are not formally managed despite the capacity to do this
CBPs established in museums and academic institutions	
Not usually home to large diverse collections, able to focus on specific projects	Staff may lack husbandry skills
Usually good facilities	Potentially limited access to veterinary care
Well suited to research	Often have high staff turn over for husbandry level positions

Table 2 continued

Advantage	Disadvantage
Good for education and awareness raising (museums) Good for capacity building	Academic funding generally revolves around short-term research projects; may be unable to guarantee longevity for a CBP. Non-academic government funding typically poor and may not cover the development of appropriate facilities
CBPs established in private sector	
Often very good husbandry skills and can serve as training institutions	Potentially serious biosecurity issues; with large phylogenetically and geographically diverse collections acquired from a variety of sources, and often at high density
Able to dedicate a lot of time to focus on specific aspects of husbandry	Difficult to regulate
No staff turn over	Reliance on only one person/small number of people; potential for personal circumstances to abruptly reduce or eliminate capacity (e.g. job loss, illness, death) Often limited participation in capacity building initiatives Limited scope for education and awareness raising

Equalisation of families at each generation can substantially reduce adaptation to captivity, although it may not significantly increase reproductive fitness in the wild (Frankham et al. 2000). This may be because employing single pair or single male—multiple female matings favours the evolution of co-operative behaviours (in both genders or in males, respectively) that are disadvantageous under competitive (i.e. wild) conditions (e.g. Holland and Rice 1999).

Lastly, managing a population as several smaller, reproductively isolated units that are combined to produce animals for reintroduction reduces genetic adaptation to captivity. This strategy also retains greater genetic diversity at the species level and generates higher reproductive fitness under competitive conditions than maintaining a single large population (Margan et al. 1998). Many amphibian CBPs involve only a single institution, however, and it may be difficult to change this given the need for dedicated single-species facilities for CBPs and the costs associated with establishing multiple such facilities. A single large population at one institution could, however, be managed as several smaller units with relatively few, if any, additional resources.

When a CBP will run for the foreseeable future, it is critical that the ability to minimise genetic adaptation is considered from the outset, and appropriate strategies are put in place. Not only can failure to do so affect the suitability of captive bred stock for release, but it can also lead to the dilution of fitness in wild populations if animals adapted to captive conditions are used to augment surviving wild populations (Ford 2002; Araki et al. 2009). The continued ability to minimise adaptation to captivity should be assessed regularly; although it may initially be possible to transfer *x* individuals of a species into the captive population from the wild every *y* years, this could change over time, adversely affecting the ability to minimise genetic adaptation to captivity if that was the primary strategy. In reality, however, CBPs rarely if ever consider the risk of genetic adaptation to captivity or employ any strategy to monitor or prevent it (Williams and Hoffman 2009); the phenomenon is not mentioned by the ACAP (Gascon et al. 2007). Moreover, flawed studbooks and population management models for captive amphibians mean that minimising adaptation to captivity is often difficult (Witzenberger and Hochkirch 2011).

Cultural significance

The potential impact of the cultural and/or socio-economic importance of a species on the success of an amphibian conservation programme, including a CBP, should not be underestimated. *Leptodactylus fallax* is of cultural importance to the people of Dominica and Montserrat (Tapley et al. 2014b). The frog was the national dish in Dominica and is emblematic, featuring on the nation's coat of arms (Tapley et al. 2014b). This cultural prominence, driven by its value as a food source, has greatly benefitted conservation efforts for the species and there is a significant national support base for the programme. Other flagship amphibian species include *Ambystoma mexicanum*. In Mexico, the species has been utilised as a food source, associated as a twin of the Aztec God Quetzalcoatl and has been an inspiration for philosophers and writers (Valiente et al. 2010). The first amphibian flagship conservation programme was successfully launched, in part, due to the cultural significance of the species (Bride et al. 2008). *Andrias japonicus* is celebrated during the annual Hanzaki festival (B Tapley, pers. obs.), it is embedded within Japanese folklore and a small ecotourism market has developed. A number of grass root community conservation organisations have been formed to protect local populations of *A. japonicas* and the associated habitat and breeding sites (Kawata 2008). The iconic status and cultural significance of amphibians is therefore an important factor to consider in the development of conservation initiatives.

Discussion

Amphibian CBPs can be successful and will be a viable option for conserving many species. However, despite commonly held perceptions (e.g. Bloxam and Tonge 1995; Bowkett 2009; Browne et al. 2011; Smith and Sutherland 2014) they are not universally appropriate for all amphibian species and promoting these generalisations, even inadvertently, could create unrealistic expectations and facilitate establishing CBPs for species that are not ideal candidates for such programmes. Given how limited conservation funding is, generalisations promoting amphibians as universally ideal candidates for CBPs could divert funding away from the CBPs that have greater chances of success.

It is clear that many threatened amphibian species fail to meet the criteria that are frequently cited as reasons why amphibians are highly suitable for CBPs. In some cases, these issues have the potential to undermine the success of CBPs and the status of any wild populations captive bred animals are used to supplement. In other cases, these issues do not necessarily threaten programme success as long as they are dealt with appropriately. In yet other cases, these issues are not necessarily the problems that they appear to be at first glance; fast growth rates and short generation times are not necessarily advantageous, for example, particularly when genetic diversity needs to be maintained and adaptation to captivity avoided in long-term programmes. The perception that amphibians are generally suitable candidates for captive programmes due to common characteristics of the class is therefore inappropriate. We therefore strongly recommend that species that have been assessed as high priorities for ex situ conservation action are subsequently assessed on an individual basis to determine their suitability for inclusion in a CBP.

Reintroduction success declines as the time between capture and subsequent release increases (Balmford et al. 1996). In addition to focussing on species that can be successfully maintained and bred in captivity and where CBPs can produce animals suitable for release to the wild, CBPs should also focus on species whose threats can potentially be ameliorated in the short to medium term. This greatly minimises the issues associated with maintaining multiple generations in captivity. These programmes can have clearly defined, realistic goals (e.g. reintroduction, supplementation or translocation of *x* individuals to *y* sites over *z* years), criteria for evaluating success and exit strategies. As a general rule, we should not continue to direct limited funds and resources towards CBPs with no foreseeable end point, particularly when there are alternatives with fewer risks and higher probabilities of success (i.e. species whose primary threats could be addressed relatively quickly, such as over-hunting, habitat destruction or invasive species). We acknowledge that this position is likely to be contentious, as many species are designated as high priorities for ex situ management due to their likely extinction in the wild as a result of threats which cannot currently be mitigated (e.g. amphibian chytridiomycosis). As previously noted, however, the number of species requiring ex situ management greatly exceeds current capacity. Given this, and the fact that amphibian species are not all equal in their suitability for CBPs, we are advocating that imminent danger of extinction in the absence of ex situ action should not, on its own, be viewed as a valid reason to establish a CBP. Rather, acknowledging the potential loss of the species in the wild should be the trigger to critically assess the likelihood that a CBP will successfully contribute to conservation efforts, with reference to the probable duration of the programme, characteristics of the species in question, suitability of the proposed facilities or host institution/s and risks involved. This may help to avoid the misdirection of resources to CBPs for species with little chance of a successful outcome and away from those that are likely to be successful.

We recognise that, in some situations, the establishment of a CBP may be viewed as warranted even though releases will not be possible for the foreseeable future (e.g. when a species is deemed to be of exceptionally high evolutionary, ecological or cultural value, or if an institution has strong links to a particular species or country, or if the species can also be used for conservation education or conservation research purposes). In these situations, it is essential that a detailed plan to properly manage populations using realistic modelling is developed and that evidence based husbandry protocols are established as quickly as possible, ideally before founders are collected. The required on-going funding also needs to be secured as soon as it is clear that the CBP is viable. Clear objectives and regular, critical review are necessary during all phases of any CBP, but are particularly important in programmes of indefinite duration; if a programme is not meeting its goals, the chances of rectifying this should be assessed and resources redirected if the likelihood of success is deemed to be low.

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