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The importance of natural history and species-specific approaches in amphibian *ex-situ* conservation

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Due to the importance of *ex-situ* components of the response to the on-going amphibian extinction crisis, the numbers of captive amphibian species and populations is growing. However, *ex-situ* projects are currently often poorly supported by knowledge of the captive husbandry requirements of individual amphibian species, many of which are being taken into captivity for the first time. Natural history data and measurements of wild environmental parameters are critical in designing appropriate captive environments, but are absent for the majority of species held in captivity. This has resulted in the failure of some *ex-situ* projects and is likely to affect many future initiatives. Publication biases away from natural history and amphibian-specific research, the inaccessibility of data in academic literature for conservation institutions and lack of time for preparative surveys before 'rescue' attempts are largely responsible for this data deficit. In many cases, conservation groups must collect their own data where existing information is insufficient. We suggest important parameters to record in the field and discuss the importance of considering the microclimates in which wild amphibians live when determining the methodology of recording parameters. Furthermore, we highlight the important role that public databases should fulfil to store and disseminate data. All in all, this perspective piece demonstrates the need for natural history data and outlines a road map for their efficient collection and for their practical integration into conservation programmes.

Key words: Amphibian, captive breeding, captive husbandry, environmental parameters, ex-situ, natural history

Natural history data can be the key to ex-situ conservation

A mphibian captive husbandry has become increasingly important in academic and conservation arenas in recent years. The focus of this review is the recent development of *ex-situ* conservation programmes for endangered amphibians in response to growing, widespread and catastrophic threats to and extinction of species in the wild (Gascon et al., 2007), as well as the growing prominence of amphibians in zoo and aquarium collections and in research laboratories.

A number of amphibian captive breeding and reintroduction events have met with some degree of success (Griffiths & Pavajeau, 2008) and are an important component of amphibian conservation (Gascon et al., 2005). However, reintroduction successes (and, in fact, all attempts at reintroduction) have largely been limited to generalist species in temperate or sub-tropical zones, which are tolerant of disturbance and a broad range of environmental conditions and are well known in terms of species biology and natural history (Griffiths & Pavajeau, 2008). Many ongoing and planned ex-situ projects, however, focus by necessity on species from the tropics, which are disproportionately data deficient (Collen et al., 2008) and include a higher degree of endemism and often associated environmental specialisation. As such, it is doubtful that Griffiths & Pavajeaus's (2008) figure of roughly one third success rate will be reflected in projects working with poorly known species, for which reintroductions have not yet taken place. During the initial phases of population foundation and captive breeding, these projects often suffer problems with basic captive husbandry protocols, although reports of these failures are rarely published. This may compromise programmes through a failure to sustain captive populations in the long term, before reintroductions are ever attempted. Problems with captive husbandry may include failure to keep founder animals alive in the short term (e.g., Gagliardo et al., 2008; Coloma & Almeida-Reinoso, 2012), long-term deterioration in the health of founder animals and associated failure to breed (e.g., development of Metabolic Bone Disease, MBD in captive Leiopelma spp. (Shaw et al., 2012) and Leptodactylus fallax (King et al., 2011)), long-term maintenance of relatively healthy animals with failure to breed (Gagliardo et al., 2008) or failure to keep larvae and young animals alive (Gagliardo et al., 2008). Indeed, Amphibian Ark (2013), the international body coordinating the organisation of the global ex-situ amphibian conservation effort, reports that only 55 of the 105 species held for conservation breeding (combining duplicate species populations and ignoring programmes starting in 2012 or later, which are unlikely to have had time to reproduce animals beyond the F1 generation) have been successfully bred and that even fewer (19 species) have been reproduced to the F2 generation or beyond. In some cases (e.g., Gagliardo et al., 2008), the production of F1 animals has been accidental and linked to the collection of wild animals primed for breeding and maintained in in-range areas where they were incidentally exposed to natural environmental stimuli, while in others reproduction has only occurred through the use of hormone treatments (Coloma & Almeida-Reinoso, 2012). This is clearly a major issue for ex-situ projects if they are to maintain viable, long-term populations in captivity and, ultimately, save species in the wild. The El Valle Amphibian Conservation Centre (EVACC) in Panama, which has provided the only peerreviewed report of failure in a conservation breeding programme, is a case in point. A number of species proved impossible to keep alive, others impossible to breed over a 3–7 year period and a number of breeding events in other species were accidental and could not be described as controlled or planned (Gagliardo et al., 2008). The issues with captive breeding at EVACC are not unique, although accounts of problems in other programs are not frequently reported.

Problems in captive husbandry and breeding can usually be traced back to gaps in the fundamental understanding of species natural history. Lack of funds or other causes may in some cases contribute by cutting projects short, but some projects listed in the Amphibian Ark (2013) records have run for 10 years (mean=5.3 years) without production of F1 animals and 14 years (mean=5.9 years) without production of F2 animals. This suggests that simple access to funds is unlikely to be a major causative factor. In most cases, when captive husbandry is based on an understanding of the wild habitat of a given amphibian species, animals thrive and breeding occurs readily. Captive enclosures can be designed to replicate wild environmental parameters, in order to maintain animals in good health for the long term, and changes in these parameters that are associated with reproductive events can be simulated to induce breeding. Godfrey & Sanders (2004), for example, found that mimicking water hardness parameters of the African Rift Lakes improved the oocyte quality and viability in captive clawed frogs (Xenopus laevis). Similarly, Tapley & Acosta-Galviz (2010) collected field data from the wild habitat of the caecilian Typhlonectes natans in Colombia. This allowed for a reassessment and modification of captive husbandry protocols at Durrell Wildlife Park, using water formulated to replicate wild measurements instead of local well water, which was shortly followed by increased health and the first captive reproduction of this species in that institution (pers. comm. B. Tapley, ZSL London Zoo, UK). In contrast, where species knowledge is poor, disaster or delay are likely to follow, as seen in the examples above.

Even when captive breeding is successful, conditions may differ from the wild in such a way that populations genetically adapt to captivity in response to relaxed or novel selection pressures (Frankham, 2008). This can lead to captive populations that are less fit in the wild than wild populations and to reintroduced animals that may fail to persist or, if wild animals still exist, may dilute the fitness of wild populations (McGinnity et al., 2003). This

phenomenon is well documented in salmonid fish farmed for reintroduction (Fleming et al., 2000; Heath et al., 2003; McGinnity et al., 2003) and was detected in captive bred Mallorcan midwife toads (Alytes muletensis), the tadpoles of which showed reduced genetic variation and failed to respond appropriately to predators after 8-12 generations in captivity (Kraaijeveld-Smit et al., 2006). Although this species was successfully reintroduced to Mallorca, had the project required a longer period of captive breeding, animals may no longer have been fit enough to re-establish wild populations. Despite the recommended use of studbooks to maintain genetic diversity and avoid changes in allele frequency, they may fail due to unrealistic model assumptions (Harrington et al., 2013; Caro & Sherman, 2013) or due to nonrandom survivorship in larvae and metamorphs, which are generally not individually registered in studbooks for highly fecund species that produce hundreds or thousands of offspring. Maintaining captive conditions closer to natural habitats will go some way towards avoiding changes in selection pressures in the first place, even if breeding programmes are not entirely able to control changes in allele frequency when they do happen.

Environmental parameters that differ from wild habitats may also impact the fitness of captive bred offspring through epigenetic effects. Environmental conditions may cause parents, particularly mothers, to influence the phenotypic fitness of offspring independent of genotype (Mousseau & Fox, 1998; Marshall & Uller, 2007). These effects have been documented in amphibians in relation to environmental parameters (including Pakkasmaa et al., 2003; Kaplan, 1987; Parichy & Kaplan, 1992; Räsänen et al., 2003b; Kaplan & Philips, 2006) and so may be an underestimated influence on ex-situ success. Although these effects could potentially improve the fitness of captive animals, for example by allowing well-fed animals to improve reproductive success (e.g., see Izquierdo et al., 2001 for a discussion in fish), it is unlikely that they will be well-understood or controlled. Crucially, captive breeding programmes should generally aim to keep animals as phenotypically similar to wild populations as possible and so should avoid changes in fitness, whether they appear positive or negative in captivity. Matching captive parameters to wild conditions will help to forestall any potential issues arising from genetic or epigenetic trans-generational inherited effects on fitness due to inappropriate captive conditions.

Genetic and epigenetic effects may occur simultaneously to drive adaptation in amphibian populations. In the moor frog (*Rana arvalis*), for example, the pH of breeding pond water affects the viability and development of embryos and tadpoles and populations rapidly adapt to local conditions through both genetic adaptation and maternal effects (Merilä et al., 2004; Andrén et al., 1989; Räsänen et al., 2003a,b). These changes occur over a relatively small number of generations (fifteen, Andrén et al., 1989), meaning that should this species be reliant on captive breeding, there is the strong possibility of producing captive bred populations adapted to pH optima different from the

Table 1. Suggested, but not exhaustive, habitat parameters to measure in the field, related to their importance to captive husbandry and breeding in captivity using evidence from the field and, where possible, from captivity.

Data Type	Specific parameters	Relevance to captive husbandry and breeding		
Environmental Pa	rameters			
Temperature	water, substrate, air	Critical for keeping animals alive (e.g. Bogaerts, 2004) and for providing thermoregulation opportunities. Affects development (e.g. captive Tylototriton wenxianensis; Gong & Mu, 2008) Seasonally dependent optima, thresholds and changes determine breeding events in many specie (Blankenhorn, 1972; Obert, 1975; Schneider, 1977; Semlitsch, 1985; Reading, 1998; Oseen & Wassersug, 2002; Wong et al., 2004; Miwa, 2007). Circannual variation is important for survival and lifetime reproductive fitness, via body size (Jørgensen, 1986).		
Substrate parameters	moisture content	Affects nest-site choice (Marangio & Anderson, 1979) and dwelling-substrate preference, with changes throughout the year (Kupfer et al., 2005).		
	рH	Affects substrate preference and nest-site choice (Wyman & Hawksley-Lescault, 1987; Horne & Dunson, 1994; Kupfer et al., 2005).		
	composition	Caecilians choose particular soil composition microclimates at different points in the reproductive cycle (Kupfer et al., 2005) and prefer certain compaction indices for making burrows (Ducey et al., 1993). Similarity to wild habitat affects growth and preference (Walsh & Downie, 2005).		
Water quality	pН	Affects development and survivorship (Pough & Wilson, 1977; Freda & Dunson, 1985; Le al., 1986; Freda, 1986; Andrén et al., 1989; Räsänen et al., 2003a;b; Merilä et al., 2004), b site choice (Strijbosch, 1979; Banks & Beebee, 1987). A drop in pH has been associated with reproductive events in the caecilian Typhlonectes natans (Parkinson, 2004).		
	nitrite, nitrate,	Nitrite and nitrate levels affect larval development and survivorship (e.g. Marco et al., 1999; Marco & Blaustein, 1999) and breeding sites are often partially defined by nitrate/nitrite content associated degree of eutrophy or oligotrophy (Strijbosch, 1979; Lindquist & Hetherington, 1998)		
	tannin and organic acid content	High levels important in survival in species living or breeding in certain habitats (e.g. treeholes of brazil-nut pods), (Tapley, 2009a) and in female oviposition site choice (Caldwell & Araújo, 1998)		
	hardness	Affects oocyte quality and viability (Godfrey & Sanders, 2004), mediate toxicity effects in larvae (Horne & Dunson, 1995) and cause calcified lesions in the skin of aquatic caecilians (Parkinson, 2004, Tapley, 2009b; Tapley & Acosta-Galviz, 2010).		
	oxygen content	Important, particularly for stream-breeding species (Lindquist & Hetherington, 1998). Influences embryonic development and larval growth (e.g. Seymour et al., 2000; Noland & Ultsch, 1981, and optima vary between species depending on breeding microclimate (Noland & Ultsch, 1981) Maintaining high oxygen saturation is an important principle in mass-rearing of plethodontic salamander eggs (Bernardo & Arnold, 1999).		
	flow rate	Preferences for lentic or lotic breeding systems, but within lotic sites, relative flow-rate can determine species distribution and potentially fitness (Odendaal et al., 1982; Baumgartner et al., 1999) and has been demonstrated in captivity in Eurycea nana (Fries, 2002).		
Light exposure	UV-B exposure	Beneficial for normal growth in some species (Verschooren et al., 2011) and corrects severe metabolic bone disease in others (Shaw et al., 2012). Conversely, excessive levels of radiation may be detrimenta to amphibians (e.g. Blaustein et al., 1995; Blaustein et al., 2003).		
	visible light; spectra and intensity	Available spectra important for identification of appropriate mates (Summers et al., 1999). Artificia light intensity affects breeding behaviour (Baker & Richardson, 2006) and mate choice (Rand et al. 1997). Moonlight intensity important in breeding events of some species (reviewed Grant et al., 2009) Seasonal changes in intensity can trigger reproduction in some amphibian species (Schneider, 1977)		
Meteorological parameters	barometric pressure and precipitation	Drops in barometric pressure are part of reproductive triggers in many species (Blankenhorn, 1972, FitzGerald & Bider, 1974; Obert, 1976; Henzi et al., 1995; Loredo et al., 1996; Oseen & Wassersug, 2002). Precipitation is also an important trigger, and is necessarily associated with low barometric pressure (Blankenhorn, 1972; Woolbright, 1985; Banks & Beebee, 1986; Gascon, 1991; Loredo et al. 1996; Tapley, 2009; Williams et al., 2009).		
Behavioural Data	specific reproductive behaviour	Behaviours involving materials that must be provided in captivity for successful reproduction, such as foldable leaves for breeding Phyllomedusa (Fenolio, 1996).		
	dietary composition and quantity	Nutritional profile affects mate choice and reproductive success (e.g. carotenoid content; Ogilvy et al., 2012). Quantity may influence reproductive success and frequency in captivity (e.g. in Typhlonectes compressicauda, Exbrayat & Delsol, 1984; Hemidactylium scutatum; Harris & Ludwig, 2004).		
	call recordings	Calls of male conspecifics stimulate breeding activity in male anurans and in attracting females to the breeding site (Bragg, 1940; Jones & Brattstrom, 1962; Brooke et al., 2000; Wong et al., 2004)		
	social interactions	Territoriality and other social interaction may influence breeding behaviour and welfare in captivity (reviews include Jaeger & Forester, 1993 (plethodontid salamanders) and Bee et al., 2012 (anurans))		
Morphometric Da	ita morphological adaptations can imply requirements through function.	Mouthpart morphology can predict specific ecological and feeding requirements of larval anurans (McDiarmid & Altig, 1999).		

wild, unless captive conditions are deliberately matched to field conditions. This phenomenon may be used to produce amphibians that are adapted to wild habitats that have undergone climate change, acidification or other alterations, allowing captive populations to track changes in the wild habitats to which they will eventually be released.

Aside from impacts on ex-situ projects, a lack of knowledge of optimal environmental parameters for captive amphibians may also impact experimental work using these organisms in the laboratory. Suboptimal environmental conditions can lead to behavioural and physiological changes in a 'stress response' that may influence the outcome of experiments, including alterations to behaviour, physiology, development, immune response and metamorphosis (Rollins-Smith, 1998; 2001; Denver, 1997b). For example, tadpoles maintained under stressful conditions are likely to metamorphose at sub-optimal sizes (e.g., Denver, 1997a,b; Denver et al., 1998), which can lead to a reduction in immune performance at metamorphosis (Rollins-Smith et al., 1988; Rollins-Smith, 1998). Longterm stress from inappropriate captive conditions can also depress the immune system in adult amphibians, leaving them open to lethal levels of infestation by parasites and pathogens (e.g., Pasmans, 2008). Research

into amphibian emerging diseases and other factors directly influences conservation policy and inaccuracies in results due to improper captive husbandry should not be overlooked or dismissed.

Natural history data are deficient or inacessible

Despite the fact that natural history data can be critical to the success of conservation breeding initiatives and the establishment of self-sustainable captive populations, there is a clear deficit of knowledge, particularly with regards to many species in need of *ex-situ* interventions. Twenty-five percent of amphibian species are listed as Data Deficient by the IUCN (IUCN, 2013), many of which are probably in need of urgent conservation intervention (Stuart et al., 2004). The reason for this gap is a combination of publication biases and practicality.

Although best practice would be to collect all necessary data from the wild before captive populations are established, the rapid development of threats in the wild may precipitate rescue operations before surveys can be completed. Just such a problem faced the EVACC initiative (Gagliardo et al., 2008) and other similar operations. This situation highlights the importance of sampling from wild habitats of potential *ex-situ* conservation targets well in advance of catastrophic events.

Table 2. Number of hits from different search term combinations in Google Scholar and ISI Web of Knowledge (version 5.12). Terms in the first column were combined individually with terms in the second column (using the AND command in ISI Web of Knowledge and the 'with <u>all</u> the words' advanced search function in Google Scholar) and search parameters set to return hits only containing both words in the title of the article. Citations and non-peer-reviewed hits were excluded. Instances where search terms were found out of context (e.g. 'Museum of <u>Natural History'</u>) or where phrases were disconnected were manually excluded. Search terms hits were grouped together by the taxonomic group to which they refer, because the number of hits was so low for most search term combinations. Searches were made on 27/11/2013.

		Numb	Number of Hits		
Search Term(s) 1	Search Term(s) 2	Google Scholar	ISI Web of Knowledge		
Amphibian		1	1		
Anura/anuran/frog/toad	environmental parameters	3	3		
Caudata/salamander/newt		0	0		
Gymnophiona/caecilian		0	0		
Amphibian		0	1		
Anura/anuran/frog/toad	habitat characteri(s/z)ation	1	1		
Caudata/salamander/newt		0	0		
Gymnophiona/caecilian		0	0		
Amphibian		0	2		
Anura/anuran/frog/toad	microclimate(s)	0	3		
Caudata/salamander/newt	microcimate(s)	2	2		
Gymnophiona/caecilian		0	0		
Amphibian		11	13		
Anura/anuran/frog/toad	microhabitat(s)	45	67		
Caudata/salamander/newt	micronabitat(s)	12	32		
Gymnophiona/caecilian		2	2		
Amphibian		4	13		
Anura/anuran/frog/toad	and well blob and	72 ¹	116 ²		
Caudata/salamander/newt	natural history	15	23		
Gymnophiona/caecilian		0	2		
Amphibian		1	2		
Anura/anuran/frog/toad	halitet og forsende	9	14		
Caudata/salamander/newt	habitat requirements	2	4		
Gymnophiona/caecilian		0	0		

¹11 hits from single work published in parts (Bragg, Observations on the ecology and natural history of Anura)

²14 hits from single work published in parts (Okuno, Studies on the *natural history* of the Japanese toad, *Bufo japonicus japonicas*)

Table 3. Mean and modal number of parameters listed in Table 1 reported in papers and number of papers using any keywords relevant to natural history data or describing specific variables. Keywords pertaining to macrohabitats were not deemed relevant. Literature surveyed consisted of papers acquired as part of the Habidata database project, see Online Appendix 1 for full citation list. Systematic sampling was impossible by definition, as many articles do not advertise natural history data content as part of the title or keywords. Where articles did not have key words (22), we generated key words from the title of the article.

Taxon	Number of parameters reported		Num		
	Mean (SD)	Mode	relevant keyword 3	specific parameter keyword	Total surveyed
Anura	3.4 (2.3)	3	7	9	37
Caudata	3.5 (2.3)	1	2	1	11
Gymnophiona	4.9 (1.7)	7	2	0	10
All combined	3.6 (2.3)	1	11	10	58

³ Complete list of keywords deemed relevant: Microclimate, Habitat requirements, Natural history, Environmental parameters. All relevant keywords found were included.

Conservationists lacking the time to conduct their own surveys are likely to find that there are few or no data already in existence, particularly in the academic literature. Conservation research is disproportionately focused on mammalian and avian taxa and on conceptual and theoretical questions, rather than species-specific observations, such that there are disproportionally few studies on herptiles and a disproportional number of those are concerned with theoretical questions, rather than descriptive work (Griffiths & Pavajeau, 2008; Griffiths & Dos Santos, 2012; Smith et al., 2009; Bonnet et al., 2002). Publication bias ultimately influences research funding through its impact on the bibliometric indices of individual researchers and so introduces a disincentive to carry out useful, though unfashionable, sampling of wild amphibian habitats. While we do not suggest that theoretical questions and research concerning mammals and birds (which are the beneficiaries of research skew; see above) are unimportant, this bias leaves little scope for species specific research, particularly in herpetofauna. Within research published on amphibians, only a very small proportion focuses on areas relevant to the collection of wild environmental parameters, including 'diet', 'reproduction' and 'husbandry/aquaculture' (Browne et al., 2011).

Although natural history data are published in academic journals (e.g., Kupfer et al., 2005; Phimmachak et al., 2012; Bernardes et al., 2013), the evidence suggests that the academic sector provides research that is, on average, less useful to frontline conservation efforts than either NGOs or Government agencies (Smith et al., 2009). We searched two major scientific search engines (Google Scholar and ISI Web of Knowledge v.5.12) using search terms pertinent to amphibian natural history data and found only a handful of hits, with a large degree of overlap, that expressly advertised that they focussed on environmental parameters and natural history in the title (see Table 2 for detailed results and methods). This highlights the difficulty of identifying this sort of information in articles, as authors simply do not advertise the fact that their work contains this data. In many cases, this is because data are collected and presented to address specific hypotheses in other research topics, rather than simply to characterise

habitats. This means that the fact that papers contain relevant environmental data is not flagged up in titles or keywords and that therefore articles cannot be identified by using search terms pertinent to natural history. Indeed, in a survey of a library of papers identified through the Habidata project (see below) as containing microhabitat environmental data, only around 1 in 5 used keywords that would allow searches for natural history to find them and a similar proportion flagged up specific parameters in their keywords (see Table 3 for results and methods). The large majority of papers used keywords relevant to the topic of the hypothesis, including population biology, taxonomy, physiology, development, ecology and conservation. This framework means that only a small number of variables are typically reported, which do not provide comprehensive enough information for the development of captive husbandry protocols; rather, they are intended to address a particular, narrow hypothesis to which other parameters are irrelevant. In the analysis of the Habidata library, the modal number of parameters reported was 1 (mean=3.6), although papers on caecilians reported more parameters (mode=7; mean=4.9) in comparison with caudate and anuran amphibians, largely due to contributions by G.J. Measey, who has tended to collect a large number of parameters from his field sites. Papers from this library that did use keywords pertinent to natural history contained similar numbers of parameters as those that did not for Anurans and Caudates (means 2.85 vs. 3.4 for Anurans and 4.5 vs. 3.5 for Caudates, respectively), but contained many more for caecilians (mean 7 vs. 4.9, respectively). Overall, this suggests that there is a need for authors to measure more parameters, whether they choose to advertise them or not. Where multiple parameters were reported, they were typically linked and often gained through a single piece of equipment; multiple water chemistry parameters was the most salient example.

A case in point here is the golden mantella (*Mantella aurantiaca*), a species that is the focus of captive breeding efforts and relatively extensive field sampling, but for which there are very few published data concerning wild habitats. Randrianavelona et al. (2010) sampled *M. aurantiaca* habitat, but present only the mean and range of one variable useful for captive husbandry, pH

of breeding ponds, as other parameters were not part of their species distribution hypothesis. Frustratingly, the authors report the collection of habitat temperatures, but do not present the data as it does not fit their model.

In the likely event that data are not already available for a conservation target species, the most obvious route for institutions to obtain the data required for successful, well-planned captive management is to arrange collection themselves. In the following sections we suggest ways of improving the efficiency of collection and dissemination of data, with the ultimate goal of improving the success of *ex-situ* conservation projects.

Field collection of data and the importance of considering microclimates

Table 1 contains the most important parameters to collect when characterising the habitat of a particular amphibian species, the majority of which can be measured rapidly using inexpensive equipment, and maps them to specific instances where they have been found to be important for survival or reproduction in captivity and/or the field. As many parameters should be measured as possible, along with key contextual information, including date and time, weather conditions, developmental stage and behavioural context (basking, breeding, feeding, hiding etc.). Physical and chemical parameters of the environment are of the highest priority, as these can rapidly affect the physiology of amphibians and can even constrain species fine-scale distribution in the wild (e.g., Freda & Dunson, 1986; Wyman & Hawksley-Lescault, 1987; Wyman, 1988).

Many of the variables listed in Table 1 could in theory be found for a given region using maps or meteorological records. However, amphibians are highly dependent on microhabitats and microclimates within the broad habitat in which they live. Microhabitats can strongly constrain distribution of a species within a macrohabit (e.g., Wyman & Hawksley-Lescault, 1987) and may be critical for survival in potentially lethal ambient conditions (e.g., Kluber et al., 2009). Amphibians use microclimates for behavioural homeostasis (Lillywhite, 1970), as refugia from inhospitable environments (Seebacher & Alford, 1999; 2002; Kluber et al., 2009), to meet metabolic demands (Lillywhite, 1973), for immune functions (Casterlin & Reynolds, 1977; Myhre et al., 1977; Bustamante et al., 2010; Murphy et al., 2011) and for reproduction (Marangio & Anderson, 1977). Data from anthropocentric measurements available through sources including meteorological records and geological surveys may be very different from the conditions required by a particular amphibian species (e.g., Kluber et al., (2009), where ambient temperatures reached lethal highs, but plethodontid salamander microclimates were remained around 10°C cooler; Michaels & Preziosi (2013) where Pelophylax frogs inhabit a lower-UVB microclimate defined by environment and behaviour). Microclimate use can vary on a circannual basis, particularly around reproductive cycles and periods of dormancy as animals migrate between major habitat types, or on a diel cycle, often around behavioural homeostasis (Lillywhite, 1970; Heath, 1975; Michaels & Preziosi, 2013). The choice of microclimate within a species also depends on life stage (e.g., aquatic larvae, terrestrial juveniles and amphibious adults in many species of newt), size class (basking juvenile and nocturnal adult Boreal toads, Lillywhite et al., 1973) and on intraspecific population (e.g., populations of *Notophthalmus viridescens*, Healy, 1973).

Annual variation in climate will interact with microhabitat choice in the animals themselves to determine the parameters of the preferred microclimate. Therefore measurements of wild environmental parameters must be taken as close to the actual position of the animal as possible and behavioural, temporal, spatial and meteorological context must be recorded as well. The combination of field data with enclosures designed to give realistic variation for a given time of year will allow animals to move between and select appropriate microclimates, while climatic changes associated with reproductive events in the wild can be used to trigger spawning in captivity, for example through the use of rain chambers (Fenolio, 1996).

Although Amphibian Ark recommends that *ex-situ* projects are conducted within the natural range of focal species, which facilitates access to natural history data by proximity to wild habitat, many existing projects are based in other countries and/or on different continents or rely on overseas funding bodies. Where *ex-situ* and *in-situ* projects are managed by different parties or separated by large distances, collaborative efforts can involve those working *in-situ* providing field data for those working in captive breeding facilities. Local governments can also sometimes provide habitat data, such as river water temperatures (Tapley & Acosta-Galviz, 2010), highlighting the importance of good relations between conservation initiatives and government.

Analogue species and data gaps

There are now more than 7000 recognised species of amphibians (Amphibiaweb, 2013) and this number is growing quickly, compared to other vertebrate taxa (Köhler et al., 2005). With so many species in existence and so few conservation and research resources available, it is inevitable that gaps in natural history data will continue to exist, despite active research efforts. Although specific expeditions may be organised to collect data on conservation targets before rescue operations must be carried out, in many cases other tactics must be used to provide emergency conservation projects with some data to work with, at least until species-specific data can be collected.

Conservation target species often fall within taxonomic groups including more common, or at least less threatened or better known, species with similar biology and natural history, which may be used as analogues in the development of captive husbandry protocols. This is not to say that analogues will have requirements identical to real conservation targets, but given careful choice of analogue species, certain data can be collected and applied to poorly known conservation targets. This may allow populations to be kept alive while species-specific requirements are assessed. For example, reproductive modes and habitat use of *Leptodactylus* frogs, including the nest-chamber construction of the critically endangered L. fallax, can be predicted by taxonomic affinities within the genus (Heyer, 1969), which would allow keepers to provide suitable breeding sites to a poorly known species. Similarly, European cave salamanders (Hydromantes), which represent diverged fragmentary populations of ancient, widespread species, share similar habitat requirements, including rock-types, humidity and temperature levels and reproductive modes (Carranza et al., 2008; Chiari et al., 2012) and data from one species might be applied to others should rapid rescue projects be required. There are many other such examples. A number of Amphibian Ark supported programmes have used analogue species to provide basic environmental parameters and to develop captive husbandry protocols that support these parameters, as well as to train staff before rescue populations arrive in facilities (Amphibian Ark Seed Grant progress report, 2013). Sister taxa that have formed recently and alloor peri-patrically and that still occur in similar habitats are perhaps most likely to share requirements and to be successful analogues. It is very important to note, however, that analogue species must not be selected simply on the basis of close taxonomic affiliation, which does not guarantee similar captive requirements. Careful analysis of natural history observations must be made where possible, either in the field or in captivity, to ensure that analogues are valid. Although they are by no means a complete substitute for species-specific data collection, the potential for analogue species data to contribute to captive husbandry of conservation targets highlights the importance of collecting natural history data for any species where it is possible

Communication of natural history research

It is critical that data, once collected, are shared and preserved in a durable form. Academic journals are important in preserving a long-term record of reports and in maintaining research standards through peer-review, but can be insufficient in ensuring the transfer of data from research to those responsible for captive amphibian husbandry. Specific information can often be scattered and difficult to identify and track down, particularly when papers revolve around hypothesis testing, rather than presentation of natural history data (see above and Tables 2 and 3). For the purposes of practicality, a centralised, open access database of pertinent species information in which data, ideally also published in academic journals, can be concentrated and made explicitly available might be of use. HabiData is such a database, which has recently been created at www.habidata.co.uk. It aims to collate disparate information from many sources into one document that is freely accessible for any individual or institution maintaining captive amphibians. Being a dynamic online tool, rather than a fixed publication, the HabiData database has the potential to grow and to evolve as new information and needs are identified, while maintaining the integrity of peer-review in its research base. HabiData is in the process of being directly linked to the British and Irish Association of Zoos and Aquaria, via its Reptile and Amphibian Working Group. It is hoped

that this link will allow HabiData to act as a direct conduit between research on the one hand and those involved in amphibian captive husbandry on the other, allowing those working with *ex-situ* amphibian populations to access information about the habitat of a species in order to replicate it in captivity. The authors strongly urge that any natural history data published as part of an academic work are also submitted to this database.

Conclusions

Many amphibian species are dependent on ex-situ conservation projects to ensure their survival. In order to achieve success, zoos and other institutions holding amphibians in captivity require information on how species live in the wild on which to base captive husbandry protocols. These data can often be collected readily, given access to field sites; if not from target species, then from similar, analogue species. It is important to create a knowledge base from which conservationists can draw information relevant to their projects. We strongly suggest that the collection of natural history data and environmental parameters becomes an integrated part of any ex-situ programme. We hope that this article will encourage the gathering of natural history data vital for the long-term survival of endangered amphibian species, both in captivity and, through ex-situ programs, in the wild.

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ONLINE APPENDIX



Appendix 1. Literature containing environmental parameters used in the analysis presented in Table 3.

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