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REVIEW

Animal personality and behavioral syndromes in amphibians: a review of the evidence, experimental approaches, and implications for conservation

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Abstract

Animal personality and behavioral syndromes can have profound effects on individual fitness. Consequently, there is growing recognition that knowledge of these phenomena may assist with animal conservation. Here we review evidence for personality and behavioral syndromes in amphibians (the most threatened vertebrate class), critique experimental approaches, and explore whether knowledge in this domain might assist with endangered species management. Despite being a neglected field (research has spanned just 24 species), there is emerging evidence that frogs, toads, salamanders, and newts show personality and behavioral syndromes along three behavioral axes: boldness, exploration, and activity. Among vertebrates, amphibians are unique in having a biphasic lifecycle defined by metamorphosis and obvious transformations in morphology, physiology, and habitat use, characteristics that enable detailed examination of behavioral changes across life stages and ecological contexts. Accordingly, recent work has started to make important contributions to our understanding of the development and proximate causes of personality and behavioral syndromes, with some emerging evidence for ontogenetic stability, genetic control, and state-dependent personality. To date, however, no study has considered the conservation implications of personality for amphibians. Drawing on a conceptual framework and empirical literature for all vertebrates, we argue that there is considerable potential for knowledge of animal personality to improve amphibian conservation programs. We propose a novel paradigm to improve (i) the mating and reproductive success of captive animals by ensuring that breeding pairs are behaviorally compatible and (ii) the post-reintroduction survival and reproductive potential of animals by facilitating the selection of optimal behavioral types for release.

Significance statement

Animal personality and behavioral syndromes appear to be widespread in nature. Here, we review animal personality and behavioral syndromes in amphibians, an understudied taxonomic group within the field. We summarize evidence, critique methodological approaches used, and emphasize that the unique behavioral ecology of amphibians makes them a model group for studying the proximate causes and ecological consequences of personality and behavioral syndromes. We also highlight that knowledge of these phenomena may have significant conservation implications for amphibian captive breeding and reintroduction programs.

Keywords Animal personality · Behavioral syndromes · Amphibians · Conservation · Behavioral axes · Metamorphosis

Introduction

Research investigating animal personality (temporally repeatable, among-individual behavioral differences) and behavioral syndromes (among-individual correlations between behavioral traits) has increased substantially over the last decade, with animals from various taxonomic groups found to display individual behavioral variation that persists

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throughout time and across different contexts. As the field of animal personality continues to progress, it has become increasingly apparent that personality and behavioral syndromes can influence an individual's ability to show optimal behavior in varying environments and, subsequently, can significantly influence an individual's survival and reproductive success (Sih et al. 2004a, 2004b; Smith and Blumstein 2008). As such, animal personality and behavioral syndromes can directly influence an individual's lifetime fitness and, in turn, have far-reaching ecological and evolutionary consequences (Réale et al. 2010; Sih et al. 2012; Wolf and Weissing 2012).

Considering these consequences, it has recently been suggested that animal personality and behavioral syndromes may also have important implications for animal conservation (Merrick and Koprowski 2017). In particular, animal personality and behavioral syndromes may influence the success of captive breeding and reintroduction programs (Merrick and Koprowski 2017). Individuals chosen for captive breeding and reintroductions are often selected based on their genetics (Miller et al. 2010), health (Saidenberg et al. 2015), and/or life history stage (Sarrazin and Legendre 2000; Bremner-Harrison et al. 2004; Robert et al. 2004). However, certain personality traits or combinations of traits may also need to be considered as they have the potential to affect the survival and reproductive success of individuals in captivity and post-reintroduction (Wielebnowski 1999; McDougall et al. 2006; Watters and Meehan 2007; Merrick and Koprowski 2017). For example, captive cheetahs (*Acinonyx jubatus*) with a shy personality have been found to have lower reproductive success in captivity (Wielebnowski 1999), while bold European mink (*Mustela lutreola*) have been shown to have higher survival rates post-reintroduction (Haage et al. 2017). Although these ideas seem intuitive, this applied area of personality and behavioral syndrome research remains relatively unstudied (Merrick and Koprowski 2017). Investment in this area would be particularly relevant to amphibians, as biodiversity loss in this group exceeds that of any other vertebrate class (Stuart et al. 2004).

To date, amphibian personality and behavioral syndrome research remains largely unexplored (Wilson and Krause 2012a, 2012b). However, it has recently been highlighted that amphibians offer an important, yet neglected, research opportunity as they undergo metamorphosis; a life history trait absent in other vertebrates. Wilson and Krause (2012b) made a convincing argument that because amphibian metamorphosis entails extreme shifts in habitat and ecological niche (more so than any other animal group), that research with amphibians stands to provide key insights into how personality differences are linked to developmental changes in physiology, morphology, and ecology, and how personality differences arise. Herein, we provide a review of personality and behavioral syndromes in amphibians, with a focus on critiquing experimental approaches and considering conservation implications. In the first part of the review, we outline the distribution of personality studies across the three amphibian orders, summarize evidence for personality and behavioral syndromes, and critique the main approaches used to test for personality. This part of the review targets animal personality researchers, with the objective of comprehensively detailing the current state of knowledge and drawing attention to unique aspects of amphibian life history, behavior, and ecology that affords research opportunities that are unavailable when working with other vertebrates. In particular, we outline how amphibian metamorphosis enables researchers to answer major questions related to the development and proximate causes of personality and behavioral syndromes. In the second part of the review, we highlight the potential for personality and behavioral syndromes to significantly influence animal conservation outcomes. Drawing on an emerging literature for all vertebrate classes, we discuss the implications of animal personality and behavioral syndromes for amphibian captive breeding and reintroduction programs. This part of the review targets amphibian conservation researchers with the objective of highlighting innovative avenues for future research and providing concrete advice on the types of experimental approaches that could be undertaken to hasten conservation success.

Contributions of amphibian research to the field of animal personality

Up until 2012, animal personality and behavioral syndrome research in amphibians lagged far behind other animal groups (see Conrad et al. 2011 for an early review), yet in the last six years, research on amphibians has gained momentum, with 80% of all amphibian personality studies published between 2012 and 2018. Although amphibians continue to stand out as being the least researched vertebrate class within the field, there is already compelling evidence that amphibians display personality and behavioral syndromes, and a growing recognition that personality may be as ecologically important in amphibians as it is in other vertebrate classes (Gruber et al. 2017a). More importantly, research with amphibians has made a number of significant contributions to our understanding of the causes and consequences of personality and behavioral syndromes. Specifically, in the last five years, amphibian personality research has not only demonstrated that personality can influence ecologically relevant behaviors such as dispersal (Brodin et al. 2013; Gruber et al. 2017a), selection of foraging sites (González-Bernal et al. 2014), and the likelihood of contracting disease or parasites (Koprivnikar et al. 2012) but has also enhanced our understanding of proximate mechanisms underpinning personality variation and syndrome structure (Gruber et al. 2017a; Kelleher et al. 2017). Most recently, research with amphibians has shown that personality differences in wild populations can persist in captive raised offspring (Gruber et al. 2017a), and has demonstrated that personality and syndrome structure can remain consistent across life stages (Wilson and Krause 2012a). Work with amphibians has also provided some of the first evidence that personality can be state-dependent (Kelleher et al. 2017) and that personality can develop in response to environmental conditions experienced during early development, such as exposure to predators and conspecifics (Urszán et al. 2015b). These early findings highlight that amphibians provide a valuable but relatively untapped model group for exploring the causes and implications of personality and behavioral syndromes.

Distribution of animal personality and behavioral syndrome studies across amphibian orders

A total of 19 studies (limited to peer-reviewed and published literature) have tested for animal personality and/or behavioral syndromes in amphibians (see Table 1). Four studies examined repeatable among-individual differences in single traits (personality), nine studies examined personality and correlations between behaviors (syndromes), and four studies examined behavioral correlations, without establishing individual repeatability. Two studies (Carlson and Langkilde 2014; Gruber et al. 2017a) examined individual behavioral differences in boldness and exploration behavior (within the animal personality framework, see Section 2) yet did not test for repeatability or behavioral correlations. Collectively, these studies span 24 amphibian species (Table 1) that are unevenly distributed across the three amphibian orders—Anura (frogs and toads), Caudata (salamanders and newts), and Gymnophiona (limbless amphibians) (Table 1). Eighty-three percent of amphibian studies have investigated personality and behavioral syndromes in the order Anura, with the remaining 17% of studies focused on species in the order Caudata (Table 1). To date, no studies have investigated personality or behavioral syndromes in the order Gymnophiona.

Within the two amphibian orders studied, research has been heavily biased towards a small number of species ($n = 24$) from North America and Europe (Table 1). The order Anura is comprised of over 5800 described species from 31 families (IUCN 2017). However, research on personality and behavioral syndromes has been restricted to just 20 species from five families (see Table 1). The order Caudata is comprised of over 560 species, from nine families (IUCN 2017), but research has been restricted to four species from three families. Of note, research has also been largely limited to amphibian species with an aquatic reproductive mode (Table 1).

Amphibians are characterized by a spectacular diversity of life histories, ecologies and reproductive biologies. They have biphasic life cycles and metamorphosis with different life stages encompassing a range of developmental environments, they can occupy a range of trophic niches, from keystone consumers to top level predators, and they have over 35 known reproductive modes, more than any other tetrapod (Haddad and Prado 2005). This variation can be expected to influence the strength of selection for animal personality and behavioral syndromes. Amphibians therefore provide excellent opportunities to investigate whether the presence or extent of animal personality varies with life history strategy and across different ecological contexts.

Evidence for animal personality in amphibians

Réale et al. (2007) developed a generalized framework for testing animal personality, with five defined behavioral axes (major personality trait categories): (1) boldness/shyness, (2) exploration/avoidance, (3) activity, (4) sociability, and (5) aggression. Within this framework, studies investigating animal personality and behavioral syndromes in amphibians have centered on three of these key behavioral axes: (1) boldness/shyness, (2) exploration/avoidance, and (3) activity (Tables 2 and 3). The evidence for animal personality along each behavioral axis in amphibians is summarized below (see Sections 2.1, 2.2, 2.3, and 2.4). We also discuss the approaches used to test for animal personality, the merits of each experimental approach and make recommendations for improvement (see Section 3).

Evidence for personality along the boldness/shyness axis

To date, a total of nine studies (representing seven anuran species) have tested for repeatable, among-individual differences in amphibian boldness behavior (Tables 2 and 3). Of the studies investigating boldness behavior in larval amphibians ($n = 5$), four have provided evidence for personality (Table 2). Five studies have investigated boldness behavior in adult amphibians, and all have provided evidence for personality (Table 3). These studies have demonstrated that boldness spans juvenile and adult life stages and has the potential to be widespread, at least in anurans. Moreover, because these studies were conducted using both wild and laboratory-raised animals, they provide evidence for boldness in both natural and captive contexts. However, the fact that so few published studies have investigated boldness behavior in amphibians is surprising because amphibians offer enormous potential to advance our knowledge of personality along the boldness/shyness axis. Most amphibians display stereotypic startle reactions in response to threatening stimuli perceived using visual and olfactory sensors (Narayan et al. 2013). As such, their predators can be easily modeled in the laboratory environment (e.g. visual signals from birds and small mammals, as well as

Table 1 Summary of taxonomic distribution, geographic distribution, and reproductive mode of amphibian species used in animal personality and behavioral syndrome research

Amphibian order	Family	Species name	Common name	Geographical region	Reproductive mode	References
Anura	Ranidae	*Rana temporaria*	European Common Brown frog	Europe	Aquatic	Brodin et al. (2013)
Anura	Ranidae	*Rana dalmatina*	Agile Frog	Europe	Aquatic	Urszán et al. (2015a); Urszán et al. (2015b).
Anura	Ranidae	*Rana ridibunda*	Marsh frog	Europe	Aquatic	Wilson and Krause (2012a)
Anura	Ranidae	*Lithobates sylvaticus*	Wood frog	North America	Aquatic	Richardson (2001); Koprivnikar et al. (2012); Carlson and Langkilde (2014).
Anura	Ranidae	*Rana catesbeiana*	American Bullfrog	North America	Aquatic	Richardson (2001); Smith and Doupnik (2005); Carlson and Langkilde (2013).
Anura	Ranidae	*Rana clamitans*	Green frog	North America	Aquatic	Richardson (2001)
Anura	Ranidae	*Lithobates sphenocephalus*	Southern leopard frog	North America	Aquatic	Richardson (2001)
Anura	Pipidae	*Xenopus tropicalis*	Western clawed frog	Africa	Aquatic	Videlier et al. (2014, 2015)
Anura	Hylidae	*Pseudacris crucifer*	Spring Peeper	North America	Aquatic	Richardson (2001)
Anura	Hylidae	*Acris gryllus*	Southern Cricket frog	North America	Aquatic	Richardson (2001)
Anura	Hylidae	*Hyla versicolor*	Gray tree frog	North America	Aquatic	Richardson (2001)
Anura	Hylidae	*Hyla femoralis*	Pine Woods tree frog	North America	Aquatic	Richardson (2001)
Anura	Hylidae	*Hyla squirella*	Squirrel tree frog	North America	Aquatic	Richardson (2001)
Anura	Hylidae	*Hyla gratiosa*	Barking tree frog	North America	Aquatic	Richardson (2001)
Anura	Hylidae	*Hyla cinerea*	American Green tree frog	North America	Aquatic	Richardson (2001)
Anura	Bufonidae	*Bufo terrestris*	Southern toad	North America	Aquatic	Richardson (2001)
Anura	Bufonidae	*Bufo americanus*	American toad	North America	Aquatic	Richardson (2001)
Anura	Bufonidae	*Bufo calamita*	Natterjack toad	Europe	Aquatic	Maes et al. (2013)
Anura	Bufonidae	*Rhinella marina*	Cane toad	North and South America	Aquatic	Gonzalez-Bernal et al. (2014); Gruber et al. (2017a, 2017b)
Anura	Myobatrachidae	*Pseudophryne corroboree*	Southern Corroboree frog	Australia	Terrestrial	Kelleher et al. (2017)
Caudata	Plethodontidae	*Desmognathus brimleyorum*	Ouachita Dusky salamander	North America	Semiaquatic	Gifford et al. (2014)
Caudata	Salamandridae	*Lissotriton boscai*	Bosca’s Newt	Europe	Aquatic	Aragón (2011)
Caudata	Ambystomatidae	*Ambystoma barbouri*	Streamside salamander	North America	Aquatic	Sih et al. (2003)
Caudata	Ambystomatidae	*Ambystoma texanum*	Small mouth salamander	North America	Aquatic	Sih et al. (2003)

chemical signals from fish predators) (see Section 3.1). Furthermore, closely related groups of amphibians display a wide range of anti-predatory defense strategies including mimicry, aposematism, and camouflage (Wells 2007). Therefore, amphibians provide excellent opportunities to explore how natural-history variation in predatory defense strategies relates to the presence of boldness personality.

Evidence for personality along the exploration/avoidance axis

A total of ten studies (representing eight anuran species and one caudate species) have tested for animal personality along the exploration/avoidance axis in amphibians (Tables 2 and 3). Of the studies investigating exploratory behavior in larval

Table 2 Summary of major findings for larval amphibian studies on personality and behavioral syndromes

Species name	Common name	Trait repeatability	Behavioral correlation	Correlations with other traits	Reference
Rana temporaria	European common brown frog	Boldness—yes Exploration—no	No	Yes (Bo/Source population) (Ex/Source population) (Ex/Body Weight)	Brodin et al. (2013)
Rana dalmatina	Agile frog	Activity—yes Boldness—yes (after prior stimulus) Exploration—yes (in later stages)	No	Yes (Ac/Age at metamorphosis) (Ac/Mass at metamorphosis) (Bo and Ex/Mass at metamorphosis)	Urszán et al. (2015a)
Rana dalmatina	Agile frog	Activity—yes (treatment dependent) Boldness—yes (treatment dependent)	Yes (Ac/Bo) (treatment dependent)	Not tested	Urszán et al. (2015b)
Rana ridibunda	Marsh frog	Activity—yes Boldness—yes Exploration—yes	Yes- (Ac/Ex) (Refuge use/Ac/Ex) (Refuge use/Ac+Ex in adult stage) (Ac+Ex/Ac+Ex adult stage)	Yes (Ac/Body length) (Ex/Body length)	Wilson and Krause (2012a)
Lithobates sylvaticus	Wood frog	Activity—not tested Boldness—not tested Exploration—not tested	Yes (Ac/Ex) (Activity level across each test)	Yes (Ac/Parasite load)	Koprivnikar et al. (2012)
Rana catesbeiana	American bullfrog	Activity—no Boldness—no Exploration—yes	Not tested	Not tested	Carlson and Langkilde (2013)
Lithobates sylvaticus	Wood frog	Boldness—not tested	Not tested	No (Bo/Survival)	Carlson and Langkilde (2014)
Ambystoma barbouri *Ambystoma texanum*	Streamside salamander Small mouth salamander	Activity—not tested	Yes (Ac in presence of CTS/ Ac in absence of CTS)	Yes (Ac/Species), (Ac/Sibship) (Ac/Body Weight)	Sih et al. (2003).
Pseudacris crucifer *Acris gryllus* *Hyla versicolor* *Hyla femoralis* *Hyla squirella* *Hyla gratiosa* *Hyla cinerea* *Bufo terrestris* *Bufo americanus* *Lithobates sylvaticus* *Rana catesbeiana* *Rana clamitans* *Lithobates sphenocephalus*	Spring Peeper Southern cricket frog Gray tree frog Pine woods tree frog Squirrel tree frog Barking tree frog American green tree frog Southern toad American toad Wood frog American bullfrog Green frog Southern leopard frog	Activity—not tested	Yes (Ac in presence of CTS/ Ac in absence of CTS)	Yes (Ac/Species)	Richardson (2001)
Rana catesbeiana	American bullfrog	Activity—yes	Not tested	Not tested	Smith and Doupnik (2005)

Correlated behaviors or traits indicated by parentheses

Behavioral axes are indicated as follows: *Bo* boldness/shyness, *Ex* exploration/avoidance, *Ac* activity, *So* sociability

amphibians ($n = 4$), three studies have provided evidence for personality (Table 2), while all seven studies on adult amphibians have provided evidence for personality (Table 3). Overall, these studies show that exploration can be significantly repeatable in both wild caught (Wilson and Krause 2012a; Carlson and Langkilde 2013) and laboratory-reared amphibians (Urszán et al. 2015a) and that exploration can vary with age and body size (Wilson and Krause 2012a; Urszán et al. 2015a). Exploration behavior has been considered important for dispersal and resource acquisition (Dingemanse et al. 2003) and is perhaps strongly selected for in later life stages when movement within and between habitats has greater fitness consequences. Gruber et al. (2017a) have already demonstrated that exploration behavior in invasive cane toad (*Rhinella marina*) correlates with dispersal patterns, with more exploratory toads dispersing further than less exploratory toads. Further research in adult amphibians may reveal that exploratory behavior is a significant predictor of individual movement patterns within and between habitats in a diversity of species, as demonstrated in other animal groups

Table 3 Summary of major findings for post-metamorphic amphibian studies on personality and behavioral syndromes

Species name	Common name	Trait repeatability	Behavioral correlations	Correlations with other traits	Reference
Rana temporaria	European common brown frog	Boldness—not tested Exploration—not tested	No	Yes (Bo/Source population) (Bo/Body weight) (Ex/Body weight)	Brodin et al. (2013)
Bufo calamita	Natterjack toad	Activity—yes Boldness—yes Exploration—yes	Yes (Ex/Ac) (Ex/Ac/Bo)	Yes (Ac + Ex/Movement speed)	Maes et al. (2013)
Rana ridibunda	Marsh frog	Activity—yes Boldness—yes Exploration—yes	Yes (Ex/Ac) (Ex/Ac/Refuge use in larval stage) (Ex + Ac/ Ex + Ac in larval stage)	Yes (Ac/Body size)	Wilson and Krause (2012a)
Xenopus tropicalis	Western clawed frog	Exploration—yes	No	No	Videlier et al. (2014)
Xenopus tropicalis	Western clawed frog	Exploration—yes	No	Yes (Ex/sex)	Videlier et al. (2015)
Rhinella marina	Cane toad	Boldness—yes Sociability—not tested	Yes (Bo/So)	Yes (Bo/Feeding rate) (Bo/Foraging competition)	Gonzalez-Bernal et al. (2014)
Desmognathus brimleyorum	Ouachita Dusky Salamander	Exploration—yes	Not tested	No	Gifford et al. (2014)
Lissotriton boscai	Bosca's Newt	Activity—not tested	Yes (Activity level across each social treatment)	Yes (Ac/Sex)	Aragón (2011)
Pseudophryne corroboree	Southern Corroboree frog	Activity—yes Boldness—yes Exploration—yes	No	Yes (Ex/Body size)	Kelleher et al. (2017)
Rhinella marina	Cane toad	Boldness—not tested Exploration—not tested	Not tested	Boldness/Population Exploration/Population	Gruber et al. (2017a)
Rhinella marina	Cane toad	Boldness—yes Exploration—yes	Not tested	Boldness/Population Exploration/Population Exploration/Source (wild vs. captive)	Gruber et al. (2017b)

Correlated behaviors or traits indicated by parentheses

Behavioral axes are indicated as follows: *Bo* boldness/shyness, *Ex* exploration/avoidance, *Ac* activity, *So* sociability

(Dingemanse et al. 2003). While larval amphibians are typically highly sedentary, adult amphibians are geared for dispersal (Wilson and Krause 2012b), and many species have large home ranges (tens of kilometers squared), traveling great distances to breed, find shelter, and food (Wells 2007). As such, we advocate the use of adult amphibians as a model group for studying the ecological implications of exploration personality.

Evidence for personality along the activity axis

To date, a total of seven studies encompassing five anuran species have tested for personality along the activity behavioral axis (Tables 2 and 3). Of the studies investigating personality along the activity axis in the larval life stage (*n* = 5), four have provided evidence for personality (Table 2), while all three studies investigating activity behavior in adult amphibians have provided evidence for personality (Table 3). Collectively, these studies have demonstrated that activity levels (1) are significantly repeatable in both wild caught and laboratory-raised individuals (over a period of several days to several weeks), (2) correlate with locomotor abilities (such as movement speed), (3) vary with body size, and (4) and can transcend life stage (discussed further in Section 4.2) (Wilson and Krause 2012a; Maes et al. 2013; Kelleher et al. 2017).

Repeatable, among-individual differences in activity levels (as well as other behavioral traits) are likely to have significant fitness consequences by influencing chances of resource acquisition and, in the adult life stage, reproductive success. For example, it has been shown in amphibians that activity positively correlates with food intake (Wells 2007). Moreover, during breeding seasons, it has also been shown that male activity (nights active in a chorus) positively correlates with mating success (Jaquiéry et al. 2010). Individual differences in activity levels may also result in important tradeoffs (Sih et al. 2004a). For instance, individuals with consistently high activity levels may have an increased predation risk yet higher resource acquisition rate (Sih et al. 2015). Alternatively, higher activity levels could result in an increase in energy use and a decrease in growth rate (Sih et al. 2015). The drivers of individual differences in activity are not well understood, though one possibility is that differences are underpinned by differences in physiological state and, in particular, metabolic rate (Careau et al. 2008; Biro and Stamps 2010; Sih et al. 2015).

As amphibians are ectothermic, they have the potential to provide some interesting insights into the relationship between metabolism and personality traits, such as activity and exploration, that affect energy expenditure (Careau et al. 2008). Metabolic rate can be easily manipulated in amphibians as standard metabolic rate (SMR) increases exponentially with temperature, as for other ectotherms (Clarke and Johnston 1999; Biro et al. 2010). Laboratory experiments which increase or decrease ambient temperature and measure personality differences may reveal that personality traits (such as activity or exploration) change with temperature and metabolic rate (for evidence in other ectotherms, see Biro et al. 2010). Thus, amphibians provide a good model for examining whether energy metabolism is a proximate mechanism underpinning personality variation. Interestingly, a study in adult salamanders (*Desmognathus brimleyorum*) has investigated whether there is co-variation between SMR, exploration, and feeding rate (Gifford et al. 2014). Despite each of these variables displaying significant among-individual variation over time, there were no significant correlations between them (Gifford et al. 2014). Small sample sizes ($n = 19$) may have resulted in insufficient statistical power to detect non-zero among-individual correlations in this study (Dingemanse and Dochtermann 2013). Alternatively, individual variation in SMR might be context dependent (Careau and Garland Careau and Jr 2012; Gifford et al. 2014). Continued investigation of whether individual differences in metabolic rate underpin personality traits that affect energy expenditure (such as activity or exploration) in amphibians will advance our understanding of the evolution and maintenance of personality in ectothermic vertebrates, so we highlight this as an important area for future research.

Behavioral axes yet to be investigated—aggression and sociability

Aggression is defined as an individual's hostile reaction to a conspecific, while sociability refers to an individual's reaction to the presence or absence of a conspecific (not including aggressive behaviors) (Réale et al. 2007). These behavioral axes have been studied in depth in other taxonomic groups, especially fish (Gosling 2001; Bell 2005; Cote et al. 2010b; McGhee and Travis 2010; Conrad et al. 2011; Wong et al. 2013), but to date have been completely overlooked in amphibians. Of the 19 amphibian studies investigating animal personality and behavioral syndromes, not one has tested for repeatable, among-individual differences in either aggression or sociability (Tables 2, 3, and 4). Overall, the deficit of studies investigating individual variation in sociability and aggression in amphibians represents a significant gap in knowledge regarding the personality repertoire of amphibians. Many amphibians engage in contests and defend resources using aggressive behaviors that typically involve both acoustic and visual displays (Wells 2007). Furthermore, many amphibians also live in groups, particularly during the larval life stage, and invest heavily in uni-parental or biparental care (Wells 2007). We encourage animal personality researchers to start testing for personality along the aggression and sociability axes and, in so doing, shed light on the ubiquity of personality across behavioral domains.

Approaches used to test for animal personality in amphibians

Approaches used to test for personality along the boldness/shyness axis

Studies testing for amphibian boldness have used three approaches: (1) the open field test (OFT), (2) the novel environment test (NET), and (3) the threat stimulus test (TST) (Table 4). During an open field test, an individual is introduced into an unfamiliar arena and behavior is observed (Carter et al. 2013). Similarly, a novel environment test also includes an unfamiliar environment, which may or may not contain novel or familiar stimuli (if it does not contain novel stimuli, it is equal to an OFT) (Carter et al. 2013). Threat stimuli tests fall into one of two categories: (1) a physical threat stimulus, such as a modified metallic rod used to simulate a predator strike (Urszán et al. 2015a), and (2) a chemical threat stimulus, such as predator chemical cues used to

Table 4 Summary of methods used to test for animal personality and behavioral syndromes in amphibians

Species name	Common name	Life stage	Behavioral axes investigated	Test	Response variables measured	Sample size	Number of repeat trials	Reference
Rana temporaria	European Common Brown frog	Larvae	Boldness	NET	Latency to leave refuge	144	2	Brodin et al. (2013)
			Exploration	NET	Total area covered			
Rana dalmatina	Agile Frog	Larvae	Activity	AFET	Movement rate in a familiar environment	80	2	Urszán et al. (2015a)
			Boldness	PTS	Latency to restart activity			
			Exploration	NET	Number of grid squares visited			
Rana dalmatina	Agile Frog	Larvae	Activity	AFET	Distance moved in familiar environment	17–20	3	Urszán et al. (2015b)
			Boldness	PTS	Latency to restart activity			
Rana ridibunda	Marsh frog	Larvae	Activity	OFT	Total time spent active	50	2	Wilson and Krause (2012a)
			Boldness	OFT + PTS	Flight initiation distance from PTS			
				NET + CTS	Latency to resume activity			
				AFET	Refuge use			
			Exploration	NET	Latency to first movement			
Lithobates sylvaticus	Wood frog	Larvae	Activity	NET	Percentage of time points spent swimming	26	0	Koprivnikar et al. (2012)
			Boldness	PTS	Time in same zone of parasite introduction			
			Exploration	Novel food test	Percentage of time sampling points tadpoles were active and present in same zone as novel food stimulus			
Rana catesbeiana	American Bullfrog	Larvae	Activity	AFET	Proportion of time spent moving	8	4	Carlson and Langkilde (2013)
			Boldness	NET	Total number of gridlines crossed in the center of open field			
			Exploration	NET	Total number of gridlines crossed			
Lithobates sylvaticus	Wood frog	Larvae	Boldness	OFT + CTS	Activity level in presence of chemical cues (proportion of time spent moving)	20	0	Carlson and Langkilde (2014)
					Proportional change in activity level from baseline conditions after adding predator cue			
Ambystoma barbouri *Ambystoma texanum*	Streamside salamander Small mouth salamander	Larvae	Activity	AFET + CTS	Activity level in presence and absence of chemical cues (Proportion of time spent out of refuge)	92	0	Sih et al. (2003)
Pseudacris crucifer *Acris gryllus* *Hyla versicolor* *Hyla femoralis* *Hyla squirella* *Hyla gratiosa* *Hyla cinerea* *Bufo terrestris* *Bufo americanus* *Lithobates sylvaticus* *Rana catesbeiana* *Rana clamitans* *Lithobates sphenocephalus*	Spring Peeper Southern cricket frog Gray tree frog Pine woods tree frog Squirrel tree frog Barking tree frog American green tree frog Southern toad American toad Wood frog American bullfrog Green frog Southern leopard frog	Larvae	Activity	AFET + CTS	Time spent active in presence of different predator chemical cues	2–9	0	Richardson (2001)
Rana catesbeiana	American Bullfrog	Larvae	Activity	NET	Time spent active	19	3	Smith and Doupnik (2005)
					Time spent in each aquarium zone			
Rana temporaria	European Common Brown frog	Juvenile	Boldness	NET	Latency to leave refuge	144	0	Brodin et al. (2013)
			Exploration	NET	Total area covered			
Bufo calamita	Natterjack toad	Juvenile	Activity	OFT	Percent time moving	118 and 152	2	Maes et al. (2013)
			Boldness	OFT	Latency time			
			Exploration	OFT	Minimum convex polygon			
Rana ridibunda	Marsh frog	Juvenile	Activity	OFT	Total time spent active	50	2	Wilson and Krause (2012a)
			Boldness	OFT + PTS	Flight initiation distance from PTS			

Table 4 (continued)

Species name	Common name	Life stage	Behavioral axes investigated	Test	Response variables measured	Sample size	Number of repeat trials	Reference
				NET + CTS	Latency to resume activity			
				AFET	Refuge use			
			Exploration	NET	Latency to first movement			
Xenopus tropicalis	Western clawed frog	Adult	Exploration	NET	Total distance moved, average, minimum and maximum speed, latency to move, average, minimum and maximum time of round trip, total and average time spent hidden between two round trips, number of complete round trips, total number of movements, number of pauses, frequency of movement, number of movements away from the wall	37	3	Videlier et al. (2014)
Xenopus tropicalis	Western clawed frog	Adult	Exploration	NET	Total distance moved, average, minimum and maximum speed, latency to move, average, minimum and maximum time of round trip, total and average time spent hidden between two round trips, number of complete round trips, total number of movements, number of pauses, frequency of movement, number of movements away from the wall	61	3	Videlier et al. (2015)
Rhinella marina	Cane toad	Adult	Boldness	NET	Time to exit a shelter and begin exploring novel environment	63	2 (Boldness) 0 (Sociability)	Gonzalez-Bernal et al. (2014)
			Sociability	Feeding site choice	Willingness to approach feeding conspecific			
Pseudophryne corroboree	Southern Corroboree frog	Juvenile	Activity	AFET	Time spent active, number of active events	24	3	Kelleher et al. (2017)
			Boldness	PTS	Latency to move, latency to forage, time spent active, time spent in strike zone			
			Exploration	NET	Distance traveled, time spent mobile, number of mobile episodes			
Desmognathus brimleyorum	Ouachita Dusky Salamander	Adult	Exploration	NET	Total number of grid squares crossed	19	3	Gifford et al. (2014)
Lissotriton boscai	Bosca's Newt	Adult	Activity	NET + social chemical cues	Time spent active	30	0	Aragón (2011)
Rhinella marina	Cane Toad	Adult	Boldness	NET	Latency to emerge from a shelter	24	0	Gruber et al. (2017a)
			Exploration	NET	Total distanced traveled, total time spent moving			
Rhinella marina	Cane Toad	Adult	Boldness	NET	Emergence from shelter, latency to emerge	68	2	Gruber et al. (2017b)
			Exploration	NET	Time spent moving and rate of movement			

NET novel environment test, *AFET* activity in familiar environment test, *OFT* open field test, *PTS* physical threat stimulus, *CTS* chemical threat stimulus simulate the presence of a predator (Wilson and Krause 2012a). Most studies of larval amphibians assess boldness using a threat stimulus in either a novel or familiar environment, while studies assessing boldness in adults use a range of approaches, including a NET, OFT, and TST (Table 2). The specific response variables measured as indicators of boldness also differ considerably across studies, and this depends, at least in part, on the approach being used. Studies employing an OFT and NET have typically measured response variables such as latency to leave a refuge and area covered in the center of the open field, while studies using physical or chemical threat stimuli typically measure response variables such as latency to restart activity and flight initiation distance (see Table 4).

Critically, the ability of each approach to detect animal personality along the boldness axis may vary considerably. Studies using an OFT or NET have argued that these approaches are useful because they have defined boldness as movement through an unfamiliar space and in reaction to novelty (Toms et al. 2010). However, these approaches have been criticized because they may be incapable of completely separating bold behavior from exploration behavior (Réale et al. 2007). In order to exclude the non-target behavior of exploration, it has been suggested that boldness might be better measured in a risky situation without any element of novelty (Réale et al. 2007). In order to achieve this in wild amphibians, boldness would be better measured in situ, in an individual's home environment. Such approaches have been used in other vertebrates (Bremner-Harrison et al. 2018) and are likely to work well with amphibians because many species have small home ranges and show high-site fidelity, particularly within seasons (Wells 2007). An alternative approach is to bring wild animals into captivity and acclimate them to the laboratory environment. Most amphibians adjust well to captivity because it is relatively easy to design environments that simulate essential elements of natural habitats (de Vosjoli 1999; Michaels et al. 2014). Moreover, combinations of environmental cues such as temperature, humidity, UV light, and photoperiod can be easily manipulated to ensure the maintenance of natural circadian rhythms (Michaels and Försäter 2017).

Another challenge when testing boldness (both in the wild and in captivity) is standardizing the threat stimulus (i.e., using a highly repeatable stimulus). Almost invariably, stimuli are imposed using rudimentary techniques. For instance, boldness has been quantified in *Rana dalmatina* tadpoles using a fine paint brush as a physical threat stimulus (tadpoles were prodded to simulate a predator attack) (Urszán et al. 2015b). The value of this approach is questionable, because the speed, distance, and force of the simulated attacks were not standardized among individuals or within individuals across repeated trials. Even if one researcher repeatedly performed the simulated attacks, variation between trials is likely to influence the measured extent and repeatability of boldness behavior. There have been attempts to standardize physical threat stimuli using gravity-based methods, specifically, dropping objects from a known height. For example, Urszán et al. (2015a) standardized the speed and force of a metallic rod used to prod tadpoles by releasing it from a set height, but the distance between the tadpole and the threat stimulus was still inconsistent between trials (interestingly, only one subset of individuals in this study showed repeatability in boldness behavior). More precise tests of boldness have come from the delivery of chemical cues. For example, in a study of tadpole response to predator cues in the lake frog (*Rana ridibunda*), Wilson and Krause (2012a) used exact quantities (1 ml) of chemical cues (water from tanks holding a known fish predator) to mimic a predator's presence. Nevertheless, because the stimulus water was manually released from a pipette, there was still potential for variation in the speed, force, and direction of the stimulus. As such, we advocate moving away from these types of approaches and towards the use of standardized, highly repeatable stimuli that will reduce variation between trials, and, in turn, increase the chance of detecting significantly repeatable behaviors.

In recent years, the use of machines to carry out precise automated actions (i.e., robotics) has increased considerably in the fields of behavioral ecology and ecology (for a detailed discussion of exciting applications, see Krause et al. 2011 and Grémillet et al. 2012), but robotics has been very slow to transcend the field of animal personality. This oversight is hindering progress because applying standardized stimuli is critical for attaining reliable measures of repeatability. In amphibians, there is considerable potential for robotics to be used to simulate physical threats (e.g., predator attacks) and accurately test for personality along the boldness-shyness axis. For example, in a study testing for personality in the critically endangered southern corroboree frog (*Pseudophryne corroboree*), Kelleher et al. (2017) recently used a robotic avian predator to control the force and rate of strikes and successfully detect significant repeatability in individual boldness behavior, even with moderate sample sizes (Kelleher et al. 2017).

Robotics could also be used to standardize stimuli when testing for personality along other behavioral axes. For instance, robotic models could be used to simulate the behavior of conspecifics when testing for sociability or aggression (Romano et al. 2017; Sanches et al. 2017). Within the amphibian-behavioral ecology literature, there are already sophisticated examples demonstrating this potential. In a study of territorial behavior, Narins et al. (2003) used a robotic poison dart frog (*Epipedobates femoralis*) to simulate an aggressive male and standardize the appearance and speed of vocal sac motion (Narins et al. 2003). More recently, in a study of female mate choice behavior, Laird et al. (2016) used a robotic green tree frog (*Hyla cinerea*) to simulate a calling male and standardize signal frequency and intensity (Laird et al. 2016). Without a doubt, robotics has enormous potential to improve the precision of personality assays and the likelihood of detecting personality along various behavioral axes, so we implore researchers to embrace this technology.

Approaches used to test for personality along the exploration axis

Exploration is typically defined as an individual's response to a new situation, such as a new habitat, new food item, or novel object (Réale et al. 2007). The approaches used to test for exploration behavior commonly include the NET, the OFT, and the novel object test (NOT). In amphibian studies, the NET predominates as the preferred test (Gifford et al. 2014; Gruber et al. 2017a; Kelleher et al. 2017), with only one study utilizing the OFT (Maes et al. 2013) and one study using the NOT (Koprivnikar et al. 2012) (Table 2). Although the NET and OFT are regularly used to measure exploration across various vertebrate groups, both tests have received criticism because the behavior expressed can be considered "forced" (Walsh and Cummins 1976; Carter et al. 2013). When individuals are placed into a NET or OFT with no opportunity to escape, it has been argued that resultant behaviors may be more reflective of anxiety or fear, rather than voluntary exploration of a new environment (Walsh and Cummins 1976; Carter et al. 2013). As an alternative approach, it has been suggested that an animals' home cage or refuge be connected to the new environment, so that entry into the unfamiliar arena can be quantified as real exploratory behavior (Walsh and Cummins 1976; Carter et al. 2013). Most amphibian studies using a NET or OFT have not provided a refuge or safe environment within the test arena, yet this approach should be considered by future studies aiming to test for exploration personality. Amphibians are known to alter their locomotor activity, hide, and/or exhibit defensive behaviors in response to acute stressors (such as handling and forced entry in a new environment) (Ricciardella et al. 2010; Narayan et al. 2013). Therefore, any attempt to measure exploration movement that is not voluntary may provide inaccurate estimates of an animal's true exploratory tendency.

Approaches used to test for personality along the activity axis

Activity is defined as the general activity level of an individual, ideally measured in a non-risky, familiar environment (Réale et al. 2007). In amphibians, three main tests have been used to measure activity levels: (1) NET, (2) OFT, and (3) activity in a familiar environment (AFET), with the majority of studies using a NET (Table 2). Using a novel environment test or open field test to measure baseline activity attracts the same criticisms as using these tests to measure boldness or exploration. Using the same test to measure multiple traits may confound measurements, and it may be hard to identify the behavioral trait an individual is expressing. For example, if activity is measured in a novel environment test, the question must be asked: is the movement rate expressed by an individual while acclimatizing to a new environment actually exploratory movement, or is it simply their baseline activity level? To avoid potential problems, we recommend that future studies aim to avoid non-target behaviors in their assays of activity by designing experiments that control for elements of novelty, risk, and disturbance (Réale et al. 2007). In captive amphibians, we recommend video recording individuals in their familiar home environment during periods without disturbance by handlers. Restricting disturbance from prey should also be considered. Amphibians are generally either active foragers or sit and wait foragers (Wells 2007), so the presence live food items may affect activity levels differently between species depending on foraging strategy. Providing food will also influence satiation levels and subsequent activity levels (i.e., an active forager might become less active with each prey item consumed).

When designing activity assays, the timing of activity assays should also be factored into experimental designs. Specifically, assays should be tailored to the natural circadian rhythms of the study species. Amphibian species are typically either crepuscular, diurnal, or nocturnal (Wells 2007). Baseline activity should be measured during peak activity periods. Measuring activity during non-peak activity periods (e.g., measuring nocturnal species activity during the day) may result in low inter-individual variation in behavior. Importantly, studies measuring baseline activity in wild amphibians have brought animals into captivity for a prolonged period of time, in order to familiarize individuals with their holding (home) containers, before measuring baseline activity levels (Aragón 2011; Maes et al. 2013). This approach allows for standardization of the test environment by removing novelty and risk, which is extremely difficult to achieve with animals living in situ (Bremner-Harrison et al. 2018). No study has attempted to measure amphibian baseline activity levels in the field, most likely because it would be difficult to achieve robust behavioral evaluation; many amphibian species are either nocturnal or cryptic (making capturing and identifying individuals for repeated measures difficult). Moreover, amphibian activity patterns vary greatly with environmental conditions such as temperature, rainfall, and humidity (Kaefer et al. 2012; Brown et al. 2013). In saying this, in situ measures of activity might be possible in groups such as poison dart frogs (family Dendrobatidae) which are typically conspicuous (displaying bright colors), diurnally active, and located in tropical environments with relatively consistent climatic conditions.

The importance of an ecologically relevant approach

When designing assays to test for animal personality, it is critical for researchers to consider the ecology of the test species. Failure to do so may increase the chance of generating insignificant results or findings that are not ecologically relevant. For example, an investigation of boldness behavior in American bullfrog larvae (*Rana catesbeiana*) failed to detect repeatable, among-individual differences in boldness, which may have occurred because the method employed was inappropriate for this species (Carlson and Langkilde 2013). The study measured boldness by quantifying the behavior of tadpoles in the center of an open field, though predators of bullfrog larvae (e.g., dragonfly nymphs) are known to reside on the periphery of ponds around vegetation (Carlson and Langkilde 2013). As such, open areas may actually be less risky for this species, and bold individuals may be those that spend less time in open water. The authors of this study may have instead measured boldness as time spent on the periphery of a model pool or time spent near peripheral vegetation. When designing assays for any species, researchers should consider the effects of species-specific ecological factors (Réale et al. 2007; Toms et al. 2010; Dall and Griffith 2014). We recommend tailoring behavioral assays to the study species by designing tests that reflect the ecology of the species, rather than using a general approach that might not capture meaningful behavior. Although this approach may not allow for direct comparisons between species, it will allow for more robust and ecologically relevant behavioral evaluation.

Evidence for behavioral syndrome correlations in amphibians

Understanding how certain behavioral traits are related to each other, and the contexts they are expressed in, is an important area of research within the animal personality field. The concept of behavioral syndromes is the notion that correlations occur between personality traits and/or functionally different behaviors across contexts or situations (Sih et al. 2004a, 2004b; Carter et al. 2013). In theory, behavioral syndromes play an important role in determining individual fitness because they imply that individuals have a limited level of overall behavioral plasticity (Sih et al. 2004b). This means that correlations between behaviors can potentially result in the expression of sub-optimal behavior in certain contexts (Johnson and Sih 2005, 2007). For example, in funnel web spiders (*Agelenopsis aperta*), a behavioral correlation between aggression and boldness (individuals who are more aggressive in conspecific contests are also bolder towards potential predators) leads to sub-optimal anti-predator behavior (Riechert and Hedrick 1993). At present, a total of 13 studies (spanning 20 anuran species and three caudate species) have investigated behavioral syndromes in amphibians (Tables 2 and 3). Of these 13 studies, eight (spanning 17 anuran species and three caudate species) have provided evidence for the existence of correlated behaviors/personality traits across contexts and/or situations.

Evidence for behavioral syndromes in amphibians demonstrates that individual behavioral traits can carry across situations, even when behavior is deemed sub-optimal (potential costs of the behavior outweigh the potential benefits, such as increasing foraging activity in the presence of a predator) (Richardson 2001; Sih et al. 2003; Aragón 2011). For example, a study by Richardson (2001) investigating the mean activity levels of 13 larval anuran species in the absence and presence of different predators found positive correlations in tadpole activity across contexts representing different levels of predation risk (Richardson 2001). However, the results of this study should be interpreted with caution because sample sizes were very low (ranging from two to nine individuals per species), which can generate false significant outcomes. Furthermore, there was no mention of whether context treatments were randomized, raising the possibility of an order effect. More recently, a study by Sih et al. (2003) found that activity levels in two species of larval salamander (*Ambystoma barbouri*) and (*Ambystoma texanum*) ($n = 92$) were positively correlated across contexts with different levels of predation risk, with treatment order for individuals randomized over a 5-day period. Salamander larvae that were more active in the absence of predator chemical cues were also more active when predator chemical cues were present, representing a carryover of activity across predation contexts (no predation vs. predation) and the presence of an activity syndrome in these species (of note, predator treatment did not have a consistent, significant effect on larval activity, however species differed in their response to predator treatment) (Sih et al. 2003). These early studies provide important evidence for behavioral carryovers across contexts in amphibians. An important next step will be to investigate the impact of such flow on effects on individual fitness.

In contrast to the aforementioned studies, five amphibian studies (spanning four species of frogs) failed to provide evidence for the existence of behavioral syndromes. For example, Videlier et al. (2014, 2015) found no evidence for behavioral syndromes in the Western clawed frog, *Xenopus tropicalis*. Both studies found that male and female Western clawed frogs displayed temporally repeatable, among-individual differences in exploration behavior (personality), and also claimed to have found evidence that that the species displayed sex-dependent behavioral syndromes (Videlier et al. 2015). However, what these studies actually identified were three distinct behavioral clusters (low, medium, and high explorers) along the exploration/avoidance axis, describing the spread of personality in Western clawed frogs (Videlier et al. 2014). Neither study specifically tested for correlations in exploration across different contexts or situations, nor did they look for correlations between exploration behavior and other behaviors expressed in varying contexts. Therefore, according to the widely accepted definition of a behavioral syndrome, although both these studies provided a comprehensive test for the presence of personality along the exploration/avoidance axis, they did not test for behavioral syndromes.

Overall, there is growing evidence that behavioral correlations and behavioral syndromes exist in various amphibians. However, evidence remains limited to a small number of species (17 anurans and three salamanders) encompassing three behavioral axes (boldness, exploration, activity) (see Tables 2 and 3), with a bias towards behavior expressed in an antipredator context. As amphibians have been shown to display personality along three of the five major behavioral axes, (with strong potential for personality to also occur along the aggression and sociability axes), they make an ideal group for studying correlations between personality traits. However, future behavioral syndrome research in amphibians should endeavor to investigate behavioral correlations in a broader range of contexts, such as foraging, competition, mate choice, and parental care contexts. It is also recommended that future behavioral syndrome studies in amphibians explore the implications these behavioral relationships have for individual survival and reproductive success. This research would provide a platform for beginning to explore the evolutionary causes of behavioral syndromes.

Beyond the five behavioral axes—other possible syndromes

To date, most behavioral syndrome research in amphibians, and indeed other vertebrate classes, has centered on the five behavioral axes—boldness/shyness, exploration/avoidance, activity, aggression, and sociability. However, there are numerous other behaviors that are relevant to the behavioral syndrome framework that require attention (Sih and Bell 2008). Examining reproductive behavior in particular would be a fruitful future research direction. It has been known for a long time that male amphibians show individual differences in mating tactics (Wells 2007). Therefore, behavioral syndromes associated with mating behavior and alternative mating tactics may be widespread in amphibians. In many amphibians, it has been shown that large males are typically dominant territory holders, while smaller, subordinate males use sneaky tactics to secure mates (Wells 2007). Although this type of mating behavior has been studied in detail, it is not known whether individual differences in amphibian mating tactics are correlated with other behaviors across contexts (Sih and Bell 2008; Schuett et al. 2010). This idea has been considered by a study in male water skinks (*Eulamprus heatwolei*) that examined behavioral differences between "territory holders," which defended resource patches, and "floaters" which moved between the territories of other males (Stapley and Keogh 2004). It was found that territorial lizards were less willing to explore new habitats and were less likely to retreat during a simulated predator attack (Stapley and Keogh 2004). Importantly, lizards displaying each tactic did not differ in body size or body condition, and presumably age, as body size and age are usually tightly correlated in lizards. These results suggest that certain alternative mating tactics may result from underlying behavioral tendencies (rather than being condition dependent), warranting further research in this area. Given the prevalence of mating tactics across amphibian species, there are excellent opportunities to investigate mating behavior (and mating tactics) within the animal personality and behavioral syndrome framework. Male territorial behavior in amphibians is often tightly linked to circulating hormone levels (i.e., testosterone controls aggression and territorial behavior), so a valuable first line of enquiry would be to investigate how changes in basal androgen levels influence male behavior in different contexts. This could be easily achieved by studying the relationship between aggressive behaviors and plasma levels of testosterone (obtained through blood samples) in different contexts (de Assis et al. 2012) or by surgically implanting subcutaneous testosterone tablets and quantifying changes in the behavioral responses of individuals to different threat types (e.g., threats from rival males versus threats from predators) (Penna et al. 1992).

Among amphibians, it is also well established that females frequently show preferences for certain males (Wells 2007). Furthermore, females are known to show variation in their preferences based on a broad suite of traits, including body size (Zhu et al. 2016), color (Dreher et al. 2017), call characters (Gerhardt et al. 2000), and nest site qualities (Felton et al. 2006). Despite such individual variation, female choosiness is yet to be considered in the behavioral syndrome framework (Sih and Bell 2008). A behavioral syndrome involving "choosiness" may be determined by evaluating the repeatability of "choosiness" across different contexts and situations (Sih and Bell 2008; Schuett et al. 2010). For example, it could be tested whether females that are choosy about their mates exhibit repeatable choosiness across different situations, such as in the presence/absence of different male traits or male abundances (Sih and Bell 2008; Schuett et al. 2010). Furthermore, it could be tested whether choosiness is displayed in different contexts. For example, are females who are choosy about their mates, also choosy when deciding on where to live (habitat preferences), or what to eat (foraging preferences) (Sih and Bell 2008)?

In amphibians, mate choice studies can easily be conducted in transportable mate choice arenas (erected in either the lab or the field), and such studies are most practical in terrestrial or semiaquatic species where behavior can easily be observed. Tests typically involve male calls or images (either real images or 3D animated images) being broadcast from speakers or monitors at the opposite end of a mate choice arena (Stange et al. 2017). In nocturnally active species, observations can be made using recording devices equipped with infrared night vision technology which uses amplified visible and near infrared radiation to enable observation under extremely low light, minimizing disturbance to test subjects. Recently, it has also been demonstrated that female movement behavior can be visualized in the dark by fitting individuals with miniature light emitting diode (LED) backpacks and tracking positional changes using continuous high definition recording of the LED coordinates (Aihara et al. 2017). In combination, changes in male calling activity in either artificial or natural choruses can be monitored, and correlated with female movement patterns, using a firefly system, whereby a miniature microphone is connected to a light emitting diode that briefly illuminates when a threshold sound pressure level is reached (Mizumoto et al. 2011, 2017). Research in this area may reveal that being choosy is the result of an individual's underlying personality and that "choosiness" is a behavioral syndrome. Testing additional behavioral axes within the behavioral syndrome framework will be an important step towards uncovering the complexity and extent of behavioral syndromes in amphibians.

Ontogenetic stability of animal personality and behavioral syndromes

An emerging question of interest is whether or not personality variation and behavioral syndromes transcend life stages (Bell and Stamps 2004; Sih et al. 2004a; Wilson and Krause 2012a; Wuerz and Krüger 2015). Most studies investigating personality and/or behavioral syndromes are conducted over a relatively short time span (days to weeks) and do not represent different stages in an organism's life cycle (Bell et al. 2009; Wuerz and Krüger 2015). Consequently, we still know very little about the development and proximate causes of personality and behavioral syndromes (Wilson and Krause 2012b; Wuerz and Krüger 2015). Animals that undergo metamorphosis provide a unique opportunity to explore the development of personality and behavioral syndromes and are increasingly being targeted for empirical research (Wilson and Krause 2012b). During metamorphosis, individuals experience rapid changes in morphology, physiology, and behavior, and each life stage is typically subject to vastly different ecological conditions (Wilson and Krause 2012a, 2012b). This provides the opportunity to explore how larval behavior is translated into adult behavior in light of profound transformations in hormonal profiles, morphology, and environment.

There are two opposing theories regarding changes in personality over life and in particular metamorphosis. The first is that animal personality and behavioral syndromes may either form or disappear during development or physical ontogenetic niche shifts (Brodin 2009; Wilson and Krause 2012b). This notion is based on the premise that different life stages are subjected to different selective pressures (e.g. natural selection will affect juveniles more strongly than adults, while sexual selection will affect adults more strongly than juveniles) so particular behavioral adaptations may be favored at each life stage (Brodin 2009; Wilson and Krause 2012b). In principle, we might expect personality and behavioral syndromes to be decoupled across life stages when a species' ecological niche or primary habitat differs dramatically between larval and adult life stages (Sih et al. 2004a; Wilson and Krause 2012b). Further to this, personality and behavioral syndromes may decouple due to a remodeling of a neural and motor systems at the time of metamorphosis (Consoulas et al. 2000). This abrupt remodeling may remove any effects of previous juvenile experience and effectively "reset" phenotype-determining processes, providing adults with a clean start (Brodin 2009; Monceau et al. 2017).

The second theory is that personality and/or behavioral syndromes will persist across metamorphosis. This notion is based on several lines of reasoning. First, personality and behavioral syndromes are expected to transcend life stages if personality is controlled by inflexible genetic mechanisms (Sih et al. 2004b; Brodin 2009). It is well established that personality traits are heritable (Dochtermann et al. 2014), and it is argued that strong genetic correlations between traits (i.e., pleiotropy where correlated behaviors are controlled by a shared genetic mechanism) could cause behavioral stability over time (Brodin 2009). Although this outcome could also arise if there is selection for optimal trait combinations (i.e., linkage disequilibrium), whereby genes (or alleles) influencing a particular personality trait are co-inherited with genes influencing another personality trait, producing an adaptive genetic correlation (Brodin 2009).

An alternative school of thought is that personality and syndromes might remain stable across metamorphosis if personality traits and behavioral syndromes are state-dependent (proximately controlled by underlying physiological state variables) (Brodin 2009; Sih et al. 2015). For instance, personality and behavioral syndromes might remain robust to developmental changes if larval and adult metabolic rate and energetic demands are similar (Wilson and Krause 2012b). Larval behavior might also have positive feedbacks on state, maintaining differences between individuals and personality across life stage (Brodin 2009; Sih et al. 2015). In addition, early experiences during ontogeny may also generate consistent patterns of behavior, despite physiological, morphological, and ecological changes (Wilson and Krause 2012b). For example, Wilson and Krause (2012b) suggested that individuals might become predisposed to certain behavioral patterns because of adverse conditions experienced during development (e.g. a pond drying out early during tadpole development may result in early metamorphosis, then a decreased body size at maturation and further flow on effects that might alter adult behavior).

Amphibians are characterized by a discrete biphasic life cycle, with each life stage subject to vastly different ecological conditions (Wells 2007). Larval amphibians typically live in aquatic environments, are primarily herbivorous, and heavily bias their investment towards somatic growth and development. By contrast, adult amphibians can inhabit a wide variety of environments (aquatic, arboreal, terrestrial), are mainly carnivorous, and are geared for dispersal and reproduction (Wilson and Krause 2012a, 2012b). If environmental conditions experienced during early development are critical for the development of personality and behavioral syndromes, we should expect selection to decouple behavioral syndromes when a species ecological niche or primary habitat differs dramatically between larval and adult life stages (Wilson and Krause 2012a). To test this prediction, Wilson and Krause (2012a) investigated whether personality variation and behavioral syndrome correlations persisted across metamorphosis in the Marsh frog (*R. ridibunda*). They expected that behavioral syndromes would be decoupled across life stages because the environmental conditions experienced during each life stage differ markedly in this species (larvae are completely aquatic while adults are semiaquatic and must perform in both aquatic and terrestrial environments) (Wilson and Krause 2012a). Instead, what they found was that animal personality and behavioral syndromes were consistent both within a life stage and across life stages (Wilson and Krause 2012a). These results suggest that behavioral traits in amphibians may be controlled by genetic mechanisms that govern their expression over ontogeny (Sih et al. 2004b; Wilson and Krause 2012a).

To date, there has been no attempt to explore the role of genetics versus environment in the development of amphibian personality. To this end, future research could make important advances by determining (i) the heritability of personality traits, (ii) isolating the genes involved in behavioral syndromes, and (iii) establishing how the expression of genes and interactions between genes are modified by environmental change. This knowledge could be attained using a combination of quantitative genetic approaches (e.g. cross-classified breeding designs and common garden experiments to determine trait heritability and the extent of gene by environment interaction), artificial selection experiments (to determine population level responses to specific selective pressures and potential for genetic correlations), quantitative trait locus mapping (to identify loci responsible for variation in personality traits), and whole genome microarrays (to elucidate changes in gene expression over time or context) (for a detailed discussion on the quantitative genetics and genomics of animal personality and behavioral syndromes, see Dochtermann and Roff 2010, van Oers and Mueller 2010, Laine and van Oers 2017, and Bengston et al. 2018).

Amphibians are ideal candidates for exploring such questions for a number of reasons. First, the external fertilization mode of amphibians means that in vitro fertilization approaches can be used to control parentage and estimate trait heritability free of confounding paternal or maternal effects (Dziminski et al. 2008). Second, because amphibians generally have small body size, high fecundity (many species produce hundreds to thousands of offspring), and a short generation time (many species reach sexual maturity in less than a year), it is relatively easy to rear multiple generations in a laboratory setting and conduct selective breeding experiments (Sumida et al. 2016). Third, researchers have already mapped full genomes for several frog species, including the Western clawed frog (Hellsten et al. 2010), the Tibetan frog (*Nanorana parkeri*) (Sun et al. 2015), and the American bullfrog (Hammond et al. 2017), placing scientists in an excellent position to interpret gene expression in different context and elucidate genetic mechanisms underpinning the ontogenetic stability of personality and behavioral syndromes.

Implications for conservation

There is growing recognition that knowledge of animal personality may facilitate animal conservation (McDougall et al. 2006; Blumstein and Fernandez-Juricic 2010; Merrick and Koprowski 2017). Surprisingly, however, there has been no attempt to investigate the conservation implications of animal personality in amphibians. Applying knowledge of animal personality to conservation programs could be particularly valuable for amphibians because biodiversity loss in this vertebrate class exceeds that of any other, with an estimated 41% of species now threatened with extinction (Wake and Vredenburg 2008; Dirzo et al. 2014). At present, the main management action to assist with the recovery of threatened amphibian species is the establishment of captive breeding and reintroduction programs (Griffiths and Pavajeau 2008). These programs have enormous potential to safeguard against the extinction of threatened species, however, the success of amphibian captive breeding and reintroduction programs has been highly variable (Soorae 2016). Two common problems contributing to the failure of amphibian captive breeding and reintroduction programs are (1) failure to produce large numbers of viable offspring for release and (2) poor survivorship post-reintroduction (Tapley et al. 2015; Soorae 2016).

We propose that knowledge of animal personality may assist in overcoming these problems by addressing behavioral issues in these two contexts. Knowledge of animal personality may be particularly relevant for amphibian captive breeding programs because reproduction in amphibians is typically a complex affair (amphibians are considered to have the highest reproductive diversity of all vertebrate groups), with considerable potential for individuals to vary markedly in their level of investment in courtship behavior, territorial behavior, mate choice, and parental care. Furthermore, all of these behaviors rely heavily on sophisticated multimodal communication systems (i.e., any behavior along the sociability behavioral axis will be impacted by signals to some degree). As amphibians have been a model group for the study of sexual selection for over 50 years, we already have a very good understanding of the proximate and ultimate causes of variation in amphibian reproductive behavior, mating systems, and communication systems. Integrating this knowledge with current theory in the field of animal personality stands to revolutionize captive breeding approaches. In regard to reintroduction, knowledge of amphibian personality is likely to be valuable because amphibians have complex biphasic life cycles, are highly vulnerable to predation, have small home ranges, and are susceptible to desiccation (and rely on freshwater), all of which expose them to a unique diversity of threats, habitat selection challenges and disease risks (Wells 2007).

The remainder of this review will outline and discuss the implications of animal personality for amphibian captive breeding and reintroduction programs, with frequent reference to unique aspects of amphibian ecology and behavior that make them excellent candidates for integrating an animal personality framework into conservation programs. This section draws heavily on research in other vertebrate classes (due to a lack of research in amphibians) and in many places is intentionally hypothetical to stimulate critical thought on the subject.

Animal personality and captive breeding

There is emerging evidence that animal personality may affect captive breeding by directly influencing both the probability of successful mating (mating success) and the number and viability of offspring produced (reproductive success) in breeding colonies (Martin-Wintle et al. 2017). Below we discuss various ways in which animal personality could influence these variables.

Behavioral compatibility and mating success

One way that animal personality may influence the probability of mating success is through effects associated with behavioral compatibility (how well individuals interact with each other) (Martin-Wintle et al. 2017). When animals are paired for breeding, certain personalities may be complimentary, while others may be conflicting. For some species, pairs with similar personalities may be better suited, while in others pairs with opposite personalities may have the highest chance of breeding success, and these effects may not necessarily be restricted to species that display monogamous pair bonds and/or biparental care. For example, in captive Black Rhino (*Diceros bicornis*), dominant more aggressive females have higher mating success when paired with submissive male partners that are less likely to engage in antagonistic interactions (Carlstead et al. 1999). To the contrary, in captive giant panda (*Ailuropoda melanoleuca*), successful mating is more likely when both partners are shy and less exploratory (Martin-Wintle et al. 2017). In amphibians, there is a high incidence of sexual conflict. Sexually active males often display aggressive behaviors, such as forced copulation, sexual coercion, and sexual harassment, and these behaviors can significantly reduce female fitness, by imposing either mortality or fecundity costs (Roberts and Byrne 2011). In many anuran species, males possess weapons such as enlarged arms or nuptial spines, and overly vigorous males can damage or even kill females (Roberts and Byrne 2011). For example, in the Quacking frog (*Crinia georgiana*), males are bigger than females and possess enlarged forearms, and competing males can drown females during mating, or interfere with effective fertilization (Byrne and Roberts 2004). While aggression in amphibians tends to be a male phenomenon, in some groups, females can also be highly aggressive. In salamanders, for example, females can sexually intimidate potential partners. In a manipulative experiment with red-backed salamanders (*Plethodon cinereus*), females were shown to violently attack partners that had recently associated with other females, intimidating males into monogamous relationships (Prosen et al. 2004).

In principle, benefits to captive breeding could come from identifying extremely aggressive personalities and either omitting these animals from breeding programs, or only pairing them with behaviorally compatible personalities, such as those who are likely to express avoidance or resistance behaviors that will minimize mating injuries. For example, in the red spotted newt (*Notophthalmus viridescens*), females can adjust their mating behavior (such as spending more time in refuge habitat), to mitigate costs of sexual harassment imposed by aggressive males (Grayson et al. 2012). In some species, evasive behavior can also be accompanied by morphological change. For example, in cane toads (*R. marina*), females can defensively inflate their bodies to ward off and dislodge unwanted males, allowing them to control mating outcomes (Bruning et al. 2010). If females that possess such abilities have different predispositions for adopting evasive tactics, this knowledge could help managers to identify optimal pairings. Importantly, in many amphibian captive breeding programs, animals can be paired and bred in small terrariums, allowing large numbers of discrete pairings during a breeding season (M. McFadden, personal communication). As such, it would be logistically feasible for managers to manipulate pairings based on personality and behavioral compatibility. In this regard, these types of benefits could also extend beyond the breeding season. Outside of the breeding season, amphibian captive colonies are typically housed in groups, often in same sex groups, and agonistic and aggressive interactions between individuals can elevate stress levels. For example, in captive male harlequin frogs (*Atelopus certus*) and (*Atelopus glyphus*) (where males aggressively fight each other), fecal cortisol levels significantly increase during group housing situations (Cikanek et al. 2014). Identifying and removing overtly aggressive personality types from captive housing groups could enable more effective and compatible group housing strategies, reduce stress, improve individual welfare, as well as reproductive viability in subsequent breeding seasons (Campbell et al. 1992).

Mate choice and mating success

Animal personality may also influence the probability of mating success if personality variation plays a role in female mate choice (Schuett et al. 2010; Merrick and Koprowski 2017). Animal personality may influence mate choice by signaling a potential mate's ability to provide parental care. For example, female fighting fish (*Betta splendens*) prefer highly aggressive and bold males, which are also better at defending territories and guarding young (Doutrelant and McGregor 2000). Alternatively, personality may influence mate choice by signaling a potential mate's genetic quality (possession of good genes or compatible genes), thought this is yet to be empirically tested (Schuett et al. 2010).

Importantly, even if certain personality traits confer a mating advantage, driving strong directional selection, genetic variation for personality traits should still be maintained by mutation-selection balance; particularly if personality traits are controlled by more than one gene (the rate of appearance of mutations affecting a trait increases where there are more genes involved) (Nettle 2006; Verweij et al. 2012). In addition, genetic variation could be maintained by heterogeneity in environmental conditions creating antagonistic selection pressure on a personality trait, either between locations or successive generations (Réale and Dingemanse 2010). In amphibians, female mate choice is extremely common, with abundant evidence that females prefer males with secondary-sexual traits (such as large body size, low call frequency, high call rate or bright coloration) that signal a male's ability to supply either direct benefits, such as fertility benefits or paternal care, or indirect genetic benefits, such as good or compatible genes (Andersson 1994; Wells 2007). At present, knowledge of sexual selection is largely ignored in amphibian captive breeding, despite emerging evidence that enabling female mate choice can improve both mating success and clutch production (Robertson 1990; Reyer et al. 1999). Exploring links between animal personality and mate choice in amphibians could provide key insights into mechanisms of sexual selection and facilitate social manipulations that enable more effective captive breeding.

Parental care and reproductive success

Once mating takes place, animal personality may continue to affect the viability of a captive population by influencing the reproductive success of individuals. There is emerging evidence that a parent's personality can influence the number and quality of offspring they raise (Both et al. 2005; Schuett et al. 2011; Mutzel et al. 2013). For example, individuals with certain personality traits might be better at raising young under particular environmental conditions (Dingemanse et al. 2004). This has been shown in wild boar (*Sus scrofa*), where less exploratory and less aggressive females raise a greater number of young than aggressive, exploratory females during years with high food availability (which may influence female risk taking behavior and predation risk) (Vetter et al. 2016). Past research has also revealed that interactions between parental personalities can influence offspring viability and thus reproductive success. This has been demonstrated in Great tits (*Parus major*), where parents with similar personalities along the exploration/avoidance axis (i.e., highly exploratory pairs and less exploratory pairs) produce a greater number of offspring, that are also in better condition, and more likely to survive and breed (Both et al. 2005).

Parental care is widespread in amphibians, with species from most families exhibiting some form of either uni- or biparental care (Wells 2007). Currently, it is not known whether or not animal personality influences the parenting ability of amphibians, but research in this area has the potential to generate knowledge that could improve the reproductive output of captive colonies. Past observational studies of captive frogs have proven effective at quantifying costs and benefits of parental care (Dugas et al. 2015), and similar approaches could be used to gain initial insights into associations between personality and care giving in threatened species.

Personality and communication: are certain personalities better communicators?

Although amphibians are widely recognized for their highly sophisticated acoustic communication abilities (males typically invest heavily in advertisement and territorial calling), communication in many groups is also facilitated by an extensive use of visual cues (De Sá et al. 2016), chemical cues (Belanger and Corkum 2009), and vibratory cues (Caldwell et al. 2010). Without question, successful communication in all amphibians plays a key role in reproduction (Wells 2007). Communication is not only essential in mate recognition and mate choice but also plays a fundamental role in the resolution of territorial disputes and parental care (Bee and Gerhardt 2001; Vargas-Salinas et al. 2014). As such, failure to facilitate successful communication in anurans stands to severely limit the success of captive breeding programs.

The relevance of personality in amphibian communication and captive breeding is yet to be considered, but it is conceivable that certain personality types might be better communicators (i.e., might more effectively send or receive signals) and that targeting such personalities for breeding (e.g., active males that invest more in calling) could significantly increase the probability of sexual encounters and successful reproduction. A number of recent theoretical and empirical studies have highlighted the potential for personality to have profound effects on the efficacy of sexual communication (Dirienzo and Hedrick 2014). In particular, there is emerging evidence that personality can influence signal quality (Ducrest et al. 2008), the frequency and duration of signaling (Naguib et al. 2010), and communication network structure (Matessi et al. 2010). With the goal of applying such principles to amphibian captive breeding, we recommend that future research focus on investigating whether personality can predict an individual's capacity to send, receive, and perceive sexual signals. It is important to bear in mind that communication traits in captive raised individuals might be linked to different personality traits than in wild individuals, because time-energy budgets differ in captivity. Such work will provide a conceptual platform for engineering captive breeding environments to maximize communication efficacy and reproductive output.

Personality and reintroduction

Following reintroduction into the wild, animal personality is likely to affect how well an individual establishes itself and survives, and in turn, the overall success of a reintroduction program (McDougall et al. 2006; Merrick and Koprowski 2017). In a new environment, animal personality may influence an individual's ability to avoid threats, disperse, select habitat, and/or avoid disease; all of which can be expected to influence the likelihood of survival and reproductive success.

Avoiding threats

An individual's personality may determine how it reacts to threatening stimuli, affecting its probability of survival post-reintroduction. Bold individuals that take more risks may suffer increased mortality due to increased exposure to predators or harmful situations (Smith and Blumstein 2008). For example, bold Swift foxes (*Vulpes velox*) (measured as latency to leave a refuge and approach novel objects) have been shown to have a lower survival rate post-reintroduction because they traveled greater distances from the release site and were less afraid of dangerous novel stimuli, such as motor vehicles (Bremner-Harrison et al. 2004). To the contrary, bold individuals that take more risks may have increased survival when the benefits of risk taking behavior outweigh the costs under certain spatial or temporal circumstances. For example, bold Tasmanian devils (*Sarcophilus harrisii*) (measured as latency to approach novel objects) have been shown to have a higher survival rate post-reintroduction, yet the reason for this remains uncertain (Sinn et al. 2013).

Personality along the exploration/avoidance axis may also influence an individual's exposure to threats. Again, however, the direction of the effect might be difficult to predict. On the one hand, highly exploratory individuals that are preoccupied with exploratory behavior, and invest less in vigilance, may be more susceptible to predation. This has been shown to be the case in convict cichlids (*Amatitlania nigrofasciata*) where highly exploratory individuals were found to be slower to react to a predator attack because they devoted more attention to foraging than to anti-predator vigilance (Jones and Godin 2010). On the other hand, less exploratory and less active individuals might have less capacity to evade predators. This has been demonstrated in captive raised voles (*Microtus rossiaemeridionalis*), where individuals who were less exploratory in their new surroundings (distance moved from release site) following reintroduction were more easily detected by predators (Banks et al. 2002). Critically, the relationship between survival and exploration personality has also been shown to vary with the spatiotemporal conditions of the release site. In a study on reintroduced European mink (*M. lutreola*), exploration personality was found to be both positively and negatively correlated with survival, depending on the time of release and release location (Haage et al. 2017), indicating that associations between personality and survival in a reintroduction context may be more complex than previously thought.

In amphibians, the association between boldness and survival has been examined in just one species. In a manipulative laboratory study, Carlson and Langkilde (2014) measured boldness behavior in wood frog tadpoles (*Lithobates sylvaticus*), subjecting individuals to a live predator in order to determine whether boldness influenced survival in a risky environment. Unexpectedly, it was found that boldness did not alter survival rates (Carlson and Langkilde 2014). Of note, however, the study did not statistically test for trait repeatability, so the findings must be interpreted with caution. Furthermore, this study only assessed boldness in 20 individuals, which may have resulted in low inter-individual variation in behavior. As such, ongoing research is needed. Knowledge gained from studies investigating whether personality influences predation risk in threatened amphibians stands to greatly benefit reintroduction programs. If associations between an individual's personality and predation risk are established, conservation managers will have the option to selectively target individuals who are best suited to the current or forecast release conditions. For instance, in environments with extremely high predation levels, releasing individuals who are shy and risk averse might reduce initial mortality rates and improve reintroduction outcomes, without the need for predator removal.

Pre-release training: can certain personalities more effectively learn to avoid threats?

Reintroduction programs can suffer catastrophic failure when naïve, captive-bred animals fail to show aversive responses to post-release threats, such as predators or toxic prey items. One way to overcome this problem is to train individuals to recognize and avoid major threats. In mammals and birds, training by associative learning has been effectively used to improve post-release survival (Griffin et al. 2000), and this approach could be of value to amphibian reintroduction programs. Amphibians have a remarkable, though somewhat underappreciated, ability to learn, with individual experience known to alter various fitness-determining behaviors, including anti-predator behavior (Epp and Gabor 2008), foraging behavior (Sontag et al. 2006), and social behavior (Ferrari and Chivers 2008). Moreover, there is evidence from work with salamanders, newts, and wood frogs that associative learning can be used to train amphibians to recognize unfamiliar potential threats, and that training is effective with adults (Woody and Mathis 1998), larvae (Crane and Mathis 2011), and even embryos (Mathis et al. 2008; Ferrari and Chivers 2010). Remarkably, amphibians can also learn to associate time of day with diel patterns of predator activity (Ferrari and Chivers 2009), and learning can be extremely rapid, occurring over just a matter of days (Ferrari and Chivers 2010).

Based on this knowledge, we predict that training schemes will be increasingly incorporated into amphibian reintroduction programs. Knowledge of personality stands to rapidly advance the development of such schemes because it has recently been demonstrated that personality underpins individual differences in learning performance in mammals (Carter et al. 2014), birds (Titulaer et al. 2012), and fish (Kareklas et al. 2017). We propose that identifying personalities that are better suited to training might be a logistically simple way to produce cohorts of captive individuals with an increased probability of post-release survival. Sophisticated training protocols have already been developed for amphibians (Heyes 2012), and this knowledge could provide a conceptual basis for designing assays to evaluate how personality functionally relates to individual variation in learning ability. Training regimes could then be tailored according to the ecology of target species. These approaches may prove to be particularly effective in species where individuals with risk averse personalities are also those that learn more effectively prior to release.

Dispersal

There is increasing evidence that animal personality variation can influence how individuals move through the environment (personality-dependent dispersal) (Cote et al. 2010a, 2010b; Chapple et al. 2012). For example, Great Tits with a higher exploratory tendency have been found to disperse further than less exploratory individuals (Dingemanse et al. 2003), and mosquito fish (*Gambusia affinis*) who are more asocial have been found to disperse further than more social individuals (Cote et al. 2010b). In amphibians, links between personality and dispersal have been explored in two studies. Brodin et al. (2013) compared personality and dispersal tendencies across populations of Common brown frogs (*Rana temporaria*) and found that individuals from isolated island populations were bolder and more exploratory than individuals from mainland populations (Brodin et al. 2013). Recent work in invasive cane toads has found that toads at the edge of the invasion front are bolder and more exploratory than toads from the center of the species current range (Gruber et al. 2017b), providing good evidence for personality-dependent dispersal.

Amphibians generally have very small home ranges compared to other vertebrates of similar size (home ranges are estimated to be 2–10,000 times smaller than mammals, birds, and reptiles under 20 g in body size) (Wells 2007). Nevertheless, amphibians can still vary greatly in space utilization and dispersal tendencies, with some species showing extreme site fidelity, while others move vast distances over just days or weeks (Wells 2007). For example, during the breeding season, small-mouthed salamanders (*A. texanum*) have been shown to travel tens of kilometers in search of mating partners (Denton et al. 2017). As such, knowledge of personality-dependent dispersal in amphibians could have considerable value for conservation programs endeavoring to manage reintroduced populations at different spatial scales (McDougall et al. 2006). Different personalities might be targeted for different release environments. For example, individuals who are more exploratory, and are more likely to disperse further in search of suitable habitats, may be better candidates for inclusion in programs aiming to establish new founder populations, or improve gene flow between isolated populations (McDougall et al. 2006). Contrastingly, in situations where suitable habitats are highly fragmented, or where habitats have been constructed specifically for animal use upon release, the use of individuals who are less exploratory and less likely to disperse may be preferable (McDougall et al. 2006). Creation of artificial habitats (such as artificial ponds) is common practice in amphibian reintroduction programs (Smith and Sutherland 2014). However, if animals disperse away from newly created habitat upon release, they are unlikely to contribute to the establishment of new populations. Conservation managers have attempted to remedy this problem by constructing amphibian-proof fences around release sites (Darcovich and O'Meara 2008). For example, during translocations of the Green and Golden Bell frog (*Litoria aurea*) in Sydney Australia, boundary fences were erected around protected and artificial habitat to stop individuals from dispersing into surrounding urban areas (Darcovich and O'Meara

2008). Selecting for individuals that are less exploratory and less likely to disperse may help mitigate the problem of high initial dispersal and reduce management costs.

Habitat selection

An individual's personality can influence its choice of habitat in a new environment, and habitat preferences have been shown to be repeatable (Merrick and Koprowski 2017). For example, in three-spined sticklebacks, highly exploratory individuals consistently prefer open habitat areas compared with less exploratory individuals, who consistently prefer sheltered areas (Pearish et al. 2013). Importantly, the type of habitat an individual chooses may influence its risk of predation, feeding rate or competitive ability, and have significant fitness consequences (Stamps and Swaisgood 2007). For example, in North American red squirrels (*Tamiasciurus hudsonicus*), active and bold individuals who preferentially use open areas are more susceptible to predation (Boon et al. 2008). In amphibians, a study by Smith and Doupnik (2005) investigated the repeatability of habitat choice and animal personality in American bullfrog tadpoles and concluded that there was no significant among-individual variation in habitat choice (Smith and Doupnik 2005). However, this study had a small sample size ($n = 19$ individuals) and did not statistically test for associations between personality and habitat choice, so the influence of animal personality on habitat selection in amphibians is yet to be comprehensively investigated.

In amphibians, habitat selection is known to have significant fitness consequences. For example, in a study of newly metamorphosed Gopher frogs (*Rana capito*), individuals who chose to shelter in underground refuges had a higher chance of survival than frogs who remained in open areas (irrespective of body mass or snout vent length) (Roznik and Johnson 2009). Considering the potential for habitat selection to influence individual fitness, future studies need to explore how personality influences habitat selection in amphibians. In principle, this knowledge would be valuable for reintroduction programs because conservation managers would be able to predict the type of habitat an individual would prefer (depending on their personality) and ensure that appropriate habitats are available at release sites. Manipulating or creating habitat is frequently done prior to amphibian reintroductions (Smith and Sutherland 2014). For instance, during Great Crested Newt (*Triturus cristatus*) reintroductions in England, providing artificial hibernacula and refuges helped to maintain stable populations (Smith and Sutherland 2014). Providing individuals with their preferred habitat (e.g., shy individuals may prefer more sheltered refuges) could potentially reduce individual stress levels post-release and increase the chance of successful establishment (Stamps and Swaisgood 2007).

Disease transmission (infectious personalities)

Animal personality may play a significant role in the transmission of disease and parasites (Barber and Dingemanse 2010; Wolf and Weissing 2012; Merrick and Koprowski 2017). It is predicted that variation in certain behavioral traits such as sociability, activity, or exploration may increase or decrease the probability that an individual will be exposed to conspecifics or habitats that carry disease or parasites (Barber and Dingemanse 2010). Individuals who are more active or exploratory and willing to approach novel objects are more likely to expose themselves to previously un-encountered sources of disease, increasing their risk of infection (Barber and Dingemanse 2010; Sih et al. 2018). The effect of personality on disease transmission might vary depending on disease transmission mode. For instance, sociability might be more relevant for diseases that spread via close range contact and aggression might be important for diseases that spread via physical contact. To date, only one study has investigated how behavioral traits relate to parasite susceptibility in amphibians. Koprivnikar et al. (2012) found that individual variation in exploratory behavior in Wood frog tadpoles (*L. sylvaticus*) was a significant predictor of parasite load, with highly active and exploratory individuals harboring more trematode worms (Koprivnikar et al. 2012). These findings may be particularly valuable for amphibian conservation because diseases such as the amphibian chytrid fungus (*Batrachochytrium dendrobatidis*) and salamander chytrid fungus (*B. salamandrivorans*) pose a significant threat to the stability and persistence of amphibian populations globally (Petersen et al. 2016).

Although chytrid fungus is a highly virulent and deadly disease, subtle, individual changes in behavior could have a major influence on disease transmission and the probability of infection. For example, recent research has shown that frogs that maintain a high body temperature through basking are less likely to contract the disease (Rowley and Alford 2013). Given that basking can be considered a “bold behavior" (it is a highly risky activity because it exposes the individual to diurnal predators), bolder individuals may be less likely to become infected. Further research in adult anurans may reveal both direct and indirect links between animal personality and disease transmission. If this proves to be the case, managers might be able to target for release personality types that reduce an individual's chances of exposure and susceptibility to infection (i.e., less infectious personalities) (McDougall et al. 2006). Such approaches have the potential to bolster threatened amphibian populations within areas of high disease risk and stem the decline of threatened species until scientific breakthroughs allow for more effective disease control.

The right mix of personalities: should multiple personalities be reintroduced?

While there may be benefits of releasing large numbers of individuals with personalities deemed to be optimal for specific reintroduction environments (as discussed above), there may also be costs. In particular, there may be long-term evolutionary consequences for populations if the selection of optimal personality traits results in removal of genetic variation and subsequent reduction in adaptive potential. Thus, it has also been proposed that benefits could come from seeding founder populations with individuals who display a wide range of personalities (Watters and Meehan 2007; Powell and Gartner 2011). The key argument being that greater diversity in behavioral phenotypes might enable greater adaptability and increase long-term reintroduction success (Watters and Meehan 2007). Costs and benefits of particular personality traits are expected to differ between ecological contexts (Dingemanse et al. 2004; Sih and Watters 2005). Therefore, by releasing groups of animals that display significant variation in personality along various behavioral axes, conservation managers might be able to strategically "hedge their bets" against environmental uncertainty and stochasticity (Watters and Meehan 2007).

To date, no study has attempted to investigate the optimal composition of personalities for reintroduction, but amphibians provide a model group for such research. Amphibians can be produced in large numbers in captivity, allowing for the release of hundreds to thousands of individuals with mixed personality types. In general, amphibians are also smaller in size than animals from higher vertebrate groups and can therefore be released into semi-natural enclosures that allow for soft releases and more intensive monitoring of individual survival and reproductive success post-reintroduction. Amphibians can also be closely monitored in situ using a variety of sophisticated tracking techniques (Rowley and Alford 2007). Radio telemetry is commonly used to track larger species, while harmonic direction and passive integrated transponders (PIT) tags are successfully being used to track smaller species (Rowley and Alford 2007; Connette and Semlitsch 2012). This form of behavioral management has enormous potential to transform reintroduction practices for a diversity of groups.

Conclusions and future directions

Animal personality and behavioral syndromes appear to be widespread in nature (Conrad et al. 2011), yet our understanding of animal personality and behavioral syndromes in amphibians remains limited. Amphibians afford excellent opportunities to investigate animal personality and behavioral syndromes because they display a spectacular diversity of easily observed and quantifiable behaviors along all of the major behavioral axes. Furthermore, they are unique in having biphasic life cycles defined by metamorphosis and obvious transformations in morphology, physiology, and habitat use, characteristics that enable detailed examination of behavioral changes across life stages and ecological contexts, as well as experimental investigation of the proximate mechanisms underpinning repeatable, individual variation in behavior. To date, studies have only investigated animal personality and behavioral syndromes in 24 amphibian species from eight families, (most from the order Anura). Nevertheless, there is emerging evidence that amphibians show animal personality and exhibit behavioral syndromes. Most recently, amphibian personality research has demonstrated that animal personality and behavioral syndromes can be stable over ontogenetic shifts, state-dependent, develop in response to environmental conditions (such as predation pressure and exposure to conspecifics) experienced during early development and that personality differences in wild amphibians can persist in captive raised offspring. These results highlight that amphibians provide a unique but untapped model group for exploring the proximate and ultimate causes of animal personality and behavioral syndromes.

To advance our understanding of animal personality and behavioral syndromes in amphibians, future work needs to examine species from a wider range of taxonomic groups with a diversity of life history strategies. Future studies should also consider the aggression and sociability behavioral axes (which have so far been ignored in amphibians) as well as examining behavioral correlations in a wide range of ecological contexts, such as mate choice, competition, and parental care contexts. Additionally, studies in amphibians should endeavor to investigate the role of genetics versus the environment in the development of personality and behavioral syndromes using a combination of quantitative genetics and genomic approaches to explore how personality changes over metamorphosis. This research would not only extend our knowledge of the personality repertoire of amphibians but also address major gaps in knowledge surrounding the development of animal personality and behavioral syndromes.

Broadening our understanding of the prevalence, causes, and consequences of animal personality and behavioral syndromes in amphibians may have applied value because there is a growing recognition that these phenomena can have important consequences for animal conservation. An emerging literature from other vertebrate groups (primarily mammals and birds) indicates that animal personality has potential to influence individual survival and reproductive success in these two contexts. Future work in amphibians should endeavor to identify whether individuals with particular personalities are more behaviorally compatible than others and whether personality influences patterns and outcomes of female mate choice. Furthermore, because many amphibians display parental care, studies should begin to explore whether personality influences the quality of maternal or paternal care provided or parental compatibility, and, in turn offspring viability. Knowledge gained from this work may help to overcome captive breeding failures linked to behavioral issues and increase colony viability through positive effects on both captive mating success and reproductive success. It is also recommended that future studies aim to monitor individuals post-release in order to determine how personality influences survival and establishment in unfamiliar natural environments. This knowledge could potentially increase the post-reintroduction survival and reproductive potential of animals by facilitating the selection of optimal behavioral types, or combinations of behavioral types, for release. This type of behavioral-based management has immense potential to enhance captive breeding and reintroduction practices for threatened amphibian species.

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Compliance with ethical standards

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