



Integrating Behavior and Physiology Into Strategies for Amphibian Conservation

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The amphibian decline crisis has been challenging to address because of the complexity of factors—and their multitude of interactive effects—that drive this global issue. Dissecting such complexity could benefit from strategies that integrate multiple disciplines and address the mechanistic underpinnings of population declines and extirpations. We examine how the disciplines of behavior and physiology could be used to develop conservation strategies for amphibians and identify eight research gaps that provide future directions for the emerging fields of conservation behavior and conservation physiology. We present two case studies on imperiled salamanders that show how studies of behavior and physiology may support amphibian conservation efforts. We found several applications of stress physiology to amphibian conservation, but long-term studies are needed to understand how stress ultimately affects individual fitness and population resilience. Additionally, multiple measures of physiological health are needed to provide a more holistic assessment of an individual's overall condition. Previous behavioral and physiological studies have been instrumental for understanding how amphibians respond to habitat modification, pathogens and parasites, contaminants, and invasive species. Some behavior-based approaches to mitigating invasive species issues have been successful in short-term studies with individual species. However, widespread application of these tactics has not yet been integrated into conservation and management strategies for ecologically similar species. A diversity of modeling approaches has enhanced understanding of how climate variability may impact amphibian populations, but model predictions need empirical tests to provide conservation managers with workable approaches to multiple perturbations associated with global environmental change. We illustrate that behavior and physiology can have broad utility for amphibian conservation, but evidence is scant that such studies have actually been used to inform strategies for amphibian conservation and management.

Keywords: amphibians, climate change, contaminants, disease, *ex situ* conservation, habitat change, invasive species, urbanization

INTRODUCTION

A substantial challenge in addressing the biodiversity crisis is the inherent complexity of environmental problems that drive population declines (Blaustein et al., 2011). Because of this complexity, there is a need to incorporate interdisciplinary approaches in conservation planning. This need has given rise to such fields as conservation genetics (Hedrick, 2001; Shaffer et al., 2015), conservation physiology (Wikelski and Cooke, 2006; Cooke et al., 2013, 2014), conservation behavior (Sutherland, 1998; Blumstein and Fernández-Juricic, 2004; Buchholz, 2007), and integrative behavioral ecotoxicology (Clotfelter et al., 2004; Peterson et al., 2017). Interdisciplinary approaches can directly address the mechanistic underpinnings of population processes (e.g., extinction risk and metapopulation connectivity), thus providing insight into the causes of biodiversity loss. The merger of physiology, behavior, and genetics with conservation, for example, has the potential to generate “cause-and-effect” relationships that can reveal how various stressors may contribute to population declines (Cooke et al., 2013; Birnie-Gauvin et al., 2017). Despite the promise that these emerging disciplines hold, a disconnect continues between basic research and applied wildlife conservation and management, particularly with behavior (Merrick and Koprowski, 2017; but see Fortin et al., 2005 for an illustrative counterexample). Moreover, the knowledge and tools that interdisciplinary approaches produce need to not only be used to document problems, but to also develop and test management strategies to solve complex conservation problems.

Integrative approaches could be particularly relevant in the case of amphibians which, among the vertebrate classes, have experienced the highest rates of diversity loss with an estimated 43% of all known species declining globally (Wake and Vredenberg, 2008). Amphibian population declines have been well-documented and are attributed to various stressors—and their synergistic interactions—such as habitat modification, disease, contaminants, competition and predation from both non-indigenous and native species, climate change, and overexploitation (Egea-Serrano et al., 2012; Grant et al., 2016; Blackburn et al., 2019). Because of the compounding effects of interacting stressors, the causes for amphibian declines are complex (Hayes et al., 2010; Blaustein et al., 2011). Studies of amphibian population declines traditionally have not addressed this complexity but, rather, have often focused on single factors (e.g., disease) affecting particular amphibian species (Blaustein et al., 2011). Because of their interactive nature, multidisciplinary approaches are well-suited to disentangle this complexity, uncover the behavioral, physiological, and other mechanisms that drive population declines and extirpations, and reveal pathways forward to developing conservation solutions.

Stressors are biotic or abiotic factors that can challenge individual homeostasis, resulting in an acute glucocorticoid (GC) stress response. During such reactions, energy stores are mobilized and rapid behavioral and physiological changes typically occur (Greenberg and Wingfield, 1987). However, severe or prolonged exposure to stressors can negatively influence reproduction, immune function, and growth, and can

impair subsequent responses to additional stressors because the hypothalamic–pituitary–adrenal/interrenal axis (HPA/HPI) becomes non-responsive (Sapolsky et al., 2000; McEwen and Wingfield, 2003). As the magnitude of a perceived stressor increases, GC levels may be upregulated or downregulated (Gendron et al., 1997; Gabor et al., 2018a), indicating that GCs may correlate with physiological health, population declines, and loss of genetic variation (Dantzer et al., 2014).

In addition to physiological indicators of environmental stress, behavioral “proxies” of population viability can also provide early indications of population decline, allowing proactive management and conservation *before* extinction risk escalates (Gerber, 2006; Janin et al., 2011; Gabor et al., 2018a; Madliger et al., 2018). Thus, given the unprecedented population declines and extirpations that amphibians are experiencing, we believe that the integration of behavior and physiology with conservation is both timely and likely urgent for this taxonomic group. We address the question: how can these disciplines be integrated and used to develop conservation strategies for amphibians? We review key studies in behavior and physiology to examine their potential to inform amphibian conservation. We then present two case studies with imperiled salamanders—one of a long-term program of behavioral research and the other from Gabor’s research on physiology and behavior—that show how such studies may support conservation efforts. Finally, we identify research gaps and potential directions that could enable future behavioral and physiological studies to help develop conservation approaches for declining amphibian populations.

EXAMPLES OF BEHAVIORAL AND PHYSIOLOGICAL STUDIES THAT SUPPORT CONSERVATION EFFORTS

We compiled studies of conservation behavior/physiology with amphibians, using Google Scholar and our knowledge of the literature (Table 1). We performed a search for publications on “conservation behavior and amphibians” and “conservation physiology and amphibians” in Google Scholar, primarily from 2000 to present (unless otherwise indicated). We additionally searched the Thomson Reuters Web of Science™ database across all years for literature on contaminants, behavior, and physiology, using the search terms “amphibian behavior and contaminants” and “amphibian physiology and contaminants.” We compiled selected studies that are relevant to five known stressors that impact amphibian populations [climate change; pathogens and parasites; invasive species; habitat modification (including urbanization); and contaminants: (Hayes et al., 2010)] and one tactic that is widely used as part of recovery strategies for threatened species (*ex situ* conservation/captive breeding). Although we include captive breeding here, we caution that captive breeding is a measure of last resort for critically endangered species that should not usurp protection of animals in the wild. This compilation, though not exhaustive, provides insight into ways behavioral and physiological studies can reveal amphibian responses to various factors, thus helping

TABLE 1 | Selected examples of studies in behavior and physiology that could help inform amphibian conservation.

Factor	Approach used/Finding	Behavior, Physiology, or Both?	Taxon	Source
CLIMATE CHANGE				
	Used knowledge of microhabitat preferences to enhance climate refugia	Both	Cane Toad (<i>Rhinella marina</i>)	Seebacher and Alford, 2002
	Used portable irrigation sprayers to artificially wet and manipulate water potentials at breeding sites because: (1) high substrate water potentials induce male calling and female oviposition and (2) could ameliorate dehydration, thus elevating resting metabolic rates	Behavior	Bibron's Toadlet (<i>Pseudophryne bibronii</i>)	Mitchell, 2001
	Studied foraging, food conversion efficiency, and stress release rates in response to increasing temperatures	Both	Eastern Red-backed Salamander (<i>Plethodon cinereus</i>)	Novarro et al., 2018
	Studied change in terrestrial moisture on stress, foraging, water uptake, and growth	Both	Spotted Salamander (<i>Ambystoma maculatum</i>)	Charbonnier et al., 2018
	Examined the effects of temperature and food availability on the timing of hibernation behavior	Behavior	Black-spotted Frog (<i>Pelophylax nigromaculatus</i>)	Gao et al., 2015
	Studied change in response to water reduction on resource allocation and stress	Physiology	Wood Frog (<i>Lithobates sylvaticus</i>)	Crespi and Warne, 2013
	Used thermal physiology, habitat associations, and biophysical models to estimate maximum body temperatures and, thus, composition of species assemblages, using simulated landcover change and climate warming	Physiology	Numerous species	Nowakowski et al., 2016
	Integrated physiological acclimatization and behavioral avoidance into simulation-based species distribution models to predict extinction risk due to climate change	Both	Southern Gray-cheeked Salamander (<i>Plethodon metcalfi</i>)	Riddell et al., 2018
PATHOGENS AND PARASITES				
	Documented how infections from pathogens and parasites may be mediated by altered thermoregulatory behavior ("behavioral fever") in amphibian hosts	Behavior	American Bullfrog (<i>Lithobates catesbeianus</i>); Red-legged Frog (<i>Rana aurora</i>); Boreal Toad (<i>Bufo boreas</i>); Panamanian Golden Frog (<i>Atelopus zeteki</i>)	Lefcort and Eiger, 1993; Lefcort and Blaustein, 1995; Richards-Zawacki, 2010; Murphy et al., 2011
	Emphasized that relationship between host behavior and infectious disease can (1) inform reserve design; (2) help predict how infectious diseases will be influenced by global changes; and (3) help develop network models to understand how parasites spread through a population	Behavior	Not specific	Hoverman and Searle, 2016
	Documented that host behavior can affect disease response	Behavior	Not specific	Woodhams et al., 2011
	Measured disease prevalence, body condition and two steroid hormones as bioindicator of health	Physiology	Wood Frog (<i>Lithobates sylvaticus</i>)	Crespi et al., 2015
	Documented the association between stress hormones, disease levels and behavior	Both	Midwife Toad (<i>Alytes obstetricans</i>)	Gabor et al., 2015
	Explored physiological mechanisms through which ultraviolet B radiation (UVBR) may affect host immune function and, thus, amphibian susceptibility to disease	Physiology	Not specific	Cramp and Franklin, 2018
	Demonstrated that individual host behavior, in particular, may influence infection success and parasite aggregation	Behavior	Pacific Chorus Frog (<i>Pseudacris regilla</i>)	Johnson and Hoverman, 2014
	Demonstrated that predators elicited behavioral (reduced activity) and morphological changes in tadpole hosts which, in turn, increased parasite transmission	Behavior	Pacific Chorus Frog (<i>Pseudacris regilla</i>)	Orlofske et al., 2014

(Continued)

TABLE 1 | Continued

Factor	Approach used/Finding	Behavior, Physiology, or Both?	Taxon	Source
	Explored the role of a contaminant as a stressor in mediating susceptibility to infection	Physiology	Cuban Treefrog (<i>Osteopilus septentrionalis</i>)	Gabor et al., 2018b
INVASIVE SPECIES				
	Demonstrated that a native mammal (Northern Quoll, <i>Dasyurus hallucatus</i>) has adapted to presence of poisonous invasive toads in some areas of Australia	Behavior	Cane Toad (<i>Rhinella marina</i>)	Kelly and Phillips, 2017
	Documented that anuran species with calls similar to those of invasive species modify their calling behavior when masked by chorus of invasive competitor	Behavior	Green Treefrog (<i>Hyla cinerea</i>); Cuban Treefrog (<i>Osteopilus septentrionalis</i>)	Tennessen et al., 2016
	Implemented predator recognition training	Behavior	Ozark Hellbender (<i>Cryptobranchus alleganiensis bishopi</i>)	Crane and Mathis, 2011
	Studied embryonic learning to novel fish predator chemical cues	Behavior	American Bullfrog (<i>Lithobates catesbeianus</i>)	Garcia et al., 2017
	Measured stress responses to evaluate effects of an invasive species on body condition, stress hormones, sex steroids, and reproductive success	Physiology	Cane Toad (<i>Rhinella marina</i>)	Narayan et al., 2015
	Used male calling behavior to attract, capture and remove an invasive toad	Behavior	Cane Toad (<i>Rhinella marina</i>)	Muller and Schwarzkopf, 2017
	Measured stress hormones and behavior to evaluate response to native and introduced fish predators	Both	San Marcos Salamander (<i>Eurycea nana</i>)	Epp and Gabor, 2008; Davis and Gabor, 2015
	Measured antioxidant enzyme activity to evaluate response to an invasive predatory snake	Physiology	Majorcan Midwife Toad (<i>Alytes muletensis</i>); Balearic Green Toad (<i>Bufoles balearicus</i>)	Pinya et al., 2016
	Measured antipredator behavior in response to aquatic invertebrates to gain insights on habitat restoration	Behavior	Barton Springs Salamander (<i>Eurycea sosorum</i>)	Davis et al., 2017
	Measured behavioral responses of salamanders to odors of native and introduced invertebrate predators/competitors	Behavior	Eastern Red-backed Salamander (<i>Plethodon cinereus</i>)	Anthony et al., 2007
HABITAT MODIFICATION (INCLUDING URBANIZATION)				
	Used conspecific call playbacks to alter amphibian distributions in ponds	Behavior	Green and Golden Bell Frog (<i>Litoria aurea</i>)	James et al., 2015
	Used chorus sounds to locate breeding habitat for anuran amphibians	Behavior	Multiple species	Buxton et al., 2015, 2018
	Used stress hormones and habitat selection to assess connectivity	Both	European Toad (<i>Bufo bufo</i>)	Janin et al., 2011, 2012
	Determined individual spatial requirements, home range size, and habitat needs	Behavior	European Toad (<i>Bufo bufo</i>); Green Toad (<i>Bufo viridis</i>)	Indermaur et al., 2009
	Measured heat tolerance and evaporative water loss to evaluate sensitivity to habitat modification	Physiology	Multiple species	Nowakowski et al., 2018
	Discovered that cognition and site fidelity in an arboreal salamander can help inform forest management strategies (clearcutting vs. retention of individual shelter trees)	Behavior	Spectacled Salamander (<i>Salamandrina perspicillata</i>)	Piraccini et al., 2017
	Studied movement behavior in fragmented landscapes vs. old forest stands and measured repeatability of behavior to understand behavioral divergence among populations in response to forest fragmentation and desiccation risk	Behavior	Eastern Red-backed Salamander (<i>Plethodon cinereus</i>)	Cosentino and Droney, 2016
	Sampled blood from individuals to test whether differences in corticosterone levels were associated with different qualities of breeding and migration habitat	Physiology	Spotted Salamander (<i>Ambystoma maculatum</i>)	Homan et al., 2003

(Continued)

TABLE 1 | Continued

Factor	Approach used/Finding	Behavior, Physiology, or Both?	Taxon	Source
	Used behavior to design irrigation and drainage systems	Behavior	Multiple species	Hou et al., 2010
	Examined movement and spatial distribution patterns to inform habitat selection and refuge construction for use in future reintroductions of captive animals	Behavior	Mexican Axolotl (<i>Ambystoma mexicanum</i>)	Ayala et al., 2019
	Used behavioral choice experiments to design road crossing structures	Behavior	Green Frog (<i>Lithobates clamitans</i>); Northern Leopard Frog (<i>Lithobates pipiens</i>)	Woltz et al., 2008
	Used learning to mitigate road mortality	Behavior	General	Proppe et al., 2016
	Measured stress hormones and activity across urban and rural streams to evaluate effect of urbanization	Both	Jollyville Plateau Salamander (<i>Eurycea tonkawae</i>)	Gabor et al., 2018a; this paper
	Measured behavioral responses to lights of various colors to understand effects of color on nocturnal migration across roads	Behavior	European Toad (<i>Bufo bufo</i>)	van Grunsven et al., 2017
	Reviewed physiological and behavioral effects of artificial night lighting in urban environments	Both	Multiple species	Perry et al., 2008
	Measured stress hormones to assess effect of intensive traffic	Physiology	Yellow-bellied Toad (<i>Bombina variegata</i>)	Cayuela et al., 2017
	Measured stress hormones to evaluate effect of traffic noise on stress and vocal sac coloration, an important cue in mate choice	Physiology	European Treefrog (<i>Hyla arborea</i>)	Troianowski et al., 2017
CONTAMINANTS				
	Reviewed physiological and behavior responses to contaminants	Both	Multiple Species	Sparling, 2003; Shuman-Goodier and Propper, 2016
	Used activity as a tool to study ecotoxicological effects of various contaminants	Behavior	3 Iberian anuran species; European Frog (<i>Rana temporaria</i>)	Denoël et al., 2010, 2012, 2013; Garcia-Muñoz et al., 2011
	Documented that a herbicide adversely affected neurotransmission and swimming performance in tadpoles	Both	Montevideo Tree Frog (<i>Hypsiboas pulchellus</i>)	Peltzer et al., 2013
	Investigated contaminant effects on tadpole activity and survival when exposed to different predator treatments	Behavior	Gray Treefrog (<i>Hyla versicolor</i>); American Bullfrog (<i>Lithobates [Rana] catesbeianus</i>); Green Frog (<i>Lithobates clamitans</i>); Spotted Marsh Frog (<i>Limnodynastes tasmaniensis</i>); Striped Marsh Frog (<i>Limnodynastes peronii</i>)	Bridges, 1999; Hanlon and Relyea, 2013; Sievers et al., 2018b,c
	Measured glycogen in tadpoles to assess stress response to aquatic pollution (nutrients and pesticides)	Physiology	Common Frog (<i>Rana temporaria</i>)	Strong et al., 2017
	Used movement and foraging behavior to inform effects of mercury contamination	Behavior	Northern Two-lined Salamander (<i>Eurycea bislineata</i>)	Burke et al., 2010
	Used water-conservation behaviors and foraging efficiency to inform effects of a contaminant (atrazine), temperature, and moisture	Behavior	Streamside Salamander (<i>Ambystoma barbouri</i>)	Rohr and Palmer, 2013
	Reviewed behavioral responses of amphibians to contaminants that are endocrine disruptors	Behavior	Various species	Clotfelter et al., 2004
	Used male calling behavior to inform effects of exposure to EE2 (an endocrine disruptor that is a component of contraceptives) on reproductive success	Behavior	African Clawed Frog (<i>Xenopus laevis</i>)	Hoffmann and Kloas, 2012
	Demonstrated that exposure to endocrine disrupting compounds alters male reproductive behavior	Behavior	Western Clawed Frog (<i>Xenopus tropicalis</i>)	Schwendiman and Propper, 2012

(Continued)

TABLE 1 | Continued

Factor	Approach used/Finding	Behavior, Physiology, or Both?	Taxon	Source
	Demonstrated that increased exposure to copper and elevated water temperatures increased the number of dragonfly attacks on tadpoles 3-fold	Behavior	Wood Frog (<i>Lithobates sylvaticus</i>)	Hayden et al., 2015
CAPTIVE BREEDING/EX SITU CONSERVATION				
	Evaluated group housing strategies	Both	Darien Stubfoot Toad (<i>Atelopus certus</i>); Pirri Range Stubfoot Toad (<i>Atelopus glyphus</i>)	Cikaneke et al., 2014
	Used captive populations to develop non-invasive tools to monitor glucocorticoid in wild populations and to evaluate physiological acclimation of wildlife brought into captive environments	Physiology	Not specific	Narayan, 2017
	Encouraged the assessment of animal behavior and personality syndromes to improve: (1) mating and reproductive success of captive animals by ensuring that breeding pairs are behaviorally compatible and (2) post-reintroduction survival and reproductive potential by informing the selection of optimal behavioral types for release	Behavior	Not specific	Kelleher et al., 2018
	Evaluated stress of captivity using multiple measures of physiology, two hormones and body mass change	Physiology	Brazilian Toad (<i>Rhinella schneideri</i>)	Titon et al., 2017
	Quantified behavior in captivity during successful breeding events to pin-point critical time periods and conditions for successful reproduction	Behavior	Ozark Hellbender (<i>Cryptobranchus alleganiensis bishopi</i>)	Settle et al., 2018

to design and improve approaches to their conservation and management.

Understanding how amphibians may cope with climatic variability has involved examining microhabitat preferences, as well as species' behavioral and physiological responses to increasing temperatures and decreasing water availability (Griffis-Kyle, 2016; Table 1). Such studies have helped develop a climate adaptation plan for at least one declining species (Mitchell, 2001). Understanding host behavior has been instrumental in revealing how amphibians can sometimes mediate (through altered thermoregulatory behavior) infections from parasites and pathogens, and physiological studies have helped elucidate how abiotic factors may affect host immune function and susceptibility to disease (Table 1). Vocalization behavior has been used to attract individuals to newly created habitats to ameliorate the effects of habitat loss and fragmentation and several physiological metrics—e.g., stress responses, heat tolerance, and evaporative water loss—have helped evaluate amphibian responses to habitat modification (including urbanization). Both behavioral and physiological studies have revealed how species respond to invasive predators and findings have generated novel ways to reduce predation risk (Table 1).

In addition to direct lethal impacts, contaminants and disease can have numerous sublethal effects—including behavioral and physiological responses—that, while not overtly causing mortality, may weaken an animal and make it more vulnerable to other stressors (Sparling, 2003; Shuman-Goodier and Propper, 2016; Rollins-Smith, 2017). For example, behavior and

physiology can be sensitive indicators of endocrine disruption (Schwendiman and Propper, 2012). Behavioral studies have provided insight into strategies for reducing the impact of emerging infectious diseases (Hoverman and Searle, 2016). Experimental studies have illustrated the role that contaminants could play in compromising reproductive success, therefore potentially contributing to the global problem of amphibian decline (Table 1). In the context of *ex situ* conservation, physiological assays have helped evaluate acclimation of animals brought into captive environments (Narayan, 2017). Likewise, an understanding of animal behavior and personality syndromes can inform the selection of optimal behavioral types for release and ensure that captive breeding pairs are behaviorally compatible, thus improving mating success, post-reintroduction survival and reproductive potential (Kelleher et al., 2018). Evidence is growing that cognitive behavior, decision making, and personality syndromes occur in amphibians (Jaeger et al., 2016; Kelleher et al., 2018) and could have many conservation and management applications (Blumstein and Berger-Tal, 2015; Owen et al., 2016; Table 1).

Despite the large body of evidence that these various stressors unequivocally affect amphibian populations, the application of this information to conservation issues—i.e., to the development of specific conservation strategies—remains uncommon. Similarly, Mahoney et al. (2018) found that an increase in conservation physiology research has not led to an increased application of physiological tools in recovery planning for threatened and endangered species in the United States. For example, for recovery plans developed over an 11-year period,

only 17% incorporated current physiological methodologies as recovery or monitoring activities. Thus, the need to integrate such knowledge into concrete conservation actions remains a critical need in recovery planning for imperiled species.

CASE STUDY 1: LONG-TERM BEHAVIORAL STUDIES INFORM CONSERVATION OF AN EXTINCTION-PRONE SPECIES

The Eastern Red-backed Salamander (*Plethodon cinereus*; hereafter, Red-backed Salamander) is widespread on forest floors of northeastern North America. By comparison, the Shenandoah Salamander (*P. shenandoah*) is restricted to only three populations, isolated on three mountain tops in Shenandoah National Park, Virginia, United States (Jaeger, 1980). These three populations inhabit Pleistocene-age talus slopes that contain sparse shade and are drier than the surrounding, deeper soil in well-shaded forests (Jaeger et al., 2016). Red-backed Salamanders are abundant in these forests and completely surround each Shenandoah Salamander population. Also, the talus slopes are slowly eroding, with Red-backed Salamanders found in these intruding soils. Jaeger (1970, 1971a,b); Jaeger (1972) hypothesized that the Shenandoah Salamander is an extinction-prone species based on these observations. He then plotted the distributions of both species and found that Red-backed Salamanders rarely entered the talus whereas Shenandoah Salamanders moved into the surrounding deeper, moister soil, but seldom are able to progress more than 3 m from the talus' edge into the forest on Hawksbill Mountain. Laboratory experiments indicated that both species prefer moist soil vs. drier rocky areas and that the Shenandoah Salamander is more tolerant of drier habitats than is the Red-backed Salamander.

Experiments in outdoor enclosures indicated that the Red-backed Salamander competitively excludes Shenandoah Salamanders from the deep-soil forest and, thus, essentially confines it to talus-refugia. Additional research indicated that the two species compete for prey on the forest floor (Jaeger et al., 2016). On Hawksbill Mountain, several small areas of talus occur below the large talus on top of the mountain. Jaeger (1980) conducted a 14-year census in these isolated talus patches and found that in one of them, the Shenandoah Salamander became extinct during a long drought. In general, amphibians have numerous adaptations that minimize water loss but, regardless, dehydration ultimately occurs when water loss exceeds an individual's physiological tolerance and ability to store water internally (Griffis-Kyle, 2016). To prevent mortality from dehydration during droughts, one management tactic could be to water talus patches during extended dry periods, as has been suggested to extend pond hydroperiods for aquatic-breeding amphibians (Griffis-Kyle, 2016).

Behavioral experiments in the laboratory showed that both species avoided pheromones of each other and that individuals preferred to reside on their own substrate pheromones (Jaeger and Gergits, 1979). This suggested that both species behaved as if territorial. Wrobel et al. (1980) also conducted

behavioral experiments in the laboratory; the two species aggressively displayed and often bit each other, again suggesting interspecific competition as a mechanism driving the spatial distributions of the two species. Later research (Griffis and Jaeger, 1998) on Hawksbill Mountain found that Red-backed Salamanders successfully defend territories (under rocks and logs) against the Shenandoah Salamander. This inhibits the latter species' movements from the source talus on top of the mountain to the sink populations below: a rare example of how interspecific competition—mediated by aggressive interference and territoriality—can lead to the endangerment of one of the competing species. Ultimately, this research contributed to listing the Shenandoah Salamander as a federally endangered species in 1989 [U.S. Fish and Wildlife Service USFWS (1989)]. Therefore, the use of observations and experiments in both laboratory and natural habitats provided the necessary information to protect and manage this vulnerable species but, to our knowledge, no specific management actions (related to interspecific competition as a factor in declines) have yet been implemented (USFWS, 2013).

CASE STUDY 2: PHYSIOLOGICAL STUDIES REVEAL THE EFFECTS OF URBANIZATION ON A THREATENED STREAM DWELLING SALAMANDER

Land-use modification (e.g., urbanization and agriculture) is often linked to higher environmental temperatures, pollution, and eutrophication in water bodies (Smith et al., 2006). Changes in water quality can affect the behavior and endocrine systems of aquatic organisms, and nitrogen and phosphorous are among the top contributors to waterway degradation (Cook et al., 2018). Nitrogen release—from fertilizers in agriculture and suburban settings, animal waste, and wastewater effluents—results in elevated levels of active forms of nitrogen (e.g., nitrate, nitrite, ammonia, and ammonium). Nitrate is a major contaminant in freshwater aquatic environments and is especially toxic to amphibians (Rouse et al., 1999; Kellock et al., 2018). Thus, understanding risks, susceptibility, and behavioral and physiological responses of aquatic species to changes in land use is necessary to mitigate potential stressors, especially as habitat conversion continues (Pauchard et al., 2006).

Gabor et al. (2018a) examined the relation between corticosterone (the main amphibian GC) and urbanization in a stream dwelling amphibian, the Jollyville Plateau Salamander (*Eurycea tonkawae*). This plethodontid is a neotenic (completely aquatic) species found in karst-associated groundwater in the Edwards-Trinity aquifer system of central Texas, United States. This spring water is oligotrophic, has constant temperatures, and supports a unique assemblage of aquatic species adapted to these conditions. A recent phylogenomic analysis revealed extensive cryptic species diversity in the salamander assemblage endemic to this aquifer system (Devitt et al., 2019). However, because of overexploitation of this groundwater resource, regional climate and hydrologic models project that these salamanders are at high risk of extinction within the next century (Devitt et al.,

2019). Indeed, the Jollyville Plateau Salamander has already been listed as threatened under the Endangered Species Act of 1973 (USFWS, 2019) due to threats from urbanization. Counts of this species have declined in areas that had the largest increases in urbanization (measured by residential development) and salamander densities were negatively correlated with residential development throughout the species' range (Bendik et al., 2014).

Gabor et al. (2018a) examined baseline corticosterone and stress response (as an indication of chronic stress) for 3 years in urban sites ($\geq 25\%$ impervious cover) vs. rural sites. They obtained corticosterone release rates using a non-invasive water-borne hormone assay and found that corticosterone was higher in urban sites than in rural ones in 2 of the 3 years of the study. Salamanders showed general stress responsiveness (to agitation) across all years and populations, indicating that even if salamanders were physiologically stressed they were not necessarily chronically stressed. They also found that "background corticosterone," measured directly from the stream in which the salamanders were sampled, was higher in urban than rural streams and was positively correlated with baseline corticosterone across populations and years. Background corticosterone provides an efficient, indirect method of evaluating stress levels and physiological health in aquatic vertebrates, allowing for more expeditious management decisions and evaluation of their effectiveness for imperiled species.

Mondelli (2016) used a behavioral assay (activity) in combination with a corticosterone assay to further examine the effects of urbanization on the Jollyville Plateau Salamander. Corticosterone and activity were positively related in two urban sites yet negatively related in two rural ones (Figure 1). The relation between activity and corticosterone release rates in urban and rural sites (albeit in opposite directions) demonstrates that measures of activity provide an additional indication of salamander responsiveness to their environment; for this species, salamanders in more urban habitats that release higher levels of corticosterone will be more active. Yet, higher activity can make individuals more vulnerable to visual predators (Epp and Gabor, 2008). This suggests a possible trade-off in consequences of behavioral activity, particularly in urban environments, for some aquatic amphibians.

These results have not yet been used directly in conservation and management strategies for amphibians. Moreover, we are unaware of any other studies in which behavioral and/or physiological findings with respect to urbanization, in general, have been used in this manner. However, because aquatic urban habitats often accumulate toxic contaminants that can affect amphibians at sublethal levels (Sievers et al., 2018a,b), behavioral and physiological assays can be additional tools in the conservation toolbox with which to assess effects of urban-associated contaminants and may serve as early warning signals of potential population declines. Although the specific contaminants that may have affected corticosterone in Mondelli (2016) are not known, exposure to nitrate and nitrite affects behavior, physiology, and survival in some aquatic species (Hecnar, 1995; Jannat et al., 2014; Pottinger, 2017). An important next step in this research will be to examine potential links

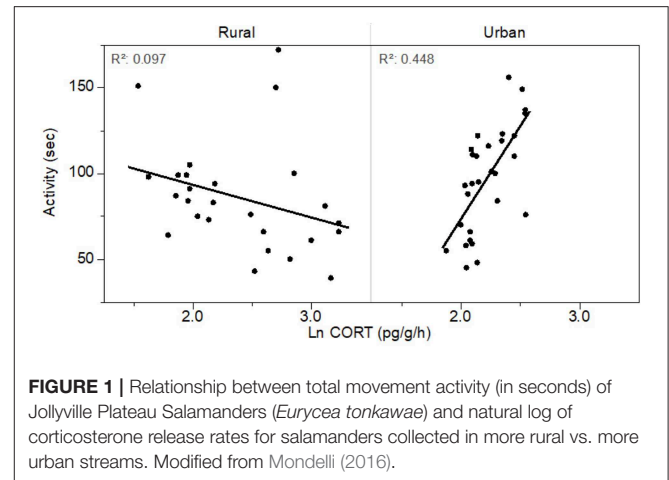


FIGURE 1 | Relationship between total movement activity (in seconds) of Jollyville Plateau Salamanders (*Eurycea tonkawae*) and natural log of corticosterone release rates for salamanders collected in more rural vs. more urban streams. Modified from Mondelli (2016).

among specific contaminants, physiology and behavior. A combination of laboratory and field studies that examine the relationship between corticosterone and behavior across a range of environmentally-relevant levels of active nitrogen could aid in understanding the consequences of urbanization on population health. If indeed nitrate affects behavior and/or physiology, then a management plan could include the use of vegetated buffer zones around water to reduce the amount of nitrate entering the water through runoff, as suggested by Rouse et al. (1999).

RESEARCH GAPS AND FUTURE DIRECTIONS

Herein we have highlighted representative examples of how studies of behavior and physiology could help inform amphibian conservation efforts, but substantial deficiencies remain. Studies with amphibians are generally under-represented in the conservation behavior and physiology literature, indicating a clear need for greater focus on amphibians in future research (Madliger et al., 2018). Long-term studies could help elucidate how behavior and physiological stress ultimately affect individual fitness and population resilience. Considerable advancements have been made in conservation behavior: for example, the scientific community now has a greater understanding of how native amphibian species respond to invasive predators, and novel behavior-based approaches have been designed to minimize the impact of invasive species (Table 1). However, widespread application of actions has not yet been integrated into conservation and management strategies for a broad array of ecologically-similar species. Other than the species-specific climate adaptation plan implemented by Mitchell (2001), it is unclear what targeted conservation strategies have been developed as a consequence of many physiological and behavioral studies. Thus, fully integrating the information gained from research in behavior and physiology into concrete conservation actions is the most critical need at the interface of these three disciplines.

In addition, there are several areas of research in amphibian behavior and physiology that could be strengthened to better integrate these disciplines with conservation. For example:

1. The terms “stress” and “stressor” are often used without a clear physiological basis in the conservation literature. Species’ threats are often identified as “stressors,” even though the physiological effects of such factors on individuals and populations may not have been empirically established (Mahoney et al., 2018) or, if examined, may have been found to not occur (Gunderson et al., 2017). Contrary to the expectation of stressor effects on amphibians, there are several examples of how pathogens (Kiesecker and Blaustein, 1999), contaminants (Boone et al., 2004; Boone, 2018), and certain predators (Werner and Anholt, 1996; Davis and Gabor, 2015) can have positive (indirect) or otherwise unanticipated effects on populations. Thus, the effects of stressors can vary within and among populations (e.g., Hopkins et al., 2016) and species, and across scales (Grant et al., 2016; Muths et al., 2017). This variation underscores the need to test assumptions about the physiological basis of stress, especially when used in the context of species’ threats.
2. Anthropogenic change can often occur over short time periods, and physiological indicators of how well a species may be able to respond to environmental disruptions could help reveal the potential for populations to persist. Steroid levels can fluctuate rapidly with environmental modifications and variation in individual responses can be high. Repeatability of these variable responses (multiple phenotypes) could indicate that endocrine traits exhibit heritable variation and, thus, the ability to evolve in response to environmental change (Hau et al., 2016). Miles et al. (2018) documented support for this hypothesis with respect to corticosterone but more work is needed. Thus, measuring repeatability in stress hormone activity is an important area of future research because it could provide an indication of how well a given species may be able to respond to environmental change.
3. Multiple measures of physiological health (e.g., glucose and lactate concentrations, metabolic rate or telomere length as a measure of metabolic cost) would provide a more holistic assessment of an individual’s condition and overall resilience of a population than would individual measures.
4. Physiological and behavioral attributes of relatively healthy populations—both of endangered and common species—need to be documented. Doing so could provide a comparative basis for evaluating responses to environmentally-induced stress. Non-threatened species can also undergo localized population declines and losses, yet typically are not the beneficiaries of conservation interventions, as are imperiled species. Proactively implementing conservation of common species could lead to early detection of conservation problems *before* endangerment occurs.
5. Behavior-based approaches to climate change adaptation are still in their infancy (Caro, 2016). Phenological shifts are key responses of species to recent climate change, yet the use of experimental approaches to gain insights into phenology are still uncommon (Gao et al., 2015). Both behavioral and physiological responses to climate change have been simulated with biophysical and species distribution models (Table 1), but these predictions need empirical tests to provide conservation managers with workable solutions to climate change.
6. The potential for behavior to mitigate disease outbreaks also warrants further study, especially as it relates to informing the design of refugia from pathogens and parasites (Hoverman and Searle, 2016).
7. Nitrate has recently been considered an endocrine disruptor that has many negative effects on amphibians and other aquatic organisms (Poulsen et al., 2018). Indeed, cortisol release rates in fish were elevated below wastewater plants where nitrate levels were high compared to upstream sites (Pottinger, 2017). More studies are needed with amphibians to examine the relationship between corticosterone and active nitrogen. If there is a link, then just measuring active nitrogen in an aquatic system could provide a first approximation of population health.
8. Last, the fundamental questions in any mechanistic study are, first, how do behavioral and/or physiological phenomena “scale up” from the individual to that of the population and community levels (e.g., Jaeger et al., 2016; Saaristo et al., 2018)? Secondly, do responses observed under controlled, experimental conditions translate into measurable effects on population demography in nature (Saaristo et al., 2018)? Answers to these questions will ultimately determine the extent to which behavioral and physiological studies may influence conservation strategies for amphibians.

CONCLUSIONS

Our review and highlighted case studies illustrate the potential utility of studies in behavior and physiology for informing strategies for amphibian conservation and management. Caro (2016) stated that examples of useful behavioral applications for conservation practitioners are “principally restricted to *ex situ* conservation.” However, we found numerous examples of behavioral and physiological studies that address key stressors known to impact amphibian populations—climate change, pathogens and parasites, invasive species, habitat change, and contaminants—in addition to *ex situ* conservation.

Our first case study highlighting Jaeger’s research (Jaeger et al., 2016) illustrates the value of long-term investigations and, together with the studies by Gabor (Mondelli, 2016; Gabor et al., 2018a), shows the dynamic nature of relationships among environmental factors, physiology, and behavioral attributes as climate change and habitat alteration escalates. These highlighted research programs illustrate how examining a species’ extinction risk through the lens of behavior and physiology can help elucidate why an extinction-prone species is currently declining, as well as provide early indicators of future population declines in at-risk species. In the future, longer-term studies, use of multiple measures of physiological health, and a focus on scaling-up from individual behavior and physiology to the

population and community levels could help pinpoint how stressor impacts compound to affect population persistence and community organization. Understanding mechanisms by which various stressors may be contributing to population declines is a fundamental first step in fostering solutions to the amphibian decline crisis. However, in many cases, specific conservation strategies based on such knowledge have yet to be developed or implemented and are priorities for future conservation and management of this imperiled group of vertebrates.

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Both authors contributed to the review through development of ideas, along with drafting, and revision of text. CG prepared the figure.

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