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Extinction Debt as a Driver of Amphibian Declines: An Example with Imperiled Flatwoods Salamanders

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ABSTRACT.—A comprehensive view of population declines and their underlying causes is necessary to reverse species loss. Historically, in many cases, a narrow view may have allowed species declines to continue, virtually undetected, for long periods of time (perhaps even decades). We suggest that extinction debt is likely responsible for numerous (perhaps most) amphibian declines and that this perspective should be incorporated into the structure of amphibian research and management. Extinction debt, originally proposed to explain changes in species richness following environmental disturbance, also may refer to the proportion of populations of an individual species that is expected to eventually be lost because of habitat change. A conservation framework to address extinction debt focuses research on threats at the individual, population, and metapopulation levels. This approach will help enhance, restore, and protect specific processes and habitats at the proper scale by directing management to the most vulnerable level and stage of a species. We illustrate this approach using Flatwoods Salamanders, *Ambystoma cingulatum* and *Ambystoma bishopi*, which occurred historically throughout the Coastal Plain of the southeastern United States but have experienced a greater than 85% loss of populations in recent years. Reversal of these losses is possible only if conservation and recovery efforts encompass individual, population, and metapopulation levels. We illustrate our framework by outlining actions that could be taken at each of these levels to help guide conservation and management of amphibians with complex life cycles and provide options for how to prioritize conservation actions in the face of logistical and budgetary shortfalls.

Declines in biodiversity are occurring across the globe at an alarming rate (Pimm et al., 1995). Amphibians are among the most affected taxa, with at least 32.5% of all species at risk of extinction (Stuart et al., 2004; Wake and Vredenburg, 2008). Since initial recognition of this global problem in the late 1980s (Wake, 1991; Blaustein et al. 1994; Houlihan et al., 2000; Wake and Vredenburg, 2008), biologists have been eager to explain why declines are occurring. By the early 2000s, biologists agreed that amphibians were being impacted by six primary threats, as well as synergisms between or among them: 1) habitat loss and alteration; 2) chemical contamination; 3) global climate change; 4) disease; 5) invasive species; and 6) commercial exploitation (Semlitsch, 2003; Collins and Crump, 2009). This stimulated a large research effort to discover the “smoking gun” that could explain amphibian declines. Although a huge body of research has now accumulated, including numerous reviews of threats and their interactions (e.g., Alford and Richards, 1999; Daszak et al., 2003; Allentoft and O'Brien, 2010; Hayes et al., 2010), seldom have we found a single factor to be responsible, and we appear no closer to a general conservation solution (Grant et al., 2016). Assessments of endangered amphibian species show continued general declines over a period of decades (McCallum, 2007, 2015; Adams et al., 2013), rather than abrupt catastrophic failures (except, possibly, for dramatic mass die-offs attributable to disease outbreaks: Daszak et al., 2003; Vredenburg et al., 2010; Martel et al., 2013; Hudson et al., 2016; Spitzen-van der Sluijs et al., 2016). In the United States, even species classified as Least Concern by the International Union for the Conservation of Nature are declining at a rate of 2.7% per year (Adams et al., 2013), and local populations are being lost from metapopulations at an average rate of 3.79% per year (Grant et al., 2016). As a result, and in spite of our best efforts to date, we are likely to continue losing species.

We assert that amphibian biologists, conservationists, and wildlife managers have generally failed to take a broader, more comprehensive view of declines and their underlying mechanisms (with some notable exceptions; e.g., Willson et al., 2012; Willson and Hopkins, 2013; Bendik et al., 2016). Rather, a typical approach has been to focus on narrower and more proximate causes of declines in hopes of solving the problem. In some cases this narrow view has allowed species declines to continue, virtually undetected, for long periods of time (perhaps even decades). Here we present a different perspective. We suggest that the mechanisms by which extinction debt affects individuals, populations, and metapopulations are likely responsible for numerous amphibian declines. If this perspective is not incorporated into our research and management structure, we will continue to allow species to go extinct while we search for the “silver bullet.”

A recent review indicates that the concept of extinction debt, originally developed at the level of species richness (Kuussaari et al., 2009; Jackson and Sax, 2010) might also be effectively applied to single species management and conservation (Hylander and Ehrlén, 2013). The rationale for this application, Hylander and Ehrlén (2013) reasoned, is that extinction debts ultimately impact species richness through the accumulation of delayed extinctions of many different species within a community. Therefore, a shift in focus—from that of species richness to that of mechanisms operating at an individual species level—is important for understanding the mechanisms underlying extinction debts (Hylander and Ehrlén, 2013). We present an overview of the application of extinction debt to amphibian declines, its hierarchical organizational structure, and some management perspectives using imperiled salamanders as a case study.

APPLICATION OF EXTINCTION DEBT TO AMPHIBIAN DECLINES

The concept of extinction debt, regarded as a future ecological cost (in terms of species losses) of present-day habitat

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destruction and fragmentation (Tilman et al., 1994), has been used to understand the disparity between predicted and observed extinctions in a community. Extinction debt occurs when an area has more species than predicted based on the amount of habitat loss or degradation observed (Kuussaari et al., 2009). This species surplus acts as a “debt” that must be “paid”: the disparity is reduced over time as species go extinct, until only the number of species that can be supported by the size and quality of the habitat remain. If this disparity or debt can be identified, an opportunity arises to understand why extinction is delayed, how each species responds, and the various mechanisms responsible for decline. This occurs during a critical period when each of the species is still present but declining. Not knowing the mechanism leading to decline for individual species can misdirect management by targeting the wrong aspects of habitat restoration or recovery, and ultimately be ineffective, missing an opportunity to affect recovery and wasting valuable limited resources.

At the level of an individual species, the concept of extinction debt corresponds to the proportion of populations in a focal landscape or a species’ range that is expected to eventually become extinct after a change in habitat (Kuussaari et al., 2009; Hylander and Ehrlén, 2013). Although every species has unique life-history characteristics, declines can generally be partitioned into three hierarchical levels at which extinction operates: the survival of individuals, populations, and metapopulations. Hence, species persistence in an area can be understood by processes or threats acting at each of these three levels and interacting with species-specific traits influencing vital rates (Hylander and Ehrlén, 2013). At the individual level, survival during each amphibian life-history stage (egg, larva, juvenile, adult) depends on biotic and abiotic habitat quality. For example, anthropogenic threats attributable to chemical contamination in the aquatic habitat may reduce larval survival, decrease size at metamorphosis, and reduce survival to maturity and fecundity of individuals. At the population level, threats such as wetland draining or the introduction of invasive fishes may reduce reproductive and survival rates that lowers recruitment and causes the population to decline over time. Local extinction occurs when the last individual in the population dies. At the metapopulation level, threats like habitat loss, alteration, and fragmentation may decrease juvenile dispersal and connectivity, reducing rescue and recolonization, and potentially increasing vulnerability to environmental stochasticity. Habitat fragmentation and degradation may accrue gradually until a species is eventually pushed beyond a tipping point; at this threshold, the system may transition from a state in which most patches are occupied to one in which the entire metapopulation goes extinct (Sheffer, 2009). Sink populations eventually go extinct when immigration is halted, and the last isolated populations eventually suffer stochastic genetic or demographic extinction, causing metapopulation collapse and rangewide species extinction. Various traits of a species may counteract the severity of a particular threat (e.g., via chemical tolerance, antipredator mechanisms, longevity, or vagility); however, once extinction debt is accrued through habitat degradation, it simply is a matter of time before species go extinct unless threats are eliminated and habitat is restored. The ability of a species to resist threats at each hierarchical level influences the size of the extinction debt and time to extinction (i.e., relaxation time). This lag period can leave biologists with the false impression, perhaps based on the presence of one stage (e.g., adults), that species may be stable,

when in fact no eggs, larvae, or juveniles are being produced to replace dying adults (e.g., Ozark Hellbender, *Cryptobranchus bishopi*; Wheeler et al., 2003). Long-lived species can prolong extinction for many years, even in the absence of juvenile recruitment but eventually will go extinct unless successful conservation efforts are implemented. Hence, the mere presence of individuals and populations or occupancy of species on the landscape can yield a false impression that things are fine and may lead to a lack of urgency in conservation action over many years.

CONSERVATION OF DECLINING AMPHIBIANS: A CASE STUDY WITH FLATWOODS SALAMANDERS

If we evaluate the persistence of a species through the lens of a hierarchical framework of extinction debt, then research focused on threats can be interpreted in terms of their effect on declines and extinction. This approach could also help direct management and resources to a species’ most vulnerable hierarchical level and life-history stage, to enhance, restore, or protect specific processes and habitats at the appropriate scale. Here, we provide an example application of this framework to declining species using the imperiled Flatwoods Salamanders, *Ambystoma bishopi* (Reticulated Flatwoods Salamander, federally listed as endangered) and *Ambystoma cingulatum* (Frosted Flatwoods Salamander, currently listed as threatened). These species are endemic to mesic flatwoods within the longleaf pine-wiregrass (*Pinus palustris*–*Aristida* sp.) ecosystem that once dominated the Coastal Plain of the southeastern United States. Historically, Flatwoods Salamanders occurred throughout this region, across southern Alabama, the panhandle of Florida, southern Georgia, and South Carolina (Palis and Means, 2005; Fig. 1A). But, like their native habitat, Flatwoods Salamanders have experienced precipitous declines and currently exist only as isolated metapopulations in a few locations within their historic range (Fig. 1).

We compiled historical locality information from museum, natural heritage (Florida [FL] Natural Areas Inventory, Georgia Department of Natural Resources [GA DNR], South Carolina DNR), and metacrawler databases (Global Biodiversity Information Facility, VertNet, HerpNet). We used GEOlocate and Google Earth to georeference records that did not contain coordinate information, and we used ArcGIS 10.3.1 to plot Cartesian coordinates to assess veracity and eliminate duplicate records.

Over time, and despite intense efforts to monitor and locate new populations, the combined range of these two species has dwindled from 476 historical locations prior to listing in 1999 to only 63 locations from 2010 to 2015 (86.8% population loss; Fig. 1A–C; Bevelhimer et al., 2008; Pauly et al., 2012). Surveys in 2015–2016 revealed previously undetected breeding wetlands for *A. bishopi* (2 in GA, 3 in FL; J. Jensen, Georgia DNR; M. Winland, Florida Fish and Wildlife Conservation Commission, pers. comm.) and *A. cingulatum* (at St. Marks National Wildlife Refuge [SMNWR] and Apalachicola National Forest, FL; J. Mott, The Nature Conservancy, pers. comm.), but the ability to identify previously unknown extant populations is challenging and limits understanding the real extent of declines. We lack published information on the causes of each population lost. However, others identify habitat loss attributable to land use change and development, habitat degradation attributable to inadequate management of long-leaf pine flatwoods and savannas, and fire suppression as primary threats to population

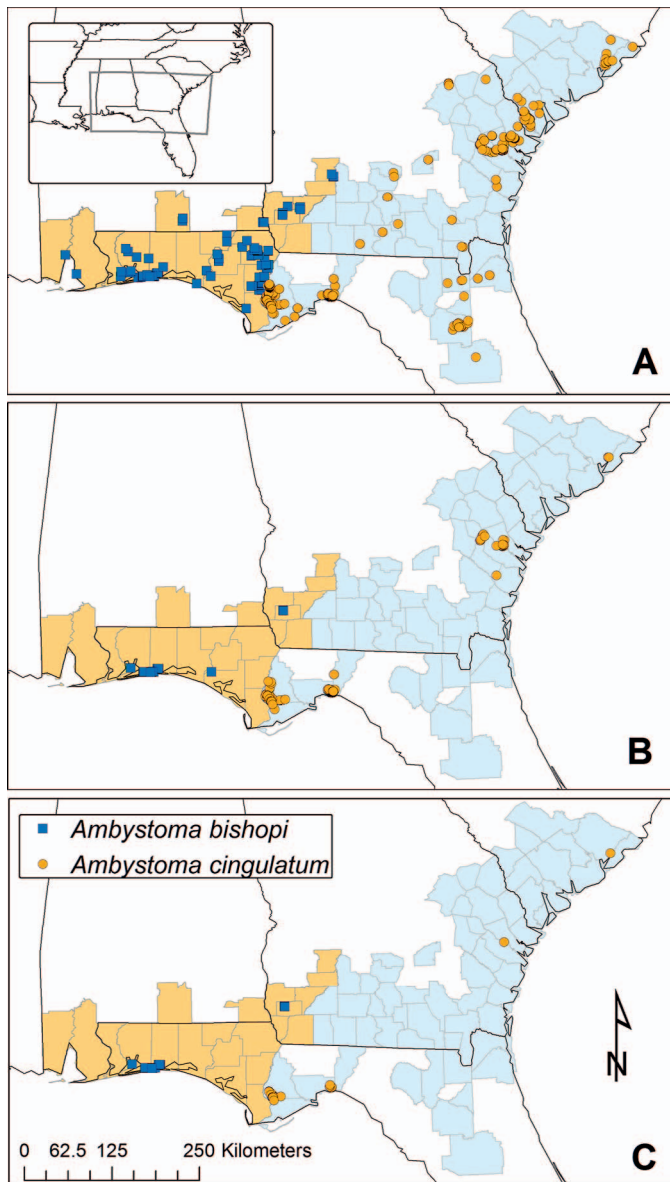


FIG. 1. Known localities of Flatwoods Salamanders (Frosted Flatwoods Salamander, *Ambystoma cingulatum*, and Reticulated Flatwoods Salamander, *Ambystoma bishopi*) in the southeastern United States over three time periods. (A) All known records; (B) 2000–2009 (post-listing); and (C) 2010 to 2015 (post-taxonomic split). Orange circles = *A. cingulatum* and blue squares = *A. bishopi*. Shaded counties indicate the range of each species.

persistence, all of which have presumably led to decreased suitability of wetlands for larvae and terrestrial habitat for juveniles and adults (Means et al., 1996; USFWS, 1999; Bishop and Haas, 2005). Even with continued assessments of both historical and extant populations, along with the development of fire management regimes in some protected areas and regions (Gorman et al., 2013), these species have gradually dwindled and could go extinct without intervention (Fig. 1C).

We suggest that management of Flatwoods Salamanders up to this point has been directed at only one level—the local population—and at two stages—the terrestrial juvenile and adult. If we ask how the presence of extinction debt can guide management, however, then we must look at each level of process: the individual, population, and metapopulation. For example, if the primary management effort is directed at

restoration of the flatwoods terrestrial habitat through prescribed burning, it will largely benefit survival of juveniles and adults (unless fire also removes accumulated duff and established invasive woody vegetation from dry wetland basins; that would benefit aquatic larvae). Over time and even in the best restored habitat, however, natural attrition of juveniles and adults will slowly cause a population to go extinct unless two additional processes are working effectively. For the population to remain stable, there must be production of metamorphosing juveniles to replace mortality of adults. This would require restoration of aquatic breeding habitats that increase egg and larval survival to metamorphosis. Further, in the absence of adequate juvenile self-recruitment, there must be connectivity among adjacent neighboring populations to enable rescue of declining populations through dispersal to compensate against stochastic local extinction and to maintain adequate genetic diversity. This necessitates maintaining terrestrial habitat suitable for dispersal and a spatial configuration of nearby ponds that enhances metapopulation sustainability. Therefore, processes that produce juveniles and allow rescue and recolonization must be functional among ponds within dispersal range and, eventually, across a species' range. Focusing management only on one mechanism of decline may allow a species to slowly wink out across its range over time.

The pattern of loss shown in Figure 1 indicates that populations across these species' ranges have gone extinct, threatening the sustainability of larger metapopulations. We used locality data (described previously) to calculate the mean distance between nearest-neighboring Flatwoods Salamander breeding ponds within each time period indicated in Figure 1. We used this metric because others have found average distance to the nearest wetland to have a direct effect on dispersal success, wetland isolation, source-sink processes and rescue of declining populations (Gibbs, 1993; Semlitsch and Bodie, 1998; Marsh and Trenham, 2001; Semlitsch, 2002; Gamble et al., 2007). Consequently, metapopulations tend to go extinct if the number of neighboring occupied patches falls below a critical threshold (Sheffer, 2009). The effect of mean interpatch distance (with a "patch" being, for example, a wetland or cluster of terrestrial vegetation) on movement and other behaviors has been examined for a variety of other herpetofauna, including Red-Legged Frogs, *Rana aurora aurora* (Chan-McLeod and Moy, 2007), Tungara Frogs, *Physalaemus pustulosus* (Marsh et al., 2000), and water snakes (*Nerodia erythrogaster* and *Nerodia sipedon sipedon*; Roe et al., 2003).

We converted coordinates from a spheroid projection into a cylindrical projection with a metric Mercator and computed Euclidian distance between all records. We determined the mean nearest neighbor to each record without replacement (i.e., if record A's nearest neighbor was B, then record B's nearest neighbor could not be A). We found that mean interpond distance increased from 8.9 km prior to 1999 (before USFWS listing of what was then a single species, *A. cingulatum*; see below), to 12.7 km from 2000 to 2009 (post-listing period), and to 28.3 km from 2010 to 2015 (post-taxonomic split into *A. cingulatum* and *A. bishopi* [Pauly et al., 2007] and designation of critical habitat [USFWS 2009]). Because individual salamanders probably do not disperse more than 1–2 km within a generation and multigeneration gene flow likely is limited to 5–10 km or less for most ambystomatid species (Semlitsch, 2008; Peterman et al., 2015), loss of Flatwoods Salamander populations over time, even prior to 1999, has evidently created severe isolation that is a critical component of an increased extinction risk. By

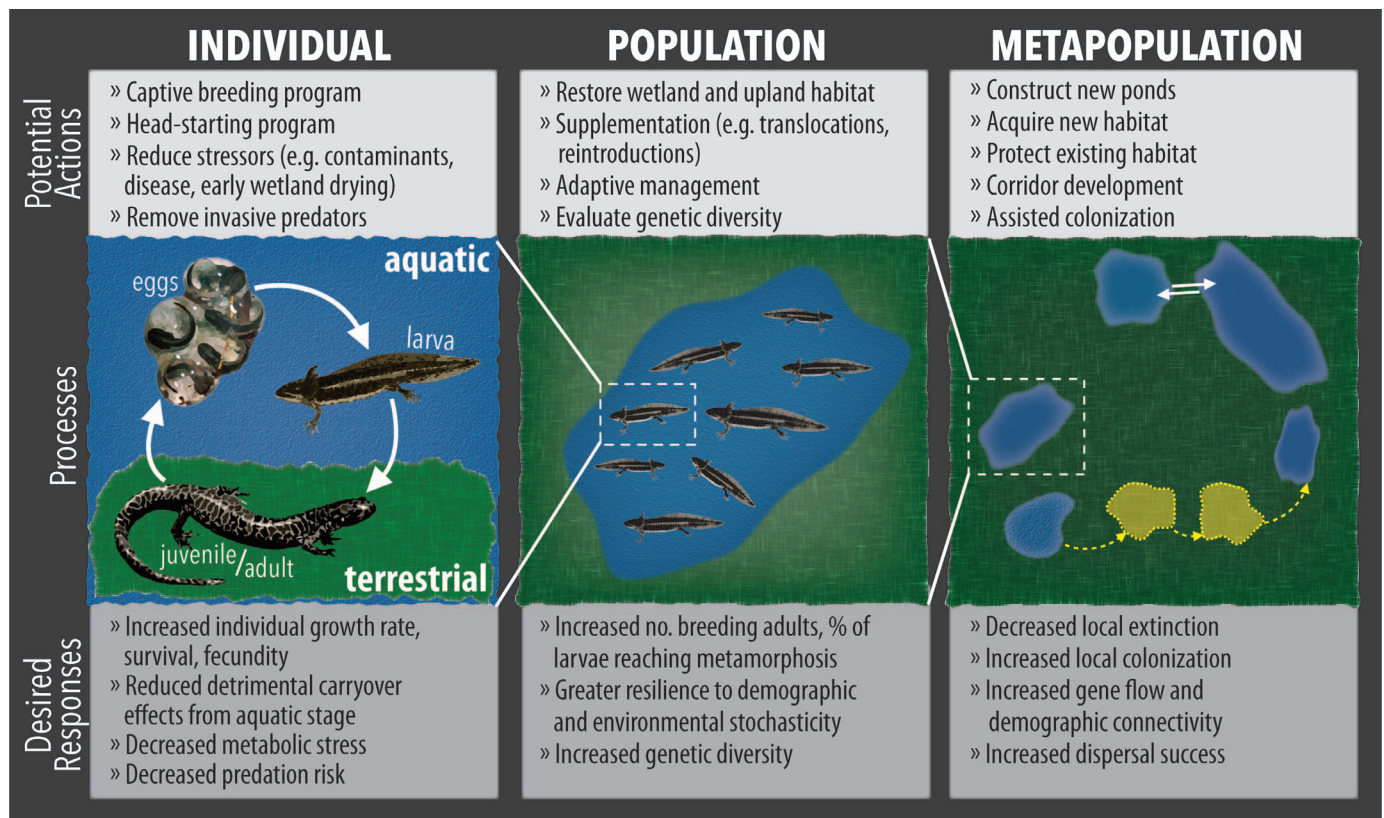


FIG. 2. Framework for a multilevel, hierarchical approach to guide conservation and management of amphibians with complex life cycles. The three panels (from left to right) represent increasing levels of scale (from individual to metapopulation). Within each panel are examples of key management actions that could be used (top), the process or level that would be targeted by those actions (middle), and the desired responses to be achieved by executing the proposed actions (bottom). At the individual level (left), the middle diagram represents the complex life cycle of Flatwoods Salamanders. At the population level (middle), the diagram represents an aquatic larval population at a single wetland. At the metapopulation level (right), shapes outlined in blue represent multiple wetlands, each supporting a breeding population that, collectively, comprise a metapopulation. Shapes outlined in yellow are “new” ponds, either created or restored to function as suitable breeding habitat; these new sites can be used as “stepping stones” (yellow arrows) for dispersing individuals en route to colonize additional sites. White arrows represent demographic connectivity between two ponds, with dispersal/exchange of individuals and, therefore, gene flow between them.

the time *A. cingulatum* (i.e., the composite species prior to its taxonomic split: Pauly et al., 2007) was listed as federally threatened in 1999, this isolation distance was already near or exceeded the maximum multigenerational dispersal distance, and isolation distance appears to be continually increasing. Even though these interpond distances are far beyond known dispersal distances, they illustrate the degree of isolation that exists for these species and underscore the need for translocations across the landscape if recovery efforts are to be successful.

Immediate reversal of losses at the individual, population, and metapopulation levels must be the focus of conservation and recovery efforts if these species are to be saved from extinction. The pattern of population loss in Flatwoods Salamanders may not be reversible, however, without massive intervention and active reintroductions at multiple levels—especially at the metapopulation and landscape level. Had the extinction debt and its hierarchical mechanisms causing decline been identified prior to this late stage, such complicated and costly recovery actions may have been avoided.

MANAGEMENT TO RECOVER DECLINING AMPHIBIAN POPULATIONS

A variety of management actions could be taken to reverse declines of imperiled amphibians with complex life cycles (Fig. 2). For example, individuals could be taken into captivity to establish assurance colonies to ensure that a species does not go

extinct. Captive propagation, if successful, along with in situ head-starting programs (Fig. 2), could be used to enhance survival of all life stages and to increase numbers of individuals that could later be introduced to suitably restored, unoccupied sites (Fig. 2). At the population level, potential management actions also could include reinforcement (through release of in situ head-started metamorphs) of existing populations to increase population viability (Seddon et al., 2014). Such actions would intend to increase the proportion of larvae that reach metamorphosis and become breeding adults and increase genetic diversity (Fig. 2). Finally, to maintain demographic connectivity, dispersal and recolonization among neighboring populations within a metapopulation (Fig. 2), specific management actions could include acquisition of additional habitat, restoration of aquatic and terrestrial habitat, and construction of new ponds that could serve as “stepping stones” within a protected dispersal corridor. In the event that individuals are unable to naturally colonize new areas if habitat suitability shifts in response to factors such as climate change, assisted colonization (i.e., “the intentional movement of an organism outside its indigenous range to avoid extinction of populations due to current or future threats”: Seddon et al., 2014) may be necessary to maintain metapopulation dynamics. At each level of this hierarchical approach, monitoring in an adaptive management framework could be used to improve manage-

ment/restoration decisions in response to observed responses to management actions.

Given the current shortfall in funding for conservation efforts (McCarthy et al., 2012), how does a practitioner proceed with implementing this approach? Implementing even a substantial subset of these management actions simultaneously could be both logistically impractical and fiscally unrealistic for many, if not most, conservation efforts. Indeed, the majority (78%) of U.S. amphibians protected under the Endangered Species Act (ESA), and which have recovery plans, actually receive only 2–70% of the budgets requested for their recovery (Gerber, 2016; SCW, unpubl. data). Moreover, 40% of federally protected U.S. amphibian species have no completed recovery plan and, therefore, lack designated funding for recovery under the provisions of the ESA (SCW, unpubl. data). Therefore, to maximize the efficient use of limited funding for conservation, resources need to be prioritized according to “the most cost-effective actions that generate the highest benefit-to-cost ratios” (Tulloch et al., 2014).

A variety of alternative guidelines exist for setting conservation priorities, most of which involve the use of formal decision theory and return on investment (ROI) approaches (e.g., Bottrill et al., 2008; Joseph et al., 2009; Wilson et al., 2009; Auerbach et al., 2014; Gerber, 2016). One option for setting such priorities is a straightforward method, proposed by Bottrill et al. (2008) and Joseph et al. (2009), that has been used to prioritize assets (species) or locations for conservation investment (Wilson 2009). We adapt this method to apply it to prioritize among management actions available for recovery of an individual species. This method involves ranking each action (i) by its cost efficiency (E_i), calculated as the product of the biodiversity benefit (B_i), species value (W_i) and probability of success (S_i), divided by the cost (C_i) (Wilson et al., 2009):

$$E_i = \frac{B_i \times W_i \times S_i}{C_i}$$

Each of these quantities is defined as follows (Bottrill et al. 2008; Joseph et al., 2009). The biodiversity benefit (B_i) of a management action or project (Fig. 2) is the gain (e.g., increase in population size of an imperiled species) from that action in progress toward a stated goal, such as ensuring the long-term viability of an imperiled species in the wild (calculated from stochastic population models, for example, or estimated through expert elicitation: Joseph et al., 2009). A species' value, W_i , could be ecological and/or economic, such as the ecosystem services a species provides, as well as evolutionary, social, or cultural. The probability of success, S_i , is the probability that the management action will result in a particular stated objective. It can be estimated, for example, using data on existing threats, the potential of a species to recover or persist (e.g., its recovery priority number), the number of partnerships involved in the recovery effort, or staff capacity. Examples of project costs (C_i) include land acquisition, equipment purchases, cost per acre to execute a prescribed burn, and labor costs. Finally, prioritization of management actions is accomplished by selecting and executing the top-ranking actions until the budget is expended (Wilson et al., 2009). Example applications of this approach to real-world conservation problems are illustrated in Bottrill et al. (2008) and Joseph et al. (2009) and could be applied to amphibian conservation issues in a relatively straightforward fashion. We propose that practitioners prioritize their conservation expenditures and, as funding and staffing allow, employ actions representative of each level of this hierarchical strategy. For Flatwoods Salamanders, we are using another decision-analytic

approach known as structured decision making—an organized approach to making decisions that focuses on identifying the problem, defining the objectives, potential actions and their consequences, and reconciling trade-offs (Gregory et al., 2012) to address key uncertainties and to develop goals to achieve recovery objectives (KMO, unpubl. data).

CONCLUSIONS

For amphibians, future management decisions need to consider a species' life cycle and life-history requirements to effectively link threats to presumed mechanisms of extinction. A more effective conservation focus for pond-breeding species could include 1) the deterioration of larval aquatic and adult terrestrial habitat for survival of individuals; 2) vital rates and demographic parameters of populations; and 3) the connectivity and recolonization that are essential for metapopulation stability. For example, studies on the effects of agricultural chemicals on growth and survival of the aquatic larval stage must be coupled with studies on carryover effects to the reproductive stage, adult survival, demographic rates, spatial population dynamics, and metapopulation persistence in agro-landscapes. Therefore, we assert that use of a comprehensive multilevel approach would be a beneficial paradigm for research, conservation and management of amphibians to help prevent further declines and extinctions. We also acknowledge that, under the universal constraint of funding limitations, actions that could be implemented at each of these levels need to be prioritized based on their benefit to a given species, the value of that species, the probability of success of a particular action, and the cost to implement that action. A coordinated response, involving multiple partners and stakeholders, will be critical to the successful implementation of our proposed approach to amphibian conservation.

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