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Forecasting changes in amphibian biodiversity: aiming at a moving target

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Amphibian population declines and sudden species' extinctions began to be noted at the beginning of the 1980s. Understanding the causes of the losses is hampered by our poor knowledge of the amphibian fauna in many parts of the world. Amphibian taxa are still being described at a high rate, especially in the tropics, which means that even quantifying species lost as a percentage of the current fauna can be a misleading statistic in some parts of the globe. The number of species that have gone missing is only one measure of the loss of biodiversity. Long-term studies of single-species populations are needed, but this approach has its limits. Amphibian populations often show great annual variation in population size making it difficult, if not impossible, to use short-term studies as a basis for deciding if a population is increasing or decreasing in the long term. Aggregating single studies into databases and searching for patterns of variation is a way of overcoming this limitation. Several databases on species and population time series are available or in development. These records show that declines are continuing worldwide with some species and populations, especially in the tropics and at higher elevations, at greater risk of extinction than others. Unfortunately, amphibian databases with population time series have much less information for the tropics compared to the temperate zone, and less for Africa and Asia compared with Europe and North America. Focusing limited resources using comprehensive statistical designs is a way to maximize the efficiency and effectiveness of monitoring efforts. It is clear that, in the first decades of the twenty-first century, the regions of the globe with the highest diversity of amphibian species will experience the greatest rates of decrease of forests and increase in human population size, fertilizer use, agricultural production, creation of new croplands and irrigation. Many of these changes are likely negatively to affect amphibian species diversity, and their influence must be understood before concluding, at least for amphibians, that the 2010 millennium assessment goal of significantly reversing the rate of loss of Earth's biodiversity can be met.

Keywords: amphibia extinction; population declines; databases

1. INTRODUCTION

Extinction occurs at different scales in both time and space—species, populations, metapopulations, regions, entire ranges—and humans typically accelerate the rate of losses at all scales. Our challenge is to protect priority taxa and their habitats through policies that reverse the loss of biodiversity (Wilson 2002). Identifying what we want to conserve and justifying the policies will require appropriate, efficient and reliable biodiversity and biodiversity-related indicators. Amphibians have many qualities of a model indicator group, starting with the fact that they are widespread. Amphibians inhabit most of Earth's freshwater and terrestrial biomes except for marine environments, the Antarctic and deep Arctic. Population sizes vary from small to large, and the complex life cycle of many species places them in water and on land where frogs and salamanders have proven sensitive to the environmental challenges of the twentieth and early twenty-first centuries (Collins & Storfer 2003). Throughout the twentieth century, competition and predation from exotic species, commercial exploitation and land use changes diminished population sizes and population numbers of many frog and salamander species. It appears that, in the last half of the century toxic chemicals, global change and infectious diseases also began contributing to declines. More research is needed before we can be confident that we understand how these six causes operate alone and more importantly, together. Unfortunately, the species themselves make some studies difficult. Many frog and salamander species are cryptic, fossorial or fluctuate greatly in population size. These factors make it harder, sometimes nearly impossible, to monitor changes in population size and population numbers. However, a variety of studies are now collectively giving us a much better grasp of how amphibian population and species' numbers are changing.

Vertebrate species reported extinct in the last 500 years include 83 mammals, 128 birds, 81 fishes,

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21 reptiles, and five amphibians; four amphibian species were recorded as extinct before the 1960s (Groombridge & Jenkins 2002). In the last 40 years eight species went missing in Australia alone—five species in the last 20 years—and are regarded as extinct. Lips *et al.* (2004) reported 31 frog populations (of 24 species) extirpated locally in southern Mexico, and assumed that 11 endemic species not seen for between 16 and 40 years were extinct. Since the early 1990s seven endemic species are presumed extinct in Honduras (Wilson & McCranie 2004), with extinctions reported in Costa Rica (Pounds *et al.* 1997; Lips 1998; Lips *et al.* 2003) and Panama (Lips 1999). Most significantly, many of these declines occurred in protected areas where habitat destruction was not a factor. There is a largely unexplained increase in the number of declining amphibian populations and the number of species that have gone missing late in the twentieth century (Houlahan *et al.* 2000). Various studies of single- and multi-species systems using data sets and databases have been developed to test the hypothesis that populations and/or species are declining and to identify the causes. Our goal is to summarize the diversity of these studies and assess some of their strengths and weaknesses. Estimating the species' number in a region is often the first challenge.

2. DATA INITIATIVES FOR MONITORING CHANGES IN AMPHIBIAN BIODIVERSITY

(a) *Monitoring changes in amphibian species' numbers*

Estimating the number of species in any group is always imprecise. Taxonomic instability is a feature of many groups as new taxa are being described. Some species' names are found to be synonyms, and what counts as a species varies among taxonomic groups (Isaac *et al.* 2004). New amphibian species, for example, are being described at a rapid rate, constantly changing the total number of species and compromising any estimate of the fractional loss of an amphibian fauna (Duellman 1999). The recent recognition of many new species in Sri Lanka suggests that the process of discovery will continue (Meegaskumbura *et al.* 2002). Tyler (1999) suspected that the total frog fauna of New Guinea is about 400 species, roughly twice the number known at the time. Ironically, some part of the increase in discovery results from an intensified search for new species before they go extinct. In a class like Amphibia where naming the fauna is incomplete, monitoring and comparing the fraction of taxa lost can be a misleading statistic because the total number of species is uncertain (Hanken 1999).

The first point, then, is that taxonomic instability is a challenge in amphibians, as it is in other taxa. But biodiversity is a more complex concept than just number of species (Balmford *et al.* 2003), so focusing only on species counts can miss the important contribution of populations to ecosystem functions and services, and this is just as true in amphibians as in other taxa (Ranvestel *et al.* 2004). Luck *et al.* (2003) proposed broadening our concept of biodiversity to incorporate population diversity, including changes in the size, number, distribution and genetic composition of populations. The convention on Biological Diversity Conference of Parties defined biodiversity loss as 'the long-term or permanent qualitative or quantitative reduction in components of biodiversity and their potential to provide goods and services at all levels' (www.biodiv.org). Likewise, Pimm *et al.* (2001, p. 2208) argued for "a greatly expanded research effort into the links between biodiversity, ecosystems, their services, and people." With the caveat of taxonomic instability in mind, what are we learning from monitoring studies of amphibians among populations, among species, and across sites?

(b) *Monitoring changes in amphibian population sizes*

Amphibian populations are monitored at three primary levels—gains and losses of species, change in population size and gains and losses of populations (Alford & Richards 1999). Studies of change in population size show extremes from no change in mean number of adult salamanders and frogs in the south-eastern U.S. over decades (Hairston & Wiley 1993; Pechmann *et al.* 1991), to rapid declines, to extinction of frog populations in north-eastern Australia (Richards *et al.* 1993; McDonald & Alford 1999), Costa Rica (Pounds *et al.* 1997; Lips 1998; Lips *et al.* 2003) and Panama (Lips 1999). Conclusions about long-term population trends are complicated by the fact that adult population sizes may vary by some 20 times over only a few years, and in any year adult number may be a poor predictor of juvenile number the following year (Pechmann *et al.* 1991). For a *Pseudacris ornata* population studied by Pechmann *et al.* (1991), Reed & Blaustein (1995) asked, do count data with this much variability have sufficient power to detect important trends? They estimated that the power was 0.17 to detect a 5% per year decline over 12 years (the period of the original data); thus, about 30 years of data would be needed to detect this level of decline with a power of 0.80. Large, annual fluctuations in population size are a significant obstacle to overcome in any effort to describe long-term trends in population sizes. Two major studies have identified declining trends in the midst of large inter-annual variation in population size.

Alford & Richards (1999) reasoned that amphibian populations are expected to decrease in more years than they increase because of the highly variable recruitment of juveniles and less variable adult mortality; that is a year of high recruitment is generally followed by years of decline. Their analysis led them to conclude that local populations of many amphibian species declined in recent years, and there are several cases of declines at and above the level of regional metapopulations. Green (2002) also concluded that amphibian populations are in decline, but found no support for the expectation that amphibian population sizes are a function of relatively rare years of high recruitment offset by intervening years of gradual decline, such that declines may outnumber decreases without negative effect.

These studies suggest two conclusions. First, long-term datasets are one way to identify meaningful population trends amidst inter-annual variability in population size; and second, another way to quantify long-term trends is to estimate changes in the number of populations, rather than focusing on changes within only one population. There is evidence that a number of amphibian species live in larger metapopulations, and in general, groups of populations may be a more appropriate level of analysis for connecting with processes at other scales that control biodiversity (Lawton 2000).

(c) *Monitoring changes in amphibian population numbers*

Individual studies are being collected as a first step in assembling the data needed to test the null hypothesis that there is no change in amphibian population numbers. The basic variable is average number of populations increasing or decreasing, and several studies using databases support at some level the conclusion that amphibians are declining; each database has assumptions and limitations. Major analyses based on databases include Waldman & Tocher (1998), Alford & Richards (1999), Houlahan *et al.* (2000) (also see the reanalysis of these data in Alford *et al.* (2001)) and Green (2002). Databases on species and population time series are available or are in development: AmphibiaWeb, AmphibiaTree, North American Monitoring Program, DAPTF's Declining Amphibian Database (DAD), Amphibian Research and Monitoring Initiative (ARMI) National Database, and ARMI Atlas for Amphibian Distributions. Several of these databases, like DAD, are not finished products but are in continuous development. We recommend linking these databases so that species names can be connected more or less automatically with readily available information on population changes. A closer look at DAD is instructive in understanding the strengths and weaknesses of these databases.

DAD has entries for 1170 species at 529 sites in 61 countries and 3020 populations (2478 frogs, 507 salamanders, 35 caecilians), where a population is a given species at a given site. It includes published and unpublished data. Names are updated as systematic revisions are published. A site is the geographical area covered by a study, which can be anything from a pond to a small country. A 'population' is not necessarily a population in the ecological sense of the word, but refers to animals of a given species at a given site. Details regarding the methods used in each study are a major feature of DAD.

What are we learning from databases and what are their limits? Whereas people have been counting birds for years, at least in places like the United Kingdom, fewer people counted amphibians before they became aware of the decline problem. Most data in DAD were collected in response to declines. As a result, we are not really in a strong position to conclude when declines began; the data must be interpreted in light of their limits. The 3020 populations in DAD sort as follows: 31 (1%) showed an increase in size; 1143 (38%) showed neither increase or decrease; 429 (14%) showed a small decline (about 25%); 75 (2.5%) showed a moderate decline (about 50%); 150 (5%) showed a major decline (about 75% or more); 313 (10%) apparently extinct; 879 (29%) population status undetermined. 'Undetermined' means too few data to reach a conclusion because the study was inconclusive (study length too short, population densities too low, or qualitative rather than quantitative data). In other cases, the species was noted as present or absent, but was not the main focus of the study.

There are too few datasets for confident conclusions about tropical population losses as opposed to species losses. For example, Green (2002) noted that most of his 617 time series and 89 amphibian species are from North America and Europe. Houlahan *et al.* (2000) included 120 populations outside North America and Europe (120/936 = 13%), including the categories Australia/New Zealand, Asia, Africa/Middle East ($n = 6$ populations), and South/Central America. DAD has 132 out of a total 529 sites (25%) in the tropics (between 23N and 23S). The point is that we have data for probably fewer than 200 tropical populations.

Overall, the databases support the conclusion that declines are occurring, but to an unknown degree that conclusion is influenced by the fact that more people are probably monitoring declining populations. Africa, Asia, the tropics and caecilians, an entire amphibian order, are poorly represented in all databases. Not surprisingly, patterns of decline vary among species with elevation and relative to a number of ecological factors. Lips *et al.* (2003) reported that aquatic, high elevation species were significantly more likely to decline in the tropics than terrestrial species; endemic species tended to decline and widespread species tended to survive; large frogs declined more than small frogs. McDonald & Alford (1999) also demonstrated that an association with streams is a risk factor for decline. Number of sites occupied changes as a function of immigration and emigration of individuals, but also as a function of the creation and destruction of sites by anthropogenic land use change (table 1) and natural processes like succession. For example Skelly *et al.* (1999) described a net change in the number of breeding populations for 14 frog and salamander species between two surveys (1967–1974 versus 1988–1992) of a set of 37 ponds in south-eastern Michigan, USA. They concluded that as a result of succession, altering pond hydroperiod and canopy cover, the average amphibian species experienced about five colonizations plus extinctions between the two surveys. Overall, there were 40 population colonizations and 34 population extinctions. The fact that declines are clearly not random and sometimes occur naturally means that any monitoring regime must account for the variation in the same sense that we use stratified sampling regimes to account for any environmental variation.

Long-term datasets increase our confidence in conclusions regarding site occupancy, which is a statistically challenging question because of detection probabilities that vary with techniques, species and a range of environmental variables (Schmidt 2003). How many instances of not observing any individuals does it take before concluding that the site is unoccupied?

Table 1. Loss of ponds (actual or potential amphibian habitats) at selected localities in Europe over the last 50 years.

location	% lost	annual rate (%)	source
all UK	20% of *ca* 350 000 between 1958 and 1988	0.7	Swan & Oldham (1993)
Sussex downland (rural)	18% of 33 lost between 1977 and 1996	0.9	Beebee (1997)
Huntingdonshire (rural)	99% lost over 40 years	2.5	Nature Conservancy Council (1982)
Milton Keynes (urban)	33% of 126 lost between 1984 and 1994	3.3	Barnes & Halliday (1997)
Geneva basin *Triturus cristatus* populations (rural/urban area)	68% of 22 lost between 1975 and 1997	3.1	Arntzen & Thorpe (1999)

Proportion of area occupied is an approach based on presence/absence data at a sample of sites across the landscape that integrates local extinction and recolonization processes into a description of metapopulation status (MacKenzie & Kendall 2002). By grouping populations, it allows for population status to be analysed at the scale of relevant ecosystem processes or at the scale of land management units such as nature reserves. Here the population-level question converges on the species-level question: How many years without being observed are needed before concluding that a species is extinct (Roberts & Solow 2003)?

3. WHAT CAN WE EXPECT IN THE IMMEDIATE FUTURE?

In the last decades of the twentieth century, amphibian species have gone missing in greater numbers than birds and mammals. We see no reason to expect this to change, even though by 2010 taxonomists will probably tell us that Earth has more amphibian species than we have today. Assessing changes in amphibians by 2010 will have to address the loss of populations and the marginalizing of frog species in the Caribbean, for example. Simultaneously, there will be an increase in the number of exotic frog species and populations in many regions, including Florida, the Hawaiian Islands, Guam and we would predict eventually any areas of Oceania with surface freshwater. Assessing changes in diversity will have to ensure that both gains by exotics and losses by endemics are seen as contributions to the negative side of the balance of biodiversity.

Loss of tropical forests through land use change (Groombridge & Jenkins 2002) means that the number of amphibian species with small ranges, many of them in the tropics, will decline. However, even in intact forests, recent experience in at least Central America, northern South America and Australia, indicates that the forest ecosystem can stay intact, but amphibian species are going missing. Chytridiomycosis is the suspected cause (Collins & Storfer 2003) and amphibian losses are continuing as shown by the IUCN's Global Amphibian Assessment (www.globalamphibians.org) (Stuart *et al.* 2004). Much current research is focused on the question of whether chytridiomycosis and other diseases have become more prevalent and/or more virulent as a result of other environmental factors, such as climate and chemical pollution.

We know most about trends in Europe and North America, which are comparatively well studied regions herpetologically. We know much less about the tropics, meaning that it is harder to make policy for these regions. The example from Michigan illustrates how populations may decline as vegetation and hydroperiod naturally change. Species will disappear locally as open ponds and marshes are converted to closed canopy forest. So, under some conditions, a natural loss of species is expected. The anthropogenic conversion of habitats is an accelerated version of the natural conversion of habitats that typifies a process like succession. Each of these dynamics alone complicates any future estimate of the number of species. Together, of course, the situation becomes more complicated as habitats undergo succession and species are lost at the same time as other habitats are converted to urban and agricultural landscapes and the mix of species changes.

Since 1990, research on amphibian declines shows considerable variation in the responses of populations and species. Some species are affected, others, even in the same community, continue to flourish. Declines correlate with elevation and microhabitat, and species with certain life histories and mean body sizes are more susceptible than others. Some regions, like Central America and Australia, are suffering a greater loss of species than other regions. Amphibian declines are not random, but show patterns that can shape statistical designs for monitoring programmes.

There are at least two major unpredictable elements in any plan to monitor changes in amphibian species and populations for a 2010 target. Global change may alter habitats so quickly that species cannot adapt and are driven to extinction. The loss of species at Monte Verde, Costa Rica, may be an example of such a rapid loss (Pounds *et al.* 1997). Second, we are only beginning to understand the effects of disease. If the loss of Central American and Australian populations and species is indeed due to chytridiomycosis as suspected, then amphibian losses to disease could exceed another case of extinction by infectious disease, that in Hawaiian birds (Warner 1968; Benning *et al.* 2002).

4. CONCLUSIONS

Amphibians inhabit most of Earth's biomes. The diversity of species and life histories coupled with late twentieth century declines and disappearances make amphibians an important model for studying the causes of global changes in biodiversity. The total number of amphibian species is still unknown, and we know little about population dynamics in many parts of the world, especially Africa, Asia and the tropics in general. Amphibian population trends are difficult to quantify because population sizes in many species naturally fluctuate a lot. However, reports suggest that populations are more likely to decline in the tropics at high elevations, if adults contact streams and if the species is relatively large bodied. These patterns are useful for creating more efficient designs for population monitoring that relates changes in population sizes and numbers to ecosystem properties and services. Several major databases summarizing changes in hundreds of populations are now available, and we recommend creating a network of linked databases sharing information on amphibian populations and species. There is a close correspondence between high areas of amphibian species richness and regions of the globe where humans are creating new croplands, increasing fertilizer use, increasing irrigation, decreasing forests and increasing human population size. In the final analysis, at least for amphibians, it is this correspondence that will likely be the greatest obstacle to meeting the millennium assessment target of ‘a significant reduction in the current rate of biodiversity loss’. Our knowledge of the causes of amphibian declines is still developing. Extinction is a complex process, but we understand some things better than we did a decade ago. Are amphibians declining faster than other taxa? Are they declining faster than some background or expected extinction rate? (Pechman & Wilbur 1994). The answer depends on whether we count species names (no), number of species gone missing in the last two decades (yes), number of populations of some exotic taxa (no), number of populations commercially exploited (yes), number of individuals or species gone missing due to land use change (yes), or toxins, global warming and disease (we do not know yet). However, we already know many things about the kinds of species and the kinds of areas that are most threatened and which would conserve the greatest number of species for a modest investment in habitat protection.

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GLOSSARY

ARMI: Amphibian Research and Monitoring Initiative
DAD: Declining Amphibian Database
DAPTF: Declining Amphibian Populations Task Force