THREATS TO AMPHIBIANS IN TROPICAL REGIONS

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Summary

Tropical amphibian populations have undergone drastic population declines and extinctions in recent decades. Threats to tropical amphibians include habitat loss, invasive species, pollution, infectious diseases, and climate change. Successful conservation of remaining amphibian populations is hindered by a lack of funding, a shortage of political and social will, and an incomplete understanding of the specific threats faced by individual amphibian populations. Unless these problems are remedied, we can expect that unacceptable numbers of amphibian species will become extinct in coming decades, resulting in irreversible consequences to the planet's ecosystems.

1. Introduction

The rapid expansion of the human population in recent centuries has had deleterious impacts on the earth's environment, and unsustainable practices have resulted in well-documented population declines and extinctions across a broad range of species (Pimm et al. 2001, Brooks et al. 2002, Ceballos and Ehrlich 2002, Stuart et al. 2004). Causes of species decline in both the terrestrial and marine environments are increasingly linked to human activities, and both the number and magnitude of threats has increased dramatically in modern times. Current threats to biodiversity include habitat loss (Vitousek et al. 1997), invasive species (Burgman and Lindenmayer 1998, Vredenburg 2004), pollution (Rowe et al. 2001, Davidson 2004), infectious diseases (Van Riper et

al. 1986, Daszak et al. 2000, Hawkins et al. 2006), and climate change (Pounds 2001, Thomas et al. 2004). Unless rapid and effective actions are immediately implemented to halt the current wave of extinctions, it is likely that we will lose a significant proportion of earth's biodiversity by the end of the century. Resolving this environmental crisis requires a combination of ecological, economic and socio-political solutions (Peres 2001).

Amphibians are among the planet's most threatened taxa. Nearly one-third of the world's 6,187 species are threatened with extinction (Stuart et al. 2004). Population declines in recent decades have been especially severe, with up to five species going extinct each year (Stuart et al. 2004). Rapid amphibian population declines have occurred in Europe (Bosch et al. 2001, Bosch and Martinez-Solano 2006), Africa (Weldon and du Preez 2004), Australia (Richards et al. 1993, Hines et al. 1999, Hero and Morrison 2004), New Zealand (Bell et al. 2004), North America (Carey 1993, Davidson et al. 2001, Green and Kagarise Sherman 2001), South America (Bonaccorso et al. 2003, Ron et al. 2003), and Central America (Pounds et al. 1997, Lips 1998, 1999, Lips et al. 2006). Unidentified processes threaten nearly half of rapidly declining amphibian species (Stuart et al. 2004), and many declines and extinctions have occurred in protected wilderness areas such as national parks and preserves, where no obvious cause can be identified (Bradford 1991, Kagarise Sherman and Morton 1993, Pounds and Crump 1994, Lips 1998, 1999, Hero and Morrison 2004).

Declines and extinctions of amphibians have been more severe in the tropics than in other regions (Stuart et al. 2004). In Australia, 32 frog species are currently listed as threatened due to population declines (Hero and Morrison 2004), and at least eight extinctions have occurred in the last three decades (Richards et al. 1993, Hero et al. 2006). At least thirty species from the neotropical toad genus *Atelopus* have not been seen in the last ten years, and are feared extinct (La Marca et al. 2005). While there have been relatively few reports of amphibian declines or extinctions in Africa or Asia, few long-term monitoring studies have occurred in these regions. Thus the threat status and population trends of a large proportion of amphibian species on these continents remain unknown (Stuart et al. 2004), and we should be hesitant to infer that amphibian populations on these continents are stable. As amphibian biodiversity is greatest in the tropics (Duellman 1999), these regions stand to lose the most numbers of species if the current threats to amphibians are not mitigated.

There are several reasons why the conservation of amphibians is important. Amphibians are an integral part of the food web. Tadpoles keep waterways clean by feeding on algae (Ranvestel et al. 2004), and adults consume large quantities of invertebrates, including disease vectors such as mosquitoes (Greenlees et al. 2006). Amphibians also serve as prey to a variety of birds, snakes, fish and other animals (Hecnar and McCloskey 1997b). Thus their disappearance could have potential negative impacts that would cascade through the ecosystem (Ranvestel et al. 2004, Whiles et al. 2006). Amphibians have permeable skin and often require suitable habitat in both the terrestrial and aquatic environment. As such, they are especially susceptible to many environmental disturbances. They are thus considered accurate indicators of environmental stress, and their health as a taxon is thought to be indicative of the health of the biosphere as a whole (Lips 1999, Cohen 2001, Wright et al. 2001, Hayes et al. 2002, Blaustein et al.

2003, Collins and Storfer 2003). Finally, important advances in human medicine have resulted from the use of amphibians in medical research (Traynor 1998, VanCompernolle et al. 2005). For example, skin secretions of three Australian frogs (*Litoria caerulea*, *L. chloris*, and *L. genimaculata*) completely inhibit HIV (VanCompernolle et al. 2005).

Herein we examine the threats to tropical amphibians, and suggest actions that must be taken to prevent future declines and extinctions, and possibly enable certain populations to recover to their pre-decline levels.

1.1. Assessing Population Decline.

Population decline can be defined as either a reduction in a species' geographic range (e.g. due to habitat loss) or a reduction in population abundance (e.g. due to overharvesting). Ultimately, population declines will lead to species extinction. A significant obstacle for evaluating declines is the lack of historical systematic, quantified surveys (number of individuals observed, distance surveyed, time surveyed, weather conditions etc.). Documenting population declines must consider the natural variation in population parameters (Yoccoz et al. 2001), as population sizes in certain species can vary by several orders of magnitude in different years (Pechmann et al. 1991), and metapopulations can go extinct and be re-colonized (Marsh and Trenham 2001). The majority of existing records are based on museum specimens and short-term follow up surveys, the results of which may or may not accurately reflect the population status of each species at that time. This highlights the importance of establishing and continuing extensive surveys and monitoring to ensure accurate assessment of species status.

When assessing amphibian populations it is necessary to consider the distinction between "population size" (the number of individuals within a population) and "number of populations" (Green 1997). The stochastic nature of amphibian populations makes interpreting changes in the former difficult without long-term data (Houlahan et al. 2000, Green 2003). In contrast, quantifying the latter (by surveying for the presence/absence of amphibian populations on a broad scale, rather than enumerating individuals within populations) facilitates the rapid assessment of species' population status (Richards et al. 1993, Ron et al. 2003).

1.2. Which amphibians are declining? (Ecological characteristics of declining frogs)

Even with the difficulties in assessing population declines, one pattern is clear: within a region, declining species co-exist with non-declining species, and within a species, some populations may decline while others do not. There are clearly factors that predispose certain species and populations toward decline and extinction. Indeed, similarities in the geographical and life-history traits of declining amphibian populations have been noted by multiple researchers. Eighty-five percent of the world's threatened frog species occur at high altitudes (Hero and Morrison 2004). Rapid population declines of montane amphibians have occurred worldwide (Bosch et al. 2001, Davidson et al. 2001, Hero and Morrison 2004, Weldon and du Preez 2004). In Australia, 41% of montane species are threatened, versus only 8% of lowland species. There are at least 4 species whose upland populations have declined precipitously, while lowland

populations have remained stable (*Litoria nannotis, L. rheocola, Nyctimystes dayi, and Taudactylus eungellensis*; Hero and Morrison 2004, Hero et al. 2006), suggesting that the causative agent of the rapid declines may be restricted to high altitudes. Most of the rapid amphibian declines in recent decades have taken place in relatively pristine, protected areas (such as national parks and preserves), where no obvious cause can be identified. Simply conferring protected area status on a locality is therefore unlikely to be sufficient for amphibian conservation in the 21st century.

Williams & Hero (1998) found that low fecundity (small clutch size), high habitat specificity (a restriction to specific vegetation associations that are geographically restricted in area), and an association with flowing streams were significant predictors of declining population status in frogs from Australia's Wet Tropics. Hero et al. (2005) examined over 60 frog species from upland areas of eastern Australia and also found that small clutch sizes and stream-dwelling behavior were primary characteristics of declining species. Furthermore, phylogenetic history was a significant predictor of declining status (certain genera had a relatively high proportion of species declining). Lips et al (2003b) examined Central American amphibians and found that the degree of association with aquatic habitat was a significant predictor of declining population status. Similarly, Stuart et al. (2004) found that nearly two-thirds of the threatened amphibian species that prefer flowing water are rapidly declining. Finally, amphibian species with narrow geographic ranges are more prone to extinction than are species with broad distributions (Williams and Hero 1998, Hero et al. 2005, Murray and Hose 2005). It should be noted though that being geographically-restricted is likely to be the long-term result of the ecological factors that led to susceptibility in the short term.

Why are species that exhibit these characteristics more susceptible to extinction than are sympatric species? How are these characteristics linked to the causes of decline? While ongoing research attempts to answer these questions, amphibian conservation efforts should focus on protecting populations that exhibit the above-mentioned characteristics (e.g. stream-dwelling frog species in the mountains of the Brazilian Atlantic forest).

2. Causes of Amphibian Declines

Amphibian declines can be clearly separated into (1) declines of predominantly lowland species, for which habitat loss is the principle culprit, and (2) unexplained declines of amphibians from relatively pristine natural habitats at high altitudes (Hero and Shoo 2003, Hero and Morrison 2004). Habitat loss is not considered to be an important factor involved in the rapid declines and extinctions that have been documented in relatively undisturbed areas in the last several decades. Determining the cause of the mysterious declines has been elusive. To date there appears to be a complexity of causes in different parts of the world. Causative agents implicated in the decline of high-altitude amphibian populations include introduced salmonid fish that predate on amphibians; pathogens (i.e. the chytrid fungus *Batrachochytrium dendrobatidis*); and global change, such as increased UV-B radiation and global warming. Increasingly complex explanations are possible as well. For instance, disease may not be the cause in isolation, but rather the result of increased stress levels in amphibians caused by increased UV radiation (Kiesecker et al. 2001) or changes to the local climate (Pounds et al. 1999, Pounds 2001).

2.1. Habitat Loss

Humans currently appropriate more than one third of the production of terrestrial ecosystems and about half of the usable fresh water on earth (Tilman et al. 2001), and the rapid growth of the human population shows no signs of slowing. It is not surprising then that habitat loss is one of the most significant threats to terrestrial biodiversity (Mittermeier et al. 1998, Pimm and Raven 2000, Brooks et al. 2002). Humans alter and destroy habitat by logging forests, draining swamps, paving grasslands, damming rivers, introducing weeds and livestock, and a variety of other actions.

Deforestation is clearly the principal cause of habitat loss, and this is concentrated in the tropical regions where biodiversity is greatest (Brooks et al. 2002). Extensive deforestation is continuing in both developed and developing countries throughout the tropical regions of the world. It is extremely difficult to halt as the subsequent development of agriculture and infrastructure is seen as the first crucial step toward economic development, and the reduction of poverty and food insecurity (Alexandratos 1999). Extensive clearing in the tropics is concentrated in lowland areas (Brooks et al. 1999, Pringle 2001), with coastal areas being particularly vulnerable, due to high rates of urban development and intensive agriculture. In South America, deforestation and subsequently intensive cattle grazing and unsustainable agriculture have severely degraded the ecosystem integrity in the Atlantic forests of Brazil, the southern plains of Brazil and Argentina, and the coastal plains of Ecuador and Peru (Ceballos and Ehrlich 2002). Each year, nearly 6 million hectares of the worlds tropical forests are logged (Whitmore 1997). The Amazon contains over half of the world's remaining tropical forest (Laurance 1998) but its size is rapidly diminishing: approximately 2 million hectares are cleared each year in the Brazilian Amazon alone (Laurance 2001).

Habitat loss, alteration and fragmentation are likely the primary causes of amphibian population declines and species extinctions worldwide (Dodd and Smith 2003). In Australia, habitat modification is associated with declines in 18 of the 40 threatened species, and is the primary cause of population declines in lowland frogs, negatively impacting 11 of the 12 threatened lowland species (Hero and Morrison 2004). Habitat alteration can directly remove amphibian breeding and feeding areas, or block access to them (Hazell et al. 2003). Deforestation alters amphibian species assemblages and reduces species diversity on the landscape scale (Corn and Bury 1989, Boyer and Grue 1995, Lowe and Bolger 2002). Livestock grazing can reduce wetland habitat quality and subsequently species diversity (Jansen and Healey 2003). Of particular concern is the stream flood mitigation process, which removes vegetation and the natural ponds associated with stream habitats (Hazell et al. 2003). Another major concern is the loss of ephemeral wetlands, which contain unique amphibian assemblages, yet often receive little legal protection (Semlitsch and Brodie 1998, Adams 1999, Gibbs 2000, Snodgrass et al. 2000). Land use change may also lead to an increased chance of direct predation by domestic animals (Crooks and Soule 1999), and may facilitate the emergence of infectious diseases (Daszak et al. 2000). While conservation of amphibians has focused on protecting breeding habitats (i.e. ponds & streams), the habitats used by all amphibian life history stages (egg, larval, juvenile & adult stages) must be protected (Taylor et al. 2006).

Although some amphibian species decline rapidly when the forest cover is removed (Ash 1988, Petranka et al. 1993, Parris 2001), most species suffer a gradual depletion of populations, and the overall impacts are not realized until the species has disappeared from a significant part of its former geographic range (Beebee 1977, Gillespie and Hollis 1996). This gradual depletion of suitable habitat through the accumulation of small-scale habitat loss (urban and rural expansion) has been described as "death by a thousand cuts". Whereby no single development (i.e. housing complex, shopping center) is responsible, the accumulation of many small developments eventually leads to the complete loss of the original habitat for the species. Loss of local populations and subsequent reduction in the area of occupancy for each species also results in loss of genetic diversity and thus a reduction in the evolutionary potential for species to adapt to environmental changes such as global warming (Crandall et al. 2000, Smith et al. 2001, Hoffmann et al. 2003). Monitoring loss of habitat, and the subsequent reduction in the area of occupancy for assessing the species' conservation status.

2.2. Over-Harvesting

Over-harvesting by humans has resulted in declines and extinctions across a broad range of mammal, bird, fish and shellfish species (Schorger 1955, Anderson 1995, Christensen et al. 2003, Edgar and Samson 2004), and currently threatens many amphibian species. Of particular concern are brightly colored species that are highly sought after by the pet trade (i.e. dendrobatids), and large, edible species. While it is difficult to quantify the number of amphibians harvested for the food industry each year, the number is likely significant. In many underdeveloped countries, the harvesting of amphibians is unregulated and is thus a likely contributor to amphibian declines. For instance, over six million Chinese Edible Frogs (*Hoplobatrachus rugulosus*) were imported to Hong Kong from Thailand in a single year, and the majority of these frogs were likely collected in the wild (Lau et al. 1999).

2.3. Introduced Species

Introduced species (both animals and plants) are a major threat to biodiversity in both terrestrial and marine ecosystems, and negatively affect a wide range of taxa. For instance, introduced rabbits and foxes have contributed to the decline and extinction of numerous Australian mammal species (Burgman and Lindenmayer 1998). Introduced species have also been implicated in the global declines of amphibians. Introduced fish, crayfish, and amphibians can harm native amphibians by competing for food resources, spreading disease, acting as toxic prey, and by predating on amphibians (Gillespie 2001, Kats and Ferrer 2003, Vredenburg 2004). Species may be introduced intentionally, such as in fish-stocking programs or the release of pets into the wild, or unintentionally, such as when a fisherman's live bait mistakenly escapes. Though the mechanisms by which invasive species cause declines are well understood, the problem is not easily remedied: it has often proven impossible to eradicate the invasive species once it has become established, as is the case with rainbow trout (*Oncorhynchus mykiss*) and bullfrogs (*Rana catesbeiana*) in the western United States, or cane toads (*Bufo marinus*) in Australia.

Introductions of salmonid fish have been associated with amphibian declines in Australia (Gillespie and Hines 1999, Gillespie 2001) and Spain (Bosch et al. 2006), and are thought to be responsible for the extinction of several *Atelopus* species in Costa Rica (Pough et al. 1998). In North America, introduced trout have been suggested as an important factor contributing to the decline of ranid frog species (Hayes and Jennings 1986, Liss and Larson 1991, Bradford et al. 1993, Hecnar and McCloskey 1997b). Similarly, the introduction of various fish species (salmonids, European carp (*Cyprinus carpio*), *Odonthestes bonariensis* and catfish (*Ictalurus* spp.)), are thought to be a principal factor leading to the decline of amphibians in southern Chile (Formas 1995).

The cane toad (*Bufo marinus*) was introduced into eastern Australia in 1935 and has since expanded its range to include a large portion of tropical and subtropical Australia (Zug and Zug 1979). Cane toads can reach large sizes (>150mm) and can achieve incredibly high densities. As such, they serve as a massive nutrient sink, significantly reducing invertebrate abundance and species richness (Greenlees et al. 2006) and thereby negatively affecting native amphibians by acting as major competitors for food resources.

Competition with the introduced bullfrog (*Rana catesbeiana*) has been proposed as contributing to the decline of *Rana muscosa* in the western USA (Hayes and Jennings 1986, Hecnar and McCloskey 1997a). Similar impacts can be expected following the establishment of wild populations of *Rana catesbeiana* that were recently introduced into China (Xu et al. 2006), Venezuela (Hanselmann et al. 2004), and Uruguay (Mazzoni et al. 2003).

The role of introduced species (e.g. *Rana catesbeiana, Bufo marinus* and *Xenopus laevis*) as potential vectors for transporting chytrid fungal disease has also been proposed (Daszak et al. 2004, Weldon et al. 2004). As these amphibian species can carry the disease without dying, and as they are being introduced to many regions around the world, they are a likely explanation for the rapid outbreak of this disease in naïve amphibian populations in various parts of the world.

2.4. Pollution

Pesticides (herbicides and insecticides) may be of critical importance to understanding amphibian declines (Boone and Bridges 2003). Pesticides are dispersed globally and have both lethal and sub-lethal effects on terrestrial fauna (Sala et al. 2000). Even low levels of pesticides can cause fatal immune suppression in frogs (Taylor et al. 1999). Many pesticides are approved by government authorities without their being tested on amphibians, and when testing is done, it generally focuses only on lethal effects. Potential sub-lethal effects may therefore easily go unnoticed by researchers.

Pesticides and other toxins that are used throughout the world have the ability to pollute geographically disparate regions via windborne transport (Datta et al. 1998). Recent studies by Davidson (2004) and Davidson and Knapp (2007) demonstrated an association between amphibian declines and amount of upwind pesticide use, strongly suggesting a link between agrochemicals and population declines. Hayes et al. (2002,

2006) showed that ecologically relevant doses of atrazine could render male *Xenopus laevis* hermaphroditic, and feminize the larynges of exposed males. Being that atrazine is one of the most commonly used herbicides in the world, (33 million kilos per year in USA alone; Hayes et al. 2002), these negative effects are clearly a cause for concern. It should be noted that many factors must be considered when implicating pesticides with amphibian declines, and that laboratory tests and experiments must be replicated in semi-natural and natural water bodies in the field to confirm cause-and-effect links (Boone and Bridges 2003).

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Biographical Sketches

Associate Professor Jean-Marc Hero has an outstanding national and international reputation as a leading amphibian research scientist. Over the last 20 years, he has worked on many aspects of amphibian ecology and conservation and more recently on the role of chytrid fungus in global amphibian declines.

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Kerry Kriger is the Executive Director of SAVE THE FROGS!, a nonprofit organization dedicated to amphibian conservation. His Ph.D. research focused on the ecology of chytridiomycosis in eastern Australia. He has written 12 refereed journal articles on amphibian diseases, and has presented his research results at conferences worldwide. His main interests are in wildlife conservation and environmental education. Dr. Kriger teaches biology, math, chemistry and music. He now resides in the USA.