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Forum

Chytridiomycosis, Amphibian Extinctions, and Lessons for the Prevention of Future Panzootics

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Abstract: The human-mediated transport of infected amphibians is the most plausible driver for the inter-continental spread of chytridiomycosis, a recently emerged infectious disease responsible for amphibian population declines and extinctions on multiple continents. Chytridiomycosis is now globally ubiquitous, and it cannot be eradicated from affected sites. Its rapid spread both within and between continents provides a valuable lesson on preventing future panzootics and subsequent erosion of biodiversity, not only of amphibians, but of a wide array of taxa: the continued inter-continental trade and transport of animals will inevitably lead to the spread of novel pathogens, followed by numerous extinctions. Herein, we define and discuss three levels of amphibian disease management: (1) post-exposure prophylactic measures that are curative in nature and applicable only in a small number of situations; (2) pre-exposure prophylactic measures that reduce disease threat in the short-term; and (3) preventive measures that remove the threat altogether. Preventive measures include a virtually complete ban on all unnecessary long-distance trade and transport of amphibians, and are the only method of protecting amphibians from disease-induced declines and extinctions over the long-term. Legislation to prevent the emergence of new diseases is urgently required to protect global amphibian biodiversity.

Keywords: chytrid, wildlife disease, amphibian declines, extinction, *Batrachochytrium dendrobatidis*, pet trade

The human-mediated transport of infected amphibians is the most plausible driver for the intercontinental spread of chytridiomycosis (Mazzoni et al., 2003; Weldon et al., 2004; Garner et al., 2006; Fisher and Garner, 2007; Skerratt et al., 2007), a recently emerged infectious disease responsible for amphibian population declines and extinctions on multiple continents (Berger et al., 1998; Bosch et al., 2001; Lips et al., 2006; Rachowicz et al., 2006). The chytrid fungus *Batrachochytrium dendrobatidis* (causative agent of chytridiomycosis) currently infects at least 287 amphibian species and occurs in at least 37 countries spanning six continents (Figure 1; Supporting Online Information Tables 1 and 2). It is widespread throughout Australia, Europe, Africa, and the Americas (Garner et al., 2005; Ouellet et al., 2005; Lips et al., 2006; Goldberg et al., 2007; Kriger et al., 2007; Pearl et al., 2007). *Batrachochytrium dendrobatidis* has been detected as far north as Alaska and as far south as Tasmania, as high as 5348 m a.s.l. (Seimon et al., 2007) and as low as nearly sea level (Kriger et al., 2007). The fungus was detected across the altitudinal gradient in all five studies that have examined its altitudinal distribution (Retallick et al., 2004; McDonald

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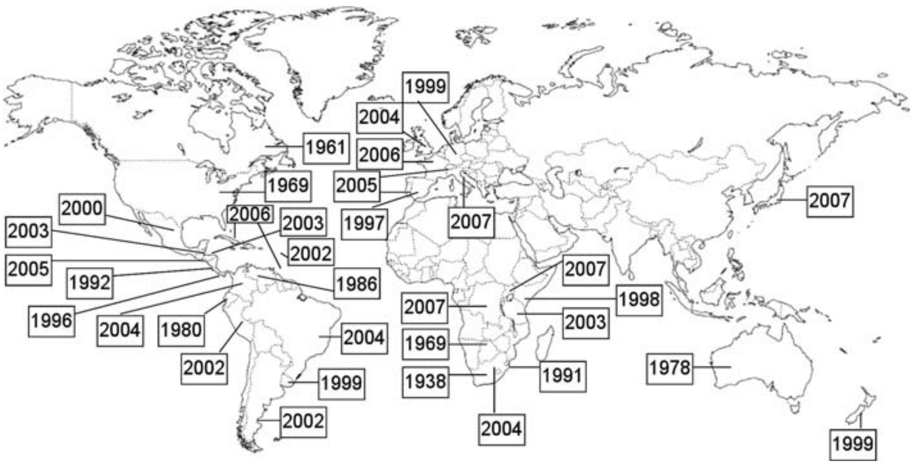

Figure 1. Global distribution of *B. dendrobatidis*. Years represent the dates of first known occurrence in the 37 infected countries.

et al., 2005; Woodhams and Alford, 2005; Puschendorf et al., 2006; Kriger and Hero, 2008), and bioclimatic modeling predicts it could occupy a significant portion of both the eastern and western hemispheres (Ron, 2005).

The apparent ubiquity of *B. dendrobatidis*, combined with the rapidity with which the fungus spreads within continents (Lips et al., 2006, 2008) and the high number of opportunities for its human-mediated transport between continents (Fisher and Garner, 2007), suggests that, barring drastic and immediate amphibian trade restrictions, *B. dendrobatidis* is likely to invade any currently unoccupied areas of its bioclimatic envelope. As approximately one-third of the world's 6350 amphibian species are already threatened with extinction (Stuart et al., 2004), preventing the further spread of chytridiomycosis and other infectious diseases represents one of the scientific community's most urgent challenges.

Herein, we define and discuss three levels of amphibian disease management: (1) post-exposure prophylactic measures, which include curing infected captive individuals, eradicating disease from infected wild populations, and facilitating evolved resistance; (2) pre-exposure prophylactic measures, such as routine diagnostic testing and quarantine of apparently healthy individuals destined for translocation, which are intended to reduce the likelihood of disease transfer; and (3) preventive measures that remove the threat of disease altogether, such as banning the translocation of amphibians.

Post-exposure Prophylactic Measures

Post-exposure disease prophylaxis is currently a viable option for only a very small proportion of the world's amphibians, namely those in captivity whose diseases can be cured by heat treatments or chemicals (Parker et al., 2002; Woodhams et al., 2003). There are no published accounts of studies that have successfully facilitated amphibians' evolved resistance to diseases, and it can be assumed that no such protocols will be imminently developed that can protect the world's amphibian populations in the short-term. This is due to: (1) the slow reproductive rate, and therefore evolutionary adaptivity of most amphibians; (2) our current lack of knowledge regarding amphibian husbandry (Lee et al., 2006); and (3) potential negative effects associated with the captive-breeding of amphibians over multiple generations (Kraaijeveld-Smit et al., 2006).

It is not currently feasible to eradicate *B. dendrobatidis* from infected sites (DEH, 2005), and it is unlikely that suitable methods will be developed prior to the fungus' initial epidemic wave wreaking havoc on any remaining naive and susceptible amphibian populations. Even if suitable eradication techniques were developed, the rapidity with which *B. dendrobatidis* causes population declines at sites in which it is newly introduced (Lips et al., 2006; Rachowicz et al., 2006) suggests that only a small proportion of the world's susceptible amphibians could be protected. The vast majority of the world's amphibians live in tropical countries (Duellman, 1999), where there are few herpetologists available to conduct regular disease monitoring, and even the best available disease detection techniques have a time-lag prior to *B. dendrobatidis* being detectable in infected amphibians (Hyatt et al., 2007). Thus, in most cases, the majority of the damage would be done before researchers would know to implement eradication protocols. In these tropical countries, most population declines due to chytridiomycosis are predicted to occur in moist areas (Ron, 2005; Kriger et al., 2007), where both amphibians and *B. dendrobatidis* are likely to persist away from water bodies, making eradication even more difficult. Further, eradication methods would likely provide only a short-term solution, as the fungus would inevitably recolonize any areas from which it had been temporarily extirpated.

The direct management of *B. dendrobatidis* in infected amphibian populations is thus futile in all but a few isolated cases, such as with endangered populations living on small islands that have only a few aquatic breeding sites (e.g., *Leiopelma hamiltoni* or *Alytes muletensis*). For such populations, the currently available management option would be to manually catch and then cure every infected individual, and repeat this process either indefinitely or until a suitable eradication method is developed. Thus, while continued research into eradication methods is important and may be necessary for protecting some critically endangered species, current (and quite possibly future) management options for the vast majority of the world's infected amphibian populations are restricted to the mitigation of all other threats to the populations (i.e., habitat destruction, invasive species, over-harvesting, loss of genetic variation, climate change, and pollutants).

As post-exposure prophylactic measures are unlikely to protect more than a small proportion of the world's amphibians, the optimal method of directly managing *B. dendrobatidis* is to prevent it from reaching new isolated locations where transport of proposed disease vectors is limited (e.g., Madagascar and Pacific Islands), and to prevent the transfer of new strains to currently affected sites, so as to facilitate amphibian populations' natural adaptation to the fungus (Berger et al., 2005; Kriger and Hero, 2006). Protecting remaining uninfected amphibian populations from *B. dendrobatidis* (and perhaps more importantly future diseases) will require drastic and immediate restrictions on the domestic and global trade and transport of amphibians, on a scale unlike any that have been implemented in the past. Appropriate restrictions would affect the pet, bait, food, zoo, and laboratory trades, all of which have been implicated as driving the global spread of chytridiomycosis (Aplin and Kirkpatrick, 1999; Pessier et al., 1999; Parker et al., 2002; Garner et al., 2006).

Pre-exposure Prophylactic Measures

The goal of a pre-exposure prophylactic measure is to reduce the likelihood of disease transfer in scenarios where infection is likely to be encountered. Such measures include quarantines and subsequent diagnostic tests to confirm infection-free status, batch-testing shipments, certifying farms as disease-free, and other similar bio-security precautions. These actions are necessary when translocations must occur, as is the case for zoos and laboratories, both of which can contribute to disease spread (Pessier et al., 1999; Parker et al., 2002), yet perform important conservation services such as captive-breeding and scientific research. As zoos and laboratories are part of the scientific community and are thus amenable to laws that benefit amphibian conservation, a reduction in trade and the enactment of appropriate quarantine and testing procedures by these sectors could likely be implemented with relative ease (Young et al., 2007). To further reduce the threat of disease transfer, captive-breeding should take place in the amphibian species' native geographical region whenever possible, and laboratories should conduct their research on either native species, or locally bred exotics.

The amphibian food trade is important in many developing countries where amphibians serve as a traditional source of protein. In these locations, amphibians tend to be harvested and consumed locally, and thus are unlikely to be significant sources of disease transfer. Such countries therefore have little reason to restrict domestic sales of amphibian species, assuming they are harvested in a sustainable manner. Conversely, most developed countries have no shortage of alternative food sources, and the amphibians they eat are seldom harvested locally. France, for instance, banned commercial frog farming in 1977 and now relies primarily on imports from southeast Asia. In such scenarios, countries should be required to either restrict their imports to dead amphibians, or to submit all imported amphibians to both quarantine periods and comprehensive disease testing and prophylactic treatment, the costs of which would be paid for by the importers and consumers. Similar restrictions should be placed on the domestic food trade if the species in question is being transported outside of its natural range.

We wish to make it clear, however, that it only takes one diseased individual to initiate an epizootic. Pre-exposure prophylactic measures are an important improvement over current laws, but are unlikely to protect biodiversity in the long-term. Diseased individuals would inevitably pass undetected, as existent diagnostic tests are seldom perfect, and many diseases have yet to be discovered. Thus, any unnecessary long-distance transfer of live amphibians, including those in a strictly regulated food trade, should eventually be phased out.

Preventive Measures

Preventing disease spread into naive amphibian populations can only be accomplished by removing the source of the problem: the translocation of infected amphibians. Unlike zoos and laboratories, whose conservation services render the translocation of amphibians an occasional necessity, the amphibian pet and bait trades are for the large part disposable, that is, they are unnecessary, serving little benefit to society. Their nearly complete dismantling would benefit amphibian populations, not only by eliminating a primary source of disease transfer, but also by simultaneously reducing the over-harvesting of wild amphibian populations, which is largely unregulated in many parts of the world (Li and Wilcove, 2005; Schlaepfer et al., 2005). At a minimum, these trades should be restricted to local sales of captive-bred individuals.

Though restricting the pet, bait, and food trades may have some initial negative economic impact, these actions may save perhaps hundreds of species from extinction, and thus will significantly reduce conservation and remediation costs (currently estimated at US$82 million per year; Gascon et al., 2007) in the long run. The free ecosystem services and benefits to human health that amphibians provide (Tyler et al., 2007) give further economic incentive that compensates for any initial economic losses. Australia successfully banned virtually all amphibian sales outside of zoo and research settings, yet remains one of the wealthiest countries in the world. There is little reason to believe that other nations would suffer undue losses were they to follow Australia's example.

Conclusions

In terms of its impact on biodiversity, chytridiomycosis may be the worst disease in recorded history (Skerratt et al., 2007). That the disease cannot be managed at affected sites should serve as a valuable lesson for the prevention of future panzootics: the continued inter-continental trade and transport of animals (be they amphibians or other taxa) will inevitably lead to the spread of novel pathogens, followed by numerous extinctions. To protect global amphibian biodiversity, we must now focus on preventing future panzootics. The immediate implementation and enforcement of appropriate biosecurity measures, including a virtually complete ban on all unnecessary long-distance trade and transport of live amphibians, should be the highest priority for the scientific and legislative communities.

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