A Plague Upon Them

Helping Wildlife Adapt to Climate Changes and Disease

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Defenders of Wildlife

Chapter 3. Chytridiomycosis

Amphibians—frogs, toads, salamanders—are in alarming decline throughout the world. The 2004 Global Amphibian Assessment classified 1,896 species of amphibians as vulnerable, endangered or critically endangered. This figure represents nearly one-third of all amphibians, a higher rate of endangerment than in birds (12%) or mammals (23%) (GAA 2004). Thirty-five species have been driven to extinction in recent years and a further 130 may be extinct. Many factors drive amphibian decline, with habitat loss and pollution long established as important threats to many species. Over the past decade, however, diseases—particularly the fungus chytridiomycosis—have emerged as another important driver. Even worse, Chytridiomycosis may be interacting with climate change and other stresses to drive species toward extinction.

Disease Life Cycle

Chytridiomycosis is caused by a fungus, the taxonomic group that includes molds, yeasts and mushrooms. Unlike mushrooms and molds, however, these fungi do not form large visible fruiting structures. Chytrids are a fairly distinct group among the fungi, as they are mainly found in aquatic habitats or in soils and each spore has a whip-like flagella for propulsion, to aid dispersal through the water. Once this zoospore lands on a suitable host, it forms a small cyst and then begins to divide and send out tiny root-like structures into the epidermal cells of its host. These rhizoids infiltrate the animal's skin cells and feed on keratin, an important structural protein within the skin. Eventually, the fungus creates new spores, which themselves go on to infect additional cells or new individuals (Longcore et al. 1999; Berger et al. 2005).

Chytrid-infected amphibians show skin lesions with cellular damage evident at the microscopic level. The damage is somewhat analogous to human cases of athlete's foot, caused by another keratin-ingesting fungus; however, the effects are much more dangerous for frogs, because their skin helps regulate the body's oxygen and water content (Berger et al. 1998). It remains uncertain whether amphibians die directly from the fungal damage, from toxins emitted by the fungus, or from secondary bacterial infection (Berger et al. 2005). Tadpoles usually survive infection, because their skin lacks keratin; therefore the fungus only attacks their keratin-containing mouthparts; widespread and often fatal infection follows metamporhosis, when a larger part of the skin becomes keratinized (Berger et al. 1998). The chytrid group contains many species; however the deadly amphibian parasite *Batrachochytrium dendrobatidis* (often abbreviated as *Bd.*) is the only species within the group to attack vertebrates (Berger et al. 1998).

The Conservation Threat

Origin and Means of Spread

A study of museum specimens found that the chytrid fungus was present on clawed frogs (*Xenopus laevis)* from southern Africa dating to 1938, 23 years earlier than the disease was found anywhere else (Weldon et al. 2004). The disease also had little impact on that species, supporting the theory that the fungus originated somewhere in Africa. A number of other amphibians from different parts of the continent have shown chytrid fungus infection without high levels of mortality, so more research is needed to pinpoint the exact origin and original host within Africa (Weldon et al. 2004).

In 1934, scientists discovered that the African clawed frog can be induced to ovulate when injected with the urine of a pregnant woman. This knowledge was used to develop a protocol for a rapid pregnancy test (Shapiro & Zwarenstein 1934). Subsequently large numbers of African clawed frogs were exported around the world (Weldon et al. 2004). Specimens were also used in embryological research and molecular biology, and feral populations that could potentially serve as infection reserviors became established in the United States, Britain and Chile (Weldon et al. 2004). The American bullfrog *(Rana catesbiana*) may have served as an additional vector for the spread of the chytrid fungus; like the African clawed frog, it is traded widely, has established feral populations in many areas, and can carry the fungus without suffering adverse effects (Weldon et al. 2004). For instance, researchers in the Venezuelan Andes have found populations of introduced bullfrogs carrying the disease but suffering only small skin lesions and low mortality (Hanselmann et al. 2004).

North America

The earliest incidence of chytrid fungus in North America dates to green frogs in Quebec in 1961 (Ouellet et al. 2005). Sampling at National Wildlife Refuges in New York, Vermont, New Hampshire, Massachusetts and Maine detected chytrid fungus in American toads (*Bufo americanus*), bullfrogs (*Rana catesbiana*), green frogs (*Rana clamitans*), pickerel frogs (*Rana palustris*), northern leopard frogs (*Rana pipiens*), mink frogs (*Rana septentrionalis*) and wood frogs (*Rana sylvatica*). The fungus was not detected in the gray tree frog (*Hyla versicolor*) and spring peeper (*Pseudacris crucifer*), possibly because both of these spend more time in trees and less in ponds and streams than the other species tested (Longcore et al. 2007).

The fungus also infects populations of the mountain yellow-legged frog (*Rana mucosa*) in California. Interestingly, the patterns of population decline in this species varies, with population extinction occuring within a few years in southern Sierra Nevada sites, but populations persisting despite infection at sites in the northern part of the range (Briggs et al. 2005, Fellers et al. 2007). The potential role of habitat and differences in temperature profile between the two areas is currently under investigation. Fungal infection has been associated with die-offs of in boreal toads, Wyoming toads and Yosemite toads (Green & Sherman 2001, Green et al. 2002).

Chytrid fungus has also been detected in the Jemez Mountains of New Mexico in an exclusively terrestrial salamander species, suggesting that the disease could potentially threaten a wider array of species than previously thought (Cummer et al. 2005). The fungus was detected in three species of Arizona frogs, one a threatened species and the other a candidate for listing. Given that all of Arizona's native frogs are experiencing population declines, the emergence of chytrid fungus there poses a serious additional concern for the southwest's amphibian fauna (Bradley et al. 2002). On the other hand chytridiomycosis detected in tiger salamanders in Arizona did not lead to mortalities, indicating that susceptibility might vary among species (Davidson et al. 2003).

Australia & *New Zealand*

Chytridiomycosis was identified in Australia after scientists discovered large numbers of dead and dying frogs in the Big Tableland area of Queensland in 1993 and 1994; these researchers subsequently found dead and dying frogs in other locations and from captive collections as well, and were able to determing that the cause of death was the chytrid fungus (Berger et al. 1998). The pathogen was probably introduced to Australia in the mid to late 1970s and had caused dramatic declines in mountain streamdwelling frog species (DEH 2006). The sharp-snouted day frog (*Taudactylus acutirostris*) was most likely driven to extinction by chytridiomycosis (Schloegel et al. 2006). The frog was previously abundant in the upland tropical areas of Queensland but populations crashed starting in 1990; by 1994 the species has essentially vanished from the wild, and the last captive specimen died in 1995 (DEH 2006).

The disease also most likely claimed the three other Australian frog species, the northern and southern gastric brooding frogs (*Rheobatrachus vitellinus* and *R. silus*) and the southern day frog (*T. diurnus*). All three went extinct before the disease was postively identified, but their patterns of decline and disapperance fit the epidemiology of chytridiomycosis (DEH 2006). Several species suffered local extinctions of their upland populations, while lowland populations have managed to persist. Overall, the disease has been detected in 49 species of amphibians in Australia, including 14 of the 27 listed as threatened. Further species are expected to be listed due to the disease (DEH 2006).

In New Zealand, where the native amphibian fauna is already greatly reduced due to introduced predators and habitat modification, the chytrid fungus was found in 1999 (Waldman et al 2001).

Central & South America

Amphibian populations in the Monteverde region of Costa Rica underwent a severe crash in 1987; this event led to the high-profile presumed extinction of two species, the golden toad and the harlequin frog (Pounds & Crump 1994), as well as declines in multiple other species (Pounds et al. 1997). Researchers postulated that temperature or moisture stress, or a pathogen, might be interacting with climate disturbance from a particularly strong El Nino event, to cause the alarming declines (Pounds & Crump 1994, Pounds et al. 1997, Ron et al. 2003). Later examination of specimens collected in 1986 from Braulio Carrillo National Park in Costa Rica confirmed the presence of chytrid fungus (Puschendorf et al. 2006a). A large-scale mortality of several species of stream-dwelling frogs observed in Las Tablas, Costa Rica and Fortuna, Panama in 1993 and 1994; these frogs exhibited the diagnostic features of infection by the keratin-attacking chytrid fungus (Lips 1998, 1999). Similar declines and possible extinctions have occurred in Honduras (Puschendorf et al. 2006b), and the disease has also been detected in Guatemala, where several species have experienced "catastrophic" declines (Mendelson et al. 2004). More recently the disease has been detected in El Salvador in two frog species, one of which is critically endangered (Felger et al. 2007).

Chytrid infection has struck frogs along the spine of the Andes, and may be a factor in the extinction of several species in genus *Telmatobius*, a group whose various species live in isolated high mountain streams in the Andes. Many *Telmatobius* were rare or endangered prior to the arrival of chytrid fungus (Barrionuevo & Mangione 2006). In 1989, the disease was detected in *T. niger*, a species that was once widespread in Ecuador. That species has not been seen since 1994 and is now presumed extinct (Merino-Viteri et al. 2005). *T. marmoratus*, which lives in the high mountains of Peru, is also in decline, with chytrid fungus as one potential cause (Seimon et al. 2005). In 2006, Bd was reported from two species of endangered Argentinean frogs (*Telmatobius atacamensis* and *T. pisanoi*) (Barrionuevo & Mangione 2006).

Chytrid fungus has probably played a role in the disappearance of several species of the brightly colored *Atelopus* toads (also called harlequin frogs) in the Venezuelan lowlands (Bonaccorso et al. 2003) and Andes (Lampo et al. 2006) and Ecuador, where the apparent extinction of the Jambayo toad (*Atelopus ignescens*) followed a warm, dry year in 1987 (Ron et al. 2003). A recent comprehensive survey of this genus found that this group has declined more severely than any other group of amphibians: 42 out of 113 putative species have declined by half and 30 species have not been seen since 1996 and are feared to be extinct (La Marca et al. 2005). These researchers also did a breakdown by country: 100% of Costa Rica's harlequin frogs were declining, 50% in Panama, 27% in Colombia, 58% in Ecuador, 11% in Peru 90% in Venezuela and 25% in French Guiana. Chytrid fungus has been documented in nine declining species and is suspected in others, particularly since many species are declining in protected areas where habitat loss is not thought to be a factor (La Marca et al. 2005).

Chytridiomycosis has been detected across a broad range of locations and altitudes in the Brazilian Atlantic rain forest (Carnaval et al 2006). While the disease has not yet been definitely linked to declines and extinctions, at least 20 species of Brazilian frogs and toads have undergone alarming population declines in recent years, and several of the species of concern are montane stream-dwelling species that have elsewhere been particularly vulnerable to chytrid fungus (Eterovick et al. 2005).

Caribbean

Chytrid fungus was first reported from the Caribbean in 2004 (Burrowes et al. 2004). At least three species of high-elevation dwelling frogs are presumed to have gone extinct in Puerto Rico over the past thirty years. Higher-elevation populations of six other endemics are in decline, and the fungus may be a factor in these declines and extinctions (Burrowes et al. 2004). More recently, the disease was found in a dead toad in Cuba, and may prove to be an emerging conservation challenge there (Diaz et al. 2007).

Europe

Chytridiomycosis was first detected in Europe in 1998, following the importation of infected frogs from Costa Rica and French Guayana (Mutschmann et al. 2000). By 1999 the disease caused an 86% crash in populations of Spain's common midwife toad; similar to patterns elsewhere, the declines took place in protected areas that had undergone very little change in habitat (Bosch et al. 2001). In 2004, the fungus was detected in a wild population of introduced bullfrogs in a pond in southeastern Britain (Cunningham et al. 2005). The extent of the disease's spread and the impacts on native British amphibian fauna are not yet known. Amphibians also tested positive for the disease in Portugal, Switzerland (Garner et al. 2005) and Italy (Simoncelli et al. 2005).

The Climate Connection

Climate disturbance, particularly extremely dry El Niño events, was proposed early on as a factor in the disappearance of the golden toad and the harlequin frog from their cloud forest habitats in Costa Rica (Pounds & Crump 1994). At first glance, however, it would appear that global warming would hinder the chytrid fungus rather than act synergistically with it. Optimal temperatures for the growth of the fungus occur between 6ºC and 28ºC (Bradley et al. 2002). The fungus is more pathogenic at moderate temperatures: for instance 100% of experimentally infected frogs died when held at 17ºC and 23ºC, but only 50% of frogs died at 27ºC (Berger et al. 2004). In Australia, chytridiomycosis is more likely to be present at sites where the summer temperature is below 30ºC (Drew et al. 2006) and the disease is more prevalent in early spring than in late summer and fall (Kriger & Hero 2006). Infected frogs held at 37ºC for fifteen hours are "cured" of the disease (Woodhams et al. 2003)

High temperatures actually inhibit the development of the fungus and increase the rates at which amphibians slough off their skin cells; thus high temperatures prevent the fungus from completing its life cycle before the infected cells are shed (Berger et al. 2005). One might expect, therefore, that warming temperatures might slow or halt the disease. However, as with many issues involving climate change, the story of how the fungus and host interact in the real world is more complicated than simply an effect of temperature.

One set of researchers believes that they have found the answer to this apparent paradox. J.Alan Pounds and colleagues have noted that in the middle elevations of the mountain regions of Central and South America, where disease-related dieoffs have been particularly severe, one of the main manifestations of climate change is an increase in cloud cover. This increase is moderating the temperatures at the middle elevations: raising the night time temperatures and lowering the daytime temperatures. At low elevations, daytime highs are still high enough to kill off the fungus, especially in sunny spots on the forest floor. At the highest elevations, night time temperatures are still low enough to inhibit the fungus. But at the middle elevations, cloud cover has moderated both the daytime and nighttime temperatures, with both periods thereby “shifting towards the growth optimum for these pathogens” (Pounds et al. 2006).

Climate conditions in Spain may also be changing in ways that favor the fungus. For instance, the number of days that fall within the most favorable conditions (21-27ºC) have increased, while the number of days hot enough to to inhibit it has not (Bosch et al 2007). Changes in humidity, night time temperatures and shorter and milder winters might also be favoring the fungus (Bosch et al. 2007).

It has also been observed that sharp amphibian declines in Ecuador (Ron et al. 2003) and Puerto Rico (Burrowes et al. 2004) were preceded by droughts. The apparent interaction between drought and amphibian die-offs led scientists to speculate about another way that the disease is interacting with a changing climate: chytrid fungus may interfere with the animals’ ability to withstand drought. As mentioned above, one of the areas that often shows damage to the skin from the fungus is the pelvic patch, a small but critically important area of skin that helps the animal control absorption of water (Berger et al. 1998). Some researchers have suggested that frogs can survive this damage during wet periods. During drought when the animals need a functioning pelvic patch in order to absorb water from dew (Pough 1983), and under these conditions the fungal damage may prove fatal because it interferes with this vital function (Burrowes et al. 2004). Increased incidence of drought is one “likely” forecast outcome of anthropogenic climate change (IPCC 2007). If this mechanism of action proves true, chytrid fungus may cause future declines in species and areas that have not yet experienced high levels of mortality from the fungus.

Researchers in Australia found that multiple-year warm trends were more likely than single-year warm periods to presage amphibian declines, and suggest that warming might stress amphibians in ways that make them more susceptible to infection (Alford et al. 2007).

Helping Wildlife Adapt to Chytridiomycosis and Climate Change

Focus monitoring and conservation efforts on vulnerable species and habitats. The chytrid fungus has caused amphibian populations in far-flung regions of the world to plummet towards extinction. To prevent further species from suffering the same fate, it will be critical to monitor amphibian population health, with particularly focus on montaine streamside habitats that are most at risk (Kriger & Hero 2007). Intensive interventions such as capture, fungicide treatments and captive breeding may be necessary to prevent further extinctions (Young et al. 2007).

Clean fishing, recreation and research practices. While the chytrid fungus is adapted to aquatic dispersal, the spore is also capable of surviving for several hours in a dry environment and up to three months in a moist environment like mud (Johnson & Speare 2005). The fungus can thus potentially be spread via recreational equipment (boats, boots, fishing gear) and research equipent (Corn 2007). "Clean" campaigns directed at other aquatic nuisance species like zebra mussels and hydrilla have raised awareness of the need to clean and dry recreational equipment before transport to new locations (see, for instance www.protectyourwaters.net). These same protocols might also help slow the spread of aquatic-borne diseaseses like chytrid fungus (Corn 2007).

Reduce the threat from release or transport of infected amphibians. Chytrid fungus was able to spread around the world from its area of origin in southern Africa because of wide-scale trade, transport and release of one of its hosts, the African clawed frog. Release of infected captive animals continues. Fungal spores can also find their way into new habitats via release of water that housed infected captive frogs. International trade in live amphibian imports has reached huge proportions: 28 million individuals passed through the three largest U.S. ports of entry from 2000-2005; and 62% of imported bullfrogs were carrying *Batrachochytrium dendrobatidis* infection (Schoegel et al. 2009). Halting the spread of the disease will require risk abatement planning to reduce the risk from amphibians in trade and captivity (Fisher & Garner 2007).

Reduce other threats, particularly those may act synergistically with chytrid fungus. Disease and climate climate are far from the only threats that amphibians face world wide. Habitat loss, exploitation, introduced species, other pathogens, ultraviolet-B radiation and a range of pollutants and toxins also take their toll on amphibians (Collins & Storfer 2003, Bancroft et al. 2008). All these threats must be abated if amphibians are to survive the climate change and disease bottleneck.