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Opinion Article

The relationship between the emergence of *Batrachochytrium dendrobatidis*, the international trade in amphibians and introduced amphibian species

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ABSTRACT

Chytridiomycosis is an emerging infectious disease of amphibians caused by the chytrid *Batrachochytrium dendrobatidis*. The disease has been associated with global amphibian declines and species extinctions, however the principle drivers that underly the emergence of chytridiomycosis remain unclear. Current evidence suggests that the world trade in amphibians is implicated in the emergence of chytridiomycosis. Here, we review the evidence that the amphibian trade is driving the emergence of chytridiomycosis by (1) spreading infected animals worldwide, (2) introducing non-native infected animals into naïve populations and (3) amplifying infection of amphibians by co-housing, followed by untreated discharge of infectious zoospores into water supplies. We conclude that the evidence that the amphibian trade is contributing to the spread of *Batrachochytrium dendrobatidis* is strong, and that specific actions are necessary to prevent the introduction of the pathogen into thus-far uninfected areas. Specifically, we recommend the development of national risk-abatement plans, focused on firstly preventing introduction of *Bd* into disease free areas, and secondly, decreasing the impact of the disease on populations that are currently infected.

Amphibian species across the globe are declining at an alarming rate and a fungal disease, cutaneous chytridiomycosis, is now known to be a major driver of these declines (Stuart *et al.* 2004; Lips *et al.* 2006). The causative agent, the nonhyphal zoosporic euchytrid *Batrachochytrium dendrobatidis* [*Bd*; phylum Chytridiomycota, class Chytridiomycetes, order Chytridiales; (Longcore *et al.* 1999; James *et al.* 2006)], is a generalist pathogen and is known to infect over 90 amphibian species on five continents (Daszak *et al.* 2003; Rachowicz *et al.* 2005). Of these species, a continuum exists in the host response to *Bd*; several species are known to carry infection without any recognised pathogenic effects, while other species suffer up to 100 % mortality, rapid species declines and in some cases, extinction (Berger *et al.* 1998; Daszak *et al.* 2003; La Marca *et al.* 2005). The scale of these declines has been such that amphibian chytridiomycosis has been described as "*the worst infectious disease ever recorded among vertebrates in terms of the number of species impacted, and its propensity to drive them to extinction*" (ACAP 2005).

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Due to its recent, and largely simultaneous, recognition as a globally widespread pathogen, chytridiomycosis has been designated an emerging infectious disease (Daszak *et al.* 2003). Two hypotheses have been advanced to account for the emerging nature of disease caused by *Bd*; on one hand, the 'novel pathogen hypothesis' (NPH) states that *Bd* has recently spread into new geographic areas, and host species, as a result of the anthropogenically-mediated spread of *Bd*. On the other hand, the 'endemic pathogen hypothesis' (EPH) states that the emergence of chytridiomycosis has been caused by amphibian hosts becoming more susceptible to pre-existing infections as a consequence of changes in the environment.

The purpose of this review is not to weigh up the evidence for the NPH versus the EPH; this was ably undertaken by Rachowicz *et al.* (2005). Ours, and other, research show that both hypotheses contribute to explaining the current pandemic. The NPH receives support from the fact that epidemic fronts of introduction have been identified (Lips *et al.* 2006), that globally-recovered isolates of *Bd* show little genetic diversity suggestive of a recent expansion from a point-origin (Morehouse *et al.* 2003) and that infected amphibians are detected in the amphibian trade (Mazzoni *et al.* 2003; Weldon *et al.* 2004; Garner *et al.* 2006). The EPH receives support from data showing that *Bd* was present in global amphibian populations decades ago [USA 1974; Canada 1961; Australia 1978; South Africa 1938 (Rachowicz *et al.* 2005)] and that there are measurable associations between amphibian condition (Reading 2006), global warming and the onset of chytridiomycosis (Bosch *et al.* 2006; Pounds *et al.* 2006). It is likely that the contemporary emergence of *Bd* is driven by a combination of NPH and EPH-like mechanisms; here we will focus on a subset of the NPH and will review the evidence that the international trade in amphibians has contributed to the emergence of chytridiomycosis by a process of continually introducing *Bd*, primarily through species introductions, into naïve amphibian populations and species.

1. Amphibian trade, introduced amphibians and the prevalence of *Bd* in commercial amphibian species

The global trade in amphibians is substantial, involves hundreds of species and occurs on every continent where amphibians and *Bd* occur (Nace *et al.* 1971; Gorzula 1996; Schlaepfer *et al.* 2005). National imports of live animals may annually run into the millions (Schlaepfer *et al.* 2005) and efforts to procure wild amphibians for trade may be so intense as to cause local population declines (Jennings & Hayes 1985; Wang *et al.* 2004). More importantly, commercial practices bring traded animals into contact with wild populations. Introductions are common and in many cases intentional, leading to the establishment of numerous feral populations (Conant & Collins 1991; Reimchen 1991; Kraus & Campbell 2002; Lever 2003; Vorburger & Reyer 2003; Weldon *et al.* 2004; Denoël 2005; Govindarajulu *et al.* 2005; Jancovich *et al.* 2005; Li *et al.* 2006; Pagano *et al.* 2003). Amphibians have been intentionally released for farming, to ornament garden ponds, as biocontrol agents and even as part of amphibian conservation efforts (Easteal 1981; Buley & Garcia 1997; Helfrich *et al.* 2001).

The data regarding amphibians known to carry *Bd* infections show that numerous species that are involved in both transient and established introductions have the capability to act as vectors of *Bd* (Table 1). We have searched the Global Amphibian Assessment (http://www.globalamphibians.org/), the Global Invasive Species Database (http://www.issg.org/database/) and the primary literature for information regarding introduced amphibian species that have successfully established a breeding population for at least one generation, or have been introduced but failed to establish a breeding population. In nearly all cases we report findings that involve well-established populations. We have cross-referenced the results of this search with the available primary literature and unpublished reports made available on the Amphibian Diseases Homepage (http://www.jcu.edu.au/school/phtm/PHTM/frogs/ampdis.htm) for evidence of infection with *Bd*. We have also taken advantage of the database we have compiled while screening tissue samples and DNA extracts from amphibians primarily sampled in Europe and Canada. Here, we have screened samples using the quantitative polymerase chain reaction (qPCR) method of Boyle *et al.* (2004), including positive and negative controls and a minimum of two-fold replication per sample (as per Garner *et al.* 2005, 2006). We have determined that a minimum of 28 species of introduced amphibians are also known carriers of *Bd* (Table 1). At least one of these species is known to be experiencing die-offs due to chytridiomycosis (*Alytes obstetricans*, Bosch *et al.* 2001), but the majority are species that are asymptomatically infected, and in some cases have been introduced on an enormous scale.

The three most widely introduced species, the African clawed frog *Xenopus laevis*, the North American Bullfrog *Rana catesbeiana* (Fig. 1) and the Cane toad *Bufo marinus*, have established feral populations in the Americas, Europe, Australia, Asia and many oceanic and coastal islands. Weldon *et al.* (2004) reported the first case of *Bd* infections in *Xenopus laevis* collected and preserved in the late 1930s. It was at this time *Xenopus* spp. were first being exported to the USA, Australasia and Europe as pregnancy assays. Subsequently, *Xenopus* has become the model amphibian genus for primary research and continues to be widely traded (Weldon *et al.* 2004). Captive colonies of *Xenopus* spp. are known to harbour *Bd*-infected animals (Parker *et al.* 2002; Fisher unpubl. data) and *Xenopus* escapes and establishments are still being reported (Cunningham *et al.* 2005). This pool of evidence has led to the popularization of the 'Out of Africa' hypothesis (Weldon *et al.* 2004). Weldon *et al.* (2004) postulated that once the trade in *Xenopus* had been established, the potential for horizontal transfer among amphibian species involved in commercial trading should speed the spread of *Bd*. This scenario seems likely, as standards at the time did not take into account the possibility of disease transmission among individual amphibians or through nonsterile handling practices, and commercial suppliers commonly traded in two or all three of these species (Nace *et al.* 1971). The first evidence of *Bd* infections in archived North American amphibians comes from frogs collected and preserved in 1961 (Ouellet *et al.* 2005). Intentional introductions of bullfrogs across western North America began in the 1930s and continued for decades afterwards

Table 1 – Introduced amphibian species known to carry *Batrachochytrium dendrobatidis* infections. References are evidence of infections

Species	Activity or trade	Introductions	Evidence of *Bd* infection	Ref
Rana catesbeiana	Food, biocont. ornamental, pet, research	Europe, Asia, Americas, islands	Native, introduced	Garner *et al.* 2006; Ouellet *et al.* 2005
Xenopus laevis	Pet, research	Europe, Americas, islands	Native, captive	Weldon *et al.* 2004; Parker *et al.* 2002; Garner & Fisher unpubl. data
Eleuthrodactylus coqui	None	Caribbean, Hawaii and Florida, USA	Native, introduced	Burrowes *et al.* 2004; Beard & O'Neill 2005
Pelophylax ridibunda	Food, research	BEL, ES, CH, UK, KAZ, Siberia, Kamchatka, RUS	Introduced	Garner & Fisher unpubl. data
Pelophylax esculenta	Food, research	ES, UK	Native	Simoncelli *et al.* 2005; Garner & Fisher unpubl. data
Pelophylax lessonae	Reintroduction[1]	UK	Native	Garner & Fisher unpubl. data
Mesotriton alpestris	Ornamental, pet, research	ES, FR, UK	Native, introduced	Garner & Fisher unpubl. data
Alytes muletensis	Research, reintroduction	Mallorca, ES	Native, introduced[2]	Garner & Fisher unpubl. data
Alytes obstetricans	Unknown	NLD, UK	Native	Bosch *et al.* 2001; Garner & Fisher unpubl. data
Dendrobates auratus	Biocontrol, pet, ornamental	Hawaii, USA	Captive	Pessier *et al.* 1999
Rana clamitans	Food, research	Western CAN/USA, Newfoundland, CAN	Native	Ouellet *et al.* 2005; Garner, St. Clair & Lesbarrères unpubl. data
Rana sphenocephala	Food, research	BHS	Native	Daszak *et al.* 2005
Rana blairi	None identified	Southeastern Arizona, USA	Native	Sredl & Caldwell 2000
Taricha granulosa	None identified	Rocky Mountains, Idaho, USA[3]	Native	Govindarajulu & Garner unpubl. data
Necturus maculosus	Pet, fish bait, research	New England, USA	Captive	Mutschmann unpubl. data
Ambystoma tigrinum	Pet, fish bait, research	Central California, USA	Native	Davidson *et al.* 2003
Hymenochirus boettgeri	Pet, ornamental	Florida, USA[4]	Captive	Raverty & Reynolds 2001
Litoria aurea	Pet	Hawaii[4], NZL, NCL	Native	Hero & Morrison 2004
Litoria raniformis	Pet, ornamental	Adelaide Hills, NZL	Native, introduced	Hero & Morrison 2004
Litoria ewingii	Pet, ornamental	NZL	Introduced	Bishop unpubl. report[6]
Bufo marinus	Biocontrol	Hawaii, USA, Peurto Rico, AUS[7]	Captive	Berger *et al.* 1998
Pseudacris regilla	Pet, ornamental	Eutsuk Lake, Queen Charlottes, BC, CAN	Native	Govindarajulu & Garner unpubl. data
Rana pipiens	Food, research, reintroduction	Western North America	Native	Carey *et al.* 1999; Adama *et al.* 2004
Limnodynastes dumerilii	Unknown	NZL[4]	Native, captive	Berger *et al.* 1999
Litoria caerulea	Pet, ornamental	NZL[4], USA	Native	Berger *et al.* 1999
Acris crepitans	Unknown	Varsity Lake, Boulder, Colorado, USA[5]	Native	Pessier *et al.* 1999
Bufo americanus	Unknown	Cuttyhunk Island, Massachusetts, USA	Native	Ouellet *et al.* 2005
Rana berlandieri	Unknown	Lower Colorado River Basin, USA	Introduced	Sredl & Caldwell 2000

1 Reintroduction program included pre-release screening for *Bd* infections.
2 Although infections reported where no introductions have occurred, locations involving released and captive-bred animals have also tested positive.
3 Possible introduction.
4 Released but did not establish.
5 Introduction extirpated.
6 Unpublished report by New Zealand chair of the DAPTF working group.
7 Most introductions were made as early attempts to use biological control against various beetle pests of sugar cane, banana and other cash crops (Lever 2001). Introduced to: Hawai'i, Puerto Rico, U.S. Virgin Islands, Guam and Northern Mariana Islands, American Samoa, and Republic of Palau: found in much of the Caribbean including Antigua, Barbados, Cuba, Dominica, Grenada and Carriacou Island, Guadeloupe, Grand Cayman Island, Haiti, Dominican Republic, Jamaica (including Cabarita Island), Martinique, Montserrat, Nevis, St. Kittis, St. Lucia, and St. Vincent. In the Pacific Australia, Japan, Papua New Guinea, Philippines, Cook Islands, Micronesia, Fiji Islands, Kiribati, Republic of the Marshall Islands, the Solomon Islands, and Tuvalu. (USGS) Other worldwide introductions include Bermuda, Egypt, Mauritius, and Diego Garcia of the Chagos Archipelago (Easteal 1981; Lever 2001).

Fig. 1 – Male *Rana catesbeiana* at a site of introduction on Vancouver Island, Canada (photo courtesy of Dina El Tounsy-Garner).

(Green 1978; Nussbaum *et al.* 1983) and there is a history of bullfrog farming in the native range (Stoutamire 1932; Baker 1942). Nace *et al.* (1971) reported 22 private outlets marketing bullfrogs for research in the 1960s (along with another 143 species, 15 of which appear in Table 1), undoubtedly representing a small component of the trade in bullfrogs dominated by the food industry (Teixeira *et al.* 2001). Introduced populations of bullfrogs are consistent in harbouring infected frogs and tadpoles (Garner *et al.* 2006). First reports of chytridiomycosis in Australia are from 1978 (Rachowicz *et al.* 2005). Cane toads were introduced in Australia as biocontrols in 1935 (Lever 2001), which precedes the hypothetical emergence out of Africa. However, like *Xenopus*, cane toads were used as pregnancy assays (Bivens 1950) in South America, the Caribbean and Australia (Lavergne & Trapido 1951; McDonald & Taft 1953; Floch & Fauran 1955). The species was commercially traded in Australia by the thousands during the 1960s (Tyler 1999). Thus, for the three most widely introduced species that asymptomatically harbour *Bd* infection, the establishment of trade and mass transport of animals and the potential for horizontal transmission among them predates the emergence of the disease.

Not all locations where amphibians suffer from chytridiomycosis have documented cases of amphibian introductions. Nevertheless, the amphibian trade usually has an influence in the area, and in many cases, a substantial one. The ongoing chytridiomycosis-driven declines of Neotropical species recorded initially in the 1990s have garnered the greatest attention of all amphibian declines related to the emergence of *Bd* (Berger *et al.* 1998; La Marca *et al.* 2005; Pounds *et al.* 2006). Many species of frogs in the region, primarily members of the family Dendrobatidae, are highly prized by researchers, hobbyists and zoological gardens. Gorzula (1996) examined the records of the World Conservation Monitoring Centre for the years 1987–1993 and reported that annual exports of wild dendrobatids ranged from 636–3506 individuals per annum (13032 individuals in total). The trade at that time involved eight neotropical countries as sources of wild animals and a further eight countries which currently maintain numerous captive breeding colonies, and in some cases, hobbyist groups with substantial memberships. Gorzula (1996) also noted that much of the trade probably goes unrecorded. Seven zoological gardens reported captive and breeding colonies of dendrobatids during the 1970s (International Zoo Yearbook, multiple years), and it is common practice for zoological organizations to exchange frogs and establish new colonies (Gorzula 1996). *Xenopus laevis* entered the zoo breeding records in 1962 (Antwerp, International Zoo Yearbook 1963), and by 1974, 11 zoos in 8 countries were breeding *Xenopus* (International Zoo Yearbook, multiple years). Cincinnati Zoo also bred bullfrogs successfully in 1970 (International Zoo Yearbook 1972). Once again the potential for cross-species transmission and trade precede disease emergence. It is important to note we could find no reports of reintroductions from captive populations of neotropical species, and instead those responsible for collecting amphibians, their equipment and associated activities would have to be the means of *Bd* introduction.

2. Assessing the risk of further *Bd* introduction into Europe, with special reference to the U.K.

Contemporary emerging infectious disease research empirically analyses the relative risk of disease introduction *via* different pathways in order to develop predictive models for disease emergence. A detailed understanding of the natural history of *Bd* is necessary for such an analysis as its biological requirements will underlie which pathways are available for introduction, amplification and spread of the pathogen. While our knowledge of *Bd*'s lifecycle is incomplete, it is clear that the organism has the ability to produce highly infectious zoospores for up to 7 weeks in lake water, and to survive in sterile moist river sand for up to 12 weeks (Johnson & Speare 2003; Johnson & Speare 2005). We have also shown that co-housed amphibian larvae (*Bufo bufo*) readily transmit the infection to each another and that the population prevalence of infection is related to the intensity of infection (Garner & Fisher unpub. obs.). This leads to two observations: (1) that co-housing amphibians during transport will amplify the population prevalence and intensity of infection and (2) that the release of infectious zoospores from infected individuals have the potential to persist in the environment for some time. Currently, it is not known whether *Bd* has the potential to form a thick-walled resting sporangia upon the onset of unfavourable conditions, as is seen in other chytrids such as *Allomyces* spp. However, if such life-cycle stages exist, or if *Bd* has the potential to survive and reproduce as a saprobe in nature, then the environmental persistence of *Bd* may be much greater than has thus far been measured, with a concomitant increase in the probability of successful transmission upon introduction.

Risk analysis for the introduction and establishment of *Bd* into a region depends on identifying the pathways through which disease introduction can occur (Daszak *et al.* 2000). As argued here, these are primarily (i) the rate of arrival of infected carrier amphibian species, (ii) the rate of arrival of water contaminated with active *Bd*, (iii) the rate of arrival of humans that are arriving from *Bd* infected areas and (iv) introduction *via* thus far unproven mechanisms, such as any species that is migratory, transported, traded and has the potential to interact with water bodies utilized by wild amphibians. For each pathway, it is then necessary to estimate the fraction of individuals that are likely to be infected (or carriers), multiplied by the probability distribution that is associated with the duration of infectiousness of zoospores. Finally, the probability of pathogen introduction must include terms that account for the likelihood associated with an infectious zoospore coming into successful contact with an uninfected amphibian, such that the basic reproductive number (R_0) for introduced *Bd* is above 1. Given our manifestly inadequate current knowledge of the biology of *Bd* and the rate at which infected amphibians are imported into countries, we are currently not in a position to accurately estimate the risk of introduction or establishment. However, it is clear that infected amphibians have been, and are, being widely traded, and that steps need to be taken to ensure that the risk of introduction of *Bd* is minimised (Daszak *et al.* 2000; Mazzoni *et al.* 2003).

Policy regarding the import and quarantine of amphibian species into Europe, and to a lesser degree among EU member states, is primarily dealt with by the EC Health and Consumer Protection Directorate – General's Animal Health and Welfare division. In the U.K. animal importation is regulated by The International Animal Health Division of the Department for Environment, Food and Rural Affairs (DEFRA) under the guidance of the Wildlife and Countryside Act 1981. Additional regulations regarding amphibian imports into the E.U. are provided through the Washington Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), and the U.K. CITES Management Authority is comprised of The Wildlife Species Conservation Division and Wildlife Habitats and Biodiversity Divisions of DEFRA. Import conditions set by the EU include veterinary checks at border inspection posts, and imports generally are only allowed from approved third countries. Within the U.K., these policies are enforced by the State Veterinary Service, Local Authorities including Port Health Authorities and Local Government Trading Standards, and Environmental Health. However, recognition of amphibian pathogens is limited. In a recent report of the meetings of the OIE (Office International des Epizooties) Aquatic Animal Health Standards Commission, no amphibian pathogens were listed, although some of the fish viral pathogens may have the ability to infect and possibly affect amphibian species (Report of the Meeting of the OIE Aquatic Animal Health Standards Commission, Paris, 1–5 August 2005). A previous report (6–10 October 2003) addresses the results of an OIE questionnaire on amphibian diseases and states…. 'the indication so far is that the trade in pet amphibians is of limited scale and may not be sufficient to present significant risk of disease transfer.' The report does acknowledge that the trade for food is larger, but that insufficient information is available to determine if there is a need to include amphibians in the Commission's remit. To the best of our knowledge, the only amphibian currently suspended from import into the EU is the North American Bullfrog (Council Regulation (EC) No. 338/97) but this suspension does not consider the ability of bullfrogs to carry and transmit *Bd*.

We have previously shown that *Bd* is broadly but patchily distributed in the EU (Garner *et al.* 2005). At least 3 species of amphibians are currently experiencing mass mortality due to chytridiomycosis in the Sierra de Guaderrama, Spain (Fig. 2, Bosch *et al.* 2001; Bosch & Martinez-Solano 2006) and we have data showing that *Bd* is currently causing mortality or disease symptoms in two of Europe's endangered amphibian species (Fisher, Garner, Bosch, Walker, Griffiths, Bovero unpubl. data). Microscopic, PCR and histological examinations of 170 amphibians collected between 1992 and 1996 from mainly the south-east England has failed to detect evidence of *Bd* infection in the UK (Cunningham 2001). An exception is the index site in Kent, where the only known breeding population of introduced North American Bullfrogs was shown to be infected with *Bd* at a prevalence of 14 % (Cunningham *et al.* 2005). Given that, globally, North American Bullfrogs have been shown to be widely infected with *Bd* and are known asymptomatic carriers of the pathogen, it seems reasonable to assume that the escape and establishment of this population led to the introduction of *Bd* (Garner *et al.* 2006). This population of bullfrogs has been the target of an eradication programme conducted by English Nature; 11,838 bullfrogs were removed from the site between 1999 and 2004 and the population is now thought to have been eradicated (Banks *et al.* 2000, Fig. 1). The status of *Bd* emergence in this area is currently uncertain and detailed surveillance is being undertaken; either *Bd* will become extinct due to stochastic causes, or will spread into native species and become endemic, perhaps broadly, within the UK.

This example illustrates a two-fold need: (1) the potential for introduction of non-native amphibians into uninfected countries/regions needs to be minimised and (2) due to the release into water of infectious zoospores, imported amphibians need to be quarantined in a manner that ensures that escape of zoospores into the general water-supply does not occur. The legal and practical infrastructure is certainly available for the appropriate steps to be taken regarding quarantine and screening of traded amphibians, and prevention of their release. Importation into the U. K. of animals such as cattle and sheep for food requires stringent veterinary evaluations that may involve quarantine and molecular examination for pathogens. Importation of pet species such as dogs, cats and ferrets requires quarantine, documentation of disease status and additional screening at the veterinary investigator's discretion. Section 14 of the Wildlife and Countryside Act 1981 prohibits the release of non-native species, and resident non-native species detailed in Schedule 9 of the Act. Nevertheless, DEFRA's website states that there are no animal health import requirements for pet amphibians, other than a letter from a vet stating the animals are healthy enough to be transported, and that there is no limit on the numbers that an owner can transport (http://www.defra.gov.uk/animalh/int-trde/imports/iins/livebalai/bal_live_8.htm). As far as we can tell, *Batrachochytrium dendrobatidis* does not appear on any list of diseases, EU or UK, that must, by law, be screened for. Given the degree of threat that *Bd* poses to European amphibians, we argue that this is a practical and legislative loophole that needs to closed, and specific actions need to be put in place in order to minimise the risk of amphibian-disease importation.

3. Specific actions necessary to control the risk of *Bd* introduction

Countries that have witnessed extreme declines in their amphibian biodiversity as a consequence of chytridiomycosis

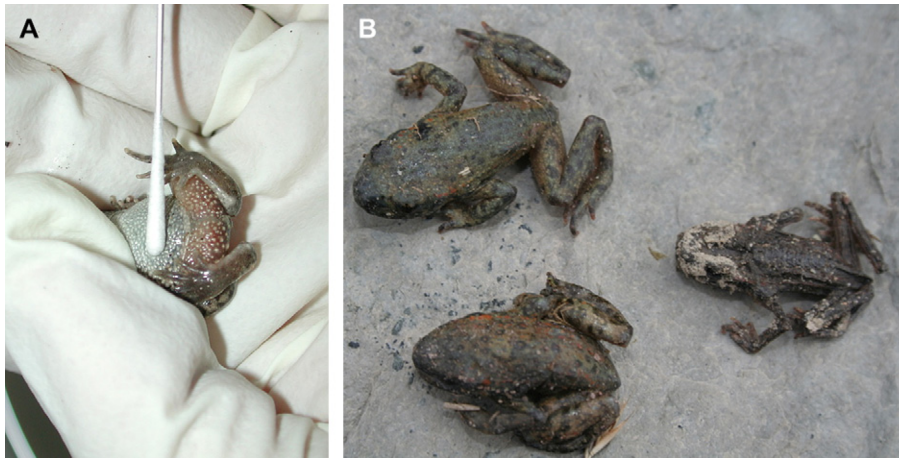

Fig. 2 – A. Swabbing the drink patch and hind-limbs of a midwife toad, *Alytes obstetricans*, to test for *Batrachochytrium dendrobatidis*. B. Midwife toads, *Alytes obstetricans*, that have died from cutaneous chytridiomycosis.

are responding by designing specific threat abatement plans. Importantly, the Australian Government has designed a strategic plan with the two broad goals of preventing introduction of *Bd* into disease free areas, and decreasing the impact of the disease on populations that are currently infected (Department of the Environment and Heritage, Commonwealth of Australia 1996). This threat abatement plan has the potential to be modified for countries that have, as yet, minimal establishment of *Bd* and/or lack appropriate legislation addressing the threat posed by this wildlife pathogen. Fig. 3 summarises the sections of the Australian threat abatement plan that we believe are necessary to action in order to control the potential for introduction of *Bd* into disease-free countries and regions, and to limit spread if introduction has occurred. Specifically,

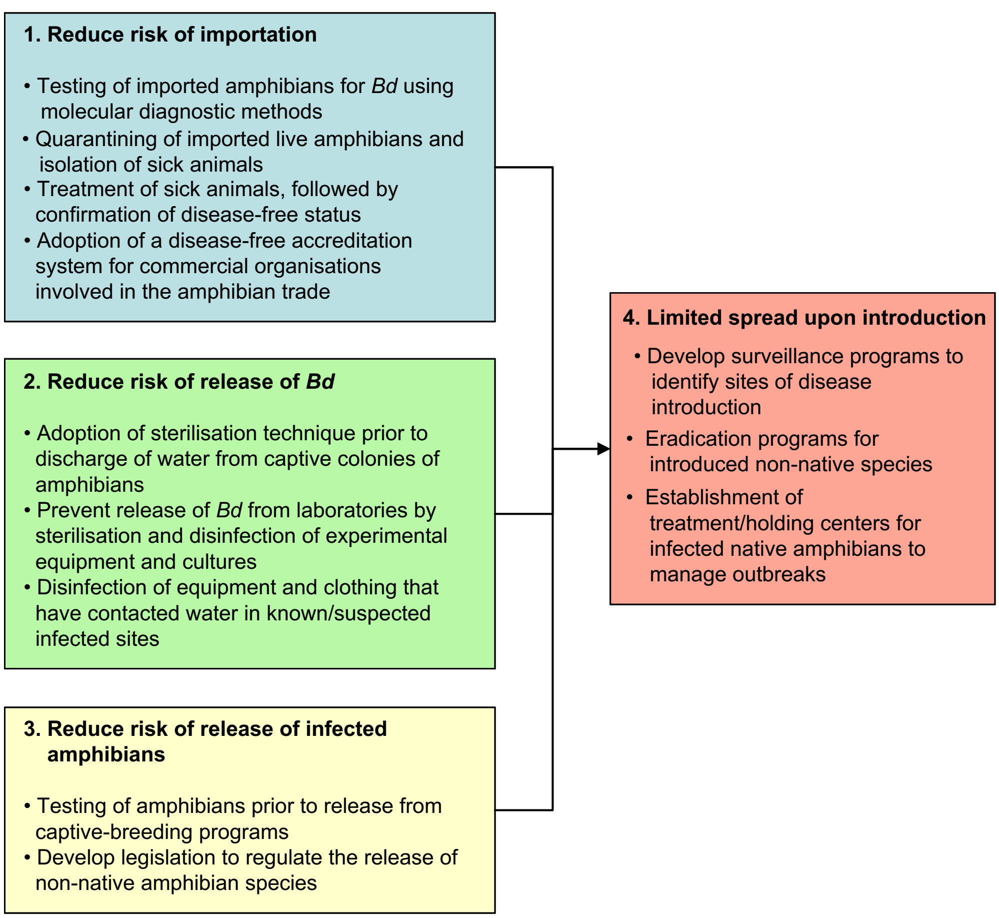

Fig. 3 – Actions to limit the introduction and release of *Batrachochytrium dendrobatidis* into uninfected countries/regions.

we feel that it is necessary to consider the steps that are necessary to (1) reduce the risk of importation, (2) reduce the risk of release of *Bd* infectious stages, (3) reduce the risk of release of amphibians and (4) limit the spread of *Bd* once release has occurred. We believe that the state of knowledge, and science, of the epidemiology of chytridiomycosis has reached the stage where a dialog can successfully be opened between major stakeholders, namely the Government, animal importers, traders and breeders, zoological gardens, scientists and research organisations. Initiating such a dialog is increasingly necessary in order to take measures to control the emergence of this increasingly destructive pandemic infectious disease.

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