ECoHEALTH

The Decline of the Sharp-Snouted Day Frog (*Taudactylus acutirostris*): The First Documented Case of Extinction by Infection in a Free-Ranging Wildlife Species?

Lisa M. Schloegel,[1] Jean-Marc Hero,[2] Lee Berger,[3] Rick Speare,[3] Keith McDonald,[4] and Peter Daszak[1]

[1]*Consortium for Conservation Medicine, 460 West 34th Street, New York, NY 10001*
[2]*Griffith University Gold Coast, PMB 50, Gold Coast Mail Centre, Queensland 9726, Australia*
[3]*James Cook University, Townsville, Queensland 4811, Australia*
[4]*Queensland Parks and Wildlife Service, PO Box 975, Atherton 4883, Queensland, Australia*

Abstract: Infectious diseases are increasingly recognized as the cause of mass mortality events, population declines, and the local extirpation of wildlife species. In a number of cases, it has been hypothesized that pathogens have caused species extinctions in wildlife. However, there is only one definitively proven case of extinction by infection, and this was in a remnant captive population of a Polynesian tree snail. In this article, we review the potential involvement of infectious disease in the recent extinction of the sharp-snouted day frog *Taudactylus acutirostris*. Our review of available evidence suggests that a virulent pathogen of amphibians, *Batrachochytrium dendrobatidis*, caused a rapid, catastrophic decline of this species, from which it did not recover. We propose that this is the first case of extinction by infection of a free-ranging wildlife species where disease acted as both the proximate and ultimate cause of extinction. This highlights a probable underreporting of infectious disease as a cause of biodiversity loss historically and currently.

Key words: amphibian decline, conservation medicine, chytridiomycosis, *Batrachochytrium*, *Taudactylus*, extinction

INTRODUCTION

The current extinction rate is estimated to be 100–1,000 times greater than the historical norm (Pimm et al., 1995). This is thought to be largely due to anthropogenic changes to the environment such as deforestation, species introduction, climate change, and others (Pimm et al., 1995; Thomas et al., 2004). A number of recent papers have

highlighted the role of infectious disease in biodiversity loss, citing examples of disease-related mass mortalities and declines of wildlife populations (Woodroffe, 1999; Daszak et al., 2000; Dobson and Foufopoulos, 2001). These include the near extinction of the black-footed ferret, the local extinction of African wild dogs, and global population declines of amphibians (Thorne and Williams, 1988; Ginsberg et al., 1995). However, infectious diseases have been hypothesized to be the cause of extinction in only a few cases, e.g., Hawaiian birds, the thylacine, and indirectly the eelgrass limpet *Lottia alveus* (Guiler, 1961; Warner, 1968;
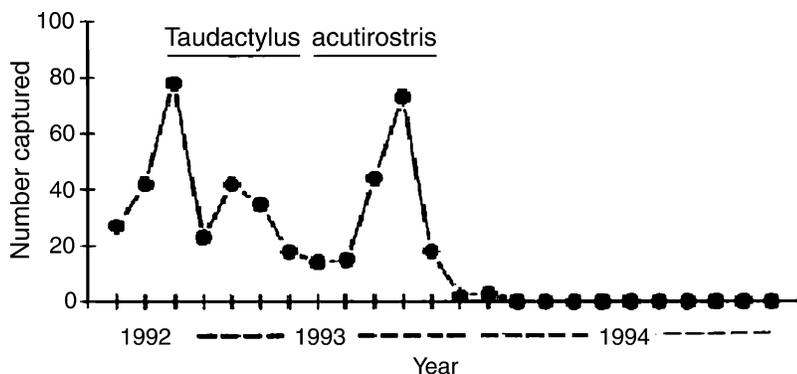
Figure 1. Number of *T. acutirostris* detected in and along a 100 m long section of stream in upland tropical rain forest, Big Tableland, northern Queensland (modified from Laurance et al., 1996).

Van Riper et al., 1986; Carlton et al., 1991; Daszak and Cunningham, 1999). Furthermore, to date, only one proven example of a species extinction due to an infectious disease has been published, that of *Partula turgida*, a Polynesian tree snail (Cunningham and Daszak, 1998; Daszak and Cunningham, 1999). Extinction by infection can occur in three ways: (1) a pathogen is documented as the cause of declines in the majority of the populations of a species where such declines lead to the extinction of the species as a whole; (2) a pathogen is proven to be responsible for the die-off of the last remnant group of a species (wild or captive) whereby the cause of declines in other subpopulations of the same species may be attributed to some other factor, known or unknown; and (3) a pathogen is shown to be the likely cause of death of the last individual of a species, where the prior declines to the verge of extinction were caused by other or unknown causes. In the case of *P. turgida*, the last remnant group of individuals died in captivity due to infectious disease but the primary cause of extirpation in the wild was the introduction of an exotic predator (Coote and Loeve, 2003).

During the past three decades, a number of amphibian populations have undergone severe declines, some of which have resulted in extinction (Blaustein and Wake, 1990; Stuart et al., 2004). In Australia, these declines have led to 40 out of 213 frog species (18.8%) being classified as threatened; at least four species disappearing from most upland areas throughout their geographic range; an additional three species almost entirely disappearing throughout their historical range; and eight species that can no longer be found in the wild (Hero and Morrison, 2003). In Australia and elsewhere, many of these declines have been causally linked to the emergence of chytridiomycosis, a disease caused by the recently discovered fungal pathogen *Batrachochytrium dendrobatidis* (Berger et al., 1998; Daszak et al., 2003).

In this article, we examine the available data on the patterns and cause of the recent extinction of the endemic Australian frog *Taudactylus acutirostris* (Figs. 1 and 2). We investigate whether chytridiomycosis, responsible for the death of some of the last known individuals, was ultimately the cause of extinction. The ultimate cause of extinction is a deterministic factor that reduces the number or size of local populations to a level where stochastic demographic and genetic factors drive population dynamics, which then represent the final and direct, or proximate, cause of extinction (Soule and Wilcox, 1980; Diamond, 1984; Wilcox, 1986). We discuss these results in the context of other recent extinctions of amphibians and the role of infectious disease in biodiversity loss globally.

RESULTS

Initial Declines

The sharp-snouted day frog *T. acutirostris*, a conspicuous inhabitant of upland rain forest streams, was once widely distributed from Mt. Graham to the Big Tableland in northern Queensland, an area of approximately 14,000 km^2 (McDonald, 1992; Hero and Morrison, 2003) (Fig. 2). The species started disappearing in the southern part of its range in the 1980s (Fig. 1). Richards et al. (1993) were able to locate *T. acutirostris* at Charmillon Creek in 1980 and 1982 but not in 1984. Similarly, it was found in Danbulla State Forest in 1984 but was absent in 1989 and 1992 (Richards et al., 1993). By 1988 it had disappeared from known sites south of the Daintree River (Richards et al., 1993). In 1989, 48 calling males were recorded along a 100 m stream transect; however, in 1990, only one adult and several tadpoles were located (Richards et al., 1993).

Mark-recapture studies conducted by McDonald (1994) revealed striking population crashes of *T. acutirostris*

Figure 2. A photograph of *T. acutirostris* from the last remnant population prior to the collection of chytridiomycosis-positive individuals. (Photograph by S. J. Richards.)

at Big Tableland during the 1993 season. In another 1993 study at Big Tableland, sick and dying anurans (including *T. acutirostris*) were collected for pathological examination and tested positive for the chytrid fungus (Berger et al., 1999).

Fate of the Last Wild and Captive Individuals

At the time of the 1993 declines, healthy tadpoles of *T. acutirostris* were collected to be raised in captivity at the Royal Melbourne Zoo; however, those that metamorphosed died (Banks and McCracken, 2002). Diagnostic examinations revealed chytridiomycosis as the likely cause of death of these individuals (Berger et al., 1998).

The pattern of declines in Queensland suggested an infectious agent, and a study to locate and collect amphibians from northern Queensland was initiated in 1993 to test this hypothesis (Laurance et al., 1996, 1997). During October 1993, ill or dead sharp-snouted day frogs were collected for diagnostic pathology examinations (Berger et al., 1998). They predominantly showed neurological signs, including abnormal sitting posture with hind legs abducted, lethargy, and slow response to tactile stimuli (Speare, 1995; Berger et al., 1998). When handled, frogs became rigid and trembled with extension of the hindlimbs and flexion of the forelimbs.

Ill or dead frogs were urgently transported from the rain forest to the laboratory at James Cook University, Townsville, where detailed necropsies were performed the same day. Thorough diagnostic examinations, including histopathology, bacterial and viral cultures, and electron

microscopy, did not reveal any pathogens except the novel amphibian chytrid fungus (Berger et al., 1998). It infected the superficial skin, causing hyperkeratosis and hyperplasia (Fig. 3). At this time, the fungus was new to science and its significance unknown. However, studies of mortality in other amphibian populations in Australia soon provided evidence that this unusual fungus was lethal to frogs (Berger et al., 1998, 1999) and a transmission experiment confirmed that it could cause a high mortality rate (Berger et al., 1998).

The last known sightings of *T. acutirostris* are of a single individual in a small tributary of the South Johnstone River in 1996 (Marshall, 1998) and of a gravid female near Mt. Hartley in 1997 (Hero et al., 1998). Apart from these two individuals, *T. acutirostris* has not been recorded during extensive searches of suitable, known sites from the previous range of this species between 1994 and 2004 (Hero and McDonald, personal communication). The species is listed as critically endangered and presumed extinct (IUCN, 2004; McDonald et al., 2004).

DISCUSSION

Previous authors have hypothesized infectious diseases as a cause of biological extinctions (Guiler, 1961; Warner, 1968; Van Riper et al., 1986; Carlton et al., 1991; Daszak and Cunningham, 1999). Linking infectious disease to extinction requires collection of population data from the last remnant group of an extinct species and pathological examination of some of these individuals (MacPhee and Marx, 1997). Investigations on archival specimens of historic extinctions are difficult due to insufficient specimens or samples or lack of adequate fixation or storage. Furthermore, knowledge of diseases of the majority of wildlife species is poor. For these reasons, there have been few concerted efforts to study the pathology of historically extinct species.

In the case of *T. acutirostris*, population surveys documented its decline to extinction at the Big Tableland site. Concurrent pathological examinations on these declining populations, including individuals from the last significant free-living remnant population, demonstrated chytridiomycosis as the probable cause of death. While chytridiomycosis may have been responsible for extirpation of this species throughout its range, the absence of pathological evidence from other sites does not allow us to make this statement with certainty. However, these data, in addition
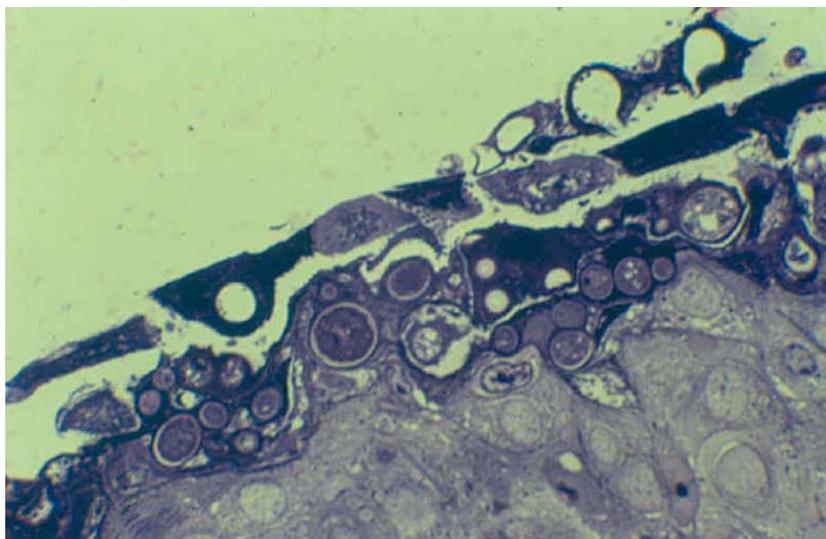
Figure 3. Micrograph of a hematoxylin and eosin-stained histological slide of formalin-fixed tissue of an individual of *T. acutirostris* from the last remnant wild population. This micrograph clearly shows keratinaceous epithelial cells on the surface of the skin infected with *B. dendrobatidis*, the causative agent of amphibian chytridiomycosis. The hyperkeratosis and hyperplasia associated with this infection were cited as the cause of death by the veterinary pathologist investigating this case (Berger and Speare, personal communication).

to lack of recovery and the subsequent finding of only two live individuals, indicate that chytridiomycosis was responsible for the decline and extinction of the last subpopulation of this species. This fits with the first criterion for extinction by infection listed above and suggests that infectious disease acted as the proximate and likely ultimate cause of extinction of *T. acutirostris*.

In Australia, little evidence has been provided for alternative hypotheses relating to amphibian declines such as increases in ultraviolet B radiation, climate change, and anthropogenic pollution within the former range of *T. acutirostris* (Richards et al., 1993; Laurance et al., 1996; Broomhall et al., 2000). Richards et al. (1993) found no evidence that drought, floods, habitat destruction, or degradation in water quality were responsible for amphibian declines in northern Queensland. The Big Tableland area, for example, has been mined since 1887 and was logged up until 1963. It is in this same area that *T. acutirostris* was at its highest density between 1991 and 1992 (Richards et al., 1993).

In Australia, declining amphibian species tend to have low fecundity, specialized habitat requirements, reproduction associated with streams, and montane distributions (Williams and Hero, 1998; Berger et al., 1999). These conditions may predispose species to heightened impact of *B. dendrobatidis*, a pathogen which has biological traits including high growth rates at relatively cool temperatures and a probable facultative parasitic nature (Daszak et al., 2003).

Models of host-pathogen dynamics predict that pathogens which rapidly deplete host populations in a density-dependent manner will reduce populations to a threshold density below which transmission is not possible (McCallum and Dobson, 1995). This occurs because the remnant host population is now composed of immune individuals or is so sparsely distributed that contact rates do not allow sufficient rates of transmission to maintain viability of the pathogen population. The presence of reservoir hosts may allow pathogens to evade threshold density (McCallum and Dobson, 1995). Previous authors have hypothesized that introduction of *B. dendrobatidis* in various areas may result from an invasive exotic host reservoir. None has so far been identified at these sites. However, 33 nondeclining species of amphibian occur throughout Australia (Hero and Morrison, 2003) and it is possible that one of these could have acted as the reservoir host for *B. dendrobatidis* providing a mechanism by which it could drive its host to extinction. Alternatively *T. acutirostris* larvae (which do not die from infection) or free-living saprobic populations of *B. dendrobatidis*, could have provided a mechanism for extinction by infection.

The IUCN classifies a taxon as extinct when there is no reasonable doubt that the last individual has died. In addition, a taxon is presumed extinct when exhaustive surveys in known and expected habitat, at appropriate times (diurnal, seasonal, annual), throughout its historic range have failed to record an individual (surveys should be over a time frame appropriate to the taxon's life cycle and life form). In 2001, the status of *T. acutirostris* was assessed and subsequently listed as critically endangered by the IUCN Red List of Threatened Species as part of the Global Amphibian Assessment 2004. The IUCN assessment for *T. acutirostris* is conservative, and the status is likely to change to extinct within 10 years.

The extinction of *T. acutirostris* appears to be part of the global emergence of *B. dendrobatidis* that has been associated with declines in Australasia (Berger et al., 1998; Waldman et al., 2001), Africa (Weldon, 2002; Hopkins and Channing, 2003; Lane et al., 2003; Weldon et al., 2004), Spain (Bosch et al., 2001), Europe (Garner et al., 2005; Simoncelli et al., 2005), and the Americas (Fellers et al., 2001; Young et al., 2001; Ron et al., 2003). In Australia, seven additional species can no longer be found in the wild (Hero and Morrison, 2003), including three species now extinct (the southern gastric brooding frog *Rheobatrachus silus* last seen in 1982, the northern gastric brooding frog *Rheobatrachus vitellinus* last seen in 1985, and the southern day frog *Taudactylus diurnus* last seen in 1979) and four critically endangered species (the armored mist frog *Litoria lorica* last seen in 1991, the mountain mist frog *Litoria nyakalensis* last seen in 1990, the peppered tree frog *Litoria piperata* last seen in 1973, and the yellow-spotted tree frog *Litoria castanea* last seen in 1975). While chytridiomycosis is suspected to have contributed to the disappearances of these species, its role in their extinctions cannot be confirmed. In the case of *T. zacutirostris*, the pathological evidence available for the last known wild and captive populations allows us to assess the role of *B. dendrobatidis* in its extinction. Such data do not exist for the above species.

Our review of the extinction of *T. acutirostris* represents the first well-supported case of extinction by infection in a free-ranging wildlife species. Here, an infectious disease appears to have acted as the proximate and the ultimate cause of extinction (Wilcox, 1986). However, logistical, technical, and other difficulties involved in assessing the role of pathogens in extinctions remain significant. For these reasons, infectious diseases are likely an underestimated cause of historical and present biodiversity loss. Continued expansion of the anthropogenic environmental factors responsible for emerging wildlife diseases suggests that their involvement in future biodiversity will also expand. For these reasons, the development of new integrated approaches to ecosystem health and wildlife medicine will likely become standard tools for conservation biology (Aguirre, 2002; Weinhold, 2003).

Acknowledgments

References

Aguirre AA, Ostfeld RS, Tabor GM, House C, Pearl MC (editors) (2002) *Conservation Medicine: Ecological Health in Practice*, New York: Oxford University Press

Banks C, McCracken H (2002) Captive management and pathology of sharp snouted dayfrogs, *Taudactylus acutirostris*, at Melbourne and Taronga zoos. In: *Frogs in the Community. Proceedings of the Brisbane Symposium of the Queensland Frog Society, East Brisbane*, Natrass AEO (editor), Brisbane: Queensland Frog Society, pp 94–102

Berger L, Speare R, Daszak P, Green DE, Cunningham AA, Goggin CL, et al. (1998) Chytridiomycosis causes amphibian mortality associated with population declines in the rain forests of Australia and Central America. *Proceedings of the National Academy of Sciences USA* 95:9031–9036

Berger L, Speare R, Hyatt A (1999) Chytrid fungi and amphibian declines: overview, implications and future directions. In: *Declines and Disappearances of Australian Frogs*, Campbell A (editor), Canberra: Environment Australia, pp 23–33

Blaustein AR, Wake DB (1990) Declining amphibian populations: a global phenomenon. *Trends in Ecology and Evolution* 5:203–204

Bosch J, Martinez-Solano I, Garcia-Paris M (2001) Evidence of a chytrid fungus infection involved in the decline of the common midwife toad (*Alytes obstetricans*) in protected areas of central Spain. *Biological Conservation* 97:331–337

Broomhall SD, Osborne WS, Cunningham RB (2000) Comparative effects of ambient ultraviolet-B radiation in two sympatric species of Australian frogs. *Conservation Biology* 14:420–427

Carlton JT, Vermeij GJ, Lindberg DR, Carlton DA, Dudley EC (1991) The 1st historical extinction of a marine invertebrate in an ocean basin—the demise of the eelgrass limpet *Lottia alveus*. *Biological Bulletin* 180:72–80

Coote T, Loeve E (2003) From 61 species to five: endemic tree snails of the Society Islands fall prey to an ill-judged biological control programme. *Oryx* 37:91–96

Cunningham AA, Daszak P (1998) Extinction of a species of land snail due to infection with a microsporidian parasite. *Conservation Biology* 12:1139

Daszak P, Cunningham AA (1999) Extinction by infection. *Trends in Ecology and Evolution* 14:279

Daszak P, Cunningham AA, Hyatt AD (2000) Emerging infectious diseases of wildlife—threats to biodiversity and human health. *Science* 287:443–449

Daszak P, Cunningham AA, Hyatt AD (2003) Infectious disease and amphibian population declines. *Diversity and Distributions* 9:141–150

Diamond JM (1984) ''Normal'' extinctions of isolated populations. In: *Extinctions*, Nitecki MH (editor), Chicago: University of Chicago Press, pp 191–246

Dobson A, Foufopoulos J (2001) Emerging infectious pathogens of wildlife. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences* 356:1001–1012

Fellers GM, Green DE, Longcore JE (2001) Oral chytridiomycosis in the mountain yellow-legged frog (*Rana muscosa*). *Copeia* 4:945–953

Garner TWJ, Walker S, Bosch J, Hyatt AD, Cunningham AA, Fisher MC (2005) Chytrid fungus in Europe. *Emerging Infectious Diseases* 11:1639–1640

Ginsberg JR, Mace GM, Albon S (1995) Local extinction in a small and declining population: wild dogs in the Serengeti. *Proceedings of the Royal Society of London Series B: Biological Sciences* 262:221–228

Guiler ER (1961) The former distribution and decline of the thylacine. *Australian Journal of Science* 23:207–210

Hero J-M, Hines H, Meyer E, Morrison C, Streatfeild C, Roberts L (1998) New records of "declining" frogs in Queensland, Australia. *Froglog* 29:1–4

Hero J-M, Morrison C (2003) Frog declines in Australia: global implications. *Herpetological Journal* 14:175–186

Hopkins S, Channing A (2003) Chytrid fungus in northern and western cape frog populations, South Africa. *Herpetological Review* 34:334–336

IUCN (2004) Global amphibian assessment Available: http://www.globalamphibians.org [accessed October 15, 2004]

Lane EP, Weldon C, Bingham J (2003) Histological evidence of chytridiomycete fungal infection in a free-ranging amphibian, *Afrana fuscigula* (Anura: Ranidae), in South Africa. *Journal of the South African Veterinary Association* 74:20–21

Laurance WF, McDonald KR, Speare R (1996) Epidemic disease and the catastrophic decline of Australian rain forest frogs. *Conservation Biology* 10:406–413

Laurance WF, McDonald KR, Speare R (1997) In defense of the epidemic disease hypothesis. *Conservation Biology* 11:1030–1034

MacPhee RDE, Marx PA (1997) The 40,000 year plague: humans, hyperdisease, and first-contact extinctions. In: *Natural Change and Human Impact in Madagascar*, Goodman SM, Patterson BD (editors), Washington DC: Smithsonian Institution Press, pp 169–217

Marshall CJ (1998) The reappearance of *Taudactylus* (Anura: Myobatrachidae) in north Queensland streams. *Pacific Conservation Biology* 4:39–41

McCallum H, Dobson A (1995) Detecting disease and parasite threats to endangered species and ecosystems. *Trends in Ecology and Evolution* 10:190–194

McDonald K, Cunningham M, Alford R, Retallick R (2004) *Taudactylus acutirostris*. Available: http://www.redlist.org/search/details.php?species=21529. [accessed December 1, 2004]

McDonald KR (1992) Distribution patterns and conservation status of north Queensland rainforest frogs. Conservation Technical Report 1, Brisbane: Queensland Department of the Environment and Heritage

McDonald KR (1994) Declining frog populations in the wet tropics. Internal Report Conservation Strategy Branch, Atherton: Queensland Department of the Environment and Heritage

Pimm SL, Russell GJ, Gittleman JL, Brooks TM (1995) The future of biodiversity. *Science* 269:347–350

Richards SJ, McDonald KR, Alford RA (1993) Declines in populations of Australia's endemic tropical forest frogs. *Pacific Conservation Biology* 1:66–77

Ron SR, Duellman WE, Coloma LA, Bustamante MR (2003) Population decline of the Jambato toad *Atelopus ignescens* (Anura: Bufonidae) in the Andes of Ecuador. *Journal of Herpetology* 37:116–126

Simoncelli F, Fagotti A, Dall'Olio R, Vagnetti D, Pascolini R, Di Rosa I (2005) Evidence of *Batrachochytrium dendrobatidis* infection in water frogs of the *Rana esculenta* complex in Central Italy. *Ecohealth* 2:307–312

Soule M, Wilcox BA (editors) (1980) *Conservation Biology: An Evolutionary-Ecological Perspective*, Sunderland, MA: Sinauer Associates

Stuart SN, Chanson JS, Cox NA, Young BE, Rodrigues ASL, Fischman DL, et al. (2004) Status and trends of amphibian declines and extinctions worldwide. *Science* 306:1783–1786

Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, et al. (2004) Extinction risk from climate change. *Nature* 427:145–148

Thorne ET, Williams ES (1988) Disease and endangered species: the black-footed ferret as a recent example. *Conservation Biology* 2:66–74

Van Riper C III, Van Riper SG, Goff LM, Laird M (1986) The epizootiology and ecological significance of malaria in Hawaiian land birds. *Ecological Monographs* 56:327–344

Waldman B, van de Wolfshaar KE, Klena JD, Andjic V, Bishop P, Norman RJDB (2001) Chytridiomycosis in New Zealand frogs. *Surveillance* 28:9–11

Warner RE (1968) The role of introduced disease in the extinction of the endemic Hawaiian avifauna. *Condor* 70:101–120

Weinhold B (2003) Conservation medicine: combining the best of all worlds. *Environmental Health Perspectives* 111:A524–A529

Weldon C (2002) Chytridiomycosis survey in South Africa. *Froglog* 51:1–2

Weldon C, Preez LHD, Hyatt AD, Muller R, Speare R (2004) Origin of the amphibian chytrid fungus. *Emerging Infectious Diseases* 10:2100–2105

Wilcox BA (1986) Extinction models and conservation. *Trends in Ecology and Evolution* 1:46–48

Williams SE, Hero JM (1998) Rainforest frogs of the Australian wet tropics: guild classification and the ecological similarity of declining species. *Proceedings of the Royal Society of London Series B: Biological Sciences* 265:597–602

Woodroffe R (1999) Managing disease threats to wild mammals. *Animal Conservation* 2:185–193

Young BE, Lips KR, Reaser JK, Ibanez R, Salas AW, Cedeno JR, et al. (2001) Population declines and priorities for amphibian conservation in Latin America. *Conservation Biology* 15:1213–1223