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Author

Hero, JM, Morrison, C

Published

2004

Journal Title

The Herpetological Journal

Version

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FROG DECLINES IN AUSTRALIA: GLOBAL IMPLICATIONS

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Amphibian declines have been reported from around the world. Here we examine life history and distributional characteristics of Australian frogs listed as threatened under the IUCN Global Amphibian Assessment guidelines, and compare these results to available information on threatened amphibians around the world. Forty of 213 Australian frog species (18.8%) are currently recognised as threatened. While eight species are listed as Vulnerable due to small or restricted populations alone (VU D2), the remaining 32 species are associated with population declines. Threatened species are concentrated in upland areas (41% of all upland species are threatened, while only 8% of lowland species are threatened). Twenty-eight of the 40 threatened species (70%) primarily occur in upland areas while only 42 of the 173 non-threatened species (24.3%) occur in upland areas. Restricted geographic range is characteristic of 31 of 40 threatened/declining species (77.5%). However, 41 non-threatened species (23.7%) also have restricted geographic ranges. Latitudinal position is not strongly associated with the degree of threat. Threatened species are strongly associated with specific reproductive habitats: 80% of species occurring in montane wetlands and 58% of species breeding in wet forest streams are threatened. For 22 of the 40 (55%) threatened species, known threats do not adequately explain the extent of decline. Habitat modification is the foremost threatening process associated with declines in 20 of the 40 threatened species (50%), including 11 of 12 threatened lowland species (91.7%). Chytrid fungus is notably associated with declines for five species and a potential contributor for an additional nine species (35% of threatened species). However, the chytrid has also been detected in an additional 33 non-threatened species (19%). Minor threats associated with threatened species include fire and global changes in weather patterns. Phylogenetic relationships of Australian frogs are poorly resolved, and there are no strong associations between phylogeny and declines within known taxonomic groups. A notable exception are frogs of the myobatrachid genus *Taudactylus* where five of the six species are threatened. Global patterns are difficult to assess, however, as declines are strongly associated with species that are primarily distributed in upland areas. Chytrid fungus has been found in both declining and non-declining species throughout Australia, and while its role as an emerging infectious disease is currently under investigation (in Australia, New Zealand, Spain, South Africa, Costa Rica, Ecuador and the USA), little is known about its distribution and prevalence in other countries.

Key words: altitude, amphibians, geographic range, IUCN, life history, status

INTRODUCTION

Amphibian declines have been reported around the world, and Australia is notably affected (Alford & Richards, 1999; Campbell, 1999; Hero & Shoo, 2003). While numerous hypotheses have been proposed to explain Australian frog declines including habitat destruction, diseases, introduced species, climate change (summarized in Campbell, 1999), to date the cause(s) of many of these declines remain unknown.

In many cases the causative mechanisms of extinction are confounded and may be difficult or impossible to detect (Gillespie, 2001; Kiesecker, Blaustein & Belden, 2001). Studying patterns is an important tool for ecologists (Lawton, 1996) and has been used to understand extinctions of species where no obvious cause

has been identified (McKinney, 1997). Williams & Hero (1998) examined frog species from the wet tropics region of northern Australia and found that low ovarian clutch size, habitat specialisation and an association with lotic streams, were the primary ecological characteristics that distinguished the declining species from the non-declining species. Examining patterns/trends in the ecological characteristics and geographic distribution shared by threatened species may help determine the specific causes of declines and identify traits that increase the likelihood of extinction or decline.

Here we present known and potential threats to Australian frogs and examine geographic and ecological traits associated with threatened species. Specifically we aimed to (1) collate data on the ecological characteristics (reproductive habitat etc.) and geographic distribution (extent of occurrence, altitude, latitudinal distribution etc) of all frogs in Australia; (2) identify trends/patterns in the threats, and ecological and geographical traits shared by threatened Australian species;

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(3) compare patterns found in Australia to those from other countries based on available geographical information; and (4) predict characteristics of potentially (but as yet unidentified) vulnerable species.

MATERIAL AND METHODS

We examined the conservation status, known and potential threats and geographic and reproductive data for the 213 frog species currently recognised in Australia. The list includes *Litoria daviesiae*, *Pseudophryne raveni* and the subspecies *L. verreauxii alpina* (three species not included in the IUCN Red List 2002 principally due to taxonomic restrictions and changes). The introduced cane toad (*Bufo marinus*) was excluded. Conservation status and threats were determined from the results of a workshop as part of the International Union for the Conservation of Nature-Global Amphibian Assessment (IUCN-GAA, see Hero, 2001; IUCN, 2002) and currently available on AmphibiaWeb (updated in 2003). Multiple threats were identified for each species and ranked as either foremost (most notable) or potential based on the GAA assessments. Geographic range (extent of occurrence) was calculated using ArcView and distribution maps generated as part of the GAA process (maps are also available on AmphibiaWeb). Altitudinal distribution was defined as either upland (predominantly distributed at elevations over 400 m asl) or lowland (predominantly distributed at elevations below 400 m asl) based on the geographic range and wherever possible published information on each species (e.g. McDonald, 1992). Natural history data was gathered from local field-guides and AmphibiaWeb (2003). The list of Australian species that have been found with chytrid fungus is summarized from Speare & Berger (2000a).

For comparative purposes we examined the conservation status of species from 46 countries listed on the IUCN (2002) Red List of Threatened Species (296 listed as threatened), and the AmphibiaWeb (2003) – Watch List (uploaded on 27 March 2002). Natural history data was gathered from AmphibiaWeb (2003) and local field-guides, and verified wherever possible by regional expert herpetologists within each country. While these data are not complete from all countries of the world they represent regions of concern (see results). A thorough analysis of this information will be completed once the IUCN Global Amphibian Assessment has been completed. The global list of species that have been found with chytrid fungus is summarised from Speare & Berger (2000b) and updated from individual publications (e.g. Bosch, Martinez-Solano & Garcia-Paris, 2001). It should be noted that limited information on the global distribution of chytrid is available. Statistical analyses are only suitable for a subset of this data and a manuscript examining upland areas of eastern Australia is currently in review (J.-M. Hero, pers. comm.). Herein we present a qualitative analysis of species characteristics associated with threatened status for all Australian frogs.

RESULTS

AUSTRALIAN THREATENED FROGS

Forty of 213 frog species in Australia (18.8%) are currently recognised as threatened and most are associated with population declines (Table 1). Eight species can no longer be found in the wild (*Rheobatrachus silus*, *R. vitellinus*, *Taudactylus diurnus*, *T. acutirostris*, *Litoria castanea/flavipunctata*, *L. lorica*, *L. nyakalensis* and *L. piperata*), an additional three species have almost entirely disappeared throughout their historical range (*Taudactylus rheophilus*, *Litoria booroolongensis* and *Pseudophryne corroboree*), and at least four species have disappeared from most upland areas throughout their geographic range (*Litoria nannotis*, *L. rheocola*, *Nyctimystes dayi* and *Taudactylus eungellensis*).

No species were listed using quantitative analysis (IUCN criterion E). Eight species were listed as Vulnerable due to restricted area of occupancy (IUCN criterion D2), although fragmentation and declines have been associated with these species. The remaining 32 species are associated with population declines, and listed under several IUCN criterion including: A ~ reduction in population size (14 species), B ~ geographic range restricted, fragmented and the population declining (17 species), C ~ small population size and declining (three species), and D ~ population very small or restricted (eight species). As such, the terms threatened and declining are synonymous for these 32 species.

Multiple threats have been identified for each species (Table 2). The principal threats to Australian frogs are currently unknown for 22 species where identified threats do not adequately explain their threatened status. Known threats include: habitat modification (foremost for 18 species and potential contributor for an additional two species), restricted geographic range (foremost for 16 species and potential contributor for an additional 15 species), chytridiomycosis (foremost for five species and potential contributor for an additional nine species), and introduced species (foremost for two species and potential contributor for an additional seven species), fire (potential contributor for six species) and global change in weather patterns/UV-B levels (potential contributor for two species).

Distribution correlates of threatened frogs are presented in Table 3. Restricted geographic range (extent of occurrence less than 20 000 km²) is a characteristic of 31 threatened species (77.5%). Eight of these (25.8%) are listed as Vulnerable (IUCN criterion D2, having an area of occupancy of less than 20 km²), however the remaining 23 species were associated with fragmentation and population declines (IUCN criterion A & B). An additional 41 non-threatened species (23.7%) have restricted geographic range (Table 4).

Twenty-eight threatened species (70%) primarily occur in upland areas (Table 3). Of the remaining 12 threatened lowland species, 11 are most notably threatened with habitat loss (Tables 2 and 3). For non-threatened species the inverse pattern is clear with

TABLE 1. IUCN categories from the Australian Global Amphibian Assessment 2001. Asterisks (*) denote species no longer found in the wild. Numbers in brackets and "x" denotes species with those characteristics but not classified using that criterion.

Species	Status	IUCN-GAA Criterion				
		IUCN 2002	A	B	C	D
		Reduction in population size	Geographic range restricted fragmented & declining	Population size fewer than 10 000mature individuals	Population very small or restricted	Quantitative analysis
<i>Rheobatrachus silus</i> *	EX	-	X	X	1	-
<i>Rheobatrachus vitellinus</i> *	EX	-	X	X	1	-
<i>Taudactylus diurnus</i> *	EX	-	X	X	1	-
<i>Geocrinia alba</i>	CR	-	2 a b(ii)	-	-	-
<i>Litoria booroolongensis</i>	CR	-	2 a b(i-v)	-	-	-
<i>Litoria castanea / flavipunctata</i> *	CR	-	X	X	1	-
<i>Litoria lorica</i> *	CR	2c	1a b(iv)	X	1	-
<i>Litoria nyakalensis</i> *	CR	2ac	1a b(iv)	X	1	-
<i>Litoria piperata</i> *	CR	-	X	X	1	-
<i>Litoria spenceri</i>	CR	-	2 a b(i-v)	-	-	-
<i>Litoria verreauxii alpina</i>	CR	1 a, b, c	X	-	-	-
<i>Philoria frosti</i>	CR	2abc	1ab(i,ii,iii) + 2 a b(i,ii,iii,iv,v)	-	-	-
<i>Pseudophryne corroboree</i>	CR	2abc+3abc	2ab(i-v)	1	-	-
<i>Pseudophryne pengilleyi</i>	CR	-	2 a b(ii,iv,v)	-	-	-
<i>Taudactylus acutirostris</i> *	CR	2ac	1a b(iv,v) + 2 b(v)	2 a(i)	1	-
<i>Taudactylus pleione</i>	CR	-	1ab(iii,v) + 2 a b(iii,v)	-	-	-
<i>Taudactylus rheophilus</i>	CR	2ac	X	-	-	-
<i>Litoria brevipalmata</i>	EN	-	2 a b(iii)	-	-	-
<i>Litoria nannotis</i>	EN	2 a	X	-	-	-
<i>Litoria raniformis</i>	EN	-	2 a b(iii)	-	-	-
<i>Litoria rheocola</i>	EN	2 a c	X	-	-	-
<i>Mixophyes fleayi</i>	EN	-	2 a b(iii)	-	-	-
<i>Mixophyes iteratus</i>	EN	-	2 a b(iii)	-	-	-
<i>Nyctimystes dayi</i>	EN	2 a c	X	-	-	-
<i>Taudactylus eungellensis</i>	EN	3 c	X	-	-	-
<i>Cophixalus mcdonaldi</i>	VU	-	X	-	2	-
<i>Cophixalus neglectus</i>	VU	-	X	-	2	-
<i>Cophixalus saxatilis</i>	VU	-	X	-	2	-
<i>Crinia tinnula</i>	VU	-	2 a b(ii-v)	-	-	-
<i>Geocrinia vitellina</i>	VU	-	X	-	2	-
<i>Heleioporus australiacus</i>	VU	2 b c	-	-	-	-
<i>Philoria richmondensis</i>	VU	-	X	-	2	-
<i>Litoria andiirrmalin</i>	VU	-	X	-	2	-
<i>Litoria aurea</i>	VU	2 a b c e	-	-	-	-
<i>Litoria freycineti</i>	VU	-	2 a b(ii-v)	-	-	-
<i>Litoria olongburensis</i>	VU	-	2 a b(ii-v)	-	-	-
<i>Mixophyes balbus</i>	VU	-	-	1+2 a(i)	-	-
<i>Pseudophryne australis</i>	VU	2 b c	X	-	-	-
<i>Pseudophryne covacevichae</i>	VU	-	X	-	2	-
<i>Spicospina flammocaerulea</i>	VU	-	X	-	2	-
Threatened Total	40	14	17 (20)	3 (7)	16	0

TABLE 2. Multiple threats identified for each species (GAA assessments), ranked as either Foremost (F) or Potential (P). Totals represent Foremost in bold, with Potential in brackets. X, an unknown threat is suspected as known threats do not adequately explain observed declines. Bold type denotes species found primarily in upland areas (see Table 3).

Species	Status	Foremost & Potential Threats						
		IUCN 2002	Restricted Geographic Range	Chytrid Infection recorded	Fire	Habitat Modification	Introduced Species	Global weather Change
<i>Rheobatrachus silus</i>	EX	F	-	-	-	P (pigs)	-	X
<i>R. vitellinus</i>	EX	F	-	P	-	-	-	X
<i>Taudactylus diurnus</i>	EX	F	-	-	-	P (pigs)	-	X
<i>Geocrinia alba</i>	CR	F	-	P	F	-	-	-
<i>Litoria booroolongensis</i>	CR	-	-	-	F	P (pigs)	-	X
<i>L. castanea / flavipunctata</i>	CR	F	-	-	F	P (fish)	-	X
<i>Litoria lorica</i>	CR	F	-	-	-	-	-	X
<i>L. nyakalensis</i>	CR	F	-	-	-	-	-	X
<i>L. piperata</i>	CR	F	-	-	F	P (fish)	-	X
<i>L. spenceri</i>	CR	F	F	-	F	F (fish)	-	-
<i>L. verreauxii alpina</i>	CR	F	-	-	F	-	-	-
<i>Philoria frosti</i>	CR	F	-	-	-	-	-	X
<i>Pseudophryne corroboree</i>	CR	P	P	P	-	-	P	X
<i>P. pengilleyi</i>	CR	F	P	-	-	-	P	X
<i>Taudactylus acutirostris</i>	CR	P	F	-	-	-	-	X
<i>T. pleione</i>	CR	P	-	-	-	P (pigs)	-	X
<i>T. rheophilus</i>	CR	F	-	-	-	-	-	X
<i>Litoria brevipalmata</i>	EN	-	-	-	F	-	-	-
<i>Litoria nannotis</i>	EN	P	F	-	-	-	-	X
<i>Litoria raniformis</i>	EN	-	P	-	F	-	-	X
<i>Litoria rheocola</i>	EN	P	F	-	-	-	-	X
<i>Mixophyes fleayi</i>	EN	P	P	-	P	P (pigs)	-	X
<i>M. iteratus</i>	EN	-	P	-	F	-	-	-
<i>Nyctimystes dayi</i>	EN	P	F	-	-	-	-	X
<i>Taudactylus eungellensis</i>	EN	F	P	-	-	-	-	X
<i>Cophixalus mcdonaldi</i>	VU	P	-	-	-	-	-	-
<i>Cophixalus neglectus</i>	VU	P	-	-	-	-	-	-
<i>Cophixalus saxatilis</i>	VU	P	-	-	-	-	-	-
<i>Crinia tinnula</i>	VU	-	-	-	F	-	-	-
<i>Eocrinia vitellina</i>	VU	P	P	P	F	-	-	-
<i>Heleioporus australiacus</i>	VU	-	P	-	F	-	-	-
<i>Philoria richmondensis</i>	VU	P	-	-	-	-	-	-
<i>Litoria andiirrmalin</i>	VU	P	-	-	-	-	-	-
<i>Litoria aurea</i>	VU	-	P	-	F	F (fish)	-	X
<i>Litoria freycineti</i>	VU	-	-	-	F	-	-	-
<i>Litoria olongburensis</i>	VU	P	-	-	F	-	-	-
<i>Mixophyes balbus</i>	VU	-	-	-	P	-	-	X
<i>Pseudophryne australis</i>	VU	F	-	P	F	-	-	-
<i>P. covacevichae</i>	VU	F	-	-	F	-	-	-
<i>Spicospina flammocaerulea</i>	VU	P	-	P	F	-	-	-
Threatened total	40	16 (15)	5 (9)	0 (6)	18 (2)	2 (7)	2	22

TABLE 3. Geographic distribution and reproductive habitats of Australia's threatened frogs. Bold type denotes species with a geographic range less than 20 000 km². TT = totally terrestrial reproductive mode.

Species	Status	Geog. range	Altitudinal range		Latitudinal range			Reproductive Habitat			
			IUCN 2002	km ²	Low-land	Up-land	Temp.	Sub-tropic	Tropic	Montane wetlands	Wet forest stream
<i>Rheobatrachus vitellinus</i>	EX	131		X				X		X	
<i>Rheobatrachus silus</i>	EX	1394		X			X			X	
<i>Taudactylus diurnus</i>	EX	1417		X			X			X	
<i>Geocrinia alba</i>	CR	164	X		X						X
<i>Litoria booroolongensis</i>	CR	135 674		X	X					X	
<i>Litoria castanea/flavipunctata</i>	CR	8520		X	X						X
<i>Litoria lorica</i>	CR	1172		X				X		X	
<i>Litoria nyakalensis</i>	CR	11 636		X				X		X	
<i>Litoria piperata</i>	CR	5030		X	X					X	
<i>Litoria spenceri</i>	CR	16 578		X	X					X	
<i>Litoria verreauxii alpina</i>	CR	3227		X	X				X		
<i>Philoria frosti</i>	CR	293		X	X				X		
<i>Pseudophryne corroboree</i>	CR	1079		X	X				X		
<i>Pseudophryne pengilleyi</i>	CR	1109		X	X				X		
<i>Taudactylus acutirostris</i>	CR	14 620		X				X		X	
<i>Taudactylus pleione</i>	CR	126		X			X			X	
<i>Taudactylus rheophilus</i>	CR	4716		X				X		X	
<i>Litoria brevipalmata</i>	EN	72 540	X				X				X
<i>Litoria nannotis</i>	EN	19 044		X				X		X	
<i>Litoria raniformis</i>	EN	433 569	X		X						X
<i>Litoria rheocola</i>	EN	15 201		X				X		X	
<i>Mixophyes fleayi</i>	EN	6 985		X			X			X	
<i>Mixophyes iteratus</i>	EN	105 945	X				X			X	
<i>Nyctimystes dayi</i>	EN	18 894		X				X		X	
<i>Taudactylus eungellensis</i>	EN	335		X				X		X	
<i>Cophixalus mcdonaldi</i>	VU	345		X				X	TT		
<i>Cophixalus neglectus</i>	VU	562		X				X	TT		
<i>Cophixalus saxatilis</i>	VU	248		X				X	TT		
<i>Crinia tinnula</i>	VU	30 272	X				X				X
<i>Geocrinia vitellina</i>	VU	32	X		X						X
<i>Heleioporus australiacus</i>	VU	80 013		X	X						X
<i>Philoria richmondensis</i>	VU	967		X				X	TT		
<i>Litoria andürrmalin</i>	VU	5 669	X					X		X	
<i>Litoria aurea</i>	VU	132 439	X		X						X
<i>Litoria freycineti</i>	VU	58 628	X				X				X
<i>Litoria olongburensis</i>	VU	8368	X				X				X
<i>Mixophyes balbus</i>	VU	110 441		X	X					X	
<i>Pseudophryne australis</i>	VU	17 504	X		X						X
<i>Pseudophryne covacevichae</i>	VU	379		X				X			X
<i>Spicospina flammocaerulea</i>	VU	562	X		X						X
Threatened total	40	31 78%	12 30%	28 70%	16 40%	9 23%	15 37%	4 (4) 10 + 10%	19 47.5%	13 32.5%	

TABLE 4. Ecological characteristics of Australian frogs. Numbers represent the number of species within each IUCN category. CR includes the subspecies *L. verreauxi alpina*.

IUCN-GAA Assessment 2001	No. of Species	Geographic Range	Altitudinal Range		Latitudinal Range			Reproductive Habitat					
			Restricted (<20K km ²)	<400m asl	>400m asl	Temp- erate	Sub- tropical	Tropical	Montane wetlands	Wet forest stream	Open forest stream	Isolated ponds & swamps	Totally terrest.
EX	3	3		3		2	1		3				
CR EN *	14	13	1	13	9	1	4	4	8		2		
EN	8	5	3	5	1	3	4		6		2		
VU*	15	10	8	7	6	3	6		2		9	4	
Threatened sub-tot. (% of 40 species)	40	31 77.5%	12 30%	28 70%	16 40%	9 22.5%	15 37.5%	4 10%	19 47.5%	0	13 32.5%	4 10%	
Near Threatened	4	2	2	2	1	2	1		3		1		
Data Deficient	22	9	19	3	7	1	14		1	2	17	2	
Least Concern *	147	30	110	37	50	34	63	1	10	7	109	20	
Non-threatened sub-tot. (% of 173 species)	173	41 23.7%	131 75.7%	42 24.3%	58 33.5%	37 21.4%	78 45.1%	1 0.6%	14 8.1%	9 5.2%	127 73.4%	22 12.7%	
All species totals (% of 213 species)	213	72 33.8%	143 67%	70 33%	74 34.7%	46 21.5%	93 43.7%	5 2.3%	33 15.5%	9 4.2%	140 65.7%	26 11.3%	
Threatened sub-total All species totals		18.8% 43%	8% 4%	41% 19%	22% 10%	20% 9%	16% 7%	80% 37%	58% 27%	0 0%	9% 4%	15% 7%	

only 42 species (24.3%) occurring in upland areas. Subsequently 41% of upland species are threatened while only 8% of lowland species are threatened (Table 4).

Latitudinal position is not strongly associated with the degree of threat. While more threatened species occur in the tropical and temperate areas than in subtropical regions (Table 3) this is primarily due to higher species richness in those regions. The percentage of threatened species in each region was 21.6%, 19.6% and 16.1% for the temperate, subtropical and tropical regions respectively (Table 4).

Threatened species are strongly associated with specific reproductive habitats: 19 threatened species breeding in wet forest streams (47.5%), 13 species breeding in isolated ponds and swamps (32.5%) and the remaining eight species breed in montane wetlands (Table 3). However, considering all species, 80% of all species breeding in montane wetlands and 57.6% of all species breeding in wet forest streams are threatened (Table 4). In contrast only 9.3% of all pond-breeding species are threatened (Table 4).

A preliminary examination of the phylogenetic relationships of Australia's threatened frogs (Table 5) suggests there are no strong associations between taxonomic groups and threatened status. One notable exception is the genus *Taudactylus* (Myobatrachidae) where five of the six species in the genus have a threatened status. Some phylogenetic associations occur within the hylid genus *Litoria* (Tyler & Davies, 1978;

Hutchinson & Maxson, 1987) however the relationships among species within this genus require further examination.

GLOBAL THREATENED SPECIES

While comparative information from other countries is scarce, the average proportion of species that are threatened is 10% (Table 6). Several countries exceeding that (with over 15% threatened) include Australia, Fiji, Jamaica, Japan, New Zealand, Philippines, Puerto Rico, Seychelles, Venezuela & Virgin Islands. There is a strong association between threatened status and high altitude in all countries for which data is available (Table 6). Research on the potential impacts of the chytrid fungus has detected numerous species carrying the disease in Australia and the USA, with limited records from five other countries (Table 6).

DISCUSSION

Approximately 18.8% of Australia's frogs are currently listed as threatened. At least eight of these species can no longer be found in the wild, despite intensive searching. This is higher than in most countries (average of 10%) and is justification for concern in Australia. Completion of the Global Amphibian Assessment throughout the world is likely to change the context of these results however concern for countries known to have high levels of threatened species (Australia, Fiji, Jamaica, Japan, New Zealand, Philippines, Puerto Rico,

TABLE 5. Geographic Distribution and Reproductive Habitats of Phylogenetic groups of Australia's frog species. Threatened species groups are highlighted in bold. **Austrochaparina* was *Sphenophryne*.

Phylogeny	No. of Species	Geographic Range		Latitudinal Range			Reproductive Habitat					IUCN GAA classification							
		Restricted <20K km ²	<400m asl	>400m asl	Temp-erate	Sub-tropical	Tropical	Mont-ane wet-lands	Wet forest stream	Open forest stream	Ponds & swamp	TT	Threatened				Non-threatened		
													EX	CR	EN	VU	NT	DD	LC
MYOBATRACHIDAE																			
<i>Adelotus</i>	1	-	-	1	-	1	-	-	1	-	-	-	-	-	-	1	-		
<i>Arenophryne</i>	1	-	1	-	-	1	-	-	-	-	-	1	-	-	-	-	1		
<i>Assa</i>	1	-	1	-	-	1	-	-	-	-	-	1	-	-	-	-	1		
<i>Bryobatrachus</i>	1	1	-	1	1	-	-	-	-	-	-	1	-	-	-	-	1		
<i>Crinia</i>	14	2	12	2	10	1	3	-	-	1	13	-	-	1	-	1	12		
<i>Geocrinia</i>	7	4	6	1	7	-	-	-	-	3	4	-	-	1	-	1	5		
<i>Helioporus</i>	6	1	6	-	6	-	-	-	-	-	6	-	-	1	-	-	5		
<i>Philoria/Kyarranus</i>	5	5	-	5	3	2	-	-	-	-	-	5	-	1	1	-	3		
<i>Lechriodus</i>	1	-	-	1	-	1	-	-	-	-	1	-	-	-	-	-	1		
<i>Limnodynastes</i>	12	1	12	-	5	3	4	-	-	-	12	-	-	-	-	-	12		
<i>Megistolotus</i>	1	-	-	1	-	-	1	-	-	-	1	-	-	-	-	-	1		
<i>Metacrinia</i>	1	-	1	-	1	-	-	-	-	-	-	1	-	-	-	-	1		
<i>Mixophyes</i>	5	2	1	4	1	4	-	-	4	-	1	-	-	2	1	-	2		
<i>Myobatrachus</i>	1	-	1	-	1	-	-	-	-	-	-	1	-	-	-	-	1		
<i>Neobatrachus</i>	10	1	10	-	5	4	1	-	-	-	10	-	-	-	-	-	10		
<i>Notaden</i>	4	1	4	-	-	1	3	-	-	-	4	-	-	-	-	1	3		
<i>Paracrinia</i>	1	-	1	-	1	-	-	-	-	-	1	-	-	-	-	-	1		
<i>Pseudophryne</i>	13	4	10	3	8	4	1	2	-	1	10	-	2	2	2	3	6		
<i>Rheobatrachus</i>	2	2	-	2	-	1	1	-	2	-	-	-	2	-	-	-	-		
<i>Spicospina</i>	1	1	1	-	1	-	-	-	-	-	1	-	-	1	-	-	-		
<i>Taudactylus</i>	6	5	-	6	-	1	5	-	6	-	-	-	1	3	1	1	-		
<i>Uperolia</i>	24	7	20	4	3	4	17	-	-	1	23	-	-	-	-	12	12		
HYLIDAE																			
<i>Cyclorana</i>	13	-	13	-	-	5	8	-	-	-	13	-	-	-	-	-	13		
<i>Litoria</i>	62	17	38	24	20	12	30	2	17	3	40	-	7	4	4	2	3		
<i>Nyctimystes</i>	1	1	-	1	-	-	1	-	1	-	-	-	-	1	-	-	-		
MICROHYLIDAE																			
<i>Austrochaparina</i> *	5	4	1	4	-	-	5	-	-	-	-	5	-	-	-	-	5		
<i>Cophixalus</i>	13	13	4	9	-	-	13	-	-	-	-	13	-	3	-	2	7		
RANIDAE																			
<i>Rana</i>	1	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	1		

TABLE 6. Conservation status of frog species listed by IUCN 2002. The proportion listed known from upland areas does not include species for which complete information on altitudinal range was unavailable. * denotes countries where altitude data was unavailable.

Country	No. species	No. species with chytrid	No. listed IUCN 2002	No. listed IUCN & Amphibia Web	Proportion listed%	No. listed from upland	Proportion listed from upland %
Afghanistan	7		1	1	14	1	100
Argentina	147		5	5	3	*	*
Australia	213	47	40	40	18.8	28	70
Bolivia	135		1	1	1	*	*
Bosnia Herzegovina	10		1	1	10	1	100
Brazil	700		6	64	3	*	*
Cameroon	165		1	1	1	*	*
Canada	40		1	1	3	1	100
Chile	44		3	3	7	3	100
China	315		1	1	0	1	100
Costa Rica	165	1	1	5	3	5	100
Côte d'Ivoire	48		1	1	2	*	*
Croatia	10		1	1	10	1	100
Dominican Republic	37		1	1	3	*	*
Ecuador	437	2	0	24	5	*	*
Equatorial Guinea	26		1	1	4	*	*
Fiji	3		1	1	33	0	0
France	40		2	2	5	2	100
Georgia	14		1	2	14	2	100
Greece	20		1	1	5	1	100
Guinea	44		1	1	2	*	*
Haiti	47		1	1	2	1	100
Honduras	91		7	7	8	7	100
India	217		3	3	1	*	*
Iran (Islamic Republic)	20		2	2	10	2	100
Italy	43		4	4	9	4	100
Jamaica	24		4	4	17	3	75
Japan	62		10	10	16	4 / 4	100
Kazakstan	9		1	1	11	1	100
Madagascar	181		2	2	1	*	*
Mexico	330		4	6	2	6	100
Namibia	26		1	1	4	*	*
New Zealand	6	2	1	1	17	0	0
Peru	355		1	1	0	*	*
Philippines	93		22	23	25	16	70
Portugal	19		1	1	5	1	100
Puerto Rico	22		3	12	55	*	*
Seychelles	12		4	4	33	4	100
Slovenia	18		1	1	6	1	100
South Africa	107	1	9	9	8	5	56
Spain	31	2	3	3	10	3	100
Turkey	21		3	1	5	1	100
United States	272	13	25	26	10	20	77
Venezuela	291		0	63	22	52 / 52	100
Vietnam	115		1	1	1	1	100
Virgin Islands (British)	4		1	1	25	0	0
Totals	4962		170	296	average 10%	134	average 85%

Seychelles, Venezuela & Virgin Islands) is likely to remain high. Amphibian biodiversity is concentrated in the tropical regions (see Crump, 2003; Hero & Shoo, 2003). However, amphibian declines in tropical countries of Asia, Africa and South America are poorly represented in the IUCN 2002 Little Red Data Book assessments (Hero & Shoo, 2003). The Global Amphibian Assessment is currently addressing this shortfall. Nevertheless, conservation effort should focus on tropical regions where biodiversity is high and threats are not well known (Hero & Shoo, 2003).

THREATS TO AUSTRALIAN FROGS

While multiple threats were identified for each species, the most alarming result of the Australian (GAA) assessment is that the threats for 23 species are currently listed as unknown. In each case the multiple threatening processes associated with these species do not adequately explain the observed declines. This result is cause for major concern as management actions are hampered by the lack of knowledge on the relative importance of threats for these species. Management actions should place equal effort firstly into mitigating the known threats (e.g. habitat modification) and secondly, continuing research focusing on testing alternative hypotheses for the unexplained declines.

Habitat modification remains a key threat to Australian frogs (associated with the status of 50% of threatened species). Legislative protection is an essential process to ensure the conservation of these species. Species currently listed as Endangered, Critically Endangered or Extinct under the Australian Commonwealth *Environment Protection and Biodiversity Conservation Act* (1999) invoke strict legislative protection. Protection of "Vulnerable" species however is less clear. Of particular concern are 10 of the 15 species currently listed as "Vulnerable" threatened by habitat modification. If habitat modification continues these species will eventually be upgraded to the "Endangered" category. Eight "Vulnerable" species have relatively large geographic ranges (>5000 km²) and information on the "area of occupancy" (the area within its extent of occurrence which is occupied) is urgently needed to assess their status. While it may not be realistic to monitor populations over such large areas, some species have well known associations with specific habitats/ vegetation types which can be mapped and the loss of area can be mapped over time. As a solution to this, Shoo & Hero (pers. comm.) propose modelling the area of occupancy (using site records in combination with spatial habitat modelling and overlaid with current land use) for each species. This management tool will estimate the predicted area of occupancy for each species and can be updated on a regular basis (e.g. five yearly) providing a dynamic picture on the potential conservation status for each species based on habitat loss and geographic distribution.

In 1998 a chytrid fungus (*Batrachochytrium dendrobatidis*) was found to have lethal effects on amphibians in Australia and in other parts of the world

(Berger *et al.*, 1998). In Australia, the chytrid fungus is directly associated with declines for five species and a potential contributor for an additional nine species (35% of threatened species). In 2002 the Australian Government listed chytridiomycosis as a "key threatening process". It should be noted, however, that *B. dendrobatidis* has also been detected in an additional 33 (19%) non-threatened species (Speare & Berger, 2000b). Clearly other factors are contributing to declines associated with chytrid infection (e.g. altitudinal distribution, breeding habitat etc.). Hero (1996), and Williams & Hero (1998, 2001) found small clutch size was associated with declining species in some areas and this relationship is currently under further examination (Hero, J.-M. unpublished).

The role of the chytrid fungus as a global threat is slowly emerging (Speare & Berger, 2000a,b; Daszak, Cunningham & Hyatt, 2001). Chytrid fungus has now been isolated from declining species in Central and South America (Lips 1999, Young *et al.*, 2001; Lips *et al.*, 2003; Ron *et al.*, 2003), several species in North America (Carey, Cohen & Rollins-Smith, 1999), Germany (Speare & Berger 2000a,b), Spain (Bosch, Martinez-Solano & Garcia-Paris, 2001) and South Africa (Lane, Weldon & Bingham, 2003). Continuing research on this emerging infectious disease is an important step in resolving global amphibian declines.

Introduced fish have been notably associated with declines in two Australian species *Litoria spenceri* and *L. aurea* and potentially contribute to the decline of several other species including *L. castanea / flavipunctata* and *L. piperata* (Gillespie & Hines, 1999). Action to mitigate these effects are feasible, e.g. introduce legislation to stop fish stocking and movement of both native and non-native fish species, and promote active management of threatened species by eradicating introduced species from their breeding habitats (Gillespie & Hero, 1999; Gillespie, 2001). Other species that are potential threats to Australian frogs include feral pigs and cattle, however the impacts of these species have not been investigated (Hines, Mahony & McDonald, 2003). Management agencies should investigate these impacts where appropriate and apply mitigation procedures where feasible.

Few studies have investigated the impacts of fire on frogs. Fire has been proposed as a potential threat to several *Geocrinia* species and *Spicospina flammocaerulea* from small isolated populations in Western Australia (Driscoll & Roberts, 1997), and to remaining isolated populations of *Pseudophryne australis* in the Sydney region (AmphibiaWeb, 2003). Following severe declines in the geographic distribution of *Pseudophryne corroboree* in the Australian Alps, wildfires affected the few remaining breeding sites in January 2003 (Will Osborne, pers. comm.). Protection measures should be investigated and an experimental approach to examine the impacts of fire on these species implemented.

Changing weather patterns (global warming and increased UV-B radiation) have not been strongly associated with frog declines in Australia. Unusual

weather appears to be an inadequate explanation for the dramatic decline of montane frogs in Queensland (Laurance, 1996). Furthermore, many threatened frog species reproduce in wet forest streams where direct UV-B radiation is limited. For Australia's montane species the effects of global warming are expected to be complex and associated with other factors (Kiesecker, Blaustein & Belden, 2001). Increased UV-B has been proposed as a contributing factor in the decline of *Litoria verreauxi alpina* in the Australian alpine region (Broomhall *et al.*, 2000). While this hypothesis has not been investigated thoroughly, we conclude that increased UV-B is currently not expected to be a major threat to frogs in Australia.

GEOGRAPHIC DISTRIBUTION AND REPRODUCTIVE ECOLOGY OF AUSTRALIAN FROGS

Restricted geographic range is characteristic of 31 of 40 threatened species (77.5%) however an additional 41 non-threatened species (23.7%) also have restricted geographic range. These data suggest that restricted geographic range (<20 000 km²) in isolation is not a threat. We propose that this distributional variable might be correlated with a species characteristic (e.g. fecundity) that would provide a biological explanation for their vulnerability to extinction processes (Smith & Quin, 1996).

Amphibian declines have been recorded from numerous high altitude areas including Australia (Campbell, 1999; this study), South Africa (Lane, Weldon & Bingham, 2003), Spain (Bosch, Martinez-Solano & Garcia-Paris, 2001), Latin America (Young *et al.*, 2001; Ron *et al.*, 2003), and the USA (Kiesecker, Blaustein & Belden, 2001). This global pattern is confirmed in our analysis (Table 6). The strong association between threatened status and high altitude both in Australia and on a global scale is not easily explained. Upland habitats contain areas of high species richness, endemism and a high proportion of geographically restricted species (Hero & Shoo, 2003). Habitat modification is more prevalent in lowland areas and unexplained threats to upland species is a major concern (in eastern Australia 8 upland species can no longer be found in the wild). Our results demonstrate this is a global phenomenon, and conservation agencies should focus on assessing the conservation status of amphibians in high altitude areas.

Morrison & Hero (2003) proposed that declines in upland areas might be associated with intrinsic changes in the life history characteristics of species associated with altitude. Amphibian populations at higher altitudes tend to: (1) have shorter activity periods and hence shorter breeding seasons; (2) have longer larval periods; (3) be larger at all larval stages including metamorphosis; (4) be larger as adults; (5) reach reproductive maturity at older ages; (6) produce fewer clutches per year; (7) produce larger clutches absolutely and smaller clutches relative to body size; and (8) produce larger eggs. The combination of these characteristics suggested that high altitude individuals, and hence

populations, may be less resilient to extinction processes (Morrison & Hero, 2003).

Species breeding in Australian montane habitats and wet forest streams are more likely to be threatened than pond breeding or totally terrestrial species. This is similar to the many species of the genus *Atelopus* that have suffered severe declines in the high altitude wet forest streams of Central and South America (Young *et al.*, 2001; Ron *et al.*, 2003). The strong association with altitude may be associated with breeding site attributes that work synergistically with other causes of decline (e.g. chytridiomycosis).

The principal threat to lowland Australian frogs is habitat loss (Table 2) – this is not surprising as land clearing for human activities is generally concentrated in lowland areas (Brooks *et al.*, 1999; Hero & Shoo, 2003). Hence we expect that more lowland species would be threatened worldwide than upland species. In Australia the principal threats to upland species are varied, often associated with restricted geographic range (however as discussed previously this association is not foremost) but more notably associated with the presence of chytrid fungus, habitat modification, introduced species and unknown causes all contributing (Table 2).

GLOBAL THREATS TO FROGS

Clearly much can be learned from the Australian assessment. Frog declines are a complex interaction of threatening processes (unknown, habitat modification, chytridiomycosis, fire and global warming) and species vulnerability (breeding habitat, altitudinal distribution and restricted geographic range). Species ecology may also play a role (e.g. reproductive ecology and population dynamics). The traits of declining frogs in Australia can be used to predict species vulnerability in countries where little is known about the status of their amphibian populations. There is a dearth of information available on the conservation status and threatening processes (e.g. chytridiomycosis) in tropical countries where amphibian biodiversity is high. Hero & Shoo (2003) proposed establishing a global network of "Research Centres for Amphibian Conservation" in biodiversity hotspots with significant species richness, endemism or both. International assistance by the global herpetological community is urgently needed to provide research training, resources and funding to scientists in tropical countries.

ACKNOWLEDGEMENTS

We thank Craig Hilton Taylor, Simon Stuart and all the participants of the Australian Global Amphibian Assessment whose cooperation and assistance brought together the known information on Australian frogs. Special thanks to Luke Shoo for calculating the extent of occurrence for all Australian species. For assisting in gathering information on the species from other continents we thank Jaime Bosch, Michael Cunningham, Ricardo Javier Torres-Cervantes, Neil Cox, Arvin Diesmos, Justin Gerlach, Brian Groombridge, Blair

Hedges, Mike Lannoo, Enrique La Marca, Alberto Veloso, Che Weldon and Larry Wilson. Luke Shoo, John Wilkinson and an anonymous reviewer provided valuable comments on an earlier draft.

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Accepted: 11.11.03