LETTER

Predicting susceptibility to future declines in the world's frogs

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Keywords
amphibian; chytridiomycosis; comparative analysis; conservation; decline; extinction risk; predictive modelling

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Received: 14 April 2008; accepted 5 May 2008.

doi: 10.1111/j.1755-263X.2008.00015.x

Abstract

The 2004 Global Amphibian Assessment demonstrated that almost 400 anuran species have recently moved closer to extinction due to a host of threat mechanisms. Of particular concern is the role of the fungal pathogen, *Batrachochytrium dendrobatidis* (Bd), for which more traditional conservation management is not effective. Determining which biological and environmental factors affect a species' susceptibility to these mechanisms would greatly aid conservation prioritisation and planning. We performed phylogenetic comparative analyses to determine which biological and environmental factors predict species' susceptibility to rapid declines, both generally and in the context of Bd. Our results extend the findings of previous finer scale studies: we find that high-altitude, restricted-range, aquatic species with low fecundity are most likely to suffer Bd-related declines. We use our findings to identify those species most at risk of Bd-related declines and global extinction in the future, and identify areas where many species are predicted to be susceptible. Identifying susceptible species in advance of their decline is particularly important in setting priorities when, as here, declines are hard to arrest once underway.

Introduction

In recent decades, amphibian species have experienced serious population declines on every continent on which they are found (Blaustein and Wake 1990; Houlahan *et al.* 2000; Wake 1991; Wyman 1990). The geographic extent and severity of amphibian population declines make the subject a conservation issue of high priority. Amphibian extinction risk and population declines are taxonomically non-random (Bielby *et al.* 2006; Stuart *et al.* 2004), even at small geographic scales (Bielby *et al.* 2006; Lips *et al.* 2003; Williams and Hero 1998), indicating that species biological attributes influence susceptibility to decline. Understanding patterns in intrinsic susceptibility is therefore an important step towards identifying locations with many species susceptible to decline in future (Cardillo *et al.* 2006), and in tailoring conservation management to the needs of particular species.

Previous analyses on susceptibility to population declines in amphibians suggest that large size, restricted range, living at high altitude, ecological specialism, and low-fecundity may all contribute to susceptibility (Lips *et al.* 2003; Murray and Hose 2005; Williams and Hero 1998), but these studies have generally considered local declines rather than species-level dynamics (but see La Marca *et al.* 2005; Sodhi *et al.* 2008). If global conservation management decisions are to be directed by research (Mendelson *et al.* 2006) we need to ensure that the information supporting decisions on the allocation of conservation resource is robust, and that species most at risk of future decline are identified. Knowing which type of species are the most likely to become globally more threatened would therefore be a powerful tool in the allocation of conservation resource.

The Global Amphibian Assessment (hereafter GAA; IUCN *et al.* 2004) provided the first evaluation of all known amphibian species according to the Red List criteria. Stuart *et al.* (2004) described a total of 398 anuran species that had experienced a genuine increase in extinction risk. These species, termed "Rapid Decline" (hereafter RD) species, may represent some of the most urgent conservation problems (Stuart *et al.* 2004) – species whose total population has declined to the point that they have moved a step closer to global extinction. The status changes of RD species were attributed to three causes: habitat reduction, over-exploitation, and enigmatic decline. While the former two categories require little explanation, the third is more complex. "Enigmatic decline" species have declined for reasons that are not fully understood. Possible mechanisms include climate change, UV-B irradiation, pollution, and infectious disease (Collins and Storfer 2003; Stuart *et al.* 2004). In particular, many of the species categorised as enigmatic RDs are thought to have declined due to chytridiomycosis (e.g., *Atelopus* species, La Marca *et al.* 2005), caused by the fungal pathogen, *Batrachochytrium dendrobatidis* (hereafter Bd).

Current understanding (Daszak *et al.* 1999; Lips *et al.* 2003; Murray and Hose 2005; Sodhi *et al.* 2008; Williams and Hero 1998) makes several predictions about how biology and threat processes interact to dictate anuran susceptibility to rapid declines. Using a large, geographically widespread dataset, and controlling for phylogeny, we aimed to test some of these predictions, particularly in the context of Bd related declines. We analysed RDs to find rules-of-thumb about which biological and environmental traits make species more susceptible to increased extinction risk in the future, and to form a basis for recommendations on future conservation efforts (Cardillo *et al.* 2006).

Methods

As 91% (398/435) of amphibian RD species are anurans (frogs), and the biology of the three amphibian orders are so different, we concentrated our analyses solely on frogs. The final dataset (available in Appendix S1) contained 553 anuran species representing 32 of the 33 anuran families, containing species from all six continents on which amphibians are present. For a detailed description of the dataset including methods of collection and sources used, please see Appendix S2.

In order to determine which biological, environmental and anthropogenic factors predicted species' RD status, we collected information on a number of life history, ecological and environmental variables. Appendix S3 gives a full description of predictor variables used and the transformations applied to meet expectations of normality.

We coded species according to their IUCN status, RD status and causal mechanism (using information from the GAA), and whether Bd infection has been reported (i.e., Bd^{+}/Bd^{-}) (see Appendix S4 for list of diagnosed species of which we are aware, and of references used). This information allowed us to make four binary comparisons, addressing four questions as follows

1. Do RD species differ biologically from other threatened species?
2. Do Enigmatic RD species differ biologically from other threatened and RD species?
3. Do Bd^{+} RD species differ biologically from Bd^{+} species that have not suffered a rapid decline?
4. Do RD species that have been infected/diagnosed as Bd^{+} differ biologically from RD species not infected/diagnosed with Bd?

When comparing threatened and non-threatened species, there are two possible problems of circularity. First, threat status might be autocorrelated with geographic range size, because species may be classified as threatened based on their narrow distribution. This could also bias comparisons between RD species (which are by definition at least Near-Threatened) and non-RD species (many of which are Least Concern). Most of our tests are structured to compare RD species with other RD or threatened species, minimising this circularity. The remaining analysis (comparison C above) also included Least Concern species in order to maximise the sample of Bd infected species. To remove the circularity from this analysis, we omitted threatened species (RD or otherwise) that had not been categorised under IUCN Criterion A (range decline, rather than small range size), following Purvis *et al.* (2000). The second possible problem is that RD status could be further autocorrelated with geographic range size if estimates of decline rate are artefactually higher in small-range species. This could occur if such species are easier to monitor, or if small ranges are mapped at a finer scale than large ranges (Thomas and Abery 1995). However, this artefact would predict that RD species tend to have smaller ranges than other threatened species, which they do not (see results of comparison A, below).

Due to the binary nature of the response variables, and the consequent non-normal error structure, we conducted the analyses using generalized linear models specifying the link function as either logit or complementary log-log, and preferred the link with the lowest residual deviance (Crawley 2002).

We accounted for the strong phylogenetic signal within the dataset (see Appendix S5) using generalised estimating equations (GEE) as described by Paradis and Claude (2002). GEE are a procedure in which model parameters in a generalised linear model framework may be estimated taking correlations among observations into account. All GEE analyses were conducted using the compar.gee function (package = ape; Paradis *et al.* 2005) in the software package R (R Development Core Team 2005). In our analyses, the correlation matrix describing the relationships among data was obtained from the recently published genus-level amphibian phylogeny (Frost *et al.* 2006) with taxonomy as a surrogate for phylogeny below the genus level. As a result of the lack of branch length information, all branch lengths were set to two units. For each of the four comparisons, A-D, we initially conducted single-predictor analyses for each of the twelve explanatory variables. In two of the 48 bivariate analyses performed, the model parameters would not converge when using one or both of the possible link functions. We have indicated where this occurred in the results section. To account for the possibility that the large number of predictors tested would result in an increased rate of Type I errors, the Holm-Bonferroni method was implemented on the bivariate analyses within each of the four comparisons made. All Holm-Bonferroni adjustments were made using the p.adjust function in the software package R (R Development Core Team 2005).

Once bivariate relationships had been modelled, we investigated multipredictor relationships, allowing determination of which variables were associated with RD status when correlated variables were accounted for. Initially, all significant single predictors were included in the model, and the predictor with the highest p-value was successively removed until the remainder were significant. To check the robustness of the resulting model, each previously excluded explanatory variable was added in turn until no more significant predictors could be found. Additionally, we conducted the analyses including variables that did not converge as single predictors in the first step of the model building process. If no significant predictors were found in the bivariate analyses, we built a minimum adequate model by including all predictors in the first model and dropping those with the highest p-values until all remaining terms had a p-value below 0.05.

For the multipredictor models obtained, cross-validation was used to obtain a measure of model fit. For each of 1000 iterations, six species from the original model were randomly selected, and brier scores calculated using the observed and fitted values of those species. Brier scores (mean squared error for binary data (Brier 1950)) are a measure of model fit: a model with perfect predictive ability would obtain a score of 0.0, while a score of 1.0 would indicate a model with very poor predictive power. For all multipredictor models, we calculated a mean brier score and standard error of the mean (SEM) for the 1000 iterations.

Using the parameters from our most predictive model, that of Bd-related RD (comparison C), and the relevant biological trait data we calculated the probability of decline for 3976 anuran species. To illustrate those locations with a high number of highly susceptible species, we mapped all species with a probability of RD of 1.0 if infected with Bd (Figure 1) using ArcMap 9.0.

Results

When RD species were compared with other threatened species (comparison A, Table 1), rapid declines were associated with aquatic life-stage in bivariate comparisons. The multipredictor model included aquatic life-stage as a significant predictor, with large geographic range approaching a significant relationship with RD ($p = 0.061$) (brier score 0.29 ± 0.002). Compared with

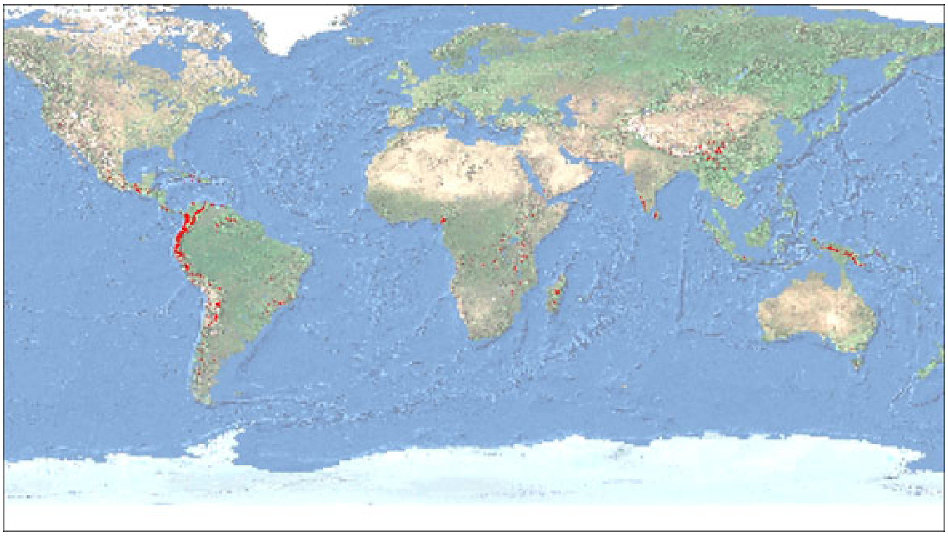

Figure 1 Global distribution of anuran species with a predicted probability of Bd-related decline = 1. Geographic ranges of those species with a predicted probability of 1 are marked in red.

Table 1 Results of univariate and multipredictor analyses of comparison A (RD species *vs* threatened species). N/A indicates that the analysis of this variable could not be completed for computational reasons related to the function compare.gee.

	Bivariate analyses			Bonferroni adjusted		MAM	
	n	Link	t	p-value	Deviance	t	p-value
log geographic range	359	clog-log[†]	2.05	0.43	111.53	1.92	0.06
log snouth vent length	358	logit	1.09	1.00	81.22		
log eggs per clutch	N/A	N/A	N/A	N/A	N/A		
log altitude	359	logit	−0.99	1.00	83.69		
log human population density	358	logit	0.33	1.00	83.70		
Net primary productivity	331	clog-log	−0.48	1.00	78.34		
Actual evapotranspiration	354	clog-log	1.05	1.00	83.54		
Isothermality	359	clog-log	−0.48	1.00	84.90		
Temp of warmest month	359	clog-log	0.44	1.00	85.73		
Precipitation seasonality	359	clog-log	0.07	1.00	84.33		
$\sqrt{}$Precipitation of driest quarter	359	clog-log	−0.15	1.00	84.20		
Aquatic life-stage	357	logit	3.90	0.00	82.02	3.06	0.00

dfp = phylogenetic degrees of freedom.

[†] log geographic range could only be analysed using the clog-log function.

In the MAM reported below, n = 357, link = clog-log, deviance = 102.74, dfp = 49.95, brier score = 0.29 S.E. ± 0.0022.

threatened species, RD species affected by enigmatic decline (comparison B) were found to live in locations with low annual temperature variation, and to have aquatic life-stages in bivariate analyses. In this multipredictor model low annual temperature variation was no longer a significant term, whereas clutch size was now significant, and high altitude approached significance with a p-value of 0.09 (Table 2, brier score 0.26 ± 0.003). When only Bd^+ species were analysed (comparison C), RD was associated with high altitude and small geographic range in the bivariate analyses (Table 3). The multipredictor analysis also included aquatic life-stage Bd^+ species alongside the significant bivariate predictors, as being more likely to have suffered an RD (Table 3, brier score 0.06 ± 0.002). When only RD species were included (comparison D) in bivariate analyses, no predictor variables were significantly associated with a species' Bd status, though large range RD species in areas of low actual evapotranspiration were more likely to be Bd^+ in the multipredictor model (Table 4).

Discussion

These global analyses of RD anuran species strengthen and extend the scope of the findings of finer scale studies

Table 2 Results of univariate and multipredictor analysis of comparison B (enigmatic RD species *vs* threatened species).

	Bivariate analyses			Bonferroni adjusted		MAM	
	n	Link	t	p-value	Deviance	t	p-value
log geographic range	359	clog-log	−0.80	1.00	87.81		
log snouth vent length	358	clog-log	−0.42	1.00	87.66		
log eggs per clutch	106	logit	−2.70	0.10	28.23	−2.569	**0.02**
log altitude	359	clog-log	0.78	1.00	88.36	1.77	0.09
log human population density	358	logit	−0.43	1.00	87.05		
Net primary productivity	331	logit	−0.51	1.00	82.35		
Actual evapotranspiration	354	clog-log	0.10	1.00	88.69		
Isothermality	359	clog-log	3.18	**0.02**	80.41		
Temp of warmest month	359	logit	−0.71	1.00	86.35		
Precipitation seasonality	359	logit	1.50	1.00	91.10		
$\sqrt{}$Precipitation of driest quarter	359	logit	−0.41	1.00	88.73		
Aquatic life-stage	357	clog-log	2.49	**0.01**	87.35	2.121	**0.04**

In the MAM reported below, n = 120, link = clog-log, deviance = 30.02, dfp = 21.53, brier score = 0.26 S.E. ± 0.003

Table 3 Results of univariate and multipredictor analysis of comparison C (Bd$^+$ RD species *vs* all other Bd$^+$ species).

	Bivariate analyses			Bonferroni adjusted		MAM	
	n	Link	t	p-value	Deviance	t	p-value
log geographic range	102	logit	−4.37	**0.01**	13.44	−2.65	0.02
log snout vent length	101	cloglog	−0.85	1.00	21.14		
log eggs per clutch	83	cloglogf	−1.80	0.81	16.97		
log altitude	102	logit	3.71	**0.02**	15.16	2.65	0.02
log human population density	102	cloglog	1.19	1.00	20.10		
Net primary productivity	102	logit	−1.18	1.00	19.25		
Actual evapotranspiration	102	cloglog	−0.84	1.00	19.53		
Isothermality	102	cloglog	1.17	1.00	25.79		
Temp of warmest month	102	logit	−2.04?	0.58	16.41		
Precipitation seasonal ity	102	cloglog	1.16	1.00	20.57		
√ Precipitation of driest quarter	102	cloglog	−0.83	1.00	20.45		
Aquatic life-stage	102	logit	0.69	1.00	19.66	2.12	0.05

† log eggs per clutch could only be analysed using the clog-log function.
In the MAM reported below, n = 102, link = clog-log, deviance = 7.37, dfp = 16.94, brier score = 0.06 S.E. ± 0.002

of anuran declines (Lips *et al.* 2003; Murray and Hose 2005; Williams and Hero 1998). Species with aquatic life-stages are particularly susceptible to rapid declines, while species with restricted distribution at high elevations are most susceptible to Bd related RD. We discuss these results and their possible implications for conservation.

Narrow geographic distribution is an important predictor of high extinction risk and declines in many taxonomic groups (Cardillo *et al.* 2005; Fisher and Owens 2004; Purvis *et al.* 2000) including amphibians (Cooper *et al.* 2008; Murray and Hose 2005; Sodhi *et al.* 2008). However, the role of geographic distribution in predicting RD status appears to be more complex. While restricted range species were indeed more susceptible to decline in one of our analyses (comparison C), two of the other comparisons (A and D) showed the opposite. This observed change of role of geographic distribution may be explained by the epidemiology and particularly the spread of chytridiomycosis. Whereas wider ranging species are more likely to be infected and diagnosed with Bd, it is restricted range species that are more likely to suffer serious consequences of chytridiomycosis.

One of the three criteria for disease-induced extinction is a restricted distribution, and associated small population size (de Castro and Bolker 2005). While wide-ranging species become infected (comparison D), and even suffer local declines (e.g., *Alytes obstetricans* (Bosch *et al.* 2001), *Salamandra salamandra* (Bosch and

Table 4 Results of univariate and multipredictor analysis of comparison D (Bd$^+$ RD species *vs* Bd$^-$ RD species). N/A indicates that the analysis of this variable could not be completed for computational reasons related to the function compare.gee.

	Bivariate analyses			Bonferroni adjusted		MAM	
	n	Link	t	p-value	Deviance	t	p-value
log geographic range	227	logit	2.48	0.19	34.05	3.24	0.003
log snout vent length	226	logit	2.64	0.14	34.55		
log eggs per clutch	79	logit	1.88	0.72	18.83		
log altitude	227	clog-log	0.48	1.00	47.05		
log human population density	227	N/A	N/A	1.00	N/A		
Net primary productivity	227	clog-log	−0.61	1.00	40.84		
Actual evapotranspi ration	227	logit	−0.34	1.00	42.64	−3.001	0.0052
Isotherm ality	227	clog-log	−0.90	1.00	38.91		
Temp of warmest month	227	clog-log	−0.45	1.00	44.75		
Precipitation seasonal ity	227	clog-log	−0.06	1.00	44.10		
√ Precipitation of driest quarte	227	clog-log	−1.62	0.92	35.71		
Aquatic life-stage	227	clog-log	0.66	1.00	43.96		

In the MAM reported below, n = 227, link = logit, deviance = 32.83, dfp = 33.82, brier score = 0.14 S.E. ± 0.003

Martinez-Solano 2006)), they are more likely to recover or at least persist through recruitment, recolonisation, and immigration than restricted range species. Of the 133 confirmed and possible amphibian extinctions in recent years (IUCN *et al.* 2004; Schloegel *et al.* 2006), many of which are likely to have involved chytridiomycosis, the majority of species had restricted ranges.

Aside from geographic range size, which other factors make a species more susceptible to the deleterious effects of Bd infection? Our analyses of both enigmatic RD (comparison B) and Bd infected species (comparison C) strongly support regional work on biological traits associated with amphibian population declines in Central America and Australia (Daszak *et al.* 1999; Hero *et al.* 2005; Lips *et al.* 2003; Murray and Hose 2005; Williams and Hero 1998): high altitude, small clutch size, partially aquatic species are most susceptible. Caution may be required when using these variables to predict RD: species with traits that place obvious restrictions on a distribution (e.g., high elevation, or aquatic life-stage) are perhaps more likely to be classified as RD simply because of a higher certainty of changes to the distribution of those species. However, there are strong biological mechanisms that could link aquatic life-stage and high altitude to RD (Lips *et al.* 2003; Williams and Hero 1998). Aquatic life-stage species are reliant on more than one type of habitat for completion of their life-cycle, and therefore may be exposed to a wider range of threats likely to cause increased mortality. Given such an increased level of mortality, one way for a population to remain stable or recover is through high recruitment in subsequent reproductive events. This may explain the importance of clutch size as a predictor of enigmatic RD with species with larger clutch size being less likely to suffer an RD.

The inclusion of high altitude as a correlate of Bd-related decline, even accounting for geographic distribution size, suggests that altitude does not increase a species' susceptibility to RD simply by limiting the species' distribution. As with restricted range species, high altitude species may be less able to offset mortality through recruitment, recolonisation, or colonisation from other populations. Additionally, factors such as Bd, climate change and pollution, may exert their influence most seriously at mid- to high-elevations (Daly *et al.* 2007; Pounds *et al.* 2006), and could perhaps work in combination to affect amphibian populations. The decline of sympatric species of reptiles and birds (which are unaffected by Bd) at sites of amphibian declines (Pounds *et al.* 1999; Whitfield *et al.* 2007), underlines the difficulty involved in ascribing an ultimate cause to a decline (Collins and Storfer 2003; Mace and Balmford 2000). Similarly, declines of Bd-infected amphibian populations as a result of climatic conditions rather than disease (Daszak *et al.* 2005) highlight the fact that the presence of Bd does not necessarily mean that it is responsible for declines in the area, something that should be remembered when interpreting the analyses presented here. So, while chytridiomycosis is a major cause for concern in amphibian conservation, the effects of other enigmatic factors, either alone or in combination with infectious diseases, must not be ignored.

The suitability of predictive models for conservation prioritisation depends upon the strength of their predictive ability, which varied greatly in the models presented here. Comparison of Bd^+ species (comparison C) resulted in a model with extremely high predictive ability (brier score of 0.064 ± 0.002) compared to the other models, particularly those for comparisons A and B (brier scores of 0.29 ± 0.002 and 0.26 ± 0.003 respectively). The key to the lower predictive ability of those models may lie with the greater geographic and taxonomic coverage in the respective datasets. The data on Bd infection were more limited geographically, taxonomically and in sample size than the data forming the basis of the other comparisons, which therefore reduced the variation in the dataset. However, given a suitable level of predictive ability, such models may be of use in guiding conservation priorities.

Using those traits highlighted in the analyses we may be able to direct conservation research and policy by predicting which species are most susceptible in the future (e.g., Cardillo *et al.* 2006; Koh *et al.* 2004). We have used the model parameters obtained in our most predictive model, comparison C, to estimate the probabilities that each of 3976 anuran species would decline rapidly if they became infected with RD (see Appendix S6). Figure 1 shows a map of the locations of those species with an estimated probability of RD of 1, and identifies areas which may be particularly heavily hit if Bd were to be introduced into the region (Figure 1). Given the susceptibility of their species, these locations represent a high priority for pre-emptive conservation policy and management efforts. We echo the call of Sodhi *et al.* (2008) for multi-foci management, which may include monitoring species population trends (Collins and Halliday 2005); directing more detailed local studies (e.g., Bosch *et al.* 2007; Pounds *et al.* 2006; Williams and Hero 1998); screening for pathogens; the introduction of legislation to reduce the possibility of pathogen introduction via the amphibian trade (Fisher and Garner 2007); preventing the spread of Bd by establishing field hygiene protocols for people working in the area (e.g., Australian Government 2006); possibly the establishment of *ex situ* populations (Mendelson *et al.* 2006); and the development of national abatement plans in countries in which Bd is already known to be present (e.g., Australian Government 2006). While some of the locations highlighted are already the subject of Bd-related declines and associated conservation attention (e.g., high altitudes in Latin America; Young *et al.* 2001), and others are already high profile recipients of conservation efforts (e.g., Madagascar), other locations (e.g., New Guinea and the Western Ghats) have received little, if any, amphibian conservation attention or management so far.

Of the 837 species with a predicted probability of RD of 1 in the event of Bd infection, 385 are listed as data deficient in the IUCN Red List. The data deficient status of so many susceptible species highlights the need for better basic information on a large proportion of anuran species, including improving our knowledge of population status and trends, particularly in Asia and Africa (Collins and Halliday 2005).

In order to maximise the utility and accuracy of such models we could incorporate more detailed information on both predictor and response variables into the models. Better knowledge of anuran life-history and ecology, and more information on Bd distribution and pathogenicity of different strains (Berger *et al.* 2005) would add greatly to the prediction of response to Bd infection. Likewise, using long-term species population data, rather than solely using coarse measures such as change of Red List status, would add further resolution to predictive modelling of species response to threatening processes, and would represent a useful future avenue for research on the subject of amphibian population declines (Collins and Halliday 2005). Although our results are generally consistent with the results of finer-scale studies, there were some differences. Our analyses, for example, did not identify any climatic predictors, or any effect of species' habitat preference on probability of decline, in contrast to finer-scale studies (Burrowes *et al.* 2004; Daszak *et al.* 2005; Pounds *et al.* 2007; Williams and Hero 1998). The advantages of studying single species or regions are the ability to include such detailed information, which is unlikely to be available globally, and the ability to inform focussed conservation goals (Fisher and Owens 2004). However, detailed studies on single species suggest heterogeneity among populations in likelihood of infection and development of disease (e.g., *Alytes obstetricans*; S. Walker pers. comm), and results of regional studies may also vary within a clade (e.g., Hero *et al.* 2005; e.g., Lips *et al.* 2003; Williams and Hero 1998). These differences may reflect local idiosyncrasies in the exact causal mechanism of decline. So while single species and regional studies have the ability to incorporate more detailed information, their findings may not be applicable to wider sets of species and locations: large-scale studies are also an important tool in identifying species' susceptibility to threat mechanisms.

As the IUCN systematically updates Red List assessments for a range of taxa, the amount of information on species status over time will increase, and so will our ability to look at trends and patterns in species' status. Determining susceptibility of species to declines in the future could complement schemes monitoring changes in Red list status (Butchart *et al.* 2006, 2007), help to set priorities for future conservation actions, and offer a useful alternative to concentrating conservation efforts solely upon species already experiencing a high risk of extinction (e.g., Ricketts *et al.* 2005).

Acknowledgments

We would like to thank Ian Owens, Georgina Mace, David Orme, Nicola Toomey, Susanne Fritz, Gavin Thomas, Shai Meiri, and Owen Jones for suggestions and comments on the manuscript; Tim Coulson for advice on statistical methods; Emmanuel Paradis for advice on the use of compare.gee function; S. Blair Hedges, Roberto Ibanez, Andres Merino-Viteri, Eugenia del Pino, Santiago Ron, and Tej Kumar Shrestha for help compiling data on eggs per clutch; Simon Stuart and Janice Chanson for information on back-classification; and Navjot Sodhi, Hugh Possingham and two anonymous referees for helpful comments on the manuscript . This work was conducted thanks to NERC studentship NER/S/A/2004/12987.

Supplementary Material

The following supplementary material is available for this article:

Appendix S1: Final dataset.
Appendix S2: Source references.
Appendix S3: Predictor variables.
Appendix S4: Bd positive species list.
Appendix S5: ANOVA for phylogenetic signal
Appendix S6: Predicted values

This material is available as part of the online article from:

http://www.blackwell-synergy.com/doi/full/10.1111/j.1755-263X.2008.00015.x

(This link will take you to the article abstract).

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Editor: Prof. Hugh Possingham