Declining amphibian populations: a global phenomenon in conservation biology

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Abstract

Declining amphibian populations: a global phenomenon in conservation biology.— The majority of the recent reductions in the Earth's biodiversity can be attributed to direct human impacts on the environment. An increasing number of studies over the last decade have reported declines in amphibian populations in areas of pristine habitat. Such reports suggest the role of indirect factors and a global effect of human activities on natural systems. Declines in amphibian populations bear significant implications for the functioning of many terrestrial ecosystems, and may signify important implications for human welfare. A wide range of candidates have been proposed to explain amphibian population declines. However, it seems likely that the relevance of each factor is dependent upon the habitat type and species in question, and that complex synergistic effects between a number of environmental factors is of critical importance. Monitoring of amphibian populations to assess the extent and cause of declines is confounded by a number of ecological and methodological limitations.

Key words: Declining amphibians, Environmental degradation, Indirect human impact, Population monitoring.

Resumen

Disminución de las poblaciones de anfibios: un fenómeno global en biología de la conservación.— La mayoría de reducciones recientes en la biodiversidad de la Tierra puede atribuirse al impacto humano sobre el ambiente. Durante la última década, es cada vez mayor el número de estudios que informan de disminuciones en las poblaciones de anfibios en hábitats inalterados. Dichos estudios sugieren el papel de factores indirectos y un efecto global de las actividades humanas sobre los sistemas naturales. Las disminuciones de las poblaciones de anfibios llevan consigo implicaciones significativas para el funcionamiento de algunos ecosistemas terrestres y pueden tener importantes repercusiones en el bienestar humano. Para explicar la disminución de las poblaciones de anfibios se ha propuesto una amplia gama de posibles factores causales. Sin embargo, parece ser que la relevancia de cada factor depende del tipo de hábitat y de la especie afectada, y que los complejos efectos sinérgicos entre algunos factores ambientales es de importancia crítica. El control de las poblaciones de anfibios con objeto de valorar la dimensión y causa de la disminución está condicionado por una serie de limitaciones ecológicas y metodológicas.

Palabras clave: Disminución de anfibios, Degradación ambiental, Impacto humano indirecto, Control de poblaciones.

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Introduction

Human alteration of the global environment namely through habitat modification, agricultural practices, anthropogenically induced climate change, and atmospheric pollutants has triggered what is widely regarded as the sixth major extinction event in the history of life (CHAPIN et al., 2000). The extent of loss of biological diversity, and alterations in the distribution of organisms shows considerable variance both with respect to geographic location but also with respect to the ecological and taxonomic characteristics of the species involved. Usually proximal factors such as habitat destruction or modification are easily identified as the responsible cause of local losses of biodiversity, and as such local reductions in biodiversity are most frequently observed across the taxonomic spectrum. Like most terrestrial species amphibians are threatened foremost by habitat destruction (SALA et al., 2000). However, in the past few decades amphibian populations have been threatened by other incompletely understood factors in areas that are perceived to be intact from human disturbance (WALDMAN & TOCHER, 1998; ALFORD & RICHARDS, 1999; CAREY et al., 2001). The suspicion that amphibians are suffering from an unprecedented and abnormally high rate of decline even in protected areas was first voiced at the First World Herpetology Conference in September of 1989, in Canterbury, England (BARINAGA, 1990), although it is clear that widespread concern existed long before this (BURY, 1999). The seriousness with which the scientific community recognised this problem was reflected in the rapid organisation of a NRC sponsored workshop in February of 1990 in Irvine USA, and in light of the perturbing reports presented (BLAUSTEIN & WAKE, 1990; WAKE, 1991), the establishment of a special task force on declining amphibian populations (DAPTF), allied with the Species Survival Commission of the IUCN. During the subsequent decade neither the scale of the problem nor the widespread concern expressed in both the scientific (WAKE, 1998), and public (BLAUSTEIN & WAKE, 1995; MORELL, 2001) community has seen any abatement. In order to tackle any problem in ecology it is essential that one is aware of the present level of understanding of its scale, diagnostic characteristics, and methodologies appropriate to its resolution. This review complements previous similar efforts (e.g. WALDMAN & TOCHER, 1998; ALFORD & RICHARDS, 1999) by exploring many important advances in the last two years. Edward Wilson recently described conservation biology as the "intensive care ward of ecology" (WILSON, 2000), and as such a conservation biologist who lacks an up–to–date appreciation of their field is failing the prescription of this definition in inadvertently advocating inefficient, repetitive, or even counterproductive research. This review seeks to provide such a revision, dealing in turn with: 1. The ecological and human importance of amphibians in natural ecosystems; 2. Evidence for population declines and caveats in their interpretation; 3. The range of candidates which have been proposed to explain such declines; 4. Some challenges presently facing conservation biologists in resolving and preventing amphibian declines.

The importance of amphibians in ecological and human environments

A world–wide decline of amphibian populations could have a significant and detrimental impact on both natural ecosystems and human welfare. Amphibians are integral components of many ecosystems, often constituting the highest fraction of vertebrate biomass (BURTON & LIKENS, 1975; BEEBEE, 1996). Their conspicuous role is noted to be of particular importance in tropical forests, where in acting as both predator and prey species, they play a key role in trophic dynamics (TOFT, 1980; BLAUSTEIN et al., 1994c). Their high collective biomass, alongside their high digestion and production efficiencies (WOOLBRIGHT, 1991), go someway to explaining their potential importance in such "functions" as the maintenance ecosystem energetics and carbon flow (PEARMAN, 1997) —namely through the maintenance of arthropod abundance (GUYER, 1990), and the provision of a critical prey base for higher order predators, such as arachnids, snakes, and birds (GUYER, 1990; WOOLBRIGHT, 1991; DUELLMAN & TRUEB, 1994). In identifying the functional significance of amphibians its is clearly of relevance to understand whether species diversity per se plays a unique role over and above species *identity* —i.e. are a few specific and perhaps more abundant frog species sufficient to maintain the natural integrity and productivity of the ecosystem? In view of the limitations on the world's resources for the conservation of biodiversity, it would seem sensible to identify the functionally important amphibian species or "guilds" in order to prioritise concern and subsequent potential conservation action following a reported decline in number. However, such an approach could be very dangerous, as it is often extremely difficult if not impossible to identify the functional role or contribution of many species (CHAPIN et al., 2000). Some (limited) empirical evidence exists to offer an explicit justification for the functional importance of species richness per se (LOREAU et al., 2001). However, a more convincing argument is that differences in the environmental tolerances of many species that may be functionally analogous to dominant species can provide critical insurance or resilience for the system in the face of climate change or altered disturbance patterns (WALKER, 1995; WALKER et al., 1999; NAEEM, 1998). In light of our ignorance of the ecology of most amphibians, and the growing domination of natural systems by human activities (VITOUSEK et al., 1997), it seems that an attitude of concern towards all populations that could be potentially at risk is prudent, if not essential. It is important to stress that concerns about the functional importance of species in no way detracts from the importance of other values humans can attach to biodiversity —including cultural, existence and intrinsic values (DOLMAN, 2000).

The second most recognised importance of amphibians is their potential role as indicators of global environmental health and resilience (BLAUSTEIN & WAKE, 1990; BARINAGA, 1990; DIAMOND, 1996). They inhabit both aquatic and terrestrial habitats, and are thus exposed to aquatic and terrestrial pollutants —to which they are particularly sensitive due to their highly permeable skin (DUELLMAN & TRUEB, 1994). Furthermore many amphibians interact with a large range of other species in the local environment during their lifetime. For example most anurans (Amphibia, Anura) play dual roles as both herbivores during larval stages and carnivores as adults, making them potentially good indicators of changes in both floristic and faunal community composition —possibly induced through environmental stress. As BARINAGA (1990) states, the fact that amphibians as a group have remained largely unchanged since the era of the dinosaurs, highlights the potentially disastrous consequences for humans and other species if their suspected demise continues unabated. Finally, from a purely anthropocentric perspective amphibians represent a storehouse of pharmaceutical products waiting to be exploited fully (BLAUSTEIN & WAKE, 1995). Some compounds already extracted are presently being used as painkillers and in the treatment of traumas such as burns and heart attacks, whilst many more undoubtedly await discovery.

Evidence for global amphibian declines

Although serious recognition of the potential problem of declining amphibians was not afforded until the last decade, individual anecdotal reports of population declines have been known since the late 18th century (BURY, 1999). However, it was during the 1980's and early 1990's that the observations of more dramatic and scientifically credible declines were made. Such declines include notable individual examples such as the Golden toad (*Bufo periglenes*) and Harlequin frog (*Atelopus varius*) (CRUMP et al., 1992; POUNDS & CRUMP, 1994), the Cascades frog (*Rana cascadae*) (FELLERS & DROST, 1993), and the Yellow and Red–legged frogs (*Rana muscosa* and *Rana aurora*) (BLAUSTEIN & WAKE, 1990). All of these declines have occurred in areas considered largely intact from human interference, which explains their common citation in justifying concern for the viability of other seemingly well protected amphibian populations. Further evidence for the apparent vulnerability of the class Amphibia as a whole comes from reports of population declines across whole communities of amphibians at the regional level, also in relatively pristine areas; the Central Valley of California (DROST & FELLERS, 1996; FISHER & SCHAFFER, 1996), the montane forests of Eastern Australia (LAURANCE et al., 1996), and the Monteverde cloud forest of Costa Rica (LIPS, 1998, 1999). It is hard to draw global conclusions from such varied examples, although a number of commonly occurring factors or attributes can be identified (LIPS, 1998; ALFORD & RICHARDS, 1999; CAREY, 2000; CAREY et al., 2001; MIDDLETON et al., 2001). These factors include:

1. Wide geographic spread in presence of declines, accompanied by significant spatial variability in their extent.
2. Significant inter–specific variability in levels of vulnerability to agents of population decline, with many species that are sympatric to others which are threatened or endangered exhibiting no change in population size or dynamics.
3. Many species extinctions or extirpations have occurred at high altitude sites (> 500 m a.s.l.).
4. Many declines have been rapid with population reductions of between 50 and 100% occurring in 1–3 years.
5. Infectious diseases, commonly fungal pathogens have been most frequently identified as the direct cause of decline, whilst a number of indirect environmental factors are thought to play key contributing roles.

Due to the heavily skewed distribution of amphibian biologists towards North America, Europe, and Australia it is possible that a number of these common attributes are at least partly artefacts of research bias. To remove some of this bias and view the declining amphibian problem from a more global perspective, it is necessary to collate information from across many sites and many species.

In attempting to draw global conclusions or patterns about a particular ecological phenomenon (such as population declines) from across different studies, one is commonly faced with two main problems; the inaccessibility of many research reports, and the extreme variability in monitoring techniques used —from the purely anecdotal to the scientifically rigorous. A number of recent reviews have attempted such a difficult collaboration in order to view the plight of amphibians from the widest possible perspective —both at spatial and temporal scales, the two most noteworthy of which are those of ALFORD & RICHARDS (1999) and HOULAHAN et al. (2000). ALFORD & RICHARDS (1999) considered 85 time series of amphibian populations spanning the period between 1951–1997, and following regression analysis concluded that more populations correlated negatively against time than would be expected under their null hypotheses of "normal" population fluctuations, with 67% of relationships being negative. However, they found no evidence that the proportion of populations decreasing changed over time —in other words there was no observation of an *increase* in the number of susceptible and affected populations which is perhaps what one would expect if the proposed agents of decline where becoming more prevalent or intense. Although continued exposure to stimulants of population declines may produce a residual number of populations and species which show heightened resilience, or adaptive shifts in geographic range to habitat refugia, it seems unlikely that such evolutionary or behavioural changes could occur at comparable speeds to many of the proposed agents of decline which are detailed above. As the authors themselves admit, it is impossible to draw firm conclusions about the global status of amphibian populations due to variance in the size of data sets, their methodological origin, and the inter–specific variance in population dynamics which renders their null model far from optimal for all amphibian species. HOULAHAN et al. (2000) made by far the most exhaustive attempt to date in collating data from 936 populations of 157 species from 6 continents, for studies of between 2 and 31 years duration. Although their results identify marked temporal variation in the speed of the decline, and spatial variation as to its extent, a definite negative relationship is clearly evident, adding perhaps the first real quantitative "weight" to the declining amphibian phenomenon. Criticism has recently been raised as to the validity of the statistical averaging methods used by Houlahan and colleagues (ALFORD et al., 2001; but see HOULAHAN et al., 2001), although re–analysis under the alterative methodology (ALFORD et al., 2001) still concluded that an overall population decline existed and disagreed only in the shape of the relationship —with the more recent interpretation identifying a increase in the rate of declines in the last decade. A number of serious inade–quacies exist in the study by HOULAHAN et al. (2000) —for example it includes only four studies from Latin America, despite the fact that this continent hosts about half the worlds amphibian species (DUELLMAN, 1999). However, a recent synthesis of published and unpublished (> 95% of the total) work from both Central and South America adds strength to the evidence for a global decline (YOUNG et al., 2001). In summarising 118 monitoring projects, population declines were found to be widespread, occurring in 13 countries, with 40 cases of recent extinction or regional extirpation affecting 30 genera and nine families of amphibians.

Candidates for amphibian decline

Physical habitat modification

The destruction or direct modification of ecological systems is widely held as the primary cause for the observed loss of much of the earth's biological diversity (SALA et al., 2000), and the loss of amphibian species together with reductions in their population size bear no exception (ALFORD & RICHARDS, 1999). In an area directly under human influence, habitat modification can usually be isolated as the cause of an observed population decline, although the actual mechanism is highly variable and can often be obscure. In addition to complete habitat destruction, a number of more subtle environmental modifications can bear particular consequences for amphibians:

1. Fragmentation of habitat. This can have two main deleterious effects. Firstly in the effect on population demographics through the distribution of regional and metapopulation processes (SJOGREN, 1991; SJÖGREN–GULVE, 1994; MARSH & TRENHAM, 2000). Both empirical (SJOGREN, 1991) and theoretical (HALLEY et al., 1996) evidence suggests that the probability of local population extinction increases with increased distance between populations —largely due to the fact that many amphibian species are thought to be highly philopatric (SJOGREN, 1991; WALDMAN & TOCHER, 1998; SCRIBNER et al., 2001). Secondly, the disruption of dispersal mechanisms can produce deleterious effects at the level of genes (e.g. HITCHINGS & BEEBEE, 1998; SEPPA & LAURILA, 1999). The genetic consequences of small and declining populations has been adequately reviewed elsewhere (e.g. FRANKHAM, 1995; HEDRICK & KALINOWSKI, 2000), although with relevance to amphibians a recent study has identified a possible relationship between reduced genetic diversity in Southern Leopard frogs (*Rana sphenocephala*) following restricted migration, and tolerance to insecticide, with possible implications for recent population declines in the western United States (BRIDGES & SEMLITSCH, 2001). In developed countries the deleterious effects of habitat fragmentation on amphibian populations is increasingly apparent with the increase in the number of roads (HITCHINGS & BEEBEE, 1998), a type of habitat modification which has also recently been acknowledged to contribute significantly to population declines through direct mortality (HELS & BUCHWALD, 2001).
2. Forest management operations which can result in a change of microclimate, soil moisture and habitat complexity. Of particular importance is land drainage for reservoirs and other developments, frequently resulting in a removal of breeding sites and fragmentation of populations.
3. The alteration of the biotic environment through the introduction of exotic predators and pathogens (see below).

More obscure and perhaps counter–intuitive examples of the deleterious impacts of habitat modification exist. For example, in the case of the Natterjack toad (*Bufo calamita*) in Britain, where the *removal* of modification (grazing) on shrub heathland led to the encroachment of tall vegetation, thus allowing the entrance of the more successful competitor *Bufo bufo* —the Common toad (BEEBEE, 1977). Such examples serve to emphasise the fragility of many ecological systems to what we may perceive to be minimal human intervention. However, habitat destruction and modification although of prime concern, are usually easily to isolate, and therefore if possible to rectify. It is the proposal that amphibian declines in largely pristine areas of the world are the result of more indirect and complex reasons that is cause for exceptional concern (WAKE, 1998; WALDMAN & TOCHER, 1998; CAREY, 2000; CAREY et al., 2001).

Ultraviolet radiation

Depletion of the stratospheric ozone layer and the observed resultant increases in ultraviolet B (UV–B) radiation at the Earth's surface (KERR & MCELROY, 1993), has prompted interest as to the possible relationship between the influence of UV–B on amphibian survival and population declines. A number of experimental manipulations of enhanced UV–B have implicated its potential contribution to amphibian declines —e.g. through evidence of; decreased hatching success and enhanced embryonic mortality (BLAUSTEIN et al., 1994a; OVASKA et al., 1997; ANZALONE et al., 1998), decreased larval survival (OVASKA et al., 1997), and negative effects on embryo and larval development (CRUMP et al., 1999). However, all of these studies report significant variation between species as to both the level and type (i.e. embryo, larvae, etc.) of susceptibility. Some resolution of this discrepancy has been proposed through inter–specific variation in the levels of the DNA repair enzyme, photolyase (BLAUSTEIN et al., 1994a; BLAUSTEIN et al., 1996). Indeed a correlation can be made between a number of species whose populations are showing a decline in number (e.g. *Bufo boreas* and *Rana cascade*) and which also show significantly low levels of photolyase activity. This can be compared against species such as the Pacific treefrog *Hyla regilla* which has characteristically high levels of the enzyme and exhibits relative stability in number (BLAUSTEIN et al., 1994a). However, this relationship is clearly not of global relevance as the Red–legged frog *Rana aurora*, has a relatively high level of photolyase but yet has suffered severe depletions in number (BLAUSTEIN & WAKE, 1990; BLAUSTEIN et al., 1996). A further quite equivocal result is seen in the declining Australian species, the Green and Golden bellfrog *Litoria aurea*, which although has a lower photolyase activity than two sympatric and non–declining species, the Bleating treefrog *L. dentata*, and Peron's treefrog *L. peroni*, shows no significant difference against them with respect to hatching success under enhanced UV–B exposure (VAN DER MORTEL et al., 1998) —thus pointing to the importance of other, independent agents of decline. Recent work by PAHKALA et al. (2001) suggests that there may be time–lags in the response of amphibians to UV–B radiation, and that whilst evidence of direct effects of enhanced radiation on early embryonic stages is rarely convincing, carry–over effects on later larval development and metamorphosis can be very important.

A number of other factors serve to shed doubt on the responsibility of UV–B in global declines. Most of the field experimental studies cited above have been conducted in shallow, clear high altitude ponds, largely in high latitude locations such as North America and South–eastern Australia. UV–B radiation is largely absorbed in the first few centimetres of the water column (NAGLE & HOFER, 1997; ADAMS et al., 2001), and the depth of penetration is negatively correlated against the dissolved organic carbon content (CRUMP et al., 1999) —factors which suggest that UV–B radiation is unlikely to be a problem in bottom laying species, or in forest (and especially tropical) species. An initial lack of evidence for significant increases in UV–B at tropical or sub–tropical latitudes since the mid–1970's (MADRONICH & GRUJII, 1993) further diminished its perceived importance in the decline of tropical amphibian populations (e.g. CRUMP et al., 1992; LIPS, 1998). However, recent remote sensing analysis (MIDDLETON et al., 2001) has identified increases in both annual and daily levels of UV–B exposure (average and maximum) between 1978–1998 at Central and South American sites where amphibian population declines have been recorded (e.g. POUNDS & CRUMP, 1994; LIPS, 1998, 1999; POUNDS et al., 1999). Further recent work by ADAMS et al. (2001) provides more correlative evidence for the importance of UV–B radiation in determining amphibian distribution, in identifying the importance of levels of UV–B exposure in determining the spatial pattern of *R. cascadae* breeding sites in Olympic National Park, USA. Although such studies report only correlative rather then causative evidence, they identify the value and urgency for further field studies on the effects of UV–B radiation on amphibian populations.

Although some of the above evidence is convincing in showing an effect of high UV–B radiation on embryo mortality and larval survival, the ecological significance of such a phenomenon at the population level is far from clear, and equally difficult to assess (ALFORD & RICHARDS, 1999). For example there may be density dependent compensation effects, through the enhanced fitness of competing individuals that survive high levels of UV–B exposure. The potential indirect effects of enhanced UV–B on amphibian dynamics, such as changes in water chemistry and food supplies, are even less well known (ALFORD & RICHARDS, 1999). Finally it is likely that unimodal experiments manipulating only levels of UV–B are inadequate, and that the crucial agent of decline could be in the interaction of UV–B with other key environmental stresses (see below).

Acidification and other chemical pollutants

The existence of amphibian extinctions and population declines in what are otherwise seen to be some of the most pristine environments on Earth has led to the frequent suggestion that atmospheric pollutants may act as indirect agents of decline (LIPS, 1998; CAREY et al., 2001). Such pollutants could originate from neighbouring and foreign agricultural depositions, as well as from factory emissions of industrialised nations, and are able to travel vast distances and persist for considerable periods of time. Recent analysis of remote sensing data in Puerto Rico has shown spatial correlations between urban and agricultural pollutants and amphibian population declines (STALLARD, 2001).

One of the most acknowledged remote impacts of human activity is increased acidity of rainfall, a phenomenon of great potential importance in light of the importance of the annual water regime to amphibians. Increased acidity of ground and pond water is suspected to have both lethal and sub–lethal effects on amphibian populations through a number of factors; enhanced embryo and larval mortality, reduced egg and larval growth, reduced reproductive output, delayed hatching times, reduced adult body size, alterations in geographic distribution, and alterations in predator–prey ratios through indirect effects on plant growth and pH sensitive competitors and predators (FREDA & DUNSON, 1986; WALDMAN & TOCHER, 1998; ALFORD & RICHARDS, 1999). Some field and laboratory work has provided evidence for such detrimental effects, for example; reduced ion exchange and larval growth in the Wood frog *Rana sylvatica* (FREDA & DUNSON, 1986), and a significant reduction in range size of Natterjack toad *Bufo calamita* following long term acidification of many British ponds (BEEBEE et al., 1990).

Observational and experimental evidence also exists for the potential role of a wide range of industrial and agricultural pollutants in precipitating amphibian population declines. Contamination from a number of major agricultural pollutants (pesticides, herbicides and fertilisers) has been correlated with observed spatial patterns of decline in a number of amphibian species (RUSSELL et al., 1995; SPARLING et al., 2001; STALLARD, 2001), with early embryonic stages being particularly vulnerable (CAREY & BRYANT, 1995). This correlative evidence for the negative impact of agricultural practices on many amphibian populations is strongly supported by a number of experimental studies. Negative effects of nitrate fertiliser including ammonium nitrate, one of the most commonly applied chemicals, have been observed on the larval mortality and development, feeding behaviour, growth rates and physical abnormalities of a number of amphibian species —including many pond and stream breeders (HECNAR, 1995; OLDHAM et al., 1997; MARCO et al., 1999; MARCO & BLAUSTEIN, 1999), and treefrogs and forest–dwelling species (SCHUYTEMA & NEBEKER, 1999; MARCO et al., 2001). Responses have been observed to be both dose–dependent and cumulative over time (MARCO et al., 1999; MARCO et al., 2001), and although there is clearly significant interspecifc variation in patterns of susceptibility (HECNAR, 1995; MARCO et al., 1999; MARCO et al., 2001), levels of fertiliser application observed to be sufficient to cause significant negative effects on individual survival and fitness are frequently no higher than officially recommend levels for field application (HECNAR, 1995; OLDHAM et al., 1997) or even for drinking water (MARCO et al., 1999).

In addition to the effects of fertiliser a number of other chemical pollutants have been identified as being of potential importance in explaining observed patterns of amphibian population decline. In the Sierra Mountains of California, a region exhibiting a high level of amphibian population declines across several species during the last 10–15 years, correlative evidence suggests the importance of pesticide contamination from the heavily agricultural downwind San Joaquin Valley (SPARLING et al., 2001). Furthermore a recent experimental study identified negative effects of ambient concentrations of atrazine —a common pesticide— on the length and weight of *H. versicolor* larvae at metamorphosis (DIANA et al., 2000), although another more recent experimental study also concerned with testing the effects of atrazine reported more equivocal results for other species, with no observed effect on either hatching success or post hatching larval morality (ALLRAN & KARASOV, 2001). The fact that such studies rarely consider longer–term or secondary effects, or even in this case report analogous measures of fitness and reproductive success, makes it difficult to make generic conclusions of the overall significance of such contaminants at the population level. Finally a number of other non–agricultural chemical pollutants have been isolated as being of potential importance in explaining population declines, including, namley: 1. Negative effects of endocrine disrupting chemicals on reproductive success, and larval development (FOX, 2001), and 2. An increasing number of experimental studies reporting negative effects of polychlorinated biphenyls (PCBs) on the larval development and feeding rates for a number of species (GUTLEB et al., 2000; GLENNEMEIER & DENVER, 2001), although the magnitude of the effect depends critically on the length of the observation period (GUTLEB et al., 1999). Alongside cases of direct mortality (CAREY & BRYANT, 1995), empirical evidence has also identified important indirect influences of agricultural pollution on populations, e.g. through altered recruitment and predator response behaviours (COOKE, 1971; BRIDGES & SEMLITSCH, 2000). The marked interspecific variation of amphibians in their susceptibility to pesticides alongside geographic variation in their deposition is highlighted as a potential explanation for the heterogeneous nature of observed declines at both taxonomic and geographic scales (BRIDGES & SEMLITSCH, 2000).

Although it is clear from the above examples that an increase in environmental acidity or other pollutants can have a negative effect on some amphibian populations, the actual physiological mechanisms remain unclear (CAREY et al., 1999). One recent experimental study provides evidence that a commonly used insecticide, endosulfan, causes impairment of the pheromonal system in Red-spotted newts (*Notophthalmus viridescens*) at very low exposure–concentrations (PARK et al., 2001). This provides one potential mechanism which could help explain reduced mating success —through the disruption of mate choice. Furthermore, and perhaps most crucially, it is once again not evident what the overall consequences of such environmental changes at the population level would be, and there is very little data implicating contaminants on the recent catastrophic population declines (ALFORD & RICHARDS, 1999). However, as in the case for enhanced UV–B levels, it is possible that the critical role of environmental contamination in population declines comes from its interaction with other causative agents (CAREY et al., 2001; STALLARD, 2001; see below).

Predation by exotics or introduced species

Biotic interactions amongst and between species can play a critical role in determining their relative local abundance, distribution and population dynamics (RICKELFS & SCHLUTER, 1993; HUSTON, 1994). Although perhaps more appropriately considered as human induced habitat modification, the introduction of exotic predators to amphibian environments has been implicated as the factor responsible for many population declines, including the collapse of whole communities (FELLERS & DROST, 1993; FISHER & SCHAFFER, 1996; HECNAR & M'CLOSKEY, 1996a). Two recent studies have analysed the spatial distribution and abundance of amphibian species against that of introduced fish stocks in mountain and alpine lakes at the landscape scale. KNAPP et al. (2001) found that the Yellow–legged frog (*Rana mucosa*) exhibited dramatic reductions in both distribution and abundance in lakes which had received artificial stocks of predatory fish when compared to those that remained naturally fishless. Also PILLIOD & PETERSON (2001) found lower abundance of both the Long–toed salamander (*Ambystoma macrodactylum*) and the Columbia Spotted frog (*Rana luteiventris*) in alpine lakes that had received artificial fish stocks, and predicted that the range restriction of amphibians to remnant shallow lakes unsuitable for fishing, in addition to severely inhibited migration patterns, could lead to the extirpation of amphibians from entire landscapes —including from sites that remained in a natural–fishless condition. Finally, although the majority of studies reporting such clear negative effects of exotic predators on amphibian populations are from temperate regions, the phenomenon is also prevalent in the tropics —for example in South America where some 30% of the amphibians are classified by the IUCN as threatened by alien invaders (RODRIGUEZ, 2001).

Aside from such convincing but co–incidental evidence, experimental manipulations of predator and amphibian distributions provide firm support as to their devastating effect on amphibian populations. Powerful examples include: 1. The significant reduction in survival of the endangered Red–legged frog (*Rana aurora*) in California, following the introduction of the two larval predators —Mosquitofish (*Gambusia affinis*), and Bullfrogs (*Rana catesbeiana*) (LAWLER et al., 1999); 2. The severe impact of both Mosquitofish, and a crayfish (*Procambarus clarki*) on the eggs and larvae of the Californian newt, *Taricha torosa* (GAMRADT & KATS, 1996); and 3. Significantly enhanced predation pressure on Spotted treefrog larvae (*Litoria spenceri*) from south–east Australia when exposed to two alien trout species —the Brown trout *Salmo trutta*, and the Rainbow trout *Onchorhynchus mykiss*— as opposed to when in the presence of the native mountain fish (GILLESPIE, 2001). Although the introduction of exotic predators such as the above is considered to be a prime cause of population decline across North America (FISHER & SCHAFFER, 1996), their role is comparatively easy to identify, and as such seems unlikely to be a global factor, especially in largely pristine tropical areas.

Disease

The remote nature of many amphibian population declines, in addition to the frequent observations of larval and adult growth abnormalities, has led to the perhaps unsurprising and widespread implication of disease (CAREY, 1993, 2000). In particular the wave–like pattern of population decline across the range of many threatened species seem to implicate the role of a biotically induced agent —as observed in both the Atlantic forest of Brazil (HEYER et al., 1988), the Eastern montane forests of Australia (LAURANCE et al., 1996), and the forests of Panama and Costa Rica (LIPS, 1998, 1999). Perhaps the most confident proposition as to the culpability of disease in precipitating the collapse of an entire amphibian community is in Australia, where 14 endemic species have decreased by more than 90% in the last 15 years (LAURANCE et al., 1996). The authors note the extreme virulence of the disease as being evidence of its potentially exotic nature, and report histological changes in infected tissue of diseased individuals as being consistent with viral infection. LIPS (1998, 1999) identified a fungal infection found on dead individuals as being the most likely cause of population decline in the forests of Panama, between 1993 and 1997. Furthermore she notes that the similarity in timing of declines, regional climatic factors, frog phylogenies, and clinical symptoms, as being suggestive of the same causal factor being responsible for catastrophic amphibian declines noted in nearby Costa Rica (POUNDS & CRUMP, 1994; LIPS, 1998). Support for this theory comes from BERGER et al. (1998) who identified the same chytridomycete (Chytridiomycota, Chytridiales) fungus on dead anurans from forests of both Central America, and also of Queensland, Australia —adding some further strength to the argument of LAURANCE et al. (1996), although the disease origin differs. The same fungus has been more recently identified to the species level (LONGORE et al., 1999), and an increasing number of reports have confirmed its presence in all of the six continents that are inhabited by amphibians (DASZAK et al., 1999; CAREY, 2000; FELLERS et al., 2001). A recent report of the expanding geographic distribution of this species, documents its arrival in Europe where it is implicated as being responsible for the disappearance of the Common Midwife toad (*Alytes obstretricans*) from more than 85% of its breeding sites in an a protected area in central Spain (BOSCH et al., 2001). The relatively sudden observation of catastrophic declines in such disparate areas of the world is suggestive of either a recent increase in virulence, or decrease in amphibian immuno–activity, perhaps due to a key interaction with a changing global climate —although the potential mechanisms behind any such interaction are poorly understood (CAREY, 2000; see below). In addition to a decrease in amphibian immuno–activity or an increase in pathogenic virulence, an increase in the level of pathogenic activity could be affecting amphibian populations through changes in the food supply or competitive ability of species (CAREY et al., 2001). Further convincing evidence as to the role of disease in population declines comes from the Pacific north–west of America, where a different species of fungus, *Saprolegina ferax* (a globally distributed fish pathogen), has been implicated as responsible for declines in the Boreal toad *Bufo boreas*, through increased egg mortality (BLAUSTEIN et al., 1994b; KIESECKER & BLAUSTEIN, 1997).

There is clearly enough convincing evidence to support the two facts that disease agents can be highly detrimental to amphibian fitness and survival, and that furthermore, evidence of them can be found in many areas where catastrophic declines have occurred. However, as for most if not all agents of decline, it is very difficult to attribute what contribution they make to the overall population dynamics of declining amphibians. Strong circumstantial evidence exists as to the role of disease in mass declines such as that observed in Australia (LAURANCE et al., 1996). However, when experimental proof is difficult to obtain, it is easy to argue for competing hypotheses which may produce equally parsimonious statistical comparisons of a potential agent of decline against the spatial distribution of population declines (ALFORD & RICHARDS, 1997; HERO & GILLESPIE, 1997). Despite the ubiquitous presence of a large range of competing hypotheses to explain any one population decline, it is crucial to the progress of science that plausible hypotheses are voiced, if only for their heuristic value in targeting future research and formulating further, refined hypotheses (LAURANCE et al., 1997). As noted below, in the case of disease it is even more likely than in other agents of decline, that interactions of disease vectors with other environmental factors plays a crucial role in determining their impact on amphibian populations (CAREY, 2000).

Climate and weather

As discussed already, amphibians are particularly sensitive to changes in their external environment, both due to their biphasic lifestyle in existing as both aquatic larvae and terrestrial adults, and due to their highly permeable skins. Perhaps the most important component of the abiotic environment to both amphibian fitness and population dynamics is the maintenance of a stable and predictable water–temperature regime (POUNDS & CRUMP, 1994; LIPS, 1998). Many amphibians are subject to both water and temperature sensitive physiological limitations on locomotive and reproductive activities. As a consequence of this the balancing of evaporative water loss against direct absorption through the skin is a critical functional attribute, as has been observed in the Marine toad *Bufo marinus* (POUNDS & CRUMP, 1994). Aside from detrimental effects of disrupting this balance (i.e. through desiccation), at the individual level, the water regime in particular can play a vital role in many other aspects of amphibian ecology, including: 1. Determination of phenological patterns of reproductive activity (WELLS, 1977; AICHINGER, 1987; GASCON, 1991); 2. Determination of the spatial distribution of community assemblages (INGLER & VORIS, 1993); and 3. In the provision of suitable breeding sites and conditions (e.g. PYBURN, 1970).

The suspected role of alterations in the annual water regime of amphibians in global population declines, follows increasing recognition of gradual changes in the global climate due to human activities. There has been a discernible human influence on world temperatures during the last century, with average temperatures projected to increase by between 1.4 and 5.8°C by 2,100, with considerably greater regional variation (IPCC, 2001). One consequence of this that is relevant here is a projected increase in activity of the tropical hydrological cycle, with the prediction of erratic and frequently severe weather patterns (GRAHAM, 1995; IPCC, 2001). The effect of climatic change on ecological systems has been observed at all levels, from population and life history alterations, to shifts in geographic range, and subsequent changes in community composition resulting in disruption of ecosystem structure and function (HUGHES, 2000; MCCARTY, 2001). It is therefore perhaps unsurprising that many changes in the population dynamics of amphibians, organisms which are so closely coupled with their environment, have been attributed to changing climatic and weather patterns.

A number of notable reports documenting multiple amphibian declines have implicated the potential role of synchronously observed climatic extremes, and in particular, periods of reduced or abnormally distributed rainfall (CORN & FOGELMAN, 1984; HEYER et al., 1988; BERVEN, 1990; CRUMP et al., 1992; FELLERS & DROST, 1993; STEWART, 1995). Owing to the sensitive response of amphibian breeding cycles it is easily conceivable that a simple shift in the commencement of the wet season in seasonal environments could either trigger premature spawning and subsequent desiccation of eggs, or if early rains are abnormally intense, the flooding of breeding ponds, and an equally disastrous loss of an entire breeding attempt (WELLS, 1977; CRUMP et al., 1992). POUNDS & CRUMP (1994) executed a detailed analysis of the infamous declines in number of Golden toad and Harlequin frog populations in the Monteverde cloud forests of Costa Rica, and concluded that coincidentally low periods of rainfall during phases of population decline were at least in part responsible. It was clear that depletions in number of the Harlequin frog populations (for which demographic data was available) matched climatic records of reduced rainfall during both the 1982–1983 and 1986–1987 El Niño induced drought periods. The potential role of long–term warming and increased intensity of precipitation patterns, when coupled with intense warm periods of El Niño —Southern oscillation cycles, has been noted to be of severe consequence for many biological communities (MCCARTY, 2001), and in light of the above, particularly so for amphibians (POUNDS, 2001). With reference to the example of CRUMP et al. (1992), it has been recently calculated that the effect of El Niño events in Central America is expected to be through severe drought periods rather than increased rainfall (HOLMGREN et al., 2001). Although the juxtaposition of the timing and extent of population declines in Harlequin frogs with the timing and intensity of periods of drought suggests that they are causally linked, it is much more difficult to identify either the environmental variable that is of crucial ecological significance, and further, the exact mechanism by which that change acts to reduce amphibian populations. POUNDS et al. (1999) in a further analysis of the situation in the Monteverde cloud forests, isolate a perhaps rather unintuitive climatic variable as being closely correlated with not only amphibian declines but also with demographic changes in many other taxa, including birds and reptiles. The climatic variable is that of decreasing "dry season mist frequency", which suggests that the important water–related mechanism affecting amphibian populations is likely to be an increase in desiccating conditions affecting egg hatching in non–aquatic species, alongside individual survival, rather than changes in reproductive phenology and breeding behaviour. Human induced climate change can be implicated here, as dry season mist frequency is negatively correlated with sea surface temperatures of the equatorial Pacific, which have increased dramatically since the mid–1970's (STILL et al., 1999). Such examples highlight the importance of studying the environment of a species under threat so as to identify the ecologically important variables, and allow an assessment of future population stability through the parameterisation of predictive ecological models —both verbal and mathematical (MCCARTY, 2001).

Aside from the above, a number of other mechanisms have been suggested to explain the potential role of climatic change in precipitating amphibian population declines. A shift in rainfall patterns could result in a change in availability of breeding sites, a reduction in which could increase levels of competition and predation, and even vulnerability to disease, resulting in a reduced overall reproductive output for that year (DONNELLY & CRUMP 1998). An increased frequency of drought periods, coupled with increased temperatures, have also been identified as having potentially severe effects on leaf litter species which don't congregate to breed, through alteration of their arthropod prey base and an increase in soil desiccation (DONNELLY & CRUMP, 1998). Finally, there is evidence of changes in spring spawning times of amphibian species in England, showing that amphibian reproductive cycles are highly sensitive to climate warming, with possible long–term consequences for population dynamics through alterations of biotic interactions (BEEBEE, 1995). However, a recent study of a number of other temperate–zone anuran populations suggests that this sensitivity of breeding patterns to changes in temperature exhibits marked inter–specific differences, although sufficient detailed monitoring information necessary to confidently describe such patterns of susceptibility is notably lacking (BLAUSTEIN et al., 2001).

However, as with all the potential agents of amphibian decline listed above, changes in climatic patterns cannot always be found to explain observed declines (LAURANCE, 1996; ALEXANDER & EISCHEID, 2001). Furthermore, due to the close coupling of amphibian population dynamics to their ecological environments, it is likely that any climatic change would affect amphibians through interactions with other biotic and abiotic factors, to which both the external climate and amphibians themselves are closely linked.

Interaction effects amongst environmental factors

Frequently, separation of the almost myriad of current hypotheses for amphibian declines in any one situation can be almost impossible, although some recent advances have been made using GIS technology to compare spatial patterns of decline with spatial patterns of potentially causal agents (Davidson et al., 2001). However, as noted above, most of the studies to date that have considered a single causal mechanism behind amphibian declines have invoked a critical interaction between multiple factors (Alford & Richards, 1999; Carey et al., 2001; Middleton et al., 2001). Such acceptance means that despite the urgency of explaining observed declines, it is important to realise that interacting suites of environmental change could produce complex effects that are often difficult or even inappropriate to isolate (Adams, 1999).

A number of recent experimental and observational studies offer support to the importance of interaction and synergistic effects between different hypothetical agents of decline. Increased UV–B exposure has been shown to increase the susceptibility of some amphibian species to disease (Kiesecker & Blaustein, 1995, 1997). Furthermore, an increase in UV–B can act synergistically with reduced pH levels to reduce embryo survival, when each factor alone is shown to have no significant effect (Long et al., 1995). Normally harmless diseases may increase their effective virulence under increased environmental pollution by contaminants such as pesticides (Carey & Bryant, 1995; Bridges & Semlitsch, 2000), and even different diseases themselves can be seen to act in concert in order to produce a detrimental effect (Cunningham et al., 1996). Temperature and water pH have been shown to interact to increase the detrimental effect of pathogenic fungi on reproductive success and survival in amphibians (Beattie et al., 1991; Banks & Beebee, 1988). An interaction between a changing environment and either the virulence and distribution of a pathogen or the immuno–activity of amphibians may not be sufficient to increase mortality directly. However, through differential responses of both different amphibian species and predators it may significantly alter the competitive and predatory dynamics resulting in a shift in the species composition or abundance rank (Kiesecker & Blaustein, 1999). The presence of carbaryl pesticide has been shown to dramatically increase the level of predation stress felt by the Gray treefrog *Hyla versicolor* with mortality being found to be 2–4 times greater when individuals were subject to predatory cues in addition to the pesticide (Relyea & Mills, 2001). Another recent study on the interaction effects of carbaryl pesticide has identified complex interactions between chemical exposure, larval competition, predation and pond drying, with results differing between species —although interestingly higher tadpole survival was observed in high density (competition) treatments which were exposed to carbaryl than in low density or control environments (Boone & Semlitsch, 2002).

Although the mechanisms are not well understood (Carey, 2000; Carey et al., 2001), it is likely that global climate change can interact importantly with virtually all local environmental factors with respect to their effect on amphibian populations (Pounds, 2001). For example an increase in drought events and the subsequent loss of many ponds and breeding sites, could greatly exacerbate the effects of local predators (Drost & Fellers, 1996). Also in relation to drought stress a recent experimental study on *H. versicolor* has identified a negative effect on larval survivorship and mass at metamorphosis from the interaction between pond drying and susceptibility to infection from the digenetic trematode parasite *Telorchis* sp. (Kiesecker & Skelly, 2001). Furthermore, an increase in temperature can increase the volatility of potentially harmful chemical deposits, the aerial concentration of which may then be increased due to a reduced frequency of rainfall events (Pounds & Crump, 1994). Due to the sensitivity of many ecological systems to climatic change (McCarty, 2001), it is likely that alterations of key environmental variables such as rainfall patterns and temperature, have the effect of reducing or even removing an important constraint on the potential of many agents of decline, both with respect to their geographic distribution but also in their physiological or biotic effect (e.g. UV–B, pH, disease) (Pounds, 2001). Just how complex an effect such changes in climatic parameters can precipitate has been illustrated in a very recent study by Kiesecker et al. (2001). Their findings illustrate that climatic induced reductions in water depth at amphibian oviposition sites have caused a high level of mortality in embryos, by increasing their exposure to UV–B radiation, and consequently their vulnerability to infection by disease. The implication of this is that elevated sea surface temperatures in the tropical Pacific, which drive large scale climatic patterns, could be the precursor for many pathogen–mediated amphibian declines world–wide (Kiesecker et al., 2001). One common theme with respect to the implication of synergistic effects in amphibian population declines is that the direct or proximate *mechanism* which increases mortality is thought to frequently be disease following immosuppression (Carey, 1993, 2000).

It should be clear from the above discussion that observed amphibian population declines seem unlikely to be the result of a small number of independent global agents, but rather the complex interaction of local effects in the context of varying regional influences and global climatic change. In order to study the existence of such effects in natural populations, and thus elucidate the relative stability and integrity of such populations, well-planned programs of observation and experimentation are needed (Alford & Richards, 1999; Carey, 2000). Furthermore, in light of the importance of both abiotic but also biotic interactions, it is important to gain an understanding of the interactions of the populations under study with both other species (amphibians and other potential competitors and predators), and their physical environment. Finally in order to identify the existence of a real population decline with confidence, development of specific "null" hypotheses or models is needed to describe how amphibian populations behave in the absence of external pressures (ALFORD & RICHARDS, 1999; MARSH, 2001).

Monitoring of amphibian populations: directions and challenges

Biological considerations: observations of temporal and spatial variability in amphibian population dynamics

In studying the proposed phenomenon of global declining amphibian populations, there are perhaps three main questions in which uncertainty remains: 1. How to determine real declines from natural population fluctuations? 2. Whether human induced agents can be isolated as the potential cause of the decline? 3. Whether global agents are responsible for the majority of observed declines? In light a growing recognition of the important implications of the mounting extinction crisis (see above), we cannot afford to be either complacent or conservative in our approach towards answering such central questions. In view of this there is a desperate need for comprehensive monitoring studies on amphibian populations world–wide (BLAUSTEIN et al., 1994c; WAKE, 1998; YOUNG et al., 2001). As can be seen from recent compilations by ALFORD & RICHARDS (1999) and HOULAHAN et al. (2000), existing studies exhibit a notable disparity with respect to length, scope, and detail. In order to draw firm conclusions at both the local and global level, it is imperative that future studies build upon previous work, and where possible incorporate recent advances in our understanding of amphibian species and their population dynamics. It is therefore instructive here to draw attention to a number of considerations, both biological and methodological, which are central to planning amphibian–monitoring programs.

The detection of real population declines which are deserving of concern, from purely natural population fluctuations can pose a serious problem in monitoring programs. It is essential that we understand the natural levels of variability inherent in amphibian populations, so as not to invoke unnecessary conservation and management action —a result that could severely compromise support for conservation in other situations (PECHMANN et al., 1991). An understanding of the levels of variability inherent in population dynamics is central to calculating both the statistical power of a monitoring program (MARSH, 2001), and the level of extinction risk from stochastic events (LEIGH, 1981; ENGEN & SAETHER, 1998; MARSH, 2001). Furthermore, an appreciation of population variability is fundamental to understanding the processes that drive population fluctuations (SEMLITSCH et al., 1996).

There exist both temporal and spatial aspects of amphibian population dynamics that can serve to confound the attempts of many monitoring programs to elucidate real declines in number. A number of ecological variables have been proposed as predictors of variability in amphibian populations, including; habitat type (WILLIAMS & HERO, 1998, 2001), reproductive mode and density dependent processes (SEMLITSCH et al., 1996; ALFORD & RICHARDS, 1999; MARSH, 2001), rainfall, taxanomic family, and latitude (MARSH, 2001). Firstly, there is strong evidence of intraspecific density dependence in many amphibian populations (BERVEN, 1990; PECHMANN et al., 1991; MEYER et al., 1998; ALFORD & RICHARDS, 1999). Crucial life history factors that appear to be regulated by density dependence include larval survival, larval size and time to metamorphosis. In a highly heterogeneous environment such as a forest, variance in such factors could produce seemingly chaotic fluctuations in population size (TURNER, 1962; BERVEN, 1990; PECHMANN et al., 1991). In the wood frog (*Rana sylvatica*) BERVEN (1990) recorded variation in R_0 (the net population replacement rate) between 0.009–7.49 over only 7 years, and as monitoring programs are rarely longer than this (BLAUSTEIN et al., 1994c; ALFORD & RICHARDS, 1999) it is easy to see how a short term population decline may be interpreted with unwarranted concern. Secondly, it is possible that at the level of the population, density dependent effects following fluctuations in resource levels may override the effect of any density *independent* environmental stress factors that may act to reduce juvenile or adult survival. However, as the judgement of "natural" levels of stability in biological populations is exceedingly difficult to make (CONNELL & SOUSA, 1983), it is consequently difficult to identify the ecological significance of any such contribution to mortality or reduction in reproductive success to overall population dynamics, even though they may be non–trivial. Aside from density dependence, a second important consideration of the temporal dynamics of amphibians is in the fact that fluctuations in breeding aggregations may be much greater than fluctuations in total population size, due to intra–population variance in breeding behaviour (PECHMANN et al., 1991). This point is of particular relevance, as due to severe logistical constraints most censuses of amphibians and especially frogs and toads (Amphibia, Anura), are conducted on aggregations at breeding sites (ALFORD & RICHARDS, 1999; see below).

Aside from temporal considerations one must also take into account the spatial aspects of amphibian population dynamics in making any conclusions about population stability or integrity. It is becoming increasingly recognised that many amphibian populations often exist in a metapopulation structure, where regional processes affecting extinction and colonisation of habitat patches, play a dominant role in determining local species assemblage composition and population size (HANSKI & GILPIN, 1991; HECNAR & M'CLOSKEY, 1996b; ALFORD & RICHARDS, 1999; MARSH & TRENHAM, 2000). It is important to recognise that from the perspective of a monitoring program effective habitat "patches" which are subject to such regional influences can represent the breeding sites or transects under human surveillance, and with respect to the actual amphibian population are often not ecologically distinct. The importance of regional processes to the persistence of local populations means that local extinction can occur due to essentially stochastic factors that are unrelated to the local environmental (abiotic or biotic) quality (SJOGREN, 1991; MARSH, 2001). Local amphibian populations are predisposed to stochastic extinctions due to the susceptibility of a peak–breeding attempt to climatic conditions (i.e. droughts or floods), their relatively short life spans (MARSH & TRENHAM, 2000), and their philopatric behaviour (WALDMAN & TOCHER, 1998). However, the essential point is that although devastating reductions in population size may be observed at a particular monitoring site, at the regional spatial scale the species may be perfectly healthy, adding doubt to the extrapolation of many population censuses to conclusions about the viability of an entire species. In order to confidently assess the stability of an amphibian population, and attribute a reason to any observed decline, it is important that such spatial factors are considered (see below).

Methodological considerations: challenges and pre–requisites for effective amphibian population monitoring

The natural variability and complexity that is inherent in both temporal and spatial amphibian population dynamics has already been highlighted above. It is crucial to recognise that such factors introduce serious practical considerations and caveats in the construction, execution, and analysis of amphibian monitoring programs. A direct consequence of such natural levels of variability is that the failure to find a significant decline in number of a particular population may frequently not be due to a lack of real decline, but rather to a lack of statistical power (GIBBS, 1995; REED & BLAUSTEIN, 1995; HAYES & STEIDL, 1997; ALFORD & RICHARDS, 1999; MARSH, 2001). The statistical power of a test for a population decline can be defined as the probability of rejecting the null hypotheses of no decline given that the null hypothesis is false and the alternative hypothesis of a declining population is true. Calculation of power requires knowledge of a number of factors, namely the sample size, the desired alpha level for avoiding Type I errors, the natural variance in sample size, and the effect size (PETERMAN, 1990). The value of conducting a prospective power analysis (HAYES & STEIDL, 1997) is severely limited by the high level of uncertainty inherent in the last two factors: 1. The natural coefficient of variability in amphibian population size —in particular in the context of the specific monitoring approach being used; 2. The level of population decline (effect) which bears ecological significance for the future stability of an amphibian population. Uncertainty in these values produces an equal level of uncertainty in level of power calculated (GIBBS, 1995). Attempts should be made to calculate the confidence in intervals associated with estimates of power, and furthermore there may be considerable merit in using Bayesian approaches to estimate levels of uncertainty (HILBORN & MANGEL, 1997; WADE, 2000). It is suggested here that in light of the serious logistical and financial limitations imposed on many, if not most amphibian monitoring projects, the "guestimating" of such variables is a dangerous game as it may render void many otherwise valuable projects which are lacking in apparent statistical rigour (and crucially lacking in ability to expand the project's sample size to achieve a satisfactory level of power). Except in situations where the species under surveillance is well studied, it may be of greater ecological significance to take a comprehensive approach to monitoring which incorporates a number of key ecological, as well as methodological considerations. This will hopefully achieve an increased understanding of the environmental requirements and population dynamics of the specific focal species, and afford greater confidence in any data interpretation. This does not nullify the clear value of prospective power analysis, but rather suggests that there is a great deal of merit in carefully considered monitoring projects which do not yet hold the minimum level of information needed to make such a preliminary analysis worthwhile. Identified below are some of the considerations deemed central to amphibian population monitoring.

For reasons emphasised earlier the two main problems facing monitoring projects are the logistical constraints on their temporal and spatial focus. Clearly in order to elucidate real declines from stochastic fluctuations, a long time series is highly favourable, although as seen from recent literature reviews few studies are longer than five years, and even less are more than 10 (ALFORD & RICHARDS, 1999; HOULAHAN et al., 2000; YOUNG et al., 2001). It is important to note however that an increase in the length of the study period will undoubtedly increase the perceived level of variability in population size and distribution due to the incorporation of a greater range of environmental conditions (PECHMANN & WILBUR, 1994; MARSH, 2001). Secondly, in light of a commonly metapopulation structure and the critical role of processes such as emigration and colonisation in amphibian populations, a regional monitoring perspective is important in order to distinguish overall regional declines from local (and essentially stochastic) extinctions (Marsh & Trenham, 2000; Marsh, 2001). For most amphibians this requires an appreciation as to the importance of the spatial arrangement, and degree of isolation between different breeding sites. It is appropriate to note here that according to a recent review of techniques used to quantify amphibian populations, most attempts focus on direct or indirect (e.g. vocal calls, egg masses) counts at breeding sites (Alford & Richards, 1999) —utilising the fact that most species congregate *en masse* to breed (Beebee, 1996). It thought that the population dynamics of a species are determined primarily by recruitment processes occurring at breeding ponds, and that such a focus can accurately determine the cause of any local or regional decline (Marsh & Trenham, 2000). However, such an exclusive focus carries a number of caveats in data interpretation: 1. Variation in population size at breeding ponds can as well be due to variation in breeding behaviour as to actual variation in population number (Pechmann et al., 1991); 2. It is often impossible to clearly distinguish variation in population size from simply variation in the size of breeding aggregations —i.e. the degree of "openness" of the population (McArdle & Gaston, 1993). Both such measures represent useful information but it is important to note that they are not synonymous; 3. In terms of adult survival and distribution an exclusive focus on breeding sites ignores the potential importance of the intervening terrestrial habitat which may be of ecological significance (Marsh & Trenham, 2000). A final note with respect to natural variability in amphibian populations is interspecific or taxonomic variance. As emphasised earlier different species exhibit different levels of susceptibility to different agents of decline (e.g. Drost & Fellers, 1996). Accordingly, any attempt to assess the stability or vulnerability of an amphibian fauna at any one regional site should consider not only the breadth of species present, but also a number of different populations of each. With relevance to all levels of variability that can serve to confound attempts to identify declining populations, a high number of intra–annual repeat visits to each monitoring site (especially during the peak breeding season) can add important, if not essential strength to the results (Alford & Richards, 1999).

Alongside data on the population dynamics of the focal species, it is important to gain an appreciation of the differential importance of key ecological variables in both the biotic and abiotic environment (e.g. climate, water quality, floral composition, and predator abundance). Such a multidimensional approach to monitoring helps to identify any potential agents of decline, but also to helps predict any secondary effects or feedbacks following a potential change in the structure of the amphibian community. This information, when integrated into demographic data of the amphibian populations can be invaluable in building a null model to predict the range and patterns of population behaviour in the absence of external pressures or agents of decline (Alford & Richards, 1999). Such null models can be used to reduce the subjectivity and ambiguity that often surrounds the evidence for a population decline (Pounds et al., 1997).

The way ahead: past lessons and future potential

In conclusion it is fair to say that conservation biology is still far from providing confident answers to the three questions posed above —how to determine real declines from simply natural population fluctuations, how to isolate the causal agents of a decline, and whether any particular factor is of global relevance. None of these are trivial questions, although each poses a significantly different challenge. With respect to the latter two questions it is becoming increasingly clear that yes human-induced agents can frequently be isolated as being causal factors behind population declines, but also that there exists a multitude of such factors operating at different scales, many of which exhibit complex interactions with both other factors and the local environment. The importance of a particular agent of decline in any one area or for any one species is likely to be context dependent, with synergistic effects that are difficult if not practically impossible to tease apart. However, as has been shown above for both specific and more general cases significant progress has been made. It is likely that further progress is only really possible through the interaction of both the many disciplines of ecology and environmental science, but also of ecosystem management, public policy and economics (e.g. Ludwig et al., 2001) —all of which contribute towards the precipitation, identification and mitigation of amphibian population declines.

In allocating limited conservation resources to the problem of declining amphibian populations the first of the three questions outlined above takes paramount importance —when are we observing real population declines and when are we just measuring natural population fluctuations? As was discussed in the final section of this review, this question has arisen through observing high levels of natural variability in amphibian population dynamics across both temporal and spatial scales —variability which serves to confront the fieldworker with a number of severe methodological challenges. The central distillation of this problem reveals a trade–off between needing enough statistical power to effectively reject the null hypothesis of no decline in cases where a decline truly exists, and the simple truth that conservation biology has insufficient funds (or historically accurate and detailed population data sets) to conduct and analyse exhaustively long monitoring programs in every case of suspected population decline. However, although this problem requires careful and objective assessment, recent progress and hard–won experience provides a number of possible alternatives for its confrontation:

1. Firstly as discussed in the previous section existing and proposed monitoring programs could be greatly strengthened in their ability to identify regional amphibian declines if they undertook a more multi–dimensional approach. Recent results from such a monitoring program in Belize provides evidence that natural variability exists in all of; species presence, relative abundance and calling activity (often taken as a surrogate of audible abundance) —across a range of temporal (within and between nights, across season, and between years), spatial (between ponds, even of similar habitat), and environmental scales (between different habitat types and climatic conditions) (GARDNER & FITZHERBERT, 2001; Gardner et al., unpublished data). Although not a substitute for long time series our ability to identify regional declines in amphibian populations would be greatly enhanced by the simultaneous monitoring of a range of both breeding sites and species, and across as many temporal scales as possible. Furthermore, such information provides a much better understanding of the underlying mechanisms which produce the observed variation.

2. Despite the value of the above recommended comprehensive approach to monitoring it still demands levels of resource allocation which may frequently be unavailable to practising conservationists. A recent application of a genetic test for bottlenecks (CORNUET & LUIKART, 1996) to distinguish between natural oscillations and true population declines in British Natterjack toads *(Bufo calamita)* (BEEBEE & ROWE, 2001) presents one potentially very useful alternative to resource intensive monitoring programs. BEEBEE & ROWE (2001) analysed a range of Natterjack populations, including ones which have experienced a recent decline, and ones which have remained comparatively stable. Microsatellite allele frequency data from these populations were tested for heterozygote excess and shifts in allele frequency distributions, and inferences from these computations about bottlenecks (i.e., persistently smaller population sizes than the recent means) were compared with demographic information. The genetic test accurately differentiated between declining and relatively stable populations (BEEBEE & ROWE, 2001). Recent theoretical (LUIKART et al., 1998, 1999) and empirical (SPENCER et al., 2000) work on the requirements for such tests suggests that to achieve sufficiently high power they only require samples of 5 to 20 polymorphic loci and approximately 30 individuals. The same work has also identified allelic diversity and temporal variation in and temporal variance in allele frequencies were most sensitive to genetic changes that resulted from the bottlenecks —but not the proportion of polymorphic loci (SPENCER et al., 2000).

3. The identification of declines in extant populations often requires a simple historical record of prior distributions of species occurrence. Recent work on a wide range of plants and animals provides encouragement that museum collections can be successfully used analyse declines, at least at a coarse spatial scale (SHAFFER et al., 1998).

4. As noted above a recent meta–analysis has been conducted on fluctuations in amphibian populations (MARSH, 2001). This work identified a number of predictive correlates of natural variability in amphibian population dynamics, notably life history type, family and latitude —correlates which could provide a rough but useful guide to the regions and species groups in which we may expect either greater or less than average natural variability in population fluctuations, and therefore help separate cases of particular concern.

5. Recent work has employed the use of skeletochronology to describe the differences in demographic composition between different populations of amphibians (e.g. DRISCOLL, 1999; REASER, 2000; KHONSUE et al., 2001). When coupled with mark–recapture data skeletochronology can provide invaluable information on age structure of a population, the stability of such age cohorts, and therefore the potential of the population to undergo large fluctuations in population size (e.g. DRISCOLL, 1999). Aside from helping to identify the potential for population variability, this technique can help isolate populations which have a skewed–senile age distribution —thus indicating a lack of recent recruitment and an accompanying higher risk of local extinction.

The above list of methodological and analytical techniques provides some undeniably valuable tools for the conservation biologist who is faced with identifying declining amphibian populations which are cause for concern, while at the same time is equipped with a limited budget. However, the list is not exhaustive, and another message that needs to be emphasised is that it is of utmost importance to maintain an open and vigilant mind with respect to new and evolving ideas and techniques. Only by adopting a flexible and holistic approach to conservation, can we profitably employ and integrate the diversity of knowledge and experience that exists in the many disciplines of ecology, environmental science and management —and thereby provide an increasingly effective response to dealing with the declining amphibian phenomenon.

A note of caution

A final note of caution in studying the declining amphibian phenomenon needs to be emphasised. Although both scientific (WAKE, 1998), and public (MORELL, 2001) opinion recognises the severity of declining amphibian populations, it is important to maintain a broad appreciation of other conservation problems and priorities (HALLIDAY, 2001). Two points should be considered at this junction. Firstly, amphibian declines have occurred in a number of pristine habitats and protected areas —removed from areas of direct human impact. This evidence bears serious implications for the effectiveness of the protected areas approach to conservation, and as such the study of amphibian populations should be integrated wherever possible into the wider context of conservation science and action. Secondly, it is important in world where resource allocation to conservation biology is seriously inadequate, that an focus or even over–emphasis on amphibians does not eclipse the equally worrying status of many other taxanomic groups (e.g. GIBBONS et al., 2000; GROOMBRIDGE & JENKINS, 2000) from both the scientific and public eye.

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