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CHICKEN LITTLE OR NERO'S FIDDLE? A PERSPECTIVE ON DECLINING AMPHIBIAN POPULATIONS

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THERE have been numerous recent reports suggesting that the populations of amphibian species in a wide array of geographic regions and habitats have apparently declined or have experienced range reductions (e.g., reviews by Blaustein and Wake, 1990; Hayes and Jennings, 1986; Honegger, 1978; Phillips, 1990; Vitt et al., 1990; Wake, 1991; Wake and Morowitz, 1991; specific examples are Beebee et al., 1990; Bradford 1989, 1991; Clarkson and Rorabaugh, 1989; Corn and Fogleman, 1984; Heyer et al., 1988; Kagarise Sherman and Morton, 1993; Semb-Johannson, 1989; Tyler and Davies, 1985). Pechmann and Wilbur (1994) evaluate the literature on amphibian declines and (1) stated that "few would dispute the fact that habitat destruction and other anthropogenic effects have reduced or eliminated many populations of amphibians as well as other taxa", (2) suggested that the declines of "isolated, protected amphibian populations" cannot be unequivocally separated from natural population fluctuations, (3) suggested that the "*implication* (italics mine) of these reports, however, is that declines and disappearances of amphibian populations represent a distinct phenomenon that goes beyond the general biodiversity crisis", and (4) questioned whether or not "amphibians are sensitive indicators of environmental stresses".

In this paper, I present my perspective on the amphibian decline problem and offer my response to points made in the paper by Pechmann and Wilbur (1994). I first presented some of the ideas in this paper at the symposium on amphibian declines at the 1990 meeting of The Herpetologists' League in New Orleans. My talk in New Orleans formed the basis of a paper that is in press in Conservation Biology (Blaustein et al., in press). In my New Orleans talk and in Blaustein et al. (in press), we came to several of the same conclusions presented by Pechmann and Wilbur (1994). Some of the points I make below are similar to those in Blaustein et al. (in press), and I liberally quote from that paper.

Pechmann and Wilbur (1994) bring a healthy skepticism to certain arguments of the amphibian decline problem. Moreover, the questions that they pose on evaluating evidence for population declines should help biologists to focus on key aspects of the amphibian decline problem. I agree with two of the general conclusions presented by Pechmann and Wilbur (1994): (1) habitat destruction and other anthropogenic effects have reduced or eliminated many populations of amphibians as well as other taxa and (2) there are not enough long term data to state conclusively, for most species, that their population declines are unusual.

I do not, however, agree with several other points made by Pechmann and Wilbur (1994). For example, in my opinion, and contrary to the views of Pechmann and Wilbur (1994), previous reviews of the amphibian decline problem did *not* imply that it was a phenomenon distinct from the general biodiversity crisis. Furthermore, despite the assertion of Pechmann and Wilbur (1994), I believe that under certain conditions, amphibians are good bioindicators of environmental stress.

TALES FROM CANTERBURY AND IRVINE AND THE TENOR OF THE TIMES

After hearing numerous anecdotal reports in conversation, and listening and reading some substantive reports in scientific sessions, many participants in the First World Congress of Herpetology, held in Canterbury, England, in 1989 began questioning whether the reports of amphibian declines represented a general trend. In February 1990, the National Research Council held a workshop in Irvine, California that addressed further the issues concerning declining amphibian populations. Several reports covering the general consensus of the Irvine participants were published (e.g., Barinaga, 1990; Blaustein and Wake, 1990; Phillips, 1990; Vitt et al., 1990; Wake and Morowitz, 1991). These reports were all very similar because they summarized the Irvine meeting. Pechmann and Wilbur (1994) criticize these reports throughout their paper as if they were original refereed scientific articles, which they were not.

After Canterbury and Irvine, the overall atmosphere was that there *might* be a problem concerning the populations of amphibians in various parts of the world. The published reports on the Irvine conference correctly conveyed the general atmosphere at the time. Phillips (1990) wrote, "By the end of the February workshop-the first to focus on the amphibian decline-the scientists agreed that anecdotal evidence indicates that at least some of the world's 5130 amphibian species are declining at an alarming rate." Blaustein and Wake (1990) stated that "The decline in populations and shrinkage in geographical range of several of these species exemplify the types of decline that are apparently occurring throughout the world." The consensus from the Irvine conference that amphibian declines may have begun in the 1970's and that the accumulation of evidence suggests the possibility of a global decline, was harshly criticized by Pechmann and Wilbur (1994). Yet, Vitt et al. (1990), in a paper co-authored by Wilbur, (cited by Pechmann and Wilbur only on page 76 and not cited or criticized along with the other reviews on the Irvine meeting), stated that "certain amphibians, even in habitats that appear to be pristine, are disappearing at an alarming rate, and the declines are widespread and have been particularly serious since the late 1970's." Moreover, Wilbur, as quoted in Barinaga (1990), stated that "The data are anecdotal, but it's so well repeated they certainly are believable."

The meetings in Canterbury and Irvine provided a good deal of anecdotal (and some empirical) evidence that *possibly* amphibian populations in various parts of the world were in decline. This was the general picture at the time—right or wrong. Since these conferences, persons have changed or modified their stance. As more information comes in, the general picture regarding the amphibian declines may change. However, the Irvine conference served as a springboard for action. Long-term studies of amphibian populations were called for. Hypotheses were constructed and, in some cases, predictions from these hypotheses are being tested.

Lag Time

Pechmann and Wilbur (1994) state that "information on some widely-cited cases [on amphibian declines] . . . is not available in the primary technical literature." This is no surprise. The lag-time from research to print takes several years. Much of the work stimulated by the Irvine conference is just now appearing in the refereed, mainstream literature. Some of the pieces to the amphibian decline puzzle are beginning to fit. For example, based on historical accounts, museum records, and intensive searches, Fellers and Drost (1993, in press for over a year) concluded that populations of the Cascades frog (*Rana cascadae*) in northern California have exhibited precipitous declines for more than 15 years. Blaustein et al. (in press; in review for eight months) identified a species of pathogenic fungus that may be one cause for the unusual mortality of toad eggs in the central Cascade Range of Oregon. The fungus is circumglobular in distribution and is commonly found on stocked fishes. It can be carried on amphibians as they disperse to other locales, and it may be very important in the overall amphibian decline picture. Kagarise Sherman and Morton (1993) recently documented changes over 20 years in the sizes of breeding populations of Yosemite toads (*Bufo* *canorus*). Other empirical papers addressing the amphibian decline problem will appear shortly. Some investigators (myself included) are waiting for enough long-term data to accumulate before publishing their results.

Pechmann and Wilbur (1994) argue that the reviews of the amphibian decline problem (primarily reviews of the Irvine conference) did not, in general, attempt "a comprehensive or random survey of the status of amphibian populations, but rather emphasize declines and disappearances." Again, this is no surprise. The reports criticized by Pechmann and Wilbur (1994) were reviews of the Irvine conference. They were not intended to provide comprehensive reviews of anything. Nevertheless, at least one report (Blaustein and Wake, 1990) did address the issue of species and areas that do not seem to be affected by "declines", by illustrating several examples of populations that were not known to be in decline.

Is the Amphibian Decline Problem a Distinct Phenomenon?

Pechmann and Wilbur state that the "*implication* (italics mine) of these reports [from the Irvine Conference] . . . , is that declines and disappearances of amphibian populations represent a distinct phenomenon that goes beyond the general biodiversity crisis." This "implication" may have been a result of the tenor of the times which included some outrageous media coverage [including a feature in the World Weekly News (17 April 1990) showing aliens taking frogs en masse to another planet to feed their kind—an unsubstantiated report from the "gray" literature]. In the reports on the Irvine conference, I simply do not see this implication. None of the reports cited by Pechmann and Wilbur (1994) state that the amphibian decline problem represents a distinct phenomenon from the overall biodiversity crisis. It is obviously one part of the overall biodiversity crisis. Rates of extinction have accelerated in recent times, in many cases because of human interference that has damaged suitable habitat (e.g., McNeely et al., 1990; Simberloff, 1986; Wilson, 1988). Numerous threatened species exist in all plant and animal groups, including amphibians (e.g., IUCN, 1990; McNeely et al., 1990).

Are Amphibians Declining in Pristine Habitats?

Pechmann and Wilbur (1994) question reports suggesting that "some of the declines and apparent extinctions have taken place in isolated, seemingly pristine areas." Too many biologists (myself included) have probably used the term pristine too loosely when describing population processes in amphibians from locations where the habitat has not obviously been altered or destroyed. For example, Wilbur, as quoted by Barinaga (1990), stated that "habitat destruction is probably the dominant thing going on—its not the whole story, because we have a lot of *pristine* (italics mine) areas where [amphibian] populations are going down the tubes as well" (see also quote above from Vitt et al., 1990).

I agree with the more recent statement by Pechmann and Wilbur (1994) that "some areas appear protected and pristine but are not so from an amphibian's point of view." It is very difficult (probably impossible) to find truly pristine habitat. Human-induced habitat alteration or destruction permeates all regions of the world. Habitat destruction or alteration may occur, for example, through overt devastation of rain forests or old-growth stands. However, some changes may be more subtle. Environmental changes may occur when exotic species (perhaps with pathogens) are introduced into areas inhabited by amphibians. Conditions may change as pollutants, not perceived by humans, are introduced into the atmosphere.

Pechmann and Wilbur (1994) state that "Reviews of declining amphibian populations have not clearly separated declines for which human activities are an obvious culprit from the others." Most of the reviews in question (e.g., Barinaga, 1990; Blaustein and Wake, 1990; Phillips, 1990; Wake and Morowitz, 1991) were summaries of the Irvine conference. They were not intended to go into detail about causes.

However, in general, they did present all the potential causes discussed at the Irvine meeting.

The "Gray" Literature

Pechmann and Wilbur (1994) state that "recent perturbations reported in other taxa share much in common with those reported in amphibians." They argue that much of the information on declines in organisms ranging from black abalone to dolphins, to sea urchins and amphibians, comes from the so-called "gray literature".

I agree that one must be cautious about using literature from unrefereed papers and personal communications. However, Pechmann and Wilbur (1994) are inconsistent in their arguments about using such information. For example, almost all of the information that they cite, in the beginning of their paper, on the leopard frog declines that seemed to have begun in the 1960's and lasted into the 1970's, were from unrefereed literature or personal communications. Although Pechmann and Wilbur stated that there are no hard data that leopard frog populations have recovered, based solely on personal communications, primarily from supply houses, they state that "*R. pipiens* populations apparently have recovered from the decline, and that bumper crops of frogs were observed during 1991 and 1992". With all the media attention regarding amphibian declines, representatives of supply houses may have a vested interest in saying that everything is fine. The information from Pechmann and Wilbur (1994) on the population recovery of *Bufo cognatus*, in Cleveland Co. Oklahoma, the site where Bragg (1960) reported their decline over 30 years ago, was based solely on one personal communication.

Long-term Studies of Amphibian Populations

In my New Orleans talk, I detailed the views of Connell and Sousa (1983) concerning the evidence needed to judge ecological stability and persistence. Connell and Sousa (1983) argued that to demonstrate that a population became extinct during a given period of time, or if it did become extinct, whether it recolonized the area within the time span, it must be monitored for at least one complete turnover of all individuals of that species at that particular site. Connell and Sousa also suggested that to demonstrate if a population is stable, it must be monitored for at least one turnover. Connell and Sousa (1983) surveyed the literature of long-term studies of organisms that fit their criteria. Their unbiased search found no such studies at all on amphibians—none showing a declining, increasing, or stable population.

A decade after Connell and Sousa (1983) published their paper, long-term studies of amphibian populations remain rare. This lack of long-term data is surprising, because anuran amphibians have been used in numerous studies as model vertebrates for studying complex life cycles, aquatic community structure and mating patterns (e.g., reviewed by Duellman and Trueb, 1986; Olson et al., 1986; Wilbur, 1980). Limited information on the long-term dynamics of amphibian populations makes it difficult to evaluate whether recently observed declines in population density are unusual in magnitude or duration. Moreover, due to the paucity of long-term data on amphibians, it is obviously difficult to distinguish between natural fluctuations and those caused by humans.

Nevertheless, there have been several long-term studies of amphibian declines published since the paper by Connell and Sousa (1983) appeared. I briefly review some of these studies below. Some of the accounts I discuss below are similar in description to those in Blaustein et al. (in press). Most of those studies that reported declines were not discussed in any detail by Pechmann and Wilbur (1994).

A study by Pechmann et al. (1991) carefully monitored the breeding population sizes of four amphibian species at one site in South Carolina for 12 years. Pechmann et al. (1991) showed that the populations of three species fluctuated and one species increased over that time span.

Semb-Johansson's (1989) study of common toads (*Bufo bufo*) on islands off the Norwegian coast is an excellent example of a long-term population study of an amphibian. Toads were monitored for 24 years (1966–1989). Their numbers declined dramatically from 1966–1975 and have remained low.

Corn and Fogleman's (1984) study documented the local extinction of leopard frogs (*Rana pipiens*) in Colorado across a number of sites. In this study, six populations of *R. pipiens* were examined for 10 years (1973–1982). Reproductive failure was seen in 1973 at one site and by 1981 no individuals of *R. pipiens* were seen at any site. *Rana pipiens* was absent from the area at the end of the study. *Rana pipiens* older than four of five years are rare (Leclair and Castanet, 1987). Thus, these populations were followed for almost two turnovers.

Kagarise Sherman and Morton (1993) documented the population changes over 20 years in *Bufo canorus* at Tioga Pass, California. Comprehensive surveys of breeding aggregations were made from 1971–1982 and less systematic observations were taken from 1983–1991 at Tioga Pass. Six additional populations in northern California were also monitored from 1973–1990. At the largest breeding pools at Tioga Pass, the populations declined about nine-fold from 1974–1982. The mean number of toads found in daily searches also declined during the 20-year period. Similar declines at the other sites were reported.

Berven's (1990) seven year study of wood frogs (*Rana sylvatica*) illustrates that their populations turn over about every 2–3 years. The populations of adult wood frogs in Berven's study showed erratic interannual fluctuations largely due to variation in juvenile recruitment. Declines in populations of adult wood frogs were followed by sharp increases in one pond and relatively low but stable numbers in another.

A 14-year study by Jaeger (1980; see also Jaeger, 1970), largely overlooked from the population perspective, showed that the Shenandoah salamander (*Plethodon shenandoah*) has been declining (and continues to do so; R. Jaeger, personal communication) probably due to competition with *P. cinereus* whose populations are relatively stable. The gradual loss in numbers of *P. shenandoah*, due to interspecific competition, may yet provide evidence of the elusive "natural" extinction event.

Declines of natterjack toads, based primarily on range reduction data collected over 20 years (e.g., Banks and Beebee, 1987; Beebee, 1977; Beebee et al., 1990), have also been reported (see discussion below).

Thus, of the seven long-term studies discussed above, two (Berven, 1990; Pechmann et al., 1991) showed species that were generally fluctuating in numbers, four (Banks and Beebee, 1987 and Beebee et al., 1990; Corn and Fogleman, 1984; Kagarise Sherman and Morton, 1993; Semb-Johansson, 1989) showed declining populations, and one (Jaeger, 1980) showed the decline of one species and a possible stable population in the other. Of course, it is possible that the populations in decline may be undergoing natural fluctuations in numbers; years with strong recruitment may be followed by years of poor reproduction during which the population declines. With a year or two of successful reproduction by older individuals (*Bufo canorus* can live for over 30 years: Goin et al., 1978), the populations could rapidly rebound from their current low levels.

In their summary of the available long-term data, Pechmann and Wilbur (1994) seem to contradict themselves by stating that "long-term census data on amphibians are too few to warrant generalizations about their variability" when in the very next sentence they generalize that "Those data that are available suggest that populations of amphibians range from the highly variable to the highly stable." Their latter statement seems inaccurate, especially in light of the long-term data (some of which reflected declines) that I presented above.

In addition to the long-term studies cited above, populations of other amphibian species have disappeared from portions of their historical ranges (without concomitant shifts in their ranges) and have failed to reestablish at such sites for periods longer than their estimated maximum life span. I will briefly discuss range reductions in three species with the caveat that much of the data concerning them have not yet been published in refereed journals.

Until the mid 1970's, the red-legged frog (*Rana aurora*) was extremely abundant in the Willamette Valley of Oregon, a relatively large valley (160 by 60 km) bounded by the Coastal and Cascade Mountain ranges (Blaustein and Wake, 1990; Nussbaum et al., 1983). *Rana aurora* is now extremely rare, and breeding populations have not been observed for at least 20 years in the Willamette Valley (Blaustein and Wake, 1990; R. M. Storm, personal communication).

The western spotted frog (*Rana pretiosa*) was abundant throughout Washington and Oregon until the mid-1970's (McAllister and Leonard 1990; Nussbaum et al., 1983), but it has become extremely rare in the western portion of its range (McAllister and Leonard, 1990, 1991; Nussbaum et al., 1983; Stebbins, 1985). Populations of *R. pretiosa* are exceptionally rare west of the Cascade Mountains in Washington, and they have not been found west of the Cascade Mountains in Oregon for at least 23 years (McAllister and Leonard, 1990, 1991; Nussbaum et al., 1983). One specimen, tentatively identified as *R. pretiosa*, was found near Olympia, Washington in 1990 (K. R. McAllister and B. Leonard, personal communication). No other specimen has been found at that site (K. R. McAllister and B. Leonard, personal communication). Thus, this species has been missing from about one-third of its range since the mid-1970's.

The intensive search of historical accounts and museum records and searches at 16 sites led Fellers and Drost (1993) to conclude that populations of the Cascades frog (*Rana cascadae*) in northern California have exhibited a precipitous decline for more than 15 years. Local extinctions of *R. cascadae* in Oregon have also been reported (Blaustein and Wake, 1990). However, based on surveys of numerous sites since the Irvine meeting, population declines of *R. cascadae* in Oregon do not seem to be as severe as they are in California (Blaustein, unpublished data).

Information on the population dynamics of *R. aurora*, *R. pretiosa*, and *R. cascadae* are being accumulated by a number of workers in Oregon, Washington, and California. These data will soon be available in the mainstream literature. The data for at least one species, *R. cascadae*, in California, have been recently published (Fellers and Drost, 1993).

Information on range reduction, sometimes in conjunction with demographic data, has resulted in many species being placed on regional threatened lists. For example, 15% of the amphibian species in the western United States are listed as candidates for threatened species status (see Walls et al., 1992, and references therein). In the Pacific Northwest, this is of special concern, because 54% of the native amphibian species in Oregon are listed as sensitive, 46% in Washington state are listed in the special concern category, and 29% are listed as threatened in Idaho (Walls et al., 1992). Of course, the listing of some species is questionable because of the lack of long-term population data.

Three Famous Cases

There are several cases concerning the amphibian decline problem that have received a great deal of attention. I will briefly discuss three of them to illustrate the importance of being cautious when interpreting reports of the population status of amphibians. These reports involve two rather unique species and the long-term study of Pechmann et al. (1991) (see Barinaga, 1990; Blaustein and Wake, 1990; Phillips, 1990; Tangley, 1990; Wake, 1991). The following accounts are liberally taken from Blaustein et al. (in press).

The gastric brooding frog (*Rheobatrachus silus*) was discovered in 1973 in relatively undisturbed areas of the Conondale and Blackall Ranges about 160 km north of Brisbane, Australia (Fanning et al., 1982; Liem, 1973). This species could have unlocked many of the mysteries of physiology and digestion because of its habit of swallowing and brooding its young in its stomach (Tyler and Carter, 1981). The decline of this species began in the late 1970's and it has not been found in nature since 1979 (Tyler, 1991; Tyler and Davies, 1985). The fact that this species was only recently discovered suggests that it may have always been rare and/or had a highly localized and little explored geographic distribution. Although this species seems to have gone extinct, it is not unusual for some species to go undetected for years.

The golden toad (*Bufo periglenes*) is a sexually dimorphic species endemic to Costa Rica (Crump et al., 1992). The males are brilliant orange whereas the females are brightly mottled. Moreover, larval golden toads have the rare habit of being facultative non-eaters (Crump, 1989). Each year from the early 1970's through 1987 the toads emerged from underground to breed in the spring (Crump et al., 1992). In 1987, more than 1500 individuals were observed by Crump et al. (1992) but recruitment was nearly zero. From 1988–1990, only 11 adult toads were found (Crump et al., 1992). While it appears that the number of golden toads has drastically dwindled, it is also possible that adults of *B. periglenes* are estivating below ground in response to unfavorable weather conditions, and may emerge when conditions become more favorable for breeding (Crump et al., 1992). Some species in the same family as *B. periglenes* can live more than 30 years (Duellman and Trueb, 1986), and many toad species within the same genus can live for more than 10 years (Bowler, 1977). Thus, populations of the golden toad can probably persist through several years of poor recruitment. Like the gastric brooding frog, the golden toad was only recently discovered (Savage, 1966), so its population dynamics have not been studied in detail and are poorly understood.

Caution should be taken when declaring that either the golden toad or the gastric brooding frog are extinct. In both cases, there is no concrete evidence that the observed declines are atypical, nor is the cause of the declines known. Because there are no long-term data for these species, we cannot reject the possibility that, under natural conditions, these species often undergo large fluctuations in numbers.

The study by Pechmann et al. (1991) has received a great deal of attention, because it was a careful long-term study and because of their conclusion that "there is no evidence that the declines in amphibian populations observed in other locations have occurred in populations at Rainbow Bay." This study was conducted at only one site in an area relatively protected from human interference. Caution should be taken not to generalize about amphibian populations in other regions based on one study site. It is possible that populations of even the same species reported to be fluctuating by Pechmann et al. (1991) might be declining or increasing in another area. Although the authors were careful not to generalize about other populations, an "implication" could easily be conjured up (as did some of the media) from this study that most reports of declines are really only the result of natural population fluctuations.

Regional Differences in Population Dynamics

The population processes and patch dynamics of amphibians may vary regionally (see examples reported in Blaustein and Wake, 1990). For example, in the southeastern United States where Pechmann et al. (1991) conducted their study, there is an extremely diverse and abundant amphibian fauna. In certain areas, such as the Savannah River site, there are relatively dense amphibian populations and a great deal of continuous suitable habitat (see discussion in Jackson et al., 1989; Wake, 1991). If populations go locally extinct in this region, it seems likely that the probability of recovery will be higher than in certain other regions (Wake, 1991). In other localities, such as some regions in mountainous western North America, where several species appear to have diminishing ranges, many species are found in habitats that are localized or fragmented and opportunities for recolonization may be much lower (Wake, 1991).

Are Amphibians "Canaries"?

Most reviews of the amphibian decline problem suggested that amphibians are good bioindicators of environmental stress. They have permeable, exposed skin (not covered by tough scales, hair, or feathers) and eggs (not covered by hard or leathery shells) that may readily absorb substances from the environment. The complex life cycles of many species potentially exposes them to both aquatic and terrestrial environmental agents. This view was amplified by statements made by Vaughn Shoemaker (at Irvine as cited in Blaustein and Wake, 1990), a highly regarded amphibian physiologist, by the keynote talk given by Henry Wilbur in New Orleans (as stated by Pechmann and Wilbur, 1994), and by Vitt et al. (1990) who noted that amphibians were "harbingers of decay".

I agree with Pechmann and Wilbur (1994) that amphibians "are more sensitive in some cases and less sensitive in others, and there is a considerable variation among species and toxicants." This statement would probably be true for organisms in almost any taxon. Moreover, I agree that it is a "quantum leap from most toxicological studies to projecting impacts on populations and communities in the field" (Pechmann and Wilbur, 1994). I am not sure how to quantify a "good" bioindicator. However, I do believe that Pechmann and Wilbur (1994) are selling amphibians short when they state that they were "not aware of any evidence available to substantiate" that amphibians were good bioindicators and that the "toxicological literature does not support a general statement that amphibians are a relatively sensitive group." Under many conditions, amphibians may be as good as other organisms as bioindicators of environmental stress. This is one reason why they are being used with increasing frequency in this regard. Their effectiveness as bioindicators, like members of other taxa, depends upon the situation and the species in question.

Thus, the U.S. Environmental Protection Agency, the U.S. Fish and Wildlife Service, and the Canadian Wildlife Service have all published extensive reports and bibliographies on the use of amphibians as bioindicators, especially in the context of toxicology (see for examples, Bantle et al., 1992; Power et al., 1989). Moreover, there are many papers in the mainstream literature that have assessed the effects of toxicants on amphibians. Many of these studies champion amphibians as bioindicators of toxic substances ranging from heavy metals to pesticides (e.g., Birge et al., 1979, 1983; Cooke, 1981; Fonovich de Schroeder and Pechen de D'Angelo, 1991; Jayaprakash and Madhyastha, 1987). After compiling more than 250 references on the effects of toxicants on amphibians, Power et al. (1989) stated that "Amphibians are particularly sensitive to metals and acidification. They are considered to be useful indicator species for measuring the effects of local changes in environmental studies."

Indeed, anuran embryos and tadpoles have become "models" for testing the toxicity of numerous chemicals (e.g., Bantle et al., 1992; Cooke, 1981). As Cooke (1981) stated "For such work, tadpoles have many advantages", including characteristic morphological changes that occur in the presence of particular pollutants. The characteristic morphological changes that occur during development when amphibian larvae are exposed to chemical pollutants is the basis of an assay and Atlas of Abnormalities in the Frog Embryo Teratogenesis Assay-Xenopus (FETAX) program (Bantle et al., 1992). The FETAX program was initiated (by James N. Dumont and coworkers of Oak Ridge National Laboratory) because of increased costs and concern over using mammalian models. Originally, the assay and atlas was intended to be used primarily for embryos and larvae of *Xenopus*. This system is now being used by several government agencies to test the effects of chemical pollutants on development in North America ranids and bufonids. The FETAX program is currently investigating the possibility of using amphibians in the field to assay chemical pollutants.

Acidification is one proposed cause for amphibian declines (Dunson et al., 1992). With regard to acid tolerance, Pechmann and Wilbur (1994) state that "most amphibians are comparatively tolerant of acid" citing Pierce (1985) and Mierle et al. (1986). In fact Pierce (1985) only tested 14 anurans and two salamanders and stated that "most amphibian species [in his study] are relatively acid tolerant." Moreover, Mierle et al. (1986) briefly reviewed the acid tolerances of only six species of amphibians showing that some were more tolerant than others. There is an extensive literature on the effects of acidity on amphibians (see symposium in *Journal of Herpetology* 26:349–442, 1992, and references therein). Certain studies show that some amphibians are very sensitive to pH, other studies show that some species are relatively tolerant to pH.

Differential sensitivity to pH has also been documented in numerous organisms from other taxa. For example, in his review of acid precipitation in aquatic ecosystems, Haines (1981) showed differential sensitivity to pH in bacteria, fungi, algae, insects, fish, and amphibians. Similarly, Roff and Kwiatkowsky (1977) showed differential sensitivity to pH in zooplankton. It is very difficult to generalize how pH affects a group of organisms. Some species within a particular taxon may be sensitive, others may be tolerant, depending upon conditions and the life history stage.

Many amphibian species are sensitive enough to acidification that they can be affected at the population and community levels. For example, Beebee et al. (1990) suggested that acidification due to pollution has adversely affected populations of natterjack toads (*Bufo calamita*) in Britain. They stated that "Natterjack toad declines have therefore almost certainly been strongly influenced by water acidifications, and this may account for the substantial number of extinctions at heathland sites." They further suggested that even small decreases in pH have substantial effects on natterjack populations. Most probably, other organisms sympatric with natterjack toads were also affected by increased acidity. I am not suggesting that natterjack toads were affected *more* than other organisms. But in this case, at least, increased acidification seems to have caused a decline in populations of the natterjack toad.

Several studies have shown that pH can affect competition and predation between amphibians. These effects can potentially alter community structure. For example, Sadinsky and Dunson (1992) showed that survival of larval *Rana sylvatica* was enhanced in conditions of relatively low pH because of reduced predation by a salamander predator. Warner et al. (1993) showed that at relatively high pH, larval *Hyla femoralis* caused decreased survival and an increase in the larval period of *Hyla gratiosa*.

In summary, in some cases, amphibians may make excellent canaries, in other situations (for example, in coal mines), canaries are probably better. The sensitivity of amphibians to certain pollutants (e.g., those causing increased acidification) may have significant ecological consequences. Finally, I agree with Pechmann and Wilbur (1994) that there may be no analyses comparing population changes in amphibians to those in other taxa to substantiate the fact that "human impacts fall more heavily upon amphibians than other taxa".

Is the Sky Falling? Is Rome Burning?

In the broad sense, the sky is falling. The world is losing an unprecedented number of species in all taxa per year, primarily due to habitat destruction and alteration (McNeely et al., 1990; National Science Board, 1989; Wilson, 1988, 1992). As rain forests and old-growth stands are destroyed, as wetlands are filled in or polluted as exotic species, or chemicals that adversely affect our atmosphere, are introduced, suitable habitat for many organisms, including amphibians, are being destroyed.

What should be the response to the number of anecdotal accounts and some recent long-term studies suggesting amphibian declines? On the one hand, it is essential that rigorous census studies of a representative sample of amphibian populations be initiated worldwide as a means of assessing the directions, magnitudes, and agents of changes in their numbers. How much information is needed before one can decide whether special efforts should be undertaken to protect or restore populations that are declining? The conservative approach of withholding intervention until extinction rates are conclusively demonstrated to be unusually high might result in an unacceptable loss of populations or entire species. The opposite approach may give mistaken conclusions that a global decline is occurring when populations are simply exhibiting normal ranges of fluctuations. This could waste resources and political capital. Therefore, one must balance the risk of lost credibility, which might seriously compromise future conservation efforts in this and other arenas, against the cost of failing to respond to a potentially serious environmental crisis.

As stated in Blaustein et al. (in press), clearly an effort should be made to initiate long-term monitoring programs for a broad array of amphibian species, populations, habitats, and geographic regions. With such long-term records, one could evaluate (1) which species have, on average, more variable populations per turnover, (2) what the average probability of local extinction is per turnover, (3) if local populations recover from extinction, how long on average recovery takes, and (4) what the spatial scale is of local extinctions. All of these comparative statements require a common relative time scale: e.g., a population turnover, so that differences in longevity of individuals do not confound the comparisons.

Without such long-term data, one cannot unambiguously state that amphibian populations are suffering unusual declines. The absence of information, however, is not license to remain indifferent to the potential crisis. Among the examples of long-term studies discussed above are several that have demonstrated recent rapid, and sometimes widespread, declines or extinctions of amphibian populations. In my view, there is a sufficient number of such cases to warrant investigation of potential links to human-caused environmental degradation.

In my opinion, only if rigorous sampling studies and ongoing assessments of the hypothesis of decline proceed *simultaneously* can the decision to intervene be made on solid scientific grounds. A case for intervention will be most convincing if the observed demographic changes can be linked to specific human-induced alterations of the habitat. Efforts to halt the declines and restore populations and their habitat to their former condition can then be undertaken.

Pechmann and Wilbur (1994) pose the question, "What should be done?" and essentially call for continued monitoring. They state that there is "no doubt that there have been numerous reductions and losses of amphibian populations worldwide because of human impacts" that include habitat destruction, pollution, and the introduction of exotic species. Yet, they do not even suggest that tests, experimentally, or otherwise, are needed for key hypotheses, until more long-term data are available. For certain regions, there are unquestionably enough baseline data (both anecdotal and empirical) to generate specific hypotheses and to test them.

Testing key hypotheses can probably best be done by implementing field experiments. For example, as referenced by Pechmann and Wilbur (1994), several reports have suggested that the introduction of bullfrogs (*Rana catesbeiana*) has caused the demise of some amphibian populations in certain regions in western North America. One paper cited by Pechmann and Wilbur was a review in a refereed journal of the bullfrog problem (Hayes and Jennings, 1986). The other two references that they cite (see Pechmann and Wilbur, 1994) were technical reports. Bullfrogs may indeed be causing the demise of certain amphibian populations, but the evidence for this remains equivocal. To my knowledge, there have been no published papers in the mainstream literature that tested this hypothesis using field experiments. One could manipulate bullfrogs experimentally, in the field. Bullfrog tadpoles or adults could be added to some ponds where other amphibians are present but which had no bullfrogs. If populations of other amphibian species in ponds where there were no bullfrogs (controls) did better than those where bullfrogs were added, the hypothesis that bullfrog presence is detrimental to other amphibians is supported. In other ponds, bullfrogs could be removed. If populations of amphibians where removals have taken place do better than populations where bullfrogs remained, the hypothesis is supported. Of course, the experiments must be conducted in an unbiased manner and with an adequate number of replicates for the results to be meaningful. Additional experiments would be necessary to determine the mechanism(s) (e.g., competition, predation) by which bullfrogs hamper populations of other amphibian species.

In fact, several studies are in progress that are incorporating field experiments in the investigation of the effects of bullfrogs on native frogs. For example, using field experiments and detailed observations, Sarah J. Kupferberg of the University of California, Berkeley, is investigating the role of bullfrog tadpoles on tadpoles of *Rana boylii* and *Hyla regilla* in the Coast Range of California. Joseph M. Kiesecker, is conducting a similar study in Oregon. Hence, within 2–5 years, there should be some insight into the impact of bullfrogs on amphibians.

Pechmann and Wilbur (1994) suggest that certain "hypothetical explanations" (e.g., increased ultraviolet radiation) may be unworthy of investigation at this time because their study "distracts us from . . . serious known problems such as rain forest destruction or stocking or exotic fish." Quick dismissal of certain hypothetical explanations is close to scientific advocacy. Just because there is scant knowledge about certain agents that could potentially harm amphibian populations (as well as populations from other taxa), this does not mean that one should not investigate them.

Conclusions

(1) The amphibian decline problem is part of the overall crisis in biodiversity. (2) Habitat destruction and habitat alteration are undoubtedly the single most important cause for declines of species in all taxa, including amphibians. (3) There probably is no such thing as pristine habitat. (4) There are not enough long-term data on amphibian populations to assess the overall significance of the amphibian decline problem. However, long-term studies are appearing with increasing frequency and in conjunction with some range reduction data, there certainly is enough evidence to suggest that populations of some amphibians, in certain regions, are declining. Whether or not specific declines are natural or human-induced must be carefully assessed. (5) Like members of other taxa, under certain conditions, amphibians are good bioindicators of environmental stress. Their overall effectiveness as bioindicators may differ with the type of stress, species, and life history stage. (6) Long-term monitoring, in conjunction with experimental tests of key hypotheses, preferably in the field, is warranted. (7) Criticizing reviews of meetings should result in a stiff fine.

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