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Andrew R. Blaustein, David B. Wake, Wayne P. Sousa

Conservation Biology, Volume 8, Issue 1 (Mar., 1994), 60-71.

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Conservation Biology

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Thu Sep 19 16:28:13 2002

Amphibian Declines: Judging Stability, Persistence, and Susceptibility of Populations to Local and Global Extinctions

ANDREW R. BLAUSTEIN

Department of Zoology
3029 Cordley Hall
Oregon State University
Corvallis, OR 97331 U.S.A.

DAVID B. WAKE

Museum of Vertebrate Zoology
1120 Life Sciences Building
University of California
Berkeley, CA 94720, U.S.A.

WAYNE P. SOUSA

Department of Integrative Biology
University of California
Berkeley, CA 94720, U.S.A.

Abstract: *Extinctions are normal biological phenomena. Both mass extinctions in geological time and local extinctions in ecological time are well documented, but rates of extinction have increased in recent years—especially in vertebrates, including amphibians—as illustrated by recent reports of their population declines and range reductions. We suggest that long-term population data are necessary for rigorously evaluating the significance of the amphibian declines. Due to the physiological constraints, relatively low mobility, and site fidelity of amphibians, we suggest that many amphibian populations may be unable to recolonize areas after local extinction.*

Declinación de anfibios: Juzgando estabilidad, persistencia y susceptibilidad de las poblaciones a las extinciones globales

Resumen: *Las extinciones son un fenómeno biológico normal. Extinciones en masa en una escala temporal geológica y extinciones locales en una escala temporal ecológica, están bien documentadas, pero en años recientes las tasas de extinción han incrementado, especialmente en vertebrados, incluyendo a los anfibios tal como ha sido ejemplificado en reportes recientes sobre la declinación de su población y la reducción de su área de distribución. Nosotros sugerimos que datos poblacionales a largo plazo son necesarios para evaluar rigurosamente la significancia de la declinación en anfibios. Nosotros sugerimos que muchas de las poblaciones de anfibios son incapaces de recolonizar áreas después de extinciones locales debido a las restricciones fisiológicas, la relativamente baja movilidad y la filopatría de los anfibios.*

Paper submitted June 1, 1992; revised manuscript accepted September 17, 1993.

Introduction

Mass extinctions of species in geological time and local extinctions in ecological time are natural occurrences (see Andrewartha & Birch 1954; Blaustein 1981; Raup & Sepkoski 1982; Connell & Sousa 1983; Stanley 1985; Jablonski 1986; Wilson 1988; Terborgh 1989; McNeely et al. 1990; Ehrlich & Wilson 1991). Even simple shifts in distribution can produce local population extinction (Connell & Sousa 1983; Davis 1986). Rates of extinction of plants and animals have accelerated in recent times, however, in many cases because of human interference that has destroyed or fragmented suitable habitat (Simberloff 1986; Wilson 1988; McNeely et al. 1990). Numerous threatened species exist in all vertebrate classes (see McNeely et al. 1990).

As part of the overall "biodiversity crisis," recent reports suggest that many species within the class Amphibia are undergoing population decline, range reduction, and even extinction (see reviews by Blaustein &

Wake 1990; Phillips 1990; Wyman 1990; Wake 1991; specific examples are provided in Table 1). In some cases, unusual mortality has been documented (see Blaustein & Olson 1991; Blaustein et al. 1994 and references therein). Habitat destruction is undoubtedly the major cause for amphibian losses, but other hypothesized causes for these declines include chemical pollution, acid precipitation, increased ultraviolet radiation, introduction of exotic species, pathogens, harvesting by humans, and natural population fluctuations (Blaustein & Wake 1990; Phillips 1990; Wyman 1990; Pechmann et al. 1991; Blaustein et al. 1994).

Amphibians are integral components of many ecosystems, and they may constitute the highest fraction of vertebrate biomass in some ecosystems (see Burton & Likens 1975). Through their contribution to trophic dynamics in a variety of communities, a world-wide decline in amphibians could have an important impact on other organisms. Adult amphibians are important carnivores in many systems and prey species in others (Por-

Table 1. Some studies of amphibians whose populations were continuously monitored (at least once per year) for at least four years.¹

<i>Species</i>	<i>Duration of Study</i>	<i>Population Trend</i>	<i>References</i>
<i>Bufo bufo</i> Common Toad	24 Years	declining	Semb-Johannson (1989)
<i>Bufo canorus</i> Yosemite Toad	12 Years	declining	Kagarise Sherman and Morton (1993)
<i>Bufo calamita</i> Natterjack Toad	9 Years	declining	Banks and Beebee (1987); see also Beebee et al. (1990)
<i>Bufo periglenes</i> Golden Toad	4 Years	declining ²	Crump et al. (1992)
<i>Rana pipiens</i> Leopard Frog	10 Years	extinction of six populations	Corn and Fogleman (1984)
<i>Rana sylvatica</i> Wood Frog	7 Years	fluctuating	Berven (1990)
<i>Pseudacris ornata</i> Ornate Chorus Frog	12 Years	fluctuating	Pechmann et al. (1991)
<i>Eleutherodactylus coqui</i> The Coqui (frog)	4 Years	increasing ³	Woolbright (1991)
<i>Plethodon jordani</i> Red-Checked Salamander	5 Years	stable	Hairston (1983)
<i>Plethodon glutinosus</i> Slimy Salamander	5 Years	stable	Hairston (1983)
<i>Plethodon cinereus</i> Red-Backed Salamander	14 Years	stable	Jaeger (1980)
<i>Plethodon shenandoah</i> Shenandoah Salamander	14 Years	declining	Jaeger (1980)
<i>Ambystoma opacum</i> Marbled Salamander	12 Years	fluctuating	Pechmann et al. (1991)
<i>Ambystoma talpoideum</i> Mole Salamander	12 Years	fluctuating	Pechmann et al. (1991)
<i>Ambystoma tigrinum</i> Tiger Salamander	12 Years	fluctuating	Pechmann et al. (1991)
<i>Ambystoma maculatum</i> Spotted Salamander	5 Years	fluctuating	Husting (1965)

¹ The population trend statements are based on the conclusions of the authors.

² See text for details.

³ This is probably only a temporary increase in numbers. According to Woolbright (1991), adults of this species increased fourfold immediately after hurricane Hugo (1989) due to an increase in retreat sites and decrease in invertebrate predators.

ter 1972); larval amphibians can be important herbivores (Dickman 1968; Seale 1980; Morin et al. 1990) as well as prey (Duellman & Trueb 1986) in aquatic habitats.

For several species, range reductions over ecological time have been documented, but local population declines leading to extinctions are less evident. Given that local extinctions or declines are common features of many apparently undisturbed animal and plant populations, we must ask whether many recent reports of amphibian population declines are cause for alarm, and, more fundamentally, whether it is true that the magnitude of amphibian population declines or the frequency of population extinctions has significantly increased in recent years. At present, this question is difficult to answer because there are few long-term data on the population dynamics of amphibians to serve as a baseline for comparison (Connell & Sousa 1983; Hairston 1987; see discussion below). Thus, there are at least two interpretations of the recent observations: (1) the phenomenon is real; long-term census data, if available, would reveal that many of the reported declines and extinctions are indeed unprecedented in ecological time; (2) the problem has been exaggerated because much of what is known about amphibian population dynamics comes from relatively brief studies or anecdotal accounts. Such studies rarely span more than a few years and may result in a misleading picture of the level of variability that occurs in the density of natural populations. Even those records that span as much as one population turnover may underestimate natural variation (Connell & Sousa 1983; Williamson 1987; Pimm & Redfearn 1988; McArdle 1989; McArdle et al. 1990) because they fail to detect infrequent, large fluctuations in density. The impression from short-term data sets is that large declines are "abnormal." As a result, biologists may simply not appreciate how commonly local extinctions occur in undisturbed amphibian populations. If longer records of amphibian population dynamics existed, they might reveal that there is nothing unusual about these observed declines; amphibian populations may simply exhibit the same variety of dynamics as any other species.

How then, in the absence of fully conclusive data, should we respond to the increasing number of largely qualitative or anecdotal accounts of amphibian decline? 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 change in numbers. But how much information is needed before one can decide whether special efforts should be undertaken to protect or restore declining populations? Adopting 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. Erring in the opposite direction, by mistakenly concluding that a global decline is occurring when populations are simply exhibiting normal ranges of fluctuation, will waste resources and political capital. It boils down to the issue of how we should 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 serious environmental crisis.

Only if rigorous sampling studies and ongoing assessments of the hypothesis of decline (incorporating experiments) proceed simultaneously, can the decision to intervene be made on solid scientific grounds. A case for intervention will be all the more convincing if 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. In the remainder of this paper, we critically discuss the evidence for a global decline of amphibians in light of what is known about natural fluctuation in their densities.

What Should Be Monitored?

Efforts to conserve threatened species or to evaluate the need for such intervention are more concerned with the persistence of populations—that density remains safely above zero—than their stability—how narrowly the density fluctuates in time about some point equilibrium or cyclic path; see Holling (1973) and Connell and Sousa (1983) for reviews of these concepts. In fact, unambiguous judgments concerning the stability of populations can be exceedingly difficult to make (Connell & Sousa 1983). Further, the relationship between variation in numbers and the likelihood of extinction is far from straightforward (Schoener & Spiller 1992). The traditional and intuitive expectation has been that more variable populations will be more prone to extinction. When, however, temporal variability in numbers increases with mean population density (as is often true), it may be inversely rather than positively correlated with the chance of extinction (Schoener & Spiller 1992).

To predict with some degree of confidence the probability that a given population will persist, one must obtain sufficient demographic information to project the future trajectory of population growth and, in particular, a population's capacity to increase from low numbers. Since age/stage distributions, schedules of natality and mortality, and rates of migration are seldom stable in natural populations, accurate projections can be made only on a "real-time" basis, from year to year, much the way that fisheries are managed. An additional consideration is the spatial scale at which demographic

information is collected and population changes are projected, because the probability of persistence will likely increase with the extent of the habitat being considered (Murdoch 1979; Connell & Sousa 1983). Populations—especially metapopulations encompassing interdependent patches of occupied and unoccupied habitat—must be monitored and managed on the landscape scale, with distinct demographic measurements being collected from all significant phases of the habitat mosaic, aquatic and terrestrial. This is particularly crucial for amphibian species whose life histories include both aquatic and terrestrial stages.

Long-Term Studies of Amphibian Populations

In their review, Connell and Sousa (1983) failed to find any published records of amphibian populations that spanned one or more turnovers of the member individuals. A decade later, long-term studies of amphibian populations remain uncommon (see Table 1). Olson et al. (1986) reviewed 20 published studies of 13 species of anurans for which size-dependent mating patterns were studied in more than one aggregation. These studies were conducted for less than one year to five years ($\bar{X} = 1.95 \pm 0.26$ SE years; a study conducted over less than one year was considered a one-year study). None of these studies lasted for more than one turnover of the sampled population. This lack of long-term data is surprising because anuran amphibians are model vertebrates for studying complex life cycles, aquatic community structure, and mating patterns in the field (as reviewed by Wilbur 1980; Duellman & Trueb 1986).

Clearly, a concerted 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) the average probability of local extinction per turnover; (3) if local populations recover from extinction; how long on average recovery takes; and (4) the spatial scale of local extinctions. All of these comparative statements require a common relative time scale, such as a population turnover, so that differences in longevity of individuals do not confound the comparisons.

Without such long-term data, we 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 below are several that have demonstrated recent rapid, and sometimes widespread, declines or extinctions of amphibian populations. There is a sufficient number of such cases to warrant investigation of potential links to human-caused environmental degradation.

The few available long-term studies of amphibian populations have documented a variety of dynamics (Table 1). Instances of sharp declines in numbers and of possible extinctions have been the most widely publicized (see Barinaga 1990; Blaustein & Wake 1990; Phillips 1990; Tangle 1990). Two such cases, involving rather unique species, the gastric brooding frog and the golden toad, have received much attention. The gastric brooding frog (*Rheobatrachus silus*) was discovered in 1973 in relatively undistributed areas of the Conondale and Blackall Ranges about 160 km north of Brisbane, Australia (Liem 1973; Fanning et al. 1982). 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 & Carter 1981). Its decline began in the late 1970s, and the species has not been found in nature since 1979 (Tyler & 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. While this species does seem to have gone extinct, it is not unusual for some species to go undetected for a number of years.

The golden toad (*Bufo periglenes*) is a sexually dimorphic species endemic to Costa Rica (Crump et al. 1992). Males are brilliant orange and females are brightly mottled. Each year from the early 1970s 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 (Crump et al. 1992), but recruitment was nearly zero. From 1988 to 1990, only 11 adult toads were found (Crump et al. 1992). While it appears that golden toad numbers had drastically dwindled, it is also possible that adult *B. periglenes* are estivating below ground in response to unfavorable weather conditions, and they 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 & Trueb 1986), and many toad species within the same genus can live for more than 10 years (Bowler 1977). Thus, golden toad populations are probably able to 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 are also poorly understood.

Declaring either the golden toad or the gastric brooding frog extinct should obviously be done with caution. 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, we cannot reject the possibility that, under natural conditions, these species often undergo large fluctuations in numbers.

Semb-Johansson's (1989) study of common toads (*B. bufo*) on islands off the Norwegian coast is one of the

best examples of a long-term population study of an amphibian. Toads were monitored from 1966 to 1989; their numbers declined dramatically from 1966 to 1975 and remain low. The trend of declining numbers suggests population instability, but this species can live for 36 years (Goin et al. 1978). As with the golden toad, the populations may be undergoing natural fluctuations in number; years with strong recruitment often may be followed by years of poor reproduction during which the population declines. With a year or two of successful reproduction by older individuals, the populations could rapidly rebound from their current low.

Corn and Fogleman's (1984) study of leopard frogs (*Rana pipiens*) in Colorado is an excellent, if rare, example of a relatively long-term study documenting extinction of an amphibian 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 *R. pipiens* were seen at any site; the species was absent from the area at the end of the study. Because *Rana pipiens* older than four or five years are rare (Leclair & Castanet 1987), these populations were followed for almost two turnovers. The question remains, how unusual are such extinctions of *R. pipiens* populations?

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

There are some amphibian species whose populations have been studied long enough to allow a convincing argument that recently observed declines in their numbers are unusual. Our knowledge of the declines for many of these species is primarily based on range reduction information rather than on demographic data per se. Thus, it is clear that certain populations of amphibians 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. For example, until the mid-1970s the red-legged frog (*Rana aurora*) was extremely abundant in the Willamette Valley of Oregon, a relatively large valley (160 km by 60 km) bounded by the Coastal and Cascade Mountain ranges (Nussbaum et al. 1983; Blaustein & Wake 1990). *Rana aurora* is now extremely rare, and breeding populations have not been observed for at least 20 years in the Willamette Valley (R. M. Storm, personal communication; Blaustein & Wake 1990).

The western spotted frog (*Rana pretiosa*) was abundant throughout Washington and Oregon until the mid-1970s (Nussbaum et al. 1983; McAllister & Leonard

1990), but it has become extremely rare in the western portion of its range (Nussbaum et al. 1983; Stebbins 1985; McAllister & Leonard 1990, 1991). 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 (Nussbaum et al. 1983; McAllister & Leonard 1990, 1991). 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-1970s.

Based on historical accounts, museum records, and intensive searches at 16 sites, Fellers and Drost (1993) concluded that populations of Cascades frog (*Rana cascadae*) in northern California have exhibited a precipitous decline for more than 15 years. Long-term disappearances and declines have been reported for several other species (Table 1).

Range reduction information, 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 (Walls et al. 1992). The Pacific Northwest is of special concern because 54% of the native Oregon amphibian species 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).

On the other hand, some amphibian populations monitored during the last two decades have persisted with relatively little fluctuation in numbers. According to Hairston (1987), the longest population study of any terrestrial salamander species is that of *Plethodon jordani* in North Carolina (Hairston 1983). Two sets of data, one covering five years (1973–1977) and the other covering eight years (1974–1981), were collected. Sympatric populations of *P. glutinosus* were also monitored for five years. The numbers of salamanders per plot fluctuated little over time, and the age structure appeared stable. Hairston (1987:40) concluded that the *Plethodon* populations were "remarkably stable and demonstrate that assumptions of equilibrium populations in those species appear to be justified." As Hairston points out, however, this study did not span a turnover time (approximately 15 years) of the salamander populations. Given their relatively long mean generation time and high survival rates (9.8 years mean generation time and 0.81 survival per year for *P. jordani*; Hairston 1983), the apparent stability in their numbers may simply reflect the persistence of long-lived individuals.

Jaeger (1980) monitored *P. cinereus* and *P. shenandoah* for 14 years. Populations of *P. cinereus* have been

remarkably stable over that time, whereas *P. shenandoah* populations have declined to near extinction, probably due to competition with *P. cinereus* (Jaeger 1970, 1980).

Pechmann et al. (1991) monitored populations of three species of aquatic salamanders and one species of frog in an ephemeral pond in the southeastern U.S. for 12 years (1979–1990). Although the populations of these species fluctuated, there was no evidence of a drastic decline in any them. Population monitoring of at least one of the salamander species (*Ambystoma talpoideum*) spanned more than one population turnover. Clearly, not all amphibian populations have suffered dramatic declines in numbers in recent times. Detailed study of such cases is central to any comprehensive investigation of the hypothesis that a global amphibian decline is occurring.

Monitoring Amphibian Populations and Assessing Extinctions

We suggest that the best method for assessing amphibian populations is to mark and release as many individuals as possible (see Gill 1978a, 1978b; see Krebs 1989 for a discussion of this technique). This can be done relatively easily in populations of amphibians that are explosive breeders and use the same discrete body of water from year to year (see review in Olson et al. 1986). For example, in many explosively breeding anurans, presumably most if not all adults aggregate conspicuously in breeding masses for a relatively short time (see reviews by Wells 1977; Olson et al. 1986). Individuals can be captured, marked, and released unharmed. By marking adults, accurate estimates of adult population sizes can be made and trends in population fluctuations can be assessed. If all the adults of a particular species are missing from their natural breeding site for a specified period of time (such as one turnover), we would consider the population to be extinct.

For some species, it is impossible to mark all the adults of a population. For example, it may be difficult to monitor adults of species that do not breed explosively, those that breed while hidden in vegetation, nonaggregating species, or those not confined to a particular breeding lake or pond. If capturing and marking adults is not practical, then it is difficult to determine if a population is in decline. This is an open demographic and statistical question that will be difficult to model in general because of the highly variable life-history characteristics of amphibians.

When amphibians fail to appear at known breeding sites and no proximal explanation (such as a dry pond) is available, it may be a matter of concern for conservation biologists. This is a special problem for many species of amphibians that breed for only a short period

each year. It is theoretically possible for a population to recover its earlier strength (measured in terms of numbers of breeding adults, or effective population size) when it has been reduced to only a few adults. But it is likely that a population that consists only of a remnant of very old individuals following a period of unsuccessful breeding seasons is in danger of extinction (see below). In making judgments and management decisions in such circumstances, use could be made of survivorship curves based on the proportion of individuals metamorphosing in a given year that survive to succeeding years. What is required for making judgments about the likelihood of survival of a local population of frogs is sufficient information on turnover and patterns of survivorship for conservation biologists to know that the population may be in severe trouble. In making judgments about the likelihood of persistence of a local population, attention must be given to the age distribution of the population, as well as to the potential capacity of the population to rebound quickly, by either recruitment or immigration. If a population has been recruiting poorly for several years and there is no immediate or obvious explanation, there may be cause for concern even in the absence of long-term data.

Nonequilibrium Dynamics and Metapopulations

The extinction of a rare or endangered species or local population may occur through a variety of mechanisms, including habitat destruction or fragmentation (Lande 1987) or natural stochastic processes (Allee et al. 1949; Andrewartha & Birch 1954). Natural fluctuations and sporadic extinction and colonization of local populations is the essence of the nonequilibrium view of community dynamics (see Hutchinson 1951; Andrewartha & Birch 1954; Connell 1978; Sousa 1979; Strong 1983; Chesson 1986; Davis 1986; Murdoch 1991).

Associated with the nonequilibrium viewpoint is the concept of the metapopulation (Levins 1969, 1970), which examines the population dynamics of a single species across a collection of spatially separated subpopulations (Lande 1987; Hanski 1991; Hanski & Gilpin 1991; see also Allee et al. 1949:328). A metapopulation is a set of geographically discrete local populations occupying suitable habitats (Levins 1969, 1970). If the extinction rate for a given local population exceeds the colonization rate, that population will become extinct (see discussions in Andrewartha & Birch 1954; Lande 1987; Hanski & Gilpin 1991). Extinction is not inherent to the concept of the metapopulation; it is one population dynamic phenomenon that is potentially influenced by spatial subdivision. While local extinctions can occur, populations can persist regionally.

For most species, it seems evident that immigration and colonization rates decrease with increased patch

isolation (Harrison 1989; Sjogren 1988, 1991; Harrison & Quinn 1989). It is more likely that a smaller number of immigrants can successfully "rescue" an extant population than colonize a new area (see Ebenhard 1991; Sjogren 1991 and references therein). Moreover, increased patch isolation has been correlated with decreased fitness in those individuals inhabiting isolated patches (see Fahrig & Merriam 1985). Thus, the rescue effect is important for population persistence and has important conservation implications (see Ray et al. 1991; Sjogren 1991). Although dispersal between patches and recolonization of vacant patches have been generally regarded as stochastic processes, the colonization process may be more deterministic, especially if dispersers are attracted to areas where conspecifics reside (Smith & Peacock 1990; Ray et al. 1991). Furthermore, the genetic composition of conspecifics in a patch may influence the behavior of a dispersing individual. Members of many species are positively attracted to related individuals (Blaustein et al. 1987), and they may be attracted to areas where there are kin.

The breeding sites of many amphibians (such as ponds, lakes, streams) may be subdivided into local populations. Populations of many amphibian species seem to display nonequilibrium dynamics, with periodic extinctions, recolonizations, and patchy spatial arrangements (for example, see Duellman & Trueb 1986; specific examples are provided by Gill 1978a; Corn & Fogleman 1984; Sjogren 1988, 1991; Berven 1990). Sjogren (1991) suggests that the extinction of certain amphibian populations is analogous to extinction patterns associated with severe habitat fragmentation when local populations become extinct and recolonization does not readily occur due to unsuitable habitat between extant and extinct groups. This, he says, may explain the sudden disappearance of amphibians from relatively undisturbed habitats. Indeed, this may explain the decline in numbers of several species of anurans found in relatively undisturbed areas of the Pacific Northwest (Blaustein & Wake 1990).

In many areas of western North America, amphibian habitat has become altered and fragmented. Anthropogenic habitat alteration may hamper recolonization. For example, Bradford's (1991) study of the mountain yellow-legged frog (*Rana muscosa*) shows that it has become extinct at many high elevation sites in the Sierra Nevada of California. Recolonization may never occur because streams connecting extant populations of *R. muscosa* are inhabited by introduced fish that eat larvae of *R. muscosa* (Bradford 1991).

The tailed frog (*Ascaphus truei*) is extremely philopatric (Daugherty & Sheldon 1982), and much of its habitat in the Pacific Northwest has been logged, with detrimental effects on its disjunct population structure (Corn & Bury 1989). Corn and Bury (1989) estimated that if *A. truei* were extirpated from certain areas, re-

establishment might take 14–40 years. Lehmkuhl and Ruggiero (1991) compiled a list of species associated with late successional Douglas Fir forests in the Pacific Northwest and modeled the risk for each species of local extinction from habitat loss or fragmentation. This model was based on the frequency of occurrence, abundance, body size, and vagility of the species. Twelve (80%) of the 15 amphibian species listed by Lehmkuhl and Ruggiero (1991) were considered to be of moderately high to high risk of extinction if their habitats were to become fragmented.

The population processes and patch dynamics of amphibians may vary regionally. For example, certain areas of the southeastern U.S. have extremely diverse and abundant amphibian fauna, with relatively dense populations and continuous suitable habitat (Wake 1991). If populations go extinct locally in these regions, it seems likely that the probability of recovery will be high. In other localities, such as in certain mountainous regions of western North America, many species live in habitats that are localized or fragmented, and opportunities for recolonization may be much lower.

Constraints on Amphibian Recolonization Following Local Extinction

In many regions, recolonization of sites vacated due to extinction of a local population may be difficult for amphibians because of (1) physiological constraints, (2) the tendency of many amphibians to move relatively short distances, and (3) because many amphibian species show extreme site fidelity.

Physiological Constraints

Although amphibians are found in a wide array of habitats, including some that are unsuitable to endotherms (Pough 1980; Duellman & Trueb 1986), they are often limited to areas where there is sufficient moisture for reproduction and survival (see Jaeger 1970, 1990; Duellman & Trueb 1986; Pough et al. 1989; Sinsch 1990). In general, amphibians—especially the more terrestrial species—are found in patches of suitable habitat surrounded by conditions that are relatively harsh to them. The glandular thin skin of amphibians lacks covering (such as mammalian hair or bird feathers) and is permeable to water (Duellman & Trueb 1986). Therefore, evaporative water loss may become a serious problem for individuals moving from one area to another (Sinsch 1990). Furthermore, because amphibians are ectotherms, they spend a great deal of time undergoing behavioral thermoregulation to avoid extremely high or extremely low temperatures (review in Duellman & Trueb 1986; Sinsch 1990). The demands of water balance and thermoregulation may limit the movements of amphibians. Movements may occur only during a nar-

row range of environmental conditions and are often limited to relatively short periods during the annual activity period (Sinsch 1990).

Movement Patterns

Amphibians generally move smaller distances than do other small-bodied tetrapods (Sinsch 1990). Small mammals, birds, and reptiles may move great distances during migrations and generally seem to move longer distances than amphibians on a daily basis (Cockrum 1962; Orr 1970, 1982; Southern 1979; Welty & Baptista 1988). Home-range sizes of terrestrial small mammals including small-bodied rodents are often several hectares in size (Cockrum 1962; Southern 1979; Vaughan 1986). Reptiles may be extremely mobile. Snakes may move hundreds of meters in several days (see Stickel & Cope 1947) or several kilometers within a few months (Porter 1972). Snake home ranges are often several hectares in size (Porter 1972). Desert tortoises (*Gopherus agassizi*) may have home ranges comprising dozens of hectares (Orr 1982). Lizards may have home ranges comprising thousands of square meters (Stamps 1983).

Although certain amphibian species may move a few thousand meters toward their summer home ranges during the spring migration (Sinsch 1990), in general amphibians move significantly smaller distances than do many other tetrapods. Semlitsch (1981) tracked mole salamanders (*Ambystoma talpoideum*) in their summer home ranges and found that their centers of activity were between 0.02 and 0.21 m². Kleeberger and Werner (1982) tagged *Plethodon cinereus* with a radioactive isotope and estimated that their daily average movement was 0.43 m; their home ranges were about 12.97 m² for males and 24.34 m² for females. Similarly tagged *Desmognathus* salamanders showed an average home range of only 0.1–3.6 m² (Ashton 1975). Even the generally more mobile anurans do not move great distances. For example, Jameson (1956) estimated that Pacific treefrogs (*Hyla regilla*) disperse less than 200 m. *Hyla cadaverina* studied by Harris (1975) moved an average distance of only 3 m per day. Common toads (*Bufo bufo*) may move as much as 50–100 m per day (Sinsch 1990). Male yellow-bellied toads (*Bombina variegata*) may move 63.8 m during a breeding season, whereas females may move only 20 m (Beshkov & Jameson 1980). The home ranges for poison dart frogs (*Dendrobates pumilio*) in Costa Rica were 2.26 m² to 15.11 m² (Donnelly 1989).

Site Fidelity and Homing

Like other vertebrates (see Greenwood 1980), amphibians of many species display extreme site fidelity (Shields 1982; Duellman & Trueb 1986; Sinsch 1990). Field experiments of numerous amphibian species illus-

trate that they are able to home relatively long distances if they are displaced. For example, although the home range for *Desmognathus ochrophaeus* was estimated to be less than 1 m² by Holomuzki (1982), individuals that were displaced more than 30 m returned to their original site. Similarly, Kleeberger and Werner (1982) noted a 90% return rate of *Plethodon cinereus* displaced 30 m from the center of their home ranges. Newts (*Taricha rivularis*) that were displaced 8 km returned to their home area within one year (Twitty et al. 1967). Of 83 treefrogs (*H. regilla*) displaced about 274 m, 77% returned to their site within a month (Jameson 1957). Numerous nonexperimental mark and release studies illustrate that many amphibian species show extreme site fidelity (see discussions in Duellman & Trueb 1986; Sinsch 1990; specific examples are provided by Brattstrom 1962; Gill 1978b; Breden 1987; Carpenter & Gillingham 1987; Berven & Grudzien 1990).

Thus, due to relatively short distances traveled, site fidelity, and physiological constraints, amphibians may not readily recolonize locally extirpated populations. For example, O'Hara and Blaustein (unpublished data) have monitored *R. cascadae* in the central Cascade Mountains of Oregon since the mid-1970s. Adults and larvae of *R. cascadae* disappeared at one site in July 1977. The species was missing at that particular site until 1989, when eggs were laid and tadpoles emerged. Recolonization did not occur for 12 years despite the presence of a population of *R. cascadae* only 2 km from the site.

Conclusions

The proposition that amphibian populations are undergoing a world-wide decline in numbers is somewhat weakened by the absence of long-term information on "typical" or "natural" patterns of numerical fluctuation in such populations. Such baseline information is essential to an objective evaluation of the hypothesis of global amphibian decline. Nonetheless, a number of the available long-term records strongly indicate unusual declines or local disappearances of some species. In such cases, links to environmental degradation should be investigated.

We strongly recommend initiation of long-term monitoring programs in conjunction with experimental tests of the hypothetical causes of decline on a wide variety of amphibian species. If possible, such studies should span at least one complete turnover of the monitored population. Whenever possible, all adult individuals should be marked and released so that longevity and survivorship can be accurately estimated. Recognizing that many amphibians live within metapopulations, these estimates should be made at more than one location for a particular species so that erroneous conclusions are not drawn regarding the overall population

status. Due to (1) physiological constraints that, in most cases, limit amphibians to moist habitats, (2) relatively low movement patterns, and (3) site fidelity, we argue that when local amphibian populations become extinct they may be less likely to recolonize than other tetrapods.

Acknowledgments

We thank Russell Lande, Martha Crump, Bruce Menge, Frank A. Pitelka, T. Beebee, Susan Walls, and several anonymous reviewers for critically reviewing our paper. The comments of the editors, David Ehrenfeld, and Gary Meffe were most helpful. We also thank Arne Semb-Johansson for his notes on the ecology of *Bufo bufo*. Additional aid was provided by Jim Vial, Lorelei Saylor, Dennis Carson, Vic Marswell, and Peter Warne. Financial support for the writing of this paper and for conducting research on amphibian populations was kindly provided to A. R. Blaustein by the National Geographic Society, the U.S. Forest Service, and the National Science Foundation (BSR-9024880).

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