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GLOBAL AMPHIBIAN DECLINES: A PROBLEM IN APPLIED ECOLOGY

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■ **Abstract** Declines and losses of amphibian populations are a global problem with complex local causes. These may include ultraviolet radiation, predation, habitat modification, environmental acidity and toxicants, diseases, changes in climate or weather patterns, and interactions among these factors. Understanding the extent of the problem and its nature requires an understanding of how local factors affect the dynamics of local populations. Hypotheses about population behavior must be tested against appropriate null hypotheses. We generated null hypotheses for the behavior of amphibian populations using a model, and we used them to test hypotheses about the behavior of 85 time series taken from the literature. Our results suggest that most amphibian populations should decrease more often than they increase, due to highly variable recruitment and less variable adult mortality. During the period covered by our data (1951–1997), more amphibian populations decreased than our model predicted. However, there was no indication that the proportion of populations decreasing changed over time. In addition, our review of the literature suggests that many if not most amphibians exist in metapopulations. Understanding the dynamics of amphibian populations will require an integration of studies on and within local populations and at the metapopulation level.

INTRODUCTION

The current wave of interest in amphibian population biology and in the possibility that there is a global pattern of decline and loss began in 1989 at the First World Congress of Herpetology (10). By 1993 more than 500 populations of frogs and salamanders on five continents were listed as declining or of conservation concern (189). There is now a consensus that alarming declines of amphibians have occurred (30, 51, 125, 147, 192). Because most amphibians are exposed to terrestrial and aquatic habitats at different stages of their life cycles, and because they have highly permeable skins, they may be more sensitive to environmental toxins or to changes in patterns of temperature or rainfall than are other terrestrial vertebrate

TABLE 1   Techniques used in 46 studies[1] to quantify populations of frogs salamanders. Many studies used more than one technique or studied both taxa, so the total number of techniques used does not equal the number of studies cited.

Technique	Habitat[2]	Frogs	Salamanders
Egg mass counts	B	4	1
Counts of individuals	B	12	1
Drift fence/pit trap counts	B	7	8
Mark-recapture estimates[3]	B	7	2
Calling male counts	B	3	N/A
Dipnet samples for larvae	B	2	2
Counts of individuals	N	1	6
Mark-recapture estimates	N	0	1
Aquatic traps	N	0	1

[1]Sources used in compiling table: 15, 19, 20, 21, 41, 49, 53, 54, 63, 64, 73, 83, 84, 86, 88, 90, 91, 92, 96, 102, 107, 111, 113, 117, 131, 136, 137, 142, 157, 158, 159, 160, 161, 165, 169, 170, 171, 174, 177, 178, 179, 180, 181, 194, 196, 202.

[2]B = Breeding, N = Non-breeding.

[3]Includes, in descending order of frequency used, Jolly-Seber, Petersen, Manly-Parr, Schnabel, and Zippin techniques.

groups (29, 190). The best-documented declines have occurred in Europe and North America, are usually associated with habitat modification (87, 116), and are often attributed to interactions among causal factors (114, 125, 147). The factors associated with population declines in relatively undisturbed habitats such as montane tropical rainforests have been more difficult to elucidate (131, 163).

Although they have been the subject of many experimental and monitoring studies, the autecology of amphibians in nature is poorly understood (87). The majority of studies of ecology and population biology of amphibians (Table 1) have been conducted on aggregations at reproductive sites. Relatively little is known of their movements or activities away from breeding sites, or of rates of exchange between populations.

Many authors have suggested that there is a need for long-term studies directed toward a combination of understanding ecological theory and increasing knowledge of the autecology of amphibians (17, 39, 79, 80, 190). Simple long-term programs that monitor the fluctuations of single populations and associated environmental factors, and then apply standard population models, are unlikely to be useful for understanding the dynamics of amphibian populations as they have not worked for that purpose when applied to other terrestrial vertebrates (164). It appears likely that understanding the problem of amphibian declines will require much more information on the ecology of the metapopulations in which many species live (87).

Our goals in this review are to summarize and synthesize the literature on potential causes of amphibian declines, and to use the literature on amphibian population dynamics to develop a null hypothesis for the behavior of amphibian populations. We then use our null hypothesis and data from the literature to determine whether the incidence of declines has recently increased. Finally, we place the dynamics of amphibian populations and their declines in the context of metapopulation dynamics.

POTENTIAL CAUSES OF AMPHIBIAN DECLINES

Ultraviolet Radiation

Depletion of stratospheric ozone and resultant seasonal increases in ultraviolet B (UV-B) radiation at the Earth's surface (119) have stimulated interest in the possible relationship between resistance of amphibian embryos to UV-B damage and population declines. Significant variation among species in levels of photolyase, a photoreactivating DNA repair enzyme that repairs UV-B damage, is correlated with exposure of natural egg deposition sites to sunlight (25, 98). In a survey of 10 Oregon amphibian species, photolyase activity, and hence ability to repair UV damage, was lowest in declining species and highest in nondeclining species (25). Field experiments demonstrated that embryos of *Hyla regilla*, a non-declining species with high photolyase activity, had significantly higher hatching success than did two declining species (*Rana cascadae* and *Bufo boreas*) with low photolyase levels (25).

A number of other studies have demonstrated that ambient (6, 24, 28, 132) or enhanced (144) UV-B radiation reduces survival or hatching success of amphibian embryos. Synergistic interactions between UV-B and other environmental stresses such as pathogens (120) and low pH (133) may also significantly increase embryonic mortality. *Rana pipiens* embryos that are unaffected when exposed to UV-B and low pH separately have significantly reduced survival when exposed to these factors simultaneously (133).

Other studies have produced more equivocal results. *Rana aurora* is a declining species with high levels of photolyase (98), and experimental hatching success is unaffected by exposure to UV-B (26). The declining frog *Litoria aurea* from eastern Australia has a lower photolyase activity than two sympatric nondeclining species, *L. dentata* and *L. peroni*, but there is no significant difference among the three species in hatching success under UV-B exposure (187). In many aquatic habitats UV-B radiation is largely absorbed in the first few centimeters of the water column (138), so increased UV-B may only affect species breeding in habitats with a narrow range of chemical and physical parameters. Ecologically relevant levels of UV-B had no effect on embryos of several Canadian amphibians, and experimental protocols used to test UV impacts have been questioned (85, 130).

Most studies that have examined the relationship between UV-B and population declines have focused their attention on species that breed in shallow, clear water,

where exposure to UV-B is expected to be greatest (6, 25, 28, 132). Exposure to intense UV-B in shallow high-altitude ponds may exclude amphibians from these habitats (138).

Even when UV-B causes higher embryonic mortality in declining species, the ecological significance of this at the population level is difficult to assess. More needs to be understood about the basic natural history of amphibian species that might be at risk. For example, information is needed on variation in oviposition site characteristics (depth, vegetation) within local populations. Experiments at "natural oviposition sites" using embryos of *Ambystoma macrodactylum* were conducted in shallow water although this species lays eggs in a variety of microhabitats (28). Loss of a large proportion of near-surface clutches to UV-B damage may have negligible impacts on populations if even a small number of deeper clutches survive, as the survivors are released from density-dependent effects (1).

Even fewer data are available to assess the indirect effects of increasing UV-B on amphibian populations. Potential indirect effects include changes in water chemistry and food supplies, and shifts in competitive and predator-prey relationships with other UV-B affected species (143). Exposure to increased UV-B may reduce survival rates of adult amphibians through damage to eyes (77), increased frequency of cancers or tumors (143), and immunosuppression (143).

Predation

Biotic interactions among amphibians, and between amphibians and other organisms, can play a significant role in determining their distribution and population dynamics (1). Larval amphibians are extremely vulnerable to vertebrate and invertebrate predators (1), and the diversity of aquatic amphibian assemblages is frequently reduced in habitats containing predatory fish (1, 100).

Larval amphibians that coexist with aquatic predators have evolved a range of antipredator mechanisms (4, 48, 118). However, widespread introductions of predatory fish have increasingly exposed native amphibians to predators with which they have not previously interacted. Inappropriate responses to novel predators may increase mortality of native amphibians (82, 121), leading to significant effects on populations.

Colonization of normally fish-free water bodies by predatory fish can result in rapid extinction of amphibian assemblages (76). The allotopic distributions of native frogs and introduced fishes in many high-elevation (>2500 m asl) Sierra Nevada lakes indicate that introduced predatory fishes have caused the extinction of local frog populations there (31). Sixty percent of lakes that frogs could formerly occupy now contain introduced fishes and no frogs. Fish introductions have had a particularly severe impact on *Rana muscosa*, which breeds in the deep lakes inhabited by fishes (31). A similar pattern of allotopic distributions has been recorded for larval newts, *Taricha torosa*, and an introduced fish (*Gambusia affinis*) and crayfish (*Procambarus clarki*) (both predators of newt eggs or larvae) in Californian mountain streams (82).

Introduced predators may also have more subtle effects. Some *Rana muscosa* populations persisting in fish-free environments have become isolated from other populations by surrounding aquatic habitats containing introduced fishes. This may eventually lead to regional extinction by preventing migration among local populations (35).

North American bullfrogs (*Rana catesbeiana*) that have become established outside their natural range have been implicated in declines of native frogs (76, 102, 127, but see 97). Adult bullfrogs consume native frogs and reach densities at which they are likely to have a severe impact on local amphibian populations (166). Experimental studies have shown that *Rana aurora* larvae exposed to adult or larval bullfrogs have increased larval periods, smaller mass, and, when exposed to both, lower survival (122).

Humans have devastated frog populations in several countries for the frog-leg trade. Before 1995, about two hundred million frogs were exported annually from Asia. By 1990 India was still illegally exporting approximately seventy million frogs each year, resulting in serious population declines (145).

Habitat Modification

Habitat modification is the best documented cause of amphibian population declines. Habitat loss certainly reduces amphibian abundance and diversity in the areas directly affected (99, 101). Removal or modification of vegetation during forestry operations has a rapid and severe impact on some amphibian populations (8). Clearcutting of mature forests in the southern Appalachians has reduced salamander populations by almost 9%, or more than a quarter of a billion salamanders, below the numbers that could be sustained in unlogged forests (149). Logging exposes terrestrial amphibians to drastically altered microclimatic regimes (9), soil compaction and desiccation, and reduction in habitat complexity (197). It exposes aquatic amphibians to stream environments with increased siltation (52) and reduced woody debris (43). Although populations may recover as regenerating forests mature, recovery to predisturbance levels can take many years (9) and may not occur at all if mixed forests are replaced with monocultures (108).

Draining wetlands directly affects frog populations by removing breeding sites (116), and by fragmenting populations (74, 168), which increases the regional probability of extinction (e.g. 53). Modification of terrestrial and aquatic habitats for urban development can reduce or eliminate amphibian populations. Populations of some amphibians in urban Florida declined after degradation of upland, dry season refuges and modification of wetlands used for breeding (62). Protection of aquatic breeding sites may be of little value if adjacent terrestrial habitats used by amphibians for feeding and shelter are destroyed (167).

More subtle alterations to habitat structure can have severe impacts on amphibian populations. *Bufo calamita* populations in Britain declined over a 40-year period due to shifts in land use practices that altered vegetation characteristics (13). Changing vegetation structure and an associated increase in shading were

detrimental to *B. calamita* and provided conditions under which the common toad *Bufo bufo* became a successful competitor.

Although habitat alterations can reduce amphibian populations, in some cases even severe habitat modifications can have little effect. The response of a savanna woodland frog assemblage at Weipa, Queensland, Australia to strip mining appears in Figure 1 (200). The structure and floristics of the plant assemblage at 60 revegetated sites vary widely; none strongly resemble the original native woodland.
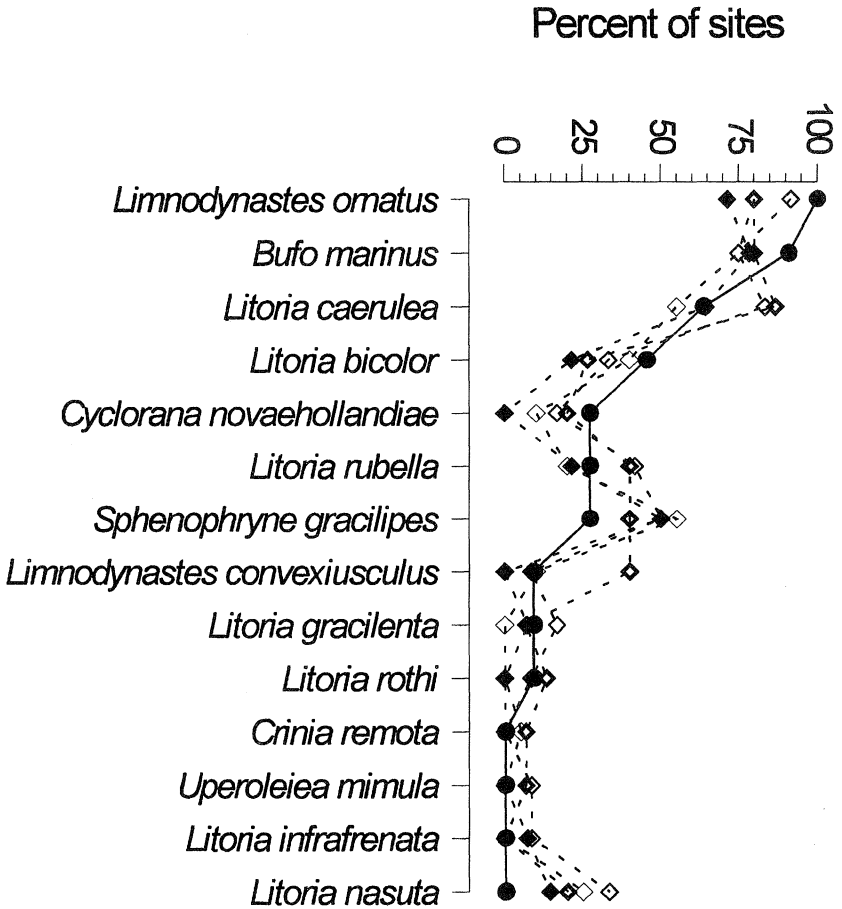
Figure 1   Profiles of percent of sites of five habitat types at Weipa, Queensland, Australia at which frogs of 14 species occurred. Species sorted in order of frequency of occurrence in native woodland. Dots and solid lines indicate native woodland habitat (13 sites). Diamonds and dashed lines indicate sites revegetated following strip mining. Density of diamonds reflects age of revegetation; from least to most dense this is: age ≤7 years, 7 years < age ≤ 10.5 years, 10.5 years < age ≤ 16 years, age >16 years. There were 15 revegetation sites in each age group in the survey.

The distance from revegetation sites to native woodland varies from a few meters to over 1 km. Despite this, within 7 years, the majority of frog species occur at revegetation sites at frequencies very similar to the frequencies at which they are found at sites in native woodland. This indicates that the frogs in this assemblage are insensitive to radical alterations in the soil characteristics, flora, and structure of their terrestrial habitat, and they can recolonize rapidly following disturbances that have eliminated them over a relatively wide area. It is possible that other amphibian species assemblages behave similarly.

Acidity and Toxicants

The acidity of aquatic habitats has major impacts on amphibian distribution, reproduction, and egg and larval growth and mortality (78, 79). Sensitivity to low pH varies among (79) and within (150) species and is influenced by complex chemical interactions among pH and other factors, particularly aluminum concentration (71, 110, 151). Mortality occurs in both the embryonic and larval stages via several mechanisms including incomplete absorption of the yolk plug, arrested development, and deformation of larvae (11, 79, 109). Sublethal effects of acidification include delayed (109) or early (36) hatching, reduced larval body size (36), disturbed swimming behavior (5), and slower growth rates resulting from reduced response to, and capture of, prey (155). Indirect sublethal effects include changes to tadpole food sources through impacts on algal communities (188), and shifting predator-prey relationships resulting from differential mortality of predatory fish and invertebrates in acidified habitats (104).

The population-level effects of acidity are less well understood. It is possible that the effects of low pH, in combination with other abiotic factors, lead to decreased recruitment into adult populations (12). Acidic breeding sites often contain less diverse amphibian assemblages, at lower densities, than do less acidic sites (205). Long-term acidification of ponds in Britain has excluded *Bufo calamita* from many sites (16). Reduced pH and increased metal concentrations in an Appalachian stream eliminated virtually all salamander larvae, causing severe long-term declines in populations of *Desmognathus quadramaculatus* and *Eurycea wilderae* (124). Low soil pH also influences the distribution, abundance, and diversity of terrestrial amphibians (204, 205).

Despite the well-documented effects of low pH on amphibians, there are few data to implicate acidification in recent, unexplained catastrophic population declines. Acid deposition was proposed as a factor in the decline of tiger salamanders, *Ambystoma tigrinum*, in the Rocky Mountains (96), but subsequent field studies demonstrated that mortality due to pond drying was equally likely to be the cause of this decline (201). Acid deposition is unlikely to be involved in population declines of frogs and salamanders at high altitudes in the Sierra Nevada Mountains (33, 34, 36) and Rocky Mountains (54, 55, 188, 201). There may be no rigorously documented cases where acidification of natural habitat has led to the extinction of an amphibian population (71). However, studies of acid tolerance have been biased toward species that are likely to have evolved tolerance to low pH (195).

Similarly, although there is an extensive literature on the toxic effects on larval amphibians of metals and chemicals used in insecticides and herbicides (154), insufficient data exist to determine their long-term impacts on amphibian population dynamics (22). Environmental toxicants act directly to kill animals, or indirectly by impairing reproduction, reducing growth rates, disrupting normal development and reproduction (endocrine disruption), or increasing susceptibility to disease by immunosuppression or inhibition of immune system development (22, 46).

Diseases

Little is known about the diseases of wild amphibians. Many disease agents are present in healthy animals, and disease occurs when immune systems are compromised (56, 57). Declines in populations of *Bufo boreas boreas* between 1974 and 1982 were associated with *Aeromonas hydrophila* infection, but Carey (47) suggested that environmental factor(s) caused sublethal stress in these populations, directly or indirectly suppressing their immune systems. A pathogenic fungus largely responsible for egg mortality in one population of *Bufo boreas* in Oregon may have been more virulent to embryos under environmental stress (27).

Epidemics can cause mass mortality of amphibians (123). In 1981 *Aeromonas hydrophila* killed all larval *Rana sylvatica* in a Rhode Island pond, and three years later few adult frogs were breeding at this site (141). The same bacterium was implicated in a well-documented decline to local extinction of a population of *Rana muscosa* in California (32). A chytridomycete fungus found on moribund anurans in Australia and Panama during mass mortality is fatal to healthy frogs under experimental conditions (18). This fungus was proposed as the proximate cause of declines in these two regions (18), but this hypothesis is untested at present.

Viruses have been isolated from dead and dying frogs during mass mortality events (59, 60) and may be the primary cause of mortality in animals where other infections such as bacteria have been identified (57). Laurance et al (129) argued that the pattern of population declines among Australian rainforest frogs was indicative of a "wave" of epidemic disease caused by an unidentified waterborne virus. This interpretation was challenged (3, 106) on statistical grounds and because numerous other explanations for the observed patterns were equally parsimonious. The involvement of a virus in these declines has now been largely discounted, but the possible involvement of a disease has not. The pattern of population declines in Central America has also led to the suggestion that a wave of epidemic disease might be responsible (131).

Climate/Weather

Immediately prior to the disappearance of golden toads, *Bufo periglenes*, the rainforests of Monteverde, Costa Rica, had the lowest twelve-month rainfall in 20 years. Toads were forced to shift their habitat use, and the dry conditions may have interacted with an unidentified factor such as disease or a pulse of contaminants

in cloud water to eliminate toad populations (152). Unusual weather conditions were dismissed as a cause of declines of Australian rainforest frogs (128). This result relies on seasonal rainfall totals calculated for fixed groups of months, while in northern Australia the date of onset of the wet season is highly variable, occurring between October and February (140). The analysis is therefore likely to have missed the extremes and underestimated the variances of rainfall, and a reexamination of the data seems warranted. Severe, short-term climatic events such as violent storms can alter the dynamics of amphibian populations. Hurricane Hugo caused extensive damage to the forests of Puerto Rico in 1989. In the short term, populations of the terrestrial frog *Eleutherodactylus richmondi* decreased by 83%, but increased availability of ground cover due to disturbance led to a six-fold increase in the densities of *E. coqui*, followed by a long period of gradual population decrease (202, 203).

Alterations in local weather conditions caused by global climate change will influence the ecology of amphibians in a number of ways. The onset of spawning in *Rana temporaria* in Finland between 1846 and 1986 shifted earlier by 2–13 days, following shifts in air and water temperature and dates of snow cover loss (182). At some sites in Britain there has been a statistically significant trend toward earlier first sighting and spawning of *Bufo calamita*, *Rana esculenta*, and *R. temporaria* between 1978 and 1994, correlated with changing patterns of spring temperatures (14).

Amphibians in Canada are affected by decreases in summer precipitation and increased temperatures and winter rainfall (105, 143). In the neotropics, increased temperatures, extended dry seasons, and increasing inter-year rainfall variability may affect litter species by reducing prey populations and altering amphibian distributions on increasingly dry soil (67). Shifting rainfall patterns will affect the reproductive phenologies of pond-breeding species. Ponds will fill later and persist for shorter periods, leading to increased competition and predation as amphibians are concentrated at increasingly limited aquatic sites (67). Frogs exposed to these stresses may also become more vulnerable to parasites and disease (67).

Interactions Among Environmental Factors

Most studies invoke multiple causes or interactions among factors. Increased UV-B exposure may alter species interactions or vulnerability to pathogens or changes in pH. Predation may eliminate local populations and have larger-scale effects by altering rates of migration between populations. Outbreaks of disease may only occur when other stresses reduce immune function. Pesticides, pollutants, and environmental acidity may interact to produce unforeseen effects. All local effects may interact with global climate change. Proving the existence of these complex effects in natural populations will require well-planned programs of observation and experimentation. To plan such studies, and to determine how stresses affect population behavior, requires an understanding of the nature of the populations being studied and the limitations of study techniques. It also requires

the development of null hypotheses regarding how amphibian populations behave in the absence of external pressures.

DEFINING AND STUDYING AMPHIBIAN POPULATIONS

Monitoring and Censusing Techniques

We have summarized the techniques used in 46 long-term population studies of frogs and salamanders in Table 1. All but one of the studies of frogs were carried out at breeding sites, while about half of the studies of salamanders included at least some data collected on densities of animals in nonbreeding habitat. The most commonly used technique is direct counts, where animals are located by intensive searching, localization of calls, or by drift fences with pitfall traps. Many studies that reported direct counts also reported the results of mark-recapture estimates. Frequently, however, the standard errors of mark-recapture estimates are very large, so that counts are regarded as being better estimates. The high standard errors typically obtained in mark-recapture estimates of animals at breeding sites probably reflect the fact that the degree of attraction of breeding sites varies widely over time, as does the activity of individual animals near them.

Problems with Studying Breeding Aggregations as Populations

Most estimates of frog populations are expressed in units such as total numbers of frogs attending a pond, numbers of frogs per m^2 of pond area, and maximum numbers of frogs at a pond on a single night during the breeding season (70). The frog groups for which data are available on densities in nonreproductive habitat tend to be species that do not aggregate at breeding sites (70, 115, 203). A few studies have examined aquatic-breeding species in nonreproductive habitats (156, 206). The use of breeding aggregations in population studies can cause problems in data interpretation.

A simple illustration of why censusing amphibians at breeding sites can cause problems in the interpretation of population dynamics appears in Figure 2. The number of frogs per unit of nonreproductive habitat (the entire rectangle) remains constant at 50. In Figure 2a, neither of the temporary pools in the habitat contains water. If censuses are carried out by visiting pool 1, a census at the time of Figure 2a would detect only 7–10 frogs in the habitat. A census carried out after pool 1 filled (Figure 2b) would detect 43 frogs, while one carried out after both pools filled (Figure 2c) would detect only 23 frogs at pool 1. Similar variations in measured density could occur over time even if the pools remain filled, because of changes in the reproductive behavior of frogs. Changes in habitat availability and in the attractiveness of bodies of water are both likely to affect the numbers of amphibians detected (191), complicating the use of data of this type as an indication of the size or density of the population occupying the surrounding habitat. Because behavior and site attributes vary seasonally and temporally with weather
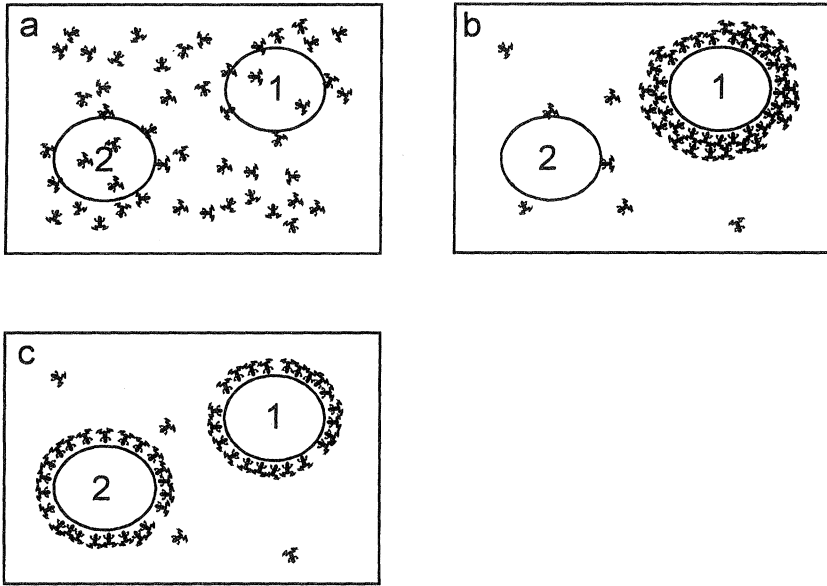
Figure 2   An illustration of the difficulties for data interpretation created by sampling animals in breeding aggregations. An area of habitat contains a fixed number of animals and two potential breeding sites. Surveys are carried out at site 1. In (*a*), animals are not attracted to breeding sites, so a census at site 1 would encounter only 9–10 individuals. In (*b*), animals are attracted to site 1, and a census would find 43 animals. In (*c*), animals are attracted to both sites, and a census at site 1 would encounter 22 animals. All of these situations may occur within a few days in many habitats, making counts at breeding sites highly variable.

and internal rhythms of the animals, the best hope for obtaining accurate estimates using censuses at breeding sites is to perform censuses frequently.

Effects of Sampling Intensity on Population Size Estimates

We used data collected by one of us (SJ Richards, unpublished data) on the number of adult males of the stream-breeding hylid *Litoria genimaculata* to investigate the effects of sampling intensity on the accuracy of count data taken at a breeding aggregation. A 60-m transect along a rainforest stream site was visited an average of 19 times each year over seven years. All frogs on the transect were counted, marked, and released. We used a resampling technique to explore how less intense sampling might have affected the results. We set the probability that a visit would occur to 0.75, 0.5, and 0.25, and resampled the data set 5000 times using each of these probabilities. It is apparent (Figure 3) that decreasing the intensity of sampling below about 0.75 times the number of visits actually made would greatly decrease the accuracy of the annual means obtained. At intensities of 0.5, 0.25,
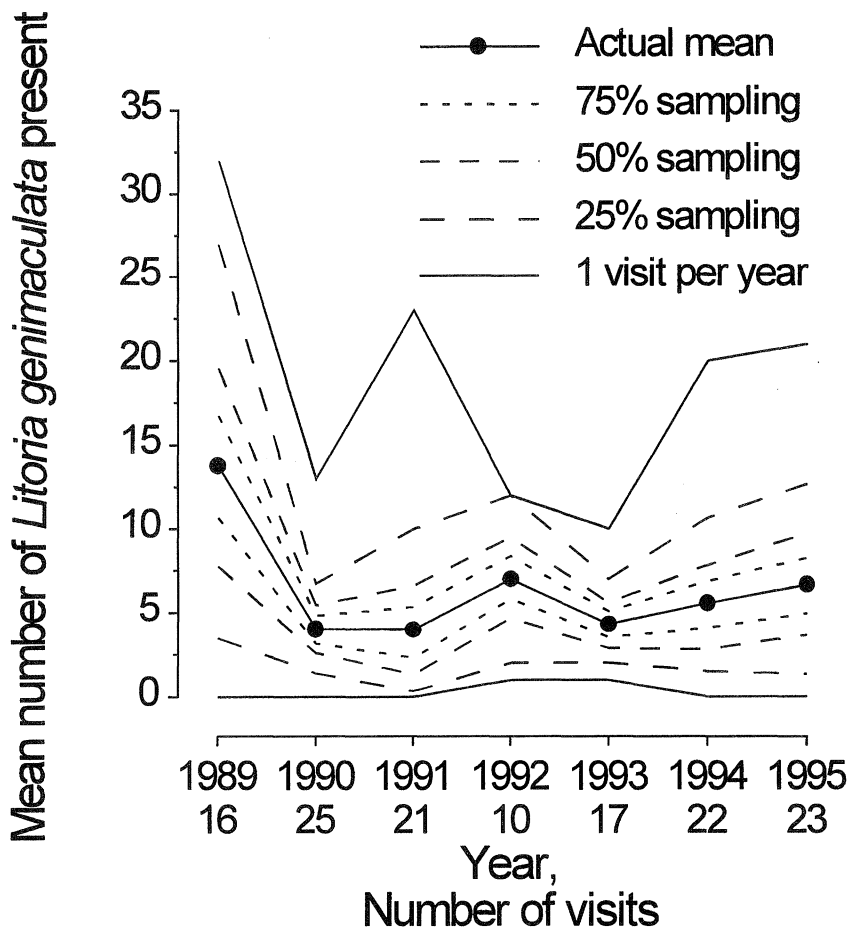
Figure 3   Results of resampling analysis on numbers of adult male *Litoria genimac-ulata* present on a 60-m transect on Birthday Creek, Mt. Spec, Queensland, Australia. Points indicate the mean number of individuals present taken over all visits in each year. The lines connecting the points are for illustration only. The dashed lines at increasing distances from the mean are the upper and lower 95% confidence limits for the location of the mean for each year at the given sampling intensity, as determined from 5000 resamplings of the data. Upper and lower solid lines are the 95% confidence limits for numbers obtained if the site was visited once annually; they are the minimum and maximum numbers encountered each year.

or one visit per year, the observed pattern of change through time would probably have differed from the pattern that appears in the full data set, and the coefficient of variation of the annual mean would have increased substantially.

Problems created by the changing attractiveness of breeding sites can also occur when animals are censused in nonreproductive habitat, because the attractiveness of patches changes. A population of *Rana arvalis* in a 2000-m^2 sampling area increased more than tenfold over the period 1984–1988 (89); this might have been due to a decrease in the local availability of water, causing animals to concentrate where it was available (89). Densities of the neotropical litter frogs *Bufo typhonius* and *Colostethus nubicola* in nonreproductive habitat varied more than tenfold over the course of a one-year study (183). This variation was probably caused by differences in the activity level and catchability of frogs, rather than by changes in population size (183).

Once a reasonable set of population estimates at a site is available, the next step in an analysis of the behavior of the population is to examine how it changes over time. It is unrealistic to expect perfect stability from any natural population; even if the population is truly constant, sampling error will introduce some variation. Given that we expect populations to fluctuate, we should try to determine how they will behave over time in the absence of directional pressures toward expansion or decline.

A Null Hypothesis for the Behavior of Amphibian Populations over Time

There has been substantial debate in recent years (23, 146, 148, 169) regarding how "normal" amphibian populations should change through time, but little theoretical work on this question. The problem has been defined clearly: Fluctuating populations of amphibians will be either increasing or decreasing at any time (146, 148). There is a very large opportunity for bias if populations are declared to be "declining" on the basis of short time series indicating that numbers are decreasing.

Amphibian Populations Fluctuate   It is almost universally agreed that most local populations of amphibians are likely to fluctuate considerably in size. This occurs because recruitment is highly variable (7, 15, 20, 44, 65, 81, 185, 186, 194). Survival rates of terrestrial stages often appear to be relatively constant, with some degree of fluctuation (7, 44, 73, 185, 186). The survival rates of eggs, hatchlings, and larvae often vary over several orders of magnitude (1, 20, 199). Pechmann & Wilbur (148) provided a useful review of approaches that have been used to examine population behavior.

Examining Changes of Numbers with Time   One approach that has been used to examine trends within populations of amphibians is simple correlations of numbers with time. Fifteen-to-twenty-year time series for six species of salamanders in the Appalachian mountains of the United States showed no evidence for consistent

trends in numbers over time (91). A lack of significant correlations of numbers with years over a long-term study may indicate that variation among years represents fluctuations in numbers rather than declines (146, 169). Significant negative correlations between population size and time have been interpreted as indicating that populations are in decline (115, 117). Of 16 studies that monitored amphibian populations for four or more years, five reported that populations were declining, one that six populations had become extinct, seven that populations were fluctuating, and three that they were stable (30). Most of the evaluations of population change were based on correlations of population size with time, and some statements that populations were not in decline were based on failure to find a significant correlation. Failure to find a significant correlation does not necessarily imply that none exists (162); it can also result from a lack of statistical power. In eight studies of amphibian populations that reported no trend in population size over time, the power of a product-moment correlation was insufficient to allow acceptance of the null hypothesis (162). Reed & Blaustein (162) suggested that studies should not conclude that populations are not in decline unless that conclusion can be supported statistically. Unfortunately, the power analysis they used, relying on simple Pearson correlations, is not statistically valid, as the adjacent annual values in time series on a single population are not independent random samples. We develop an alternative approach below.

A Simple Model of Population Behavior   In order to suggest how more appropriate tests might be carried out, we explored how time series data on amphibian populations should be analyzed and interpreted, and what the "normal" patterns in such data might be. We constructed a simple verbal model of frog population dynamics and compared its predictions with the behavior of 57 time series of frog abundances and 28 salamander time series (all studies cited in Table 1; details are available on the World Wide Web in the Supplemental Materials section of the main Annual Reviews site [www.AnnualReviews.org]). Finally we compared the behavior of those 85 time series with that of a simulated population. The simple verbal model is:

> Assumptions: 1. amphibian populations often persist for many generations, neither decreasing to extinction nor exploding to infinity; 2. survival rates of terrestrial stages may vary, but that variation is typically over less than a single order of magnitude; 3. survival rates of aquatic stages often vary over several orders of magnitude. Deductions: (A) Assumption 1 implies that recruitment must on average be sufficient for replacement to occur. (B) Assumptions 1 and 2 together imply that most variation in the size of terrestrial populations must be due to fluctuations in recruitment from the aquatic stages. (C) Assumptions 1, 2, and 3 together imply that when aquatic survival is high, populations must rapidly increase, but that aquatic survival must frequently be below replacement level, so that the increases do not tend to lead to sustained explosions. Deductions (A–C) taken together

suggest that populations should decrease more often than they increase, because increases can be very rapid and must be counterbalanced by slower decreases.

This model suggests that populations of species with highly variable recruitment from the aquatic to the terrestrial stage might be expected to decrease during more than 50% of time intervals. This is a potentially important point in the context of the problem of amphibian declines: If populations naturally decrease in numbers more often than they increase, relatively short-term population studies may often find that the population or populations studied appear to be in decline.

Comparing the Predictions of the Model with Data   To examine this problem in more detail, we extracted data from a database of information on time series of population sizes of frogs and salamanders collated from the literature and available from the United States Geological Survey (USGS) (72). Most of the populations studied were not regarded as being in decline. We modified the database from its raw form in several ways. The database includes a number of time series collected using different techniques on the same species at the same sites and times. We included only one time series of data on any species for any site and set of dates. We did not use data on larvae or juveniles in our analysis because they reflect reproductive input modified by highly variable aquatic mortality rates and so are least likely to reflect the dynamics of adult populations. When data were available for both male and female adults, we combined them. When count data and other estimates such as mark-recapture values were available, we included the count data if they had been collected in a manner that was likely to be comparable among years; otherwise we used the estimated numbers. When only data on numbers of egg masses were available, we included them in our analyses, as they should be highly correlated with numbers of adult females. We included only time series taken over four or more years. We also included data from Cohen (50) that were not present in the USGS database. A summary of the original sources of the data we used appears in Table 1, and details of the data for each time series appear on the World Wide Web in the Supplemental Materials section of the main Annual Reviews site (www.AnnualReviews.org).

We classified each yearly population estimate as either the initial number in a series, an increase, a decrease, or no change. Three families of frogs (Bufonidae, Hylidae, and Ranidae) and two families of salamanders (Ambystomatidae and Plethodontidae) contained sufficient numbers of time series. We used nonparametric statistics (Table 2) to determine whether the percentage of the time in which populations decreased from one year to the next varied among families. In both orders, families differed in the percentage of the time that populations declined between years. In the Caudata, populations of species in the family Ambystomatidae, which are pool-breeding species with relatively large clutch sizes, decreased between years an average of 59.2% of the time. Species in the Plethodontidae, primarily terrestrial egg layers and stream-breeders with smaller average clutch

TABLE 2   Means, standard deviations, and numbers of time series analyzed for the percentage of year-to-year changes in population size that are decreases, for amphibians of five families, and tests for significant differences in the mean among families within orders.

| Family | Percent of population changes that are decreases | | |
	Mean	Standard Deviation	N
Salamanders. Wilcoxon 2-sample test, $Z = 2.43, P = 0.015$			
Ambystomatidae	59.2	18.1	12
Plethodontidae	42.0	16.1	14
Frogs. Kruskal-Wallis test, $\chi^2 = 8.82$, 2 d.f., $P = 0.012$			
Bufonidae	55.5	19.8	19
Hylidae	47.3	6.7	15
Ranidae	60.6	13.0	23

sizes (see references in Table 1), declined between years only 42% of the time. In the Anura, species in the families Ranidae and Bufonidae decreased in more than 50% of intervals, while species in the family Hylidae decreased in slightly less than 50% of intervals. (Table 2). The ranids and bufonids included in the database generally produce larger clutches of eggs and often have highly variable offspring survival, while hylids produce smaller clutches and may have less variable rates of offspring survival (references in Table 1).

The results of this analysis suggest strongly that the expected behavior of populations over time varies among families of frogs and salamanders, and that the adult populations of species that have more variable survival of premetamorphic offspring tend to decrease between years more often than they increase. This result has implications for the ability to draw conclusions about population trends from simple time series of numbers over years. A species in the family Plethodontidae, in which the mean population behavior is to decrease between 40% of years, has a probability of four successive decreases of only 0.031, and finding four successive decreases between years in a censused population might be cause for alarm. However, a ranid species would need to decrease in numbers six times in succession before the probability of that sequence of decreases was less than 0.05.

Our data set included populations from many times and places, some of which might have been undergoing declines caused by external pressures. This would bias the results of our analysis. To erect a null hypothesis independent of the data from natural populations, we examined the behavior of a simulated population with known characteristics.

A Numerical Model of Population Behavior   For comparison with our verbal model and the results of our data analysis, we used a simulation model based on a

long-term study of the population dynamics of *Bufo marinus* in northern Australia
(2). Our model incorporated simple density-dependence in the adult stage and
lognormal variation in recruitment success. Mean recruitment rates were adjusted
so that populations tended to fluctuate about a mean size rather than explode or
decline rapidly to extinction. The population arbitrarily started with 100 adult
female toads. Year-to-year survival of adult females was set at the lower of 50%
or 50 total. Each female produced 9000 eggs, which survived to reach maturity as
females in one year at variable rates equal to 0.00047^{ea+1}, where a is a normally
distributed random variable with mean 0, standard deviation 1. The number of
adults was truncated to an integer following survival and recruitment in each
year.

   We ran the simulation 5000 times, for 1000 "years" each time. On average,
the population persisted for 423 years before extinction and contained 296 adult
females while extant. Within a run, recruitment differed on average approximately
300-fold between the lowest and highest years, while adult survival differed 15-
fold as a consequence of density-dependence. While the population persisted,
it decreased in 56.32% of intervals between years, a result that is in very close
agreement with the observation (Table 2) that populations of bufonids declined
between 55.5% of years. This suggests that our initial verbal model was correct:
When population fluctuations are driven by highly variable recruitment, it is likely
that population dynamics will be characterized by occasional outbreaks with longer
intervening periods of decrease, so that they are "in decline" more than 50% of the
time. This result is similar to the "storage" effect in open populations (45, 193).

   It is clear that a population decreasing in more years than it increases is not nec-
essarily in decline. However, if there has recently been an increase in the general
tendency of amphibian populations to decline, there should be a correlation be-
tween the year in which a study ended and the frequency of decreases in that study.
We tested this hypothesis using the 85 time series in our database. We correlated
the final year of each study with the percentage of intervals across which the studied
population declined. We analyzed the data for each family of frogs and salaman-
ders separately, as combining them might have confounded real effects of time with
the effects of changes in the proportions of studies that were carried out on each
taxon. We calculated Spearman rank correlations because these straighten nonlin-
ear relationships and decrease the effects of outliers and data that are not normally
distributed. We found no evidence for any significant correlation of proportion
decreases with time in any family (maximum $r_s = 0.327$, minimum $P = 0.234$),
an outcome supported by examination of the data (Figure 4), which do not suggest
any strong trend for either frogs or salamanders.

   The proportion of years in which a population declines may be a weak indicator
of trends and is potentially subject to difficulties in deciding how large a change in
population size represents a real decrease rather than noise in the data. Correlations
between population size and time might be a better indicator of population status
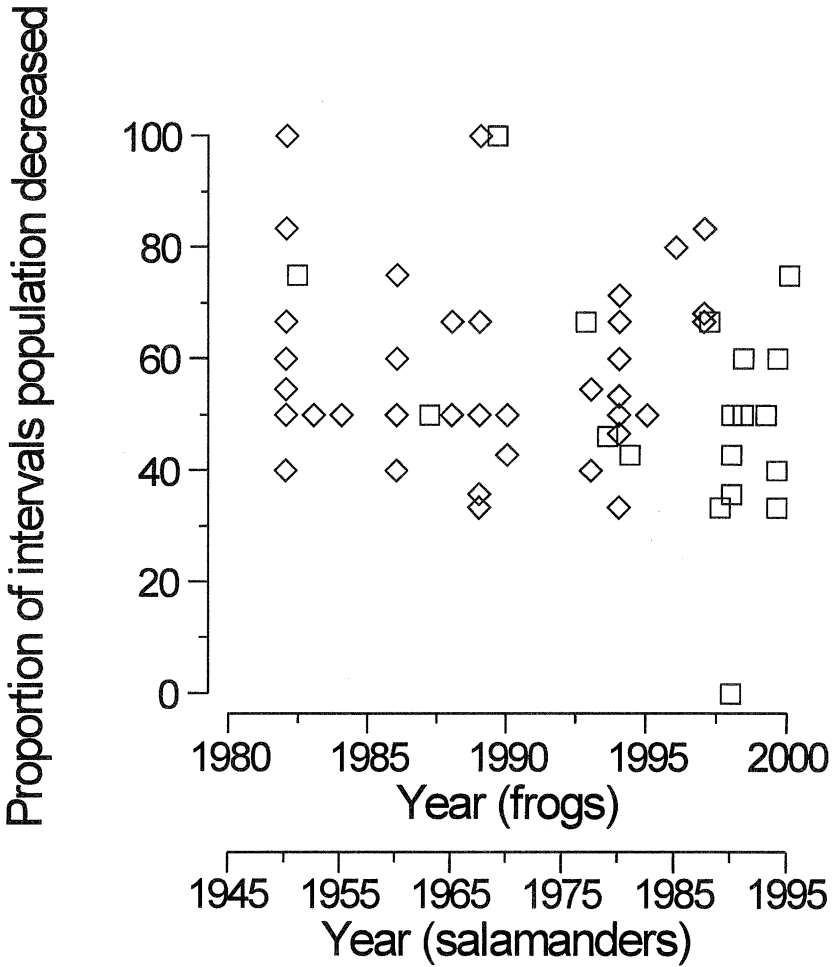(30, 148).

Figure 4   Proportion of the intervals from one year to the next over which populations decreased during long-term studies (4 or more years) of 85 local amphibian populations (28 of salamanders, shown as squares, 57 of frogs, shown as diamonds). The abscissa is the final year of each study.

CORRELATIONS OF POPULATION SIZE WITH TIME

If there is a general global phenomenon acting on all amphibians and increasing their tendency to decrease in numbers, we would expect that recently completed studies would show more or stronger negative relationships between population size and time than would older ones. For each of the 85 time series in our database, we regressed $\log_{10}(N+1)$ on year of the series. We used $\log_{10}(N+1)$ because this

stabilizes variances and because a population increasing or decreasing at a constant proportional rate will show a linear relationship of $\log_{10}(N + 1)$ with time. Years were adjusted within each time series so that the first year was year zero, to reduce possible influences of rounding errors on the regressions. We used the correlations and slopes of these regressions in further analyses to determine whether there was any evidence for an overall trend toward an increase in the incidence or intensity of negative relationships between population size and time. In these analyses we examined the data for frogs and salamanders separately because trends might be present in one but not in the other. We first looked for correlations of either the slope or the correlation coefficient with the year in which each time series ended, using Spearman rank correlations because of the unknown sampling properties of these two measures. None of the correlations of the correlation coefficient or the slope with final year were significant (salamanders: $r_s = -0.021$, $P = 0.917$ and $r_s = -0.024$, $P = 0.905$; frogs: $r_s = 0.175$, $P = 0.174$ and $r_s = 0.161$, $P = 0.232$; respectively).

Although there was no trend in either order for changes over time in the relationship of population size to year of study, it is still possible that a general declining trend was present throughout the period. To examine this possibility, we plotted the correlations of population size with year and the slopes of the regressions of population size on year against final year of the study (Figure 5a and 5b). Initial examination of these figures could be a source of alarm because there are many more negative than positive correlations and because most of the apparently significant correlations and slopes are negative. Further analysis shows that both of these effects are probably artifacts of the population dynamics of amphibians and the fact that standard assessments of significance should not be applied to time series data. In order to more rigorously assess the significance of these correlations and slopes, we returned to the results of our population simulation. On each of the 5000 iterations of the time series, we calculated correlations and slopes for regressions of $\log_{10}(N + 1)$ on year for time series containing 4 through 9, 11, 12, 14, 15, 16, 23, and 28 years, starting arbitrarily at year 20 of the simulated time series to allow the effects of initial conditions to disappear. This resulted in at least 4904 coefficients for each combination of parameter and series length (less than 5000 because a few populations went extinct before the final year of each simulated series). We sorted the vector of coefficients for each combination of parameter and series length into ascending order, and we took the coefficients at 0.025 from the bottom and top of the series as the upper and lower 95% confidence limits for the correlation and slope of regressions of an amphibian population on year. These confidence limits appear in Figure 5, c and d, with plots of the correlations and slopes obtained from the time series in our database. Using the criterion that to be significant a parameter must fall outside these empirical 95% confidence limits, only a single correlation and four slopes are significant, well within the number that would be expected due to Type I error when 85 comparisons are made.

Although we must conclude that there is no evidence in the 85 time series we analyzed to suggest that correlations or slopes of regressions of $\log_{10}(N + 1)$ against
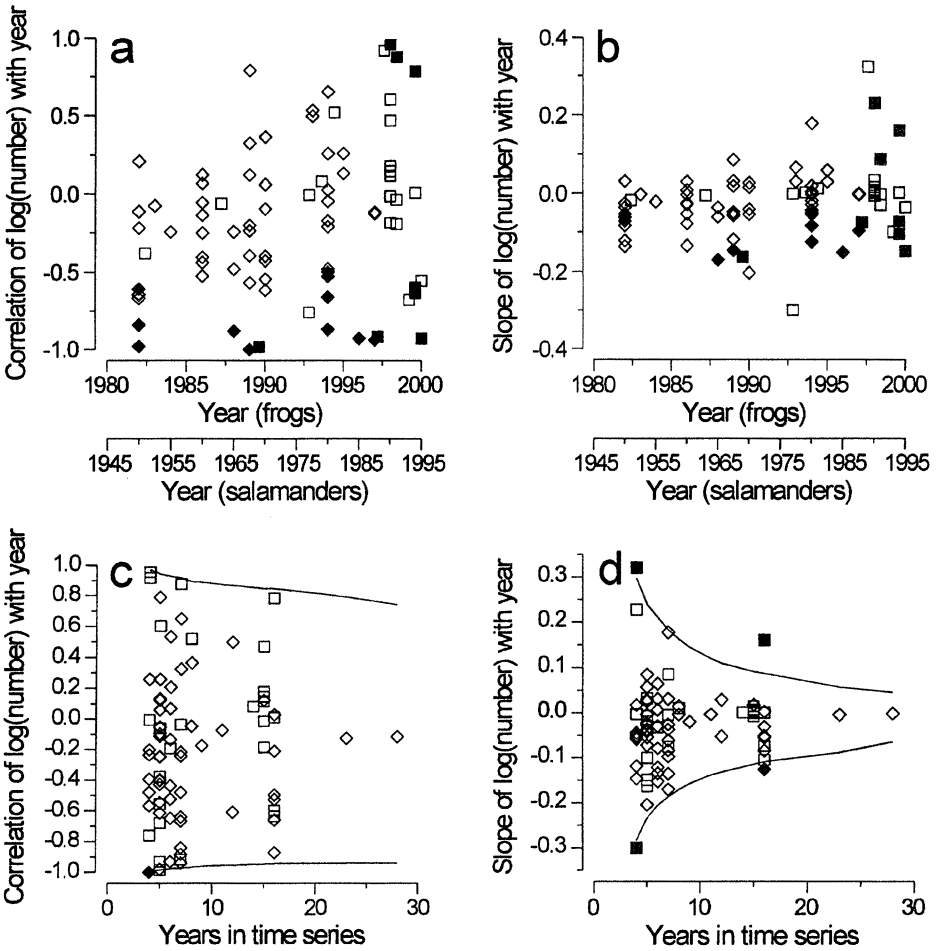
Figure 5 (*a*) Product-moment correlation of $\log_{10}(N + 1)$ with year of study for 85 time series of four or more years of data on local populations of amphibians, plotted against final year of the study. Data for salamanders shown as squares, frogs as diamonds. Correlations that would be significant at $\alpha = 0.05$ using standard parametric criteria are indicated by filled shapes. (*b*) Slopes of regressions of $\log_{10}(N + 1)$ on year of study, other details the same as in (*a*). (*c*) The same correlation coefficients as in (*a*), plotted against number of years in the time series from which the correlation was derived. Lines indicate upper and lower 95% confidence limits derived from correlations calculated on 5000 simulated time series of each length. Only the single correlation outside these confidence limits should be considered significant (indicated by the filled shape). (*d*) The same slopes as in (*b*), plotted against number of years in the time series from which they were derived. Lines indicate 95% confidence limits, derived as in (*c*). Only four of the 85 slopes should be regarded as significant at the 0.05 level (*filled shapes*).

time have changed in recent years, we might still be concerned over the apparent excess of negative relationships of population size with time (Figure 5, *a* and *b*). Fifty-seven of the 85 relationships of population size with time (67%) are negative. The proportion of negative correlations from our simulation increased with length of the time series from 54.8% negative with a series length of 4 years to 57.5% with a series length of 28 years. We used these expected proportions, weighted by the number of each of the real time series that were of each length, to calculate the expected numbers of correlations that should have been greater and less than 0 (37.6 and 47.4, respectively), and compared these with the observed numbers (28 and 57) using a chi-squared goodness-of-fit test (chi-squared $= 4.42$, $P = 0.037$). This significant result indicates that the amphibian populations we examined had a greater number of negative correlations with time than would be expected, as compared with our simulated populations. This could reflect a general tendency toward decline, but it could also reflect the fact that our simulation model, while it probably provides a more realistic null hypothesis than the simple assumption that effects in both directions should be equal, does not perfectly reflect the population behavior of all amphibians. Using a greater variety of models to generate null hypotheses more appropriate for each family, genus, or even species would obviously be preferable. It would also be useful to examine the sensitivity of our conclusions to variations in model parameters and form.

The use of appropriate null hypotheses will allow more rigorous examination of the behavior of individual populations. However, many amphibians appear to live in local populations that interact strongly with other populations, so that understanding the implications of local population dynamics for species persistence requires a knowledge of their metapopulation biology.

AMPHIBIAN METAPOPULATION BIOLOGY

A metapopulation consists of a group of local populations inhabiting more or less discrete patches of habitat (94). A metapopulation differs from a collection of independent populations in that there is substantial migration between local populations, so that no local population is likely to remain extinct for any length of time. Migration rates may be high enough to affect rates of local population increase and decrease (95, 139). A metapopulation differs from a single subdivided population by having sufficiently low rates of migration between local populations that they exhibit some degree of independence in their dynamics, including the possibility of declining to extinction (93).

Metapopulation Studies on Amphibians

Although it has been suggested that amphibians are generally highly philopatric (30, 61, 172), many species depart from this pattern. One of the problems that plagues mark-recapture studies of amphibian populations at single sites is the high

rates at which animals disappear from local populations (2, 31, 40, 111, 134, 156). Substantial rates of dispersal among local populations have been documented in many species (2, 21, 37, 38, 42, 58, 66, 81, 112, 161, 173, 198)). Additional evidence that many amphibians live in metapopulations comes from explicit metapopulation studies (175). Breeding populations of the newt *Notophthalmus viridescens* act as cells in a regional metapopulation (83). The European pool frog *Rana lessonae* lives in spatially complex metapopulations; the quality of potential breeding sites and their degree of isolation from other sites determines their probability of occupancy and the probability of local extinction (176). Increases in the isolation of habitat patches due to natural succession or habitat destruction decrease the persistence of local populations (176). Surveys of *Rana clamitans* occupancy at 160 ponds in three distinct regions (103) demonstrated the existence of regional metapopulations. Colonization rates varied from 0 to 0.25 ponds · (pond occupied · year)$^{-1}$, while local extinction rates were between 0 and 0.5 ponds · (pond occupied · year)$^{-1}$. Small populations were more prone to local extinction than were large ones, and there was no overall trend in occupancy rates when all three metapopulations were considered (103). Ten other species examined at 97 ponds in the same regions (101) also exhibited metapopulation dynamics, with rates of turnover from 0.07 to 0.30 species · (pond · year)$^{-1}$. Pool size and isolation both affected species richness in 77 pools in the southern Netherlands (126) and 332 habitats in Bavaria (68).

Models of Amphibian Metapopulations and Their Implications

Because amphibians often live in metapopulations, declines and extinctions of local populations may be common events. Detailed studies of local populations may give useful insights into the autecology of species, but they are of limited use in evaluating the status of regional metapopulations. One approach to examining the behavior of metapopulations is to examine simple probabilistic models for the frequency with which local populations might change in status (184). A probabilistic null model for population declines and disappearances was used to examine whether the declines and disappearances of frogs that occurred in the 1980s at Monteverde, Costa Rica, might be due to chance (153). Pounds et al (153) used long-term studies to estimate probabilities of disappearance. They then compared the numbers of species disappearances at their study sites to the numbers of disappearances predicted by the cumulative binomial distribution, and they found that far more species had disappeared than would have been predicted.

The probabilistic approach (153) seems to be a useful way to quantify the idea that, when certain regions or taxa are considered, species are disappearing at a rate "too great to be coincidental." Several studies have produced data that could be examined using this technique. It seems likely that the disappearances of seven species from all sites at elevations above 400 m throughout the Australian Wet Tropics (135, 163) would be shown to be extremely improbable, as would the

disappearances of three species and large declines in site occupancy of four others in the Yosemite area of California (69), the disappearance of *Rana cascadae* from the southern end of its range (75), and the disappearances of many species at Las Tablas, Costa Rica (131).

A more complex analytical model was used to predict the rates of extinction of local populations of the common toad *Bufo bufo* and the crested newt *Triturus cristatus* in Europe, and to examine how those rates should respond to the size of the local habitat patch and its distance from a source of migrants (92). The persistence of populations of both species should increase with the carrying capacity of the local habitat and should decrease with increasing distance to a source of migrants. Over a wide range of carrying capacities, the critical distances are approximately 10 times as great ($\sim$5 km) for toads as they are for newts ($\sim$500 m) (92). This study suggested that both patch size and spatial distribution must be taken into account when managing amphibian metapopulations. Information on patch occupancy from a geographically referenced database (168) indicates that small, relatively isolated wetlands are important in the metapopulation dynamics of amphibians in South Carolina, USA. Loss of these habitats might lead to disproportionately large rates of extinction in regional metapopulations that depend upon them as stepping stones in colonization and as refuges from local extinctions (168).

Delineating and monitoring the status of metapopulations requires extensive sampling, but because metapopulation dynamics are concerned mostly with the presence or absence of species in local populations, sampling of local populations does not need to be intense (87). Fully understanding the dynamics of amphibian metapopulations will require much more information on movements and dispersal among local populations than is presently available.

CONCLUSIONS

It is clear that local populations of many amphibian species have declined in recent years, and there are several well-documented cases of declines at and above the level of regional metapopulations. Although many environmental factors can adversely affect the growth, survival, and reproduction of amphibians, few studies have convincingly demonstrated that these effects alter their population dynamics. Studies linking factors that negatively affect amphibians in the laboratory or in artificial field trials with effects on population dynamics in more natural settings are urgently needed.

Local populations of amphibians tend to fluctuate, and our results show it is likely that many normally decrease more often than they increase. It is therefore important to develop realistic null hypotheses for their behavior. If we had not based our null hypothesis on a simulation of frog population dynamics, we would have reached very different conclusions in our analysis of population behavior. Additional data on an ecologically diverse range of species will allow the development of more sophisticated and specific null hypotheses for a greater range of

populations. This is necessary to make rigorous tests of the responses of local populations to environmental factors possible.

Many amphibian species occur as metapopulations, so the dynamics of local populations may be poor indicators of their status. Declines and extinctions of metapopulations are likely to result from interactions between changes in the dynamics of local populations and habitat modification or loss (93, 94, 168). For many species, understanding the factors affecting the status and dynamics of metapopulations should therefore be the ultimate goal of studies aiming to prevent or reverse declines. Monitoring metapopulations requires different data collection techniques than monitoring isolated populations, so the first step in designing any monitoring program should be to determine whether the species of interest forms a metapopulation. Studies integrating research within local populations with investigations at the metapopulation level are most likely to discover the causes of amphibian declines and provide a basis for the conservation of amphibian diversity.

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