DISTRIBUTIONS OF POND-BREEDING ANURANS:
AN OVERVIEW OF MECHANISMS

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ABSTRACT

Concern over the fate of amphibians has led to increasing attention on the mechanisms that underly their distribution. Among pond-breeding anurans, surveys have revealed that most species are restricted to a minority of ponds, but distributions can shift over time. The mechanisms for these patterns fall into two broad classes: variation in environmental attributes among ponds, and the impact of spatial context surrounding ponds.

There is abundant evidence that embryonic and larval anurans are sensitive to variation in a large number of abiotic and biotic variables. In some cases these effects on performance have been linked to variation among natural ponds, and compelling evidence suggests that anuran distributions may be restricted by the action of local conditions. While these explanations are often discussed in terms of single variates (e.g., hydroperiod), field experiments suggest that elimination will often result from the joint action of multiple factors (e.g., low pH and high metal concentrations). While variation among ponds is usually considered in terms of the direct impacts on the survival, growth, and development of offspring, there is mounting evidence that adult behavior may regulate distributions via the selection of oviposition sites.

Spatial context for ponds can impact anuran distributions in distinct ways. Metapopulation models suggest that pond isolation may influence patterns of occupancy, a hypothesis supported by survey data. In addition, most pond-breeding anurans utilize terrestrial uplands as adults. The amount and quality of terrestrial habitats also can impact distributional patterns. Thus, via either mechanism, spatial context can impact distributional pattern in the absence of any impact due to between-pond variation.

Current evidence suggests that the restricted yet dynamic nature of anuran distributions results from factors operating within as well as surrounding breeding ponds. The dynamic natures of both ponds and surrounding uplands appear to have sizable impacts on distributional patterns. Recognition of this dynamism has critical importance for the development of effective conservation measures for anurans.
INTRODUCTION

During the last decade, the study of amphibian distributions has been thrust into the limelight by reports of declines and population disappearances from around the world. Recent reviews of declines emphasize the large number of instances and, in all but a few cases, the lack of mechanistic understanding (e.g., Pechmann and Wilbur, 1994; Sarkar, 1996; Alford and Richards, 1999). Understanding patterns of population distribution and abundance is a difficult task under the best of circumstances. These challenges are magnified manyfold when populations have already crashed (e.g., Pounds and Crump, 1994; Pounds et al., 1999). In this study I review findings emanating from observational and experimental studies of anurans and focus on distributions among ponds and the factors that affect such patterns. While much of this research has centered on species not suspected to be declining, my objective is to use these studies to highlight what we know about the distributions of anurans in general: What limits them, and why do they change? The hope is that answers to these questions, even in partial form, will strengthen our efforts to understand reverse declines and to plan for the conservation of amphibians not in decline.

This review is focused on pond-breeding anurans. The exclusion of salamanders (and caecilians for that matter) is largely pragmatic. However, in addition to allowing me to focus the review, I have chosen a subset of the Amphibia for which there is both a large literature and a large measure of concern over the fate of species. Anurans are a diverse group. Even among pond-breeding species, there is enormous variety in many aspects of life history, physiology, and behavior (Duellman and Trueb, 1986; McDiarmid and Altig, 1999). Like most organisms, pond-breeding anurans typically exhibit restricted distributions. Figure 1 summarizes data from nine observational studies designed to document anuran distributions among potential breeding ponds. The studies were conducted on four continents and include 45 species from six anuran families. The average prevalence among studies is just 34%, with very few species exceeding 70%.

In order to be meaningful, these values must be placed into context. Notably, prevalence depends on the group of ponds included in a survey pool. A survey which included any body of water, no matter how ephemeral, would yield a much lower prevalence of occupancy than would a study with a more restrictive definition of potential breeding ponds. However, among the studies included in Fig. 1, the group of surveyed ponds tended to be selected using relatively restrictive definitions. Most studies employed (1) minimum surface or depth of hydroperiod cutoffs, or (2) cutoffs defined by the presence of at least one breeding amphibian species.

Despite the near pervasiveness of restricted distributions, there is mounting evidence that anuran distributions are dynamic (Sjogren-Gulve, 1994; Skelly et al., 1999). Even over relatively short time periods, species can disappear from some breeding ponds and appear at others (Hecnar and M’Closkey, 1996a). Whatever limits species distributions, these factors prevent ubiquity without preventing distributional change. Local extinction rates can be measured as the disappearance of a species from a breeding pond. Studies spanning a decade or more suggest that the per year probability of population extinction
Fig. 1. Prevalence among ponds for 45 anuran species. For each study, the average percentage of surveyed ponds occupied by a species is given + 1 SE. Data were taken from nine studies: Azevedo-Ramos et al., 1999 [40 ponds; 13 species; Bradford et al., 1993 [312 ponds; 1 species; Glooschenko et al., 1992 [118 ponds; 8 species; Heenan and M'Closkey, 1996b [180 ponds; 10 species; Mann et al., 1991 [280 ponds; 4 species; Pavignano et al., 1990 [61 ponds; 4 species; Sjogren-Gulve, 1994 [116 ponds; 1 species; Skelly et al., 1999 [37 ponds; 8 species; Skelly, unpublished data [22 ponds; 14 species; collected in New South Wales, Australia].

within a pond can range as high as 2 to 2.5% (Sjogren-Gulve, 1994; Skelly et al., 1999). Numbers of colonizations are known to match or exceed local extinctions. The net effect of this dynamism can be surprisingly high rates of turnover in the presence–absence pattern of a species. Thus, even when a species is not declining, it may be inappropriate to assume that its distribution will be static (Skelly et al., 1999).

An ideal model would succeed in predicting the restricted nature of anuran distributions, account for intra- and interspecific differences in such patterns, and be able to forecast changes in distributions over time. While we have not yet reached this level of understanding, in recent years ecologists have greatly increased their knowledge of anuran distributions. The task of organizing this understanding is made easier by recognizing that the distributions of all patchily distributed species can be affected by (1) variation in attributes among patches, and (2) the spatial context for those patches. Because pond breeding anurans depend in distinct ways on ponds and the uplands that surround them, this perspective is a useful starting point for describing the mechanisms underlying distributional patterns.
VARIATION AMONG PONDS

Perhaps the most straightforward mechanism for a restricted distribution is the action of one or more factors that exclude a species from some patches. This mechanism of local exclusion requires that patches vary and that the performance of the focal species is a function of that variation. If this impact is sufficiently extreme, the species' distribution in space will map its tolerance for the factor (Brown, 1995).

In fact, there is extraordinary variation in physical, chemical, and biotic attributes of lentic environments (Hutchinson, 1957). In the context of amphibian studies, ecologists have noted variation in abiotic factors such as hydroperiod (e.g., Smith and Van Buskirk, 1995) and dissolved oxygen (e.g., Werner and Glennemeier, 1999). Biotic factors such as the density and composition of predators (e.g., Smith and Van Buskirk, 1995) and potential competitors (e.g., Skelly, 1995a) also are well-documented through surveys.

Correspondingly, there has been a strong tradition of evaluating the effect of this variation (also reviewed by Alford, 1999). Table 1 shows that experiments have been conducted on a great variety of factors. Broadly speaking, this work has revealed a correspondence between factors that show variation among ponds, and those associated with impacts on survival, growth, or developmental rates in experiments. Does this mean that anurans are prevented from using many ponds because their embryos or larvae are negatively impacted by local conditions?

<table>
<thead>
<tr>
<th>Factor</th>
<th>References</th>
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<tbody>
<tr>
<td>Hydroperiod</td>
<td>Wilbur, 1987; Skelly, 1995a; Smith and Van Buskirk, 1995</td>
</tr>
<tr>
<td>Predation</td>
<td>Wilbur, 1987; Skelly, 1995a; Smith and Van Buskirk, 1995</td>
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<tr>
<td>Predator cues</td>
<td>Skelly and Werner, 1990; Skelly, 1992; Lardner, 2000</td>
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<tr>
<td>Interspecific competition</td>
<td>Wilbur, 1982; Woodward, 1982; Morin and Johnson, 1988</td>
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<tr>
<td>Intraspecific competition</td>
<td>Brockelman, 1969; Wilbur, 1977; Skelly, 1995b</td>
</tr>
<tr>
<td>Food</td>
<td>Kupferburg, 1994; Britson and Kissell, 1996; Babbitt and Meshaka, 2000</td>
</tr>
<tr>
<td>Parasitism/Disease</td>
<td>Kiesecker and Blaustein, 1995</td>
</tr>
<tr>
<td>pH</td>
<td>Cummins, 1989; Jung and Jagoe, 1995; Fioramonti et al., 1997</td>
</tr>
<tr>
<td>Metal</td>
<td>Lefcort et al., 1998; Loumbardis et al., 1999</td>
</tr>
<tr>
<td>Pesticide</td>
<td>Ankley et al., 1998; Berrill et al., 1998; Bridges, 2000</td>
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<td>Forest canopy</td>
<td>Werner and Glennemeier, 1999</td>
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<tr>
<td>Temperature</td>
<td>Berven and Gill, 1983; Newman, 1998; Blaustein et al., 1999</td>
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<tr>
<td>Dissolved oxygen</td>
<td>Moore and Townsend, 1998; Plenet et al., 2000</td>
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<tr>
<td>Salinity</td>
<td>Dunson, 1977; Uchiyama and Yoshizawa, 1992</td>
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<tr>
<td>Ultraviolet radiation</td>
<td>Kiesecker and Blaustein, 1995; Broomhall et al., 2000</td>
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Previous commentators have noted the gulf between the evidence necessary to show that a factor has a measurable impact on performance and that necessary to show an impact on an organism’s distribution (e.g., Peckarsky, 1998). Salient issues include the duration and spatial scope of a study as well as the nature of the evidence. Specifically, anuran experiments have been conducted in a variety of venues including laboratory containers, mesocosms (often using cattle watering tanks), field enclosures, and, rarely, manipulations of entire ponds.

Perhaps the ideal experimental study of variation among ponds would involve manipulating entire breeding ponds and monitoring population dynamic responses in order to verify the link between treatment and occurrence or nonoccurrence of distributional shifts. To my knowledge, there have been no such experiments conducted. The great majority of experiments have been conducted outside of the field context altogether and, generally, have lasted short periods of time, larval period or less. It is worth noting that these experiments were conducted with a variety of goals in mind; for many of these goals, shorter experiments conducted in more tractable settings are expedient and appropriate.

Whatever their original intent, this large body of experiments provides indications of possible impacts on natural populations. The degree to which they represent strong evidence for distributional mechanisms is, basically, a personal decision based on one’s notion of a standard of evidence. Rather than entering that debate, I present below a selection of four case studies. I suggest that these cases offer compelling evidence for a link between inter-pond variation and distributional patterns. The research embodied in each case varies in its particulars. However, each of the cases features a careful field survey in order to document patterns of distribution and the existence of variation in putative factors. Survey efforts have been followed up using some kind of field manipulation, often involving the transplant of focal species into ponds where they do not naturally occur.

\[ pH \]

Acidity is among the oldest published hypotheses for the regulation of anuran distributions (e.g., Noble and Noble, 1923; Gosner and Black, 1957). Later concern over acidic deposition spurred further research into the impacts of acidity on anurans (Dale et al., 1985; Pehek, 1995; Heenar and M’Closkey, 1996b). The association of some anurans with pine barrens environments and their acidic breeding ponds led biologists to speculate that these species were particularly adapted to acidic conditions and that low pH may prevent other species from utilizing acidic ponds. Experiments have confirmed that pine barrens specialists do, in fact, have a greater tolerance for acidity than other species (Gosner and Black, 1957; Freda and Dunson, 1986). In addition, it appears that pH can decrease performance in field enclosures. Available evidence suggests that pH may limit distributional patterns in conjunction with other factors. Concentrations of metals, notably aluminum, may be particularly important, as the impact of acidic conditions may be manifested in large part by the mobilization of toxic elements in ponds with low buffering capacity (e.g., Sadinski and Dunson, 1992, Rowe and Dunson, 1993; Horne and Dunson, 1995a, 1995b; Pehek, 1995). In many cases, acidic waters are associated
with shifts in terrestrial vegetation. A number of authors have noted that larval distributions attributed to pH also may be influenced by adult responses to the terrestrial environment (e.g., Glooschenko et al., 1992; Pehek, 1995).

THE HYDROPERIOD GRADIENT

Perhaps the best-studied factor affecting anurans is the hydroperiod, or permanence, gradient (Wilbur, 1980, 1997; Wellborn et al., 1996). For anurans, the duration of the pond forms a fundamental constraint. Species may successfully recruit only from those ponds that last long enough to allow adults to breed, embryos to hatch, and larvae to reach metamorphosis. That hydroperiod is an active force frequently revealed by the partial or complete loss of larval cohorts at the time of pond drying (Pechmann et al., 1991; Skelly, 1996). Hydroperiod is a useful predictive axis because of its obvious relationship to life history attributes of species (breeding phenology, larval period). Ecologists have used this axis to develop hypotheses for interspecific differences in distribution and interannual variation in recruitment, as well as local extinctions brought on by unusually dry conditions (Collins and Wilbur, 1979; Pechmann et al., 1989; Skelly, 1995a).

In fact, the obvious and immediate impacts of pond drying can obscure the role of other correlated changes which may be no less critical for anurans. In particular, the strong association between hydroperiod and the composition and abundance of predatory taxa has been documented in a number of regions (Skelly, 1995a, 1996; Smith and Van Buskirk, 1995; Spencer et al., 1999). For many of the same reasons that anuran distributions appear to be limited by hydroperiod, those of their predators may be constrained as well. As hydroperiod increases, the potential pool of predators increases. The presence of some of these predators in longer hydroperiod ponds may explain the absence of some anurans (e.g., Skelly 1995b). As an example, the transition from nonpermanent to permanent water is often associated with the entry of fish into freshwater communities. The consequent impact of fish on prey taxa is well studied (Werner and McPeek, 1994). Among anurans, there are relatively few species that can survive in the presence of substantial fish populations. Those that do, appear to persist by being unpalatable or extremely cryptic (Kats et al., 1988).

These patterns suggest that the limits of each species' distribution might be anchored on one end by the ability to develop rapidly enough to metamorphose prior to drying, and, on the other end, by the ability to survive in the presence of increasing predation threat. Results from independently conducted field transplant experiments on spring peeper (Pseudacris crucifer) and chorus frog (P. triseriata) larvae are supportive of this hypothesis (Skelly, 1995a; Smith and Van Buskirk, 1995). In addition, these studies find no evidence that interspecific competition contributes to the segregation in distribution between species.

BULLFROGS

The invasion of bullfrogs (Rana catesbeiana) in western North America has yielded an unfortunate opportunity to witness a change in the distributional pattern of anuran. During its spread, several researchers have noted corresponding declines and disappear-
ances of native species (e.g., Moyle, 1973). Subsequent experiments have been aimed at quantifying and understanding the mechanism underlying the "bullfrog effect" (e.g., Kupferberg, 1997; Kiesecker and Blaustein, 1998; Adams, 2000).

Experimentation has revealed evidence for competitive impacts on natives, as well as negative effects of predation. For example, Kupferberg (1997) has shown that larvae of *R. boylii*, a native species, suffer a 48% drop in survival when in the presence of bullfrog larvae. Correspondingly, bullfrog larvae in field enclosures alter the composition of algal food resources in a manner that may negatively affect native species. Both larvae and adults appear to contribute to the impact of bullfrogs, and at least one experiment suggests that native species may suffer particularly from the interactive effects of the two life stages (Kiesecker and Blaustein, 1998). The rapid evolution of behavior by native species along the invasion front is further evidence of the dramatic impact of bullfrogs (Kiesecker and Blaustein, 1997).

While the case for the effects of bullfrogs seems particularly strong, it has been noted that the spread of introduced bullfrogs is often coincident with the introduction of nonnative fish species. Surveys have revealed strong negative associations between introduced fish and native frog species (Knapp and Matthews, 2000), while experimentation has shown that the impacts of bullfrogs and introduced fish may cause disproportionate impacts on native anurans relative to the effects expected from each invader alone (Kiesecker and Blaustein, 1998).

**FOREST CANOPY**

Small ponds surrounded by successional vegetation often become overtopped by shoreline trees or by emergent shrubs. In many parts of the world such woodland ponds are the most common breeding environment available for anurans. The observation that distribution of both anurans and caudates may be linked to forest canopy has been made in both Europe (Bussler, 1982) and North America (Skelly et al., 1999). A number of species are known to be entirely restricted to ponds that have low levels of canopy development. Relatively few species are known to inhabit heavily shaded ponds.

Recently, Werner and Glennemeier (1999) published the results of a larval transplant experiment showing that some "open canopy obligate" species are unable to survive in deeply shaded ponds. Because canopy is likely to have a number of subsidiary impacts on other aspects of ponds, more research remains to be done. Candidate factors impacted by canopy include water temperature, dissolved oxygen, and the composition of food resources.

This selection of four cases includes examples which are nominally abiotic or biotic, and which are often discussed in terms of a single variable. However, in each case it is clear that upon closer examination, impacts on anurans are precipitated through the joint actions of multiple variables which themselves may be mechanistically linked.

The tendency for mechanisms to be best represented by the intersection of multiple variables extends to other examples for which distributional impacts are suspected, but less known. One example is the impact of disease. Disease has been implicated in declines, but thus far conclusive evidence is lacking. The documented impacts of disease
make it clear that pathogens by themselves can have little impact on performance. As an example, the negative effects of a fungal pathogen on the embryos of some anurans appear to be enhanced by UV-B radiation. The distribution of the fungal pathogen itself may be related to past stocking of introduced fish (Kiesecker et al., 2001). While neither UV-B radiation nor the fungus are nearly as potent alone as in combination, their joint effect appears to reflect aspects of the pond basin and its location on the one hand, and the history of fish stocking on the other hand.

In general, it appears that the opportunities to describe distributions in terms of single factor variation among ponds may be relatively infrequent. Much more commonly, distributions appear to be impacted by two or more factors acting in concert.

The regularity of the associations between anuran distributions and the variation among ponds appears to reflect the broad extent to which anurans are “habitat specialists.” Restricted distributions often may be due to the intolerance of embryos and larvae for the concordant changes associated with water chemistry, hydroperiod, and physical variables. While some variables may be important for a wide array of species, it is equally clear that both the available range of ponds and the tolerances for variation differ among species.

SPATIAL CONTEXT

The spatial context for ponds can impact distributions in two distinct ways. The fate of a population within a pond may be influenced by its connections to other ponds. Ponds can become more isolated when other ponds are located farther away or when the intervening landscape is somehow inhospitable to dispersers. In addition to isolation, the spatial context for ponds matters because the terrestrial uplands form the habitat for juveniles and adults for many pond-breeding anurans. For this reason, variation in the structure, amount, and proximity of different kinds of terrestrial environments also can affect distributions apart from any issues related to connectivity among ponds. In this section, I briefly review the effect of spatial context on anuran distributions mediated through both connectivity and juvenile–adult habitat.

AMPHIBIAN METAPOPULATIONS

The typical characteristics of anuran distributions (restriction, dynamism) may be explained in terms that do not rely on between-habitat variation. In the 1960s, Richard Levins showed that, in the absence of any variation among patches, a species could have a limited distribution among patches that could change rapidly over time (Levins, 1969). The classic metapopulation model predicts that the equilibrium fraction of patches occupied will reflect a balance between the likelihood of local population extinction, and the rate at which dispersers arrive from other populations. Most recent incarnations of metapopulation models include the notion that some measure of isolation from the nearest patches will drive the rate of immigration (Harrison and Taylor, 1997).

Since the development of the metapopulation concept, the idea has been linked frequently with pond-breeding amphibians (e.g., Gill, 1978; Sjogren-Gulve, 1994; Harrison and Taylor, 1997). In fact, many of the assumptions of both classic and modern
metapopulation models seem to be remarkably well met. It has been suggested that pond-breeding anurans have their populations demographically focused around insular habitat patches, that there are discrete local extinction and colonization events, that adults are generally highly philopatric, and that juveniles do disperse among ponds (Harrison and Taylor, 1997). The superficial congruence between the assumptions of metapopulation models and the pond-breeding amphibian system has encouraged ecologists to suggest that inter-pond variation may not be as important to distributions as the spatial arrangement of ponds and the pattern of landscape structure in between ponds (e.g., Marsh et al., 1999).

There is substantial evidence for the impact of isolation on anuran distributions. In particular, it appears that the isolation of breeding ponds does affect distributions (Semlitsch and Bodie, 1998). Figure 2 shows the relationship between the occupancy status of ponds and their isolation from the nearest breeding pond for an amphibian assemblage in Michigan, USA (Skelly et al., 1999). Even in this landscape with low density of human settlement, few barriers to movement, and a high density of ponds, the tendency for ponds to be occupied is related to their proximity to other ponds. In other landscapes with lower pond densities and lower connectivity, these effects appear to be magnified; a number of studies show that pond occupancy is lower and the likelihood of extinction is higher when a pond is more isolated (Sjogren-Gulve, 1994; Vos and Stumpel, 1996; Kolosvary and Swihart, 1999; Lehtinen et al., 1999). Using data from a long-term survey of pool frogs \( (Rana lessonae) \), Sjogren-Gulve (1994) concluded that most observed extinctions were related to pond isolation. Recently, Marsh et al. (1999) published the first experimental evaluation of the impact of isolation on anurans. Consistent

Fig. 2. Isolation of ponds according to population status during two surveys (1967–74 and 1988–92) in which the distributions of 14 amphibian species were described for 32 ponds. Population status was defined as follows: not present in the pond during either survey (Never), present during 1988–92 survey only (Invaded), present during 1967–74 survey only (Extinct), present during both surveys (Stable). Bars represent mean + 1 SE. Figure is reprinted from Skelly et al. (1999).
with most observational evidence, they found that tungara frogs (*Physalaemus pustulosus*) were more likely to breed in artificial ponds placed nearer to source ponds.

Despite evidence that isolation can impact occupancy patterns, amphibian ecologists remain divided over the utility of the metapopulation framework (Gill, 1978; Berven and Grudzien, 1990). In part, this is a definitional issue. If a metapopulation is defined in its strictest sense, then it would probably apply to very few species of any taxon. However, metapopulation biologists have argued, convincingly, that even if species residing in patches are more connected to each other than they would be in a strict metapopulation, the fragmentation of the species into patches can still influence demography. We should expect the pattern revealed in Fig. 2 to arise under a variety of conditions, each sharing some resistance to movement associated with distance. The relevant concern is that the spatial arrangement of ponds may impact distributional patterns among ponds and demographic processes within ponds. Figuring out the extent to which it does influence spatial pattern awaits further experimentation.

**THE ROLE OF LANDSCAPE CONTEXT**

A recent spate of landscape studies provides evidence that the structure of the intervening upland environment also can affect distributions. Several studies suggest positive effects of forest cover (Pavignano et al., 1990; Gibbs, 1998a; Heenan and M'Cluskey, 1998) or negative effects of urban cover (Knutson et al., 1999) and road density (Vos and Chardon, 1998) on the presence of anurans. Correspondingly, there is a small but growing number of studies that show that movement behavior of anurans is impacted by land cover. deMaynadier and Hunter (1999) report that emigrating juveniles preferentially utilize mature forest. A separate study by Gibbs (1998b) showed that amphibians are sensitive to landscape boundaries, tending to avoid crossing open areas and roads. While a number of these studies have emphasized the importance of the findings for understanding the role of landscape connectivity, the impact of landscape variation on adult habitat is difficult to separate in observational studies. The most direct way to dissect such impacts would involve landscape-scale experiments involving the manipulation of both the amount of adult habitat and the connectivity (or proximity) of breeding habitats.

**OVIPOSITION SITE CHOICE**

Most conceptions of anuran distributions among ponds have focused on the impacts of abiotic and biotic factors on embryos and tadpoles and their variation among potential habitats. However, prior to being subjected to the vagaries of their aquatic environment, offspring are placed there by one or both parents as a fertilized egg. Oviposition site choice by adults is an equally tenable hypothesis for an anuran distributional pattern (Blaustein, 1999).

There is mounting evidence that breeding amphibians are capable of sensing and altering oviposition patterns in response to a variety of cues (Table 2). While most experiments have manipulated predators (including cannibal morphs of the focal spe-
Table 2

Studies experimentally evaluating the influence of different factors on oviposition site selection by anurans. For each study, the focal species, experimental setting, significant factors, and authors’ interpretation are presented.

<table>
<thead>
<tr>
<th>Study</th>
<th>Species</th>
<th>Setting</th>
<th>Factor</th>
<th>Interpretation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Resetarits and Wilbur (1989)</td>
<td><em>Hyla chrysoscelis</em></td>
<td>Wading pools</td>
<td>Conspecific larvae</td>
<td>Competition avoidance</td>
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<td></td>
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<td></td>
<td>Fish</td>
<td>Predation avoidance</td>
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<td></td>
<td></td>
<td></td>
<td>Salamander larvae</td>
<td>Predation avoidance</td>
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<td></td>
<td></td>
<td></td>
<td>Heterospecific Larvae</td>
<td>No effect</td>
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<td></td>
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<td></td>
<td>Adult salamanders</td>
<td>No effect</td>
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<td></td>
<td>Insect larvae</td>
<td>No effect</td>
</tr>
<tr>
<td>Crump (1991)</td>
<td><em>Hyla pseudopoma</em></td>
<td>Plastic containers</td>
<td>Conspecific larvae</td>
<td>Predation avoidance</td>
</tr>
<tr>
<td>Hopey and Petranka (1994)</td>
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<td>Artificial ponds</td>
<td>Depth</td>
<td>Desiccation avoidance</td>
</tr>
<tr>
<td>Petranka et al. (1994)</td>
<td><em>Bufo americanus</em></td>
<td>Artificial ponds</td>
<td>Fish</td>
<td>Predation avoidance</td>
</tr>
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<td>Spieler and Linsenmair (1997)</td>
<td><em>Hoplobatrachus occipitalis</em></td>
<td>Rock pools</td>
<td><em>R. sylvatica</em> larvae</td>
<td>Predation avoidance</td>
</tr>
<tr>
<td>Laurila and Aho (1997)</td>
<td><em>Rana temporaria</em></td>
<td>Rock pools</td>
<td>Conspecific larval</td>
<td>Predation avoidance</td>
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<td>Kiesecker and Skelly (2000)</td>
<td><em>Hyla versicolor</em></td>
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<td>Snails</td>
<td>Infection avoidance</td>
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cies), other studies demonstrated significant responses to potential competitors and to the presence of a pathogen. Researchers have interpreted these responses as avoidance of predation, competition, desiccation, and infection. When researchers have followed up choice experiments with larval assays, avoided habitats have tended to yield inferior larval performance (e.g., Petranka et al., 1994). While still not numerous, the studies in Table 2 represent a diversity of taxa from a variety of regions. The results are even more remarkable when one realizes that some of the focal species are known to spend relatively short periods of time in the water (e.g., Ritke and Mumme, 1993) and may not even submerge completely during their stay.

The demonstration that adult choice of oviposition sites is facultative and sensitive to a variety of cues is of extreme importance to researchers interested in anuran distributions. Most fundamentally, it means that we must be cautious in interpreting patterns of distributional change (discussed below). The arrival or disappearance of a species may be because of local demographic responses, or because adults have moved elsewhere to breed. The two alternatives have large implications for assumptions concerning the relationship between distributions and declines or increases in regional density of a species. In addition, it means that managers intervening by altering pond attributes must be aware that their actions could alter the status of cues that anurans use to choose breeding sites. On the one hand this may be a problem, on the other it may represent an underexploited opportunity.

A DYNAMIC PERSPECTIVE

There is a wealth of evidence that the demography of amphibians is volatile (Pechmann et al., 1989, 1991; Semlitsch et al., 1996). Booms and busts in recruitment appear to be routine for many species (Alford and Richards, 1999). Less well-documented have been the longer term patterns of establishment and extinction of breeding populations (Sjogren-Gulve, 1994; Semlitsch et al., 1996; Skelly et al., 1999). However, even this smaller body of work implies that shifts in distributions should not be surprising. Despite this evidence, many discussions of anuran distributions tacitly assume that distributional change is not normal.

Either because of stochastic fluctuations, or because of deterministic shifts, ponds change over time. Because the performance of embryos and larvae can be sensitive to these changes and because adults may alter their oviposition site choice, we can expect changes in ponds to beget changes in distributions (e.g., Sjogren-Gulve, 1994). If distributional change is viewed as a natural backdrop for anurans, the detection of declines or other anthropogenically mediated changes in distributions becomes more challenging. Nevertheless, we must expect that such changes will occur, sometimes rapidly, and may have distinct effects on different species.

Sjogren-Gulve’s (1994) study of pool frogs shows how the long-term processes associated with the creation and succession of pond environments may drive distributional dynamics. The region occupied by these populations is slowly being raised out of
the Baltic Sea (60–80 cm per century). Depressions in the bedrock become ponds that may last for up to 400 years before being filled in during the course of successional changes in the basin. While these ponds exist, they may be occupied by pool frogs whose populations blink in and out of existence until successional changes render the basin no longer habitable. In this case, it appears that stochastic and deterministic changes co-occur and together drive distributional patterns.

In a second example from the United States, the probability of extinction for two anuran species is presented as a function of changes in the overhead forest canopy of their breeding ponds (Fig. 3). Spring peeper (*P. crucifer*) populations tended to disappear from ponds where canopies closed over ponds during forest succession, but not from ponds that remained open. In contrast, the extinction pattern of wood frog (*R. sylvatica*) populations was unrelated to canopy closure. The rapid loss of populations of one species was associated with natural regrowth of forests occurring over less than 20 years. The persistence of the second species despite these changes may be related to its ability to maintain rapid growth and development in a colder, less productive environment (Skelly, et al., in press). Because wood frogs are less sensitive to an important change in pond environments, their large-scale dynamics may more closely echo those of a stochastically-driven metapopulation, whereas the dynamics of spring peepers and other canopy-intolerant species may be more driven by the pattern of environmental change, a hypothesis currently under evaluation.

![Graph](image_url)

**Fig. 3.** The probability that a population became extinct in ponds where forest canopy remained open (white bar) between two surveys (1967–74 and 1988–92) versus ponds in which canopy closed over (black bars) pond basins between surveys. Data are presented for two anuran species, the spring peeper (*Pseudacris crucifer*) and the wood frog (*Rana sylvatica*) at the E.S. George Reserve in Michigan, USA (Skelly et al., 1999).
IMPLICATIONS FOR CONSERVATION

The wealth of information uncovered during studies of anuran distributions yields some useful conclusions that may be applied to their conservation:

- Anuran distributions are both restricted and dynamic. A single anuran species rarely occupies a majority of the ponds used by anurans as a group. Therefore, we should expect absences. In addition, long-term studies show that local extinctions of anuran populations can occur relatively frequently even in the absence of long-term decline. This means that evidence of declines is most readily available from landscape-scale studies incorporating many populations.

- Experiments have revealed that anuran embryos and larvae are sensitive to alterations in a great variety of factors. For any change in distribution pattern, there are many candidate explanations.

- While amphibian declines are often discussed in terms of the impact of single factors (nowhere more so than in the media), the real causes for amphibian distributions, including declines and disappearances, often may be the result of multiple, interacting factors. Understanding these intricacies and communicating them effectively to policymakers will be critical in developing effective conservation measures.

- Despite more than three decades of intensive study, there are relatively few instances for which we have developed convincing links between natural patterns of distribution and experimentally supported explanations for those patterns, even among nondeclining species. Given the time expediency of conservation action, practitioners often will be forced to take action in the absence of local knowledge of those links.

- The metapopulation perspective remains appealing for the study of amphibians, but is generally underevaluated. Particularly important issues include the effect of landscape change on connectivity among populations and the potential importance of presently unoccupied ponds for the long-term persistence of anuran species. In addition, there has been a tacit assumption that the breeding pond is an appropriate unit of conservation concern. In fact, viable demographic units may require larger scale protection efforts. These issues will remain unresolved in the absence of landscape scale, long-term experiments.

- The terrestrial landscape represents adult habitat for most pond-breeding amphibians (Semlitsch, 1998). The status and dynamics of uplands are likely to have a large impact on the fate of breeding populations; these impacts are only dimly understood.

- Oviposition decisions by anurans have received less attention than they deserve. There is compelling evidence that landscape scale changes in embryonic and larval distributions arise from adult behavior. Understanding how anthropogenic changes influence oviposition decisions is likely to be important to the success of amphibian conservation efforts.
CONCLUSIONS

The study of anuran ecology is unusual compared with many other taxa. Anuran ecologists have emphasized experimentation to a degree matched in few other systems. We know a great deal about how a variety of factors act alone and in concert to influence cohorts of larval anurans. These efforts have made larval anurans a model system in ecology. Consequently, I have found that many ecologists working in other systems have been surprised by the inability of anuran ecologists to account for declines and disappearances of anuran populations. There are many reasons for this lack of understanding that would be familiar to scientists in other disciplines (e.g., fisheries). However, to a significant extent, the documentation of anuran distributions and the building of inferential bridges between distributions and experimental outcomes have not been emphasized among practitioners until recently. During the last decade, concern over the fate of species has precipitated a tidal shift in the priorities of anuran ecologists.

This shift will speed the development of a more predictive conceptual framework for anuran distributions. If the ideal model will need to be able to forecast changes in distribution over large scales of time and space, then it stands to reason that we must start conducting experiments over those same scales. These experiments will be costly, time consuming, and will be completed successfully only with great effort. However, compared with most animals of conservation concern, anurans are relatively tractable. Techniques including manipulations of whole ponds offer the promise of a greatly enhanced understanding of the mechanisms which underly distribution patterns.

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REFERENCES


Copelia 1999: 22–33.


Ecol. Manage. 1: 3–11.


