Metapopulation Dynamics and Amphibian Conservation

DAVID M. MARSH* AND PETER C. TRENHAM†

*Department of Biology, Washington and Lee University, Lexington, VA 24450, U.S.A., email marshd@wlu.edu
†United States Environmental Protection Agency, Mid-continent Ecology Division, 6201 East Congdon Road, Duluth, MN 88504, U.S.A.

Abstract: *In many respects, amphibian spatial dynamics resemble classical metapopulation models, in which subpopulations in breeding ponds blink in and out of existence and extinction and colonization rates are functions of pond spatial arrangement. This "ponds-as-patches" view of amphibian spatial dynamics is useful in several respects. First, it highlights the importance of regional and landscape processes in determining local patterns of abundance. Second, it offers a straightforward, pond-based approach to monitoring and managing amphibian populations. For many species, however, the ponds-as-patches view may be an oversimplification and metapopulation structure may be more apparent than real. Changes in distribution may be caused by processes other than extinction and recolonization, and most extinctions probably result from deterministic factors, not stochastic processes. In addition, the effects of pond isolation appear to be important primarily in disturbed environments, and in many cases these isolation effects may be better explained by the distribution of terrestrial habitats than by the distribution of breeding ponds. These complications have important implications for both researchers and managers. For researchers, future efforts need to determine the mechanisms underlying patterns of abundance and distributional change and patterns in amphibian populations. For managers, effective conservation strategies must successfully balance metapopulation considerations with careful attention to local habitat quality. Furthermore, translocations and active management may be indispensable tools for conserving amphibians in landscapes containing multiple breeding ponds.*

Dinámicas Metapoblacionales y Conservación de Anfibios

Resumen: *La dinámica espacial de anfibios se asemeja de muchas maneras a los modelos metapoblacionales clásicos donde las subpoblaciones en los estanques de reproducción aparecen y desaparecen y las tasas de extinción y colonización son funciones de la disposición espacial de los estanques. Esta visión de "estanques-como-parches" de las dinámicas espaciales es útil de diversas maneras. Primero, resalta la importancia de los procesos regionales y de paisaje en la determinación de patrones locales de abundancia. Segundo, ofrece una estrategia directa, basada en los estanques, para monitorear y manejar poblaciones de anfibios. Sin embargo, para muchas especies la visión de estanques-como-parches puede ser una sobresimplificación y la estructura de metapoblación puede ser más aparente que real. Los cambios en la distribución pueden ser ocasionados por procesos diferentes a la extinción y la recolonización y la mayoría de las extinciones probablemente resulten de factores determinísticos y no de procesos estocásticos. Además, los efectos del aislamiento de estanques parecen ser importantes principalmente en ambientes perturbados y en muchos casos, estos efectos de aislamiento pueden ser explicados de mejor manera por la distribución de hábitats terrestres que por la distribución de los estanques de reproducción. Estas complicaciones tienen implicaciones tanto para los investigadores, como para los manejadores. Para los investigadores, los esfuerzos a futuro deben determinar los mecanismos fundamentales de los patrones de abundancia, los cambios en la distribución y los patrones en las poblaciones de anfibios. Para los manejadores, las estrategias de conservación efectivas deberán balancear exitosamente la consideración de la metapoblación, con especial atención en la calidad del hábitat. Además, el desplazamiento y el manejo activo pueden ser herramientas indispensables para conservar anfibios en paisajes que contienen múltiples estanques de reproducción.*

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Introduction

Metapopulation theory is an increasingly popular basis for conserving species in patchy or fragmented environments (e.g., McCullough 1996). Most studies of metapopulations consider the dynamics of populations divided into a number of subpopulations that exchange migrants and that may be subject to local extinction and recolonization (Hanski & Simberloff 1997). These studies are important to conservation biology because they provide an empirical basis for assessing the influence of habitat patch geometry and connectivity on local and regional population persistence (Harrison et al. 1988; Sjögren 1991; Kindvall & Ahlen 1992; Hanski et al. 1995*a*). They also provide a framework for predicting the effects of future habitat loss and fragmentation on populations of interest (Lindenmayer & Possingham 1996; Sjögren-Gulve & Ray 1996).

Metapopulation approaches have been applied to taxa ranging from protozoa (Holyoak & Lawler 1996) to butterflies (Harrison et al. 1988; Hanski et al. 1995*b*) to grizzly bears (Craighead & Vyse 1996). Recently, a number of studies have addressed the metapopulation biology of pond-breeding amphibians (e.g., Gill 1978; Berven & Grudzien 1990; Sjögren 1991; Sinsch 1992; Sjögren-Gulve 1994; Edenhamn 1996; Hecnar & M'Closkey 1996; Driscoll 1997; Skelly & Meir 1997; Trenham 1998; Skelly et al. 1999). The growing popularity of a metapopulation approach to amphibian ecology has two likely causes, one applied and one methodological. From an applied perspective, spatial processes such as habitat fragmentation and the loss of dispersal corridors may be increasingly important causes of amphibian population declines (Bradford et al. 1993; Blaustein et al. 1994; Hecnar & M'Closkey 1996; Sjögren-Gulve & Ray 1996; Beebee 1997; Semlitsch & Bodie 1998). On a methodological level, amphibians lend themselves particularly well to metapopulation studies because breeding ponds form discrete habitat patches that can be easily identified and characterized.

Because of this methodological issue, most amphibian metapopulation studies take a "ponds-as-patches" approach to metapopulation dynamics (e.g., Gill 1978; Sjögren 1991; Sjögren-Gulve 1994; Edenhamn 1996; Hecnar & M'Closkey 1996; Skelly & Meir 1997; Trenham 1998), in which ponds are used to delineate subpopulations that exchange migrants and that are subject to local extinction and recolonization from other pond subpopulations. Metapopulation dynamics are then studied by observing interpond migration rates and by using yearly surveys to document patterns of pond occupancy, extinction, and recolonization.

Based on this ponds-as-patches view, an amphibian metapopulation might be expected to have the following characteristics: (1) population dynamics are due primarily to processes occurring at breeding ponds, such that a focus on ponds can accurately determine the cause of local or regional declines, (2) local extinction and recolonization of pond subpopulations are common occurrences, (3) many local extinctions result from stochastic processes in otherwise suitable breeding habitats, and (4) limited dispersal ability leads to effects of pond isolation on colonization, extinction, or occupancy.

This view of amphibian metapopulations is obviously a caricature, and few would argue that the four characteristics listed above apply to all systems. Nevertheless, because a ponds-as-patches view of amphibian metapopulations has direct implications for the study, monitoring, and managing of amphibian populations, it is important to know whether this caricature is in fact useful for understanding the dynamics of amphibian populations. We use this caricature of amphibian metapopulation dynamics as a starting point from which to review the literature on amphibian metapopulation dynamics and conservation. Our goal here is not to criticize previous work; in fact, most of the issues we raise have been addressed in some form by previous authors. Rather, our goal is to compare this simple caricature of ponds-as-patches metapopulations to the dynamics of real systems and to ask when the discrepancies do or do not matter for amphibian conservation. Based on this review, we provide two sets of recommendations: one set for researchers that outlines the important gaps in our understanding of amphibian spatial dynamics and one set for managers that summarizes the conservation implications of our findings.

Do Amphibian Population Dynamics Result from Processes that Occur at Breeding Ponds?

Empirical studies of metapopulations in insects (Harrison et al. 1988; Kindvall & Ahlen 1992; Hanski et al. 1994, 1995*b*), plants (Ouborg 1993; Harrison et al. 2000), and mammals (Moilanen et al. 1998) have analyzed the dynamics of populations in networks of habitat patches. Habitat patches in these studies encompassed primary habitat for all life-history stages and were easily distinguishable from the nonhabitat matrix surrounding the patches. For amphibians, however, breeding ponds are simply the most convenient sites for sampling organisms. Most adult amphibians spend little time at breeding ponds, and many species are characterized by explosive breeding whereby mature adults breed over a period as short as a few days (reviewed by Wells 1977). Even species with prolonged breeding seasons commonly spend the majority of their lives in terrestrial habitats that may or may not be directly adjacent to the breeding site (Wilbur 1984). Although metapopulation studies do not explicitly assume that population dynamics are determined only by processes occurring within the habitat patches studied, exclusively pond-based studies will generally lead to pond-based explanations for patterns of abundance and persistence. As a result, it is important to know the relative contributions of breeding ponds and terrestrial habitats to amphibian metapopulation dynamics.

Numerous experimental studies have demonstrated that density, interspecific competition, and predation can have strong effects on larval survival (reviewed by Wilbur 1997), but the strength of these effects in natural systems is less well understood. Semlitsch et al. (1996) did find significant positive correlations between breeding adult population size and the number of metamorphs in previous years for 5 of 12 amphibian species and positive trends for 6 of the remaining 7 species. Meyer et al. (1998) detected density dependence in one of three ponds containing *Rana temporaria.* Berven (1990) found that fluctuations in the size of adult populations of wood frogs (*Rana sylvativa*) are well explained by previous recruitment. Similarly, Beebee et al. (1996) determined that the number of *Bufo bufo* metamorphs was highly correlated with the number of breeding adults in the following year.

Nevertheless, a growing body of evidence suggests that terrestrial habitats may also play an important role in population dynamics. For example, Schwarzkopf and Alford (1996) found that shelter-site quality was an important determinant of growth in *Bufo marinus.* Similarly, Loredo et al. (1996) demonstrated the importance of ground squirrel burrows for California tiger salamanders (*Ambystoma californiense*) and suggested that loss of these terrestrial habitat features may have strong negative consequences for salamander populations. The recent work of Skelly et al. (1999) on the effects of terrestrial succession on local extinction also makes a strong case for the role of terrestrial habitat in determining local (i.e., within-pond) population dynamics.

In addition to affecting local demography, terrestrial habitat may also have a strong influence on regional dynamics. In Table 1 we present the results of studies that have considered isolation from essential terrestrial habitats as a potential influence on breeding pond use. Where isolation from terrestrial habitats has been assessed, it has been correlated with amphibian abundance or diversity in every case. In several cases (e.g., Laan & Verboom 1990; Edenhamn 1996), the evidence for terrestrial isolation effects is stronger than the evidence for aquatic (i.e., pond-to-pond) isolation effects. Thus, pond occupancy may be more indicative of the spatial arrangement of terrestrial habitat than the arrangement of breeding ponds.

One clear implication of these results is that terrestrial habitats, and not just breeding ponds, must be protected. Recognizing this need, Semlitsch (1998) used movement data for ambystomatid salamanders to estimate appropriate terrestrial buffer zones for wetlands used by these species. A less obvious implication of terrestrial habitat use is that it may lead to misinterpretation of metapopulation structure. For example, Trenham (1998) found that California newts (*Taricha torosa*) often disperse much longer distances between ponds and terrestrial habitats than between different ponds. An exclusively pond-based study would therefore underestimate the mobility of individuals and the spatial scale over which the population should be monitored or protected. Thus, to the extent that terrestrial habitat use remains a black box, conservation biologists must be cautious in identifying the factors that are responsible for local amphibian declines and extinctions.

Are Local Extinction and Recolonization Common Occurrences?

In metapopulations, patch occupancy and persistence are functions of extinction and colonization rates (Levins 1969; Hanksi & Gilpin 1991). Thus, estimating these rates is a primary goal of metapopulation studies. For studies that take a pond-as-patches approach to amphibian metapopulations, local extinction and recolonization are generally assessed by analyzing year-to-year changes in the presence or absence of adults or larvae at breeding ponds (here, "turnover") (Sjögren-Gulve 1994; Edenhamn 1996; Hecnar & M'Closkey 1996). Ponds that are

Table 1. Effects of isolation from terrestrial habitats on use of breeding ponds by amphibians.

Species	*Terrestrial habitat variable*	*Effects found*	*Effects not found*	*Reference*
Rana lessonae	ditching between ponds	predicted persistence	—	Sjögren-Gulve & Ray 1996
Hyla arborea	percent intervening natural pasture, forest	colonization, extinction	—	Edenhamn 1996
Hyla arborea	shrub, herb density within 1 km	pond occupancy	—	Vos & Stumpel 1996
Rana moorea	moorland within 2 km	pond occupancy*	pond occupancy*	Vos & Chardon 1998
Rana temporaria	distance to forest	pond occupancy	—	Loman 1988
Rana dalmatina	distance to forest	egg masses	—	Wederkinch 1988
10 species	distance to forest	diversity	—	Laan & Verboom 1990
11 species	distance to forest	diversity	—	Lehtinen et al. 1999

**Aquatic and terrestrial isolation variables were highly correlated and therefore confounded.*

used one year but unused the next indicate local extinctions, whereas ponds that go from unused to used indicate colonization. Many studies of amphibian populations have documented turnover in this context, some at remarkably high rates (Table 2).

Nevertheless, a number of processes other than the extinction and recolonization of local subpopulations may contribute to observed turnover. Most obviously, sampling error can cause apparent local turnover. That is, if species are missed in surveys, local populations appear to go extinct and be recolonized when they were present all along. Although sampling error is a problem for all species, it may be particularly common for amphibians because of their short reproductive periods (Wells 1977) and large fluctuations in breeding population size from year to year (e.g., Pechmann et al. 1991; Semlitsch et al. 1996).

Several biological processes may also contribute to observed turnover. First, turnover could result from subpopulations of long-lived species that skip breeding seasons when climatic conditions are unfavorable (Twitty 1966; Semlitsch et al. 1996). Similarly, turnover could be caused by pulse-breeding coupled with extended prereproductive periods (Edenhamn 1996). This is analogous to seed banks in plants, which make it difficult to interpret local fluctuations in adult density (Doak et al. 2001). Finally, turnover could occur through the regular movement of groups of adults from one pond to another. Active selection of breeding sites, by both calling males and females, has been observed in numerous studies (e.g., Resetarits & Wilbur 1989, 1991; Crump 1991; Spieler & Linsenmair 1997), indicating that some amphibians move between ponds in response to biotic or abiotic cues. When individuals move frequently between ponds, groups of amphibians at individual ponds are more properly regarded as breeding aggregations than as local subpopulations subject to extinction and recolonization.

As a result of these complications, some of the extinction and colonization rates in Table 2 are likely to be overestimates. Does this matter? From a conservation perspective it may not always be important what biological processes cause turnover in pond use. All biological causes of turnover reinforce the conclusions that apparent local extinctions are not necessarily permanent, that unused habitats may be important for the long-term persistence of species, and that maintaining connectivity between habitat patches should be a priority. In addition, the conclusions from monitoring programs based on surveys of multiple ponds may not depend on the causes of distributional change. Substantial declines in the number of used breeding ponds over many years will be a concern regardless of whether previously used ponds were abandoned or breeding populations went extinct (Fisher & Shaffer 1996; Shaffer et al. 1997).

In other cases, understanding the mechanisms behind observed turnover is important for amphibian conservation. First, the correlates of breeding-site selection may differ from the factors that cause local extinction. Thus, correlations between biotic or abiotic factors and amphibian disappearances may not be informative without knowledge of the underlying processes (McArdle & Gaston 1993). Second, understanding the causes of turnover in pond use may have important implications for predicting population persistence. High rates of local extinction and recolonization may imply that a metapopulation is highly unstable and that stochasticity in extinction or colonization rates alone can drive metapopulation extinction. Conversely, if this same amount of turnover represents the movement of individuals between ponds or skipped breeding seasons, the overall population size may remain quite constant from year to year and expose the metapopulation to low extinction risk.

Several steps may be taken to distinguish among the processes that cause apparent turnover. First, sampling

Table 2. Rates of turnover in amphibian metapopulations, given as extinction or colonization per species per year.

Study	*Species*	*Total/ occupied ponds*	*Years*[a]	*Extinction rate*	*Colonization rate*[b]
Sjögren-Gulve 1994	*Rana lessonae*	≅200/49	22 (resurvey)	0.017	0.009
Sjögren-Gulve 1994	*Rana lessonae*	≅200/71	5 (yearly)	0.021	0.023
Edenhamn 1996	*Hyla arborea*	≅1500/227	8 (resurvey)	0.07	0.04
Edenhamn 1996	*Hyla arborea*	≅1500/452	3 (yearly)	0.24 to 0.27	0.27 to 0.46
Hecnar & M'Closkey 1996	11 species	97/4-95	3 (yearly)	0.16 to 0.30[c]	0.07 to 0.29[c]
Skelly & Meir 1997	14 species	32/32	12 (resurvey)	0.007[c]	0.008[c]
Semlitsch et al. 1996	13 species	1/1	16 (yearly)	0.056[c]	0.051[c]
Berven 1995	*Rana sylvatica*	6/6	7 (yearly)	0.0	0.0
Gill 1978	*Notophthalmus viridescens*	7/7	5 (yearly)	0.0	0.0
Sinsch 1997	*Bufo calamita*	5/5	5 (yearly)	0.0	0.0
Meyer et al. 1998	*Rana temporaria*	3/3	23-28 (yearly)	0.0	0.0

[a] *We indicate whether turnover was estimated from yearly surveys (yearly) or from two surveys several years apart (resurvey).*
[b] *Colonization rates are calculated assuming that all unoccupied ponds are potentially suitable.*
[c] *Data are given as averages across species.*

error can be reduced by calibrating observed presences and absences with known distributions or species lists obtained by independent methods (e.g., Hecnar & M'Closkey 1996) and by visiting ponds a sufficient number of times (Driscoll 1998). Turnover due to extended prereproductive periods can be eliminated by requiring that the population be absent from a breeding pond for longer than the time to maturity before it is deemed locally extinct (Edenhamn 1996). Turnover related to skipping breeding seasons or movement between ponds can be distinguished only when individuals are marked. Although mark-recapture studies are labor-intensive, they may be necessary for developing species conservation strategies that require a detailed understanding of population dynamics.

Do Local Extinctions Result from Stochastic Processes?

Some disappearances of amphibians from breeding ponds do represent local extinctions. For a ponds-as-patches metapopulation approach to be useful, however, extinctions must occasionally occur in suitable habitats (i.e., "stochastic" extinctions), not just in habitats that have become permanently degraded (i.e., "deterministic" extinctions). If the latter situation predominates, then landscape-scale patterns in distribution and abundance are explained by local pond characteristics and not by metapopulation characteristics such as isolation or connectivity.

Several authors have recently highlighted the deterministic nature of local amphibian extinctions. Beebee (1997) noted that either pond destruction or the introduction of fish could explain most recent disappearances of the crested newt (*Triturus cristatus*) from dewponds in Sussex England. Sinsch (1992) observed that local extinctions in a metapopulation of natterjack toads (*Bufo calamita*) were due entirely to habitat destruction. Processes other than habitat destruction may also result in deterministic local extinctions. Sjögren-Gulve (1994) documented deterministic extinctions in pool frog populations caused by pond succession, and Skelly et al. (1999) found that succession in terrestrial habitats surrounding ponds explained much of the observed turnover in species distributions in a Michigan assemblage. Finally, strong inverse correlations between the presence of amphibians and the presence of fishes (Bronmark & Edenhamn 1994; Fisher & Shaffer 1996) and strong correlations between amphibian distributions and abiotic habitat characteristics (Beebee 1985; Pavignano et al. 1990; Ildos & Ancona 1994; Stumpel & van der Voet 1998) also suggest that deterministic factors may explain many local disappearances.

Conversely, classifying extinctions as stochastic is difficult, because disappearances from apparently suitable ponds may indicate insufficient understanding of the abiotic or biotic conditions that determine pond quality. For example, the well-known extinction of golden toads (*Bufo periglenes*) from Costa Rica was originally ascribed to stochastic factors (Pounds & Crump 1994) until better data on climate changes became available (Pounds et al. 1999). Nevertheless, a number of factors may predispose amphibian populations to stochastic extinction. First, amphibian reproduction may fail completely due to climatic events such as drought (Gill et al. 1983; Pechmann et al. 1991; Semlitsch et al. 1996). Second, many amphibians are short-lived, such that a few consecutive "bad" years may be sufficient to eliminate a breeding population. Indeed, at least some of the extinctions observed in previous metapopulation studies appear to be related to factors other than pond quality (e.g., Sjögren 1991; Edenhamn 1996).

Is it important whether local extinctions are stochastic or deterministic? Conservation and recovery plans certainly need to consider both types of extinction as potential threats. But the issue of whether local extinctions are primarily stochastic or deterministic is crucial because it determines whether amphibian monitoring and management strategies should focus on local habitat conditions or on landscape factors. Given that conservation efforts are always subject to financial constraints, expanding the landscape component of amphibian surveys may entail a loss of information on the characteristics of individual ponds. If such a trade-off is unavoidable, the decision about whether to focus on local or landscape-level threats to persistence should not be made without concrete natural-history data on the relevant species and their habitat affinities.

Is Pond Isolation Important to Pond Use or Population Persistence?

Amphibians have generally been viewed as highly philopatric organisms with poor dispersal abilities (Sinsch 1990; Blaustein et al. 1994; Duellman & Trueb 1994). This has led many to hypothesize that pond isolation, measured as some function of distance between ponds, should be a critical determinant of pond use and population viability for amphibians (Laan & Verboom 1990; Sjögren 1991; Bradford et al. 1993; Blaustein et al. 1994). Understanding the role of pond isolation is also vital to amphibian conservation because loss of breeding habitats and disruption of dispersal routes leaves remaining habitats increasingly isolated from one another (Sjögren-Gulve & Ray 1996; Semlitsch & Bodie 1998).

But the dispersal abilities of amphibians may not be as limited as has often been suggested. Long-distance dispersal is notoriously difficult to detect and is usually underestimated by mark-recapture studies (Porter & Dooley 1993). For example, Szymura and Barton (1991) found that genetic estimates of dispersal rates in fire-bellied toads (*Bombina bombina*) are more than double estimates obtained from mark-recapture data, and that rare long-distance dispersers may move up to 11 km. Many other species may disperse over similarly large distances. In Table 3 we present data from some of the better-dispersing amphibians; recorded dispersal distances of some species exceed 10 km. Although long-distance dispersers may be rare, these individuals may nevertheless dominate habitat colonization and patterns of spatial dynamics (Kot et al. 1997; Lewis 1997). If even a few dispersing amphibians are able to reach all suitable ponds, the effects of pond isolation (i.e., the distance between ponds) on pond colonization or extinction may be negligible. Indeed, several studies found no detectable effects of pond isolation (Table 4). In addition, for several systems not included in Table 4, dispersal apparently occurs often enough that there are no isolation effects to be examined. That is, all suitable ponds are occupied at any given time because of high dispersal frequencies (Gill 1978; Sinsch 1992; Berven 1995; Trenham 1998).

Although some studies did not detect isolation effects, others have found significant isolation effects in amphibian populations (Table 4). Sjögren (1991) found strong effects on both colonization and extinction in *Rana lessonae* near the species' northern range limit. In addition, two genetic studies have found steep increases in genetic differentiation with increases in interpond distance (Reh & Seitz 1990; Hitchings & Beebee 1997). One common feature of these genetic studies is highly disturbed habitats: both studies found that urban development is positively correlated with genetic divergence among populations. A number of other studies have found that urbanization and roads may limit amphibian dispersal or abundance (Fahrig et al. 1995; Gibbs 1998; Knutson et al. 1999; Lehtinen et al. 1999). In contrast, most of the studies that found no significant isolation effects (Gill 1978; Berven 1995; Trenham 1998; Seppa & Laurila 1999; Skelly et al. 1999) were conducted at sites where the habitat between ponds was relatively undisturbed. Studies examining interpond dispersal in relatively undisturbed habitats have often found dispersal rates on the order of 20% per generation (Table 5). Because many amphibians appear to be adapted for regular interpond dispersal, isolation effects are probably not inherent aspects of amphibian spatial dynamics. Rather, the strength of isolation effects may reflect the degree to which the landscape has been altered by human development.

This view has several implications for conservation. First, it suggests that connectivity may be an important issue primarily at a regional scale where highly developed areas intervene between breeding ponds. Within biological reserves or other protected areas, connectivity and the effects of pond isolation may be much less of an issue. Second, if isolation effects occur primarily in highly disturbed habitats, species translocations may be necessary to promote local and regional population persistence. Because most amphibians lack parental care, they are prime candidates for egg and larval translocations. Indeed, translocations have already proven successful for several species of amphibians (Andren & Nilson 1995; Bloxam & Tonge 1995; Zvirgzds et al. 1995; Denton et al. 1997). In addition, translocations may prove more cost-effective than attempts to promote local persistence with habitat corridors of unknown efficacy.

Recommendations for Researchers

We lack sufficient understanding of the role of terrestrial habitats in determining patterns of abundance at breeding ponds. Although collecting this sort of information is difficult,it can be accomplished with increasingly reliable marking methods (e.g., Spieler & Linsenmair 1998) and by experimentally manipulating terrestrial habitat features of interest (e.g., Stewart & Pough 1983; Donnelly 1989).

Although advances have been made in describing amphibian metapopulation dynamics, much less is known about the underlying processes. Investigating processes such as dispersal and local demography is time-consum-

Table 3. Longest reported dispersal distances of some amphibians.

Species	*SLV (cm)*[a]	*Dispersal (km)*	*Method*	*Reference*
Bufo marinus	8–12	15.1 km/year	rate of spatial spread	Easteal & Floyd 1986
Rana lessonae	7–11	15 km	mark-recapture	Tunner 1992[b]
Hyla arborea	4–6	12.6 km/year	mark-recapture	Stumpel & Hanekamp 1986
Hoplobatrachus occipitalis	7–9	6 km/year	radiotelemetry	Spieler & Linsenmair 1998
Taricha torosa	7–9	4.0 km/year	mark-recapture	Trenham 1998
Rana aurora	8–12	2.8 km/year	radiotelemetry	J. Bulger et al., personal communication
Rana sylvatica	4–6	2.5 km/year	mark-recapture	Berven & Grudzien 1990
Hyla regilla	3–5	2.5 km/year	rate of spatial spread	Reimchen 1991

[a] *Mean adult snout-vent length.*
[b] *As cited in Spieler and Linsenmair (1998).*

Table 4. Isolation effects in amphibian metapopulations.[a]

Species	*Effects found*	*Effects not found*	*Reference*
Rana lessonae	colonization, extinction	—	Sjögren 1991
Hyla arborea	extinction (large pop.)[b]	colonization, extinction (small pop.)[b]	Edenhamn 1996
Hyla arborea	pond occupancy	—	Vos & Stumpel 1996
Rana moorea	pond occupancy[c]	pond occupancy[c]	Vos & Chardon 1998
Physalaemus pustulosus	colonization	—	Marsh et al. 1999
12 species	—	colonization, extinction	Skelly et al. 1999[d]
10 species	diversity in old ponds	diversity in new ponds	Laan & Verboom 1990
11 species	diversity	—	Lehtinen et al. 1999
Rana temporaria	—	genetic differentiation	Seppa & Laurila 1999
Rana temporaria	genetic differentiation	—	Reh & Seitz 1990
Rana temporaria	genetic differentiation	—	Hitchings & Beebee 1997

[a] *All studies examined correlations between some function of distance to other breeding ponds and pond use, extinction, or colonization.*
[b] *Effect observed only in populations of ≤ 5 calling males.*
[c] *Aquatic and terrestrial isolation variables were highly correlated and therefore indistinguishable.*
[d] *Isolation effects were marginally significant.*

ing, but studies that focus on both spatial patterns and dispersal behavior have been useful in connecting patterns and processes for other taxa (Harrison et al. 1988; Hanski et al. 1994; Lewis et al. 1997). In addition, analytical and simulation models (e.g., Pulliam 1988; Sutherland 1996) can be used to explore the population consequences of dispersal behavior.

Correlative studies relating amphibian distributions to landscape factors are useful starting points, but few experimental studies have been conducted to separate landscape effects from the effects of local habitat quality on amphibian populations. Manipulative experiments are possible for amphibians; for example, fragmentation can be simulated by inducing habitat isolation with artificial barriers (e.g., Murdoch et al. 1996), and pond distributions can be manipulated with artificial ponds (Wilbur & Travis 1984).

For most species, we lack realistic protocols for species translocation and the creation of suitable breeding habitat (but see Denton et al. 1997). These issues are perhaps less theoretically interesting than those outlined above but are likely the most practical for amphibian conservation.

Clearly, amphibian species vary widely in dispersal and colonization ability, risk of local extinction, and sensitivity to habitat fragmentation. Beyond saying that "all species are different," we need to explore the ecological basis for interspecific variation in these responses. This will greatly enhance our ability to identify threatened species and predict their responses to environmental change.

Table 5. Annual rates of interpond migration of amphibians.*

Amphibian	*Adult*	*Juvenile*	*Meters*	*Reference*
Salamanders and newts				
Ambystoma californiense	18% M	20% M	300–670	Trenham 1998
	18% F	20% F		
Ambystoma maculatum	0 (322)	NR	800	Whitford & Vinegar 1966
Ambystoma opacum		6%	NR	Scott 1994
Ambystoma talpoideum	4 (629)	NR	150, 400	Raymond & Hardy 1990
Notophthalmus viridescens	1 (8500) F	NR	1000	Gill 1978
Taricha torosa	2.8% M	NR	60–1260	Trenham 1998
	1.5% F			
Frogs and toads				
Bufo americanus	15%	NR	30–250	Oldham 1966
Bufo bufo	20.1% M	17% M	60–180	Reading et al. 1991
	25.7% F			
Bufo calamita	2% M	0% M	NR	Sinsch & Seidel 1995
	20% F			Sinsch 1997
Bufo woodhousei	17%	27%	200–2000	Breden 1987
Rana catesbeiana	9 (22)	NR	150–1600	Ingram & Raney 1943
Rana lessonae	<1%	35%	NR	Sjögren-Gulve 1994
Rana sylvatica	0%	21% M	264–2530	Berven & Grudzien 1990
		13% F		

**Percentages are given where total number of recaptures was reported. In other cases, the number of interpond migrants is given, with the total number of marked animals in parentheses. NR indicates data were not reported, M indicates males, and F indicates females.*

Recommendations for Conservation Planners and Managers

Terrestrial habitat may be exceptionally important to the conservation of amphibian populations. Management plans that focus only on preserving ponds or wetlands will probably fail to maintain viable amphibian populations. Identifying and protecting critical terrestrial habitats should be a conservation priority.

Aggregations of amphibians at individual breeding ponds may not represent distinct populations and in many cases should not be managed as distinct units. Although amphibians are often regarded as philopatric, many species regularly disperse between ponds. As a result, groups of ponds may often be a more meaningful unit of management than individual ponds.

Because deterministic processes frequently drive amphibian populations to extinction, simply protecting clusters of breeding ponds may not be sufficient to maintain viable populations. Instead, active management may be necessary to protect amphibian populations. Important aspects of active management may include the removal of non-native predators and the maintenance of appropriate successional stages, both within the ponds and in adjacent terrestrial habitats.

Pond isolation may be a concern primarily in disturbed environments where interpond dispersal is impeded by barriers such as roads or urban development. Ameliorating isolation effects may be possible through the selection of sites for mitigation and wetland protection that are less isolated by roads and urban development. Where most ponds are severely isolated, translocations into extinct subpopulations may be the best strategy to promote regional population persistence.

Conclusions

Pond-based studies of amphibian spatial dynamics allow for efficient sampling of amphibians over large areas and over many years. As a result, these studies may provide a reliable database for the assessment of regional population trends, regardless of whether or not all species surveyed actually exhibit metapopulation dynamics. Because of this advantage, the utility of pond-based studies is without question. Nevertheless, amphibian spatial dynamics are more complex than might be inferred from studies that take a ponds-as-patches approach. In the preceding discussion we argued four main points with respect to these complexities. First, terrestrial habitats make critical contributions to both local and regional population dynamics, and exclusively pond-based studies may miss important causes of local and regional declines. Second, turnover in use of a breeding pond may result from biological processes other than local extinction and recolonization within metapopulations. Third, when local extinctions do occur in amphibian populations, they often result from deterministic factors and not environmental or demographic stochasticity. Fourth, the effects of pond isolation are not ubiquitous but appear to be important primarily when the terrestrial habitats surrounding ponds are highly altered.

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