

# Differentiating Migration and Dispersal Processes for Pond-Breeding Amphibians

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**ABSTRACT** Understanding the movement of animals is critical to many aspects of conservation such as spread of emerging disease, proliferation of invasive species, changes in land-use patterns, and responses to global climate change. Movement processes are especially important for amphibian management and conservation as species declines and extinctions worldwide become ever more apparent. To better integrate behavioral and ecological data on amphibian movements with our use of spatially explicit demographic models and guide effective conservation solutions, I present 1) a synopsis of the literature regarding behavior, ecology, and evolution of movement in pond-breeding amphibians possessing biphasic life cycles to distinguish between migration and dispersal processes, 2) a working hypothesis of juvenile-based dispersal, and 3) a discussion of conservation issues that follow from distinguishing the spatial and temporal movements of amphibians at different scales. I define amphibian migration as intrapopulation, round-trip movements toward and away from aquatic breeding sites. Population-level management, in general, can be focused on spatial scales of <1.0 km with attention focused on adult population and juveniles that remain near the natal wetland. I define amphibian dispersal as interpopulation, unidirectional movements from natal sites to other breeding sites. Metapopulation- or landscape-level management can be focused on movements among populations at spatial scales >1.0–10.0 km and on importance of terrestrial connectivity. The ultimate goal of conservation for amphibians should be long-term regional persistence by addressing management issues at both local and metapopulation scales. (JOURNAL OF WILDLIFE MANAGEMENT 72(1):260–267; 2008)

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Spatial and temporal aspects of animal movement are foundational to population regulation, metapopulation dynamics, and long-term persistence of species. Understanding movement of animals also is critical to many aspects of management and conservation such as the spread of emerging disease, proliferation of invasive species, impact of land use, and responses to global climate change. Movement processes are especially important for amphibian persistence as species declines and extinctions worldwide become ever more apparent (Stuart et al. 2004). For amphibians with a biphasic life cycle (aquatic larval phase and terrestrial juv–ad phase), movements to and from breeding sites are essential for reproduction and survival of local populations. Also, at broader landscape or regional scales, movement among populations is essential for recolonization after local extinction and maintenance of metapopulations (Marsh and Trenham 2001). Therefore, understanding behavior, ecology, and evolution of movement and distinguishing its importance at both population and metapopulation level is critical for effective management and conservation of amphibians (Semlitsch and Rothermel 2003). Further, any differences between local and regional scales are important for linking theoretical constructs, such as how and why ecological processes at different scales interact, which is important for landscape ecology (Wiens 1992).

Although advances in technology such as radiotelemetry, stable isotope analysis, and use of microsatellite genetic markers have yielded greater resolution of the movement ecology of amphibians, the framework regarding the biological importance of movement at different scales (migration vs. dispersal) has not been clarified. The terms

migration and dispersal are often used interchangeably when discussing important amphibian conservation issues (Lemckert 2004, Smith and Green 2005). Using migration and dispersal interchangeably can lead to increased confusion in the use of empirical data. For example, focusing management of a local adult population using small vernal pools in the northeastern United States at scales of >1-km radius based on data from juvenile dispersal rather than resident adult migration from breeding sites can unnecessarily increase conflict in land use between development and conservation (Calhoun et al. 2005). Further, the lack of a clear mechanistic basis and its scale of operation may even misdirect future studies.

To better integrate behavioral and ecological data on pond-breeding amphibian movements with our use of the spatially explicit demographic models, to effectively apply management and conservation solutions, and to guide future studies, I present 1) a synopsis of the literature regarding the behavior, ecology, and evolution of movement in pond-breeding amphibians possessing biphasic life cycles to distinguish between migration and dispersal processes, 2) a working hypothesis of juvenile-based dispersal, and 3) a discussion of conservation issues that follow from distinguishing the spatial and temporal movements of amphibians at different scales.

## MIGRATION

I define amphibian migration as movements, primarily by resident adults, toward and away from aquatic breeding sites (Fig. 1A; Savage 1935, Oldham 1966, Shoop 1968, Semlitsch 1985, Sinsch 1988). During the breeding season, adults migrate across land from overwintering sites to ponds to mate and deposit eggs. After breeding, postreproductive

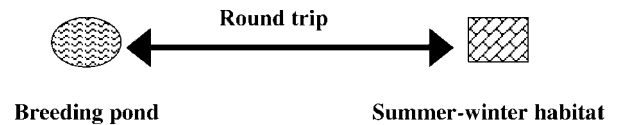
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males and females return to terrestrial habitats. Secondary migrations can occur between foraging habitat, summer refugia, and over-wintering sites (Lamoureux and Madison 1999, Lamoureux et al. 2002). For the adult residents using a breeding pond, migrations are reoccurring events (often, but not always annually), round-trip, and intrapopulational (Fig. 1A). Although a local population consisting of residents can be centered on a single pond, the use of multiple ponds in a relatively small area has also been described; thus, a cluster of ponds can constitute a single breeding unit that is genetically distinct (Ritke et al. 1991, Sinsch 1997, Marsh et al. 1999, Petranka et al. 2004, Zamudio and Wiczorek 2006). I use the term local population to describe either one pond or clusters in close proximity occupied by one breeding group.

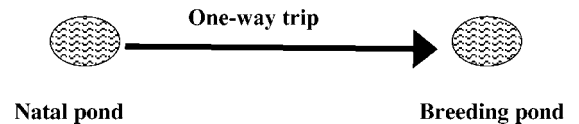
Adults typically migrate away from breeding sites in a nonrandom manner, entering and exiting in the same place, and preferentially using some habitats as travel routes more than others (Marty et al. 2005, Sztatecsny and Schabetsberger 2005, Rittenhouse and Semlitsch 2006). During postbreeding migration, most adults make several long terrestrial movements oriented in a straight line, roughly perpendicular to the pond shoreline, and these movements can be directed towards landscape features such as drainages or seeps (Semlitsch 1981, Madison 1997, Lamoureux and Madison 1999, Rittenhouse and Semlitsch 2007). The average distance adults migrate away from ponds ranges from 142 m to 289 m from the pond edge (mean min. estimates for 32 species; Semlitsch and Bodie 2003). There are some reliable records using radiotelemetry of postbreeding adults migrating up to 2,440 m (e.g., western toad [*Bufo boreas*]; Bartelt et al. 2004) but these represent extreme values for a few species and from a small portion of the local population. Such extreme movements are likely important for occasional dispersal of adults to new populations or for recolonization but less important for local population management issues. Frogs (*Rana* spp.) and toads (*Bufo* spp.) have been found to move significantly farther than salamanders (*Ambystoma* spp.; Rittenhouse and Semlitsch 2007); toads move farther than true frogs or treefrogs (*Hyla* spp.; Lemckert 2004), and for some species, females move farther than males (Muths 2003, Bartelt et al. 2004, Johnson 2005, McDonough and Paton 2007). These long-distance movements are followed by short movements in small activity centers, a few square meters in area, to gain access to microhabitats (e.g., cover, thermal and hydric refugia) and food (Semlitsch 1981).

Evolution of migratory behavior probably results from natural selection for movement to follow resources that vary in time and space (Dingle 1980). For amphibians with a biphasic life cycle, natural selection has maintained an aquatic and a terrestrial stage to exploit benefits of both aquatic and terrestrial environments (Wassersug 1975, Wilbur 1980). Migratory behavior and use of ponds as breeding sites likely evolved to find transient but high-quality reproduction sites each year. The particular seasonal timing of reproductive migrations is presumably the out-

### A. Migration (intra-populational):



### B. Dispersal (inter-populational):



**Figure 1.** Summary of the salient features of (A) migration and (B) dispersal in pond-breeding amphibians with arrows indicating movement. A local population is defined by the residents of a single breeding pond or cluster of ponds in close proximity.

come of tradeoffs among seasonal availability of water and food resources for aquatic larvae, favorable environmental conditions for terrestrial migration, terrestrial resources for foraging during the nonbreeding season, and safe over-wintering habitats. Migrations are often triggered by nocturnal rainfall that is conducive to overland movement by desiccation-prone organisms (Hurlbert 1969, Semlitsch and Pechmann 1985, Pechmann and Semlitsch 1986, Todd and Winne 2006). Timing of migration varies geographically with climatic conditions. For example, breeding migration of spotted salamanders (*Ambystoma maculatum*) in the northeastern United States occurs in spring (Apr–May), when ponds are full, and is timed to coincide with melting of ice and snow, making open water (at least along the edge) available for mating and oviposition (Shoop 1965, Whitford and Vinegar 1966). At southern latitudes, breeding migrations of the same species occur during winter when ponds are full and when temperatures are mild enough for overland movement (Dec–Feb; Semlitsch 1985; R. D. Semlitsch, University of Missouri, personal observation).

Sexual and interspecific differences in timing of migration have evolved to maximize reproductive success. Males often arrive earlier than females, which maximizes mating opportunities, whereas females often arrive later, which maximizes mate choice (Douglas 1979). Females may also arrive later to ensure eggs are deposited after potential for pond freezing is past, when water levels in ponds are at maximum depths, and when food resources for larvae, such as zooplankton, are readily available (Harris 1980). Autumn breeding in species like the marbled salamander (*Ambystoma opacum*) is thought to represent an alternative adaptation to allow larvae the earliest opportunity to hatch and maximize development in seasonal ponds (Jackson et al. 1989). Larvae that overwinter in the pond usually attain relatively large body sizes before other spring-breeding species arrive and

are, thus, strong competitors and sometimes, due to their large relative size, predators on the larvae of spring-breeding anuran and caudate species (Boone et al. 2002).

Philopatry (i.e., site fidelity) of adults to a breeding site may have evolved to take advantage of a favorable and relatively stable pond at a known locality rather than searching for a new pond when reaching maturity or during yearly breeding attempts. Assuming adults have no knowledge of location or condition of alternative but distant ponds relative to their current breeding pond, individuals may accumulate higher reproductive success, higher survival, or both, if they simply return to the same pond each year (Johnson and Gaines 1990). Although better breeding sites may occur in the landscape, the critical problem for amphibians is obtaining knowledge of alternative sites. Finding alternative breeding sites at unknown distances requires exploratory behavior and ability to perceive cues from ponds at long distances. Exploratory behavior has not been observed and is unlikely because of physiological and ecological constraints resulting from water loss, heat stress, and predation (O'Connor and Tracy 1992, Tracy et al. 1993). Further, most amphibian species probably lack true navigation ability (Sinsch 1990). Perception of olfactory cues to detect ponds likely occurs only at relatively short distances (McGregor and Teska 1989, Joly and Miaud 1993). Thus, philopatry has probably evolved among amphibians because of high costs of dispersal. In addition, once an alternative pond is found, reproductive success at the new site must be higher than that of the abandoned site to account for high dispersal costs (Morris 1987). The same selection pressures probably result in philopatry to refugia in the terrestrial environment, although currently, data showing terrestrial philopatry is only suggestive (Dole and Durant 1974).

Philopatry is fairly widespread among pond-breeding amphibians but its intensity varies by species and perhaps regionally because of the distribution of ponds (Smith and Green 2005). For example, in species like the common toad (*Bufo bufo*; 93–96% ad return; Reading et al. 1991), wood frog (*Rana sylvatica*; 100% ad return; Berven and Grudzien 1990), and great crested newt (*Triturus cristatus*; 99% ad return; Kupfer and Kneitz 2000), a high proportion of surviving adults return to their first breeding ponds or natal ponds. Yet, we know that when a new pond is created, breeding adults of some species, like narrow-mouth toads (*Gastrophryne carolinensis*; Pechmann et al. 2001) colonize it fairly quickly. Breden (1987) estimated that adult and juvenile dispersal to new breeding ponds was as high as 49% for Woodhouse's toad (*Bufo woodhousii*), which illustrates that not all species are strictly philopatric and not all individuals within species populations are likely to be philopatric.

I suggest that species form a continuum of philopatric behavior dependent on breeding site requirements. Behavior of species varies from highly faithful, favoring stable ponds in late-successional stages (e.g., forested closed-canopy vernal pools for woodfrogs and spotted salamander [*Ambys-*

*toma maculatum*]), to highly vagile, favoring new ponds in early successional stages (e.g., grassy, open-canopy ponds for Natterjack toad [*Bufo calamita*], Woodhouse's toad, small-mouthed toad [*Gastrophryne carolinensis*], gray treefrog [*Hyla versicolor*], chorus frog [*Pseudacris triseriata*], and eastern spadefoot [*Scaphiopus holbrookii*]). Evolutionary models have indicated that dispersal for aquatic insects is favored by natural selection when environmental conditions in ponds change temporally and become unfavorable naturally, for example, through succession (McPeck and Holt 1992). Colonizing newly created ponds is likely associated with high fitness via enhanced offspring performance of any adults changing ponds or for successfully dispersing juveniles breeding for the first time. Dispersal or switching of breeding ponds by adults has also been observed in natural populations and when stochastic or anthropogenic factors cause ponds to deteriorate (Pechmann et al. 2001, Petranka and Holbrook 2006, Gamble et al. 2007). Switching by adults may happen most frequently when a newly created pond occurs within close proximity of existing ponds and within an individual's migration path.

## DISPERSAL

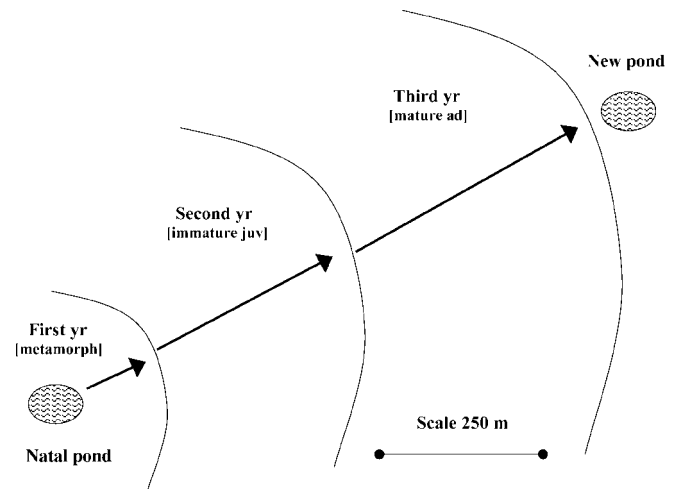
I define amphibian dispersal as unidirectional movements from natal sites to breeding sites that are not the pond of birth and not part of the local population (Fig. 1B). For dispersing juveniles, movements are ultimately greater in distance than for migrating adults, probably occur only once in a lifetime, and are interpopulational in scale (Fig. 1B). Sometime after adults leave the breeding pond, depending on species, larvae metamorphose and move onto land away from the pond. A portion of the juveniles will remain near the breeding site, reach sexual maturity, and return to breed in their natal pond, thereby joining the local breeding adult population. The remaining portion of surviving juveniles will disperse into the terrestrial habitat and presumably colonize nonnatal ponds.

There are few explicit and comprehensive studies of juvenile dispersal, notably on newts (*Notophthalmus viridescens*; Gill 1978), woodfrogs (Berven and Grudzien 1990), and recently, on marbled salamanders (*Ambystoma opacum*; Gamble et al. 2007). In the metapopulation study of newts (Gill 1978), he suggested that the immature eft stage was specialized to colonize newly formed beaver ponds that had a moderately rapid turnover rate. Although he did not present empirical data on eft movements, he argued that dispersal by efts should be favored by natural selection when there is a relatively rapid turnover of breeding sites or when there is frequent change in the quality of breeding sites. He also suggested that a simple diffusion distance model could adequately explain varying dispersal distances among regions and was dependent on spatial pattern and density of ponds. Berven and Grudzien (1990) showed that overall juvenile dispersal rates among 5 montane ponds averaged 18.5% and dispersal distance averaged 1,276 m (SD = 435 m; max. = 2,530 m). Gamble et al. (2007) conducted a 7-year mark-recapture study at 14 seasonal ponds and found that an

average of 9% of all successful breeding juveniles dispersed to new ponds. They also showed that some experienced breeding adults (1.7–1.9%) dispersed to new ponds. Further, they found that dispersal distance averaged 440 m (SE = 120.9 m; range = 142–1,297 m).

Numerous field studies have supported the idea that juveniles are more likely to disperse to nonnatal sites or new sites than adults and, therefore, likely constitute the dispersal stage for pond-breeding species (Dole 1971, Breden 1987, Berven and Grudzien 1990, Kupfer and Kneitz 2000). Yet, in many respects, juveniles are seemingly maladapted for sustained long-distance terrestrial movement, often >1 km (Smith and Green 2005). Juveniles of most species are small, have less locomotor capacity, and are subject to more rapid water loss than adults and, thus, are highly constrained in moving great distances. Locomotor studies have consistently shown, for a wide range of species, that small individuals travel shorter distances, have lower rates of travel, and have lower stamina than large individuals (Goater et al. 1993, Beck and Congdon 2000). In studies where direct monitoring was possible, the average movement distance for recently metamorphosed salamanders indicates they travel less than half the distance of adults after metamorphosis when studied over the same period of time (spotted salamander, juv 92.2 m vs. ad 252 m [Williams 1973]; mole salamander [*Ambystoma talpoideum*], juv 47.0 m vs. ad 178 m [Semlitsch 1981]). Also, metamorphosing amphibians have been found to incur high mortality as they leave the pond, primarily due to desiccation in summer and from predation near ponds (Jameson 1956, Shoop 1974, Wassersug and Sperry 1977, Semlitsch 1981, Rothermel and Semlitsch 2002).

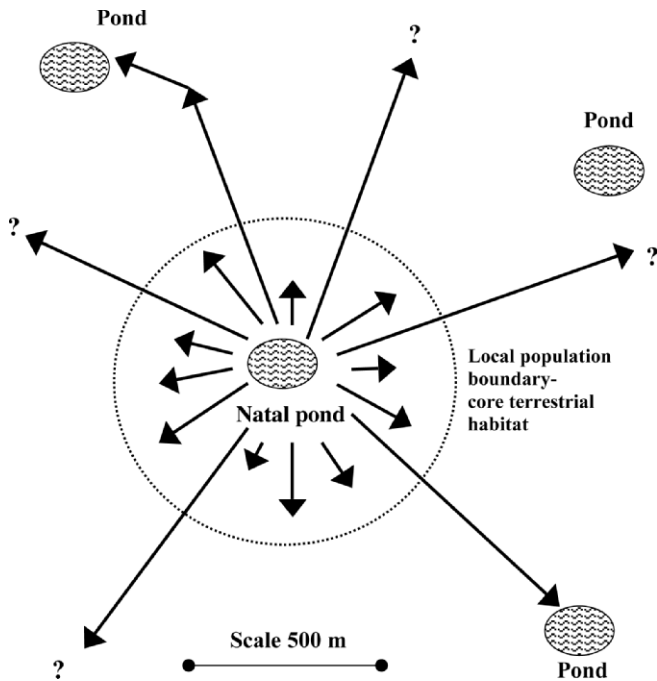
Yet, we know that individuals are found colonizing new ponds, sometimes at great distances from any other ponds and that individuals are sexually mature when they first appear. So, if newly metamorphosed amphibians are dispersing long distances in their first season of terrestrial activity, they likely must wait a year or two in areas adjacent to the new pond until they become mature. Although some species may mature before dispersing, I propose an alternative model of dispersal that is better aligned with our knowledge of physiological and morphological limitations and reproductive maturation. I suggest for most species, especially those metamorphosing at a small size and taking several years to mature, that juvenile dispersal is divided into several discrete events that allow individuals time to reach a larger body size more conducive to terrestrial movement and enables them to travel longer distances (e.g., 5.2 km after 2 yr for 3 M marked as metamorphs [Dole 1971]; Fig. 2). For most species, individuals metamorphose during the summer and at a time least favorable to long-distance movement, so movement in the first year is most likely limited to areas adjacent to the breeding pond where they feed, continue to grow, and find over-wintering sites. I suggest that it is not until later in the season or after the second or third year, when juveniles are larger, that they move great distances that are consistent with observations



**Figure 2.** Model of juvenile-based amphibian dispersal with arrows indicating movement. The ultimate distance achieved by individuals occurs over discrete intervals (e.g., yr).

and then find a new breeding pond (Smith and Green 2005; Fig. 2). Juveniles may have this opportunity because they cannot breed in the first several years due to slow reproductive development. I assume that dispersal ceases upon achieving reproductive maturity and after first reproduction at a new pond. Species metamorphosing at a large body size (e.g., bullfrogs [*Rana catesbeiana*]) or reaching maturity in their first year (e.g., *Acris* spp. and *Pseudacris* spp.) may already be large enough to disperse overland without any delay. Because of lack of techniques to directly follow metamorphs, studies purporting to examine dispersal of new metamorphs may have only examined movement behavior and distances during initial dispersal into the terrestrial environment and not to an ultimate destination.

There is no evidence to suggest that juvenile amphibians have specialized perceptual abilities to find new or alternative breeding sites, such as water-finding ability or by using sounds of breeding choruses of anurans, which might indicate that juveniles exhibit target-oriented dispersal (i.e., directed movement toward a specific habitat; Sjogren-Gulve 1998). When leaving from pools in pastures, 2 species of newly metamorphosed amphibians (spotted salamander and American toad [*Bufo americanus*]) did not orient toward or successfully reach the forest at distances of >60 m, which might suggest they have limited perceptual ability (see Rothermel 2004). Further, movement patterns that might suggest searching behavior (systematic or loop-like movements; Heinz et al. 2006) have never been observed during initial amphibian dispersal; rather, they move in a linear manner, roughly perpendicular to the pond edge, similar to adults but not equal to the distance achieved by adults (Semlitsch 1981). Further, dispersion patterns of juveniles leaving the pond are often less directional and more random than movements of adults (Sinsch 1997, Rittenhouse and Semlitsch 2006). Exceptions have been found and suggest that indirect cues may be used for orientation in some cases (Patrick et al. 2007). However, in

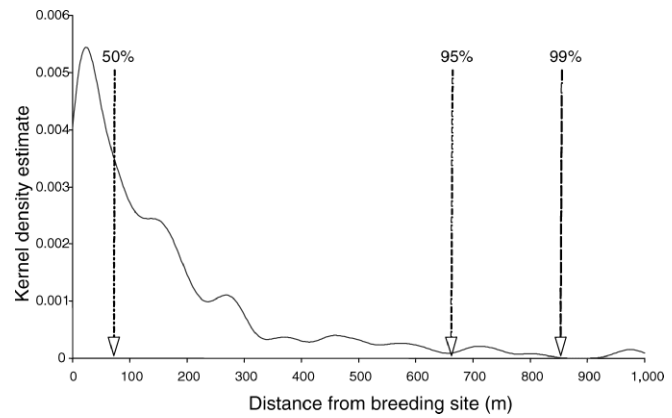


**Figure 3.** Model of juvenile-based amphibian dispersal with arrows indicating movement. The ultimate location achieved by individuals occurs randomly with respect to colonizing new ponds in the landscape.

most cases the simplest explanation would be that newly metamorphosed individuals disperse from natal ponds in a random pattern relative to landscape features beyond the pond perimeter (i.e., acknowledging there is nonrandom dispersal at the pond edge), and subsequently, find new or nonnatal breeding ponds primarily by chance (Fig. 3). The hypothesis of random dispersal is consistent with Gill's (1978) model for efts in which he proposed that the pattern of dispersal is best described by a simple diffusion distance model. Probability of colonizing a pond is likely a consequence of density of ponds in the landscape, distance traveled, barriers, and habitat resistance (Rothermel and Semlitsch 2002). In years when species produce large numbers of metamorphs, waves of thousands of metamorphs have been found moving far away from breeding ponds in no apparent orientation to known ponds in the area (R. D. Semlitsch, personal observation). Yet, by virtue of their great numbers a few individuals periodically reach ponds many kilometers away and are consistent with observations of colonization by mark-recapture and genetic analyses (Dole 1971, Gibbons et al. 2006, Zamudio and Wicczorek 2006, Gamble et al. 2007).

## DISCUSSION

Dispersal is critical to the conservation of species in fragmented and altered landscapes (Kareiva and Wennergren 1995, Hanski and Ovaskainen 2000). Thus, distinguishing between migration and dispersal processes is essential to effectively address management and conservation issues concerning amphibians at the proper temporal and spatial scales. Further, understanding the limitations of migration and dispersal ability for amphibians is also critical so that



**Figure 4.** Univariate kernel density estimate for 408 individuals from 13 radiotelemetry studies (modified from fig. 1 of Rittenhouse and Semlitsch 2007). This composite estimate was calculated from 1,000 bootstrap samples drawn equally from each study to correct for sample size differences among studies. Arrows represent the 50% (93 m), 95% (664 m), and 99% (852 m) isopleth values.

conservation solutions designed for other taxa, such as reptiles, birds, and mammals are not applied to amphibians without recognizing important differences among taxa in ability and motivation to move (Semlitsch and Rothermel 2003).

Our current knowledge indicates that adult migration in amphibians is associated with a local breeding population and restricted to terrestrial habitats surrounding one breeding site or a cluster of ponds in close proximity. The spatial extent of migrations for pond-breeding species can be effectively estimated by measuring the emigration distance of resident adults using direct tracking techniques such as radiotelemetry and by mark-recapture with concentric drift fences at multiple distances (Madison 1997, Trenham and Shaffer 2005). Conservation issues directed at single populations rely on accurate estimates of the size of core terrestrial habitat used to complete life-history functions for persistence of the population. It also is important that the area encompass all habitats needed by individuals, including foraging, overwintering, summer, and breeding habitat, and that the core conservation area contain a large portion of the breeding population. Although we do not know what portion of the population or what numbers of adults are necessary for long-term persistence of most species (but see Taylor et al. 2006), reliable estimates of core habitat averaged across 13 studies and 11 species have included 50%, 95%, and 99% of the population to yield radii of 93 m, 664 m, and 852 m, respectively, from the breeding site (Fig. 4; Rittenhouse and Semlitsch 2007). These boundaries of migration distance have also indicated that the probability distribution of individuals is strongly skewed, with more individuals found close to the breeding site (Fig. 4). Even for individual species, especially frogs or toads that move longer distances, estimates for 95% of the population still average 703 m. Thus, population-level conservation, in general, can be focused on spatial scales of <1.0 km with attention focused on the majority of the adult population nearest the wetland, but special attention might also be

directed at females near the outer limits (McDonough and Paton 2007, Rittenhouse and Semlitsch 2007).

At present, the phenomenon of dispersal in amphibians is poorly understood and needs more attention. In particular, the potential relationship of sex, body size, density-dependence, population size, habitat quality, and land use to dispersal tendency and behavior needs to be empirically examined (Heinz et al. 2006, Gamble et al. 2007). Empirical data on juvenile dispersal measured from direct monitoring of individuals combined with genetic analyses indicates metapopulation-level processes are likely to occur at distances 2.0–10.0 km (Smith and Green 2005). Recent fine-scale genetic analyses for spotted salamanders indicate that nonrandom genetic structure occurs at a scale of approximately 4.8 km (Zamudio and Wieczorek 2006).

Thus, a primary distinction between migration and dispersal is the spatial scale of amphibian movement and the number of populations affected. I believe that the distinction between migration and dispersal is real and not an artificial division of a continuum of movement across the landscape because individuals are driven by different selective pressures and consequences to their movement (Johnson and Gaines 1990). Selective pressures (detailed above) drive the movement process in different directions, either movement towards (philopatry and migration) or away from (dispersal) natal ponds. I suggest that philopatry and migration are driven by fitness gains within the local population when habitats remain favorable for relatively long periods of time and dispersal costs are high (Morris 1987). Dispersal is driven by fitness gains from colonizing a new pond that counter negative effects of succession, deterioration of habitats, and potential for inbreeding depression.

A second distinction between migration and dispersal is the implicit difference in temporal scale of movements. Migrations at the local population level are driven by demographic processes occurring over relatively short time periods, annual events or within generations (1–5 yr), whereas dispersal at the metapopulation level is driven by benefits of recolonization processes occurring over relatively longer periods of time, perhaps 10–20 years or among multiple generations. It is also important to recognize that genetic dispersal data typically integrates gene flow over multiple generations of dispersal events, whereas behavioral migration data usually encompass one year and measure the movement of individuals. This distinction is especially important for rapid conservation solutions in highly altered habitats where dispersal of new individuals on an ecological (demographic) time scale is necessary for recolonization, rescue, and preventing regional collapses of species populations. Further, dispersal might be a relatively rare event to detect, compared to annual mass breeding migrations, and occurs at a low rate or only frequently enough to counterbalance extinctions. Yet, the importance of maintaining dispersal for metapopulation or regional species persistence and, thus, for effective conservation, is far greater than maintaining any single local population and local migration,

especially in fragmented and disturbed landscapes (Marsh and Trenham 2001).

## MANAGEMENT IMPLICATIONS

A distinction between migration and dispersal is relevant to a number of conservation issues for pond-breeding amphibians. Knowing the spatial area (i.e., core terrestrial habitat) needed for local protection of individual populations of an endangered species from various land uses might be necessary before regional protection is achieved. Although local and regional protections ultimately are critical for effective conservation of any species, prioritizing recovery efforts in a conservation plan might be necessary. For example, short-term restoration efforts might be directed at the core terrestrial habitat of a local population whereas long-term restoration efforts could be directed toward larger scale efforts like connectivity among populations and improvement of matrix habitat. Further, an understanding of the behavioral tendency of species or stages of dispersal also might be critical to directing conservation efforts. For example, resources might be focused on protecting or restoring natal ponds and surrounding terrestrial core habitat for species with late-successional requirements and philopatric tendencies. Alternatively, periodically creating early successional breeding ponds needed by many dispersing species or protecting adequate terrestrial habitat, managing matrix habitat to increase permeability, or building corridors to enhance connectivity between natal ponds and new breeding sites is also critical. Thus, metapopulation- or landscape-level conservation, in general, should be focused on dispersal among populations at spatial scales >1–10 km, longer periods of time, and on the importance of pond density and distributions, terrestrial connectivity, and isolation effects due to land use (Marsh and Trenham 2001). By understanding temporal and spatial priorities for movement, and limitations of pond-breeding amphibians, we can better apply existing knowledge, direct management efforts, and develop conservation solutions.

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