7 Ecology and Conservation of Pool-Breeding Amphibians

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CONTENTS

Amphibian Complex Life Cycle 128
Amphibian Distributional Patterns 131
Vernal Pool Amphibians 131
Hydroperiod 132
Canopy 132
Population Dynamics 134
Community Dynamics 136
Spatial Ecology 137
Conservation Implications 139
Summary 142
Acknowledgments 142
References 142

Our concern over the decline of amphibian populations and species extinctions has raised many questions about the causes and potential solutions (e.g., Blaustein et al. 1994, Houlahan et al. 2000, Semlitsch 2003). Recently, it was determined that amphibians are more threatened than either birds or mammals (Stuart et al. 2004). Although no single cause for all declines has surfaced, six common threats are known: disease, introduction of exotic species, chemical contamination, commercial exploitation, global climate change, and habitat loss and alteration (Semlitsch 2003). Among these, most biologists agree that habitat loss and alteration is the number one factor contributing to global declines. This is especially true in North America, where aquatic breeding habitats such as vernal pools receive little, if any, protection and are disappearing at an alarming rate (Comer et al. 2005; but see state exceptions Burne and Griffin 2005). To combat the loss of these small wetlands, it is important to understand what role they play in the larger forested ecosystem where they are found and discuss how their loss might affect other components of forest biodiversity and function (e.g., importance of amphibians in local food chains; Paton 2005). We can advance this understanding by focusing on the ecology of amphibians, and their dependence on both vernal pools and the surrounding forested habitat for completion of their life cycle and for long-term persistence.

The majority of amphibian species worldwide have a complex life cycle (Semlitsch 2003). Within the northeastern North America region, roughly 48 species of amphibians occur (Conant and Collins 1998, Petranka 1998) and fully 28 of 48 species regularly use either vernal or other seasonal pools (Colburn 2004; Table 7.1). All of the 28 species using seasonal pools have a complex life cycle and may play important ecosystem roles such as the following:

Larval anurans (frogs and toads) are consumers of primary production in the form of periphyton and phytoplankton (e.g., Seale 1980).

All larval caudates (salamanders) and some anurans are consumers of secondary production in the form of zooplankton, aquatic insects (including mosquitoes), and larval anurans.

On land, all amphibians consume small invertebrates often not available to other vertebrate groups. Amphibians comprise a large amount of protein biomass that is readily available in the forest food chain (e.g., to fish, snakes, birds, mammals; reviewed by Davic and Welsh 2004). They serve as nutrient vectors connecting aquatic and terrestrial ecosystems through seasonal emigration and immigration processes that disperse protein and nutrients between habitats (e.g., Regester et al. 2006).

Our objectives in this chapter are to provide: (1) an overview of the ecology of pool- breeding amphibians drawing on studies from across North America, (2) a framework for how amphibians are dependent on vernal pools as well as the surrounding terrestrial habitats in forested ecosystems in the northeastern region, and (3) the essential features that are necessary for conservation of pool-breeding amphibians.

AMPHIBIAN COMPLEX LIFE CYCLE

All pool-breeding amphibians in northeastern North America possess a complex life cycle that has an aquatic larval stage and a terrestrial juvenile/adult stage. Aquatic larvae feed, grow, and develop in pools until metamorphosis is complete. After metamorphosis, they emigrate as juveniles to forested terrestrial habitats where they remain until they reach reproductive maturity and, eventually, most migrate back to aquatic breeding sites (Wilbur 1980). Thus, the pool and the surrounding terrestrial habitat are essential to completion of the species' life cycles. Metamorphosis is the developmental mechanism that allows individuals to make the transition between the two environments and produces a radical change in morphology, physiology, ecology, and behavior. In contrast, some amphibians in the Northeast have simple life cycles; the redback salamander, (*Plethodon cinereus*) has direct development, having lost the aquatic larval stage, and is completely terrestrial, whereas the mudpuppy (*Necturus maculosus*) does not metamorphose and is completely aquatic.

TABLE 7.1
Amphibian Species in Northeastern North America That Regularly or Occasionally Breed in Vernal Pools

What is this?

Common Name	Scientific Name	Vernal Pools Are Primary Breeding Habitat
SALAMANDERS	**CAUDATA**	
Jefferson salamander	*Ambystoma jeffersonianum*	Yes
Blue-spotted salamander	*A. laterale*	Yes
Spotted salamander	*A. maculatum*	Yes
Marbled salamander	*A. opacum*	Yes
Small-mouthed salamander	*A. texanum*	Yes
Eastern tiger salamander	*A. tigrinum*	Yes, in parts of range
(Formerly) silvery salamander (JJL)	*Formerly A. platineum*	Yes
(Formerly) Tremblay's salamander (JLL)	*Formerly A. tremblayi*	Yes
Four-toed salamander	*Hemidactylium scutatum*	Yes
Eastern red-spotted newt	*Notophthalmus viridescens*	No, but commonly used
FROGS AND TOADS	**ANURA**	
Eastern spadefoot	*Scaphiopus holbrookii*	Yes
American toad	*Bufo americanus*	No
Fowler's toad	*B. fowleri*	No
Blanchard's cricket frog	*Acris blanchardi*	No
Northern cricket frog	*A. crepitans*	No
Spring peeper	*Pseudacris crucifer*	No, but commonly used
Upland chorus frog	*P. feriarum*	No
Mountain chorus frog	*P. brachyphona*	No
Western chorus frog	*P. triseriata*	Yes, in parts of range
Cope's treefrog	*Hyla chrysoscelis*	No
Gray treefrog	*H. versicolor*	No, but commonly used
American bullfrog	*R. catesbeiana*	No
Green frog	*R. clamitans*	No
Pickerel frog	*R. palustris*	No
Northern leopard frog	*R. pipiens*	No
Southern leopard frog	*R. utricularia*	No
Wood frog	*R. sylvatica*	Yes

Source: Conant, R. and Collins, J.T. (1998). *A Field Guide to Reptiles and Amphibians of Eastern and Central North America*. 3rd ed., Houghton Mifflin Company, New York; Colburn, E.A. (2004). *Vernal Pools: Natural History and Conservation*. The MacDonald and Woodward Publishing Company, Blacksburg, VA.

It is thought that the amphibian complex life cycle is maintained evolutionarily by natural selection to exploit the benefits of both the aquatic and terrestrial environments (Wassersug 1975). The length of time larvae remain in pools is quite variable and is generally thought to be an adaptation to exploit resource-rich but ephemeral aquatic habitats. Generally, larvae that remain in the aquatic environment longer reach a larger size at metamorphosis and achieve a greater portion of their final adult size (Wilbur and Collins 1973, Werner 1986). Larger size at metamorphosis is associated with increased fitness (and hence ability to survive to reproduce) of adults in both frogs and salamanders (e.g., Smith 1987, Semlitsch et al. 1988, Berven 1990). Ephemeral aquatic habitats also generally contain fewer anuran predators than permanent water bodies, as many predatory species cannot survive and complete their lifecycles when pools dry. Because pools are temporary habitats and are only seasonally available, metamorphosis is maintained to escape into more "permanent" terrestrial habitats that do not carry the risks associated with drying pools. Thus, natural selection also maintains variability in the timing of metamorphosis to escape the dangers of desiccation in ephemeral pools and to track spatial and temporal variability in drying rates of pools. Although little is known about the terrestrial stage of many amphibians, most species spend the majority of their life on land, where they grow and reach reproductive maturity after 2–3 years and can often live for 515 or more years. Dispersal to new pools over land also occurs only in the terrestrial stage.

One of the most important aspects of amphibian life histories is how closely many aspects of their life cycle are associated with the filling and drying of vernal pools. The timing of their life cycle varies geographically with climatic conditions. For example, the breeding migration of spotted salamanders (*Ambystoma maculatum*) in the Northeast occurs in very early spring when pools are full and timed to coincide with melting of ice and snow, making open water (at least along the edge) available for mating and egg deposition (e.g., Shoop 1965, Whitford and Vinegar 1966). Males often arrive earlier than females to maximize the number of mating opportunities, whereas females often arrive later to maximize mate choice. Females may also arrive later to ensure eggs are deposited after the potential for pond freezing is past (Harris 1980), when the water levels in pools are at their maximum depths, and when food resources for larvae such as zooplankton are readily available. Autumn breeding in species like the marbled salamander (*Ambystoma opacum*) is thought to represent an extreme adaptation to allow larvae the maximum potential to hatch and develop early in seasonal pools. Adults often arrive from August to September in the Northeast when pools are completely dry, mate on land, and deposit and guard eggs under debris or grass clumps along the margin of the dry pool bed. Eggs begin development but do not hatch until flooded by water when low oxygen triggers hatching (Petranka et al. 1982). Larvae then overwinter in the pool and attain relatively large body sizes before other spring-breeding species arrive. They are often predators on the larvae of spring-breeding anuran and caudate species due to their large relative size.

Timing of metamorphosis also closely coincides with the drying of pools during the summer months, allowing larval growth to be maximized, while minimizing the risk of larval desiccation. Some species of anuran tadpoles such as the American toad (*Bufo americanus*) can speed up development in rapidly drying pools in response to reliable environmental cues (e.g., water level, higher temperature, crowding). In this way, they metamorphose before they become trapped and die. Species such as the red-spotted newt (*Notophthalmus viridescens*), under certain environmental conditions, can adjust to periods of long inundation by delaying metamorphosis for extended periods and can even reproduce in the larval stage (i.e., paedomorphosis or neoteny; Healy 1973). Thus, northeastern amphibians with complex life cycles have numerous features of their biology that make them well adapted to exploit vernal pools.

AMPHIBIAN DISTRIBUTIONAL PATTERNS

Glaciation defines the geographic scope of this book, as well as the amphibian membership of vernal pools within northeastern North America (see Chapter 2, Rheinhardt and Hollands). Virtually every pool in the region is home to species that arrived from somewhere not covered by Pleistocene ice. This fact is of enormous importance to understanding the distribution of northeastern vernal pool amphibians. Amphibians have moved hundreds of kilometers to reach their present day distributional limits. In general, fewer species are found farther from areas of glacial refugia — that is, farther north. But the south–north axis also defines a gradient of climate that appears strongly limiting to amphibians (Duellman and Sweet 1999). Most species tend to have ranges centered in the southern portion of the region. Amphibians in boreal and sub-boreal environments must contend with extremely short growing seasons and winter cold (Duellman and Sweet 1999). Many species appear unable to cope with these extremes. The southernmost part of the focal region (Illinois) is home to 41 amphibian species, whereas just a single species, the wood frog (*R. sylvatica*), is found in northern Labrador. Although northward attrition implies strong variation in species composition across the Northeast, this impression is, in part, misleading. Across much of the region, roughly 20 species of amphibians are found and turnover in species composition (gamma diversity) is extremely low. Amphibian biologists from Maine airdropped into Wisconsin would be able to identify 14 of the 18 species found 1200 km away from their home state. Constancy in species composition likely reflects the common geographic origins of colonists as well as the recent upheaval that created and then exposed one of the densest concentrations of vernal pools on earth.

Vernal Pool Amphibians

What is a vernal pool amphibian? Any answer to this nontrivial question must be provided with the caveat that there are numerous definitions and policies offered by many different institutions and agencies that use vernal pool associations of amphibians as a criterion for defining and protecting wetlands (see Calhoun and deMaynadier 2004, Calhoun et al. 2005). From a purely biological perspective, it is easy to make the case that vernal pools are important for most amphibians. Even when they are not used by a species for breeding, smaller pools tend to be the most numerous wetlands (Semlitsch and Bodie 1998, Gibbs 2000) and provide hospitable habitat for amphibians moving through the terrestrial environment (Table 7.1). Even if we restrict our definition to just those species breeding in vernal pools, the picture is not simplified. If vernal pools are monitored long enough, most species present within a region can be discovered breeding there, if only sporadically or in some part of the region (Skelly et al. 1999, Halverson et al. 2003, Skelly et al. 2003, see

Whiting 2004). One reason is the tremendous climate-driven temporal variation in vernal pool inundation periods. During a run of wet years, a vernal pool that dries during a season of average rainfall can remain filled for a year or more (e.g., Semlitsch et al. 1996, see Chapter 3, Leibowitz and Brooks). This will allow species like green frogs (*R. clamitans*), most often described as permanent pond inhabitants, time to arrive and breed (Skelly et al. 2005). In the same pool during an extreme drought, successful breeding can be restricted to one or two species that breed in early spring and have extremely rapid larval development (e.g., wood frogs [*R. sylvatica*], eastern spadefoot toads [*Scaphiopus holbrookii*]). These patterns have sometimes been portrayed as aberrant phenomena. Such a characterization misses the important point that vernal pools are highly dynamic environments: they vary among pools and across years to an extreme degree. It can be misleading to characterize vernal pools according to an average condition or by their typical inhabitants.

Nevertheless, we can restrict our definition further to include only those species that breed primarily or solely within vernal pools. This is the perspective familiar to regulators and other environmental professionals. For example the U.S. Environmental Protection Agency and various state governments define species such as wood frogs, spotted salamanders, eastern spadefoot toads, and others that are broadly distributed across the Northeast as "vernal pond indicators." In some cases, presence of breeding individuals of such species is used to define a wetland as a vernal pool (e.g., Calhoun et al. 2003; see Chapter 10 Mahaney and Klemens). Because of their interest from both regulatory and scientific perspectives, these amphibians have been subject to close ecological study, yielding an extensive catalog of the factors that can affect distribution (reviewed by Skelly 2001). Here, we focus on two abiotic factors, hydroperiod and canopy, that are particularly important for understanding vernal pool species distributions.

HYDROPERIOD

Vernal pools are defined by periodic drying. The likelihood and timing of drying within a pool have enormous effects on which amphibian species will breed (Semlitsch et al. 1996, Skelly et al. 1999, Snodgrass et al. 2000, Babbitt et al. 2003, Gamble et al. 2006) and how they fare (Skelly 1996). In general, species with longer larval periods tend to restrict their breeding to pools of longer duration (Skelly 1996, Skelly et al. 1999, Baldwin et al. in press). Egg mass densities also tend to be higher in longer duration vernal pools (Egan and Paton 2004, Baldwin et al. in press). In a year of near-average rainfall, entire cohorts of larval wood frogs failed due to drying in 35% of their breeding pools at the Yale Myers Forest, Connecticut (E. Lee, personal communication). These and comparable findings (Semlitsch et al. 1996, Skelly 1996) imply that annual drying serves as an active distributional constraint on vernal pool amphibians.

CANOPY

A second factor affecting many vernal pools is the presence of forest canopy. Most of the focal region is coincident with the forested realm of North America. Because pools drying seasonally also tend to be small in surface area, vernal pools are susceptible to overtopping by terrestrial woody vegetation. As this vegetation grows and matures, it can deeply shade a vernal pool (Skelly et al. 2002, Halverson et al. 2003, Skelly et al. 2005). Light levels in closed canopy pools can be indistinguishable from those measured above the floor of a mature forest (Halverson et al. 2003). Shading has important consequences for vernal pool amphibians, as it does for terrestrial organisms. Foremost among these is alteration of temperature. Average water temperature can differ by as much as 2–3˚ C and peak daytime temperatures can be more than 10˚C higher in an open wetland (e.g., Skelly et al. 2002). For ectothermic ("cold-blooded") animals such as amphibians, rates of both development and growth are functions of temperature. The consequences of shading are magnified by the time boundary imposed by hydroperiod. Although it might seem that shaded pools should survive longer due to lower rates of evaporation from the pool surface, the opposite is generally true. Forest growth moves water demand up to the canopy where rates of evapotranspiration more than compensate for any decreased evaporation from the pool surface (Brooks 2004). Long- term observations suggest that hydroperiod of wetlands beneath accreting forests can decline as much as one week (Skelly et al. 1999).

Canopy has a separate set of effects mediated through changes in the rate and constitution of primary production. Both decreases in standing crop and alterations in composition of attached algae and other food sources (Skelly et al. 2002) are characteristic of closed canopy pools, which in turn are associated with decreased digestive efficiency of vernal pool tadpoles (Skelly and Golon 2003) and lower rates of growth and development (Skelly et al. 2002). Field experiments showing that food addition has greater positive effects on growth and development in shaded vs. open pools underscore the importance of food mediated effects of canopy development (Skelly et al. 2002).

Whatever their origin, canopy has strong effects on the amphibian composition within vernal pools (Figure 7.1). Many species are sensitive to canopy closure and are found infrequently in shaded pools (Skelly et al. 1999, Skelly et al. 2005). There are also a number of specialized amphibian breeders, including spotted and marbled salamanders and wood frogs that are dependent upon shaded conditions. Field transplant experiments confirm that open canopy specialists perform relatively poorly when placed in closed canopy environments (Werner and Glennemeier 1999, Skelly et al. 2002, Skelly et al. 2005). These findings highlight the challenging nature of closed canopy vernal pools. Exceptions, such as marbled salamanders, spotted salamanders and wood frogs that perform well under these conditions, are the very species that we identify most closely with closed canopy vernal wetlands (Table 7.1).

When considering the role of canopy cover, however, we need to include the effects on the terrestrial as well as the aquatic environment. Although open canopy over pools increases productivity, many vernal pool species are heavily dependent on forested terrestrial habitat, either avoiding open areas or suffering negative effects from factors such as dehydration (Rothermel and Semlitsch 2002). Because of this, species such as the wood frog, spotted salamander, and marbled salamander are unlikely to be found breeding at pools surrounded by large areas of open habitat. These are the most abundant vernal pool dependent species in much of the northeast

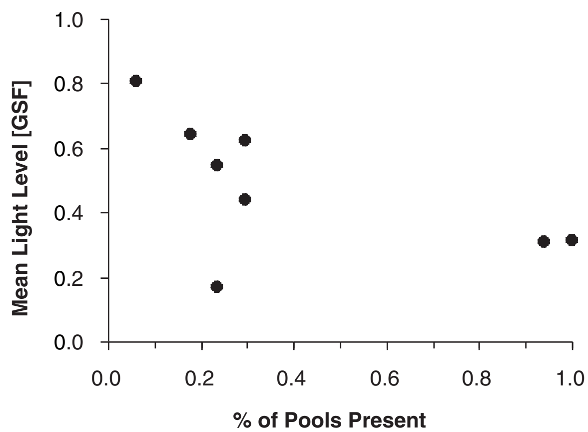

FIGURE 7.1 The data points represent the proportion of pools where each species was found breeding, plotted against average light level (measured as global site factor [GSF] during the leaf-on period). Data are derived from the distribution of 8 amphibian species across 17 vernal pools at the Yale Myers Forest, Connecticut. The 8 species are *Bufo americanus, Pseudacris crucifer, Hyla versicolor, Rana clamitans, R. sylvatica, Ambystoma maculatum, A. opacum,* and *Notophthalmus viridescens*. With the exception of *A. opacum*, which was present exclusively in heavily shaded ponds, species found in fewer locations tend to be found in more open pools. Species found in most or all of the pools (*A. maculatum, R. sylvatica*) bred in ponds that ranged from extremely low light (GSF = 0.08) to extremely sunny (GSF = 0.96) but were on average shaded (GSF = 0.31). (Data from Skelly, D.K., Halverson, M.A., Freidenburg, L.K., and Urban, M.C. (2005). *Wetlands Ecology and Management* 13: 261–268. With permission.)

U.S. (e.g., Patrick et al. 2006). Because shade is more likely to be reduced, rather than increased, by anthropogenic habitat change, populations of these species are also more likely to be at risk than are species such as green frogs or spring peepers that frequent open areas. A further consideration when evaluating the consequences of shade over vernal pools comes from recent studies of amphibian population biology (summarized in the following section). These studies suggest that changes in aquatic life-history stages, such as increased production of larvae, are unlikely to be driving population trends alone, and that terrestrial habitat conditions and adult survival should be of primary conservation concern. Thus removing forest around a breeding pool may increase larval productivity, but, for obligate vernal pool species, any beneficial population effects may be outweighed by the potential reduction in adult survival and breeding in subsequent years.

POPULATION DYNAMICS

The historic view of population dynamics in pool-breeding amphibians is that regulation occurs primarily in the larval aquatic stage, although theoretically, it could also occur in the terrestrial stage or both stages (Wilbur 1980). This historic view follows from the high larval densities observed in natural populations (e.g., up to

4,000 per m^2 for anurans; Woodward 1982, Petranka 1989) and high species diversity in many aquatic habitats (e.g., < 14 species in northeastern pools but > 20 in the southern U.S., Dodd 1992, Semlitsch et al. 1996). It was long thought that density-dependent and species interactions are likely important for regulating natural larval populations (Wilbur 1980, Pechmann 1994). Field studies have demonstrated a strong negative effect of density on growth and survival of larvae (Smith 1983, Petranka 1989, Van Buskirk and Smith 1991, Scott 1994). These studies show that as larval density increases, larvae grow and develop more slowly, larval period increases, size at metamorphosis is reduced, and fewer individuals reach metamorphosis (< 5% of larvae normally metamorphose; Herreid and Kinney 1966, Licht 1974, Semlitsch 1987). Small size at metamorphosis can result in poor physiological and locomotor performance in the terrestrial environment (Goater et al. 1993), lower juvenile survival, later first reproduction, and smaller size at first breeding (Smith 1987, Semlitsch et al. 1988, Berven 1990). As larval density decreases, the same larval traits are positively affected and populations experience higher metamorphic success. But in most species, successful larval development to metamorphosis in natural aquatic habitats is affected by the interaction of multiple factors, typically related to the drying rate of pools, interspecific competition for food, and the presence and abundance of predators (Semlitsch et al. 1996). All of these factors are consistent with density-dependent regulation in the larval stage.

Several recent findings, however, suggest that regulation of amphibian populations can also occur in the terrestrial stage and likely interacts with density-dependence in the aquatic stage. First, a field experiment that manipulated the density of metamorphs in terrestrial pens indicated that survival was higher at lower densities, and survival was enhanced even more when metamorphs originated from low-density aquatic habitats and were reared in low-density terrestrial habitats (Pechmann 1994). Second, the use of ecological sensitivity models and demographic population models indicate that postmetamorphic vital rates and adult habitat size strongly influence population dynamics of amphibians (Biek et al. 2002, Halpern et al. 2005). The most interesting implication stemming from this new paradigm — that of terrestrial regulation of amphibian populations -— is that loss of terrestrial habitat surrounding vernal pools could be just as detrimental to population persistence as loss of the wetland.

Thus, populations are likely regulated in both the aquatic and terrestrial stage such that they persist over time by a combination of the number and quality of metamorphosing larvae leaving a pool and the number of terrestrial juveniles that survive to be recruited into the adult breeding population. A set of species persists in a given area because each species episodically and under the right environmental conditions produces large numbers of metamorphosing juveniles (e.g., Gill 1978, Semlitsch 1983, Berven 1990, Pechmann et al. 1989, Semlitsch et al. 1996). Reproductive failures are common among amphibians, at least in regions where wetlands are subjected to rapid drying or other catastrophic events (e.g., in South Carolina depressional wetlands reproductive failure rates were 42–56% for 13 species over 16 years; Semlitsch et al. 1996). Yet, adults reproduce over multiple years and many species (especially *Ambystoma* salamanders) have a life expectancy great enough (5–15 years) to experience a few "booms" in metamorph recruitment that compensates for adult attrition. Short-lived (<2 years) species like spring peepers (*Pseudacris crucifer*) or chorus frogs (*P. triseriata*) are vulnerable to local extinction after just a couple years with negligible metamorph recruitment. Modeling of amphibian populations indicates that long-lived species can "store" recruits in terrestrial habitats during these infrequent reproductive booms, whereas short-lived species cannot and depend more directly on larval success in aquatic habitats (Halpern et al. 2005). This pattern of "boom or bust" population dynamics contrasts greatly with the constant low-level, annual reproductive success exhibited by most mammals and birds. This characteristic of amphibian populations means that multiple years of reproductive failure due to unfavorable pool conditions such as rapid drying during drought years or from anthropogenic factors like building ditches or introducing fish can result in decline and eventual extinction of species at the pool level (e.g., Semlitsch et al. 1996, see Chapter 8, Gibbs and Reed), and local landscape level.

Because breeding adults have a strong preference to return to ponds where they first breed (e.g., Oldham 1966, Breden 1987, Berven and Grudzien 1990), metamorphosing juveniles are likely the primary dispersal stage (sensu Gill 1978). A high rate of successful metamorphosis is critical to maintain local adult populations and act as dispersers to reestablish extirpated populations or found new populations. So, although vernal pools are especially critical for reproduction in short-lived species; terrestrial habitats are especially critical for adult populations in long-lived species, and the connections among pool populations are essential for higher-level regional persistence.

COMMUNITY DYNAMICS

Vernal pool amphibian species typically are found in multispecies assemblages that include other amphibian taxa and a wide variety of invertebrates. During recent decades there have been many experiments that have found strong effects of competition and predation on focal amphibian species (reviewed by Wilbur 1997, Skelly and Kiesecker 2001). These findings have been widely interpreted to mean that vernal pool amphibian distributions in nature are likely to be functions of both predator and interspecific competitor distributions (Alford 1999). Specifically, because pools with longer hydroperiods tend to have more diverse and voracious predators (Wellborn et al. 1996), it has been hypothesized that predation would reduce density to a greater degree in longer duration pools. In the most ephemeral pools, the effects of interspecific competition are assumed to be strongest where low levels of predation would allow for high densities of larval amphibians (Morin 1983).

Collectively, this synergism among hydroperiod, predation, and interspecific competition has been predicted to lead to segregated distributions among larval amphibians. Stronger competitors should have more rapid development, be more susceptible to predators, and therefore concentrate in ephemeral ponds lacking fish and other predators. Slow-developing species should be less susceptible to predators and should be present in ponds of longer duration. In a general sense, natural history patterns are consistent with these predictions; a number of studies have shown that related species fall out on the hydroperiod gradient as expected (Werner and McPeek 1994, Skelly 1995a, 1995b, 1996).

It is clear that biotic interactions are critically important for the distributions of vernal pool amphibians. Some of the strongest biotic effects on amphibians are widely agreed to come from fish predators (e.g., Maret et al. 2006). Field observations and whole pond manipulations show that fish presence is a critical determinant of amphibian oviposition patterns. Some species such as wood frogs breed rarely if at all in the presence of fish (Hopey and Petranka 1994) and are known to move into wetlands following local extinction of fish due to winterkill or drought-related drying (E. E. Werner et al., unpublished data). Experiments and anecdotal reports show that many important predatory fish species can have devastating effects on amphibian species commonly associated with vernal pools (Smith et al. 1999). Because fish are only associated with northeastern vernal pools under unusual conditions (e.g., floodplain pools, abandoned beaver flowages), fish predation may be most helpful in understanding why many species are restricted to vernal pools (Skelly et al. 1999).

SPATIAL ECOLOGY

Understanding vernal pool amphibian population dynamics requires an understanding of spatial context due to their use of multiple habitats and the patchy distribution of breeding pools (see Chapter 3, Leibowitz and Brooks; Chapter 14, Baldwin et al.). In this section, rather than considering the ways in which pools can differ from each other, we consider the ways in which terrestrial context can influence amphibians breeding in vernal pools. Specifically, we review evidence suggesting that isolation among pools and the state of the uplands surrounding pools affect amphibian populations. The metapopulation concept (a cluster of populations) has long been used as a framework for thinking about the spatial ecology of amphibians (Gill 1978; see Chapter 8, Gibbs and Reed).

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Whereas vernal pool amphibians spend much of their lives in the terrestrial environment, most adults migrate no more than tens to hundreds of meters from breeding pools (Color Figure(XX*); Regosin et al. 2003, Semlitsch and Bodie 2003). This generalization has two critical implications. First, it means that landscape changes within the core terrestrial habitat surrounding a vernal pool can have direct impacts on a large fraction of the terrestrial members of its breeding population (Semlitsch and Bodie 2003, Trenham and Shaffer 2005). Second, the incremental destruction of breeding pools and other small wetlands increases pond isolation, potentially severely impairing connectivity among populations (Gibbs 2000, Semlitsch and Bodie 1998, see Chapter 16, Windmiller and Calhoun).

Loss of connectivity can be important for vernal pool amphibian populations that depend on dispersal among ponds. Can a species be absent from a vernal pool because of isolation from other pools? The answer appears to be yes, even within the northeastern region where interpool distances can be relatively modest (Skelly et al. 1999). Sparsely available long-term data show that species are less likely to be present, and are less likely to persist, when the nearest sources of colonists are farther away (Skelly et al. 1999). These are important results implying that long-term

* See color insert following page xxx.

persistence of a species within a pool may depend on successful dispersal of individuals from other pools (the "rescue effect").

There is even stronger evidence that terrestrial landscape composition surrounding vernal pools is critical for amphibian populations. Although results vary among species, a number of recent studies show quite clearly that vernal pool species are more likely to be present in landscape contexts dominated by forest cover and that increasing landscape conversion and fragmentation by agriculture, roads, and suburban or urban land uses is associated with species absences (Gibbs 1998, Homan et al. 2004, Porej et al. 2004, Price et al. 2004). Some studies have gone beyond simple positive and negative associations to reveal strong scale dependence in patterns between land cover types and species presence-absence (e.g., Price et al. 2004). As one example, Homan et al. (2004) estimated thresholds describing changes in the relationship between forest cover and vernal pool species presence. For spotted salamanders, there was a strong overall relationship between percentage of forest cover and the likelihood of species presence regardless of scale of estimation, which ranged from 100 to 1000 m radius (Figure 7.2). Finer scales of estimation focusing on the uplands immediately surrounding pools, however, revealed an additional threshold requirement for forest cover of 30%. Below this value, spotted salamanders were unlikely to be present.

In addition to providing nonbreeding habitat, the structure of uplands may influence amphibian distributions by affecting dispersal. A number of studies show that vernal pool amphibians have strong preferences for different land cover types

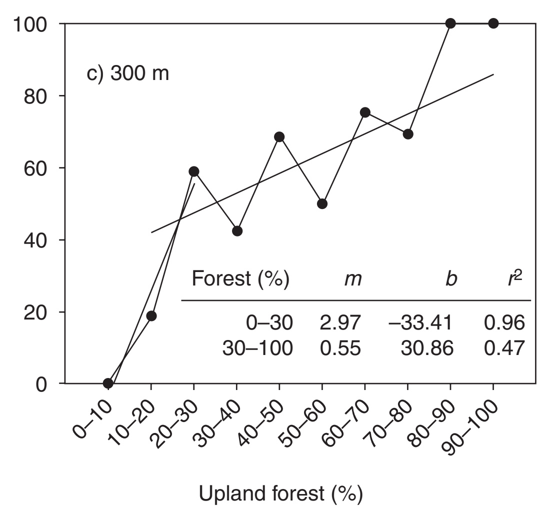

FIGURE 7.2 Percent occurrence of spotted salamanders (*Ambystoma maculatum*), as a function of land cover (percentage of upland forest within a 300 m radius) measured from the edge of suitable breeding pools. Two regression lines are joined at the point of a critical threshold in the relationship between forest cover and salamander presence. (Figure reproduced from Homan, R.N., Windmiller, B.S., and Reed, J.M. (2004). *Ecological Applications* 14: 1547–1553. With permission.)

(Gibbs 1998, deMaynadier and Hunter 1999, Montieth and Paton 2006), with most species in the focal region selecting partially to mostly closed canopy forest settings. Further evidence for preference for closed canopy forest is provided by studies showing that amphibians placed in open, unforested areas do not move as far and survive poorly compared with amphibians moving within forested habitat (Rothermel and Semlitsch 2002, Mazerolle and Desrochers 2005), perhaps because amphibians desiccate more rapidly when moving in the open. Open environments may also affect the ability of amphibians to navigate (Rothermel 2004, Mazerolle and Desrochers 2005).

Either because of habitat changes or because of loss of connectivity, landscapes altered by humans typically have lower species abundance even when vernal pools remain (Gibbs 1998, Skelly et al. 2006). In a study of forested, suburban, and urban landscapes in Connecticut, Skelly et al. (2006) found a reduction in amphibian species richness of more than two thirds (from >3 species per pool to <1 species) with increasing urbanization. Vernal pool indicator species such as wood frogs are particularly hard hit by landscape conversion, disappearing in degraded landscapes even where vernal pools are still present (Gibbs 1998, Skelly et al. 2006).

CONSERVATION IMPLICATIONS

There are three essential components that need to be addressed in conservation plans for amphibians using vernal pools: (1) the area containing the local population that includes the breeding pool, the surrounding terrestrial nonbreeding habitats, and the juxtaposition of the two (= complementation sensu Dunning et al. 1992), (2) the metapopulation, including the terrestrial matrix between populations, and (3) natural disturbance processes that create new pools or reset succession of pools or terrestrial habitat (Semlitsch 2000, Semlitsch and Rothermel 2003).

The number and quality of metamorphosing larvae leaving a pool, and the number of juveniles surviving to maturity and recruited into the terrestrial adult population determine success at the local population level. Juvenile survival and time to maturity depend on the size and quality of core terrestrial habitat (carrying capacity) adjacent to pools (Semlitsch and Bodie 2003). The radius of habitat required by most adult amphibians ranges from 142–289 m (462–939 feet) from the wetland edge (mean minimum estimates for 32 species from Semlitsch and Bodie 2003). Frogs, in general, require significantly more habitat than salamanders (Rittenhouse and Semlitsch 2006 data), and females have been shown to travel and overwinter farther from pools than males (Regosin et al. 2005). Estimates compiled for 12 species common to the Northeast region indicate an average distance of 121 m (393 ft) and a maximum of 260 m (845 feet) from pools is needed to encompass local populations around vernal pools (Table 7.2). Land use activities that degrade or truncate the terrestrial core habitat will limit the carrying capacity of populations and potentially their long-term viability (Halpern et al. 2005). Because edge effects from surrounding land use can also impact amphibians, an additional 25–50 m (81–163 ft) buffer is required to protect the terrestrial core habitat (Murcia 1995, deMaynadier and Hunter 1998).

TABLE 7.2
Summary of Terrestrial Migration Distances for Adult Salamanders and Frogs Surrounding Vernal Pools and Other Aquatic Breeding Sites

	State	Mean/Range/Maximum (in Meters)	Reference
Caudata			
Ambystoma jeffersonianum	Indiana	Mean = 252, range: 20–625 (86)	Williams 1973
	Kentucky	Mean = 250 (10)	Douglas and Monroe 1981
	Michigan	Mean = 39, range: 8–129 (8)	Wacasey 1961[a]
	Michigan	Mean = 92, range: 15–231 (45)	Wacasey 1961[b]
	Vermont	Mean = 93, range: 30–205 (6)	Faccio 2003
Ambystoma laterale	Massachusetts	Maximum > 300 (7)	Regosin, Homan, and Windmiller, unpublished data
Ambystoma maculatum	Indiana	Mean = 64, range: 0–125 (7)	Williams 1973
	Kentucky	Mean = 150, range: 6–220 (8)	Douglas and Monroe 1981
	Michigan	Mean = 67, range: 26–108 (2)	Wacasey 1961[a]
	Michigan	Mean = 103, range: 15–200 (14)	Wacasey 1961[b]
	Michigan	Mean = 192, range: 157–249 (6)	Kleeberger and Werner 1983
	New York	Mean = 118, range: 15–210 (8)	Madison 1997
	Vermont	Mean = 137, range: 52–219 (5)	Faccio 2003
Ambystoma opacum	Indiana	Mean = 194, range: 0–450 (12)	Williams 1973
	Kentucky	Mean = 30 (6)	Douglas and Monroe 1981
	Massachusetts	Range: 114–381 (20)	Gamble, unpublished data [c]
Ambystoma texanum	Indiana	Mean = 52, range: 0–125 (10)	Williams 1973
Ambystoma tigrinum	New York	Mean = 60, range: 0–286 (27)	Madison and Farrand 1998
Anura			
Acris crepitans	Illinois	Range: 8–22 (189)	O'Neil 2001[a]
Bufo americanus	Ontario	Range: 23 - 480 (176)	Oldham 1966[a]
Hyla versicolor	Missouri	Mean = 172, maximum = 271 (20)	Johnson et al. 2006
Pseudacris triseriata	Indiana	Mean = 75, maximum = 213 (9)	Kramer 1973
Rana clamitans	New York	Mean = 121, maximum = 360	Lamoureux and Madison 1999
	Ontario	Mean = 137, maximum = 457	Oldham 1967[a]
Rana sylvatica	Maine	Mean = 192.5, range: 102–340 (8)	Baldwin et al. 2006
	Massachusetts	Maximum = 472	Windmiller 1996

Note: Sample sizes, where reported, are given in parentheses.

[a] Hand collecting marked individuals.
[b] Hand collecting unmarked individuals.
[c] Incidental recaptures of individuals traversing drift fences at fixed distances from known breeding ponds.

Source: References are taken from Appendix 1 in Semlitsch and Bodie (2003) or provided in the literature cited.

Metamorphs are also critical to maintain other local populations through dispersal (i.e., in source-sink dynamics; Pulliam 1988). We know that local species populations are subjected to extinction periodically, even under natural conditions, primarily due to stochastic events like drought (Semlitsch et al. 1996), and through anthropogenic factors like draining, ditching, filling, pollution, and fish introduction. Dispersal occurs mostly by juveniles (e.g., Breden 1987, Berven and Grudzien 1990) and connectivity among pools is critical to maintaining amphibian metapopulations. Alteration and loss of pools reduces the total number or density of pools where amphibians can reproduce and provide dispersers. Reduced pool density increases the distance between neighboring pools, thereby affecting critical recolonization processes (e.g., Semlitsch and Bodie 1998). This adverse effect is critical because most individual amphibians cannot migrate long distances due to physiological limitations of water loss (Spotila 1972). An estimate of genetic dispersal distance for wood frog populations averages only 1,126 m, suggesting that migration and gene flow are near zero beyond these distances (Berven and Grudzien 1990). Semlitsch and Bodie (1998) demonstrated in South Carolina that the loss of all natural wetlands <4.0 ha in size would increase the nearest-wetland distance from 471 to 1,633 m. This distance is likely greater than can be traversed by most species. In addition, land use that alters the matrix between populations can render it unusable or less permeable to migrating amphibians (e.g., peat mining; Mazerolle 2001, pastureland; Rittenhouse and Semlitsch 2006, roads; deMaynadier and Hunter 2000) might reduce or disrupt recolonization (Joly et al. 2001). Thus, the loss or alteration of wetlands as well as the terrestrial matrix could severely impede rescue and recolonization processes, and place populations of amphibians in remaining wetlands at increased risk of extinction (Laan and Verboom 1990, Joly et al. 2001, Marsh and Trenham 2001).

Natural disturbance processes responsible for resetting succession or in some cases even creating new wetlands must not be ignored or suppressed by management (Semlitsch and Rothermel 2003). Although glacial processes originally created most vernal pools in the northeastern region (e.g., kettle holes; Colburn 2004; see Chapter 2, Rheinhardt and Hollands), some were created by the scouring process of flooding in river floodplains, landslides, and windfalls (e.g., tip-ups in shallow forested wetlands). Maintaining these disturbance processes is important to balance the loss of seasonal pools in certain areas due to the deterministic process of succession. Reversing succession by fire is also potentially important where wildfires were historically common, such as in dry, sandy coastal regions (e.g., pine barrens of New Jersey and Long Island). In more inland regions, beaver were likely important to reverse succession by flooding forests and killing trees to create open canopy ponds (sensu Gill 1978). Without these disturbance processes present on the landscape, amphibian species favoring early successional breeding habitats (e.g., chorus frogs, toads, tiger salamanders) will decline or disappear from local populations, thereby favoring species associated only with later successional stages (Skelly et al. 1999, Table 7.1). Every effort should be made to preserve the structure, function, and diversity of vernal pools, their spatial arrangement and connectivity, and the surrounding terrestrial habitat for pool-breeding amphibians so that costly and problematic species recovery and habitat restoration or mitigation procedures are not necessary.

SUMMARY

We have emphasized important features of the ecology of amphibians in the northeastern region that use vernal pools. These amphibians share a common historical and biogeographic context that may account for broad similarity in species complements inhabiting vernal pools over a relatively large area. Yet, species composition within individual pools is highly variable among pools and even between years. Forest canopy conditions over vernal pools can have strong effects on amphibian species composition. Many species are sensitive to canopy closure and are found infrequently in cool, shaded pools. There are also a number of specialized amphibian breeders, including ambystomatid salamanders and wood frogs, that are often associated with shaded pool conditions. Although amphibians are well adapted to natural variability in pool flooding and drying, anthropogenic influences can significantly increase or decrease the length of time pools are inundated with negative impacts to some species. Regulation of population size is determined by metamorph recruitment from aquatic habitats, but for long lived species, the carrying capacity of terrestrial habitats is likely more important. Composition of the terrestrial habitat surrounding pools is important to amphibians because it contains the adult breeding populations; removal of surrounding forests would be detrimental to many species. Further, if terrestrial habitats are altered by incompatible land use, they can offer resistance to dispersal among pools, thereby affecting rescue and recolonization processes important to the persistence of species at a regional level.

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