Marbled Salamander (*Ambystoma opacum*) Conservation Plan for Massachusetts

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1. INTRODUCTION

In 1998, we initiated an intensive study in western Massachusetts to examine the critical issues of dispersal and metapopulation dynamics in vernal pool breeding amphibians, focusing on the Massachusetts-"Threatened" marbled salamander (*Ambystoma opacum*). With the help of our partners (see below), we have completed our tenth season of intensive monitoring of amphibian populations at a cluster of 14 vernal pools in western Massachusetts with the aim of carefully examining population spatial structure and dynamics of the marbled salamander. Using computer-aided photo identification techniques (Gamble et al. 2007b) and mark-recapture procedures, we have documented the movement of nearly all individuals to and from all ponds during this period. Among other things, we have quantified the timing and orientation of movement to and from the breeding ponds, dispersal probabilities and distances, degree of natal and breeding site fidelity, adult survival, and spatial and temporal variability in local population demographics (Gamble 2004, Jenkins et al. 2006, Timm et al. 2007a-c, Gamble et al. 2007a, Gamble et al. submitted). Our findings confirm a high level of philopatry and the prominence of local factors (e.g., reproductive success) in determining local population trends. Our results indicate that hydrology, and a host of ecological conditions linked to hydrology, including predation by a range of aquatic predators that preferentially inhabit long hydroperiod ponds, may be the key to understanding these local population dynamics. However, we have also documented dispersal rates of 3-9%, with several individuals exceeding distances of 1,000 m. Overall, our findings suggest that individual ponds support relatively small and highly dynamic local populations and that these populations operate interdependently in a metapopulation context. Importantly, it seems that dispersal probably plays a key role in maintaining population connectivity and that connectivity is essential to metapopulation persistence in our study area. This field study has begun to shed light on the importance of movement and dispersal to the structure and dynamics of marbled salamander populations.

Building on the empirical results of the intensive field study, in 2002 we initiated a separate but related study to develop a spatial-analytical method of evaluating vernal pool connectivity (a vital landscape function) for amphibian metapopulations. Specifically, we developed a spatial computer algorithm (known as a “kernel”) that models the spread of dispersing amphibians across the landscape (Compton et al. 2007). Our modeling framework assesses the potential effects of roads, development, and other land cover types on connectivity for ambystomatid populations. Our model employs a new metric, the resistant kernel estimator, to assess functional inter-pond connectivity at the local, neighborhood and regional scales. In our initial application, we parameterized this model for the four ambystomatid salamanders that occur in Massachusetts (*A. opacum*, *A. maculatum*, *A. jeffersonianum*, and *A. laterale*) based on a combination of empirical data (deMaynadier & Hunter 1999, Rothermel & Semlitsch 2002, Gamble 2004, Montieth & Paton 2006, Gamble et al. 2007a, McDonough and Paton 2007) and expert opinion and applied it to the nearly 30,000 potential seasonal ponds across the state. Our multi-scale connectivity model represents a novel approach for assessing connectivity in pond-breeding amphibian populations, and it can be an important tool in prioritizing conservation efforts for pond-breeding amphibian populations at broader scales than traditional pond-based protection.

Our findings from the intensive field study and the resistant kernel model in combination provide a foundation for establishing a strategic conservation plan for marbled salamanders in Massachusetts. This conservation plan represents an attempt to integrate our current knowledge on marbled salamanders into a strategic plan for their conservation.

2. GOALS

The goals of this conservation plan are to guide the Commonwealth and interested environmental and local groups in a strategy for conserving marbled salamanders (and other associated vernal pool species), specifically:

- To conserve populations in perpetuity across the Massachusetts range.
- To identify and protect (i.e., maintain ecological integrity) the most important habitats and minimize degradation to the remaining habitats.
- To provide a framework for prioritizing conservation actions, surveys, and future research.

3. SPECIES ECOLOGY

3.1. Distribution

Marbled salamanders occur across much of the eastern United States from southern New England (including southern New Hampshire, Massachusetts, Connecticut and Rhode Island) to eastern Texas (Petranka 1998)(Fig. 1). In Massachusetts, marbled salamanders are broadly distributed, although they are notably absent from in the Berkshire and Taconic Mountains, northern Worcester Plateau, and the Cape and Islands (Fig. 2). As of 2006, the Natural Heritage element occurrence database indicated that there were 75 towns in Massachusetts where marbled salamanders had been observed. Seventy-eight occurrences have been documented since 1981, as well as 27 historic occurrences that were documented prior to 1981. In 2008, marbled salamanders were documented in the lower Housatonic River Valley, extending their documented range to the western third of the state.

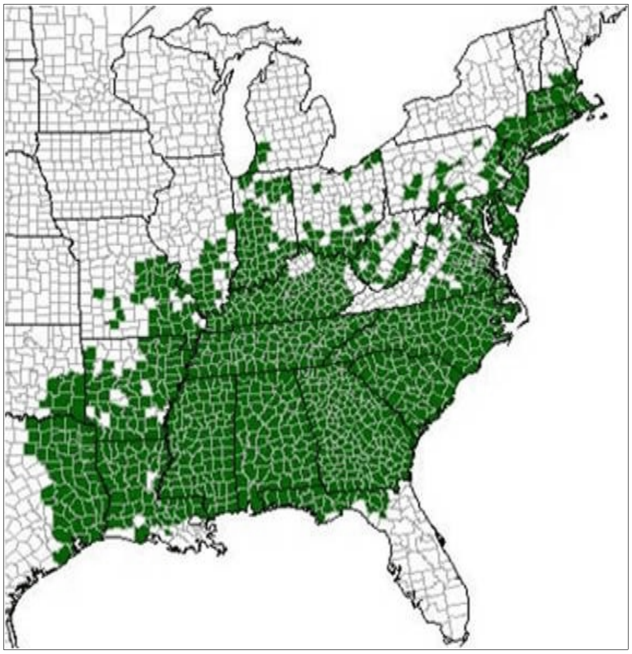

Figure 1. Range of the marbled salamander (*Ambystoma opacum*).

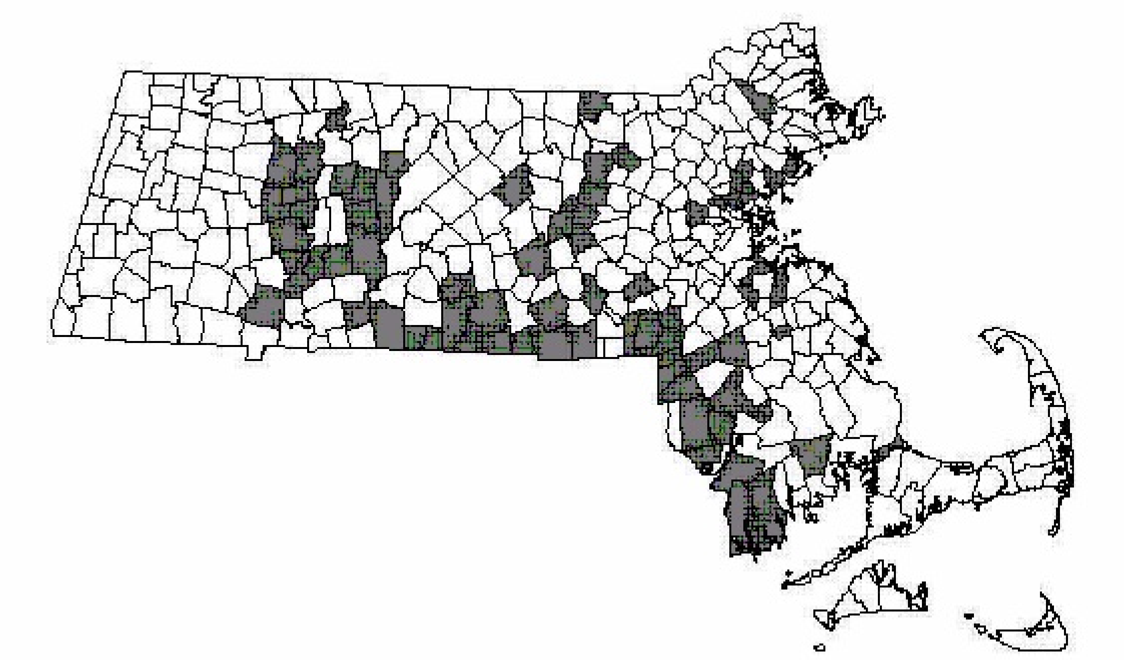

Figure 2. Marbled salamander distribution in Massachusetts based on the Natural Heritage Database records from 1980-2006.

3.2. Life History

Like other ambystomatids, marbled salamanders have a bi-phasic life history consisting of an aquatic larval phase and a terrestrial juvenile and adult phase (Fig. 3). The species is considered an ephemeral-wetland "obligate" species, relying on fish-free aquatic habitats to complete its larval stage. The required ephemeral wetlands are typically seasonal ponds or pools, also commonly referred to as “vernal pools”. In the late summer and early fall, adults migrate from terrestrial refugia in upland or floodplain forests to receded or dry seasonal pond basins to breed. After courtship, females deposit eggs under cover objects and in shallow leaf litter and commonly brood their egg clutches (Petranka 1998). In favorable conditions, the eggs are inundated by rising pond water in the subsequent weeks or months, and soon thereafter hatch into aquatic larvae. The larvae overwinter in the ponds and metamorphose into terrestrial juveniles in the following spring and summer. While terrestrial egg laying and larval overwintering appear to be risky (e.g., late pond inundation and susceptibility to freeze or desiccation), this early development strategy may give surviving larvae a competitive advantage over spring-breeding amphibians (i.e., all other species in Massachusetts); larval forms of other species such as the wood frog (*Rana sylvatica*) and spotted salamander (*Ambystoma maculatum*) are commonly depredated by larger marbled salamander larvae (e.g., Stenhouse 1985, Cortwright and Nelson 1990). In Massachusetts, marbled salamanders complete metamorphosis in June and July, emerging on rainy nights in this period to move into surrounding woodlands (Timm et al. 2007b). After a sub-adult stage of 1 to 6 years (Scott 1994), the majority of individuals return to natal ponds to breed, but a small percentage of animals disperse to breed in new ponds (Gamble et al. 2007).

Figure 3. Life history stages of the marbled salamander.

3.3. Breeding Site Fidelity and Dispersal

There is some evidence of breeding site fidelity among adults (Williams 1973, Scott 1994), but to our knowledge this has not been quantified rigorously with multiple-breeding site investigations except in Massachusetts, where we found that 96.4% of experienced breeders maintained breeding site fidelity through multiple seasons (Gamble et al. 2007). These findings confirm a high level of philopatry among adults, but indicate that adults do on rare occasion disperse to new breeding sites. In addition, rates of successful dispersal in sub-adult age classes have been estimated at less than 15% (Scott 1994). In Massachusetts, we found that 91.0% of first-time breeders returned to their natal ponds to breed; the remaining 9% of juveniles dispersed to new ponds to breed as adults (Gamble et al. 2007).

3.4. Survival and Breeding Frequency

Several studies have indicated that ambystomatid salamanders are generally characterized by high annual survival, ranging from 60% to 90% (Husting 1965, Whitford and Vinegar 1966, Raymond and Hardy 1990, Trenham et al. 2000), and may frequently skip breeding seasons. For example, non-breeding adult tiger salamanders (*Ambystoma tigrinum*) survived at annual probabilities around 68%, but attempted breeding in any given year at probabilities less than 25% and 50% for females and males, respectively (Church et al. In Press). Female tiger salamanders appeared to mitigate the risks of breeding by remaining in upland habitat during especially dry years. Survival estimates for spotted salamanders in a Michigan population averaged 72% and 87% for females and males, with fewer than 40% of individuals breeding in any given year (Husting 1965).

Marbled salamanders appear to be characterized by lower annual survival and higher breeding probabilities than other ambystomatids. Taylor and Scott (1997) estimated 50% annual survival for adult marbled salamanders in South Carolina. We estimated a similar annual survival rate of 55% for adult marbled salamanders in western Massachusetts, indicating that very few individuals likely live beyond 12-15 years. Moreover, the majority of males (~95%) in our study attempted to breed in every season, and the minority of females that skipped a season (<45%, on average) almost always bred in the year following. One potential explanation for this difference is that individual marbled salamanders, faced with relatively poor odds for surviving to another breeding season (approximately 65% for non-breeders), may derive the greatest fitness benefit from "making the best of it" regardless of conditions or energetic readiness in a particular season. In addition, these other species are aquatic breeders for whom weather cues that favor migration may also have some value in predicting good breeding conditions (e.g., are pond basins full or dry), possibly strengthening selective pressures for selectivity. Precipitation patterns during the breeding period of marbled salamanders seem less likely to correlate dependably with favorable nesting conditions that depend more on precipitation amounts in later months.

Based on these annual survival rates and breeding frequencies, we estimated that approximately 55% of females and males that survived to breed lived one or more additional years, but fewer than 5% lived beyond 6 additional years (Fig. 4). Overall, the average female (i.e., that survived to breed) survived 1.3 years beyond first breeding and the average male 1.4 years. Given higher probabilities of skipping breeding seasons, average lifetime breeding events for females (2.0) were lower than for males (2.5). Our simulations of longevity suggest that while many individuals may live to breed a second or third time, fewer than 10% survive beyond 5 breeding seasons. These results may also be interpreted to mean that 5 successive years of reproductive failures could reduce population size by over 90%, suggesting that this form of stochasticity alone may present significant extinction risks.

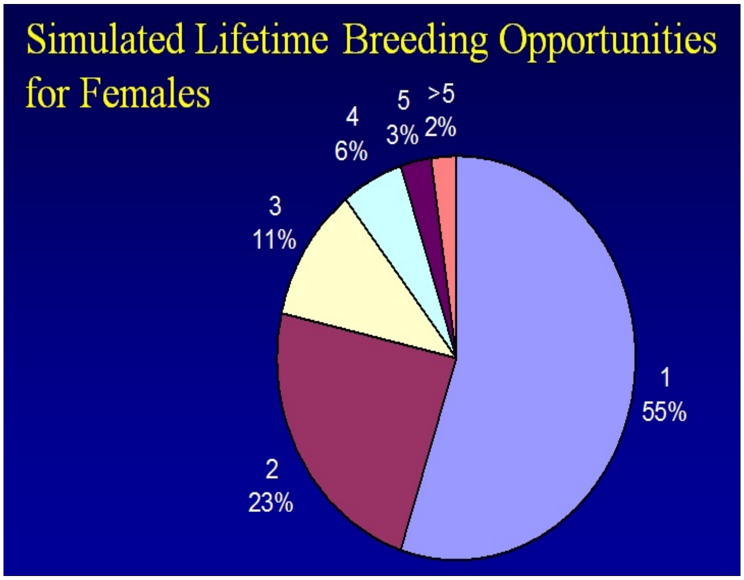

Figure 4. Simulated lifetime breeding opportunities for female marbled salamanders.

3.5. Habitat Selection

Breeding habitat.--As noted above, marbled salamanders are considered obligate seasonal pond (or vernal pool) breeders throughout their range (Fig. 5). Unfortunately, very little else is

Figure 5. Season ponds have an annual wet-dry cycle that is required breeding habitat for marbled salamanders.

known about their breeding habitat requirements. In Massachusetts, marbled salamanders have been observed breeding in a wide range of seasonal ponds, including ponds of widely varying sizes and depths and amounts and types of aquatic and riparian vegetation. In western Massachusetts, we found that some ponds were consistently more productive than others and some years more productive than other years (Gamble et al. Submitted). While the causal factors are difficult to confirm, our observations suggest that there may be several important factors. Hydroperiod, or the length of the period the pond holds water through the spring/summer, appears to be the most important factor (Fig. 6). Long hydrologic regimes appear to preclude successful larval development, possibly due to increased rates of larval predation by larger populations of vertebrate predators and predacious aquatic invertebrates. Our observations of low breeding population sizes coupled with high reproductive success at intermediate hydroperiod ponds strengthen the conclusion that conditions in long hydroperiod ponds are inhospitable for marbled salamander larvae.

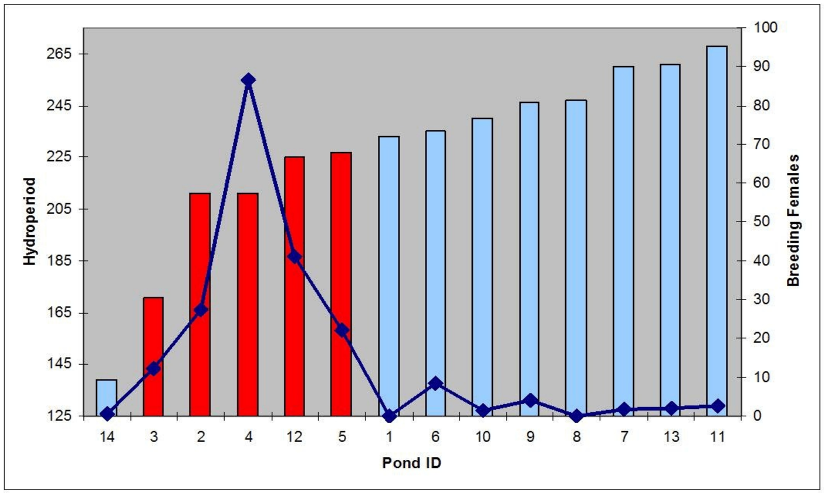

Figure 6. Relationship between pond hydroperiod (left axis and colored bars) and number of breeding female salamanders (right axis and solid line) for 14 seasonal ponds in western Massachusetts (shown in rank order from shortest to longest hydroperiod). The "optimal" spring hydroperiod (date of pond drying) was June 20 to August 18.

Non-breeding habitat.--Little is known about the terrestrial ecology of this species (Taylor and Scott 1997). Based on radio telemetry studies of other eastern mole salamanders (e.g., Madison 1997), it is believed that marbled salamanders are nocturnal and spend most of the non-breeding season as "sit-and-wait" predators in crevices and small mammal burrows in upland forests surrounding breeding sites. It is generally believed that adults select mature deciduous or mixed forested uplands of the southern hardwood type, dominated by oak and hickory species with white pine and containing a well developed understory with abundant coarse woody debris and deep litter, although this is mostly anecdotal and/or derived from studies on other species or in other environments (e.g., Perkins and Hunter 2006, Rothermel and Semlitsch 2002, deMaynadier and Hunter 1998, but see Morris and Maret 2007).

Dispersal habitat.–Even less is known from empirical studies about the habitat requirements of dispersing individuals, adults or juveniles. However, experts generally agree that mature forest is preferred and early-successional forest (e.g., shrublands, grasslands) and non-forested environments are avoided during dispersal and that developed lands, especially roads with high traffic intensity, are strongly avoided.

3.6. Movements and Home Range

Marbled salamanders exhibit three distinct types of movement: 1) movement within the uplands during the non-breeding season, 2) migration to and from the breeding site, and 3) dispersal from the natal site (Fig. 7). Nothing is known about movement within the uplands during the non-breeding season, but it is assumed that individuals maintain strong fidelity to small areas based on observations of related species (e.g., McConough and Paton 2007). With regards to seasonal migrations between the uplands and breeding sites, Williams (1973) tracked 12 individuals (with radioactive tags) and found that they moved on average 194 m with a standard deviation of 129 m and a range of 0-450 m from the pond (before settling down). Semlitsch (1998) reviewed upland habitat use of six Ambystoma species (n=265 individuals) and found that on average they resided or were found 125 m from the breeding habitat (sd=73 m). McDonough and Paton (2007) radio tracked spotted salamanders emigrating from ponds near a

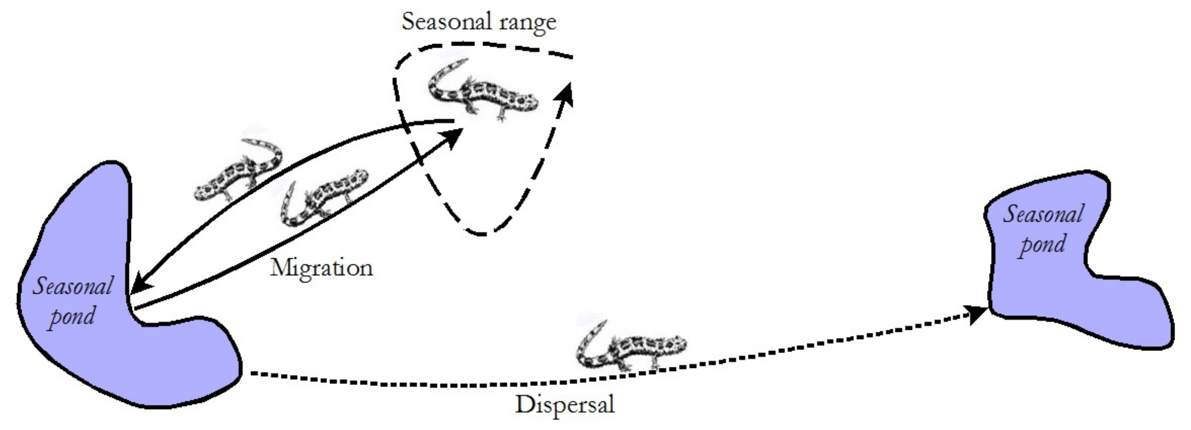

Figure 7. Three major types of movements of marbled salamanders: seasonal home range movements in the uplands, migration to and from the breeding site, and dispersal from the natal pond to a new breeding site.

golf course and in undisturbed forest (control). Around the control pond males emigrated a mean maximum distance of 85 m (sd=40 m, N=10), while females had a mean of 124.9 m (sd=37 m, n=8). Thus, it appears that 95% of salamanders are likely to be found within 200-450 m of the breeding pond during the non-breeding season.

Little is known about dispersal movements outside of Massachusetts. Our findings indicate that approximately 95% of successful dispersers occur within roughly 800 m of their natal pond, but that a number of individuals represented by the tail of this distribution might be expected to disperse farther (Gamble et al. 2007). We recorded 12 individuals (16% of successfully dispersing FTBs) breeding at ponds greater than 1000 m from their natal ponds with a maximum dispersal distance of 1350 m. Because these observations were bound by the scale of our study area, it is likely that longer distances are occasionally traversed (Smith and Green 2005). Previous maxima recorded for pond-breeding ambystomatids include 1000 m for marbled salamanders in South Carolina (personal observation noted in Pechmann et al., 2001) and 756 m for spotted salamanders (Madison 1997). Nonetheless, our findings considerably extend the distances that we understand ambystomatids to be capable of moving, which are critical as we consider population dynamics at broader scales.

3.7. Population Structure and Dynamics

Much interest has centered around the question of whether amphibians occur as metapopulations. A strict view of metapopulation theory describes assemblages of local populations that are individually prone to extinction but collectively persistent as a result of dispersal and recolonizations (Hanski and Gilpin 1997). Many pond-breeding amphibians have been considered likely candidates for metapopulation models because they have high breeding site fidelity and are characterized by high levels of population variability (Semlitsch 2000). However, other authors have suggested that the applicability of metapopulation theory may be overestimated. This may result from inflated estimates of extinctions and recolonizations from incorrectly interpreted field data (Marsh and Trenham 2001) and underestimates of dispersal distances and probabilities (Smith and Green 2005).

In the case of many species that occur in spatially-subdivided populations with limited dispersal, the relevance of metapopulation models ultimately depends on the level of demographic variability experienced by local populations and the level of independence in this variability over space and time. Several studies have established the potential for wide fluctuations in amphibian populations over time (Semlitsch et al. 1996, Meyer et al. 1998) and the susceptibility of local populations to extinction (Blaustein et al. 1994, Skelly et al. 1999). However, most research on population regulation in pond-breeding amphibians has focused on factors affecting success in aquatic stages (Pechmann 1995) and/or has been limited in scale to individual breeding populations (Semlitsch 2002).

Our work on marbled salamanders in Massachusetts confirms limited (but non-zero) dispersal among ponds, a wide range of variability in productivity among ponds and from year to year, and moderate levels of asynchrony in reproductive success among ponds (Gamble 2004, Gamble et al. 2007, Gamble et al. Submitted). These observations allow us to consider conceptual models which might best describe landscape-level population structure and dynamics in this system. A range of well-known conceptual and mathematical models have been proposed to describe dynamics in spatially-structured populations, ranging from panmictic populations at one extreme to classic metapopulations at the opposite extreme. These models might best be viewed as different points along a continuum rather than as categorical divisions. While the use of metapopulation terminology has varied widely, most would agree that its appropriate application be limited to the portion of this continuum where populations are characterized by pronounced spatial structure (e.g., discrete breeding habitats) and where dispersal rates are not so high as to completely dilute demographic independence among local populations (Hanski & Simberloff 1997; Stacey et al. 1997).

In the metapopulation portion of this continuum, source-sink dynamics as originally presented by Pulliam (1988) emphasized conditions where some habitats consistently supported more productive populations than others (thus the term "habitat-specific demography")(Fig. 8). Through the frequent export of dispersers, these source habitats were expected to maintain overflow populations in less productive, or sink habitats. Classic metapopulation dynamics, in contrast, described theoretical populations characterized by frequent and independent local extinctions (Fig. 8). Under the assumption of equal probability of dispersal among local populations, an equilibrium condition might result as increases in unoccupied patches were met by increased rates of recolonization. Though few real-world examples of a classic model have been described, it has been considered particularly relevant to species dependent on spatially dynamic habitats (e.g., brief successional stages) where "true" extinctions and recolonizations are relatively common.

An intermediate condition between these models appears to best describe marbled salamander populations in Massachusetts. In these "rescue-effect metapopulations" (Stacey et al. 1997)(also referred to as dynamic source-sink metapopulations)(Fig. 8), any brief snapshot in time would likely resemble a source-sink structure, but over longer time periods of years or decades, those habitats supporting source populations may be expected to change as the result of

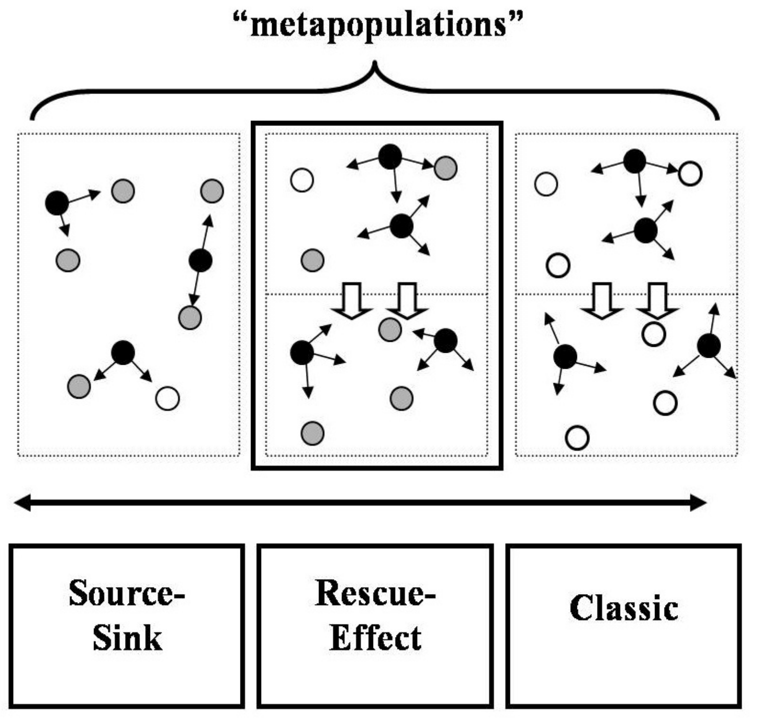

Figure 8. Alternative metapopulation models used to describe marbled salamander populations.

stochastic local variability and/or deterministic successional dynamics. Gill (1978) provided an early example in his work with red-spotted newts in Virginia. In this case, most breeding sites were clearly reproductive sinks; however, populations were maintained (and extinctions prevented) through the apparent abundance of dispersers from productive ponds. More recent work by Trenham et al (2001) with California tiger salamanders offers a closer taxonomic comparison. They observed distance-dependent dispersal rates and considerable independence among local populations; however, as in the previous example, true extinctions were deemed to be rare or unlikely due to high dispersal rates from productive ponds.

In the case of marbled salamanders in Massachusetts, pond hydroperiod appears to largely drive community composition and the specific conditions under which this species is able to be successful. To the degree that approximate hydroperiod/hydrologic regime is maintained over time and long hydroperiod ponds attract dispersers, it can be expected that they will act as persistent sinks in a metapopulation context. Among breeding sites within an optimal hydroperiod range, there is some tendency towards temporal synchrony as the result of regionally dominant events (e.g., premature floods or fall/winter droughts), but this is countered significantly by the differentiating effects of local variables such as premature pond drying, post-inundation freezes (in shallow ponds) and/or disease outbreaks. The result is that individual breeding sites may vary significantly over time both in their intrinsic growth rates and their relative contributions to metapopulation-level recruitment (and thus their status as sources or sinks).

Unlike the other amphibian examples described, it is unclear that dispersal from productive centers will constantly maintain populations at other sites potential breeding sites, at least in our study area. There is evidence of high site fidelity among both adult and juvenile marbled salamanders (Pechmann et al. 1991 L. Gamble et al. 2007), and even the possibility that some level of active habitat selection is preventing the attempted colonization of less-desirable, long-hydroperiod ponds (L. Gamble, unpubl. data). In our study, for example, 2 of 14 ponds have never been visited by adult females over a ten years even though one is surrounded by other breeding sites and the other is isolated by less than 300 m. Population sizes observed in our study - while reasonably representative of marbled salamander populations in the region (Shoop & Doty 1972 and P. Paton pers. com.) - are small relative to those in more southern localities (D. Scott, pers. com) or of other ambystomatid salamanders in the Northeast (e.g., Paton & Crouch 2002; Windmiller 1996). Given the high level of year-to-year variability in recruitment success and small breeding population sizes, it appears that local extinctions are possible, if not likely, at most sites over the long-term. We observed at least one possible local extinction during the course of our study. Re-emphasizing the continuous nature of population models under discussion, it is likely that marbled salamanders emulate rescue-effect metapopulation dynamics in areas where breeding sites are in closer proximity and dispersing individuals more abundant while more closely approximating extinction-recolonization dynamics at more isolated or peripheral sites (Stacey et al. 1997).

Finally, there is the possibility that the distribution of suitable breeding sites, perhaps largely determined by hydroperiod, may change over longer time periods. Though most seasonal ponds in southern New England are generally considered to be the result of long-term geologic/geomorphic events (and thus spatially-fixed), the hydrologic regimes of these wetlands may be subject to change as the result of forest successional dynamics. In a study of 37 wetland sites in Michigan, for example, Skelly et al (1999) found that ponds appeared to be drying approximately 2.5 weeks earlier than they were in surveys dated 25 years previous, a magnitude of change which would bring many unestablished breeding sites in our study area under the apparent hydroperiod threshold described. This observation was concurrent with a significant increase in canopy closure over this time interval. Canopy closure, in turn, was shown to have significant effects on amphibian community composition and productivity (Halverson et al. 2003; Skelly et al. 2002), though specific effects on ambystomatid larvae are not known. The potential for dynamic change in breeding habitat quality and/or distribution would likely be greater still in floodplain forests, where ephemeral wetlands may be less permanent features in the landscape. Moreover, future climate changes are likely to effect precipitation patterns and thus hydrologic regimes, but the potential consequences of these changes to marbled salamander populations is largely unknown.

4. CURRENT STATUS

The global status assigned by NatureServe is “G5”, which means that the species is considered “demonstratably widespread, abundant, and secure” on a global scale. The marbled salamander is not listed as threatened or endangered at the federal level in the United States. Though locally abundant in parts of their range, marbled salamanders are considered vulnerable to decline due to the widespread loss of seasonal ponds that remain largely unprotected by existing state and federal wetlands regulations (Scott 2005) and the widespread loss and degradation of upland forests surrounding and connecting breeding sites caused by development. In Massachusetts, they approach the northern limits of their natural range and are listed as a state-"Threatened" species under the state Endangered Species Act (M.G.L c.131A and regulations 321 CMR 10.00). The fact that the marbled salamander is near the northern limit of its range in Massachusetts is a contributing factor to its rarity in the state. Furthermore, the species is difficult to locate and census accurately. Although marbled salamanders are widespread throughout Massachusetts lowlands, populations tend to be very small and localized surrounding breeding ponds. For yet unknown reasons, many seasonal ponds do not support them.

5. CONSERVATION CONCERNS

While considered common throughout much of their range, marbled salamanders and other pond-breeding amphibians are threatened by the loss, degradation and fragmentation of both breeding and terrestrial habitats (Semlitsch 1998). These threats affect vital population processes including reproduction, survival, dispersal and gene flow.

5.1. Habitat loss

Habitat loss is perhaps the greatest overall threat to marbled salamander population viability as it results in a quantitative reduction in the space (and thus resources) available for salamanders to meet their life history needs. Habitat loss results in a direct reduction in population size as a result, and smaller populations are always less viable. The major cause of habitat loss is residential and commercial development, which results in the draining and filling of seasonal wetlands (breeding habitat) and the deforestation of uplands (non-breeding habitat). Seasonal wetlands receive some protection under the Massachusetts Wetlands Protection Act, but many of the seasonal ponds that provide breeding habitat for marbled salamanders are not protected under the current law due to their small size and landscape position. Massachusetts Audubon estimates that roughly 40 acres of land are lost to development per day. In addition, activities associated with developing the land (e.g., clearing and plowing) cause direct mortality of individuals. Given the low annual survival rates of marbled salamanders (discussed previously), any activity that reduces survivorship has the potential to significantly effect population viability.

5.2. Habitat degradation

Habitat degradation is the reduction in the quality of habitat without completely eliminating it; in other words, the reduction in survival and/or reproductive success leading to lower (but not zero) individual fitness. Habitat degradation is a major conservation concern because it is difficult to detect and measure directly and is caused by both natural and anthropogenic factors that are sometimes confounded. Major threats affecting the quality of aquatic breeding habitat and terrestrial non-breeding habitat including the following:

- Disruption of hydrologic regime.–Maintaining natural hydrologic regimes of the aquatic breeding habitat is critical for the conservation of marbled salamanders. As noted previously, the quality of the aquatic breeding habitat appears to be strongly determined by its hydrologic regime. In particular, reproductive success appears to be much higher over time in ponds with an intermediate Spring hydroperiod (i.e., drying between late June and late July). In addition, successful reproduction apparently also depends on favorable hydrologic conditions in the Fall; specifically, dry pond basins in August and September followed by sustained filling in October or early November. Thus, activities that disrupt hydrologic regimes by altering surface or ground waters is potentially detrimental to reproductive success. Of course, these same activities may actually improve habitat quality in some places. Of particular concern is the unknown effects of climate change on hydrologic regimes. Spring hydroperiod and the refilling of pond basins in the Fall are strongly tied to the period of leaf-on in the deciduous vegetation due to transpiration. Any climate-induced change in the timing and duration of leaf-on in the deciduous vegetation will likely have an affect on ground water patterns, which will in turn affect Spring hypdroperiod and/or the timing of pond refilling in the Fall, which will in turn affect marbled salamander reproductive success. In addition, an increase in the magnitude, frequency and/or timing of major storm events in the late summer or early fall may adversely affect breeding conditions, for example by causing the ponds to fill prematurely before eggs can be laid or to fill and then dry after the eggs have hatched.

- Alteration of vegetation.–Maintaining mature forested upland habitat surrounding the breeding ponds is essential for the conservation of marbled salamanders. The major anthropogenic source of vegetation alteration in the uplands is commercial timber harvesting. Timber harvesting activities, such as the operation of heavy machinery and the felling of trees, can result in the direct mortality or injury of individuals leading to a reduction in survival. The reduction in canopy cover caused by tree removal affects the forest floor microclimate. Salamanders are sensitive to dessication and prefer high canopy cover. The altered vegetation and microclimate together affect the invertebrate community that provides the food resources for the salamanders. In addition, timber harvest affects ground water levels (and thus spring hydroperiods) by reducing water loss via transpiration, although these effects may be ephemeral.

- Pesticides and other toxic chemical pollutants.–Maintaining water quality in the aquatic breeding habitat is essential for the conservation of marbled salamanders. Excessive pesticide levels may adversely affect the productivity and diversity of the aquatic invertebrate community that forms an essential food base for larval salamanders. Road salts are perhaps a more ubiquitous concern as they have been shown to affect amphibian reproductive success in wetlands up to several hundred meters from roadways.

- Meso-predator populations.–In recent decades, human-subsidized meso-predators such as raccoon, opossum and skunk populations have benefitted from the availability of additional food sources such as garbage, bird seed and food for pets, provided by humans in residential and commercial areas. These mammals are efficient predators and can cause high rates of mortality for adults and juveniles as they enter and leave the breeding ponds since the animals are concentrated and offer minimal predator defenses. The impacts can be significantly increased in areas of residential and commercial development.

5.3. Habitat fragmentation

Habitat fragmentation is the disruption in the continuity and connectivity of habitat. Habitat fragmentation is perhaps more insidious than habitat loss and degradation because its affects are often indirect and difficult to observe except over very long periods of time. As noted previously, marbled salamanders have a metapopulation structure in which periodic dispersal of individuals between ponds is critical. Dispersal allows for the redistribution of individuals from source populations to sinks, which increases the size of the metapopulation (and therefore its persistence), allows for recolonization of breeding habitats after stochastic extinction events, and provides gene flow among local populations that is essential for evolutionary adaptation in a changing environment.

- Roads.–Other than the obvious disruption of connectivity caused by residential and commercial development, the major cause of fragmentation is roads. Roads cause the direct loss of habitat as well as the degradation of habitat due to salt, sediment and other pollutants that runoff roads into nearby wetlands and reduce water quality. However, the principal effect of roads is to impede the movement of individuals across the landscape. Mortality on roadways is a major concern for all amphibians, but is especially so for slow-moving species such as salamanders. Several studies have documented road mortality of hundreds of individual amphibians on single road segments (e.g., Wyman, 1991; Ashley and Robinson, 1996; Mazerolle, 2004; Aresco, 2005). In addition, theoretical models incorporating movement rates across roads in relation to traffic intensities have estimated annual road mortality rates potentially exceeding 20% of the total adult population for several species (Hels and Buchwald, 2001; Gibbs and Shriver, 2005). Highways with high traffic volumes become impenetrable barriers that isolate salamander populations and prevent dispersal to and, therefore, gene flow with neighboring populations. Even smaller roads with moderate traffic volumes can cause enough mortality to cause a local population to decline.

The threat of roads is expected to increase in the future. Although mass transit will likely increase over the next 20 years, automobiles will undoubtedly remain the most prevalent form of transportation. Traffic volume in the Boston area is projected to increase more rapidly than the miles of road needed to accommodate the increase (Woods and Poole 2000). The Woods Hole Research Center reported that in the last 50 years the expansion of high volume expressways has had the largest single influence on southeastern Massachusetts. Car volumes have increased 35 percent in 27 towns in the southeastern part of the state (Woods Hole Research Center in press.). Given the rate of development, in addition to the new roads built to support the new development, it is almost certain that traffic intensity will increase on arterial roads leading to greater road kill of salamanders and other species.

6. CONSERVATION FRAMEWORK

Given the complex life history and ecology of marbled salamanders and the current threats facing this species in Massachusetts, we propose a multi-scale conservation framework. Here we describe the conservation scales, present a strategy for conservation action across scales, and discuss potential conservation tactics that can be used at one or more scales.

6.1. Conservation Scales

We recognize four discernable scales for conservation of marbled salamanders (Fig. 9):

- The breeding seasonal pond or basin.– The seasonal pond itself is likely a primary determinant of population size and stability, and largely exerts control on populations through effects on reproductive success. Because adults exhibit high breeding-site fidelity (Whitford & Vinegar 1966; Pechmann et al. 1991; Gamble et al. 2007), each seasonal pond generally supports a distinct breeding population. Seasonal ponds vary in habitat quality, supporting populations that vary widely among pools and across years (Pechmann et al. 1991; Skelly et al. 1999, Gamble 2004). Pond hydroperiod seems to be the most important

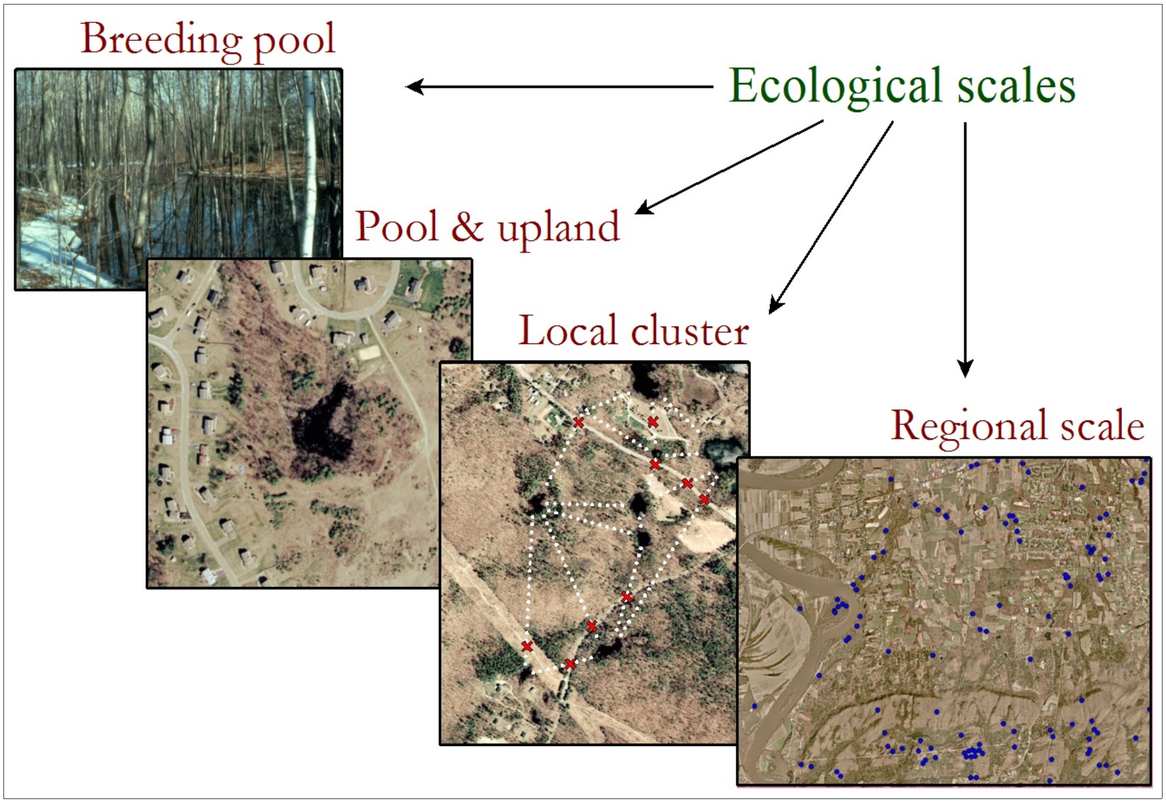

Figure 9. Ecological scales for the conservation of marbled salamanders. The breeding pool is required breeding habitat and supports local reproduction; the pool and upland scale provides required non-breeding habitat at the scale of seasonal migrations; the local cluster scale provides local habitat and the connections among local populations to support metapopulation processes such as dispersal; and the regional scale consisting of clusters of clusters of seasonal ponds and intervening habitat supports long-term processes such as gene flow.

variable structuring vernal-pool communities (Semlitsch et al. 1996; Skelly et al. 1999; Snodgrass et al. 2000; Colburn 2004) and appears to be a major determinant of marbled salamander reproductive success Gamble 2004).

- The breeding seasonal pond with surrounding upland habitat.--The second scale is the seasonal pond with its surrounding upland habitat, or the "life zone" (Semlitsch 1998), which largely exerts control on populations through effects on juvenile and adult survival during the non-breeding season. Marbled salamanders and other ambystomatids spend 90–95% of their lives in upland forests, up to several hundred meters from breeding pools (Semlitsch 1998), and upland habitat may overlap for several breeding pools. Clearly, protecting pools without this upland habitat does little for even the short-term persistence of populations. Although the details of upland habitat use is an area of active research (e.g., see Madison & Farrand 1998; Faccio 2003; Regosin et al. 2003; McDonough-Haughley & Paton 2007), a reasonable surrogate for the availability of upland habitat is simply the amount of forested area surrounding a pool that is accessible to individual salamanders (e.g., not across a major road; Guerry & Hunter 2002; Homan et al. 2004).

- Neighboring seasonal ponds and upland habitat.–At a third scale, connectivity among local populations represents the degree to which dispersal may support metapopulation processes. If dispersal (defined as demographic and genetic exchange among populations, as opposed to migration, which is annual upland movement within a population) among pond-centered populations is low but not zero, then seasonal ponds and their surroundings represent discrete populations with the potential for occasional gene flow and demographic interactions (such as colonization and the rescue effect; Brown & Kodric-Brown 1977). If all populations have a high potential for extinction over time, and if these extinctions are neither synchronized nor deterministic, then populations show metapopulation structure (Hanski & Gilpin 1991). Our research on marbled salamanders provides evidence for metapopulation structure in at least some populations (Gamble 2004, Gamble et al. 2007, Gamble et al. Submitted). If marbled salamanders do generally operate in metapopulations, conservation at the scales of ponds and local upland habitat is insufficient to ensure persistence over the long term because even in the absence of anthropogenic stressors, many (or even all) populations are expected to become extinct due to stochastic fluctuations over decades or centuries. If connectivity among pools is interrupted, natural dispersal that enables recolonization, rescue effects, and gene flow will not support metapopulation processes.

- Clusters (groups of groups) of seasonal ponds in a broader regional framework.–Over long time periods connectivity takes place at even broader spatial scales than neighboring seasonal ponds (i.e., well beyond the scale of individual salamander movements) because the contribution of dispersers from neighboring ponds depends in part on how connected these ponds are to more distant ponds. Metapopulations in broader connected clusters may be more likely to persist than those in smaller clusters. Thus, regional connectivity is structured by the connectivity among clusters of ponds at multiple spatial scales. For the sake of convenience, we lump these poorly understood broader scales into a fourth, broadly defined, "regional scale."

6.2. Conservation Strategy

Given the conservation scales above, we propose a three-step conservation strategy. Our strategy is hierarchical, starting from the broad regional scale and allows for flexibility in matching planning and conservation efforts to available resources, as follows:

Step 1.–The first step is to select regional clusters (groups of groups) of highly connected *potential* seasonal ponds, where metapopulation processes such as dispersal and gene flow are effectively unimpeded. Ideally, these clusters would be well distributed across the full extent of the planning area (Fig. 10). We developed a *resistant kernel model* for this purpose (see Compton et al. 2007 for the details). Conservation planners can use the results from our model statewide or across a smaller region of interest (e.g., ecoregion, watershed, or town) to select regional clusters. The model results are available as an ArcGIS shapefile and can be downloaded from the UMass Landscape Ecology website (www.umass.edu/landeco/research/vernal/vernal.html). Potential seasonal ponds with high scores for regional connectivity can be identified. Such identification can take other variables into account, such as proximity to protected open space. Depending on the resources available, this could include the top 1%, 10%, or more of the ponds—such use of qualitative metrics is to some extent a political, rather than a biological decision (e.g., what percentage of seasonal ponds need protection at all scales?). The result of this step would be the identification of "hotspots" of potential seasonal ponds with high regional connectivity to other ponds and intact upland habitat, where metapopulation persistence and long-term processes such as gene flow and evolutionary adaptation are most likely to occur. These regional clusters would provide a strategic regional landscape context for focused conservation efforts at the next scale.

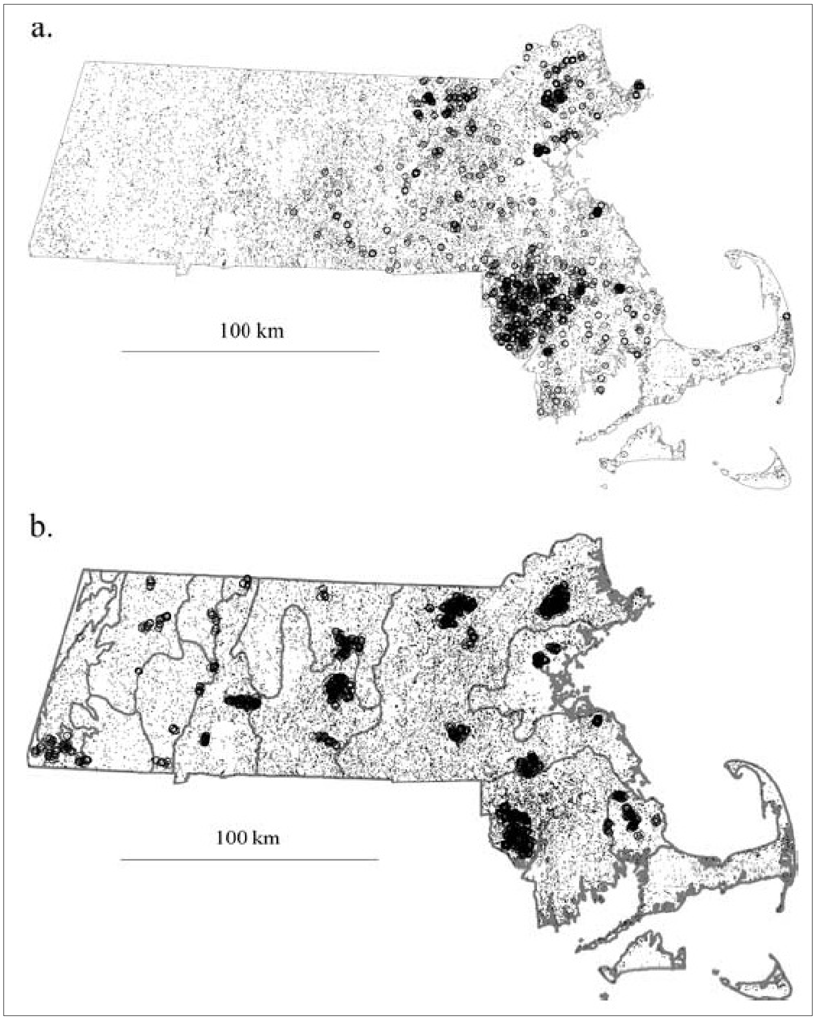

Figure 10. Vernal-pool connectivity scores (integrated across all three scales) for all pools across Massachusetts: (a) combined pool scores across Massachusetts and (b) pool scores by ecoregion (black circles, 10% most connected pools; small dots, 90% least connected pools; gray lines [in b], ecoregion boundaries)(From Compton et al. 2007).

In addition to these regional clusters, individual potential seasonal ponds with high local and/or neighborhood connectivity based on the resistant kernel model (i.e., abundance of accessible upland forest and connections to nearby seasonal ponds) that are not included in the targeted large regional clusters should be identified and targeted for opportunistic conservation actions in step 3 below. These individual ponds and small clusters of ponds may function as stepping stones to promote connectivity between the larger regional clusters and therefore should be protected whenever opportunities arise.

Step 2.–Once regional clusters of high-ranking *potential* seasonal ponds are identified, the next step is to field validate these subsets of pools (Fig. 11). Such proactive efforts could make use of volunteers through citizen science programs, as has been previously done effectively in Massachusetts. Depending on available resources, field validation could range from confirming the existence of standing water during various seasons as an estimate of hydroperiod (e.g., from aerial photos), to biologically-based vernal pool certification, to more intensive work targeted at confirming the presence of marbled salamanders (and other seasonal pond breeding species) and estimating populations sizes.

This two-step process is a highly efficient way to identify seasonal ponds with high conservation value for marbled salamanders and other ambystomatids. The result of this step would be the confirmation of integral seasonal ponds and intervening uplands within regional clusters, where vital population processes such as survival and reproduction are most likely to exist and metapopulation processes such as dispersal and gene flow are intact. Once verified, these seasonal ponds and intervening uplands would become Habitat Conservation Areas (HCAs) that provide the focus for local conservation effects in the next step.

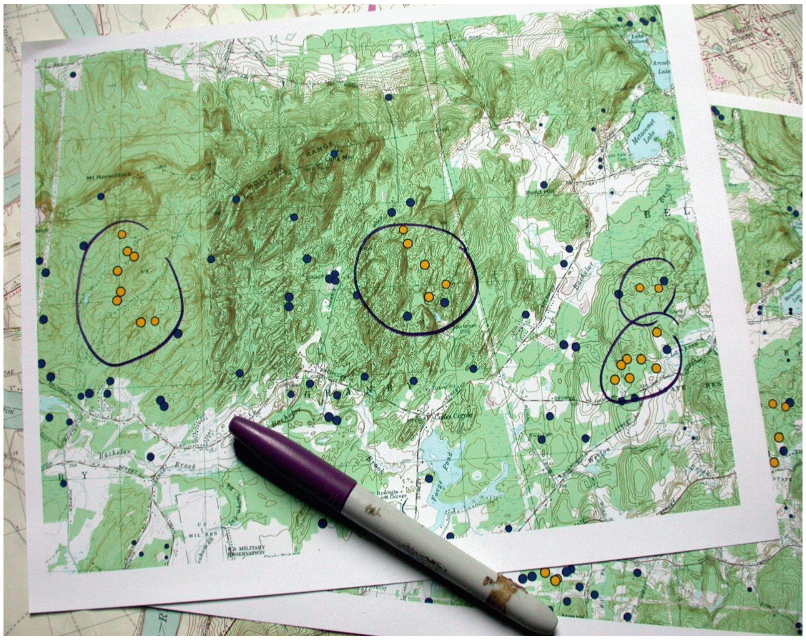

Figure 11. Example of using model results to target field work aimed at confirming the existence and functionality of habitat for marbled salamanders.

In addition to validating the integrity of habitat in the large regional clusters (HCAs), similar efforts should be made to confirm the condition of high-valued individual ponds and small clusters of ponds that are intended to function as stepping stones in the intervening matrix between HCAs. However, in contrast to the proactive field work needed to confirm the integrity of strategic HCAs, field confirmation of these stepping stone sites is more likely to be done in reaction to a conservation opportunity in the matrix.

Step 3.–Once high-integral seasonal ponds and intervening upland are identified, either within designated HCAs or in the intervening matrix, the final step is conservation action to maintain the integrity of the seasonal ponds, their surrounding upland habitat, and the connections among ponds. There are numerous conservation tactics that can be employed within this strategic conservation framework; these are discussed in the next section.

6.3. Conservation Tactics

In this section, a number of current and potential tactics for marbled salamander conservation are discussed. Tactics are listed in order of priority, from most important and useful, to most speculative.

Land acquisition/conservation restrictions

Protecting large tracts of high-quality marbled salamander habitat that can support metapopulation and evolutionary processes over the long term is the keystone of a conservation strategy. Without such concerted land protection, all other tactics will ultimately fail. Protecting these sites must consist primarily of preventing roads and development between and near seasonal ponds, especially within strategic HCA's. Lower-impact land use, such as low-intensity forestry and recreation, pose a relatively low risk to marbled salamanders. Although marbled salamander habitat would ideally be managed as natural areas, land that is permanently protected for forestry (but not agriculture) can be considered as protected marbled salamander habitat.

The most prevalent development threat in much of Massachusetts is the incursion into undeveloped blocks of subdivisions or industrial parks. These developments not only result in the direct loss of available habitat but can degrade the quality of nearby habitat, for example by disrupting local hydrologic regimes, providing sources of water pollution, and increasing meso-predator populations. Moreover, because these developments can divide previously undeveloped blocks and are likely to cut across salamander travel paths, they pose a fundamentally greater threat than the constant increase in traffic rates on existing roads associated with development along existing roads or within towns.

Given limited conservation funds, alternatives to outright purchase of conservation land are necessary. These can include conservation restrictions and land trusts. One tactic for protecting large blocks of land is building small or clustered roadside developments in conjunction with protecting large areas of back land. The Groton Land Foundation has recently used this approach to protect 60 acres that include important wetlands and surrounding land, funded by the construction of 2 houses off Old Dunstable Road. Although roadside developments do increase traffic and are undesirable for a number of conservation, aesthetic, and social reasons, they do serve to limit access to backlots for large subdivisions.

Given the rapid increase in suburban and rural development across Massachusetts, the cost of protecting land is likely to continue to increase. Our knowledge of marbled salamander's habitat requirements is sufficient to prioritize land for protection. Further research will modify and refine these priorities somewhat, but the cost of delay is much greater than the cost of errors from our incomplete knowledge. Ten years from now, many blocks of marbled salamander habitat that are now potentially viable will be lost if they are not protected now. Other more technically demanding conservation actions, such as road mitigation, are a much lower priority than protecting required habitat.

Regulation: environmental review

Current environmental review methods are of limited use in protecting marbled salamander populations. Because marbled salamanders are highly secretive and therefore extremely difficulty to find, and move considerable distances during migration and dispersal, developments that devastate populations may be undetected by Element Occurrences. As of 2006, there were only 105 Element Occurrences (EOs) for marbled salamanders in Massachusetts, and their geographic distribution reflects numerous biases. Clearly, the current EOs for marbled salamanders is inadequate as the basis for environmental regulation. Moreover, simply knowing the point location of a marbled salamander gives little insight into the area required to protect the population and metapopulation it is a member of. At the same time, historic EOs may occur in locations that can no longer support viable populations. Protecting such "ghost populations" with regulation can waste time, money, and goodwill.

Instead of relying exclusively on EOs, we suggest a two-tiered approach based upon both field knowledge (including EOs) and modeling results, as follows:

<ins>Tier 1 – Landscape-level assessment</ins>.–The first tier is to classify all undeveloped land into three categories based on the resistant kernel model results (Fig. 12): (A) all land and water falling within designated HCA's (see above); (B) all land and water falling within 1 km of an EO or any high-value seasonal pond in the intervening matrix (where the threshold for "high" value is determined through a political process); and (C) all other land and water.

<ins>Tier 2 – Site-level assessment</ins>.–The second tier is to conduct a site-level assessment in the field if the area in question falls into category A or B; category C sites would receive no environmental review. The site-level assessment would involve standardized field work to confirm the existence of a functional seasonal pond (based on biologically-based vernal pool certification standards), confirm the presence of marbled salamanders and estimate populations sizes, and assess the amount, quality and accessibility of upland forest. Assessments should weigh not only current

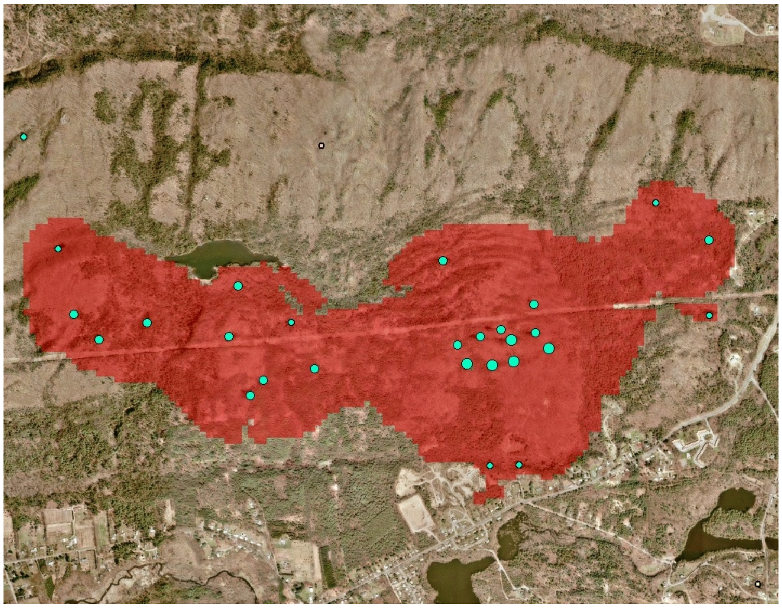

Figure 12. Example of a proposed Habitat Conservation Area (regional cluster) containing seasonal ponds and intervening uplands, classified as Category A lands (highest priority) for environmental regulatory purposes.

conditions, but the potential for long-term change or successional dynamics at breeding sites and the terrestrial landscapes in which they are embedded. Restrictions on development would be imposed based on the findings and the category of land. Category A sites are the highest priority for proactive conservation measures as well as protection by uncompromising environmental review and thus should receive the highest level of protection. Category B sites would be protected more flexibly. Populations at individual Category B sites may be unlikely to persist over the long-term, but by protecting all Category B sites, we increase the probability that some of them will persist or that they will serve as temporary stepping stones between Category A sites (HCAs). These sites should be protected by environmental review. If mitigation-based conservation permits are granted, mitigation should be focused on gaining significant protection of Category A sites as well as minimizing impacts on the Category B project sites.

Education

Public education is an important tactic. Our ability to protect marbled salamander populations depends to a great extent upon citizen-activists who are willing to help protect land, support conservation efforts, and influence their friends and neighbors, as well as a general level of appreciation by the public of conservation issues. The following messages are the most important to convey to the public:

- Marbled salamander life history strategy is key to understanding why they are fundamentally different from most pond-breeding organisms. Once people understand that marbled salamanders spend almost their entire life in the uplands, often at great distances from their breeding pond, and must periodically disperse large distances across the landscape to find new breeding sites and exchange genetic material with other populations, they can appreciate the importance of protecting not just the seasonal ponds, but the uplands adjoining the breeding ponds and the connections between them as well.
- Salamanders crossing roads should be helped across in the direction they are going, and never moved to a "better" site. If a fairly large percentage of drivers stop to help salamanders across roads, road mortality-the biggest threat to salamander metapopulations-could be reduced significantly.
- Collecting salamanders as pets or moving them is devastating to populations, and is illegal.
- Land protection requires active, caring citizens with an appreciation of the distances salamanders move, their habitat needs, and the size of tracts that are necessary for their conservation.

Public education can (and must) take many forms: education in public schools, outreach through environmental groups, public talks, stories in newspapers and other media.

Tunnels & barriers

Once marbled salamander habitat is protected, existing roads may continue to pose a threat to populations, and certainly can divide populations, preventing rescue effect and gene flow. Road mitigation measures may be an important element in protecting populations at some sites. In theory, a well-designed barrier-and-tunnel system will allow salamanders and roads to coexist. In practice, there are several problems with road mitigation structures:

- Expense – Tunnels, bridges, and salamander-proof barriers are expensive.
- Dispersed movement – Marbled salamanders seldom seem to travel in well-defined corridors, and populations are usually small and scattered. Thus, even a well-placed and well-designed tunnel will be unlikely to be used by many animals.
- Long-term maintenance – Mitigation structures must either be essentially maintenance-free, or provide permanent funding and personnel for maintenance over many decades. The Henry Street "salamander tunnels" require considerable volunteer effort each year to maintain. If maintenance and longevity are treated as afterthoughts, mitigation measures will fail.
- Lack of knowledge and experience – Road mitigation structures are not well-tested and thus must still be viewed as experimental at this point.

These considerations suggest that tunnels and curbs are inappropriate as mitigation for new development in conjunction with conservation permits. In order to provide a "net benefit" to a population, it is necessary to have confidence that the benefit is more than speculative. On the other hand, mitigation structures should be considered at strategic sites on existing roads. In particular, appropriate mitigation structures should be considered for bridge and culvert upgrade and road-widening projects. If an attempt to improve a site failed, the cost would be financial, but not a loss of a marbled salamander population.

In some extreme situations, absolute barriers rather than barrier and passage arrangements should be considered. Busy roads such as expressways and primary highways may kill 100% of the salamanders that attempt to cross. In these situations, a relatively inexpensive barrier, such as Jersey barriers, would be effective. Such barriers fragment populations, preventing gene flow and rescue effect, but they stop juvenile and adult mortality, an important short-term goal. Controlled experiments on barrier-and-tunnel designs should be conducted before future designs are approved. For less than the cost of a single permanent concrete tunnel, a 1-2 year experiment with movable plywood tunnels of varying designs on an abundant surrogate species (such as spotted salamanders) could be conducted to determine which designs work best.

Wetland modification/creation

When direct loss of seasonal ponds is unavoidable (e.g., because of economic cost-benefit), creation of artificial seasonal ponds is sometimes proposed for mitigation. While such artificial ponds have been constructed for wetland mitigation purposes, the engineering of functional seasonal ponds is exceedingly challenging and may fail to produce ponds that emulate natural hydrologic regimes more often than not. Moreover, while such artificial ponds have been successful in some cases in attracting pond-breeding amphibians, we know of NO cases where they have been successful in establishing new marbled salamander populations. Thus, mitigation wetlands for purposes of marbled salamander conservation should be used sparingly and only in the most extreme cases when no other options are available, and they should be viewed as experimental. Mitigation in the form of land protection in category A lands should be viewed as a much higher priority.

Relocation/population seeding

What if we are able to secure a large, intact tract of land in a designated HCA (category A) that has no marbled salamanders? Does it make sense to seed a new population at the site? Perhaps. The first questions that must be answered are, why are there no marbled salamander at this site? Is it really suitable marbled salamander habitat? A site that could not support an earlier population is unlikely to support a colonizing population, unless the factors that caused extirpation have been removed. For example, if the hydroperiod of the seasonal pond is too short too long to support successful reproduction on a regular basis, then no amount of seeding will establish a persistent population. If, on the other hand, the site lacks salamanders due to a chance extinction in the past, or has only recently become suitable habitat (e.g., via reforestation) and by chance has not yet been colonized, then seeding may prove effective.

Given that an appropriate site is found, seeding must be based on introducing larvae, not adults. Adults exhibit high fidelity to their established breeding site and may become "lost" if displaced to a new site. In addition, given the small size of must breeding populations in Massachusetts, removal of adults would represent an excessive loss to their source population. Larvae, on the other hand, are not particularly valuable to a population since most will die anyways, and in some circumstances could be safely harvested from a large population. Care must be taken not to disrupt the genetic structure of populations by introducing hatchlings from far away or to introduce diseases carried by animals. Population seeding efforts would require releasing large numbers of animals, and success would be far from assured. In any case, success of such efforts would not be measurable until several years had passed, since marbled salamanders generally take 3 to 4 years to mature. Population seeding should not be considered a primary element of a marbled salamander conservation plan.

7. CONCLUSION: PRIORITIES FOR CONSERVATION AND FURTHER RESEARCH

Conservation policies targeting wetlands remain focused on protecting individual breeding sites, in some cases with limited terrestrial "buffer zones" and generally without regard to landscape context. While these policies provide limited habitat protection critical in short-term conservation efforts, long-term objectives of protecting viable populations may not be met if breeding sites are effectively isolated. It thus remains critical that policies and conservation strategies outside of the policy framework evolve with our increased understanding of complex dynamics in pond-breeding amphibian populations. The scientific community should continue to advance this understanding with much-needed research at larger spatial and temporal scales (in particular to quantify rates of dispersal in intact landscape settings, the effects of modern land use practices on species-specific landscape permeability and the importance of dispersal events to local population viability) and make efforts to better communicate new findings to the practitioning conservation community.

The top priority for marbled salamander conservation is the protection of large regional clusters of highly connected seasonal ponds and the intervening uplands. These Habitat Conservation Areas (HCAs) are compatible with low-impact human uses (e.g., low intensity forestry and recreation), but they must preclude roads and development to the extent possible. Given continued development trends, without protected areas of sufficient size, efforts at marbled salamander conservation in Massachusetts can achieve little more than delaying extirpation. Results from our intensive research, the resistant kernel model, and other survey work is sufficient as an initial guide to land protection. Our approach to marbled salamander conservation will be refined as additional research is carried out. Any such work must be done in the context of protecting ecosystems and associated communities of wetland and upland species (Klemens 2000).

Future research

Future research falls into three categories: (1) modeling; (2) extensive surveys; and (3) intensive study. The ongoing UMass study is primarily an intensive study that has provided many of the data necessary for both direct conservation efforts and for modeling. Several important questions remain that can only be answered by further intensive work. Extensive surveys for the presence and abundance of marbled salamanders will be necessary to help guide site-specific conservation decisions. Ideally, modeling and surveys will be done in concert, with results from modeling guiding surveys, which in turn provide refinements in modeling. The resistant kernel model, based upon our intensive work, is a first step in this process. We plan to use model results to guide surveys during the upcoming field seasons.

- <u>Modeling</u>.--The resistant kernel model is a useful start for identifying sites that are likely to support viable salamander populations. However, it has several limitations (discussed in detail in Compton et al. 2007). Briefly, it is based on photo-interpreted “potential” vernal pools with known errors of omission and commission. It is static, i.e., based on a current snapshot of the landscape and thus does not account for land history or future changes in land use. It ignores the variability among seasonal ponds in breeding habitat quality. It depends on several poorly known parameters associated with the resistance of various land uses and road types. Finally, because it does not directly address population viability, the resistant kernel model cannot answer the most important conservation questions: What is the relative viability of populations at each site or cluster of sites? How will this change if land parcels are protected, developed, or an underpass added?

  Some of these issues are being addressed in a spatially-explicit population model for marbled salamanders being developed at Umass. This model uses empirical data from the UMass intensive study, as well as published literature, along with GIS data to explicitly model metapopulation dynamics in a yearly time step over decades or centuries. Like a traditional PVA, this model simulates demographic processes (using a stochastic simulation, allowing for variance in vital rates). Unlike a traditional PVA, this model explicitly incorporates the composition and spatial configuration of the landscape. Thus, the spatial structure of populations are incorporated into the demographic model, allowing for interactions among subpopulations, such as metapopulation dynamics and the rescue effect. This model will provide several useful results:

- The ability to rank both known and unknown populations by likely viability
- Identify new sites likely to have viable salamander populations
- The ability to evaluate pond clusters of alternative sizes and configuration by likely viability
- Exploration of alternative scenarios, such as changes in forest management practices, increases in road density, or the construction of road mitigation structures (e.g. tunnels)
- Sensitivity analysis of possible management actions (e.g. road mitigation structures vs. road closings).

The salamander PVA model has been fully designed and software has been written and tested. Simulation experiments are currently underway.

- Extensive surveys.–Field surveys are needed to verify the existence of marbled salamander populations in areas that seem to provide habitat for viable populations (e.g., areas ranked high in the resistant kernel model). Surveys would be most useful if based on modeling - there is little reason, for instance, to document "ghost populations" that are not viable, while ignoring sites more likely to support populations. Modeling can help direct surveys to areas most likely to contain viable populations of salamanders.

  Surveys can take two forms: visual walk-throughs or intensive trapping. Visual surveys are most effective during a few weeks in early spring, say April and early May, when the marbled salamander are active, reasonably well-developed, and are the only larval amphibian in the ponds (i.e., before the spring-breeding amphibian larvae emerge). Larval surveys are most effective if done at night, as the larvae are usually inactive and hidden in the substrate during daylight hours. Use of a strong flashlight during slow walks through the pond basin usually results in observations of larvae if they are present in sufficient numbers. The relative abundance of larvae can provide an indication of the breeding effort that year, but are generally unreliable as indicators of local population size because of the numerous factors that can affect reproductive success in any given year and pond.

  Intensive pitfall trapping of juveniles and adults entering and leaving the pond is a more effective way to survey ponds for marbled salamanders, although it is far from efficient. Trapping can be done from late May through October. Juveniles generally emerge from late May through July and adults migrate to and from the ponds between mid-August and October. To be effective, drift fencing must be installed around the perimeter of the pond with pitfall traps place at intervals on both sides of the fence. Given the effort required to install and maintain drift fence arrays around ponds, surveys with the goal of determining population size or relative abundance are generally impractical for extensive surveys. The effort required to gain a reliable estimate of population size should be considered an intensive study, and the ability to make inferences to other sites is low.

- Intensive research.–Several questions remain for future intensive studies:
    - Breeding habitat requirements. While we understand the requirement for seasonal ponds, very little is known about the characteristics of seasonal ponds that affect their habitat suitability for marbled salamanders. We have observed a strong relationship between spring hydroperiod and reproductive success in our intensive study of 14 ponds, but this relationship needs to be confirmed with a much larger sample over a broader geographic range. Other factors beside hydroperiod need to be examined as well.
    - The life history of juveniles after they emerge from the natal pond is mostly unknown, including movement ecology and habitat selection. Given the important role of juvenile dispersal in the metapopulation, it is imperative to gain a better understanding of environmental factors in the uplands affective dispersal behavior and success.
    - Habitat selection and movement ecology of adults during the nonbreeding season. Adults spend 95% of their life in the uplands outside of the breeding season, yet almost nothing is know about habitat requirements and home range in the uplands.
    - Rates and sources of mortality of larvae, juveniles and adults. No systematic study of mortality sources has been done. Although adult survival is a more important demographic parameter, decreased survival of eggs and larvae to predation could also limit population growth.
    - Mitigation structures-tunnels and barriers. Although salamander tunnels have been installed for use in a few locations, these have been "uncontrolled" experiments. Controlled experiments with surrogate species (such as spotted salamanders) to determine the elements of an effective tunnel and barrier system.

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8. LITERATURE CITED

Alford, R. A., and Richards, S. J. 1999. Global amphibian declines: A problem in applied ecology. - Annual Review of Ecology and Systematics 30:133-165.

Babbitt, K. J. 2003. Patterns of larval amphibian distribution along a wetland hydroperiod gradient. - Canadian Journal of Zoology 81:1539-1552

Berven, K. A. 1990. Factors affecting population fluctuations in larval and adult stages of the wood frog, Rana sylvatica. Ecology 71:1599-1608.

Berven, K. A., and T. A. Grudzien. 1990. Dispersal in the wood frog (Rana sylvatica) - implications for genetic population structure. Evolution 44:2047-2056.

Bishop, S. C. 1941. Salamanders of New York. New York State Museum Bulletin 324:1-365.

Bol, L. 2006. Massachusetts Forestry Conservation Management Practices for MESA-Listed Mole Salamanders, Natural Heritage and Endangered Species Program, Westborough, MA.

Breden, F. 1987. The effect of post-metamorphic dispersal on the population genetic structure of Fowler's toad, Bufo woodhousei fowleri. Copeia 1987:386-395.

Brooks, R. T., and Hayashi, M. 2002. Depth-area-volume and hydroperiod relationships of ephemeral (vernal) forest pools in southern New England. - Wetlands 22:247-255.

Brooks, R. T. 2000. Annual and seasonal variation and the effects of hydroperiod on benthic macroinvertebrates of seasonal forest ("vernal") ponds in central Massachusetts, USA. Wetlands 20:707-715.

Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography - effect of immigration on extinction. Ecology 58:445-449.

Buonaccorsi, J. P., Elkinton, J. S., Evans, S. R., and Liebhold, A. M. 2001. Measuring and testing for spatial synchrony. - Ecology 82:1668-1679.

Burne, M. R. 2001. Massachusetts aerial photo survey of potential vernal pools. Natural Heritage and Endangered Species Program, Massachusetts Division of Fisheries and Wildlife, Westborough, Massachusetts.

Calabrese, J. M., and W. F. Fagan. 2004. A comparison-shopper’s guide to connectivity metrics. Frontiers in Ecology and the Environment 2:529–536.

Colburn, E. A. 2004. Vernal pools: natural history and conservation. McDonald and Woodward, Blacksburg, Virginia.

Compton, B.W., K. McGarigal, S.A. Cushman, and L.R. Gamble. 2007. A resistant-kernel model of connectivity for amphibians that breed in vernal pools. Conservation Biology 21(3):788-799.

Cortwright, S. A., and Nelson, C. E. 1990. An examination of multiple factors affecting community structure in an aquatic amphibian community. - Oecologia 83:123-131.

Daszak, P., Cunningham, A. A., and Hyatt, A. D. 2003. Infectious disease and amphibian population declines. - Diversity and Distributions 9:141-150.

DeGraaf, R.M. and M. Yamasaki. 2001. New England Wildlife: Habitat, Natural History, and Distribution. University Press of New England, Hanover, NH.

deMaynadier, P. G., and M. L. Hunter. 1999. Forest canopy closure and juvenile emigration by pool-breeding amphibians in Maine. Journal of Wildlife Management 63:441–450.

Faccio, S. D. 2003. Postbreeding emigration and habitat use by Jefferson and spotted salamanders in Vermont. Journal of Herpetology 37:479–489.

Findlay, C. S., and J. Bourdages. 2000. Response time of wetland biodiversity to road construction on adjacent lands. Conservation Biology 14:86–94.

Flageole, S., and R. Leclair. 1992. Demography of a salamander (Ambystoma maculatum) population studied by skeletochronology. Canadian Journal of Zoology 70:740–749.

Frankel, O. H., and M. E. Soule 1981. Conservation and evolution. Cambridge University Press, Cambridge, England.

Gamble, L. R. 2004. Landscape-level population structure and local variability in marbled salamanders (Ambystoma opacum) of western Massachusetts: applied lessons from metapopulation theory. M.S. thesis. Department of Natural Resources Conservation, University of Massachusetts, Amherst, Massachusetts.

Gamble, L.R., K. McGarigal, D.B. Sigourney, and B.C. Timm. (Submitted). Survival and breeding frequency in Marbled Salamanders (Ambystoma opacum): implications for spatio-temporal population dynamics. Copeia.

Gamble, L. R., K. McGarigal, C. L. Jenkins, and B. C. Timm. 2006. Limitations of regulated “buffer zones” for the conservation of marbled salamanders. Wetlands 26(2):298-306.

Gamble, L.R., K. McGarigal, and B.W. Compton. 2007. Fidelity and dispersal in the pond-breeding amphibian, *Ambystoma opacum*: Implications for spatio-temporal population dynamics and conservation. Biological Conservation 139:247-257.

Gamble, L. R., S. Ravela, and K. McGarigal. 2008. Multi-scale features for identifying individuals in large biological databases: an application of pattern recognition technology to the marbled salamander Ambystoma opacum. Journal of Applied Ecology 45:170–180.

Gibbs, J. P. 1993. Importance of small wetlands for the persistence of local-populations ofwetland-associated animals.Wetlands 13:25–31.

Gibbs, J. P., and W. G. Shriver. 2005. Can road mortality limit populations of pool-breeding amphibians? Wetlands Ecology and Management 13:281–289.

Gill, D. E. 1978. Metapopulation ecology of red-spotted newt, Notophthalmus viridescens (Rafinesque). - Ecological Monographs 48:145-166.

Gill, D. E. 1978. Effective population size and interdemic migration rates in a metapopulation of the red-spotted newt, Notophthalmus viridescens (Rafinesque). Evolution 32:839-849.

Gill, D. E. 1979. Density dependence and homing behavior in adult red-spotted newt Notophthalmus viridescens (Rafinesque). Ecology 60:800-813.

Gotelli, N. J. 1998. A primer of ecology, second edition. Sinauer Associates.

Green, D. E., Converse, K. A., and Schrader, A. K. 2002. Epizootiology of sixty-four amphibian morbidity and mortality events in the USA, 1996-2001. - Annals of the New York Academy of Sciences 969:323-339.

Guerry, A. D., and M. L. J. Hunter. 2002. Amphibian distributions in a landscape of forests and agriculture: an examination of landscape composition and configuration. Conservation Biology 16:745–754.

Hall, B., G. Motzkin, D. R. Foster, M. Syfert, and J. Burk. 2002. Three hundred years of forest and land-use change in Massachusetts, USA. Journal of Biogeography 29:1319–1335.

Halverson, M. A., Skelly, D. K., Kiesecker, J. M., and Freidenburg, L. K. 2003. Forest mediated light regime linked to amphibian distribution and performance. - Oecologia 134:360-364.

Hanski, I. 1997. Metapopulation dynamics: from concepts and observations to predictive models. - In Hanski, I. and Gilpin, M. E. (ed.), Metapopulation biology: ecology, genetics, and evolution. Academic Press, pp.69-91.

Hanski, I., and M. Gilpin. 1991. Metapopulation dynamics: brief history and conceptual domain. Biological Journal of the Linnean Society 42:3–16.

Hanski, I., and D. Simberloff. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. Pages 5-26 in I. Hanski, and M. E. Gilpin, editors.

Metapopulation biology: ecology, genetics, and evolution. Academic Press, San Diego, California.

Holyoak, M. and Ray, C. R. 1999. A roadmap for metapopulation research. - Ecology Letters 2:273-275.

Homan, R. N., B. S.Windmiller, and J. M. Reed. 2004. Crtitical thresholds associated with habitat loss for two vernal pool-breeding amphibians. Ecological Applications 14:1547–1553.

Husting, E. L. 1965. Survival and breeding structure in a population of Ambystoma maculatum. - Copeia 1965(3):352-362.

Jenkins, C. L., K. McGarigal, and B. C. Timm. 2006. Orientation of movements and habitat selection in a spatially-structured population of marbled salamanders (*Ambystoma opacum*). J. of Herpetology 40(2):240-248.

Jenkins, C. L., K. McGarigal, and L. Gamble. 2002. A comparison of aquatic surveying techniques used to sample *Ambystoma opacum* Larvae. Herpetological Review 33:33-35.

Jenkins, C. L., K. McGarigal, and L. Gamble. 2003. Comparative effectiveness of two trapping techniques for surveying the abundance and diversity of forest floor vertebrates along drift fence arrays. Herpetological Review 34:39-42.

Keitt, T. H., D. L. Urban, and B. T. Milne. 1997. Detecting critical scales in fragmented landscapes. Conservation Ecology 1(1): http://www.consecol.org/vol1/iss1/art4/.

Kenney, L. P., and M. R. Burne. 2000. A field guide to the animals of vernal pools. Massachusetts Division of Fisheries and Wildlife, Natural Heritage and Endangered Species Program and Vernal Pool Association, Westborough, Massachusetts.

Kiesecker, J. M., Blaustein, A. R., and Belden, L. K. 2001. Complex causes of amphibian population declines. - Nature 410:681-684.

Koenig, W. D. 1999. Spatial autocorrelation of ecological phenomena. - Trends in Ecology & Evolution 14:22-26.

Lefkovitch, L. P. 1965. The study of population growth in organisms grouped by stages. - Biometrics 21:1-18.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America 15:237-240.

Levins, R. 1970. Extinction. Pages 75-107. in M. Gerstenhaber, editor. Some mathematical problems in biology. American Mathematical Society, Providence, Rhode Island.

Madison, D. M. 1997. The emigration of radio-implanted spotted salamanders, Ambystoma maculatum. Journal of Herpetology 31:542-551.

Madison, D. M., and L. Farrand. 1998. Habitat use during breeding and emigration in radio-implanted tiger salamanders, Ambystoma tigrinum. Copeia 402–410.

Marsh, D. M., Fegraus, E. H., and Harrison, S. 1999. Effects of breeding pond isolation on the spatial and temporal dynamics of pond use by the tungara frog, Physalaemus pustulosus. - Journal of Animal Ecology 68:804-814.

Marsh, D. M., G. S. Milam, N. R. Gorham, and N. G. Beckman. 2005. Forest roads as partial barriers to terrestrial salamander movement. Conservation Biology 19:2004-2008.

Marsh, D. M., and P. C. Trenham. 2001. Metapopulation dynamics and amphibian conservation. Conservation Biology 15:40-49.

McCarthy, M. A., and K. M. Parris. 2004. Clarifying the effect of toe clipping on frogs with Bayesian statistics. Journal of Applied Ecology 41:780-786.

McDonough-Haughley, C., and P.W. C. Paton. 2007. Spotted salamander dispersal across a forested landscape fragmented by a golf course. Journal of Wildlife Management 71: in press.

Mills, L. S., and F. W. Allendorf. 1996. The one-migrant-per-generation rule in conservation and management. Conservation Biology10:1509–1518.

Moran, P. A. P. 1953. The statistical analysis of the Canadian lynx cycle. II. Synchronization and meteorology. - Australian Journal of Zoology 1:291-298.

Noble, G. K., and Brady, M. K. 1933. Observations on the life history of the marbled salamander, Ambystoma opacum Gravenhorst. - Zoologica 11:89-132.

Noble, G. K., and M. K. Brady. 1933. Observations on the life history of the marbled salamander, Ambystoma opacum Gravenhorst. Zoologica 11:89-132.

Ott, J. A., and D. E. Scott. 1999. Effects of toe-clipping and PIT-tagging on growth and survival in metamorphic Ambystoma opacum. Journal of Herpetology 33:344-348.

Paton, P. W. C., and Crouch, W. B. 2002. Using the phenology of pond-breeding amphibians to develop conservation strategies. - Conservation Biology 16:194-204.

Pechmann, J. H. K., R. A. Estes, D. E. Scott, and J. W. Gibbons. 2001. Amphibian colonization and use of ponds created for trial mitigation of wetland loss. Wetlands 21:93-111.

Pechmann, J. H., D. E. Scott, R. D. Semlitsch, J. P. Caldwell, L. J. Vitt, and J. W. Gibbons.

1991. Declining amphibian populations: the problem of separating human impacts from natural fluctuations. Science 253:892–895.

Petranka, J. G. 1998. Salamanders of the United States and Canada. Smithsonian Institution Press, Washington, DC.

Petranka, J. W., and Petranka, J. G. 1981. On the evolution of nest site selection in the marbled salamander, Ambystoma opacum. - Copeia 2:387-391.

Petranka, J. W., C. K. Smith, and A. F. Scott. 2004. Identifying the minimal demographic unit for monitoring pond-breeding amphibians. Ecological Applications 14:1065-1078.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. - American Naturalist 132:652-661.

Pyke, C. R. 2005. Assessing suitability for conservation action: prioritizing interpond linkages for the California tiger salamander. Conservation Biology 19:492–503.

Ray, N., A. Lehmann, and P. Joly. 2002. Modeling spatial distribution of amphibian populations: a GIS approach based on habitat matrix permeability. Biodiversity and Conservation 11:2143–2165.

Regosin, J. V., B. S. Windmiller, and J. M. Reed. 2003. Influence of abundance of small-mammal burrows and conspecifics on the density and distribution of spotted salamanders (Ambystoma maculatum) in terrestrial habitats. Canadian Journal of Zoology 81:596–605.

Ricketts, T. H. 2001. The matrix matters: effective isolation in fragmented landscapes. The American Naturalist 158:87–99.

Rosenberg, D. K., B. R. Noon, J. W. Megahan, and E. C. Meslow. 1998. Compensatory behavior of Ensatina eschscholtzii in biological corridors: a field experiment. Canadian Journal of Zoology 76:117-133.

Rothermel, B. B., and R. D. Semlitsch. 2002. An experimental investigation of landscape resistance of forest versus old-field habitats to emigrating juvenile amphibians. Conservation Biology 16:1324–1332.

Rustigian, H. L., M. V. Santelmann, and N. H. Schumaker. 2003. Assessing the potential impacts of alternative landscape designs on amphibian population dynamics. Landscape Ecology 18:65–81.

Scott, D. E. 1994. The effect of larval density on adult demographic traits in Ambystoma opacum. - Ecology 75:1383-1396.

Scott, D. E. 1990. Effects of larval density in Ambystoma opacum - an experiment in large-scale field enclosures. - Ecology 71:296-306.

Semlitsch, R. D. 1998. Biological delineation of terrestrial buffer zones for pond-breeding salamanders. Conservation Biology 12:1113–1119.

Semlitsch, R. D. 2000. Principles for management of aquatic-breeding amphibians. - Journal of Wildlife Management 64:615-631.

Semlitsch, R. D. 2002. Critical elements for biologically based recovery plans of aquatic-breeding amphibians. Conservation Biology 16:619-629.

Semlitsch, R. D., editor. 2003. Amphibian conservation. Smithsonian Books, Washington, D.C.

Semlitsch, R. D., and J. R. Bodie. 1998. Are small, isolated wetlands expendable? Conservation Biology 12:1129–1133.

Semlitsch, R. D., D. E. Scott, J. H. K. Pechmann, and J. W. Gibbons. 1996. Structure and dynamics of an amphibian community: evidence from a 16-year study of a natural pond. Pages 217-248 in M. L. Cody, and J. A. Smallwood, editors. Long-term studies of vertebrate communities. Academic Press, San Diego, California.

Shoop, C. R., and Doty, T. L. 1972. Migratory orientation by marbled salamanders (Ambystoma opacum) near a breeding area. - Behavioral Biology 7:131-136.

Silverman, B.W. 1986. Density estimation for statistics and data analysis. Chapman & Hall, London.

Sinsch, U. 1992. Structure and dynamic of a natterjack toad metapopulation (Bufo calamita). Oecologia 90:489-499.

Sjogren, P. 1991. Extinction and isolation gradients in metapopulations - the case of the pool frog (Rana lessonae). - Biological Journal of the Linnean Society 42:135-147.

Skelly, D. K., Freidenburg, L. K., and Kiesecker, J. M. 2002. Forest canopy and the performance of larval amphibians. - Ecology 83:983-992.

Skelly, D. K., E. E. Werner, and S. A. Cortwright. 1999. Long-term distributional dynamics of a Michigan amphibian assemblage. Ecology 80:2326–2337.

Smith, M. A., and D. M. Green. 2005. Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations? Ecography 28:110-128.

Smyers, S. D., Rubbo, M. J., Townsend, V. R., and Swart, C. C. 2002. Intra- and interspecific characterizations of burrow use and defense by juvenile ambystomatid salamanders. - Herpetologica 58:422-429.

Snodgrass, J. W., Bryan, A. L., and Burger, J. 2000. Development of expectations of larval amphibian assemblage structure in southeastern depression wetlands. - Ecological Applications 10:1219-1229.

Snodgrass, J. W., M. J. Komoroski, A. L. Bryan, and J. Burger. 2000. Relationships among isolated wetland size, hydroperiod, and amphibian species richness: implications for wetland regulations. Conservation Biology 14:414–419.

Stacey, P. B., M. L. Taper, and V. A. Johnson. 1997. Migration within metapopulations: the impact upon local population dynamics. Pages 267-291 in I. Hanski, and M. E. Gilpin, editors. Metapopulation biology: ecology, genetics, and evolution. Academic Press, San Diego, California.

Stenhouse, S. L., Hairston, N. G., and Cobey, A. E. 1983. Predation and competition in Ambystoma larvae - field and laboratory experiments. - Journal of Herpetology 17:210-2220.

Thomas, C. D. and Kunin, W. E. 1999. The spatial structure of populations. Journal of Animal Ecology 68:647-657.

Timm, B.C., and K. McGarigal. (Submitted). Resource partitioning between subadult Fowler's toads (*Bufo fowleri*) and Eastern spadefoots (*Scaphiopus h. holbrookii*) at Cape Cod National Seashore, USA. Copeia.

Timm, B. C., K. McGarigal, and B. W. Compton. 2007a. Timing of large movement events of pond-breeding amphibians in western Massachusetts, USA. Biological Conservation 136:442-454.

Timm, B. C., K. McGarigal, and L. R. Gamble. 2007b. Emigration timing of juvenile pond-breeding amphibians in western Massachusetts. Journal of Herpetology 41(2):243-250.

Timm, B.C., K. McGarigal, and C.L. Jenkins. 2007c. Emigration orientation of juvenile pond-breeding amphibians in western Massachusetts. Copeia 3:685–698.

Trenham, P. C., W. D. Koenig, M. J. Mossman, S. L. Stark, and L. A. Jagger. 2003. Regional dynamics of wetland-breeding frogs and toads: turnover and synchrony. Ecological Applications 13:1522-1532.

Trenham, P. C., W. D. Koenig, and H. B. Shaffer. 2001. Spatially autocorrelated demography and interpond dispersal in the salamander Ambystoma californiense. Ecology 82:3519–3530.

Urban, D., and T. Keitt. 2001. Landscape connectivity: a graph-theoretic perspective. Ecology 82:1205–1218.

Vanbuskirk, J. 1988. Interactive effects of dragonfly predation in experimental pond communities. - Ecology 69:857-867.

Wellborn, G. A., Skelly, D. K., and Werner, E. E. 1996. Mechanisms creating community structure across a freshwater habitat gradient. - Annual Review of Ecology and Systematics 27:337-363.

Whitford, W. G., and A. Vinegar. 1966. Homing, survivorship, and overwintering of larvae of spotted salamanders, Ambystoma maculatum. Copeia 1966:515–519.

Wilbur, H. M. 1987. Regulation of structure in complex systems - experimental temporary pond communities. - Ecology 68:1437-1452.

Wilbur, H. M. 1997. Experimental ecology of food webs: complex systems in temporary ponds - The Robert H. MacArthur Award Lecture - Presented 31 July 1995 Snowbird, Utah. - Ecology 78:2279-2302.

Wilbur, H. M., and Fauth, J. E. 1990. Experimental aquatic food webs - interactions between 2 predators and 2 prey. - American Naturalist 135:176-204.

Williams, P. K. 1973. Seasonal movements and population dynamics of four sympatric mole salamanders, genus Ambystoma. Doctoral dissertation. Indiana University, Bloomington, Indiana.

Windmiller, B. S. 1996. The pond, the forest, and the city: spotted salamander ecology and conservation in a human-dominated landscape. Dissertation. Tufts University.

Wojnowski, D. 2000. Hurricane Floyd's effect on the nesting success of the marbled salamander (Ambystoma opacum) at Falls Lake, North Carolina. - Journal of the Elisha Mitchell Scientific Society 116:171-175.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168.