LIMITATIONS OF REGULATED ''BUFFER ZONES'' FOR THE CONSERVATION OF MARBLED SALAMANDERS

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Abstract: Most amphibians that breed in seasonal wetlands are predominantly terrestrial animals that require ''upland'' habitats for the majority of their life cycles. However, wetland regulations aimed partially at protecting wildlife values are often limited to the wetland basins and small terrestrial ''buffer zones'' that typically extend 30 m or less from the wetland edge. In this study, we assessed whether a common buffer zone (i.e., 30 m) is sufficient for the conservation of marbled salamanders (*Ambystoma opacum*). We installed and monitored two concentric and continuous drift fence arrays (3 m and 30 m from the pond margin) around each of three seasonal ponds in western Massachusetts, USA. We quantified the numbers and percentages of breeding adults and emerging juvenile salamanders that immigrated from and/or emigrated beyond the 30-m fences. In addition, we recorded incidental year-of-emergence captures of juveniles at more distant drift fences that were in place for a broader study. Of the breeding adults captured immigrating to the basins at 3-m fences, 84–96% were first captured at 30-m fences, and corrections for capture probabilities suggested that nearly 100% of these individuals originated beyond 30 m from their breeding sites. Of the newly emerging juveniles captured emigrating from the basins at 3-m fences, 58–85% were subsequently captured at 30-m fences and 284 juvenile captures were recorded at distances between 111 and 1,230 m (median = 269.2 m) from natal ponds. Our findings highlight the dramatic limitations of existing wetland regulations with regard to upland habitat use by mole salamanders (family Ambystomatidae) and the need to approach conservation of these animals both at broader scales and with more comprehensive and innovative strategies.

Key Words: amphibian, marbled salamander, *Ambystoma*, seasonal wetland, ephemeral wetland, vernal pool, buffer zone, wetland regulation, terrestrial habitat, dispersal

INTRODUCTION

Seasonal wetlands and the terrestrial communities surrounding them provide critical habitats for many amphibians (Dodd 1992, Semlitsch 1998, Snodgrass et al. 2000, Comer et al. 2005). In the northeastern USA, five species of ambystomatid salamanders and two anurans are known to rely almost exclusively on seasonal wetlands for breeding, and numerous other amphibians use them facultatively (Hunter et al. 1999, Colburn 2004). As many as 27 amphibian species were associated with a Carolina bay wetland in the southeastern USA (Semlitsch et al. 1996), of which at least 10 may be considered seasonal wetland obligates. Seasonal wetlands may also play vital roles for amphibians in a broader landscape context, acting as ''stepping stones'' between otherwise isolated breeding sites and/or contributing to broad-scale population dynamics (e.g., Gill 1978, Sjogren 1991, Skelly et al. 1999).

Despite much research documenting the extensive use of terrestrial habitats (Semlitsch 1998, Semlitsch and Bodie 2003), many pond-breeding amphibians are still widely perceived as being primarily aquatic. This is reflected in state and federal wetland regulations that offer little or no protection to terrestrial (i.e., ''upland'') communities adjacent to wetlands (Calhoun and Klemens 2002, Burne and Griffin 2005). For example, in the state of New York, no regulatory protection is afforded to non-wetland areas surrounding vernal pools except under endangered species legislation (Calhoun and Klemens 2002). In Massachusetts,

where some of the strictest state wetland standards apply, a 100-foot (30 m) "buffer zone" is protected around vernal pools in cases where they meet specific criteria for size, volume, and significance to wildlife (Massachusetts Wetlands Protection Act. MGL c.131 s.40; also see Griffin 1989). In the strictest case, the performance standard is for no adverse effects to wildlife from activities in this zone; however, this zone is not a "no build" zone, and habitat alterations are commonly permitted.

Most studies that quantified migratory distances in mole salamanders (family Ambystomatidae) have involved tracking a few individuals with implanted radioactive wire tags or small radio transmitters. Semlitsch (1998) estimated that adult *Ambystoma* (five species grouped) moved an average of 125 m from breeding ponds and that a 164 m "critical life zone" would be necessary to protect >95% of most populations. In telemetry studies, Madison (1997) and Faccio (2003) found that adult spotted salamanders (*Ambystoma maculatum* Shaw) and Jefferson salamanders (*Ambystoma jeffersonianum* Green) moved up to 219 m from breeding ponds and spent the majority of the year in and at the entrances to small mammal burrows. Related studies of upland habitat use indicate that several ambystomatids are positively associated with percent forest cover at scales exceeding 200 m (Guerry and Hunter 2002, Homan et al. 2004, Herrmann et al. 2005) and negatively associated with roadsides (deMaynadier and Hunter 2000), road densities (Porej et al. 2004), and forest clearcuts (deMaynadier and Hunter 1999). Despite this growing body of information, no studies have directly investigated cumulative movement and habitat use at the population level (i.e., all individuals and age classes) to evaluate the possible effectiveness or limitations of explicitly defined "buffer zones" as described in existing regulations or guidelines.

As part of a larger investigation into the metapopulation dynamics of the marbled salamander (*Ambystoma opacum* Gravenhorst), we directly measured the percentages of adult and juvenile salamanders that would be encompassed by a commonly regulated zone extending approximately 30 m beyond the high-water line at each of three breeding ponds. We accomplished this through the use of two continuous, concentric drift fences surrounding each of three ponds. In addition, the presence of numerous other drift fences installed for the broader study allowed us to report a range of distances moved by marked juveniles during their years of emergence. We present these findings in both a biological and regulatory context and discuss some alternative, more proactive approaches to the conservation of pond-breeding amphibians.

METHODS

Study Organism

The marbled salamander is a predominantly terrestrial amphibian. Its geographic range extends across the eastern half of the United States from southern New England to eastern Texas (Petranka 1998). This species is considered a seasonal-pond "obligate" species, relying on fish-free aquatic habitats for egg deposition and larval development. Unlike most pond-breeding amphibians, adult marbled salamanders migrate to their breeding sites in the late summer and early fall when the ponds are receded or dry, courting and laying eggs terrestrially (Petranka 1998). The eggs hatch into aquatic larvae shortly after inundation, and the larvae overwinter in the ponds. In spring or early summer, marbled salamanders metamorphose and emerge from ponds on rainy nights to move into surrounding woodlands, where they spend most of the remainder of their life cycle.

Field Methods

Our study area spanned approximately 300 ha of contiguous mixed-deciduous hardwood forests on the Holyoke Range in western Massachusetts. A total of 14 seasonal ponds were identified in this area, ranging in size at high water from 0.03 to 0.35 ha. To monitor marbled salamander movements, we completely encircled all seasonal ponds with continuous drift fences and pitfall traps. These drift fences were made from 35-cm aluminum flashing and installed approximately 3 m beyond the estimated high-water line of each pond (see Jenkins et al. 2003 for details on fence construction). We buried pitfall traps (#10 tin cans) along both sides of each fence at 10-m intervals. We checked traps daily from May through November of each year from 1999 to 2003, fully encompassing the emergence and breeding periods of marbled salamanders, and released animals on the opposite sides of the fences. Juveniles received a double toe-clip cohort mark (Ott and Scott 1999) associating them with their pond of origin. Adults were measured, sexed, and digitally photographed for individual identification. For one year only (pre-breeding 1999 to post-emergence 2000), we placed and monitored a second concentric drift fence around each of the three ponds supporting the largest breeding populations. These three fences were made from pre-staked silt fence and were installed 30 m beyond the high-water line with pitfall traps identical to those at 3-m fences. During the off-season, all traps were closed and doors were opened along all fences to allow passage of non-target animals.

Data Analysis—Local Captures

We identified individual captures and recaptures of adult marbled salamanders at the three ponds with 30-m fences by manually matching digital photographs of their dorsal patterns. We then indexed the matched capture records into a list of all unique individuals and their capture histories. To minimize errors in this procedure, a second observer independently repeated this process for each pond and results were compared and resolved.

For each pond with a 30-m fence, we determined the minimum number and/or percentage of adult marbled salamanders (males and females) that a) immigrated from beyond the 30-m fence prior to capture (during immigration) at the 3-m fence and b) emigrated beyond the 30-m fence after capture (during emigration) at the 3-m fence. In addition, we estimated the number and percentage of adults that approached but did not enter each basin (captured at 30-m fences but did not traverse 3-m fences). For newly emerging juveniles, we determined the minimum number and percentage of individuals that emigrated beyond the 30-m fence. In the case of juveniles and adults last captured emigrating at 3-m fences, a class of ''unknown fate'' animals not captured at 30-m fences included not only those that stayed within the proximate upland zone, but also those that 1) passed the 30-m fences undetected, 2) died before reaching the 30-m fence, and/or 3) sought temporary refuge close to basins but possibly moved farther away in a later, unmonitored time period.

The interpretation of capture-recapture data for breeding amphibians can be complicated by partial observability (some animals skip breeding seasons and therefore are not subject to capture) and imperfect detection probabilities (drift fences do not capture all breeding animals; Bailey et al. 2004). Since our goals were not to estimate *total* population sizes or demographic rates, partial observability was not problematic. However, we calculated detection probabilities for observable (i.e., migrating) individuals at the three ponds with 30-m fences to assess the potential magnitude of bias in our raw capture data. Specifically, we calculated detection probability as the number of individuals *observed* crossing a fence divided by the total number *known* (or reasonably assumed) to traverse the fence (see Appendix 1). Except where explicitly noted in the text, we present unadjusted capture numbers and percentages but occasionally refer to the detection probabilities in their interpretation.

Data Analyses—Interpond Captures

Through the duration of the study, numerous instances occurred in which juveniles originally marked at their natal pond were subsequently captured entering or traversing another fenced basin during their year of emergence. We would not label these as ''true'' dispersal events unless these individuals were captured entering other basins as breeding adults. Rather, these individuals may simply be seeking terrestrial refugia and incidentally encountering other pond basins in the process. Nonetheless, this information is useful and demonstrates the potential for movement (and possibly dispersal) at various distances in this age class. We report the number of capture events recorded in each 100-m distance interval (0–1300 m) among our study ponds, omitting captures at the 30-m fences since they were only present at three ponds during one year of the study. Since individuals in this age class remain indistinguishable from dorsal patterns, repeated captures could not be identified; however, a 50% conversion (assuming two captures of each individual at a new basin—one entering and one departing) provides a conservative estimate of the number of individuals captured in any given distance class.

RESULTS

Total Captures

At the three ponds with 30-m fences in breeding year 1999, we recorded a total of 1,062 capture events of 366 adult marbled salamanders (172, 73, and 121 adult individuals at ponds 4, 5, and 12; Table 1) with male:female sex ratios ranging from 2.7 to 1.1 (ponds 4 and 5). Total captures of juveniles at 3-m fences were 1418, 360, and 504 at the same three ponds, respectively.

Upland Habitat Use by Adults

The vast majority of adult salamanders immigrated from beyond the 30-m fences, and most of these individuals emigrated from this area shortly after the breeding period. Specifically, 93%, 96%, and 84% of adults that entered the pond basins were first captured at the 30-m fences at ponds 4, 5, and 12, respectively (Figure 1A). Of the adults captured emigrating from the basins at 3-m fences, 60–79% were subsequently captured at the 30-m fences. Approximately 10–25% of adults captured at the 30-m fences while approaching the pond basins were not subsequently captured at the 3-m fences. These individuals were almost all males (>87%) at ponds 4 and 12 but included many females (44%) at pond 5. Small sample sizes limited further exploration, but no striking differences in size (snout-vent length or weight) or timing of capture at 30-m fences occurred between groups of individuals that did and did not enter pond basins.

Table 1. Summary of 1999 capture events by pond, fence (3-m or 30-m), direction of movement, and sex. Numbers in parentheses indicate captured individuals with a damaged or missing image file that consequently could not be included in individual-level capture histories.

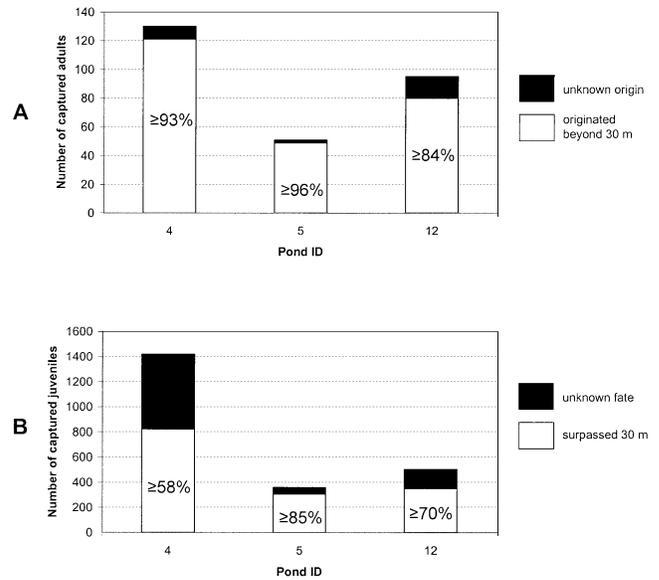| Direction	Fence	Pond 4 ♂	Pond 4 ♀	Pond 4 Juveniles	Pond 5 ♂	Pond 5 ♀	Pond 5 Juveniles	Pond 12 ♂	Pond 12 ♀	Pond 12 Juveniles	Total Adult Captures
Immig.	30-m	116(+3)	44(+1)	—	39	39	—	67(+7)	29	—	345
Immig.	3-m	94	38	—	28(+1)	31	—	65(+4)	32	—	293
Emig.	3-m	46(+2)	19	1,418	20	16	360	62(+1)	30	504	196
Emig.	30-m	65	25	1,109	22	25	349		22	459	229
Total capture events		321(+5)	126(+1)	2,527	109(+1)	111	709	264(+11)	113	963	1,062
Total individuals		126	46	—	38	35	—	88	33	—	366

Figure 1. Minimum percentages of a) adults immigrating (pre-breeding) from beyond 30-m fences and b) juveniles emigrating past 30-m fences after emergence. Adults of unknown origin may have been initially located within the 30-m fence boundary or evaded capture at this fence. Juveniles of unknown fate may have remained within 30-m boundary, died after first capture, or evaded capture at 30-m fence.

Juvenile Movements

Similar to adult salamanders observed in this study, the majority ($\geq 58\%$, $\geq 70\%$, and $\geq 85\%$) of emerging juveniles first captured at 3-m fences as they left the pond basins were subsequently captured at the 30-m fences (Figure 1B). In addition, in the five seasons from 1999 to 2003, we recorded a total of 284 capture events of juveniles entering or traversing other basins in the study area during their year of emergence (Figure 2). Euclidean distances between capture points of individuals ranged from 111 to 1,230 m, with 90.8% (n=258) of these instances occurring between 100 and 400 m.

Capture Probabilities

With the exception of emigrating adults, capture probabilities were relatively consistent among ponds, fences (3-m versus 30-m), and age classes in 1999 (Table 2). Capture probabilities for immigrating adults ranged from 77% to 98% at the 30-m fences and from 83% to 91% at the 3-m fences. Similarly, capture probabilities for emigrating juveniles at the 3-m fences were estimated at minima from 75% to 90% (e.g., a minimum of 90% of emigrating juveniles were captured at the 3-m fence at pond 5). In contrast, adults emigrating from the basins evaded capture much more
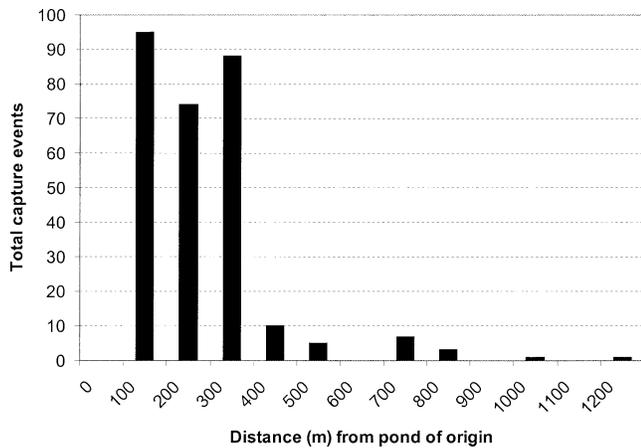
Figure 2. Distance distribution of incidental capture events of juvenile age class individuals entering or traversing other fenced pond basins during their year of emergence. All recorded movements from natal ponds to traversed ponds are aggregated into 100-m distance classes. Sampling effort (i.e., possibility for recapture) was not evenly distributed among distance classes but, instead, was a function of the natural configuration of ponds relative to each other. A total of 11,203 juveniles were captured and marked while emigrating from natal pond basins during this period.

frequently, with capture probabilities as low as 52% and 68% at two ponds.

DISCUSSION

Adult Movements

An important finding of this study was that almost all juvenile and adult marbled salamanders resided in forest habitats that were beyond 30 m from pond edges. In the case of breeding adults, for example, the percentages of individuals first captured at 30-m fences (93%, 96%, and 84% at ponds 4, 5, and 12) corresponded closely with the capture probabilities at these fences (93%, 98%, and 77%, respectively), suggesting that the unadjusted figures were in fact minimum estimates of true percentages that approach 100%. This finding is not completely surprising, as the majority of studies assessing terrestrial movements in this genus have recorded mean distances greatly exceeding 30 m (see review by Semlitsch 1998); however, it dispels a

common misperception that most pond-breeding salamanders are concentrated in close proximity to their breeding sites during non-breeding seasons. In addition, an interesting ecological question is posed by our results—that is, why do we not observe *more* use of terrestrial habitats proximate to the pond basins?

We can only speculate about this limited adult use of proximate uplands. For example, natural selection may have favored behaviors that minimize crowding in upland habitats and subsequent density-related effects. As individual salamanders move greater radial distances from a pond basin, they may benefit from the squared increase in terrestrial area available to them. Marbled salamander survival rates to first reproduction were not affected by maintaining animals in terrestrial enclosures at double ''natural'' densities (Pechmann 1995); however, spotted salamanders emerged at low rates from terrestrial enclosures with high densities (Regosin et al. 2003). Other hypotheses include the possibility of interspecific interactions such as competition for terrestrial refugia (e.g., see Smyers et al. 2002) and/or the possibility that individuals move further away from basins in search of favorable upland habitat conditions. Additional research would clearly be needed to investigate these and other possibilities.

Significant numbers of adult salamanders (approximately 6–21% of those captured at 30-m fences *after* adjustments for capture probabilities) never entered the pond basins, with an apparent bias toward males in this subset. These observations are consistent with those of Krenz and Scott (1994), who found that as many as 30–50% of female marbled salamanders collected before entry into pond basins were already carrying fertilized eggs, strongly suggesting that some males initiate courtship outside the basins. In addition, rains from two consecutive major storms filled the basins in our study earlier in 1999 than in any of the other four years observed. As a result, some individuals may have remained outside inundated areas and/or deposited eggs above the high-water line and beyond our 3-m fences (Wojnowski 2000).

Juvenile Movements

The timing and distance distributions of juvenile movements among the ambystomatids are consider-

Table 2. Summary of drift fence capture probabilities in 1999 for three ponds with 30-m fences. Numbers of individuals used to calculate probabilities are indicated in parentheses. Please refer to Appendix 1 for a detailed explanation of calculations.

Life Stage	Fence	Direction	Pond 4	Pond 5	Pond 12
Adults	30-m	Immig.	93% (83)	98% (44)	77% (87)
Adults	3-m	Immig.	87% (61)	91% (32)	83% (90)
Adults	3-m	Emig.	52% (60)	68% (31)	85% (69)
Juveniles	3-m	Emig.	≥75% (1,099)	≥90% (342)	≥78% (450)

ably less well-understood than those of adults; however, our work suggests that newly metamorphosed salamanders are also capable of extensive terrestrial movements. We observed minima of 58–85% of juveniles surpassing our 30-m fences. These represent conservative estimates since we cannot account for post-emergence mortality or unknown capture probabilities at the 30-m fences. In addition, some of the ''unknown fate'' individuals may have remained close to their natal ponds post-emergence (Windmiller 1996) but moved greater distances in subsequent seasons.

In previous studies with relatively small sample sizes (n < 15), Williams (1973) and Semlitsch (1981) recorded juvenile Jefferson salamanders and mole salamanders, respectively, at distances ranging from 3 to 247 m from their natal ponds using radioactive wire tags. The majority of juveniles captured traversing other basins in our study were captured at distances between 100 and 400 m. We also captured 12 juveniles at distances greater than 700 m (Figure 2). Although we cannot determine whether these individuals were true dispersers colonizing new breeding sites, this range of distances shows the potential for connectivity among breeding populations separated by more than a kilometer, which has significant implications for potential metapopulation dynamics in this species. It is important to note that the distance distribution displayed in Figure 2 does not represent equal sampling effort across distance classes but, rather, is biased by the configuration of ponds (and therefore the number of potential capture opportunities) within each distance class in our study area.

Our study area contains no paved roads and is continuously forested with the exception of a 30-m-wide powerline corridor. Notably, numerous juveniles crossed a perennial stream and/or the powerline corridor, and most crossed one or more narrow (3 m) logging roads; however, the relative effects of these potential landscape ''filters'' on movement could not be assessed in this study. Other studies indicate that newly metamorphosed spotted salamanders tend to avoid open canopy or clearcut conditions compared to forest (deMaynadier and Hunter 1999, Rothermel and Semlitsch 2002, Vasconcelos and Calhoun 2004) and experience higher mortality rates in fields versus forests (Rothermel and Semlitsch 2002). One recent study investigating orientational cues in newly emerged amphibians showed that less than 15% of juvenile spotted salamanders survived and reached forest edges located across 50 m of pasture from pond locations (Rothermel 2004). Cumulatively, these studies demonstrate that numerous aspects of landscape composition and configuration are likely to have significant effects on rates of successful dispersal and movement distances in terrestrial salamanders.

Regulatory Implications

In light of our findings and those of previous studies, existing regulatory frameworks alone are inadequate to meet the long-term conservation needs of marbled salamanders and other seasonal wetland breeding amphibians with similar terrestrial habitat requirements. These shortfalls exist for several reasons.

(1) Many seasonal wetlands do not qualify for protection under state wetlands regulations due to minimum size or volume thresholds or because they do not meet other criteria in wetlands definitions. For example, five of the 14 study ponds at our Massachusetts site are too small to qualify as jurisdictional resource areas (must exceed 308 cubic meters of water to qualify as ''isolated lands subject to flooding'') and are therefore exempt from protections under the Massachusetts Wetlands Protection Act (MGL c.131 s.40).

(2) In cases where wetlands regulations do apply, they often provide protections only within the wetland boundary or to small terrestrial buffer zones (e.g., 30 m from wetland edge). While these areas usually perform other critical functions (e.g., supporting amphibian emergence and breeding migrations, reducing siltation or nutrient loads), they fall far short of protecting terrestrial habitats required by marbled salamanders.

(3) Most or all wetlands regulations are applied on a case-by-case basis in response to permit applications and therefore are poorly suited to assessing cumulative impacts (i.e., incremental impacts may appear insignificant) or broad-scale dynamics (e.g., Sjogren 1991, Skelly et al. 1999, Trenham et al. 2003) that may be critical to some amphibian populations.

(4) Endangered species regulations are typically not applicable until after a species has suffered extensive decline. In these cases, recovery efforts may be more costly, restrictive, and less likely to succeed since fewer conservation opportunities remain and reconnecting habitats fragmented by roads and development may be difficult or impossible. In addition, endangered species legislation often depends on documented occurrences of listed species, and systematic surveys for such occurrences are rarely available.

Future Directions

In order to be effective, land-management and conservation strategies targeting pond-breeding amphibians must evolve with our increased understanding of these animals' life history requirements. For example, research has shown that many ambystomatid salaman-

ders not only require intact seasonal wetlands to breed, but also require substantial upland habitats to support the remainder of their life cycle. While existing wetland legislation in many states may provide reasonable protection to these breeding sites, several authors have recently proposed that we view seasonal wetlands and their surroundings as nested biological zones with corresponding management guidelines (e.g., see Calhoun and Klemens 2002, Semlitsch and Bodie 2003). These guidelines recognize the terrestrial areas immediately surrounding pond basins (corresponding roughly to the 30-m zone studied here) as critical staging areas for adult amphibians and temporary refugia for newly metamorphosing individuals, as well as for their values in protecting the integrity of the breeding sites. Larger zones extending up to 290 m are proposed for their significance as terrestrial habitats, and indeed, larger areas may need to be considered in cases where metapopulation dynamics are evident.

Rigid regulatory frameworks such as no-build zones may not be politically feasible or most appropriate to address these broader spatial scales (e.g., beyond 30 m); however, innovative and proactive planning strategies may offer potential alternatives. For example, Calhoun and Klemens (2002) offered the example of a residential development in Connecticut that was planned specifically to accommodate life-history requirements of Jefferson salamanders through strategic limitation and placement of house footprints, roadways, conservation easements, and the use of specially-designed curbs to minimize barrier effects. At a broader scale, the Massachusetts Natural Heritage and Endangered Species Program has completed a statewide ''Biomap'' assessment to identify priority natural areas for management and acquisitions (Massachusetts Division of Fish and Massachusetts Division of Fisheries and Wildlife 2001). Similar strategies may be appropriate at town or county levels.

Further research in the areas of amphibian dispersal and metapopulation dynamics, landscape permeability and connectivity, compatible land uses, and terrestrial density dependence would all be helpful in guiding these strategies. In addition, and perhaps most fundamentally, educational efforts are necessary at all levels to help the general public and policy makers understand that many amphibians that we associate with wetlands are predominantly terrestrial animals. Increased public understanding of this basic point is likely to increase public support for diversified conservation efforts.

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Appendix 1: Detection Probability Calculations and Assumptions

To estimate detection probabilities for drift fences at each of the three ponds with concentric fences, we needed to know or be able to assume reasonably the number of individuals that traversed a fence line (whether or not they were captured) and calculate the percentage of these that were captured. Since we had different data available to us with regard to these conditions, the methods and assumptions for calculating detection probabilities differed slightly for each fence (3-m or 30-m) and direction of salamander movement. To calculate detection probabilities for immigrating adult salamanders at the 30-m and 3-m fences, we assumed that all individuals captured emigrating from the pond originated (pre-breeding) outside of the respective fence line. We then calculated the percentage of these individuals that were captured at the fence during immigration. For example, 61 adult salamanders were captured at the 3-m fence when emigrating from pond 4 after the breeding period. Of these individuals, 53 were previously captured on the outside of the 3-m fence when immigrating to the basin. Thus, we estimated the capture probability for immigrating adults at this pond's 3-m fence as 53/61, or approximately 87%. For adults emigrating from basins at the 3-m fences, the number of individuals that were captured immigrating at the 3-m fence (thus known to enter the basin) *and* later emigrating at the 30-m fence (thus known to still be alive) formed the denominator, and the subset of these individuals captured emigrating at the 3-m fence was the numerator. Capture proba-

bilities for juveniles emigrating from basins at 3-m fences were estimated as the proportion of individuals captured at the inside of the 30-m fence that had previously been captured and marked at the 3-m fence. Capture probabilities for juveniles and adults emigrating from basins at 30-m fences could not be calculated as their subsequent fate was not known.

To estimate the percentages of adults that approached the pond basins (i.e., were captured at the 30-m fences) but did not enter 3-m fenced areas, we adjusted the raw capture data to account for individuals that may have entered and/or departed the 3-m fenced areas undetected. This adjustment was calculated as

$$Y = (1 - \text{3-m immigrating capture probability}) * (1 - Z)$$

where $1 - Z$ represents the percentage of animals that remained (or died) within the basin or emigrated without detection at the 3-m fence. Z is calculated as the fraction of captured immigrating individuals (at 3-m fence) that were subsequently captured emigrating at this fence. At Pond 4, 53 of the 131 individuals captured immigrating were later captured emigrating, so $Z = 53/131$, or 0.40). Thus,

$$Y = (1–0.87) * (1–0.40) = 7.8\%$$

Completing the Pond 4 example, although 31/159 (19.5%) of adults captured immigrating at the 30-m fences were not subsequently captured immigrating or emigrating at the 3-m fences, we estimated that $19.5\% - 7.8\%$, or approximately 11.7% of the individuals approaching the basin actually did not enter the basin proper. The same adjustments were made to interpret capture data at ponds 5 and 12.