BIOLOGICAL CONSERVATION 139 (2007) 247–257

available at www.sciencedirect.com

journal homepage: www.elsevier.com/locate/biocon

Fidelity and dispersal in the pond-breeding amphibian, *Ambystoma opacum*: Implications for spatio-temporal population dynamics and conservation

Lloyd R. Gamble, Kevin McGarigal, Bradley W. Compton*

Department of Natural Resources Conservation, 160 Holdsworth Way, University of Massachusetts, Amherst, MA 01003, USA

ARTICLE INFO

Article history:
Received 25 July 2006
Received in revised form
15 March 2007
Available online 28 August 2007

Keywords:
Metapopulation
Wetland
Seasonal pond
Marbled salamander
Movement ecology

ABSTRACT

The spatio-temporal dynamics of amphibian populations and the models that describe them are largely influenced by the frequency of dispersal among breeding sites; however, dispersal has rarely been addressed rigorously in empirical studies. In a 7-year landscape-level investigation, we monitored breeding populations of marbled salamanders (*Ambystoma opacum*) among 14 seasonal ponds in western Massachusetts, USA, to quantify dispersal probabilities and distances. Emerging juveniles ($n = 11{,}168$) received cohort marks and adults ($n = 5560$ capture events) were photographed for individual identification using computer-aided dorsal pattern analysis. We found that 91.0% of first-time breeders returned to natal ponds to breed and 96.4% of experienced breeders maintained breeding site fidelity through multiple seasons. These findings confirm a high level of philopatry in this species and the prominence of local factors in determining local population trends. However, the remaining survivors dispersed to other ponds, with several individuals exceeding distances of 1000 m. Though breeding populations were clearly subdivided, dispersal at these rates may offset effects of genetic drift and inbreeding depression by increasing effective population size (through the aggregation of breeding populations). Outward dispersal probabilities were higher at ponds with small breeding populations and inward dispersal was biased toward larger populations, suggesting that salamanders were cueing to the presence of other individuals and/or to unmeasured habitat characteristics. Our findings suggest that small and dynamic local populations may operate inter dependently in a metapopulation context. Effective conservation strategies targeting these and similarly structured amphibian populations must address landscape-level processes (e.g., dispersal) as well as local demographic factors.

1. Introduction

Much debate has centered on whether the metapopulation paradigm accurately describes many amphibian populations (Semlitsch, 2000; Marsh and Trenham, 2001; Smith and Green, 2005). Though the terminology has been applied broadly, metapopulations are generally defined as groups of populations that experience routine local extinctions but may persist regionally as a result of dispersal and recolonization (Levins, 1969, 1970; Hanski and Gilpin, 1997). Broader interpretations include source-sink populations (Brown and Kodric-Brown, 1977), rescue-effect populations (Stacey et al., 1997),

---

* *Corresponding author*: Tel.: +1 413 887 8557.

E-mail addresses: lloydgamble2@gmail.com (L.R. Gamble), mcgarigalk@nrc.umass.edu (K. McGarigal), bcompton@nrc.umass.edu (B.W. Compton).

0006-3207/$ - see front matter © 2007 Elsevier Ltd. All rights reserved.
doi:10.1016/j.biocon.2007.07.001

or virtually any spatially subdivided populations connected by occasional dispersal. Where the paradigm applies, it carries clear conservation implications, such as the need to focus on landscape-level connectivity (e.g., see Cushman, 2006) and to maintain both occupied and potential habitat patches. However, misapplication of the paradigm can be risky, as in cases where a fragmented population in decline may be viewed as a metapopulation at equilibrium or where deterministic local factors may be more important to population persistence than regional connectivity (Marsh and Trenham, 2001).

At face value, the metapopulation paradigm appears well suited to many amphibians. For example, pond-breeding amphibians: (1) are associated with discrete aquatic breeding sites, (2) often experience wide population fluctuations (Semlitsch et al., 1996; Green, 2003) that may vary temporally among proximate sites (Trenham et al., 2003) and (3) often appear to have high fidelity to natal ponds (i.e., philopatry) (Pechmann et al., 1991). The degree to which populations exhibit philopatry is critical in determining the scales at which populations operate; however, this is often the condition we know least about in real populations. For example, how often do individuals successfully disperse in a true ecological sense – that is, to leave a natal site and breed at a new location – and what factors regulate this behavior? Is dispersal a density-dependent response to local conditions or does it occur at more constant, predictable rates? How is dispersal success mediated by distance, landscape permeability, and/or active habitat selection? Addressing these types of questions is necessary to assess the applicability of the metapopulation paradigm and its conservation implications for pond-breeding amphibians (Semlitsch, 2002).

Though a number of studies have concluded that pond-breeding amphibians exhibit philopatry, most of these studies have been limited primarily to observations of returning individuals at a single breeding site. For example, both Husting (1965) and Whitford and Vinegar (1966) conducted multi-year studies on spotted salamanders (*Ambystoma maculatum*) that were focused on single breeding sites with limited sampling at nearby ponds. In both cases, no marked animals from the primary sites were observed elsewhere and it was concluded that little or no dispersal occurred. Findings have differed in studies that have incorporated numerous breeding sites. For example, in a study of the California tiger salamander (*Ambystoma californiense*), Trenham et al. (2001) directly observed interpond dispersal at probabilities exceeding 20% in both first-time and experienced breeders. Gill (1978) documented perfect breeding site fidelity among adult red-spotted newts (*Notophthalmus viridescens*) but inferred dispersal by juveniles based on the persistence of several apparent sink populations. Multi-site studies of anurans have documented abundant dispersal in some cases (Breden, 1987) and infrequent, age-specific dispersal in others (Berven and Grudzien, 1990). To our knowledge, no published studies have directly measured dispersal in any Ambystomatids in eastern North America.

Here we present results from a 7-year field study in which we continuously monitored breeding populations of the marbled salamander (*Ambystoma opacum*) at 14 seasonal ponds in a western Massachusetts landscape. Our primary objectives in this paper are to:

1. address pond fidelity in marbled salamanders by measuring successful return and dispersal probabilities among first-time and experienced breeders,
2. use these empirical data to fit a distance-dispersal function that can (a) help to generalize our findings to different landscapes (with several important limitations) and (b) be used to set parameters for spatial population and connectivity models,
3. describe several observations that reveal elements of dispersal behavior and may be used to frame future experimental work,
4. discuss the implications of our findings for spatio-temporal population dynamics in this species and for conservation approaches to pond-breeding amphibians in general.

2. Methods

2.1. Study organism

The marbled salamander is a terrestrial salamander whose natural range extends across the eastern United States from Florida to southern New England (Petranka, 1998). The marbled salamander is one of several species in its genus that breed primarily in seasonal ponds and spend the majority of their lives in upland forests surrounding these ponds. In contrast to most of their eastern congeners, however, adult marbled salamanders court in the late summer and early fall and subsequently lay eggs terrestrially in receded or dry pond basins (Noble and Brady, 1933; Bishop, 1941). Eggs are typically inundated by rising waters in the fall or winter months and then hatch almost immediately into aquatic larvae. These larvae overwinter in the ponds and surviving individuals metamorphose into terrestrial salamanders in the late spring and early summer. In Massachusetts, breeding populations of marbled salamanders are fairly small (likely due to proximity to northern range limits) and the species is listed as “Threatened” under the state Endangered Species Act (M.G.L c.131A and regulations 321 CMR 10.00). High pond fidelity in this species is suspected (Pechmann et al., 1991), in which case local “pond-populations” even in close proximity may be effectively discrete, related only by occasional dispersal of juvenile animals (but see Petranka et al., 2004).

2.2. Study area

The study area encompasses approximately 300 ha of mixed-deciduous hardwood forests on the Holyoke Range in western Massachusetts, USA. The site is mostly undeveloped, but is bisected by a 30-m wide power line corridor and contains numerous carriage roads and trails. Estimated modal stand age is 70 years. Ten seasonal ponds are clustered tightly in the western section of the study area and four are distributed more widely to the east, with interpond distances ranging from 50 to 1500 m. The ponds range in surface area at high water from 0.03 to 0.35 ha, and vary considerably in structure – including shrub-dominated, open-deep water, and shallow (open and/or vegetated) ponds. Hydroperiods and water level fluctuations vary among ponds and years. Most ponds typically dry between June and September but some occasionally hold water continuously throughout the year.

Marbled salamander breeding populations (number of breeding individuals per pond per year) at these ponds range from 0 to approximately 150 breeding females with male-biased sex ratios (Gamble, 2004). For purposes of evaluating population structure in this area, the study area appears to be effectively closed to the north (steep slopes and high ridge line), east and south (major roadway and residential development). While there are no barriers to the immediate west, the nearest seasonal ponds are approximately 800 m away, and we have not detected marbled salamanders at any ponds within 1250 m of our study ponds.

2.3. *Field methods*

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 2005, fully encompassing the emergence and breeding periods, and released captured animals on the opposite sides of the fences. All marbled salamanders (adults and juveniles) were first inspected for previous marks and the sex of adults was determined by inspecting the cloacal region for swelling. Unmarked juveniles received a double toe-clip cohort mark (Ott and Scott, 1999) to associate them with their natal pond. Given the number of productive ponds and our desire to minimize the potential impacts of the marking method (e.g., see McCarthy and Parris, 2004), it was not feasible to administer a year- or individual-specific mark to juveniles. Adults were digitally photographed for individual identification based on their unique dorsal patterns. We later matched these photographs with a computer-based pattern recognition program (Gamble et al., in press) and matching results were cross-referenced to original data to construct individual capture histories. During the off-season, we closed all traps and opened doors along all fences to allow passage of non-target animals.

2.4. *Analytical methods*

We estimated dispersal probabilities and dispersal distance functions separately for first-time breeders (FTBs) and experienced breeders (EBs) because some studies have suggested that dispersal in amphibians may be age-specific (e.g., Gill, 1978; Berven and Grudzien, 1990). FTBs were individuals that were marked at emergence and returned to breed a first time during the study period. EBs were individuals that we captured as adults in more than one breeding season, and thus include a small number of individuals who were also evaluated as FTBs.

First-time breeders. First, we estimated the probability of *successful* dispersal by FTBs in our study area. To do this, we identified all capture events of breeding adults with cohort marks (issued at emergence). Then, using the results of the pattern recognition analyses, we reviewed the capture histories of these individuals to eliminate repeat captures or cases where cohort marks were not consistently interpreted across captures. For each pond of origin, we then calculated the percentage of FTBs that attempted to breed elsewhere (at non-natal ponds). As an example, at Pond 2, there were 39 capture events through the course of the study that represented 15 unique returning individuals. In addition, there were 15 capture events at other ponds representing five individuals that originated from Pond 2. Thus, the probability of successful dispersal from this pond was estimated as 5/(15 + 5), or 25%. Note that we emphasize *successful* dispersal because it is not possible to quantify failed dispersal attempts and/or associated mortality (e.g., an individual cannot definitively be classified as a disperser until it survives and attempts to breed at a non-natal pond). Instead, we present dispersal probability as the percentage of survivors from a given breeding population that disperse versus those that are philopatric (see Trenham et al., 2001, for a similar example). At the time of this analysis, the pattern recognition analysis of FTBs was complete for returning individuals through 2004 and for dispersing individuals through 2005. For this reason, data from 2005 were excluded from the calculation of dispersal *probabilities* described here, but were included in the distance analysis described below.

Sources of potential error in dispersal probability estimates for FTBs included regrowth of toe-clips, misinterpretation of natural marks as toe clips and variability in capture probabilities between origin and destination ponds. Regrowth should not create a systematic bias because both returning and dispersing individuals should experience similar probabilities of regrowth. Similarly, malformations resembling cohort marks should be rare and presumably random in their distribution. Though we did not have a means of estimating these, the confirmation of marks across multiple captures for most individuals should have minimized this type of error. Lastly, we estimated capture probabilities for each pond in each year by calculating the percentage of immigrating animals that were actually captured upon entry into a pond basin (see Gamble et al., 2006 for full explanation). Because these probabilities were both high and very similar across ponds and years (i.e., approximately 80–90%), adjustments to calculated dispersal probabilities were negligible and were not reported.

Experienced breeders. To estimate probabilities of dispersal among EBs, we used capture histories constructed from the pattern recognition analysis to identify all individuals that were captured at more than one pond during the study period. Since a single data entry error could result in a misinterpretation of these data (e.g., incorrectly identifying a dispersal event from an incorrectly entered pond number), each apparent case with interpond captures was reviewed individually for errors before being assigned to one of three categories:

(1) *Clear dispersal event* – capture history showed incontrovertibly that an individual spent different breeding periods at different ponds (e.g., an individual captured both immigrating and emigrating at Pond 12 in one year and at Pond 6 in a later year).

(2) *Probable dispersal event* – capture history showed that an individual spent at least one breeding period in one pond, and in a different breeding period was captured exclusively at a different pond, but for an unknown duration (e.g., captured only once either immigrating or emigrating).
(3) *Probable traverse event* – typically, these were same-year captures of an individual at different ponds, in which one pond appeared to be traversed *en route* to a destination pond (based on timing, direction of movement and/or brevity of stay).

To estimate a minimum dispersal probability from these data, we divided the number of individuals with clear dispersal events from a given pond (category 1, above) by the total number of returning and dispersing individuals (originating from this pond) captured in two or more breeding seasons. This denominator represented the total sample of individuals that could possibly be observed as returning to the same breeding pond or dispersing. Clear and probable dispersal events were summed in the numerator to provide a second (and probably more accurate) dispersal estimate for each pond.

Two types of errors in the matching process, mismatches and missed matches, could create bias in the estimation of EB dispersal probabilities. Mismatches should be extremely rare or non-existent because all matches were double-checked for accuracy and no ambiguous cases of identity were encountered. Missed matches, however, were more common in the data, typically occurring when a poor image (associated with a specific capture event) did not match to one or more other images of the same individual, resulting in an artificially subdivided capture history (e.g., an individual captured two times each in 1999, 2000 and 2001 could incorrectly appear as two individuals – one captured once in 1999 and the other captured once in 1999 and twice in each of the subsequent years). There is no reason to suspect that missed matches would occur more frequently among returning or dispersing individuals, and the most common cases would decrease the numerator and/or increase the denominator in our calculations, suggesting that our EB dispersal estimates would also be conservative.

Dispersal distance function. Dispersal success is a function of several variables, including proximity to other potential breeding ponds, propensity to disperse from a specific source pond (e.g., density-dependent dispersal), landscape permeability, and degree of active habitat selection. Therefore, an unadjusted distribution of observed dispersal across distance classes in our study area may be confounded by these variables. Though our data were not sufficient to address all of these variables, we could adjust our dispersal data for sampling bias (across distance classes) that results from the specific configuration of breeding ponds in our study area and variable productivity among these ponds. We estimated this sampling bias based on the number of pond-to-pond linkages in each 100 m distance class (from 0 to 1500 m) and the number of potential dispersers produced by each pond (see Appendix A for a detailed description and statistical validation of this methodology). We then fitted a normal curve (see Section 4) centered on 0 m to the adjusted levels of dispersal in each distance class to model the effect of distance on dispersal success.

3. Results

3.1. Dispersal probabilities and natal site fidelity

Marbled salamanders in our study area showed a high degree of natal site fidelity (FTBs) and breeding site fidelity (EBs); however, occasional dispersal occurred among breeding sites in both age classes. Specifically, of 11,168 individuals marked at emergence, 395 returned to breed within the study period, and 39 (9.0%) of these FTBs dispersed to new breeding sites (Table 1). Fates of the remaining marked individuals can be attributed to later maturation, mortality, lost marks and/or dispersal outside the study area (see Section 4). Pond-specific estimates of outward dispersal varied widely from approximately 5% at the three ponds with the most surviving FTBs ($n \geqslant 40$) to 100% at two ponds with only one or two recaptured individuals.

In the case of EBs, a total of 782 individuals were captured in multiple breeding seasons, of which only 28 (3.6%) appeared to change breeding sites. Thirteen of these individuals (1.7%) were classified as clear dispersers and 15 (1.9%) as probable dispersers. An additional 19 individuals were classified as probable traverse events, entering and/or departing more than one pond basin within a breeding season. Some of these traversing individuals repeated similar capture routes (e.g., through Pond 13 *en route* to Pond 12) in more than one year. Similar to the FTBs, dispersal probabilities varied considerably by pond, but were less than 10% at all ponds with sample sizes exceeding 10 individuals.

Twenty-four of the 39 dispersing FTBs were males (sex ratio = 1.6:1) as were 16 of the 28 dispersing EBs (sex ratio = 1.3:1). These sex ratios were slightly less male-biased than those of non-dispersing breeders for all breeding populations combined (2.1:1 and 1.7:1 for FTBs and EBs, respectively).

3.2. Dispersal distance

Including dispersal data from the 2005 breeding season, a total of 76 FTBs dispersed from 142 to 1297 m with the majority (68%) concentrated between 200 and 400 m. After adjusting for sampling bias across distance classes in our study area, these data were reasonably well described ($r^2 = 0.56$) by a normal curve (centered on zero) with a standard deviation 440.1 m (standard error of estimate = 120.9 m; $p = 0.003$); Table 2 and Fig. 1). This distribution should be interpreted to mean that, by this estimate, approximately 95% of successful dispersers would occur within 862 m (1.96 × SD) of their natal pond, but that a small number of individuals represented by the tail of this distribution might be expected to disperse farther. Compared to FTBs, dispersal distances of EBs were shorter, ranging from 105 to 439 m ($n = 28$). After corrections for sampling bias by distance classes, these were best described by a normal distribution with a standard deviation of 331.5 m (standard error of estimate = 160.8; $r^2 = 0.36$; $p = 0.031$; Table 2 and Fig. 1).

Table 1 – Successful dispersal probabilities for *Ambystoma opacum* among 14 breeding sites in western Massachusetts

Pond ID	First-time breeders				Experienced breeders		
	Total juveniles marked (1999–2003)	Returning individuals (2000–2004)[a]	Dispersing individuals (2000–2004)[b]	Dispersal probability (%)[c]	Returning individuals (1999–2004)[d]	Dispersing individuals (1999–2004)[e]	Dispersal probability (%)[c]
1	0	0	0	–	1	0	0.0
2	1701	15	5	25.0	84	5	5.6
3	612	38	2	5.0	40	4	9.1
4	6393	287	16	5.3	412	3	0.7
5	1224	10	10	50.0	27	0	0.0
6	19	0	2	100.0	37	2	5.1
7	0	0	0	–	0	1	100.0
8	0	0	0	–	0	0	0.0
9	67	0	1	100.0	10	1	9.1
10	0	0	0	–	0	0	0.0
11	15	0	0	–	2	4	66.7
12	1337	45	3	6.2	140	5	3.4
13	0	0	0	–	1	3	75.0
14	0	0	0	–	0	0	0.0
Total	11,168	395	39	9.0	754	28	3.6

a Number of individuals that returned to natal pond between 2000 and 2004.
b Number of individuals that originated from this pond and were captured as first-time breeders at other ponds.
c Dispersing individuals divided by sum of dispersing and returning individuals.
d Number of individuals captured in two or more breeding seasons at the same pond.
e Total of "clear" and "probable" dispersers (see text) first captured at this pond and subsequently at a different pond.

Table 2 – Observed distribution of *Ambystoma opacum* dispersal events by distance class with associated sampling bias

Distance class	First-time breeders				Experienced breeders			
	Observed dispersal (number of individuals)	Observed dispersal (%)[a]	Sampling bias[b]	Adjusted dispersal[c]	Observed dispersal (number of individuals)	Observed dispersal (%)[c]	Sampling bias[b]	Adjusted dispersal[c]
0–99	0	0.00	0.00	–	0	0.00	0.00[d]	0.00
100–199	4	0.05	0.04	1.32	16	0.57	0.07	8.16
200–299	24	0.32	0.10	3.16	6	0.21	0.11	1.95
300–399	28	0.37	0.08	4.61	3	0.11	0.10	1.07
400–499	3	0.04	0.02	1.97	3	0.11	0.04	2.68
500–599	0	0.00	0.06	0	0	0.00	0.04	0.00
600–699	0	0.00	0.00	–	0	0.00	0.00	–
700–799	4	0.05	0.06	0.88	0	0.00	0.05	0.00
800–899	1	0.01	0.13	0.10	0	0.00	0.10	0.00
900–999	0	0.00	0.01	0.00	0	0.00	0.00	–
1000–1099	8	0.11	0.19	0.55	0	0.00	0.17	0.00
1100–1199	0	0.00	0.18	0.00	0	0.00	0.13	0.00
1200–1299	4	0.05	0.11	0.48	0	0.00	0.13	0.00
1300–1399	0	0.00	0.01	0.00	0	0.00	0.02	0.00
1400–1499	0	0.00	0.02	0.00	0	0.00	0.03	0.00
Total	76	1.00	1.00	–	28	1.00	1.00	–

a Number of observed individuals divided by total.
b Proportional level of sampling opportunity in each distance class given the configuration and varying productivities of ponds in our study area (see Section 2 and Appendix A).
c Observed dispersal divided by sampling bias for each distance class (see Section 2 and Appendix A). This value has little absolute meaning, but demonstrates relative levels of dispersal across distance classes and allows a distance function to be fitted (Fig. 1).
d This is a non-zero value (0.003) that rounded to 0.00, so the quotient can be calculated.

4. Discussion

The large majority of marbled salamanders in our study system were philopatric. Ninety-one percent of individuals surviving to a first breeding event returned to their natal ponds and almost all adults continued to breed at the same pond year after year. These results are consistent with those of several "single breeding site" studies documenting high return

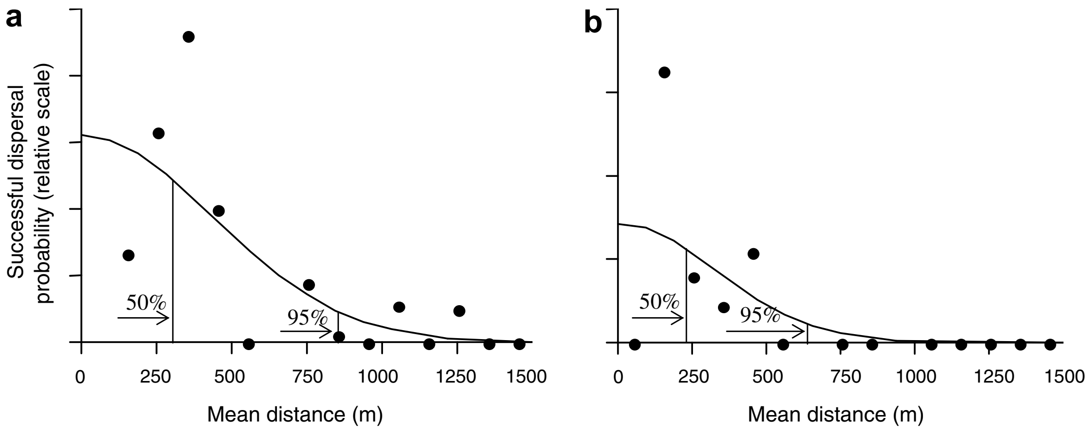

Fig. 1 – Normal curves fitted to relative dispersal probabilities for marbled salamanders by distance (see text) for (a) first-time breeders (SD = 440.1 m, standard error of estimate = 120.9 m, $r^2 = 0.56$, $p = 0.003$) and (b) experienced breeders (SD = 331.5 m, standard error of estimate = 160.8 m, $r^2 = 0.36$, $p = 0.031$) among 14 seasonal ponds on the Holyoke Range in western Massachusetts, USA. Each circle is placed at the midpoint of a 100 m distance class between 0 and 1500 m (x-axis) and corresponds to adjustments (y-axis) calculated in Table 2.

probabilities in ambystomatid salamanders (e.g., Whitford and Vinegar, 1966; Williams, 1973). However, our findings went a step further, as we documented the fates of individuals that survived and dispersed to other breeding sites as well. Though these dispersers represent a small percentage of the overall population(s) being studied, they may contribute disproportionately to broader scale population dynamics in this system.

4.1. *Demographic considerations*

First, we consider the demographic impacts of dispersing individuals. In the larger populations (in our study area, $n \geqslant 10$ breeding females/year), dispersers represented only a small percentage of individuals leaving from or arriving to any particular breeding population. For this reason, it can be expected that their short-term impact on local population growth or decline would be minimal. Instead, the status of local populations is likely driven primarily by local habitat variables affecting reproductive success and survival of returning individuals. In a previous analysis, for example, we found that specific elements of pond hydroperiod (e.g., date of inundation relative to nesting) explained much of the variability in reproductive success among ponds (Gamble, 2004). Reproductive success, in turn, likely explains much of the variability in subsequent breeding population size (Semlitsch et al., 1996).

Though local demographic rates are the primary drivers of dynamics in larger populations, the effects of dispersal may be more significant when drawing from or adding to smaller populations. Interestingly, though sample sizes were low in these cases, we observed the highest outward dispersal probabilities of both first-time and experienced breeders from the smallest breeding populations (Fig. 2). In the case of experienced breeders, for example, outward dispersal exceeded 66% at three of four ponds with fewer than 10 experienced breeders, yet never exceeded 10% in the remaining, larger populations. This may be an indication that some individuals are abandoning ponds due to a lack of potential mates and/or are responding to local environmental variables that are responsible for the lack of previous success. However, the data from these small breeding populations are sparse and they coincide with closer proximity to neighboring ponds, presenting at least one alternative explanation for these patterns. If marbled salamanders are exhibiting active habitat selection among ponds, it seems to be occurring across breeding seasons, because very few individuals are captured at more than one pond within a given breeding season, and most of these cases appear to be chance encounters with other ponds en route to a particular destination pond.

A bias appears to affect the selection of destination ponds for successful dispersers. Only five of 27 dispersing EBs arrived at breeding sites with small populations, and five ponds with few or no breeding individuals received no dispersing EBs at all. Similarly, only seven of the 76 dispersing FTBs appeared at ponds with small breeding populations, and five of these appeared at the same pond in the same year. This apparent selectivity contrasts with movement patterns of

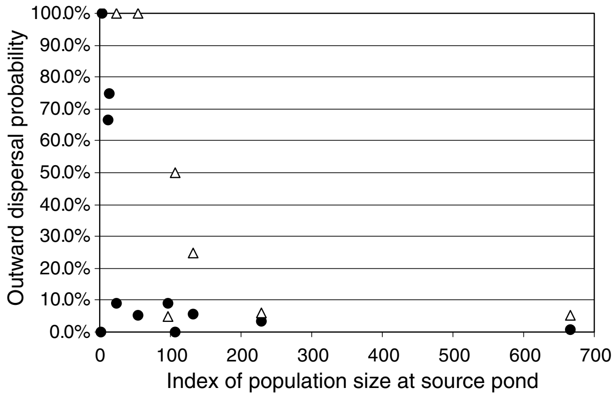

Fig. 2 – Marbled salamander dispersal probability for each breeding pond plotted against an index of population size (total number of unique breeding individuals captured throughout study period). Solid circles indicate experienced breeders. Open triangles indicate first-time breeders.

juvenile marbled salamanders during their year of emergence (Gamble et al., 2006); these individuals were captured entering and/or traversing virtually all pond basins in the study area as they moved away from natal ponds. These observations strongly suggest that breeding individuals are cueing to the presence of other individuals and/or are exhibiting active selection of breeding habitats based on other physical variables. If the presence of other individuals is an important cue, this behavior would tend to reinforce established breeding populations in a metapopulation context and possibly impede colonization of new sites.

Sex ratios were slightly less male-biased among dispersing versus returning individuals, but did not indicate strongly sex-biased dispersal. These findings are consistent with those of Berven and Grudzien (1990) and Trenham (2001) documenting no sex-biased dispersal in wood frogs (*Rana sylvatica*) and California tiger salamanders (*A. californiense*), respectively. In contrast, female natterjack toads (*Bufo calamita*) were found to have less fidelity to natal ponds than males (Sinsch, 1992). Male-biased sex ratios are often observed in amphibian breeding populations, and may result from a combination of factors including later sexual maturity in females (with associated differences in survival to breeding) and differences in breeding frequency (Berven, 1990).

4.2. *Genetic considerations*

Dispersing individuals may also play a role in a conservation genetics context through effects on genetic drift and inbreeding. All of the populations we studied were relatively small: peak numbers of females captured in any one breeding season for the four largest breeding populations were 143, 58, 40 and 31, and sex ratios were typically skewed at approximately 1.6 males/female. Although “true” population sizes (N) were likely to be larger due to some individuals skipping breeding seasons (Petranka, 1998), several factors (e.g., population fluctuations and likelihood of unequal reproductive contributions among individuals) suggest that effective population sizes (N_e) would be considerably smaller. In this case, several of these populations would be below effective population sizes at which drift and inbreeding become potential concerns (Frankel and Soule, 1981). However, the rates of dispersal we observed could lessen the effects of inbreeding and drift.

Although dispersal distances of EBs were limited to less than 400 m, the dispersal we observed could be considered substantial in a number of ways. For example, several dispersing FTBs spanned some of the longest interpond distances in our study area (Fig. 3) and only three of 14 ponds received no dispersers at all in the seven years of this study. The remaining ponds were interconnected by as few as one and as many as 24 dispersal events and the mean number of dispersers received by a pond was 4.8 (SD = 6.5). Dispersal events to any one breeding population came from between 1 and 4 different breeding populations. Assuming dispersers were successfully breeding in these populations, these dispersal frequencies exceeded minimum rates necessary to prevent significant genetic differentiation among breeding populations that would result from the effects of genetic drift (Mills and Allendorf, 1996). Although these breeding populations are clearly subdivided, this frequent exchange of individuals may serve to increase N_e via aggregation of breeding populations. This level of genetic exchange among ponds could also lessen the effects of inbreeding depression. A direct assessment of the degree to which dispersers are genetically integrated into the breeding populations and subsequent relationships with inbreeding depression (e.g., association between the degree of heterozygosity and fitness) would be necessary to further understand these effects.

4.3. *Fate of remaining marked individuals*

Of the newly emerging metamorphs given cohort marks between 1999 and 2003, only 3.5% were identified as recaptured breeding adults during our study. This estimate is not surprising, particularly given low survival expectations for this age class and estimated time needed to reach sexual maturity. For example, in a study of marbled salamanders in South Carolina, Scott (1994) found that approximately 6% and 21% of individuals marked upon emergence (from high and low density larval treatments, respectively) survived to breed a first time, and these animals required 1–6 years to reach sexual maturity. Trenham (2001) estimated that 3.4% of newly metamorphosed California tiger salamanders (*A. californiense*) survived to breeding age, requiring 4–5 years to reach maturity. In our study, 59% of the individuals marked as metamorphs emerged in the summer of 2003, and many of these likely did not reach breeding age by 2004, the last breeding year incorporated into the dispersal probability analysis. In addition to natural mortality and late maturation, it is also feasible that some marks were not discernable due to regrowth of digits and/or that some individuals may have dispersed outside the study area. Similar forested habitats exist to the west; however, no seasonal ponds occur within 800 m of the western extent of our study area. Our results suggest that we captured much of the range of variability in dispersal distances within our study area and that our estimates of dispersal probabilities would not be particularly sensitive to the exclusion of these more distant ponds.

4.4. *Dispersal distances and distance functions*

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 *A. maculatum* (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.

As mentioned previously, the probability of dispersal success from any given population is affected by several factors, including the propensity of individuals to disperse, the permeability of the surrounding landscape, the proximity and abundance of other potential breeding sites and the degree of active

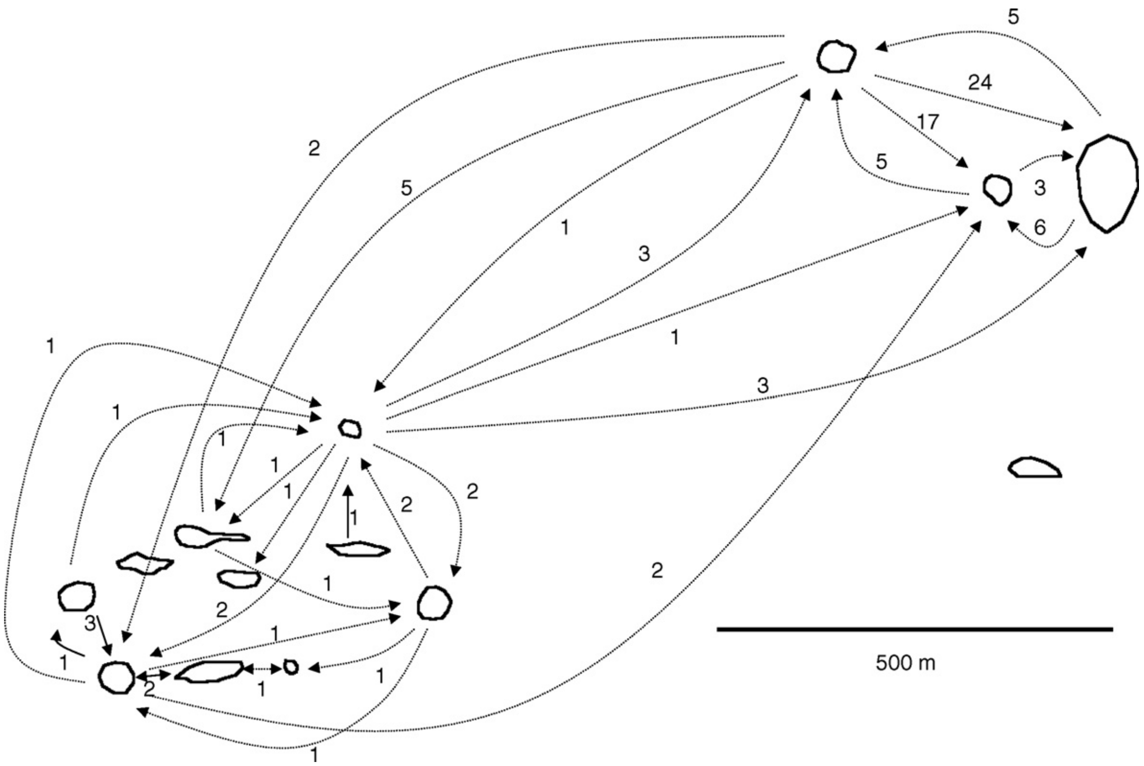

Fig. 3 – Binary depiction of ponds and numbers of dispersing first-time and experienced breeding marbled salamanders between 1999 and 2005, displayed by origin and destination ponds. Labels of two-sided arrows indicate an equal number of individuals dispersing in both directions.

habitat selection by individuals. For these reasons, one should be cautious in generalizing dispersal probabilities quantified in one landscape to other areas. In this regard, our estimates are likely to be high relative to many landscapes given the proximity of numerous potential breeding sites in a continuously forested area. However, with certain limiting assumptions, the sampling bias correction and curve-fitting procedure that we used (see Appendix A) allowed us to estimate the relative effects of distance on dispersal success in a manner that was not restricted to the specific configuration of ponds in our study area. In turn, these results have been useful in the parameterization of kernel-based spatial population models that investigate landscape connectivity for this and closely related species at broader scales (Compton et al., 2007) to facilitate identification of priority sites for conservation.

It is important to distinguish the distance function we present from one calculated to describe upland habitat use of migrating (non-dispersing) individuals. For example, Semlitsch (1998) reviewed numerous studies that documented movement distances of Ambystomatids in eastern and midwestern states, and concluded that a buffer zone extending 164 m from pond edges would be necessary to encompass 95% of these populations. As the author noted, such a zone may minimize short-term impacts on a local population, but it does not account for dispersing individuals and their potential significance to long-term and broader-scale dynamics. Interestingly, the distance distribution we report for dispersing FTBs resembles that of emigrating juveniles captured in their year of emergence (Gamble et al., 2006), suggesting that the first terrestrial season may be a critical time for dispersing individuals.

The most limiting factors and assumptions in our distance analysis were: (1) all ponds were imbedded in a continuously forested landscape (thus, we cannot infer movement distances in highly fragmented systems), (2) numbers of potential dispersers leaving each pond were assumed to be proportionate to the numbers of surviving and returning individuals, and (3) it was assumed that no systematic relationship existed between pond “attractiveness” and our distance classes (e.g., that the “best” breeding sites happen to all occur 300–400 m from the majority of other breeding sites). In addition, the selection of a statistical distribution to fit to the data can significantly affect their interpretation, particularly with reference to the tail of the distribution (e.g., see Smith and Green, 2005). Indeed, rare long distance dispersal events are both implicitly unpredictable and difficult to quantify (Clark et al., 2003). Amphibian movement distances have previously been described by a normal distribution (e.g., Semlitsch, 1998), as well as by a negative exponential (e.g., Berven and Grudzien, 1990; Trenham et al., 2001) and a power law (Smith and Green, 2005); however, amphibian dispersal data in general have been too sparse to suggest what distributions are most appropriate. We chose the normal distribution both for parsimony and because we were excluding returning individuals (dispersal distance = 0) from the analysis. We found that a normal distribution best fit our data, but suggest that the far tail of the distribution be interpreted cautiously.

4.5. *Implications for metapopulation dynamics and conservation*

To understand the implications of our findings for the spatial ecology and conservation of marbled salamanders, we consider where these populations appear to fit along a continuum of conceptual spatial population models. First, given the high level of fidelity to natal sites, we assert that these populations have clearly defined spatial subdivision based largely on the configuration of suitable breeding sites. We cannot definitively assess the contribution of terrestrial habitats to this spatial structure; however, because our study site is continuously forested with relatively homogeneous stand age and composition, we assume that upland habitat characteristics are of secondary importance to breeding habitats in this landscape.

The continuum then, is defined by varying levels of connectivity as dictated by dispersal probabilities and distances. At one extreme, populations are completely isolated from each other due to distance and/or inhospitable land cover types. Some would consider this an extreme form of a non-equilibrium metapopulation, where extinctions are likely but recolonizations cannot occur (Hanski and Simberloff, 1997). In the middle, a "classic" metapopulation typically describes cases where dispersal among patches occurs, but at low enough rates to be insignificant relative to local environmental variables and their demographic implications. Then we consider a "patchy" population – one in which dispersal occurs frequently enough that local extinctions do not occur (i.e., all breeding sites receive a study inflow of dispersers) or are extremely rare. In our study, based on dispersal frequency alone, breeding populations seem to fall between the latter two conditions. Dispersal occurs frequently enough that the arrival of immigrants at any potential breeding site is probable over the course of several years. However, short-term local extinctions appear plausible, if not likely, as the result of local environmental stochasticity and/or catastrophic events.

Several other factors that we have not addressed in this analysis may contribute significantly to this assessment and its conservation implications. Most importantly, we do not know explicitly what combination of factors leads to decline and extinction in local populations and whether these factors are stochastic or relatively persistent over time. For example, if pond-level variables (e.g., predator or prey abundance) significantly affect year-to-year reproductive success and are themselves highly variable over time and space, then classic extinction-recolonization dynamics are likely to be important. In contrast, if more persistent variables (e.g., average hydroperiod) predominate, then it is likely that a less dynamic source-sink model would better describe these populations. In the latter case, the identification and protection of source populations should be an obvious conservation priority; however, less productive populations may still offer significant conservation value as stepping stones to other potential source populations and/or to seed recoveries at source populations after catastrophic local declines (e.g., from a pathogen outbreak).

Regardless of the exact placement of this real population along a theoretical continuum of population structures, several conservation implications are apparent. First, since breeding populations are both spatially subdivided and highly dynamic, dispersal may serve to increase regional persistence probabilities through (1) recolonizations after local extinctions, (2) rescue-effects at sites which have the potential to become self-sufficient "source" populations, and/or (3) genetic exchange at levels which may decrease risks of genetic drift and inbreeding depression. Given the range of dispersal distances observed and high potential fecundity in this species, these effects could extend to distances well over 1000 m in a continuously forested landscape. Further, if factors such as climate change or habitat fragmentation increase local stochasticity, dispersal may play a more important role as a stabilizing process by offsetting increased probabilities of local declines or extinctions.

Designing and implementing experimental work around such a large-scale process as amphibian dispersal can be exceedingly difficult if not logistically impossible. Displacement studies (Gill, 1979; Marsh et al., 2005) and runway experiments (Rosenberg et al., 1998; Rothermel and Semlitsch, 2002) have proven to be useful approaches to address elements of movement behavior; however, landscape-level investigations are also essential to offer baseline information on processes that occur at broader scales. Our findings offer new information about the dispersal behavior and capabilities of marbled salamanders and are likely to have relevance to other Ambystomatids with similar habitat requirements. In particular, they reveal the capacity for long-distance dispersal and the potential significance of this process to population dynamics at scales exceeding 500–1000 m. Additional empirical work on how dispersing amphibians respond to different cover types (i.e., landscape permeability) and on specific mechanisms driving dispersal behavior and habitat selection would add much to our understanding of pond-breeding amphibians and our ability to design appropriate conservation strategies to maintain viable populations.

Acknowledgements

Many thanks to S. Jackson, S. Melvin, C. Griffin, A. Richmond, B. Timm, C. Jenkins, S. Fowle, and M. Neel for valuable input throughout this project and for critical feedback on previous versions of this manuscript, to Sai Ravela for the development of pattern recognition algorithms, and to the Valley Land Fund and several private landowners for permitting access to their properties. We thank K. Berger, N. Bovaird, D. Brennan, M. Contois, C. Eiseman, M. Grgurovic, M. Hey, K. McKenney, K. Montieth, J. Roberts, and E. Weymouth for their long hours in the field and D. Pepin for field support. This work was funded by the Natural Heritage & Endangered Species Program of the Massachusetts Division of Fisheries and Wildlife, Sweet Water Trust (Boston, MA), the US Geological Survey Amphibian Research & Monitoring Initiative (ARMI), the Silvio Conte National Wildlife Refuge (Challenge Grant #50181-1-J045A), the Massachusetts Environmental Trust (Boston, MA) and the Robert & Patricia Switzer Foundation. Handling of animals was conducted under the University of Massachusetts Amherst Institutional Animal Care and Use Protocol #22-02-02 and annual collection permits granted by Massachusetts Division of Fisheries and Wildlife.

Appendix A. Methodology and validation for estimating dispersal-by-distance function

A.1. *Methodology*

We took the following steps to adjust our raw dispersal data (i.e., successful dispersal events) for sampling bias across distance classes in our study area. The result is a distribution of relative dispersal probabilities across distance classes. We first discuss the steps used for first-time breeders (FTBs), and then explain the minor modifications necessary for a parallel analysis of experienced breeders (EBs).

1. To estimate the relative output of dispersers from each pond in our study area, we used the total number of *returns* (FTBs returning to their natal pond). This index incorporated potential pond-level variability in productivity, survivorship and time to sexual maturity, but not in propensity to disperse. We chose this index over total reproductive output because the latter would have addressed only the first of these potentially confounding variables. We also tested an alternative index based on total surviving FTBs (returning or dispersing). In this case, results were nearly identical to the selected method and therefore were not detailed in this paper.
2. For each pond, we multiplied the total number of returns (#1) by the number of potential "recipient" ponds in each distance class relative to the source pond. Ponds with no individuals surviving and returning were assumed to produce no dispersers.
3. We summed these values within each 100 m distance class from 0 to 1500 m for all possible source ponds, creating a relative distribution of capture opportunities across distance classes. We then converted this to a proportional distribution summing to 1. One may view this distribution as representing the relative levels of opportunity, given the configuration of our study area and variable productivity of ponds, to capture dispersers in each distance class.
4. We grouped observed dispersal events into corresponding distance classes and created a proportional distribution summing to 1.
5. In each distance class, we report the quotient of the two normalized distributions (i.e., observed proportion of dispersers divided by proportional level of sampling opportunity) to represent an adjusted measure of dispersal per unit "sampling opportunity."
6. We fitted a normal curve (centered on 0 m) to the corrected levels of dispersal to model the effect of distance on dispersal success (see Section 4 regarding choice of distribution). This distribution can be interpreted to mean, "of those individuals that survive and successfully disperse, this is our expectation of how they will be distributed over distance."

For EBs, we followed the same procedure except for the following:

1. We used the total number of breeding individuals at each pond (that were captured in more than one breeding season) to estimate the relative output of potential dispersers across ponds. For example, a pond with 100 individuals breeding in more than one year would be expected to produce twice as many potential dispersers as another pond with 50 individuals.
2. The relative distribution of observed dispersal events (#4, above) was estimated from the sum of "clear" plus "probable" dispersal events in each distance class.

A.2. *Validation*

We validated this method by applying it to simulated dispersal data randomly drawn from a known distribution. We randomly placed seven pools (the number of pools in our study site that produced dispersers) in a grid with a 1 m cell size and fixed to the size of our study site (1390 × 845 m). We assigned population sizes to source pools by drawing from a negative exponential distribution because populations are not distributed uniformly among pools. We then generated a dispersal probability for each pool-to-pool combination based on the source population and a normal function of dispersal distance ($h = 440$). We distributed a fixed total number of successful dispersers ($n = 39$, the number of dispersing FTBs we captured) across all pairs of source-recipient pools by drawing from the relative probabilities of pool-to-pool dispersal. We then used the linkage method described in Section A.1 (using 100 m distance classes) to estimate $\hat{h}$. We iterated 1000 times and estimated bias as $(h - \text{median } \hat{h})/h$ and precision as both (interquartile range of $\hat{h})/h$ and $(Q_{0.975} - Q_{0.025})/h$.

Our simulations gave a median $\hat{h}$ of 435.2, thus bias was a negligible 1.2%. The interquartile range of $\hat{h}$ was (324.1, 540.0), and the 95% range was (82.5, 921.1). Our simulations showed that given the parameters and sample sizes from our study site, the method was unbiased but not particularly precise, with a 50% confidence interval of ±26%, and a 95% confidence interval of ±95%. Given the necessarily small sample sizes inherent in studies of vertebrate dispersal, estimates of dispersal by any method will likely be relatively imprecise. Although it is beyond the scope of this paper, a more thorough set of simulations could be useful in selecting the extent, number of pools, and necessary sample sizes for a desired level of precision when designing future dispersal studies.

REFERENCES

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., Grudzien, T.A., 1990. Dispersal in the wood frog (*Rana sylvatica*) – implications for genetic population structure. Evolution 44, 2047–2056.

Bishop, S.C., 1941. The Salamanders of New York. New York State Museum, New York.

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.

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

Clark, J.S., Lewis, M., McLachlan, J.S., HilleRisLambers, J., 2003. Estimating population spread: what can we forecast and how well? Ecology 84, 1979–1988.

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

Cushman, S.A., 2006. Effects of habitat loss and fragmentation on amphibians: a review and prospectus. Biological Conservation 128, 231–240.

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

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., Ravela, S., McGarigal, K., in press. 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.

Gamble, L.R., McGarigal, K., Jenkins, C.L., Timm, B., 2006. Limitations of regulated "buffer zones" for the conservation of marbled salamanders. Wetlands 26, 298–306.

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.

Green, D.M., 2003. The ecology of extinction: population fluctuation and decline in amphibians. Biological Conservation 111, 331–343.

Hanski, I., Gilpin, M.E., 1997. Metapopulation Biology: Ecology, Genetics, and Evolution. Academic Press, San Diego, CA.

Hanski, I., Simberloff, D., 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. In: Hanski, I., Gilpin, M.E. (Eds.), Metapopulation Biology: Ecology, Genetics, and Evolution. Academic Press, San Diego, CA, pp. 5–26.

Husting, E.L., 1965. Survival and breeding structure in a population of *Ambystoma maculatum*. Copeia 1965, 352–362.

Jenkins, C.L., McGarigal, K., Gamble, L.R., 2003. Comparative effectiveness of two trapping techniques for surveying the abundance and diversity of reptiles and amphibians along drift fence arrays. Herpetological Review 34, 39–42.

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. In: Gerstenhaber, M. (Ed.), Some Mathematical Problems in Biology. American Mathematical Society, Providence, Rhode Island, pp. 75–107.

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

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

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

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

Mills, L.S., Allendorf, F.W., 1996. The one-migration-per-generation rule in conservation and management. Conservation Biology 10, 1509–1518.

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

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

Pechmann, J.H.K., Scott, D.E., Semlitsch, R.D., Caldwell, J.P., Vitt, L.J., Gibbons, J.W., 1991. Declining amphibian populations – the problem of separating human impacts from natural fluctuations. Science 253, 892–895.

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

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

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

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

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

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

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., Scott, D.E., Pechmann, J.H.K., Gibbons, J.W., 1996. Structure and dynamics of an amphibian community: evidence from a 16-year study of a natural pond. In: Cody, M.L., Smallwood, J.A. (Eds.), Long-term Studies of Vertebrate Communities. Academic Press, San Diego, CA, pp. 217–248.

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

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

Stacey, P.B., Taper, M.L., Johnson, V.A., 1997. Migration within metapopulations: the impact upon local population dynamics. In: Hanski, I., Gilpin, M.E. (Eds.), Metapopulation Biology: Ecology, Genetics, and Evolution. Academic Press, San Diego, CA, pp. 267–291.

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

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

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

Williams, P.K., 1973. Seasonal movements and population dynamics of four sympatric mole salamanders, genus *Ambystoma*. Ph.D. Dissertation, Indiana University, Bloomington, Indiana.