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The importance of understanding spatial population structure when evaluating the effects of silviculture on spotted salamanders (*Ambystoma maculatum*)

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ABSTRACT

Current silvicultural practices in the northeastern United States create diverse vegetation patterns and microclimates that provide a mosaic of terrestrial habitats for amphibian species. We inferred patterns of habitat use by the spotted salamander, *Ambystoma maculatum*, by studying colonization of four newly created breeding pools each surrounded by four different forest treatments: a control, partial cut, clearcut with coarse woody debris (CWD) removed, and clearcut with CWD retained. Created pools were rapidly colonized, indicating that breeding salamanders readily bred in new pools they encountered. This suggests that in our study area pool-specific philopatry and site fidelity may not be high and that particular pools may not define local breeding populations. In the experimental silvicultural treatments, juvenile salamanders preferred the control forest to the clearcuts, whereas adult salamanders showed no significant preferences among the treatments. Although silvicultural practices such as clearcutting may reduce juvenile movement between pools, inter-pool movement by adults that are more tolerant of habitat change may ameliorate this effect in our study area. If juveniles are the primary life-history stage dispersing between local populations (i.e., moving between more isolated groups of pools), however, there is potential for clearcutting to reduce the connectivity between local populations.

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1. Introduction

Loss and degradation of forested habitats is a principle cause of the on-going declines in amphibian populations (IUCN et al., 2006; Stuart et al., 2004), with changes in the vital rates of terrestrial life-history stages of amphibians playing an important role in driving patterns of abundance and population persistence (Biek et al., 2002; Conroy and Brook, 2003; Harper, 2007; Vonesh and De la Cruz, 2002). Forest practices such as clearcutting have been shown to affect amphibians (Patrick et al., 2006), but sustainable forest harvesting is far less invasive than development or agriculture. In the

northeastern United States, silviculture usually generates a shifting mosaic of forest patches, including small clearcuts, partial harvests, and older stands. Predicting how amphibian populations will be affected by this heterogeneous landscape is complex, requiring knowledge of how individuals evaluate and respond to changes in habitat, and how these patterns translate into changes in the abundance and viability of local and regional populations (Patrick et al., in press).

Patterns of movement and the spatial structure of populations varies among amphibian species (Carr and Fahrig, 2001; Gibbs, 1998; Rothermel and Semlitsch, 2002); within the same

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species in different geographic regions, (Calhoun et al., 2003; Harper, 2007; Patrick et al., 2006; Rittenhouse and Semlitsch, 2007); and between sexes (Faccio, 2003; McDonough and Patton, 2007). In areas where breeding sites are isolated and terrestrial conditions inhospitable, movement including dispersal may be risky, resulting in high rates of philopatry (Solomon, 2003). Conversely, if a population is found in an area where breeding sites are close together and terrestrial conditions favorable, dispersal may be more common (Johnson and Gaines, 1990).

Historically, pool-breeding amphibian populations have been characterized as rarely dispersing between breeding sites, and correspondingly conforming to a metapopulation paradigm (Gill, 1978; Sjogren Gulve, 1994). This assumption has recently been called into question (Smith and Green, 2005). Where amphibians can readily move through terrestrial habitats (due to intrinsic adaptation of the species, and/or favorable conditions in a locale), and breeding sites are abundant, frequent movement between breeding sites makes it less likely that local populations are defined by single breeding sites. Conversely, if breeding sites are isolated and terrestrial habitat inhospitable, the “pond as a population” and metapopulation paradigms may well be applicable. Understanding the spatial structure of amphibian populations is vital if we are to be able to evaluate the effects of habitat change and develop conservation strategies for amphibian populations (Petranka et al., 2004; Smith and Green, 2005).

Our research focuses on understanding how the terrestrial ecology of the spotted salamander in our study area influences the likely effects of silviculture on population processes. This forest-dependent ambystomatid salamander is widely found in eastern North America, spending most of its time in the terrestrial environment (Duellman, 1999). Previous research has highlighted the sensitivity of ambystomatids to changes in forest habitat, including lower abundance when forest canopy is reduced (Cromer et al., 2002) and near forest edges (deMaynadier and Hunter, 1998), higher juvenile survival in forests compared to old fields (Rothermel and Semlitsch, 2006), and higher adult survival when migrating to a breeding pond from a forest compared to a clearcut (Raymond and Hardy, 1991). Spotted salamanders have also been shown to avoid leaving forested habitat when emigrating (Rittenhouse and Semlitsch, 2006). Because of this sensitivity of spotted salamanders to changes in forest habitat quality, their high abundance throughout much of their range (Gibbs and Shriver, 2005; Patrick et al., 2006), and the importance of salamanders in forest ecosystem processes (Burton and Likens, 1975; Regester et al., 2006), alteration of forest habitat quality and the corresponding effects on salamander populations could influence ecosystem structure and function.

Our study consists of two components. Initially, we focus on patterns of colonization of newly created breeding pools by adult salamanders. Next, we focus on how local populations of spotted salamanders respond to changes in terrestrial habitat due to silvicultural practices, with attention to differences in terrestrial habitat selection between juvenile and adult spotted salamanders. We conclude by combining these two aspects to draw conclusions about the likely effects of silviculture on spotted salamanders in our study area.

2. Methods

2.1. Study area

Our study was conducted in the Dwight B. Demeritt and Penobscot Experimental Forests, near Orono, Maine (44° lat., –68° long.). We established four replicate experimental arrays (separated by a minimum of 300 m of forest) in which four silvicultural treatments surrounded a central breeding pool. The breeding pools were approximately 10 m in diameter and 0.5–0.75 m deep, and were created by mechanically excavating depressions in existing forested wetlands from December 2003 to March 2004, with the goal of mimicking the natural vernal pool habitat of our focal species. The pools did not dry during the duration of the study, but they remained fishless, the key feature of vernal pools. Small numbers of spotted salamander egg masses (<5 at each site) had been seen in the wetlands where three of our pools were created. The nearest breeding pools to our study pools were a minimum of 200 m away. At each array, the silvicultural treatments extended 164 m in radius from the central pool's edge (Semlitsch, 1998). This 164-m radius circle was divided into four quarters (each ~2.1 ha in size, intersecting at the breeding pool), with each quarter randomly assigned one of the treatments (with the caveat that the two clearcut treatments were opposite one another) (Fig. 1). The treatments included an uncut control, a partial cut where 50% of the forest canopy was removed, a clearcut where coarse woody debris (CWD) <10 cm in diameter was retained, and a clearcut where CWD was removed. Harvesting occurred from November 2003 to April 2004.

Before the experimental treatments were established, the forest consisted of mature mixed deciduous and coniferous stands (primarily balsam fir, *Abies balsamea*, eastern white pine, *Pinus strobes*, northern white cedar, *Thuja occidentalis*, red maple, *Acer rubrum*, eastern hemlock, *Tsuga canadensis*, red oak, *Quercus rubra*, and paper birch, *Betula papyrifera*), with the most recently harvested stands being at least 60 years old.

2.2. Field methods

We established drift fences and pitfall traps encircling each of the pools (hereafter termed “pool fences”). At these pool fences, a pair of pitfall traps were established every 5 m along the fence, with one trap on the outside, and one on the inside of the fence. Fences were also placed at 16, 50, 100, and 150 m into the silvicultural treatments (“terrestrial fences”). Each of these terrestrial fences was 10 m in length with a pitfall trap (two 0.45 kg coffee cans [~15 cm in diameter, 40 cm deep] duct-taped together) on each end and one on each side in the center. We established one fence at 16 m, 3 at 50 m, 6 at 100 m, and 9 at 150 m in each treatment at each site collectively covering 38% of the arc (Fig. 1). As the breeding pools were created at the start of the experiment, 70 spotted salamander *Ambystoma maculatum* egg masses were randomly assigned to each pool in May 2004. We collected eggs from wetlands surrounded by continuous forest and within 1 km of the study sites.

All captured animals were identified to species, and sexed where possible. We measured snout-vent (SVL) on marked

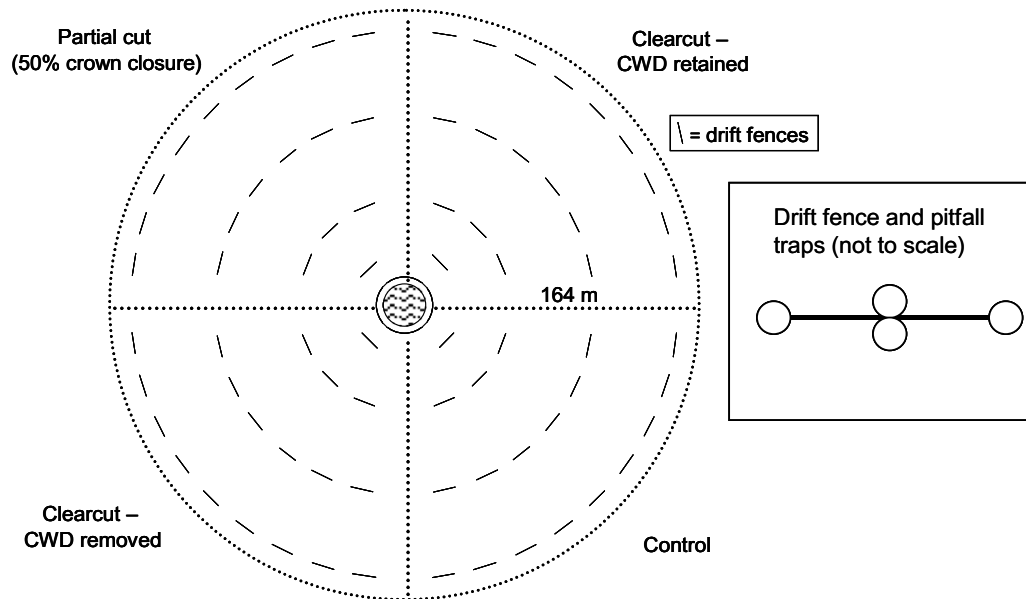


Fig. 1 – Representation of one of the four experimental arrays, showing position of the drift fences. The dotted lines represent boundaries between the forestry treatments and the outer perimeter of the array.

spotted salamander. Two periods of sampling were conducted each year: a shorter period starting when the first adults moved to the pools to breed in early spring and ending when the adults left the pools after breeding (termed “breeding migration”) and a longer period starting when the first metamorphs emerged from the breeding pools in late spring (“non-breeding period”). The latter period was longer in the first year of the study (2004) to ensure documentation of all movement of juveniles. We closed the traps between sampling periods. During the breeding migration, only the traps at the pool fences were opened (and traps at 16 and 50 m in 2005 as explained below), because the ground was still frozen and traps were difficult to open during the breeding migration. All traps were open continuously during the non-breeding period each year. Traps were checked every other day during both sampling periods. Data were analysed using Program R version 2.4.1. (R Development Core Team, 2006) with $\alpha = <0.05$ for all tests. Normality was assessed using the Shapiro-Wilk test. Where normality was violated, data were transformed via a natural logarithmic function ($X' = \ln[X + 1]$). For both parametric and non-parametric tests, array was used as a blocking variable.

2.3. Breeding migration

We collected data on adult spotted salamander movements during the breeding migration from 24 April to 6 May 2005 and 2 April to 20 April 2006, with capture data referring to salamanders entering the pools (as soon as the first salamanders were captured leaving the pool, outside traps were closed to avoid multiple captures of the same unmarked individuals). One array was not sampled in 2006 due to flooding of the traps. In 2005, we examined habitat use farther from the pools during adult migration by opening traps at the 16 and 50 m terrestrial fences and marking salamanders at the pool fences using visible implant elastomer (VIE) based on the

treatment they emerged into. Using batch rather than individual marks throughout this study means that we were unable to identify if we were recapturing the same animals. In previous research with wood frogs in the study area, multiple recaptures of the same individuals were very rare (<5%, Patrick, unpublished data).

We compared the frequency of captures of breeding adults at the edge of the pools in the four treatments in 2005 and 2006 using analysis of variance (ANOVA), excluding the array that was not sampled in 2006. The dependent variable used was the number of captures per trap (to account for slight differences in trap numbers among treatments).

Because our study pools were created at the start of our research and sex-dependent movement rates have been shown for our study species, we were also interested in looking at patterns of adult sex ratios during breeding. We used a three-way contingency table and the chi-square statistic to test if the frequency of captures of male and female adult salamanders were mutually independent of year and array (removing the array flooded in the 2006 breeding migration), followed by partial independence tests between factors if non-independence was found (Zar, 1999).

2.4. Non-breeding period

We gathered data on juvenile and adult habitat use outside the breeding season by opening traps at the pool and terrestrial drift fences from 30 June to 27 October 2004, 30 June to 13 September 2005, and 30 June to 20 August 2006. We captured and marked juvenile spotted salamanders emerging from the breeding pools using VIE to indicate the treatment they entered. We also captured unmarked spotted salamanders that did not originate from the study pools. These were not marked and were released on the opposite side of the fence to the point of capture.

To test for differences in recaptures of marked juveniles among the silvicultural treatments, we used Friedman's non-parametric ANOVA, because assumptions of normality could not be met (Zar, 1999). Unaltered frequencies were used as the dependent variable, as all traps were kept open during the period of juvenile emigration in the three years of the study (Patrick et al., 2006). We also compared the mean SVL of recaptured marked juveniles among the silvicultural treatments using parametric ANOVA.

For captures of unmarked salamanders (which we continued to capture outside of the period of juvenile emigration), we accounted for differences in trap effort between the study years by using captures per day as the dependent variable. To test for differences in captures of unmarked adults in the four treatments outside of the breeding season, we used Friedman's tests. To test for differences in captures of unmarked juveniles, we used parametric ANOVA, initially testing if there were a difference in frequencies of captures in each treatment between the three years of the study, followed by testing for differences among the four treatments.

3. Results

3.1. Breeding migration

We captured 641 adult spotted salamanders at the pool fences (mean total captures per array per year [± 1 standard deviation]: 2005 = 85.25 ± 54.91 , 2006 = 100 ± 78.17) (Table 1). Based on captures at the pool fences, adult spotted salamanders entering the breeding pools did not show a significant preference for any of the silvicultural treatments (mean captures per trap: control = 1.20 ± 0.74 , partial cut = 2.62 ± 1.47 , clearcut CWD retained = 3.03 ± 1.57 , clearcut CWD removed = 4.33 ± 4.20), with captures at the pool fences differing among arrays (ANOVA, $F_{2,3,6,12} = 45.93$, $P = <0.0001$), but not among treatments (ANOVA, $F_{2,3,6,12} = 1.82$, $P = 0.20$), or years (ANOVA, $F_{3,1,3,16} = 0.06$, $P = 0.81$). Of the 129 adults marked with VIE on leaving the pools in 2005, 8 (6.2%) were recaptured at the terrestrial 50 m fence: 6 in the partial cut, 1 in the control, and 1 in the clearcut with CWD removed.

When comparing the sex ratio of breeding adults, the three factors (sex, array, and year) were not mutually independent ($\chi^2_{10} = 31.93$, $P = <0.001$). Tests for partial independence showed that array was independent of sex and year ($\chi^2_7 = 6.55$, $0.50 < P < 0.25$), but that sex ($\chi^2_9 = 31.38$, $P = <0.001$) and year ($\chi^2_7 = 24.33$, $P = <0.001$) were interrelated. Removing site from the model, we found that the sex ratio varied between the two years of the study ($\chi^2_1 = 24.23$, $P = <0.01$). Comparing the observed male to female sex ratio with that expected under a null hypothesis of equal numbers of each sex, we found both years to be female-biased (2005: 4.3:1 F:M sex ratio, $n = 339$, $\chi^2_1 = 102.736$; 2006: 1.65:1 F:M sex ratio, $n = 300$, $\chi^2_1 = 18.253$, $P = <0.001$ for both years), but that the strength of the female bias had weakened in 2006.

3.2. Non-breeding period

We marked 1038 juvenile spotted salamanders at the pool fences (mean marks per year per array: control 25 ± 17.82 , partial cut 28.91 ± 19.88 , clearcut CWD retained 26.46 ± 21.50 , clearcut CWD removed 19.27 ± 15.76). Of these, 81 (7.8%) were recaptured at terrestrial fences (mean recaptures per year per array: control 5.67 ± 7.18 , partial cut 2.67 ± 2.92 , clearcut CWD retained 0.44 ± 0.53 , clearcut CWD removed 0.22 ± 0.44). We found a significant difference between the numbers of recaptures in each treatment ($\chi^2_{4,4} = 12.49$, $0.01 < P < 0.005$). Pairwise rank comparisons could not show a difference between treatments due to low statistical power, but 51 of the recaptures were in the control and 24 in the partial cut treatments, compared to only 4 in the clearcut with CWD retained, and 2 in the clearcut with CWD removed. Thirteen of these recaptures were at the 16 m fences, 35 at 50 m, 22 at 100 m, and 9 at 150 m (Table 2).

We captured 314 adult spotted salamanders during the non-breeding period from 2004 to 2006 (mean captures per sample day per array: control 0.09 ± 0.13 , partial cut 0.07 ± 0.08 , clearcut CWD retained 0.05 ± 0.08 , clearcut CWD removed 0.03 ± 0.05). Analyses of captures of adults for each of the three field seasons revealed no significant differences between treatments (Friedman's non-parametric ANOVA:

Table 1 – Captures of breeding adult spotted salamanders at the pool fences in traps bordering each of the four forestry treatments [control, partial cut (PC), clearcut with CWD retained (CWD Ret), and clearcut with CWD removed (CWD Rem)] in 2005 and 2006

Site	Silvicultural treatment ^a									
	Control		PC		CWD Ret		CWD Rem		Total	
	2005	2006	2005	2006	2005	2006	2005	2006	2005	2006
Gilman	13	33	32	22	20	28	35	33	100	106
N. Chemo	8	na	22	na	9	na	36	na	75	na
S. Chemo	23	22	46	37	48	46	32	70	149	175
Smith	6	5	6	6	3	8	2	0	17	9
Total	50	50	106	65	80	82	105	103	341	300

Data only include salamanders migrating into the breeding pools. Data are unavailable for the N. Chemo site in 2006 due to flooding of pitfall traps.

^a PC = partial cut, CWD Ret = clearcut with coarse woody debris (<10 cm diameter) retained, CWD Rem = clearcut with coarse woody debris removed.

Table 2 – Marked juvenile spotted salamanders recaptured at different distances from pools ($n = 4$) in 2004–2006

Distance (m)	Silvicultural treatment ^a				Total
	Control	PC	CWD Ret	CWD Rem	
16.6	6	4	3	0	13
50	23	12	0	2	35
100	15	7	0	0	22
150	7	1	1	0	9
Total	51	24	4	2	81

a PC = partial cut, CWD Ret = clearcut with coarse woody debris (<10 cm diameter) retained, CWD Rem = clearcut with coarse woody debris removed.

$\chi^2_{4,4} = 5.7, -0.23, 1.28; P = >0.1, >0.99, >0.75$ for 2004, 2005, and 2006 respectively).

We captured 2762 unmarked spotted salamanders during the study (mean captures per sample day for each array \pm std. dev.: control 1.50 ± 1.48 , partial cut 0.68 ± 0.54 , clearcut CWD retained 0.34 ± 0.28 , clearcut CWD removed 0.28 ± 0.30). Captures of unmarked juveniles differed among the four treatments (ANOVA: $F_{3,2,6,36} = 5.66, P = 0.003$) but not among the three years of the study (ANOVA: $F_{3,2,6,36} = 0.23, P = 0.79$). With year removed from the model, unmarked captures were found to differ significantly between both treatments (ANOVA: $F_{3,3,9,32} = 11.00, P = <0.001$) and arrays (ANOVA: $F_{3,3,9,32} = 7.73, P = <0.001$). Significantly more juveniles were caught in the control compared to the two clearcuts (Tukey post-hoc tests, $P < 0.05$), but there were no significant differences between other treatments.

Snout-vent length (SVL) of recaptured marked juveniles did not differ among the four terrestrial treatments (mean SVL [mm]: control 25.35 ± 3.56 , partial cut 26.0 ± 3.23 , clearcut CWD retained 25.75 ± 3.78 , clearcut CWD removed 27.5 ± 3.54) (ANOVA: $F_{3,72} = 0.38, P = 0.77$).

4. Discussion

4.1. Pool colonization and spatial population structure of spotted salamanders

Rates of pool colonization have been shown to be dependent on pool isolation, levels of philopatry, size of nearby populations, and dispersal ability (Gamble et al., 2007; Laan and Verboom, 1990; Pechmann et al., 2001). Ambystomatid salamanders typically show high philopatry and are relatively slow to colonize new habitats in comparison to other pool-breeding amphibian species (Pechmann et al., 2001; Scott, 1994; Semlitsch, 1981; Semlitsch et al., 1988; Vasconcelos and Calhoun, 2006). In contrast to these studies, breeding adult spotted salamanders in our study were abundant in the year following creation of the pools (between 13 and 16 months after excavation). At all of our pools, the number of breeding adults captured represents at least an order of magnitude more than the number breeding at the location prior to construction (inferred from egg mass counts). Thus, we can be quite confident that most of the adults breeding in our pools had originated from other breeding pools.

Where did these spotted salamanders come from? In comparison to previous colonization studies from the southeast-

ern United States (Pechmann et al., 2001; Semlitsch, 1981), terrestrial habitat in our study area is more suitable for amphibian movement (Rittenhouse et al., 2007; Rothermel and Semlitsch, 2002), with an abundance of moist forested lowlands, relatively consistent and frequent rainfall, and low summer temperatures (National Weather Service, 2007). Spotted salamanders in this area primarily breed in vernal pools and larger beaver-created wetlands, but will also make use of roadside ditches and ruts created by logging (DiMauro and Hunter, 2002). All of these habitats are relatively transient, resulting in temporal variability in the location of breeding sites. Thus, our region is characterized by conditions where terrestrial movement of spotted salamanders is less stressful compared to many places where amystomatids are found, and where strong philopatry and breeding site fidelity may not be a selective advantage.

We also observed a clear female-skewed sex-ratio in our breeding adults (4.3:1 F:M in initial colonization year, and 1.65:1 in year 2). Spotted salamander breeding populations are typically male-skewed (Sexton et al., 1990), but female spotted salamanders tend to move farther from pools than males (Faccio, 2003; McDonough and Paton, 2007; Regosin et al., 2003). The increased movement range of females may result in a greater chance of their coming into contact with novel breeding sites such as the study pools. If the differential movement translates into differences in the breeding sex ratio of spotted salamanders (as would be the case in a newly colonized pond), there may be consequences for recruitment. Where sex ratios are highly female-skewed, some females might remain unfertilized. However, most female spotted salamanders have been shown to collect multiple spermatozoa during a single breeding event (Myers and Zamudio, 2004), suggesting that a reduced number of males may not change fertility rates.

Our pool colonization data suggest that spotted salamanders are abundant in the study area, and will breed in suitable habitat they encounter during terrestrial movement. Our data also suggest that females are more likely to colonize new sites but the resulting female-skewed sex ratio may not be enough to affect population dynamics. Given these findings, local breeding populations of spotted salamanders within continuous forest are unlikely to be defined by individual breeding sites. These results support the findings of recent studies of the spatial distribution of pool-breeding amphibian populations (Marsh et al., 1999; Petranka et al., 2004; Smith and Green, 2005).

4.2. The effects of silviculture on habitat use

Previous research into terrestrial habitat use by spotted salamanders has shown a high sensitivity to canopy removal for both adult and juveniles (deMaynadier and Houlahan, 2007; Rittenhouse and Semlitsch, 2006; Rothermel and Semlitsch, 2002). In contrast, our results show a clear difference between the sensitivity of juvenile and adult spotted salamanders to terrestrial habitat change. As in previous research, juvenile spotted salamanders were sensitive to canopy removal (deMaynadier and Hunter, 1998; Rittenhouse and Semlitsch, 2006; Rothermel and Semlitsch, 2002), with lower abundance of both marked and unmarked juveniles in the clearcuts compared to the uncut controls, and some evidence of a reduction in abundance of unmarked spotted salamanders in the partial cuts. Furthermore, fewer juvenile spotted salamanders emigrated through the clearcut treatments, with a single recapture > 100 m from the pool in the three years of the study versus 30 recaptures in the control and partial harvest (Table 2).

In contrast to juveniles, adult spotted salamanders in our study were more tolerant of forest harvesting with no statistical differences seen in captures among treatments. Adult spotted salamanders are relatively mobile, moving over 150 m in a single night (Madison, 1997), and previous research has shown that they are capable of crossing open areas such as golf courses (McDonough and Paton, 2007) and roads (Gibbs and Shriver, 2002). Based on previous research, juveniles are unlikely to be able to make long-distance crossings through open areas (Rothermel and Semlitsch, 2002).

4.3. Management implications

Our combined results help in understanding the likely effects of silviculture on spotted salamanders in our study area. Our data suggest that before any changes to natural habitat in the study area, spotted salamanders are likely to move widely through the moist forested lowlands, with local breeding populations occupying groups of sites close together, and rapidly colonizing new sites. Silvicultural practices similar to those in the study design (i.e., small-scale [~2 ha] cuts surrounded by mature forest) are unlikely to result in major changes in these patterns for adult spotted salamanders, but will result in changes in patterns of abundance and movement of juvenile spotted salamanders.

Previous research has shown that reduced juvenile abundance in clearcuts could be due to both emigration into closed-canopy forest (Rittenhouse and Semlitsch, 2006), or to higher mortality in open-canopy areas (Rothermel and Semlitsch, 2002). Emigration from clearcuts would increase the density of spotted salamanders in the remaining area of forested habitat, potentially resulting in increased density-dependent mortality (Harper, 2007; Harper and Semlitsch, 2007). Bearing in mind the sensitivity of amphibian populations to changes in vital rates of terrestrial life-history stages (Vonesh and De la Cruz, 2002), any changes in juvenile survival could reduce the probability of long-term persistence.

The single juvenile recaptured at or beyond 100 m from the pool in clearcut habitat suggests that successful juvenile dis-

persal between pools through such habitat is likely to be greatly reduced, potentially increasing genetic isolation, and reducing the probability of recolonization (Hanski, 1999). Frequent movement of adults between pools within a local population, and the higher tolerance of these adults to habitat change may negate some of these effects at the local population level. If juvenile amphibians are the dispersing life-history stage, however, reduced dispersal may have consequences for regional populations persistence. Given the differences in how juvenile and adult spotted salamanders are affected by silviculture, determining the contribution of these life-history stages to dispersal is a vital next step in research.

Our research also has clear implications for the creation of pools during wetland mitigation. In places similar to our study area, where abundant breeding sites are surrounded by suitable terrestrial habitat, colonization of created pools is likely to be rapid. Many of the spotted salamanders colonizing new pools, however, are likely to be individuals that were intercepted in their normal terrestrial movement. If the created pool is not suitable breeding habitat, this may result in a decrease in the reproductive output of these individuals (DiMauro and Hunter, 2002). Alternatively, our results suggest that if created pools are suitable, placing pools in close proximity to known breeding sites may result in rapid colonization.

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