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An experimental assessment of buffer width: Implications for salamander migratory behavior

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ABSTRACT

Upland buffer zones are the primary proposed management tool for vernal-pool-breeding amphibians; however, experimental validation of the utility of buffers is lacking. We used clear cutting to experimentally manipulate upland buffer widths at 11 vernal pools in east-central Maine. Each pool was randomly assigned to one of three possible treatments: >1000-m buffer, 100-m buffer, or 30-m buffer. We radio-tracked 40 adult spotted salamanders at these pools and modeled their migratory behavior with mixed-effects regression. Mean maximum distance salamanders moved from their breeding pool was 106.0 ± 15.4 m (range = 1.6–427.6 m). Salamanders were able to enter and cross clear cuts. We observed differences in migratory behavior between the 100-m buffer and reference treatments and between forest and clear-cut habitat; however, weather conditions and a salamander's distance from the vernal pool strongly mediated the impact of buffer treatment on migration behavior. Our findings indicate that clear cuts are semi-permeable to adult spotted salamanders, but that degree of permeability and the effects of buffer treatment largely depend on weather conditions.

1. Introduction

Sustainable forest management has become a priority for forest managers world-wide (UN General Assembly, 1992, 2007) and requires balancing competing interests including harvest, recreation, and maintenance of ecosystem services and biodiversity (UN FAO, 2005). Since the 1970s, the international community has recognized the vital role that wetlands play towards achieving sustainability (Ramsar Info Paper No. 2, 2008). Wetlands are particularly important for preserving biodiversity, since 12% of global wildlife species depend on freshwater wetlands for some portion of their lifecycle (The Ramsar Bureau, 2001). Though large percentages of wetland-dependent species require adjacent uplands during critical life history stages (e.g., Boyd, 2001; Gibbons, 2003; Roe et al., 2006), only recently have the inextricable connections between wetlands and their surrounding landscapes gained significant attention (Semlitsch, 1998; Gibbons, 2003; Talley et al., 2006). Given the links between uplands, wetlands, and sustainability, an emerging objective for forest managers is to understand how upland management activities impact wetland-dependent species.

Upland forest alteration may modify both the quality and permeability of forested habitat patches, affecting a species' capacity for patch use (Hanski and Gilpin, 1991; Begon et al., 1996; Guerry and Hunter, 2002). Anthropogenic habitat fragmentation often creates habitat edges that are more permanent and less permeable than those created by natural disturbances (den Boer, 1970; Hansen et al., 1991; Noss and Cooperrider, 1994; Marsh and Trenham, 2001). Forest clear cutting is an intense, but non-permanent, form of anthropogenic habitat disturbance. Clear cutting can be highly detrimental to individual species (e.g., Ash, 1988, 1997; Petranka et al., 1993, 1994; Herbeck and Larsen, 1999; Knapp et al., 2003), but can also reset succession, possibly enabling greater diversity across a landscape and through time (Enge and Marion, 1986; Cromer et al., 2002; Renken et al., 2004). Where cutting exceeds the natural disturbance regime, however, species which find clear cuts inhospitable may not persist in a region because the migration and dispersal processes of these species may be disrupted (Hunter, 1990; Bunnell, 1995; McGee et al., 1999).

1.1. Focal species

Spotted salamanders (*Ambystoma maculatum*) are found throughout much of eastern North America and use forested uplands for refuge, overwintering, and foraging during about 95% of the year (Semlitsch, 1998), but migrate annually from the uplands to breed in vernal pools (i.e., isolated wetlands). This species can use non-forested areas, but is generally averse to edges and open habitat (e.g., Gibbs, 1998b; Montieth and Paton, 2006; Rittenhouse and Semlitsch, 2006). Salamander abundance tends to decrease with increasing canopy removal and across forest-clear cut edges

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(deMaynadier and Hunter, 1998, 1999; Renken et al., 2004; Patrick et al., 2006, 2008; but see Morris and Maret, 2007). The likelihood of a salamander migrating through a clear cut may depend on the cut's configuration; geographic location; landscape and historical context; habitat-edge permeability; salamander size, sex, and age (Windmiller, 1996; Faccio, 2003; Regosin et al., 2005); and weather conditions (Douglas and Monroe, 1981; Sexton et al., 1990; Madison, 1997; Vasconcelos and Calhoun, 2004).

Though much is known about spotted salamander habitat requirements, it is still unclear how its movements are affected by forest harvests. Leaving forested buffers around vernal pools is the most common approach to managing vernal pool ecosystems in eastern North America, and buffers have been integrated into many state policies (e.g., ME, 1993, 2002; MA, 2005). Semlitsch (1998) suggested that a biologically-based upland buffer zone of 164.3 m around vernal pools would protect 95% of the local salamander population. Recent research suggests that greater buffer widths may be necessary (Faccio, 2003; Montieth and Paton, 2006; McDonough and Paton, 2007; Rittenhouse and Semlitsch, 2007). Calhoun and deMaynadier (2004) provide forestry-specific guidelines with a two-tiered buffer and different activities allowed at varying distances from the pool. Although the use of buffers has been widely suggested as a viable management approach, experimental validation of the benefits of buffers is lacking.

1.2. Improved statistical technique

Radiotelemetry is a popular method used to study migratory movements and habitat use. Typically, radiotelemetry data are analyzed using *t*-tests, analyses of variance (ANOVAs), or their nonparametric equivalents (e.g., Madison, 1997; Faccio, 2003; Montieth and Paton, 2006; McDonough and Paton, 2007). There are several problems, however, with past analyses of radiotelemetry data. First, most studies focus on summary statistics, ignoring the wealth of data available from individual tracking events. Where individual tracking events are examined (e.g., Madison, 1997), three further problems arise. First, typical analyses assume that repeated observations of each individual are statistically independent. While observations may be independent if the inter-observation period is sufficiently long, this does not occur in practice (Madison, 1997; Faccio, 2003; Montieth and Paton, 2006). The resultant inter-observation correlation violates test assumptions and can obscure data patterns. The typically-used techniques are also ill-equipped to deal with highly unbalanced data (e.g., where repeated measures were not taken at the same points in time for all individuals or at equal intervals for any one individual) and between-subject variability (i.e., variability attributed to unique differences between individuals). When present, these data characteristics can confound effects and obscure underlying population-level patterns.

Generalized linear mixed-effects modeling (GLME) is an alternative analytic technique used to examine time-series data in other disciplines (e.g., Pinheiro and Bates, 2000; Andreozzi et al., 2006) and has recently been applied in ecological studies (e.g., Cooper et al., 2002; Venables and Dichmont, 2004). Because GLME allows the analyst to model both fixed and random effects, separate between-group from between-subject variability, use unbalanced data, and specify the variance–covariance matrix (i.e., to model serial correlation and heterogeneous variance), GLME effectively addresses past limitations of, and provides a preferable analytic framework for radiotelemetry analyses.

1.3. Objectives

To determine the usefulness of buffer zones and the short-term impacts of clear cutting on spotted salamander migration and upland habitat use, we used clear cutting to experimentally manipulate upland buffer widths at vernal pools. We then used radio-telemetry and GLME to observe and analyze the interactions between clear cutting and buffer zones and their effects on: (1) the odds of salamander movement; (2) the rate of salamander movement (i.e., meters moved per day); and (3) the straight-line distance of a salamander from the edge of its breeding pool, on any given day during the tracking period.

2. Methods

2.1. Study site

We conducted this research in east-central Maine (latitude: 44°60′N, 44°48′N; longitude: 68°26′W, 68°02′W). The landscape is characterized by moderate hills and abundant wetlands, including numerous vernal pools. The forest is actively-logged second-growth, dominated by mixed hemlock (*Tsuga canadensis*)-hardwood (*Fagus grandifolia, Acer saccharum, Betula alleghaniensis*) at lower elevations, and balsam fir (*Abies balsamea*) and red spruce (*Picea rubens*) at higher elevations. In 2002, we located 300 vernal pools in this landscape and selected 40 of similar size (i.e., 0.1–0.3 ha) and surrounding forest (i.e., uncut within 1000 m), for which we conducted egg mass counts in spring 2003. Of these 40 pools, we identified 35 with breeding populations of both wood frogs (*Lithobates sylvaticus*) and spotted salamanders and hydroperiods of at least five months post-ice out. From these 35 pools, we randomly selected 12 for inclusion in this study. During the first field season, we discovered that one of the 12 pools had a permanent inflow, and subsequently eliminated this pool from the study.

2.2. Buffer creation

Between September 2003 and March 2004, the landowner created the study buffers by clear cutting forest around selected vernal pools. Clear cutting involved mechanically-removing all merchantable trees of $\geqslant 5$ cm diameter at breast height and slash, though an incidental amount of woody debris remained. We randomly assigned each pool to one of three possible treatments: >1000-m buffer (i.e., a reference or uncut treatment), 100-m buffer, or 30-m buffer. In the two cut treatments, we left intact an upland buffer of 100 m and 30 m, respectively, immediately adjacent to the vernal pools and then created a concentric 100-m-wide clear cut around the buffer (Fig. 1). We based buffer widths on extant Best Management Practices, laws, and the literature (Semlitsch, 1998; Calhoun and deMaynadier, 2002; M.G.L. c. 131, § 40). Once

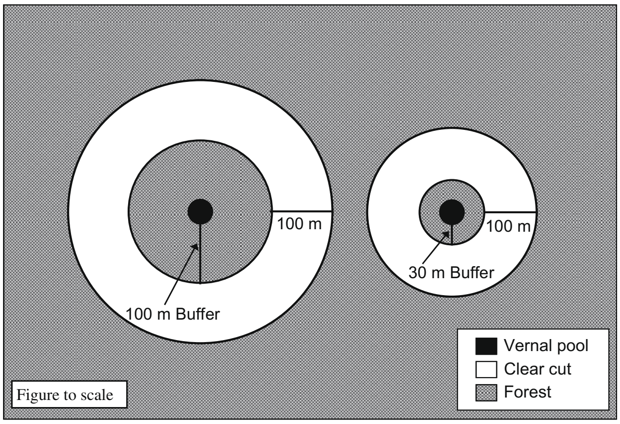

Fig. 1. Experimental design implemented at 11 vernal pools in east-central Maine. Clear-cut treatment buffers were either 100 m (left; $n = 4$) or 30 m (right; $n = 4$) wide. Clear cuts were 100 m wide. Beyond the clear cut was undisturbed forest. No cutting occurred at reference vernal pools (not shown; $n = 3$).

cutting was complete, we used a Trimble Pathfinder Pro XR GPS unit (Trimble Navigation Limited, Sunnyvale, CA; accurate to 0.5 m) and ArcViewGIS 3.3 (Environmental Systems Research Institute, Inc., Redlands, CA) to map study pool perimeters, buffers, and clear cuts.

2.3. Radiotracking

We tracked 40 adult spotted salamanders (21 in 2004, 19 in 2005; 25 females, 15 males) using radio-telemetry. We captured study salamanders as they were leaving the pools after breeding (i.e., from mid-April to early May), in pitfall traps placed along drift fence arrays encircling each pool. We only selected salamanders that weighed more than 13 g so that an implanted transmitter would not exceed 14% of a salamander's mass (Madison, 1997; Faccio, 2003). To the extent possible, we selected equal numbers of females and males, and equal numbers from each treatment and vernal pool. Ultimately, we tracked 13, 21, and 6 salamanders in the reference, 100-m, and 30-m treatments, respectively. While GLME is robust to unbalanced designs (Pinheiro and Bates, 2000), we note that the small sample size for the 30-m treatment may have limited our ability to detect statistical differences between the 30-m and other treatments.

In the lab, we surgically implanted a radio-transmitter into each selected salamander (transmitter mass: 1.8 g; model: BD-2H, Holohil Systems LTD, Carp Ontario, Canada; Madison, 1997; Faccio, 2003). Post-surgery, we allowed each salamander to recover for about 24 h in a plastic bucket containing damp paper towels. We then returned each salamander to a natural burrow located 1–3 m from the trap where it was caught, outside the fence encircling its breeding pool. Mid-summer, when transmitter batteries were nearing depletion, we recaptured the radio-tagged salamanders and replaced their transmitters. After recovery, we returned each salamander to the burrow whence we removed it or to a burrow within 0.25 m of that location if salamander retrieval rendered its former burrow unusable. In the fall, we excavated salamanders prior to the first hard freeze, permanently removed their transmitters, and returned each salamander to the field as described above.

We radiotracked the salamanders from 2 May to 7 November in 2004 and from 27 April to 28 October in 2005. We based starting and ending dates on salamander migration dates and weather conditions. In 2004, we recorded the position of all radio-tagged individuals, on average, every 6 days (range = 1–29 days). In 2005, the average radiotracking interval was 2.5 days (range = 1–23 days). We tracked salamanders with a Communications Specialists Inc. (Orange, CA) R1000 receiver and a hand-held, 3-element Yagi antenna. We used direct overhead localization to pinpoint salamander locations to within 10 cm (Madison, 1997). At each location, we noted the general habitat type (i.e., forest or clear cut). We also recorded each location with a Trimble Pathfinder Pro XR GPS unit and mapped the location using GIS. For each salamander, we then calculated the distance between each pair of consecutive locations, and between each location and the nearest point on the vernal pool trap line.

We obtained daily precipitation and air temperature data from the nearest functional National Climatic Data Center station. This station is located in Wesley, Washington County, Maine and is between 20 and 60 km from our vernal pools.

2.4. Data analysis

To test for treatment effects on salamander fate (i.e., alive, dead, or missing at the study's end) and the number of days tracked per salamander, we conducted ANOVAs in SPSS 15.0 for Windows (SPSS Inc., 2006). We then created three mixed-effects regression models, each capable of predicting different aspects of daily salamander movement, using the "GLME" and "LME" functions in the correlatedData library of S-PLUS 7.0 Enterprise Developer (Insightful Corporation, 2005). We modeled movement-odds using mixed-effects logistic regression. We classified a salamander as having moved if it was $\geqslant 1$ m from its last location. We modeled movement rate using mixed-effects Poisson regression, with distance moved as the outcome variable and log (number of days since a salamander was last tracked) as the offset. We analyzed movement-odds and rate separately because the number of days when salamanders did not move (i.e., migration rate was 0 m/day) was too great for movement to be described by any single distribution. Such zero-inflated data are better described by a mixture of distributions (Lambert, 1992; Hall, 2000). We used logistic regression to examine differences between movement and no-movement days, then removed the no-movement days and modeled migration rate with Poisson regression. Finally, we modeled distance-from-the-pool using mixed-effects linear regression.

In mixed-effects regression, fixed effects are parameters that apply to the entire sample population, describe experimental treatments, or are suspected sources of systematic variance (e.g., buffer treatment; Pinheiro and Bates, 2000). Random effects, however, apply only to individual sampling units (i.e., subjects), randomly drawn from the population (Pinheiro and Bates, 2000). Random effects are used to account for within-subject correlation that arises because a subject's behavior depends partly on the subject's unique characteristics, some of which are unobserved and cannot be accounted for by other predictors (Landau and Everitt, 2004). If random effects are not correctly specified, then one cannot assume that outcome observations are independent (Landau and Everitt, 2004) or that variance attributed to fixed effects is properly quantified (Pinheiro and Bates, 2000). Random effects consist of intercepts and/or slopes. For random intercepts, a different intercept is estimated for each random-effects subject. Random intercepts indicate how much a subject's mean outcome differs from the mean outcome for all subjects combined (Pinheiro and Bates, 2000). A random slope is similar to an interaction: a unique regression slope (based on a user-defined variable) is fit for each subject (Landau and Everitt, 2004). For telemetry studies, assigning random intercepts to individual animals is a useful starting point for the model-building process.

As discussed in Bolker et al. (2009), methods for fitting GLMEs are still an active area of statistical research, and the approach one takes (i.e., iterative model building, a priori model selection, or Bayesian methods) depends more on the researcher's philosophy than statistical correctness. We used an iterative process to develop our three models. For each model, we started with the same pool of 23 potential fixed effects and 19 potential random effects (Appendix A). By the end of the process, we had distinguished a unique subset of these effects for each of our three models. Potential fixed effects described treatment, time, weather, and physical parameters of both salamanders and habitat, and were derived from past research on salamander movement. To select among these fixed effects, we conducted a manual, step-wise regression, using individual salamander as the default random-subject parameter. We assessed the relative importance of each predictor using plots of fitted versus observed values, plots comparing predicted values between successive models, biological relevance, marginal ANOVAs, *t*-tests (for dummy variables representing categorical predictors), effect coefficients, and effect confidence intervals.

After the fixed effects were determined, we refined the random effects, comparing models with different random-subject variables, intercepts, and slopes using likelihood ratio tests (LRTs) and Akaike Information Criteria values (AIC; Sakamoto et al., 1986; Appendix A). Ultimately, for the movement-odds model, we assigned a random slope to each salamander based on numbers of days between tracking events. For the migration-rate model, we assigned random intercepts to each salamander. For the distance-from-the-pool model, we assigned a random slope to each salamander based on log (cumulative days tracked).

After refining the random effects, we modeled the variance/covariance structure in a two-part process. First, we fit the correlation structure. We suspected that repeated measures for each salamander were not independent, such that observations closer together in time were more highly correlated than observations farther apart in time (Pinheiro and Bates, 2000). To account for repeated-measure correlation, we used empirical autocorrelation function plots, LRTs, and AIC to compare models with different auto-regressive and/or moving average correlation structures. Ultimately, we modeled within-salamander correlation as a second-order autoregressive process with day of the year as the time variable for the movement-odds model, and as a first-order autoregressive process with cumulative days tracked as the time variable for the migration-rate and distance-from-the-pool models. Second, we modeled the variance structure, using residual plots to examine within-group variance patterns. For heteroscedastic variances, we used LRTS, AIC, and confidence intervals to select the appropriate variance structure. In general, each fixed effect listed in Appendix A was tested as a possible variance covariate; and fixed, identity, and exponential variance functions were compared (Pinheiro and Bates, 2000). The movement-odds model showed homoscedastic variance, but we observed heteroscedastic variance for the migration-rate and distance-from-the-pool models. We ultimately modeled within-salamander variance as a linear function of maximum temperature during the week preceding a tracking event for the migration-rate model; and as an exponential function of maximum temperature during the 48 h preceding a tracking event, with separate variances for each year, for the distance-from-the-pool model. To completely correct heteroscedasticity for the distance-from-the-pool model, we also log-transformed two of the model parameters (Table 4).

After fitting the variance/covariance structure, we used a process that mimicked fixed-effects selection to assess the need for first-order interactions. We tested only interactions we thought were biologically plausible, using only fixed effects as interaction terms. We then verified that the random and fixed effects and the correlation and variance structures were still valid, and assessed whether the model satisfied GLME assumptions. Finally, we used marginal ANOVAs to determine the contributions of individual predictors to each final model. All three models violated the assumption of normally-distributed random effects, despite attempts to normalize random effects (Pinheiro and Bates, 2000). Since the fixed effects structure is relatively robust to violations of this assumption (Venables and Dichmont, 2004) and since no a priori hypotheses were made with respect to random effects, however, it was reasonable to ignore the violation and infer from the fixed effects portions of the models. For each model, all other assumptions were satisfied. Overall the models fit the data reasonably well. For the final movement-odds model, 79% of cases were correctly classified as having moved or not moved. Fitted versus observed plots for the other two final models showed that the migration-rate model tended to slightly underestimate movement rates (Fig. 2), but the distance-from-the-pool model reproduced observed results relatively well (Fig. 3).

Although mixed-effects regression can be used for a priori hypotheses testing, we applied it to an exploratory study of a relatively-large predictor set. We did not adjust *p*-values to account for the potential increase in Type I error that may occur with large predictor sets, so results may overestimate the significance of individual predictors.

Three additional issues arose during the analysis. First, log (cumulative days tracked) and cumulative precipitation fallen since tracking of the salamander started were both significantly predictive of distance from the pool. These two variables were also strongly correlated ($r = 0.87$). Correlation between fixed-effects is only problematic, however, when the significance of one fixed effect depends on whether another fixed effect is included in the model. If both fixed-effect variables are simultaneously significant (as in our case), then both should be retained in the model regardless of their correlation (McCullagh and Nelder, 1989; Neter et al., 1990; Kennedy, 1992). The risk incurred from the high correlation is that of greater uncertainty as to the exact values of the coefficients for each variable. Where the two variables are positively correlated (as in our case), then the coefficients for the two variables could be increased or decreased in tandem, and the model would still fit the data relatively well.

Second, salamanders were sometimes not re-located for long periods (e.g., several weeks; due to equipment failure and/or weather constraints). We assumed each salamander used the whole between-observation period to move the recorded distance. Data from other salamanders suggest, however, that during the missing interval, salamanders likely moved at quicker rates on some days and not at all on other days. Thus, our models likely underestimate salamander movement rates.

Third, of the 40 salamanders tracked, 23 dropped out of the study (i.e., disappeared and could not be tracked) before mid-October (Appendix B). Though all but one of the 30-m treatment

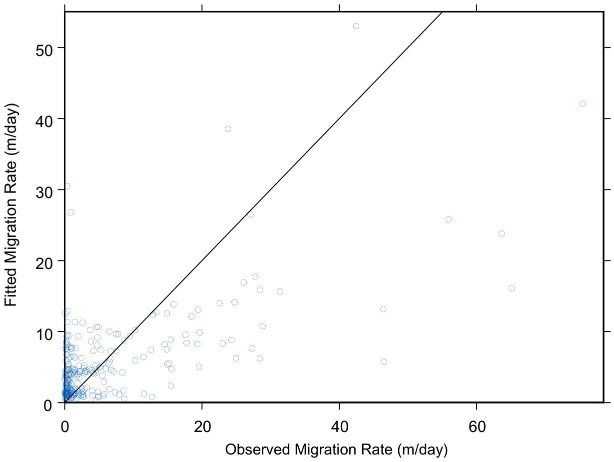

Fig. 2. Fitted migration rate (m/day) versus observed migration rate (m/day) for spotted salamanders at 11 vernal pools in east-central Maine.

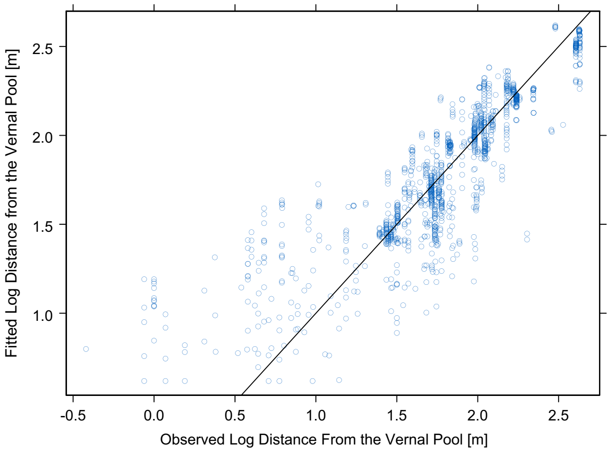

Fig. 3. Fitted log (distance from the vernal pool [m]) versus observed log (distance from the vernal pool [m]) for spotted salamanders at 11 vernal pools in east-central Maine.

salamanders were drop-outs, we did not find a significant difference between treatments with respect to salamander fate (i.e., alive, dead, or dropped-out; $F_{(2,37)} = 0.406$; $p = 0.669$). We do not know whether drop-out salamanders died, remained stationary but undetectable, or moved beyond the search area. We were thus unable to classify and model drop-out bias. Reduced sample size due to drop-out may have led to decreased statistical power at the ends of the tracking seasons. We tried to compensate for drop-out by testing interactions between day of the year and treatment, and between season and treatment. These interactions were not significant, indicating that, with respect to slope of the regression lines, drop-out and non-drop-out salamanders behaved similarly across treatments. We had no good method, however, to test for potential differences in regression-line length between drop-out and non-drop-out salamanders across treatments. Nevertheless, GLME is robust to unbalanced sampling over time (Pinheiro and Bates, 2000). Further, the fall season is important from a natural history perspective, because salamanders sometimes undertake significant fall movements (Madison, 1997; Faccio, 2003; Regosin et al., 2005; McDonough and Paton, 2007). For these reasons, we determined it was important and justified to analyze our fall data, and so included all 40 salamanders in our analysis.

3. Results

We recorded 1357 salamander locations (i.e., fixes) for 40 salamanders over two years. We tracked 13, 21, and 6 salamanders in the reference, 100-m, and 30-m treatments, respectively (Appendix B). The number of days each salamander was tracked did not differ between treatments ($F_{(2,37)} = 0.342$; $p = 0.712$). Mean maximum distance from the vernal pool was 106 ± 15.4 m (range = 1.6–427.6 m; Table 1). Mean migration rate was 5.6 ± 0.63 m/day (range = 0.08–75.5 m/day). Salamanders entered and crossed clear cuts, though behavior with respect to cuts varied between years. Among the 14 clear cut-treatment salamanders tracked in 2004, 29% entered clear cut areas, but none completely crossed a cut area. Two of these 14 salamanders were still in the buffer when they dropped out of the study in May (one salamander was lost and the second was eaten by a garter snake), however, and might have entered the clear cut if they were tracked longer. Among the 13 clear cut-treatment salamanders tracked in 2005, 77% entered, and 46% completely crossed, the clear cut. Mean percent of time, and mean duration, spent in the clear cut by salamanders at cut-treatment pools were 27.2 ± 7.2% (range = 0–99%) and 30.7 ± 9.1 days (range = 0–167 days), respectively. Salamander migratory paths varied widely, even at a single wetland (see Appendix C for examples of salamander pathways).

3.1. Odds of salamander movement

Salamander movement-odds differed between the 100 m and reference treatments (Table 2; Fig. 4). At low cumulative precipitation, salamanders were more likely to move in the 100 m treatment; however, above about 390 mm of cumulative precipitation, salamanders were more likely to move in the reference treatment. This volume of precipitation fell by mid-August in 2004 and early August in 2005. The main effect of the 30-m treatment was not significant, but the interaction between cumulative precipitation and the 30-m treatment was marginally significant ($t_{(1246)} = -1.714$, $p = 0.087$). Both the main effect and interaction with cumulative precipitation were significant for the 100-m treatment ($t_{(36)} = 2.735$, $p = 0.010$; $t_{(1246)} = -2.677$, $p = 0.008$, respectively). The lack of significance at the $\alpha = 0.05$ level for the 30-m treatment may be due to small sample size and low power or because the effect of a 30-m buffer is truly similar to that of the uncut treatment. In general, though, these results suggest that with increasing cumulative precipitation, movement-odds at the treated sites decreased relative to the odds for the uncut, reference sites.

Salamander movement-odds were also negatively correlated with the previous week's minimum temperature. On average, for every 1 °C increase in the previous week's minimum temperature, movement-odds decreased by a factor of 0.92. Similarly, in 2005, movement-odds were negatively correlated with the previous week's maximum temperature (Fig. 5). On average, for each 1 °C increase in the previous week's maximum temperature, movement-odds in 2005 decreased by a factor of 0.94. In 2004, however, previous-week-maximum-temperature and movement-odds were positively related, such that for every 1 °C increase in maximum temperature, movement-odds increased by a factor of 1.06.

3.2. Migration rate

Salamander migration rate was positively correlated with the volume of precipitation fallen during the week preceding a tracking event (i.e., weekly precipitation), but negatively, and less strongly, correlated with cumulative precipitation (Table 3). For every 1 mm of weekly precipitation, salamander migration rate increased by a factor of 1.01. Conversely, for every 1 mm increase in

Table 1
Summary of tracking statistics describing movements for 40 adult spotted salamanders at 11 vernal pools in east-central Maine.

All Pools				
	Mean[a] ± SE		Range	
Number of fixes	34 ± 3.8		2–80	
	All salamanders	*Salamanders tracked through mid-October*	*All salamanders*	*Salamanders tracked through mid-October*
Max. distance from pool (m)	106.0 ± 15.4	118.4 ± 25.9	1.6–427.6	32.2–427.6
Max. cumulative dist. moved (m)	140.4 ± 18.0	166.0 ± 30.6	6.0–593.0	64.5–593.0
Final location dist. from Pool (m)	99.1 ± 14.2	105.6 ± 22.8	1.0–405.9	15.9–405.9
Length of individual migratory movement, by season (m)				
spring	28.3 ± 3.7	28.8 ± 5.5	0.10–271.0	0.10–271.0
summer	3.3 ± 0.7	2.8 ± 0.6	0.01–80.8	0.01–44.5
fall	7.0 ± 1.7	7.3 ± 1.8	0.03–127.3	0.03–127.3

Clear-cut treatment pools only					
	2004 and 2005	*2004*	*2005*	*2004*	*2005*
% Entered clear cut	51.9	28.6	76.9		
% Crossed clear cut	22.2	0	46.2		
% Time in clear cut	27.2 ± 7.2	19.9 ± 9.1	35.1 ± 11.3	0–94	0–99
Duration in clear cut (days)	30.7 ± 9.1	27.5 ± 13.9	34.5 ± 11.6	0–167	0–121

[a] Value is the mean except where indicated.

Table 2
Summary of mixed-effects logistic regression predicting logit of odds of spotted salamander movement at 11 vernal pools in east-central Maine.

	Mean ± SE	Range	F value$_{(df)}$[d]	t Value$_{(df)}$[e]	Coefficient ± SE
Move[a]	0.22 ± 0.01	0–1			
Minimum temperature during the week preceding the tracking event (°C)	5.79 ± 0.1	−5.6–15.6	$10.8_{(1,\ 1246)}^{*}$	$-3.3_{(1246)}^{*}$	−0.079 ± 0.024
Maximum temperature during the week preceding the tracking event (prvwkTmax; °C)	25.2 ± 0.2	12.2–33.3	$4.2_{(1,\ 1246)}^{*}$	$2.1_{(1246)}^{*}$	0.062 ± 0.030
Year			$13.6_{(1,\ 36)}^{**}$	$3.7_{(36)}^{**}$	2.999 ± 0.814
Cumulative precipitation since tracking of the salamander started (cumppt; mm)	309.3 ± 5.4	0–942.8	$0.9_{(1,\ 1246)}$	$1.0_{(1246)}$	0.001 ± 0.001
Treatment: 30 m[b]			$3.7_{(2,\ 36)}^{*}$	$1.2_{(36)}$	0.543 ± 0.453
Treatment: 100 m[c]				$2.7_{(36)}^{*}$	0.868 ± 0.317
PrvwkTmax × year			$15.3_{(1,\ 1246)}^{**}$	$-3.9_{(1246)}^{**}$	−0.127 ± 0.032
Cumppt × treatment: 30 m[b]			$3.9_{(2,\ 1246)}^{*}$	$-1.7_{(1246)}$	−0.002 ± 0.001
Cumppt × treatment: 100 m[c]				$-2.7_{(1246)}^{*}$	−0.002 ± 0.001
Intercept					$-2.568 \pm 0.783^{*}$

[*] $p < 0.05$.
[**] $p < 0.001$.
[***] $p \leqslant 0.0001$.
[a] Outcome variable. Coded: 0 = did not move or moved less than 1 m and 1 = moved ⩾ 1 m.
[b] Dummy variable. Coded: 0 = reference treatment and 1 = 30-m treatment.
[c] Dummy variable. Coded: 0 = reference treatment and 1 = 100-m treatment.
[d] Results from the marginal ANOVA testing overall significance of each variable and results provided just once for each categorical variable.
[e] Results from the t-test, used to determine significance of individual dummy variable coefficients.

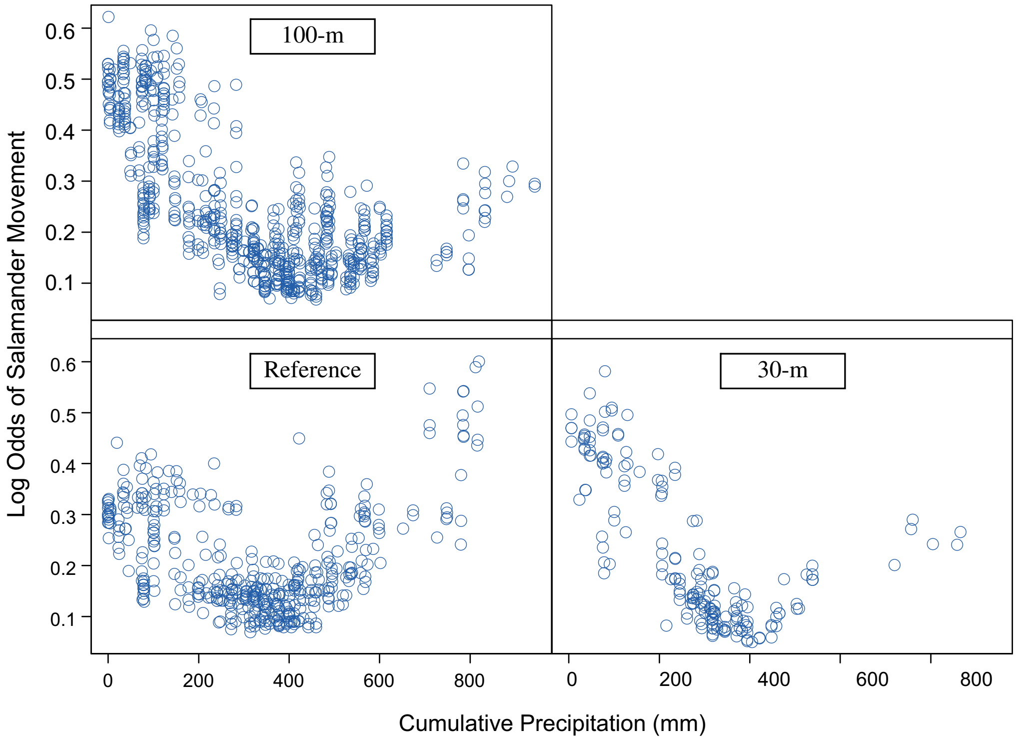

Fig. 4. Predicted log-odds of movement versus cumulative precipitation fallen since start of tracking (mm), grouped by buffer treatment, for spotted salamanders at 11 vernal pools in east-central Maine.

cumulative precipitation, migration rate decreased by a factor of 0.997. The interaction between weekly precipitation and cumulative precipitation was not significant and was not included in the final model.

Salamanders also moved at different rates depending on their distance from the pool and the previous week's minimum temperatures (Fig. 6). At low minimum temperatures, salamanders moved faster when they were far from the pool; however, above minimum temperatures of about 9.5 °C, salamanders moved faster when they were close to the pool.

Including treatment in the final model did not alter these results. Treatment was not a significant predictor of migration rate ($F_{(2,37)} = 0.1487$; $p = 0.862$). The estimated effect sizes for treatment were small with relatively-large standard errors ($\beta \pm \text{SE} = -0.085 \pm 0.248$ and 0.027 ± 0.196, for the 30-m and 100-m treatments, respectively, compared to the reference treatment).

3.3. Distance from the vernal pool

As main effects, log (cumulative days tracked), cumulative precipitation, and habitat were positively related to distance from the pool (Table 4); however, interactions between cumulative precipitation and habitat, respectively, and log (cumulative days tracked) were both negative. The patterns resulting from these combined effects are as follows (Fig. 7). First, on any given day, whether in the forest or the clear cut, the greater the cumulative precipitation,

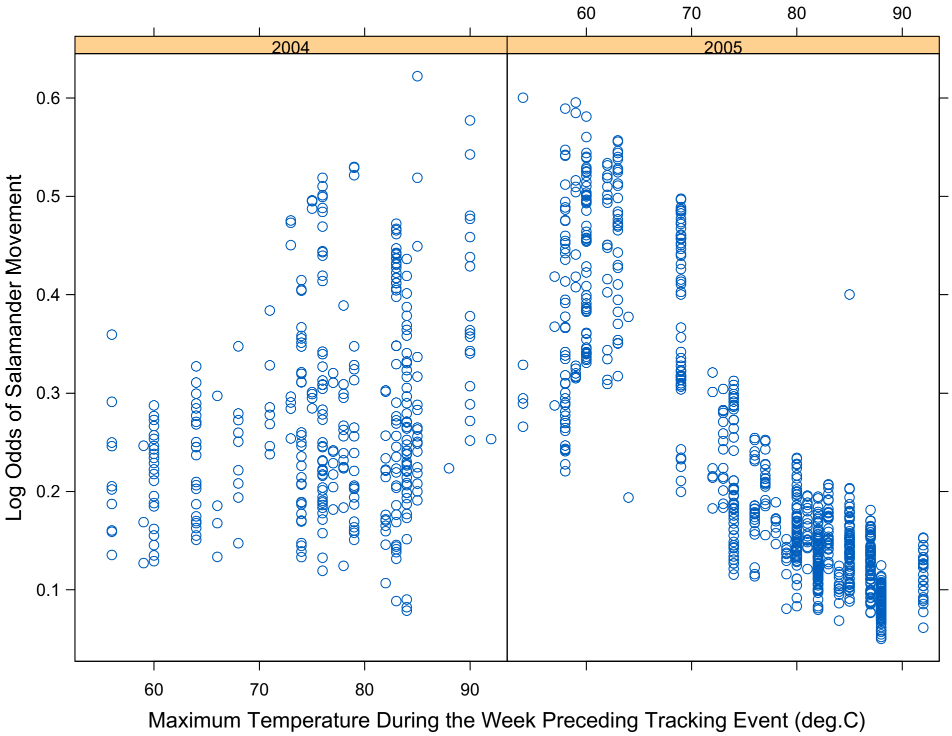

Fig. 5. Predicted log-odds of movement versus maximum temperature during the week preceding the tracking event (°C), grouped by year, for spotted salamanders at 11 vernal pools in east-central Maine.

Table 3

Summary of mixed-effects Poisson regression predicting migration rate of spotted salamanders at 11 vernal pools in east-central Maine. Migration rate was calculated by: distance moved since previous radio-fix (m)/# days since previous radio fix. Distance moved was the outcome variable, # days was the offset, and a log link function was used in the regression.

	Mean ± SE	Range	F value$_{(df)}$	Coefficient ± SE
Distance moved (m)	19.6 ± 2.2	0.5–271		
Number of days (days)	3.8 ± 0.2	1–29		
Distance from pool (m)	84.7 ± 5.4	0–427.6	$62.4_{(1,238)}^{***}$	0.010 ± 0.001
Cumulative precipitation since tracking of the salamander started (mm)	268.7 ± 13.4	0–942.8	$67.0_{(1,238)}^{***}$	−0.003 ± 0.0004
Cumulative precipitation over previous 7 days (mm)	35.7 ± 2.0	0–181.1	$28.3_{(1,238)}^{***}$	0.010 ± 0.002
Minimum temperature during the week preceding the tracking event (prvwkTmin; °C)	4.2 ± 0.3	−5–14.4	$0.0007_{(1,238)}$	−0.0008 ± 0.032
Distance from pool × prvwkTmin			$16.7_{(1,238)}^{***}$	−0.001 ± 0.0003
Intercept				$1.346 \pm 0.163^{***}$

* $p < 0.05$.
** $p < 0.001$.
*** $p \leqslant 0.0001$.

the farther a salamander was from the pool. This pattern was most strongly expressed early in the year. Second, in the clear cut, as cumulative days tracked increased, distance from the pool decreased, with the greatest reductions occurring at high cumulative precipitation. Third, in the forest, the longer a salamander was tracked, the farther the salamander moved from the pool when cumulative precipitation was low, but the closer the salamander moved to the pool when cumulative precipitation was relatively high (i.e., >168 mm). Note that 168 mm of precipitation fell by early July in 2004 and late May in 2005. Fourth, by the end of the tracking season and irrespective of cumulative precipitation, predicted distances from the pool converged at about 54 m and 40 m for salamanders in the clear cut and the forest, respectively.

Including treatment in the final model did not alter these results. Treatment was not a significant predictor of distance from the pool ($F_{(2,37)} = 0.6979$; $p = 0.5040$). The estimated effect sizes for treatment were small with relatively-large standard errors ($\beta \pm \text{SE} = -0.081 \pm 0.105$ and 0.102 ± 0.088, for the 30-m and 100-m treatments, respectively, compared to the reference treatment).

4. Discussion

This is the first study to examine how experimentally-manipulated buffer widths around vernal pools impact the migratory behavior of spotted salamanders. We observed that salamander movement-odds differed between the 100-m buffer and reference treatments, and that a salamander's distance from the vernal pool was influenced by habitat type (i.e., forest or clear cut). Weather conditions, however, strongly mediated the impact of buffer treatment on migration behavior.

4.1. Odds of movement

Salamanders were significantly more likely to move in the 100-m treatment, compared to the reference treatment, when cumulative precipitation was relatively low (i.e., below 390 mm). This suggests that early in the season, when emigrating from breeding pools to uplands, salamanders in an area disturbed by clear cutting search more actively for suitable habitat, and potentially have less suitable habitat available, than salamanders in an

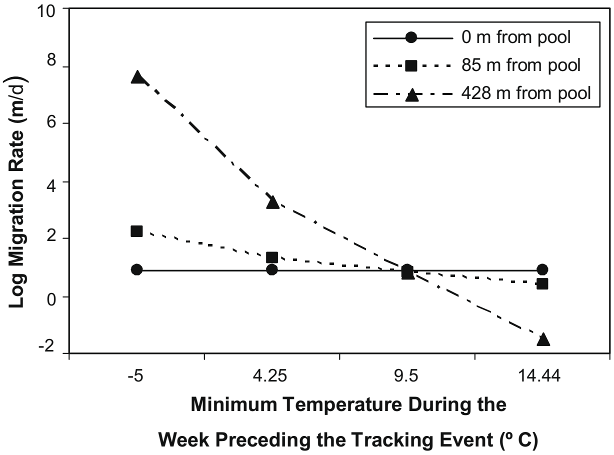

Fig. 6. Predicted log (migration rate [m/day]) versus minimum temperature during the week preceding the tracking event (°C), at selected distances of from the vernal pool (m), and mean values for cumulative and weekly precipitation, for spotted salamanders at 11 vernal pools in east-central Maine.

uncut forest (Graeter et al., 2008). At higher cumulative precipitations, salamanders in the 100-m treatment were less likely to move than salamanders in the reference treatment. This suggests that salamanders in the 100-m treatment either settled into acceptable microhabitat earlier or were unwilling to search for more suitable habitat as the year progressed, despite precipitation, which is frequently linked with salamander movement (Shoop, 1965; Sexton et al., 1990; Madison, 1997; Vasconcelos and Calhoun, 2004). We observed a similar, though marginally-significant, interaction between movement-odds and cumulative precipitation at the 30-m treatment, but our ability to interpret this interaction is limited by the small sample size at the 30-m treatment. Movement-odds in the reference treatment were not significantly influenced by cumulative precipitation, indicating that other factors drive the likelihood of salamander movement in undisturbed forests.

Salamanders were less likely to move as minimum temperatures increased, across all treatments and years. This trend is consistent with existing research, as salamanders experience greater desiccation risks at higher temperatures (summarized in Duellman and Trueb, 1986; Spotila, 1972; Pough and Wilson, 1970). The relationship between maximum temperature and movement-odds differed between years, however (Fig. 5), probably due to unseasonable spring warmth in 2004 that may have facilitated rather than inhibited movement.

4.2. Migration rate

Two different measures of precipitation were important for predicting salamander migration rate. On the more immediate timescale, and independent of season, salamanders moved faster when weekly precipitation was higher, indicating that salamanders capitalized on wet conditions, moving quickly to new locations before dry weather returned. This behavior might be expected given that spotted salamanders move selectively on rainy or moist nights (Shoop, 1965; Sexton et al., 1990; Madison, 1997; Vasconcelos and Calhoun, 2004). On a longer timescale, however, higher cumulative precipitation was correlated with slower salamander movements. If cumulative movement opportunities increase with cumulative precipitation, then at high cumulative precipitation, salamanders have had ample opportunity to find suitable habitat and may travel slower because they are only moving for small-scale activities such as foraging. Further, if higher cumulative precipitation creates a moister habitat, then desiccation risk and the need to move quickly to find a moist refuge might be reduced (Duellman and Trueb, 1986).

Temperature also influenced migration rate, but mostly through its interaction with a salamander's distance from the pool. Given the physiological constraints to moving that heat creates for salamanders, it is not surprising that, overall, migration rate decreased as temperature increased. At low temperatures, however, salamanders moved faster when they were farther from the pool; while at high temperatures, salamanders moved slower when they were farther from the pool. These interactive effects on migration rate could represent a combined function of variable habitat quality at different distances from the pool (Rittenhouse and Semlitsch, 2007; Semlitsch, 2008), non-temperature cues that signal a changing migratory environment (Patrick et al., 2007; Homan et al., 2008), and the physiological demands of breeding and migration (Finkler et al., 2003). For example, early in the year, when temperatures are low, salamanders that are close to the pool may still be recovering from breeding (Finkler et al., 2003), while more distant salamanders have presumably recovered from breeding and are capable of moving more quickly. Later in the year, salamanders that endured a long migration may experience physiologic or energetic constraints to moving when temperatures, and thus desiccation risks, are high. Salamanders that migrated only a short distance may possess ample energetic reserves which enable them to move quickly, even at high temperatures. While the causal mechanisms discussed for this interaction are merely hypotheses and run the risk of being over-interpretation of the results, the large effect size for the interaction (as shown in Fig. 6) makes it worthy of discussion and such hypothesis generation.

4.3. Distance from the vernal pool

Distance from the pool was most strongly tied to whether a salamander was in forested or clear-cut habitat, but was also impacted by cumulative precipitation and the duration a salamander was tracked. Our model indicates that salamanders in both clear cut and forested habitat initially emigrated away from the pool,

Table 4
Summary of mixed-effects linear regression predicting distance of a salamander from the vernal pool for 11 vernal pools in east-central Maine.

	Mean ± SE	Range	F value$_{(df)}$	Coefficient ± SE
Log (distance from vernal pool [m])	1.78 ± 0.01	−0.42–2.63		
Habitat[a]			$381.0_{(1,1235)}^{***}$	1.186 ± 0.061
Log (cumulative days tracked)	1.70 ± 0.01	0–2.26	$108.5_{(1,1235)}^{***}$	0.475 ± 0.046
Cumulative precipitation since tracking of the salamander started (cumppt; mm)	309.3 ± 5.4	0–942.8	$190.8_{(1,1235)}^{***}$	0.007 ± 0.0005
Log (cumulative days tracked) × habitat			$173.4_{(1,1235)}^{***}$	−0.570 ± 0.043
Log (cumulative days tracked) × cumppt			$177.2_{(1,1235)}^{***}$	−0.003 ± 0.0002
Intercept				0.619 ± 0.047***

* $p < 0.05$.
** $p < 0.001$.
*** $p \leqslant 0.0001$.
[a] Coded 0 = forested habitat and 1 = clear-cut habitat.

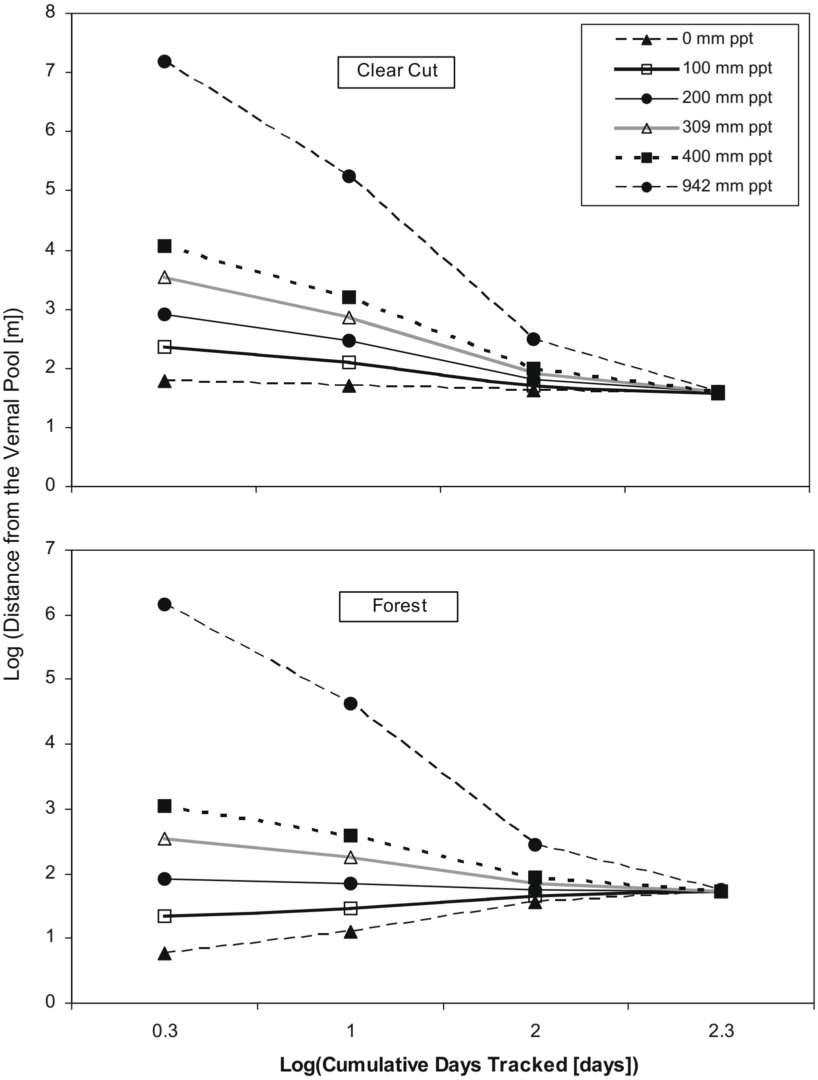

Fig. 7. Predicted log (distance from the vernal pool [m]) versus log (cumulative number of days tracked [days]), grouped by habitat (clear cut = upper graph; forest = lower graph), at selected values of cumulative precipitation fallen since start of tracking (mm ppt), for spotted salamanders at 11 vernal pools in east-central Maine. Habitat refers to a salamander's location for a given radio-fix (e.g., at clear cut-treatment pools, a salamander was classified as in forest if it was located in the buffer or in the forest on the far side of the clear cut).

but returned towards the pool before the end of the tracking season. These results suggest that emigrating salamanders moved farther from the pool than they ultimately overwintered. McDonough and Paton (2007) similarly found that about 50% of the male salamanders they tracked through the fall returned to within 40 m of the pool. Previous research also indicates that spotted salamanders are relatively inactive during the summer, but sometimes undertake shorter migratory movements in the fall, presumably in search of overwintering habitat (Madison, 1997; Regosin et al., 2005; McDonough and Paton, 2007). Our model results suggest that salamanders in the clear cut actively begin returning towards the pool during the spring and continue to move closer to the pool throughout the summer and fall, when weather conditions were conducive to movement. This early return response may be a reaction to poor habitat quality in clear cuts; salamanders may be returning to more suitable habitat in the forested buffers (Rothermel and Semlitsch, 2002; Rothermel, 2004; Semlitsch et al., 2008). For salamanders in the forest, return movements were associated more with cumulative precipitation than with the fall season or cool fall temperatures.

A perceived discrepancy between our model results and field observations, however, highlights the difficulty of predicting individual salamander distance from a vernal pool. The model would appear to predict that a salamander in the clear cut will always be moving closer to the pool, but our field data show that 22% of the salamanders we tracked in cut treatments were able to cross the clear cut and enter the forest on the far side of the cut. Proper interpretation of the model results, however, is that, on average, salamanders in the clear cut will move closer to the pool over time when all other variables are constant. As such, some individuals may move farther from the pool, some may remain at equal distance from the pool, and some may move toward the pool. The combination of these movements, though, is an average pattern of movement towards the pools over time. One of the powerful aspects of GLME is that individual heterogeneity in behavior is directly accounted for in the random effects, thus allowing us to make statements about the average even when individuals are behaving differently.

4.4. Clear cut permeability

Six of the 27 salamanders we tracked at cut-treatment pools were able to cross through 100-m wide clear cuts, indicating that clear cuts are semi-permeable to adult spotted salamanders. Past research has similarly shown that spotted salamanders are capable of selectively migrating out of clear cuts into forest (Semlitsch et al., 2008), and that other non-forest land covers are semi-permeable to adult spotted salamanders (e.g., golf fairways, meadows; Shoop, 1968; Windmiller, 1996; Montieth and Paton, 2006; Rittenhouse and Semlitsch, 2006). Spotted salamanders thus demonstrate some resilience to forest fragmentation in that they are able to migrate through significantly-altered habitat. Other evidence suggests that clear cuts, though semi-permeable, are inferior habitat for adult spotted salamanders. For instance, this species tends to be less abundant in clear cuts and along forest-cut edges (deMaynadier and Hunter, 1998; Renken et al., 2004).

The relative permeability of clear cuts in our study strongly depended on temperature and precipitation. Given that these weather parameters can vary widely from year to year, migratory patterns likely exhibit great interannual variation, even within a single salamander population. In our treatments, clear cuts are likely inhospitable to salamanders in some years, due to the high temperatures and low moisture associated with canopy loss (Feder and Burggren, 1992; Rothermel and Semlitsch, 2002; Finkler, 2006). In other years, the clear cuts may not be as hostile a habitat because salamanders are able to capitalize on transient or spatially-discrete, moist, cool conditions in the cut. Spotted salamanders typically select microhabitat with abundant deciduous leaf litter, coarse woody debris, and small mammal burrows (Madison, 1997; deMaynadier and Hunter, 1998, 1999; Faccio, 2003; Regosin et al., 2003). In clear cuts, adult salamanders tend to be more numerous when coarse woody debris is retained versus removed, suggesting that a lack of cool, moist microhabitats might limit salamander use of cuts (Patrick et al., 2006). In New England, however, mechanical soil preparation is an uncommon forestry practice (Barrett, 1980; M. Ducey, pers. comm.), much of the forest floor is left undisturbed by cutting, and moist microhabitats might not be as limiting as expected. Though we did not quantify the abundance of suitable microhabitat in cuts relative to salamander needs, we did observe microhabitat conditions conducive to salamander survival. For example, the essential soil structure of a mature forest was maintained throughout much of our cuts. Cues derived from forest soil that may guide salamander migration (Rittenhouse et al., 2004) would thus still be intact. We observed a substantial, buried leaf layer in our cuts, which provided insulation and trapped moisture near the soil surface. We also observed abundant potential subterranean refuges. In our treatments, tree stumps remained rooted after cutting. Soil near these stumps was not compacted, since cutting equipment usually did not approach within several meters of the tree being cut (pers. obs.). Salamanders were often found in burrows associated with these stump roots. Additionally, vegetation in cuts regenerated rapidly, providing some shade and leaf litter, even by the end of the first growing season (Patrick et al., 2006; pers. obs.). Finally, salamanders generally move on rainy nights when clear cuts are relatively wet and cool. If a salamander migrating through the clear cut is able to locate a suitable refuge before high temperatures arrive and/or precipitation ceases, then this salamander is likely to survive while in the cut. With time, as shade and leaf litter increase in the cuts, the probability of that salamander finding a suitable refuge also likely increases.

4.5. Mixed-effects modeling

Our experience confirms that mixed-effects regression is an appropriate and preferred technique for analyzing radiotracking data. Within our data, we found significant correlation among repeated tracking events, heteroscedastic variance, and unbalanced sampling, but were able to control for these problems with mixed-effects regression. We believe that previous tracking studies may not have sufficiently accounted for serial correlation and other statistical problems commonly encountered with tracking data. We note, however, two difficulties in applying this statistical method.

First, we used mixed-effects regression to assess mean salamander migration behavior on a multi-day scale. Our models, therefore, poorly describe rare, long-distance emigration movements that occur in shorter time periods. This deficiency was compounded because we sometimes could not locate salamanders for several days or weeks during these extended movements. Such long emigration movements are of conservation interest, however, since they define the outer-bounds of adult salamander upland habitat use around vernal pools. Alternative techniques might better elucidate the factors driving these long movements. We assessed movement-odds, and then predicted migration rate, when salamanders did move. A better approach might be a multi-part process which assesses movement-odds and then describes factors influencing long-distance and short-distance movements separately. Second, we assumed throughout this analysis that factors influencing movement-odds and movement rates all do so in a linear fashion. Non-linear relationships, including thresholds and tipping points, were not considered. Future salamander-migration research might explore non-linear mixed-effects models.

4.6. Conservation implications

Forested buffers have been promoted as a method for maintaining viable populations of wetland-breeding amphibians. Our study provides an experimental assessment of the impact of forested buffers on spotted salamander migration, when forests have been fragmented by clear-cut harvesting. With respect to migratory behavior, we found that salamander movement-odds differed between the 100-m buffer and reference treatments; and that the presence of clear-cut habitat affected the distance of a salamander from the vernal pool.

Although we did not observe significant effects of the 30-m treatment on migratory behavior, we suspect this lack of significance resulted from a small sample size and low statistical power for the 30-m-treatment. Despite our best efforts to select equal numbers of salamanders from each treatment, we were limited by the availability of salamanders large enough to carry radio-transmitters. Ultimately, we tracked 13, 21, and 6 salamanders from the reference, 100-m, and 30-m treatments, respectively. Data trends suggest that salamanders at the 30-m and 100-m treatments responded similarly to the clear cuts. For instance, the interactive effect of the 30-m treatment and cumulative precipitation on movement-odds was marginally significant. Additionally, the direction of the relationship between cumulative precipitation and movement-odds was more similar between the 30-m and 100-m treatments, than between either of the cut-treatments and the reference treatment (Fig. 4). These trends suggest that salamanders in the 30-m treatment were more likely to move at low cumulative precipitation and less likely to move at high cumulative precipitation, than salamanders in the reference treatment. When combined with the 100-m treatment results, the trends imply that salamander migratory behavior changes in response to 100-m-wide clear cuts located within 200 m of a vernal pool.

We cannot, however, rule out the possibility that the effects of the 30-m treatment were the same as those of the reference treatment. Because our 30-m treatment results are inconclusive, the question of what buffer width is adequate to maintain substantially-unaltered salamander migratory behavior remains unanswered. Since 30 m is a buffer width commonly invoked in wetland-protection and timber-harvesting policies, there is a strong need for additional research that examines individual salamander behavior with respect to 30-m-wide buffers surrounded by clear-cut habitat. Despite the need for additional research, we offer the following recommendations towards achieving a sustainable balance between wildlife and human forest-needs.

First, managers must ensure that sufficient small mammal burrows, coarse woody debris, and leaf litter are preserved as microhabitat for salamanders both in forested and cut areas, as these habitat features provided critical refuges for salamanders, and may partly determine whether a salamander uses the habitat (Madison, 1997; deMaynadier and Hunter, 1998; Rothermel and Luhring, 2005; Patrick et al., 2006). Foresters in other geographic regions, especially where mechanical site preparation is more common and weather is hotter or drier (e.g., the southern United States) can accomplish this by leaving more stumps in the ground, more of the soil structure intact, and more coarse woody debris post-harvesting.

Second, managers must plan on both landscape and local scales. In our research and other recent tracking studies, 20–38% of spotted salamanders emigrated farther than the 164-m buffer that Semlitsch (1998) calculated would encompass 95% of salamanders around a given pool (Faccio, 2003; Montieth and Paton, 2006; McDonough and Paton, 2007), indicating that adult spotted salamanders regularly emigrate greater distances than previously believed. It seems impractical to expect private-land managers to preserve upland buffers of 164 m or wider. In a forestry context, where succession leads to rapid revegetation of clear cuts, the buffer management model might not be most appropriate. A better strategy might be to focus generally on preserving a certain percent of intact forest at the landscape scale, while maintaining key microhabitat features in close proximity to vernal pools. Spotted salamanders tend to be absent from vernal pools, or present but at significantly reduced densities, when forests occupy less than 30% of land area within about 200 m of the pool (Gibbs, 1998a; Homan et al., 2004; Porej et al., 2004; Herrmann et al., 2005) or less than 50% of land area within 1000 m of the pool (Homan et al., 2004). To manage spotted salamanders on a landscape scale in a forestry setting, therefore, forest should cover at least 30% of the land within 200 m, and at least 50% of the land within 1000 m, of a pool. Protecting key local habitat features is a necessary complement, however, to landscape-scale forest preservation (Cushman 2006). By using spatially-explicit buffers that preserve only the most important local features, instead of using the more-typical circular buffers, the amount of land removed from timber production can be greatly reduced (Baldwin et al., 2006). For spotted salamanders, key local features that should be protected include the microhabitat elements described in our first recommendation (e.g., small mammal burrows) and a narrow circular buffer (i.e., 30–60 m) that would preserve wetland water quality and serve as a staging area for salamanders that have recently emerged from the pool (Semlitsch and Bodie, 2003; Herrmann et al., 2005). By combining landscape and local scale management, spotted salamanders should be able to find suitable habitat even when much of the surrounding landscape has been disturbed by timber harvesting.

Finally, management policies should specifically incorporate salamander behavior in dry, hot years, when salamanders are most limited by weather. In our study, salamander movement with respect to cutting treatment (including whether a salamander crossed a clear cut to suitable forest habitat or not) depended on weather conditions. Additionally, climate change models predict increased summer temperatures and variability in precipitation (NAST, 2000; Levy et al., 2008), and greatly reduced runoff (Huntington, 2003) for the northeastern United States over the next century. On average, these changes will likely make upland habitats, especially recent clear cuts, drier, less predictable, and more hostile to spotted salamanders. In turn, these habitat changes will likely exacerbate the altered behavior migrating salamanders exhibited in the 100-m treatment and decrease the likelihood of salamanders successfully crossing clear cuts.

To accommodate both the natural variability in weather conditions and predicted climate changes, management policies will need to be crafted with a sense of precaution. At the landscape scale, this will likely mean leaving more than 30–50% of the land area as relatively-intact forest. Additionally, managers may need to stipulate habitat configuration such that vernal pools and upland forest patches are connected via continuous forest corridors. At the local scale, clear cut size may need to be increasingly restricted, if clear cuts become less permeable to salamanders. In our study, clear cuts were 100-m wide and were not crossed by salamanders in the drier of the two years, suggesting that 100-m-wide clear cuts will present a substantial barrier to migrating salamanders if conditions become even more hot and dry. Finally, management plans should be explicitly adaptable so that conservation prescriptions can be adjusted to reflect actual climatic changes.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2009.04.024.

References

Andreozzi, V.L., Bailey, T.C., Nobre, F.F., Struchiner, C.J., Barreto, M.L., Assis, A.M.O., Santos, L.M.P., 2006. Random-effects models in investigating the effect of vitamin A in childhood diarrhea. Annals of Epidemiology 16, 241–247.

Ash, A.N., 1988. Disappearance of salamanders from clear cut plots. Journal of the Elisha Mitchell Scientific Society 104, 116–122.

Ash, A.N., 1997. Disappearance and return of plethodontid salamanders to clear cut plots in the southern Blue Ridge Mountains. Conservation Biology 11, 983–989.

Baldwin, R.F., Calhoun, A.J.K., deMaynadier, P.G., 2006. Conservation planning for amphibian species with complex habitat requirements: a case study using movements and habitat selection of the wood frog *Rana sylvatica*. Journal of Herpetology 40, 442–452.

Barrett, J.W., 1980. Regional Silviculture of the United States, second ed. John Wiley and Sons, Inc., New York.

Begon, M., Harper, J.L., Townsend, C.R., 1996. Ecology, third ed. Blackwell Science, Inc., Cambridge, Massachusetts.

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., White, J.-S.S., 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology and Evolution 24, 127–135.

Boyd, L., 2001. Buffer Zones and Beyond: Wildlife Use of Wetland Buffer Zones and their Protection Under the Massachusetts Wetland Protection Act. University of Massachusetts, Massachusetts, Amherst, Wetland Conservation Professional Program.

Bunnell, F.L., 1995. Forest-dwelling vertebrate faunas and natural fire regimes in British Columbia: patterns and implications for conservation. Conservation Biology 9, 636–644.

Calhoun, A.J.K., deMaynadier, P.G., 2002. Forestry habitat management guidelines for vernal pool wildlife in Maine. Maine, Orono, a cooperative publication of the University of Maine, Maine Department of Inland Fisheries and Wildlife, Maine Audubon, and Maine Department of Conservation.

Calhoun, A.J.K., deMaynadier, P.G., 2004. Forestry habitat management guidelines for vernal pool wildlife. MCA Technical Paper No. 6, Metropolitan Conservation Alliance, Wildlife Conservation Society, Bronx, New York.

Cooper, A.B., Pinheiro, J.C., Unsworth, J.W., Hilborn, R., 2002. Predicting hunter success rates from elk and hunter abundance, season structure, and habitat. Wildlife Society Bulletin 30, 1068–1077.

Cromer, R.B., Lanham, J.D., Hanlin, H.H., 2002. Herpetofaunal response to gap and skidder-rut wetland creation in a southern bottomland hardwood forest. Forest Science 48, 407–413.

deMaynadier, P.G., Hunter Jr., M.L., 1998. Effects of silvicultural edges on the distribution and abundance of amphibians in Maine. Conservation Biology 12, 340–352.

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

den Boer, P.J., 1970. On the significance of dispersal power for populations of carabid beetles (Coleoptera: Carabidae). Oecologia (Berl.) 4, 1–28.

Douglas, M.E., Monroe, B.L., 1981. A comparative study of topographical orientation in *Ambystoma* (Amphibia: Caudata). Copeia 1981, 460–463.

Duellman, W.E., Trueb, L., 1986. Biology of amphibians. The Johns Hopkins University Press, Baltimore, Maryland. 670 pp..

Enge, K.M., Marion, W.R., 1986. Effects of clearcutting and site preparation on herpetofauna of a north Florida flatwoods. Forest Ecology and Management 14, 177–192.

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

Feder, M.E., Burggren, W.W., 1992. Environmental Physiology of the Amphibians. University of Chicago Press, Chicago.

Finkler, M.S., 2006. Effects of temperature, sex, and gravidity on the metabolism of small-mouthed salamanders, *Ambystoma texanum*, during the reproductive season. Journal of Herpetology 40, 103–106.

Finkler, M.S., Sugalski, M.T., Claussen, D.L., 2003. Sex-related differences in metabolic rate and locomotor performance in breeding spotted salamanders (*Ambystoma maculatum*). Copeia 2003, 887–893.

Gibbons, J.W., 2003. Terrestrial habitat: a vital component for herpetofauna of isolated wetlands. Wetlands 23, 630–635.

Gibbs, J.P., 1998a. Distribution of woodland amphibians along a forest fragmentation gradient. Landscape Ecology 13, 263–268.

Gibbs, J.P., 1998b. Amphibian movements in response to forest edges, roads, and streambeds in southern New England. Journal of Wildlife Management 62, 584–589.

Graeter, G.J., Rothermel, B.B., Gibbons, J.W., 2008. Habitat selection and movement of pond-breeding amphibians in experimentally fragmented pine forests. Journal of Wildlife Management 72, 473–482.

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

Hall, D.B., 2000. Zero-inflated Poisson and binomial regression with random effects: a case study. Biometrics 56, 1030–1039.

Hansen, A.J., Spies, T.A., Swanson, F.J., Ohmann, J.L., 1991. Conserving biodiversity in managed forests: lessons from natural forests. BioScience 41, 382–392.

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

Herbeck, L.A., Larsen, D.R., 1999. Plethodontid salamander response to silvicultural practices in Missouri Ozark forests. Conservation Biology 13, 623–632.

Herrmann, H.L., Babbitt, K.J., Baber, M.J., Congalton, R.G., 2005. Effects of landscape characteristics on amphibian distribution in a forest-dominated landscape. Biological Conservation 123, 139–149.

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

Homan, R.N., Wright, C.D., White, G.L., Michael, L.F., Slaby, B.S., Edwards, S.A., 2008. Multiyear study of the migration orientation of *Ambystoma maculatum* (spotted salamanders) among varying terrestrial habitats. Journal of Herpetology 42, 600–607.

Hunter Jr., M.L., 1990. Wildlife, Forests, and Forestry: Principles of Managing Forests for Biological Diversity. Prentice Hall, Englewood Cliffs, New Jersey.

Huntington, T.G., 2003. Climate warming could reduce runoff significantly in New England, USA. Agricultural and Forest Meteorology 117, 193–201.

Insightful Corporation, 2005. S-PLUS Enterprise Developer, Version 7.0, Insightful Corporation, Seattle, Washington.

Kennedy, P., 1992. A Guide to Econometrics, third ed. MIT Press, Cambridge, Massachusetts.

Knapp, S.M., Haas, C.A., Harpole, D.N., 2003. Initial effects of clearcutting and alternative silvicultural practices on terrestrial salamander abundance. Conservation Biology 17, 752–762.

Lambert, D., 1992. Zero-inflated Poisson regression, with an application to defects in manufacturing. Technometrics 34, 1–14.

Landau, S., Everitt, B.S., 2004. A Handbook of Statistical Analyses Using SPSS. CRC Press, Boca Raton, Florida. 354pp.

Levy II, H., Shindell, D.T., Gilliland, A., Schwarzkopf, M.D., Horowitz, L.W., 2008. Executive Summary in *Climate Projections* Based on Emissions Scenarios for Long-Lived and Short-Lived Radiatively Active Gases and Aerosols. In: Levy, H., II, Shindell, D.T., Gilliland, A., Schwarzkopf, M.D., Horowitz, L.W. (Eds.). US Climate Change Science Program and the Subcommittee on Global Change Research, Washington DC.

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

Maine. Maine revised statues. Title 38, Chapter 3, Section 480, Rev. 1993.

Maine. Maine revised statues. Public Law Chapter 618, 2002.

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

Massachusetts. Wetlands protection act regulations. Code of Massachusetts Regulations, Title 310, Section 10, Rev. 2005.

McCullagh, P., Nelder, J.A., 1989. Generalized Linear Models, Monographs on Statistics and Applied Probability Number 37. second ed. Chapman and Hall, London.

McDonough, C., Paton, P.W.C., 2007. Salamander dispersal across a forested landscape fragmented by a golf course. Journal of Wildlife Management 71, 1163–1169.

McGee, G.G., Leopold, D.J., Nyland, R.D., 1999. Structural characteristics of old growth, maturing, and partially cut northern hardwood forests. Ecological Applications 9, 1316–1329.

Montieth, K.E., Paton, P.W.C., 2006. Emigration behavior of spotted salamanders on golf courses in southern Rhode Island. Journal of Herpetology 40, 195–205.

Morris, K.M., Maret, T.J., 2007. Effects of timber management on pond-breeding salamanders. Journal of Wildlife Management 71, 1034–1041.

National Assessment Synthesis Team (NAST). 2000. Climate Change Impacts on the United States: the Potential Consequences of Climate Variability and Change. US Global Change Research Program, Washington DC.

Neter, J., Wasserman, W., Kutner, M.H., 1990. Applied linear statistical models: regression, analysis of variance, and experimental design, third ed. Richard D. Irwin, Homewood, Illinois.

Noss, R.F., Cooperrider, A.Y., 1994. Saving Nature's Legacy. Island Press, Washington DC.

Patrick, D.A., Hunter Jr., M.L., Calhoun, A.J.K., 2006. Effects of experimental forestry treatments on a Maine amphibian community. Forest Ecology and Management 234, 323–332.

Patrick, D.A., Calhoun, A.J.K., Hunter Jr., M.L., 2007. Orientation of juvenile wood frogs, *Rana sylvatica*, leaving experimental ponds. Journal of Herpetology 41, 158–163.

Patrick, D.A., Calhoun, A.J.K., Hunter Jr., M.L., 2008. The importance of understanding spatial population structure when evaluating the effects of silviculture on spotted salamanders (*Ambystoma maculatum*). Biological Conservation 141, 807–814.

Petranka, J.W., Eldridge, M.E., Haley, K.E., 1993. Effects of timber harvesting on southern Appalachian salamanders. Conservation Biology 7, 363–370.

Petranka, J.W., Brannon, M.P., Hopey, M.E., Smith, C.K., 1994. Effects of timber harvesting on low elevation populations of southern Appalachian salamanders. Forest Ecology and Management 67, 135–147.

Pinheiro, J.C., Bates, D.M., 2000. Mixed-Effects Models in S and S-PLUS. Springer, New York.

Porej, D., Micacchion, M., Hetherington, T.E., 2004. Core terrestrial habitat for conservation of local populations of salamanders and wood frogs in agricultural landscapes. Biological Conservation 120, 399–409.

Pough, F.H., Wilson, R.E., 1970. Natural daily temperature stress, dehydration, and acclimation in juvenile *Ambystoma maculatum* (Shaw) (Amphibia: Caudata). Physiological Zoology 43, 194–205.

The Ramsar Bureau, 2001. Wetland values and functions: reservoirs of biodiversity. Switzerland, Gland, 2pp. <http://www.ramsar.org/info/values_biodiversity_e.pdf> (retrieved 20.11.08.).

Ramsar Information Paper No 2, 2008. Additional guidance for the implementation of the wise use concept. <http://www.ramsar.org/index_about_ramsar.htm#info> (retrieved 12.11.08.).

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

Regosin, J.V., Windmiller, B.S., Homan, R.N., Reed, J.M., 2005. Variation in terrestrial habitat use by four pool-breeding amphibian species. Journal of Wildlife Management 69, 1481–1493.

Renken, R.B., Gram, W.K., Fantz, D.K., Richter, S.C., Miller, T.J., Ricke, K.B., Russell, B., Wang, X., 2004. Effects of forest management on amphibians and reptiles in Missouri Ozark forests. Conservation Biology 18, 174–188.

Rittenhouse, T.A.G., Semlitsch, R.D., 2006. Grasslands as movement barriers for a forest-associated salamander: migration behavior of adult and juvenile salamanders at a distinct habitat edge. Biological Conservation 131, 14–22.

Rittenhouse, T.A.G., Semlitsch, R.D., 2007. Distribution of amphibians in terrestrial habitat surrounding wetlands. Wetlands 27, 153–161.

Rittenhouse, T.A.G., Doyle, M.C., Mank, C.R., Rothermel, B.B., Semlitsch, R.D., 2004. Substrate cues influence habitat selection by spotted salamanders. Journal of Wildlife Management 68, 1151–1158.

Roe, J.H., Gibson, J., Kingsbury, B.A., 2006. Beyond the wetland border: estimating the impact of roads for two species of water snakes. Biological Conservation 130, 161–168.

Rothermel, B.B., 2004. Migratory success of juveniles: a potential constraint on connectivity for pond-breeding amphibians. Ecological Applications 14, 1535–1546.

Rothermel, B.B., Luhring, T.M., 2005. Burrow availability and desiccation risk of mole salamanders (*Ambystoma talpoideum*) in harvested versus unharvested forest stands. Journal of Herpetology 39, 619–626.

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

Sakamoto, Y., Ishiguro, M., Kitagawa, G., 1986. Akaike Information Criterion statistics. Reidel, Dordrecht, Netherlands.

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

Semlitsch, R.D., 2008. Differentiating migration and dispersal processes for pond-breeding amphibians. Journal of Wildlife Management 72, 260–267.

Semlitsch, R.D., Bodie, J.R., 2003. Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. Conservation Biology 17, 1219–1228.

Semlitsch, R.D., Conner, C.A., Hocking, D.J., Rittenhouse, T.A.G., Harper, E.B., 2008. Effects of timber harvesting on pond-breeding amphibian persistence: testing the evacuation hypothesis. Ecological Applications 18, 283–289.

Sexton, O.J., Phillips, C., Bramble, J.E., 1990. The effects of temperature and precipitation on the breeding migration of the spotted salamander (*Ambystoma maculatum*). Copeia 1990, 781–787.

Shoop, C.R., 1965. Orientation of Ambystoma maculatum: movements to and from breeding ponds. Science, New Series 149, 558–559.

Shoop, C.R., 1968. Migratory orientation of Ambystoma maculatum: movements near breeding ponds and displacements of migrating individuals. The Biological Bulletin, 230–238.

Spotila, J.R., 1972. Role of temperature and water in the ecology of lungless salamanders. Ecological Monographs 42, 95–125.

SPSS Inc., 2006. SPSS 15.0 for Windows. SPSS Inc., Chicago.

Talley, D.M., Huxel, G.R., Holyoak, M., 2006. Connectivity at the land–water interface. In: Crooks, K.R., Sanjayan, M. (Eds.), Connectivity Conservation. Cambridge University Press, New York, pp. 97–129.

UN General Assembly, 1992. Report of the United Nations conference on environment and development, Annex III: Non-legally binding authoritative statement of principles for a global consensus on the management, conservation, and sustainable development of all types of forest (A/CONF.151/26), New York.

UN FAO, 2005. Global forest resources assessment 2005: progress towards sustainable forest management. FAO Forestry Paper 147, Rome.

UN General Assembly, 62nd Session. 2007. Non-legally binding instrument on all types of forests (A/C.2/62/L.5), New York.

Vasconcelos, D., Calhoun, A.J.K., 2004. Movement patterns of adult and juvenile *Rana sylvatica* (LeConte) and *Ambystoma maculatum* (Shaw) in three restored seasonal pools in Maine. Journal of Herpetology 38, 551–561.

Venables, W.N., Dichmont, C.M., 2004. GLMs, GAMs, and GLMMs: an overview of theory for applications in fisheries research. Fisheries Research 70, 319–337.

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