

Winter 2006

Effects of forest clear cutting on spotted salamander (*Ambystoma maculatum*) migration

Jessica Susannah Veysey
University of New Hampshire, Durham

Follow this and additional works at: <https://scholars.unh.edu/thesis>

Recommended Citation

Veysey, Jessica Susannah, "Effects of forest clear cutting on spotted salamander (*Ambystoma maculatum*) migration" (2006). *Master's Theses and Capstones*. 252.
<https://scholars.unh.edu/thesis/252>

This Thesis is brought to you for free and open access by the Student Scholarship at University of New Hampshire Scholars' Repository. It has been accepted for inclusion in Master's Theses and Capstones by an authorized administrator of University of New Hampshire Scholars' Repository. For more information, please contact nicole.hentz@unh.edu.

EFFECTS OF FOREST CLEAR CUTTING ON SPOTTED SALAMANDER
(*AMBYSTOMA MACULATUM*) MIGRATION

BY

JESSICA SUSANNAH VEYSEY
Bachelor of Arts, Dartmouth College, 2000

THESIS

Submitted to the University of New Hampshire
in Partial Fulfillment of
the Requirements for the Degree of

Master of Science
in
Natural Resources: Wildlife

December, 2006

UMI Number: 1439299

INFORMATION TO USERS

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleed-through, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

UMI[®]


UMI Microform 1439299

Copyright 2007 by ProQuest Information and Learning Company.


All rights reserved. This microform edition is protected against unauthorized copying under Title 17, United States Code.

ProQuest Information and Learning Company
300 North Zeeb Road
P.O. Box 1346
Ann Arbor, MI 48106-1346

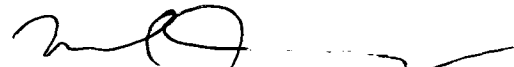
This thesis has been examined and approved.




Thesis Director, Dr. Kimberly J. Babbitt,
Associate Professor of Wildlife Ecology



Dr. Andrew B. Cooper, Research Assistant
Professor of Natural Resources



Dr. Mark J. Ducey, Associate Professor of
Forest Biometrics and Management



Dr. Bryan S. Windmiller, Visiting Scholar,
James Cook University, Queensland,
Australia

29 NOV 2006

Date

ACKNOWLEDGEMENTS

I am most grateful to my advisor, Dr. Kimberly Babbitt, for her guidance, patience, and support of this research. I am deeply indebted to Dr. Andrew Cooper for the amount of time and energy he spent teaching me about statistics. I am extremely appreciative of the help and thoughtful suggestions of Dr. Mark Ducey and Dr. Bryan Windmiller, both members of my master's committee.

I would like to thank everyone who assisted with field work for this project, including: Emma Carcagno, Nicole Freidenfelds, Sarah Emel, Ryan Killoran, Chris McLean, Sarah McClellan, Jim Pannaccione, and Lisa Plagge; and especially Dr. Matthew Baber, who collected field data, but also helped select the vernal pools and install the drift fences. My special thanks are extended to Stephen, for his uncomplaining help with field and lab work; to Dr. John Veysey, for his enthusiastic advice about statistics; and to Shelby, who is skilled at dishing out humor, empathy, and indignation, in all the right doses. I am also glad for both the advice and moral support offered by fellow graduate students.

I am thankful beyond words to my parents, brothers, sister-in-law, and Stephen, whose inspiration and rock-solid support got me here, and absolutely helped me through this process. Finally, I am beholden to all of the salamanders that were poked, prodded, sliced, and generally harassed, but made this research possible.

TABLE OF CONTENTS

ACKNOWLEDGEMENTS.....	iii
LIST OF TABLES.....	vi
LIST OF FIGURES.....	vii
ABSTRACT.....	viii

CHAPTER	PAGE
I. INTRODUCTION.....	1
Study Organism.....	2
Migration and Upland Habitat Requirements.....	5
Buffer Zones and Timber Harvesting.....	11
Traditional Analysis Methods.....	14
II. METHODS.....	18
Study Site.....	18
Buffer Creation.....	19
Radiotracking.....	21
Selection of Individuals.....	21
Implant of Transmitters.....	21
Data Collection.....	23
Data Analysis.....	25
Mixed-Effects Regression Modeling.....	25

III. RESULTS.....36

 Probability of Salamander Movement.....48

 Migration Rate.....56

 Distance From the Vernal Pool.....62

IV. DISCUSSION.....68

REFERENCES.....81

APPENDIX A. Institutional Animal Care and Use Committee Approval Letters.....91

LIST OF TABLES

TABLE		PAGE
Table 1.	List of parameters considered in the modeling process.....	27
Table 2.	Summary of tracking statistics for individual spotted salamanders.....	37
Table 3.	Summary of tracking statistics describing movements for all 40 adult spotted salamanders.....	39
Table 4.	Summary of mixed-effects logistic regression predicting logit of odds of salamander movement.....	50
Table 5.	Summary of mixed-effects Poisson regression predicting migration rate.....	58
Table 6.	Summary of mixed-effects linear regression predicting distance from the vernal pool.....	64

LIST OF FIGURES

FIGURE	PAGE
Figure 1. Diagram depicting cutting treatments.....	20
Figure 2. Migratory paths of 3 salamanders tracked at a 30-m buffer treatment pool.....	43
Figure 3. Migratory paths of 2 salamanders tracked at a 100-m buffer treatment pool.....	44
Figure 4. Migratory paths of 3 spotted salamanders tracked at a reference wetland.....	45
Figure 5. Percent of salamanders at clear-cut treatments pools that remained in the buffer; entered the cut; and both entered and crossed the cut.....	47
Figure 6. Distribution for the number of days that salamanders at clear cut-treatment pools spent in the clear cut.....	47
Figure 7. Probability of salamander movement versus day of the year.....	52
Figure 8. Predicted probability of salamander movement versus cumulative precipitation, grouped by snout-vent lengths.....	55
Figure 9. Predicted migration rate as a function of distance of from the vernal pool, grouped by minimum temperature.....	60
Figure 10. Predicted migration rate as a function of cumulative precipitation.....	61
Figure 11. Predicted migration rate as a function of weekly precipitation.....	61
Figure 12. Predicted log (distance from the vernal pool) as a function of log (cumulative days tracked), grouped by both habitat and cumulative precipitation.....	65

ABSTRACT

EFFECTS OF FOREST CLEAR CUTTING ON SPOTTED SALAMANDER (*AMBYSTOMA MACULATUM*) MIGRATION

by

Jessica S. Veysey

University of New Hampshire, December, 2006

Upland buffer zones are a proposed management tool for vernal-pool-breeding amphibians. Substantial validation of buffers, via experimental upland habitat disturbance, is lacking. Specifically, no studies have examined immediate effects of clear cutting on spotted salamander (*Ambystoma maculatum*) migration. I used clear cutting to experimentally manipulate upland buffer widths at 11 vernal pools. I then radiotracked 40 adult spotted salamanders at these pools, and modeled their migration with mixed-effects regression. Mean maximum distance from the pool was 106.0 ± 15.4 m (range = 1.6 to 427.6 m). At clear cut-treatment pools, mean percent of time in the cut was $27.2 \pm 7.2\%$ (range = 0 to 99%). Salamanders entered and crossed cuts. Buffer treatment was not significantly predictive of movement. Precipitation, season, days tracked, and distance from the pool were among the strongest predictors. Clear cuts are semi-permeable to adult spotted salamanders, but degree of permeability depends largely on precipitation patterns.

CHAPTER I

INTRODUCTION

In eastern North America, wildlife habitat is increasingly impacted by resource extraction, and threatened by suburban sprawl and industry (e.g., Klemens 1993; Knox 1999; Petranka 1998; Windmiller 1996; Sundquist and Stevens 1999; Breunig 2003). Consequently, eastern states have expanded some natural resource laws (e.g., MA Wetlands Protection Act; MA Forest Cutting Practices Act; NH Best Management Practices for... Timber Harvesting) to include protection of wildlife habitat, reasoning that where wildlife habitat is maintained, wildlife is protected. For vernal-pool-breeding amphibians, however, these protective laws are likely ineffective (Boyd 2001; Gamble et al 2006; Semlitsch and Bodie 2003; Semlitsch 1998; Dodd and Cade 1998). The laws preserve the wetland, but not upland habitat of these amphibians; even though the amphibians spend most of their lives in the uplands surrounding their breeding pools (i.e., between 85.9% and 98.9 % of the year for some salamander species; Semlitsch 1998). One potential reason that upland habitat protection for vernal-pool-breeding amphibians has been withheld is a lack of data and understanding about their upland habitat requirements.

Study Organism

Spotted salamanders (*Ambystoma maculatum*) are among the amphibians that depend upon vernal pools and surrounding uplands for survival. In northern New England, adult spotted salamanders typically emerge from hibernation and migrate to breeding wetlands in early April (Babbitt, unpub. data), during a major rainfall event. Although it can breed in a variety of wetland habitats, vernal pools are particularly productive breeding sites for this species because the pools lack fish predators (Klemens 1993; Hunter et al. 1999; Petranka 1998).

In a given year, only a portion of the adult spotted salamander population breeds. The percent of breeding adults varies by population, and can range from about 33% to 90% (Husting 1965; Windmiller 1996; Douglas & Monroe 1981; Whitford and Vinegar 1966). In New England and south-eastern Canada, spotted salamanders can reach sexual maturity as early as 2 years of age, but most males attain sexual maturity closer to 5 years, and most females at 6 or 7 years of age (Flageole and LeClair 1992; Homan et al., unpub. data). Individual spotted salamanders usually return to breed in their natal pools (Shoop 1974; DeGraaf and Yamasaki 2001; Vasconcelos and Calhoun 2004) but sometimes breed in non-natal pools, possibly when a disturbance occurs near their breeding pool (Petranka et al. 2004). Breeding spotted salamanders spend from a few days up to about 5 weeks in the vernal pools, before returning to the uplands (Windmiller 1996).

By the end of May, most adults have reemerged from the vernal pools and migrated back into the surrounding uplands. Following this post-breeding migration,

salamanders are largely inactive during the summer months (Windmiller 1996). In northern New England, from September to early November, movement of adults, juveniles, and metamorphs increases again (Veysey and Babbitt unpub. data). Similar autumnal migrations have been observed in other locations (Duellman 1954; Wacasey 1961; Williams 1973; Jackson 1990; Windmiller 1996; Madison 1997; Regosin et al. 2005). In New England, the salamanders are generally inactive during the winter months, although Windmiller (1996) did observe minimal salamander movement in Massachusetts throughout the winter.

Spotted salamanders are integral to forest nutrient and energy cycling (Davic and Welsh 2004). During their annual breeding migrations, adult salamanders leave significant captured energy and nutrients in the vernal pools, in the form of egg masses. Nutrients and energy are transported back into the uplands, in the form of salamander biomass, when metamorphs disperse from the pools (Wassersug 1984; Regester et al. 2006). Spotted salamanders are also important predators and prey within the forest ecosystem. Spotted salamanders consume a variety of forest insects, worms, and other invertebrates, and are prey to a variety of forest vertebrates. Windmiller (1996) estimated that upland spotted salamander biomass around one vernal pool in Massachusetts was nearly 4 times greater than the total breeding bird biomass, and almost one half of the total small mammal biomass, in that same forest area. He suggested that vernal-pool-breeding salamanders strongly influence forest ecology, and are especially important as predators of the forest floor arthropod community.

Previous research suggests that spotted salamanders are organized into metapopulations, comprised of a network of local populations, each occupying a habitat patch composed of upland centered on an individual vernal pool, and linked by dispersal between these habitat patches (Marsh and Trenham 2001; Semlitsch 2000). Regional persistence of spotted salamanders requires maintenance of both local populations and dispersal opportunities between local populations (Semlitsch 1998 and 2000, Gibbons 2003, Hecnar and M'Closkey 1996).

Persistence of local salamander populations depends on availability of suitable upland habitat. Despite their vital reproductive connection to vernal pools, spotted salamanders are largely terrestrial as juveniles and adults, inhabiting the uplands around their breeding pools about 95% of every year (Semlitsch 1998). Salamanders return to the pools only to breed or as stopover points during migration. Spotted salamanders use the surrounding uplands for migration, shelter, foraging, over-wintering, and, dispersal habitat.

Juvenile and adult spotted salamanders experience high survival rates, compared to larval salamanders (0.6 and 0.7 vs. 0.04, respectively), and can live up to 32 years in the wild (Flageole and LeClair 1992; Petranka 1998). Additionally, juveniles may be the primary dispersers for the species (Rothermel and Semlitsch 2002; Rothermel 2004). Demographically, therefore, the juvenile and adult life stages are particularly important (Gibbs 2005).

Given the strong association between juvenile and adult spotted salamanders and upland habitat use, and the demographic importance of these life stages, the key to spotted salamander regional persistence is proper upland habitat management. It is

impossible to successfully manage uplands for salamanders, however, without detailed knowledge of the species' upland habitat needs and movement patterns.

Migration and Upland Habitat Requirements

Migratory success, like dispersal success, is a function of the distance that must be traveled (Hanski 1997; Sjogren 1991); the migratory capacity and requirements of the migrating species (Hansson 1991; Hanski and Gilpin 1991; Hanski 1997); the spatial arrangement of habitat patches (Marsh and Trenham 2001; Sjogren 1991); habitat permeability (Joly et al. 2001; Wiens 1997; Moilanen and Hanski 1998); and potentially, habitat patch quality (Hansson 1991). In particular, habitat fragmentation may change the permeability of migratory habitat; and prevent, limit, and/or delay migration (Hanski and Gilpin 1991; Hansson 1991; Marsh and Trenham 2001; Joly et al. 2001), which may lead to local population collapse. Habitat fragmentation caused by humans may have stronger negative impacts on movements than habitat fragmentation caused by non-human processes, because anthropogenic disturbances tend to create more abrupt edges, to be associated with stronger negative edge effects, and often are more permanent and less permeable than natural disturbances (den Boer 1970; Marsh and Trenham 2001; deMaynadier and Hunter 1998; Noss and Cooperrider 1994; Hansen et al. 1991). In general, amphibian movements may not be as limited (in frequency or distance) as previously supposed, but may become quite limited or become a liability to amphibian populations in human-disturbed landscapes (Marsh and Trenham 2001; Gibbs 1998b).

Information about spotted salamander migration and upland habitat needs is limited and variable, and derives from studies that differ widely in observation technique, numbers of salamanders studied, duration and season of study, geographic location, and landscape type. Research into the spotted salamander's migratory and upland habitat requirements is complicated by the species' behavior. In particular, spotted salamanders are fossorial. Windmiller (1996) found that this species spent 76.8% of its time in the uplands inside small mammal burrows. They are also nocturnal and tend to travel only during rain (Faccio 2003; deMaynadier and Hunter 1999). Additionally, they migrate relatively long distances from their breeding pools into the uplands (Semlitsch 1998). A review of existing research into spotted salamander upland habitat use and migratory patterns follows.

In undisturbed habitats, the maximum net distance spotted salamanders emigrated from breeding wetlands ranged from 0 to 249 m, with mean distances varying from 64 to 192 m (see review in Semlitsch et al. 2003; Kleeberger and Werner 1983; Faccio 2003; Rittenhouse and Semlitsch 2006). In one study, cumulative distance moved from spring to fall varied from 18 to 243 m, with a mean of 124 m (Faccio 2003). Regosin et al. (2005) found that 60% of spotted salamanders overwintered at distances greater than 100 m from their breeding pool.

During migration, salamanders moved both in straight lines and zigzag patterns (perhaps in response to landscape features) away from breeding pools (Madison 1997; Rittenhouse and Semlitsch 2006). Spotted salamanders, like other ambystomatids, may utilize home ranges, ranging from 0.11 to 23 m², once emigration is complete (Faccio 2003; Rittenhouse and Semlitsch 2006; Semlitsch 1981).

Research indicates a positive relationship between salamander size (i.e., mass and/or snout-vent-length [SVL]) and net distance emigrated from the breeding pool (Faccio 2003; Regosin et al. 2005). Additionally, each sex may use upland habitat differently. Females tended to overwinter farther from pools than males (Regosin et al. 2005). In general, females moved further from pools than males (Windmiller 1996; Faccio 2003). Different use of upland habitat may stem from different locomotor capacities between the sexes. In the laboratory, males crawled faster than females; and both post-gravid females and males sustained crawling on a treadmill for longer periods than gravid females (Finkler et al. 2003).

There is a strong connection between weather and spotted salamander movement. Salamanders moved during rainy nights, when temperatures were above freezing. Minimum temperatures required for salamander movement varied between studies, from 0 to 12 ° C (Douglas and Monroe 1981; Baldauf 1952; Wright and Allen 1909; Duellman and Trueb 1986; Madison 1997). Sexton et al. (1990) found that 98% of migratory salamander movements at the pond edge occurred when the mean 3-day temperature was greater than 5.5 °C, and at least 4 mm of rain had fallen in the last 24 hours. Madison (1997) found that all salamander movements occurred on nights when the mean temperature was between 5 and 14° C, and rainfall during the previous month was at least 4 cm. Vasconcelos and Calhoun (2004) also found significant correlations between rainfall, temperature, and salamander movements near the wetland edge. As an upper threshold, the critical thermal maximum for spotted salamanders is 39.7 °C (Pough and Wilson 1970).

Spotted salamanders tend to use small mammal burrows (including both horizontal tunnels in the duff, and vertical tunnels extending into soil) almost exclusively as refuges during the non-breeding season (Windmiller 1996; Madison 1997; Faccio 2003). Vertical burrows, especially those close to large tree trunks, were the preferred overwintering refuges (Madison 1997; Faccio 2003). Regosin (2003) found that spotted salamanders were 3 times more likely to leave experimental plots when small mammal burrows were removed, suggesting that burrow abundance may influence salamander migration distances and terrestrial density. Spotted salamanders frequently chose tunnels that are under pit and mound topography, live root boles, logs, and/or stumps (Faccio 2003; Windmiller 1996). Spotted salamander refuges were positively associated with percent cover of leaf litter, low shrubs, logs, and saplings; number of log, stumps, and vertical tunnels; soil moisture; and land slope; and were negatively associated with mid-story canopy cover (Faccio 2003). Other habitat characteristics positively associated with spotted salamander non-breeding use included: mature closed canopy cover, leaf litter depth, density of coarse woody debris, well-drained soils, south-facing slopes, and availability of root channels (Windmiller 1996; deMaynadier and Hunter 1998, 1999).

The 2 studies to-date that radio-tracked spotted salamanders during the non-breeding season in relatively undisturbed landscapes found wide variation among individual salamanders in time, direction, and distance moved, leading to the conclusion that it is nearly impossible to predict when salamanders will undertake major migratory movements (Madison 1997; Faccio 2003).

By contrast, spotted salamanders may exhibit significantly different migratory behavior and upland habitat use in disturbed and fragmented landscapes. For instance,

salamanders near sites that are actively being disturbed, may migrate farther distances (e.g., 467 m from the breeding pool, the furthest emigration distance yet recorded for a spotted salamander) than salamanders in undisturbed or previously-disturbed habitats, and may delay migration (Montieth and Paton 2006). Salamanders in actively-disturbed and previously-disturbed landscapes may also alter their macro-habitat use choices (e.g., proportion of time spent in forested uplands), compared to choices in undisturbed landscapes (Montieth and Paton 2006). At a micro-scale, however, spotted salamanders in disturbed landscapes seem to choose similar habitat characteristics to those in undisturbed landscapes (e.g., small mammal burrows; areas where vegetation and vegetative debris create a moist microclimate; Montieth and Paton 2006).

Spotted salamanders seem to distinguish between different types and extents of disturbance, avoiding some, while traversing others. Adult and juvenile spotted salamanders seem to favor emigration into forested versus grassland habitat (Vasconcelos and Calhoun 2004; Rittenhouse and Semlitsch 2006; Regosin et al. 2005; Windmiller 1996). When presented with a choice between forest and old-field, juvenile spotted salamanders preferentially selected, moved further into, and experienced less dehydration and mortality in forested habitat (Rothermel and Semlitsch 2002). When presented with soil and/or leaf litter from forest versus grassland, adult and juvenile salamanders tended to occupy the forest soil, especially when forest leaf litter was also present (Rittenhouse et al. 2004). Despite their apparent preference for forested versus grassland habitats, spotted salamander adults and juveniles can migrate through fields and will even take refuge in grassland (Regosin et al. 2005, Rothermel 2004, Madison 1997). Additionally, though spotted salamander adults tend to avoid, and were never found “residing” in golf

course fairways, they are capable of crossing fairways and lawns (Montieth and Paton 2006, Windmiller 1996). Spotted salamanders have also been observed crossing roads and parking lots (Windmiller 1996; Homan et al. 2003; Mazerolle 2004). Spotted salamanders' selection of forest versus non-forest may partly reflect relative availability and proximity of each habitat type. Apparent habitat preferences may also be complicated by study design. Several of the studies that found strong salamander preferences for forested habitat (e.g., Rothermel and Semlitsch 2002; Rittenhouse et al. 2004; Rittenhouse and Semlitsch 2006) used artificial ponds, constrained salamanders to narrow enclosures, and/or displaced salamanders to unfamiliar locations. Studies that documented salamanders moving through both forested and non-forested habitat, however, were observations of natural salamander populations (e.g., Montieth and Paton 2006; Homan et al. 2003; Regosin et al. 2005; Windmiller 1996).

Use of non-forested habitats seems to partially depend on the size and configuration of the habitat patch. Rothermel (2004) found that migratory success of juvenile salamanders moving through pastures was a direct function of distance to the nearest forest, with only 15% of juveniles that were released 50 m from the forest succeeding in reaching the forest (Rothermel 2004). Windmiller (1996) observed salamanders crossing a 20-m-wide parking lot, a 20-m-wide mowed field, and a 35-m-wide power line cut, but observed no salamanders crossing a 50-m-wide golf course fairway, 130-m-wide mowed field, or a 40-m-wide parking lot. Similarly, the golf course fairway traversed in the Montieth and Paton (2006) study was 38-m wide, while the traversed lawn was 40-m wide.

Finally, there seems to be a hierarchy in the relative permeability of different types of edges to spotted salamander movement. While salamanders may cross or occur in various grassland types and must sometimes cross roads and parking lots, forest-road edges are less permeable to spotted salamanders than are forest – open land edges (Montieth and Paton 2006; Regosin et al 2005; Rothermel 2004; Gibbs 1998a; Gibbs 2005, Mazerolle 2004, Windmiller 1996).

As a summary, in uplands, spotted salamanders seem to prefer closed canopy forests, which contain abundant deciduous leaf litter, stumps, logs, and small mammal burrows. Spotted salamanders are capable of utilizing non-forested areas, but are generally averse to edges and open habitat. The likelihood of a salamander using non-forested habitat may depend on the size, type, shape, history, and landscape context of that habitat patch; on the geographic location of the salamander population; and on the size, sex, and age of the salamander.

Buffer Zones and Timber Harvesting

Despite the growing body of knowledge about spotted salamander upland habitat use, there are substantial gaps and variation in the data. It remains unclear how uplands should be managed to sustain salamander populations, and how resistant this species truly is to disturbance. Semlitsch (1998) suggested a biologically-based upland buffer zone of 164.3 m around vernal pools, which would encompass 95% of pond-breeding salamander populations. Subsequently, this “life” zone was tentatively updated to 175 m and then to 185 m, when additional data, including some from salamander movement at disturbed

sites, became available (Faccio 2003; Montieth and Paton 2006). Legal upland habitat protections in New England nominally range from 0 to 30.5 m of buffer zone around breeding pools (although individual municipalities may have larger buffer zones; CT 2005; MA 2005; ME 1993, 2002; NH 1996; VT 2002).

Substantial validation of these suggested buffer zones, in the form of experimental upland habitat disturbance, is lacking, however. (But see Windmiller et al., in press, for evidence of spotted salamander population decline following non-experimental upland habitat disturbance near a vernal pool where an upland buffer was maintained). Specifically, no studies have examined the immediate effects of clear cutting, and its interaction with buffer zone size, on spotted salamander migration.

Clear cutting is an intense, but non-permanent form of habitat disturbance. Its effects may be highly detrimental to some species (e.g., Knapp 2003; Ash 1988, 1997; Petranka et al. 1993, 1994; Herbeck and Larsen 1999), but clear cutting also resets succession. The vegetative, soil, and microclimatic conditions in clear cuts change with time; possibly enabling greater regional amphibian diversity across a landscape and through time (Cromer 2002; McLeod and Gates 1998; Phelps and Lancia 1995; Enge and Marion 1986; Renken et al. 2004). If, on a landscape scale, clear cutting mimics the natural disturbance regime, then clear cutting may have only temporary negative impacts (Hunter 1990; Bunnell 1995; McGee 1999). If clear cutting differs greatly from the natural regime, then the resulting negative impacts are likely to permanently alter the regional species assemblage. Particularly where clear cutting exceeds the natural disturbance regime, species for which clear cuts are impermeable or inhospitable may not be able to persist in the region.

Additional research is needed to understand the interplay of time, buffer zones, clear cuts, and geographic location, with spotted salamander upland habitat requirements. DeMaynadier and Hunter (1998, 1999), McLeod and Gates (1998), Renken et al. (2004), and Patrick et al. (2006) found fewer spotted salamanders in clear cut versus uncut areas. More specifically, Patrick et al. (2006) found that adult spotted salamanders were more abundant in uncut, partially cut, and clear cut areas where coarse woody debris was retained, compared to clear cut areas where coarse woody debris was removed. They also found that juvenile spotted salamanders were more abundant in uncut versus partially cut areas, and in clear cuts where coarse woody debris was retained versus clear cuts where coarse woody debris was removed. However, clear cuts in deMaynadier and Hunter's studies were at least 2 years old, and those in McLeod and Gates' study were at least 12 years old. Furthermore, none of these studies documented the migratory origins of captured salamanders, nor the fate of salamanders found within clear cuts; and were thus unable to determine distances traveled from breeding pools, and the success with which salamanders were able to pass through clear cuts (i.e., the permeability of clear cuts). Gibbs (1998a, 1998b) found spotted salamanders sensitive to forest edge gradients, but he examined forest-road and forest-residential edges, not forest-clear cut edges.

Forest management research related to other amphibian species, suggests a range of potential effects of cutting on spotted salamanders. Numerous studies demonstrate that plethodontid salamanders respond poorly to both clear cutting and partial harvests. In general, local plethodontid populations tended to collapse within 2 years of a logging event and took decades to recover pre-cut abundances (Knapp 2003; Ash 1997, 1988; Petranka et al. 1993, 1994; Petranka 1999; Dupuis et al. 1995; Herbeck and Larsen 1999).

Similarly, Means et al. (1996) attributed a drastic decline in a flatwoods salamander (*Ambystoma cingulatum*) population to disturbances caused primarily by mechanical preparation and secondarily by clear cutting, of a pine plantation. Moseley et al. (2003) observed that marbled salamanders (*Ambystoma opacum*) were more abundant in unburned versus burned forest stands. In contrast, Ford et al. (2000) found no difference in abundance of *Plethodon jordoni*, *Desmognathus ocoee*, and *Eurycea bislineata* between logged and uncut forest stands. Likewise, Chazal and Niewiarowski (1998) documented no difference in several indicators of growth and fecundity between mole salamanders (*Ambystoma talpoideum*) raised in clear cut versus mature forest conditions. Knutson et al. (1999) indicated that forests act as dispersal corridors for anurans; while Joly et al. (2001) found that the width of pasture corridors linking ponds and forest was a strong predictor of newt abundance. Finally, studies of long-toed salamanders (*Ambystoma macrodactylum*; Naughton et al. 2000) and the mole salamander (Raymond and Hardy 1990) indicate that clear cut areas are less permeable to dispersing amphibians than areas that receive partial-cuts, and that clear cut areas may act as dispersal barriers. Although they suggest additional salamander upland habitat requirements, none of these studies focused on spotted salamanders or forestry practices in New England.

Traditional Analysis Methods

Radiotelemetry is an increasingly popular method used to study migratory movements and habitat use in adult amphibians. This method involves attaching radio-transmitters to a set of amphibians, then releasing those individuals back into their

habitat, and using a radio-receiver to obtain information about the location of each tagged amphibian. Over the course of the battery-life of the transmitters, the observer makes repeated location observations for each animal being tracked.

Traditionally, data gathered via amphibian radiotelemetry studies have been analyzed using t-tests, Analyses of Variance (ANOVAs), or their non-parametric equivalents (e.g., Madison 1997; Faccio 2003; Montieth and Paton 2006). These analyses usually compare differences in summary statistics such as: total distance moved or net distance from the breeding pool, at the end of the migratory season. There are 3 major, potential problems with using these techniques to analyze amphibian radiotelemetry data.

First, such analytic techniques assume that repeated observations made on each tagged individual are statistically independent of each other. While observations may be independent if significant time is allowed between observations, in practice, amphibian researchers probably do not use inter-observation periods that are long enough to achieve statistical independence (e.g., in salamander telemetry studies, individuals were tracked at least once every 3 days or at least once a week; Madison 1997, Faccio 2003, Montieth and Paton 2006). The resultant correlation among observations violates the assumptions of the traditionally-used tests, and can obscure actual patterns in the data.

Second, the traditional analytic techniques are not well-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). When these irregularities are present in the data, the traditional techniques tend to confound the effects of different factors.

Finally, the traditional techniques do not have a mechanism to deal with between-subject variability. This is variability that can be attributed to unique differences in behavior between individual amphibians. While these unique differences may be intriguing, population or species-level traits are generally more useful in a research context. Where between-subject variability is present, it can obscure underlying population or species-level patterns.

Generalized linear mixed-effects modeling (glme) is an alternative analytic technique that has been used to examine time series data in other disciplines (e.g., medicine; Pinheiro and Bates 2000; Andreozzi et al 2006), and has recently been applied in ecological studies (e.g., Golet et al, in press; Bishop et al 2004; Venables and Dichmont 2004; Millar and Anderson 2004; Cooper et al. 2002). Glme is equipped to deal with each of the above problems. Glme allows the analyst to include both fixed and random effects in the model (i.e., to separate between-group from between-subject variability), to use unbalanced data sets with relative impunity; and to specify the variance-covariance matrix when necessary (i.e., to model serial correlation and heterogeneous variance). Glme results in the creation of regression models that can be used to describe population-level phenomena.

To help determine the usefulness of buffer zones to, and the immediate impacts of clear cutting on spotted salamander migration and upland habitat use, I used clear cutting to experimentally manipulate upland buffer widths at vernal pools. Subsequently, I used radio-telemetry and generalized linear mixed effects modeling to observe and analyze the

interactions between clear cutting and buffer zones, in their effects on salamander migration and upland habitat use.

The objectives of this study were to track individual spotted salamanders to determine the effects of forest clear cutting and buffer zone width on: 1) the probability of salamander movement; 2) the rate of salamander movement; and 3) the net distance a salamander moves from the edge of its breeding pool. In general, I expected salamanders to avoid clear cuts, but to move more quickly through clear cuts than forest, were they to enter the clear cut. Consequently, I expected net distance migrated from the vernal pool to increase with buffer width, but also expected a few outliers representing the rare salamander that crossed the clear cut to forest on the far side.

CHAPTER II

METHODS

Study Site

This research was conducted in eastern-central Maine on land that is owned and managed by International Paper (IP) / Sustainable Forestry Technologies (latitude: 44°60'N, 44°48'N; longitude: 68°26'W, 68°02'W). The landscape is characterized by moderate hills, valleys, 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, with increasing dominance of balsam fir (*Abies balsamea*) and red spruce (*Picea rubens*) at higher elevations and in riparian areas (Babbitt, pers. comm). Access roads are abundant within the forest.

In 2002 to 2003, twelve vernal pools within this landscape were selected for study. The vernal pools were selected from about one hundred potentially-suitable pools based on the criteria described below. These criteria were established in an effort to standardize the biotic and abiotic factors affecting salamander populations at both the landscape and within-wetland levels.

The chosen vernal pools were all embedded within relatively-undisturbed, hemlock-northern hardwood forest (i.e., in general, forest within a 1000-m radius of the pool could not have been logged within the past 60 years). The chosen pools were all about 0.2 ha, a size typical of vernal pools in the region (Gibbs 1993; Babbitt pers. comm.). To ensure that the pools were fishless, but inundated long enough to allow full development of larval salamanders in most years, the hydroperiods of the chosen pools were all between 5 and 6 months (post ice-out). Finally, the selected pools had a similar amphibian species composition and similar abundances of salamanders. Salamander abundances were estimated from salamander egg mass counts conducted in April and May of 2002 (Babbitt, unpub. data).

Buffer Creation

Between September 2003 and March 2004, International Paper created the study buffer zones by clear cutting forest (i.e., removing all merchantable trees of ≥ 5 cm diameter at breast height (dbh)) around selected vernal pools. Each pool was randomly assigned to 1 of 3 possible treatments: >1000-m buffer (i.e., a reference or uncut treatment), 100-m buffer, or 30-m buffer. In the 2 cut treatments, an upland buffer of 100 m and 30 m, respectively, was left intact immediately adjacent to the vernal pools; then, a concentric, 100-m-wide clear cut was created around the buffer (See Figure 1). Buffer widths in the cut treatments were based on extant BMPs, laws, and/or the literature (Semlitsch 1998; Calhoun and deMaynadier 2002; M.G.L. Chapter 131, § 40).

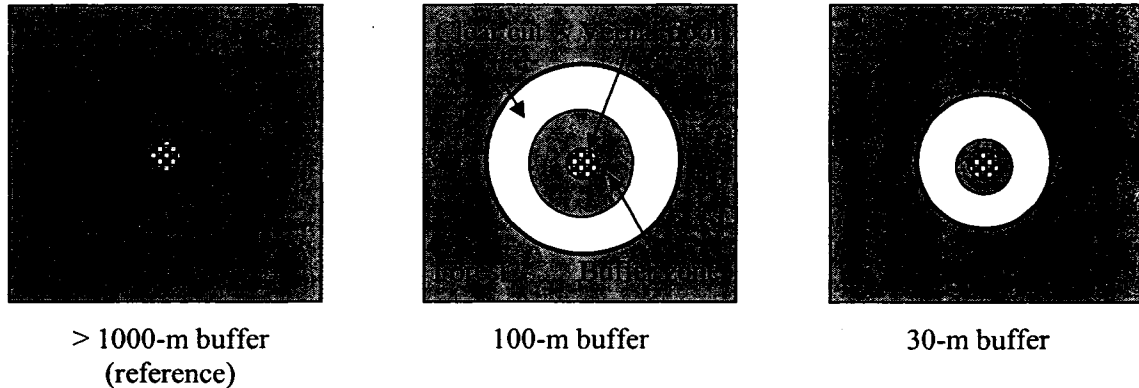


Figure 1. Experimental design for each of the 3 cutting treatments: > 1000-m buffer (reference treatment), 100-m buffer, or 30-m buffer. No cutting occurred at reference vernal pools. At clear-cut treatment vernal pools, buffer zones were either 100 m or 30 m wide. Clear cuts were 100 m wide. Outside the clear cut was undisturbed forest. Figure not to scale.

Once cutting was complete, I used a Trimble Pathfinder Pro XR GPS unit (Trimble Navigation Limited, Sunnyvale, CA) and ArcViewGIS 3.3 (Environmental Systems Research Institute, Inc., Redlands, CA) to map the perimeter of each vernal pool; the buffer and clear cut edges; and major landscape features (e.g., access roads, streams).

I also installed 2 max/min air thermometers and 2 rain gauges at each vernal pool. One of each instrument was located at 9 m east of the pool (i.e., in a forested region). The second of each instrument was located at 60 m (for the 30-m buffer treatment), or at 130 m (for the 100-m buffer and the uncut treatments; i.e., within the clear cut, if there was a clear cut) east of the vernal pool.

Radiotracking

Selection of Individuals

Forty adult spotted salamanders (21 in 2004, 19 in 2005; 25 females, 15 males) native to the selected vernal pools were tracked using radio-telemetry. Tracked subjects were captured in pitfall traps as they were leaving the vernal pools, post-breeding (i.e., from mid-April to early May). Subjects were selected for tracking based on mass, sex, and cutting treatment. Previous research indicates that transmitters should not comprise more than 13 to 15% of a salamander's body mass (Faccio 2003; Madison 1997). Since my radio-transmitters were 1.8 g each; only salamanders weighing more than 13 g were considered for tracking (mean: 18.0 g; range: 13.2 to 22.5 g). To the extent possible, I tried to select equal numbers of females and males; and equal numbers from each cutting treatment, for tracking.

Implant of Transmitters

The selected salamanders were transported to the lab, and surgically implanted with radio-transmitters (model: BD-2H, Holohil Systems LTD, Carp Ontario, Canada), according to the methods of Madison (1997) and Faccio (2003). Madison (1997) concluded that this surgical procedure and tracking method does not pose a long-term threat to spotted salamanders.

Post-surgery, salamanders were kept overnight in individual plastic buckets, that each contained a moistened paper towel. The following morning, the salamanders were

returned to their native pools, and placed in a natural burrow located 1 to 3 m upgradient from the trap line, opposite to the trap where they were originally caught. The entrance to the burrow was then covered with leaves. In instances where the surgery was particularly long, or when the salamander did not seem recovered enough to be returned the morning following surgery, the salamander was held for an additional 24 to 48 hrs, then transported to a burrow near its pool.

Transmitter batteries were designed to last 14 weeks. At about 13.5 weeks post-surgery, salamanders were recaptured and transported to the lab, so their transmitters could be replaced, using the same surgical procedure as before. After recovery, the salamanders were returned to the burrow whence they were removed, or to a burrow within 0.25 m of that location (if excavation of the salamander rendered its former burrow unusable). In one instance, when a salamander was retrieved, its original incision was found to have reopened. Its transmitter was removed, but not replaced. I simply restitched its incision and released it to its previous location. Salamanders were excavated and their transmitters surgically and permanently removed, at the end of October / beginning of November.

I tried to be as un-intrusive as possible when retrieving the salamanders. However, an unfortunate consequence of this tracking method is that retrieving the salamanders required excavation around their location, which often resulted in substantial destruction of the burrow system and underground integrity at the location. I believe this habitat alteration caused some salamanders to move in search of a better refuge. I observed 6 salamanders that resettled from their post-surgery point of release to a less disturbed location, during the first 2 weeks following surgery. Resettlement distances

ranged from 0.5 to 7.5 m. Movements greater than 7.5 m were not observed during those first 2 weeks. This behavior probably led to increased estimates of summer movements, than would otherwise have been observed. Additionally, some of the fall movements may be attributed to excavation, which likely made some summer refuges unsuitable for overwintering.

Data Collection

Radio-tracking was conducted from 2 May to 7 November in 2004, and from 27 April to 28 October in 2005. The starting and ending dates were determined by salamander availability and weather conditions.

In 2004, I recorded the position of all radio-tagged individuals, on average, every 6 days (range = 1 to 29 d). In 2005, the average radio-tracking interval was 2.5 days (range = 1 to 23 d). I did not radio-track during substantial rain events to avoid damage to receiving equipment. Individuals were tracked using a Communications Specialists Inc. (Orange, CA) R1000 receiver and a hand-held, 3-element Yagi antenna.

I used direct overhead localization (Madison 1997) to pinpoint the precise location of each individual. I used the receiver without the antenna to gauge the relative depth of the salamander below ground. The maximum distance from which radio signals were detected ranged from < 3 m (when salamanders are deep in burrows) to a maximum of about 40 m. At least once a week, I peeled back the leaf layer to try and visually confirm the presence of the salamander.

If a salamander moved, I systematically searched for the salamander, by zigzagging across adjacent, 10-m-wide strips, using the salamander's last known location as a focal point, and moving up to 350 m distance from that location. Multiple person-hours were devoted to finding each lost salamander (search duration per salamander in 2005 ranged from 3 to 13 hr).

Each salamander location was marked with a labeled flag, and recorded with a Trimble Pathfinder Pro XR GPS unit (which is accurate to 0.5 m), and subsequently plotted on a GIS map of the site. For every salamander, I then calculated the distance between each pair of consecutive locations, and between each location and the nearest point on the vernal pool trap line, using x, and y coordinates for each point.

In addition to salamander location, I also recorded the general habitat type (i.e., whether the location was in forest, in edge [i.e., 0 to 10 m from the edge of the clear cut], or in the clear cut) and the general microhabitat type (e.g., above-ground, below-ground, in a tunnel) at each location. Since only 3 salamanders were ever located at an edge, I reduced the general habitat type categories to either forest or clear cut, for analytic purposes. Numerous other habitat characteristics (relating to vegetative and microhabitat structure) were also cataloged at each salamander location and at semi-random locations in the surrounding uplands. These more specific habitat data are not analyzed as part of this thesis.

Finally, I recorded max/min air temperature and precipitation at each of the weather gauges at each pool weekly in 2005. I also obtained daily weather data from the nearest National Climatic Data Center climate station for which data was available for the

duration of this study. This station is located in Wesley, Washington County, Maine, and was between about 20 km and 60 km from my vernal pools. To ascertain if the Wesley station data sufficiently depicted weather patterns at my vernal pools, I used Pearson correlations to compare my field-based precipitation data to the Wesley station data. Correlations between the field and Wesley station data were relatively high (mean = 0.84 \pm 0.03, range = 0.71 to 0.95). Despite micro-climatic differences that certainly exist between pools, I concluded it was reasonable, based on these high correlation values, to use the Wesley station data to represent the relative, daily weather patterns at all of my study pools.

Data Analysis

Linear and generalized linear, mixed-effects models were used to examine daily salamander movements.

Mixed-Effects Regression Modeling

Three mixed-effects regression models, each capable of predicting different aspects of daily salamander movement, were created using the “glme” and “lme” functions in the “correlatedData” library of S-PLUS 7.0 (Insightful Corporation, Seattle WA). Respectively, these models describe a) the probability of a salamander moving on a given day; b) its movement rate, if that salamander did move, and c) the distance a salamander was from the vernal pool.

The probability of a salamander moving (a), was modeled using mixed-effects logistic regression. A salamander was classified as having moved, if it was ≥ 1 m from its

last tracked location. Movement rate (b) was modeled using mixed-effects Poisson regression. The offset for the Poisson regression was a log-transformation of the number of days since a salamander had last been radiotracked. Distance from the vernal pool (c) was modeled using mixed-effects linear regression (i.e., based upon the normal distribution).

Movement probability and rate were analyzed separately because the number of days when salamanders did not move (i.e., when migration rate was 0 m/d) was too great for movement to be described by any single distribution. Such zero-inflated data is better described by a mixture of distributions (Lambert 1992; Hall 2000). I used logistic regression to examine differences between movement and no-movement days; then removed the no-movement days from the data, and modeled migration rate with Poisson regression.

Random effects were included in the models because I expected salamanders to sometimes exhibit individualized behaviors, and/or exhibit behaviors unique to their breeding pool. I was not, however, interested in quantifying the nature and strength of these particular effects. By including salamander and/or vernal pool as random effects, I was able to account for such atypical behaviors without complicating the main part of my analysis.

In general, models were constructed as follows. Overall, parsimony (i.e., fewer variables) was favored over minimal improvements resulting from additional variables. First, fixed effects were selected. Parameters considered as possible fixed effects are given in Table 1.

Table 1. List of parameters considered in the modeling process.

Parameter	Possible values	Abbreviation
cutting treatment	reference, 30-m buffer, 100-m buffer	treat
habitat	not in clear cut, in clear cut	habitat
reference category ^a	reference pool, not a reference pool	ref
sex	male, female	sex
year	2004, 2005	year
day of the year		day of the year
season ^b	spring, summer, fall	
day on which salamander was first tracked		first day
cumulative number of days tracked		CumDays
number of days since salamander was last tracked		no.days
distance from the vernal pool ^c		distvp
snout-vent length		svl
mass		mass
cumulative precipitation over previous 48 hours ^d		2dppt
cumulative precipitation over previous 7 days ^e		weekppt
cumulative precipitation since first date tracked		cumppt
minimum temperature over previous 48 hours ^d		2dTmin
maximum temperature over previous 48 hours ^d		2dTmax
minimum temperature over previous 7 days ^e		prevweekTmin
maximum temperature over previous 7 days ^e		prevweekTmax
mean temperature over previous 3 days ^f		3dTmean
cumulative number of days (since first date tracked) when temperature ranged from 0 to 33.3 °C ^g		cumdays0to33
cumulative number of days (since first date tracked) when temperature ranged from 5.5 to 33.3 °C ^g		cumdays5to33

Notes: ^a Included in case habitat / treatment effects were confounded by the pre-determined distance of each habitat type, as dictated by cutting treatment.

^b Spring = 27 April to 14 June; Summer = 15 June to 31 August; Fall = 1 September to 7 November.

^c Only used as a possible fixed effect in the logistic and Poisson regressions.

- ^d Interval for parameter based on the mean tracking interval in 2005, which was 2.5 d.
- ^e Interval for parameter based on the mean tracking interval in 2004, which was 6 d (i.e., about 1 week).
- ^f Sexton (1990) indicated this temperature-related parameter was strongly associated with spotted salamander movement.
- ^g Parameter derived from previous studies of *Ambystoma* movement, and preliminary screening of data from this study.

Selection of fixed effects occurred as follows. First, I ran a series of regressions, each including one possible fixed effect (plus the offset where applicable), using individual salamander as the default random grouping parameter. I tested the significance of each possible fixed effect's contribution to the model via marginal analyses of variance (ANOVAs). In the case of categorical variables with more than 2 categories I used t-tests to determine if the coefficients for each of its individual dummy variables were significantly predictive of the outcome. Throughout, only those fixed effects found to explain a significant portion of the variance were considered further. Next, I used F values to determine the relative importance of each fixed effect. The effect (x) with the highest F value was retained in the model.

This process was then repeated: a series of regressions and marginal ANOVAs were used to test whether each remaining fixed effect, in turn, significantly contributed to the existing model. To judge the contribution of each potential new fixed effect, I generated scatter plots of the predicted values from the existing model versus predicted values from each updated version of the model (i.e., predicted: predicted plots). The degree of difference between the original and updated models (i.e., the amount of scatter in the predicted: predicted plot) was used as an index of the relative contribution of each new fixed effect to the model. I considered the amount of scatter in the

predicted: predicted plots, the F values, the biological relevance, effect coefficients, effect confidence intervals, and fitted: observed plots in deciding which parameter to retain in the model. Only those parameters that, relatively, added a medium to large amount of scatter were candidates for retention. This serial process was repeated until the predicted: predicted plots of any additional parameters revealed only very little scatter (i.e., difference between the models was negligible). I did not use likelihood ratio tests (LL) to compare relative contribution of fixed effects because LL tests, in the context of linear mixed-effects models, tend to be “anticonservative” and generate inaccurate p values (Pinheiro and Bates 2000; Cooper et al. 2002).

After the fixed effects were determined, the random effects structure was refined. I used LL ratio tests and Akaike Information Criteria (AIC, Sakamoto et al. 1986) values to select the most appropriate random grouping parameter and random effects. I compared grouping by salamander, wetland, year, and salamander nested within wetland, respectively, in addition to several different random effects. Consistently, for all 3 models, random grouping by salamander (i.e., random intercepts), but no random effects (i.e., random slopes) generated the best fit random effects structure.

After updating the random effects, I specified the correlation structure, in order to account for dependence between repeated observations taken on each salamander. Additionally, I suspected that observations made closer in time would be more highly correlated than those further apart in time. Initial examination of empirical autocorrelation function (ACF) plots confirmed that the correlation structure needed to be specified for all 3 models. I used LL ratio tests, AIC values, and empirical ACF plots to select from a mixture of auto-regressive and/or moving average correlation structures.

After choosing the correlation structure, I assessed whether the variance structure needed specification. To make this determination, I examined plots of standardized residuals versus fitted values, both across groups for categorical variables and across continuous parameters. If these plots indicated that the assumption of homogeneity of variance was violated, I proceeded to model the variance structure. The variance structure was selected based upon LL ratio tests, AIC values, confidence intervals of the model parameters, and residual plots. Possible variance structures included:

Fixed variance: Variance is fit during the first iteration of the model, and held fixed throughout the rest of the iterations. Variance is structured as a linear function of a covariate.

Identity variance: A different variance is fit for each level of a grouping parameter.

Constant-power variance: Variance is a function of a constant plus a power of a covariate.

Exponential variance: Variance is an exponential function of a covariate.

After choosing the variance structure, I tested whether any first-order interactions should be included in the model. The process for selecting interactions mimicked the fixed effects selection process. Potential interactions were chosen based upon biological relevance.

Once the interactions were selected, I verified that the random effects, correlation, and variance structures were still valid for the updated model. Then, using predicted: predicted plots, I dropped each fixed effect / interaction, in turn, from the model, to confirm that each effect contributed significantly to the model. After effects were dropped from the model, as needed, I re-verified the validity of the chosen random

effects, correlation, and variance structure. If necessary, this process was repeated, until a final model was achieved, in which all fixed effects / interactions contributed highly to the predictive power of the model, and all other pieces of the model were fitted optimally to those fixed effects. This modeling method, in many ways, resembles a step-wise, forward and backward regression.

The final model was then assessed to determine whether it satisfied the assumptions of linear or generalized linear modeling. In the case of the “distance from vernal pool” model, the variance was not homogenous across groups, even after a tailored variance structure was added to the model. Log-transformations of 3 of the variables included in the model corrected the variance heterogeneity. Log transformations were appropriate since field observations indicated that salamander movement, with respect to distance from the vernal pool, was a log-type process. Salamanders tended to make large movements early in the year, bringing them some distance from the pool. Later in the year, movement lengths tapered off, such that the salamander’s distance from the pool did not change much after their initial exodus into the uplands.

All 3 models violated the assumption of normally-distributed random effects. (Pinheiro and Bates 2000). Attempts to normalize the random effects (i.e., by transforming variables or altering the hierarchy of the random grouping structure) were unsuccessful. However, since the fixed effects structure is relatively robust to violations of this assumption (Cooper, pers. comm.; Venables and Ripley 2004), and since no a priori hypotheses were made with respect to random effects, I concluded it was reasonable to ignore the violation, and safely draw conclusions about the fixed effect

portions of the models. All other assumptions relating to linear and generalized linear modeling were satisfied.

I did find, however, strong correlations among several of the predictors, including 3 that were used in the final models: day of the year, CumDays, and cumppt (see Tables 1, 2, and 3). The problem with including highly correlated variables in an analysis is that if the variables describe a similar phenomenon, they may compete to explain the same portion of variance in the data, and thus each may weaken the apparent effect of the other. Each of the above 3 variables, in some way, describes the passage of time. Initially, I decided there might be legitimate differences between the 3 variables, and inclusion of all 3 was warranted. I found, however, that day of the year and CumDays were too closely related, and did in effect, cancel each other out in my analyses. (Cumppt seemed to operate fairly independently of day of the year and CumDays). I therefore decided that either day of the year or CumDays could be used in a model, but not both. Selection between the 2 was based on my understanding of the biology of the situation, and the relative strength of each in the given model.

Four other problematic issues arose during the course of the analysis. First, SVL and mass measurements were not recorded for 7 and 5 of the salamanders, respectively. To determine the impact of this missing data on my analysis, I created binomial variables to represent whether a salamander's SVL and mass measurements were, or were not recorded. I then tested these variables as fixed effects in the early stages of each model to ascertain whether missing these size measurements might bias the results of my modeling. For both the migration rate and distance from vernal pool models, regressions including the missing measurement variables were not significantly different than the null

model. For the “probability of a salamander moving” model, the missing-mass variable was significant when it was the only fixed effect included in the model. Once a second fixed effect was added to the model, however, the missing-mass variable was no longer significant. Given this, and since mass itself did not contribute significantly to the model, I concluded that the results of my modeling would be valid, despite these missing size measurements.

The second potential problem was that salamanders were sometimes not re-located for long periods of time (i.e., several weeks). In 2004, standard protocol was to locate salamanders once a week. Frequently, however, salamanders were only located every 10 to 14 days. Occasionally, salamanders were not located for 18 to 29 days. In 2005, 5 salamanders moved long distances during extended periods of rain. Because I could not track during the rain, and due to the limited range of the telemetry equipment, it took about 1 week to find 4 of these salamanders, and about 3 weeks to find one of these salamanders. The problem with these extended tracking intervals is that I do not know the rate at which salamanders were actually moving during the interval. For instance, the 2005 salamander that was missing for 3 weeks moved 165 m during that period. It is impossible to know whether that salamander moved 165 m over the course of the 3 weeks, or in just a couple of days. I modeled these uncertain migration rates as if the salamander used the whole between-observation period to move the recorded distance. Observations from other salamanders suggest, however, that the missing salamanders were probably moving at quicker rates for some periods, and not moving at all, during other days of that interval. Thus, my models likely underestimate the true rates at which the salamanders moved.

The third potential problem was that when I went to retrieve 6 of the salamanders (3 in 2004, 3 in 2005) I found the transmitter, but not the salamander. I do not know for certain when these salamanders died / lost their transmitters (i.e., how long I was tracking a transmitter, but not a salamander). Based on the movement histories of these 6 salamanders, the longest I may have tracked a transmitter without its salamander ranged from 11 to 46 d. I am reasonably confident, however, that no movements greater than 2 m occurred when just the transmitters were being tracked. For the analyses, I assumed the salamander was alive up to the tracking event which preceded the tracking event during which the transmitter alone was found. The problem with this uncertainty is that I could be overestimating the length of time that the salamander spent at its final location.

The fourth potential concern stems from premature drop-out of several salamanders in the study. Of the 40 salamanders tracked, 21 dropped out before mid-October. Among the 30-m treatment salamanders, all but 1 were drop-outs. I do not know whether these salamanders died; remained stationary but undetectable (e.g., due to transmitter failure or because the salamander was too deep for detection); or moved a great distance, and were lost from the study. Likely, it was some combination of the 3. I was therefore unable to classify the direction of the bias caused by drop out, and fully incorporate it into my models. The reduced sample size caused by drop-out likely led to decreased statistical power for the end of the tracking season. Reduced power would make detection of significant movement patterns representative of the entire population more difficult.

I tried to compensate for drop-out, however, by testing whether day (e.g., day of the year) X treatment and season X treatment interactions were significant. These

interactions were not significant in any of the models. This indicated that, with respect to slope of the regression lines, drop-out and non-drop-out salamanders behaved similarly across treatments. These interactions did not address, however, potential differences in lengths of regression lines between drop-out and non-drop-out salamanders and between treatments (i.e., the regression lines may be parallel, but one may be longer than another). I had no good mechanism to test whether this occurred. I decided, however, to keep the drop-outs in the analysis for two reasons: a) 77% of the drop-outs occurred during the summer or fall (i.e., after the major migratory movements of spring were complete); and b) I thought including the drop-outs increased the sample size at the beginning of year sufficiently to offset the risk associated with the using drop-out data.

Because of my particular application of the mixed-effects regression technique, I might be accused of data mining and gross inflation of Type I error. Mixed-effects regression can be used for, and limited to testing of a priori hypotheses. In my study, however, I wanted to examine the potential effects of a relatively large predictor set. I therefore intentionally accepted the risk of Type I error inflation associated with large predictor sets, in order to establish a baseline understanding of the relationships between each predictor and salamander migration. Due to the large number of variables involved, I did not adjust my p values to account for the potential increase in Type I error, so my results may overestimate the significance of individual predictors.

CHAPTER III

RESULTS

A total of 1357 observations of salamander locations (hereafter referred to as fixes) were made over the 2 years of the study. On average each salamander was located 34 ± 3.8 times (range = 2 to 80 fixes). Refer to Table 2 for a summary of individual salamander tracking statistics, and to Table 3 for a summary of combined statistics for all 40 salamanders.

Table 2. Summary of tracking statistics for individual spotted salamanders. Salamanders are grouped according to the length of time tracked (i.e., dropped-out versus tracked through at least mid-October), and year.

Treatment	Salamander	Sex	Mass (g)	SVL (mm)	Fate	Days tracked	MaxDist ^a (m)	CumDist ^b (m)	Final Dist ^c (m)	% Time in CC ^d	Final Habitat ^d
Salamander That Dropped Out of Study Before mid-October											
2004											
30-m	150.148	F	17	81	Dead ^e	72	37.4	41.2	37.4	0	Buffer
100-m	150.341	F	22.2	92	Missing	127	124.1	139.9	124.1	69	CC
100-m	150.421	M	17.5	82	Dead ^e	69	4.4	11.4	4.0	0	Buffer
100-m	150.600	M	13.2		Alive	88	99.8	105.6	99.8	49	CC
100-m	150.606	M			Missing	71	47.3	61.7	47.3	0	Buffer
100-m	150.221	F	19.5	85.5	Missing	6	2.4	43.7	1.0	0	Buffer
100-m	150.279	F	19	92	Missing	87	80.2	99.3	80.2	0	Buffer
100-m	150.631	F	19	86	Dead ^e	4	13.9	46.55	13.9	0	Buffer
Reference	150.188	M	18.7	75	Missing	52	3.8	6.0	3.8		Forest
Reference	150.371	F	19	91	Alive	64	1.55	13.0	1.0		Forest
Reference	150.438	M			Missing	7	12.3	15.3	12.3		Forest
Reference	150.500	F			Dead ^e	59	61.5	66.1	60.3		Forest
Reference	150.581	F			Missing	15	201.9	210.4	201.9		
2005											
30-m	150.020	F	15.6	78	Missing	89	121.1	206.8	108.5	87	CC
30-m	151.300	F	18.5	82	Alive	101	168.4	171.7	168.4	24.8	FBC
30-m	151.008	F	17.0	66	Missing	60	65.7	119.6	65.7	99	CC
30-m	151.021	F	16.9	68	Dead ^e	92	173.9	183.1	173.9	22	FBC
100-m	150.288	M	17.5	78	Dead ^f	38	287.5	302.7	287.5	26	FBC
100-m	151.029	M	14.5	78	Dead ^g	68	221.6	298.4	220.1	1 to 16 ^h	FBC
100-m	151.045	F	17.5		Alive	87	151.0	153.6	150.9	99	CC
100-m	151.320	M	16.5	81	Missing	160	110.3	164.3	96.2	81	Edge

Table 2. Continued from p. 37.

Treatment	Salamander	Sex	Mass (g)	SVL (mm)	Fate	Days tracked	MaxDist ^a (m)	CumDist ^b (m)	Final Dist ^c (m)	% Time in CC ^d	Final Habitat ^d
Salamanders Tracked Through mid-October											
2004											
100-m	150.351	F	18.5	85	Alive	176	101.6	124.8	97.2	0	Edge
100-m	150.621	F	22.2	92	Alive	183	141.5	204.0	141.5	94	CC
100-m	150.228	F	18.7	89	Missing	164	54.3	114.3	40.7	0	Buffer
100-m	150.270	F	22	93	Missing	162	155.3	186.6	155.3	67	CC
100-m	150.300	F	19	94	Alive	175	43.6	113.4	43.6	0	Buffer
100-m	150.329	F		92	Alive	175	55.9	90.7	52.7	0	Buffer
Reference	150.206	M	18.3	84	Alive	169	106.2	137.6	98.5		Forest
Reference	150.561	M	14.7		Alive	183	50.3	73.9	50.3		Forest
2005											
30-m	150.045	F	22.5	91	Alive	178	427.6	593.0	302.0	8	FBC
100-m	151.160	M	16.5	78	Alive	179	52.9	113.0	15.9	0	Buffer
100-m	151.170	F	18.5	77	Missing	169	405.9	450.3	405.9	8	FBC
100-m	151.208	F	15	70	Alive	176	77.3	145.8	56.5	0	Buffer
100-m	151.261	F	18.5	84	Alive	183	59.9	87.6	59.9	0	Buffer
Reference	151.267	M	18	73	Alive	170	33.5	104.6	28.9		Forest
Reference	151.329	M	18.7	75	Alive	174	32.2	64.5	32.1		Forest
Reference	150.036	M	17.5	77	Dead ^e	167	68.2	88.5	65.6		Forest
Reference	150.087	F	20	81	Alive	171	181.7	192.9	181.7		ESF
Reference	151.220	F	20	75	Alive	174	96.6	133.6	82.5		ESF
Reference	151.227	M	14	80	Dead ^e	174	105.26	135.4	96.3		ESF

Notes: ^a Max Dist = Maximum straight-line distance moved from the nearest edge of the vernal pool.

^b Cum Dist = Maximum cumulative distance moved during the period tracked.

^c Final Dist = Straight-line distance of the salamander from the vernal pool on the last day the salamander was tracked.

^d CC = Clear cut; FBC = Forest beyond clear cut; Edge = Edge between clear cut and forest; ESF = Early successional spruce field.

^e Death due to predation. ^f Death due to being crushed by skidder. ^g Death due to unknown causes.

^h Salamander was never fixed in the clear cut per se, but did cross through the clear cut to forest on the far side. Eleven days passed (i.e., 16% of the time it was tracked) between when it was fixed in the buffer, and next fixed (in the forest on the far side of the clear cut).

Table 3. Summary of tracking statistics describing movements for all 40 adult spotted salamanders.

All Pools					
	Mean ^a ± SE			Range	
Number Fixes	34 ± 3.8			2 - 80	
	<i>All Salamanders</i>	<i>Salamanders Tracked Through mid-October</i>	<i>All Salamanders</i>	<i>Salamanders Tracked Through mid-October</i>	
Max. Distance From Pool (m)	106.0 ± 15.4	118.4 ± 25.9	1.6 - 427.6	32.2 - 427.6	
Max. Cumulative Distance Moved (m)	140.4 ± 18.0	166.0 ± 30.6	6.0 - 593.0	64.5 - 593.0	
Final Location Distance From Pool (m)	99.1 ± 14.2	105.6 ± 22.8	1.0 - 405.9	15.9 - 405.9	
Clear Cut Treatment Pools Only					
	<i>2004 & 2005</i>	<i>2004</i>	<i>2005</i>	<i>2004</i>	<i>2005</i>
% Entered Clear Cut	51.9	28.6	76.9		
% Crossed Clear Cut	22.2	0	46.2		
Percent of Time in Clear Cut	27.2 ± 7.2	19.9 ± 9.1	35.1 ± 11.3	0 - 94	0 - 99
Duration in Clear Cut (d)	30.7 ± 9.1	27.5 ± 13.9	34.5 ± 11.6	0 - 167	0 - 121

Notes: ^a Value is the mean except where indicated.

Of the 40 salamanders, 19 were tracked through at least mid-October. The other 21 salamander dropped out of the study on various dates and for various reasons. Five salamanders dropped out during the spring, 14 during the summer, and 2 in early fall. Many of the summer dropouts occurred just prior to the time when transmitter batteries were expected to stop working; these salamanders may have been lost because their transmitters were no longer emitting signals. Known drop-out causes were attributed as follows: 5 salamanders were predated; 2 died of other causes; and transmitters were not replaced in 3 salamanders during the mid-summer surgeries. (One salamander had dropped too much weight; and 2 experienced complications during surgery, though they survived and were healthy post-surgery). One predation was observed when tracking led to a garter snake (*Thamnophis sirtalis*) which had recently consumed one of my tagged salamanders. Of the 2 salamanders that died from other causes, one was found, above-ground, in the process of dying. Its incision had split open (possibly from attempted predation). I brought this salamander back to the laboratory with the intention of removing the radio, re-closing the incision and nursing the salamander back to health, but the salamander died en-route. The other salamander was crushed by a skidder when a selective logging operation commenced in the area where it was located. This salamander had crossed a 100-m buffer and a 100-m clear cut, and moved about 100-m into the forest on the far side of the clear cut. It had been at this location about a week, when logging in the area started, a skidder trail was made across its location, and it was crushed. A second salamander also crossed the clear cut and moved into the same forest area just prior to the partial cut. Although cutting occurred all around this second salamander and up to 3 m from its burrow, this salamander survived, stayed in that one burrow throughout the

logging, and did not move until mid-fall (presumably to find a more suitable overwintering habitat). The remaining 11 drop-out salamanders were likely lost due to battery failure, predation, and/or salamanders moving beyond the area tracked.

Burrows (likely small mammal burrows) were the predominant refuge used by salamanders in this study. Often these burrows were along tree roots. Only once was a salamander observed outside of a burrow. This occurred at the end of July; the salamander was curled under the leaf litter. Another salamander migrated to a spruce (*Picea* sp.) stand that was underlain by thin, flat, horizontally layered rocks, with only about 5 cm of soil between the surface and the rocks. On excavation for its mid-summer surgery, this salamander was found in the tunnels formed by the layered rocks. It quickly dropped within these tunnels from about 5 cm to 18 cm deep, at which point, it was submerged in the groundwater that flowed through these rocks.

Interestingly, there was a 1-ha section of forest within 50 m of one of my reference pools that appeared to be prime spotted salamander habitat (i.e., deciduous upland forest). None of the 5 salamanders tracked at this pool settled in this forested area, however. In fact, 3 of the 5 salamanders at this pool crossed a stream, in order to settle in an early successional spruce field, instead of the nearby deciduous forest. Extremely heavy rainfall in fall 2005 provided insight into the salamanders' possible avoidance of this section of seemingly ideal forest habitat. During the rains, the entire forest hectare essentially turned into a continuous swath of overland flow. The soil in this forest section must have been saturated, and any burrows were likely flooded.

The maximum straight-line distance that a tracked salamander moved from the vernal pool was 427.6 m. Mean maximum distance from the vernal pool for all

salamanders was 106.0 ± 15.4 m (range = 1.6 to 427.6 m), and for salamanders tracked through at least mid-October was 118.4 ± 25.9 m (range = 32.2 to 427.6 m).

The mean maximum cumulative distance moved over the entire tracking period by a salamander was: 140.4 ± 18.0 m (range = 6.0 to 593.0 m) for all salamanders in the study, and 166.0 ± 30.6 m (range = 64.5 to 593.0 m) for salamanders tracked through at least mid-October. Salamanders did not always take direct routes away from the pool, but frequently zigzagged across the landscape (Figures 2, 3, and 4). This behavior, in conjunction with the small movements salamanders sometimes made once settled into an area, largely explain the differences between straight-line distances from the pools and cumulative distances moved.

The mean distance of a salamander from the vernal pool at its final fix of the year was: 99.1 ± 14.2 m (range = 1.0 to 405.9 m) for all salamanders in the study; and 105.6 ± 22.8 m (range = 15.9 to 405.9 m) for salamanders tracked through at least mid-October.

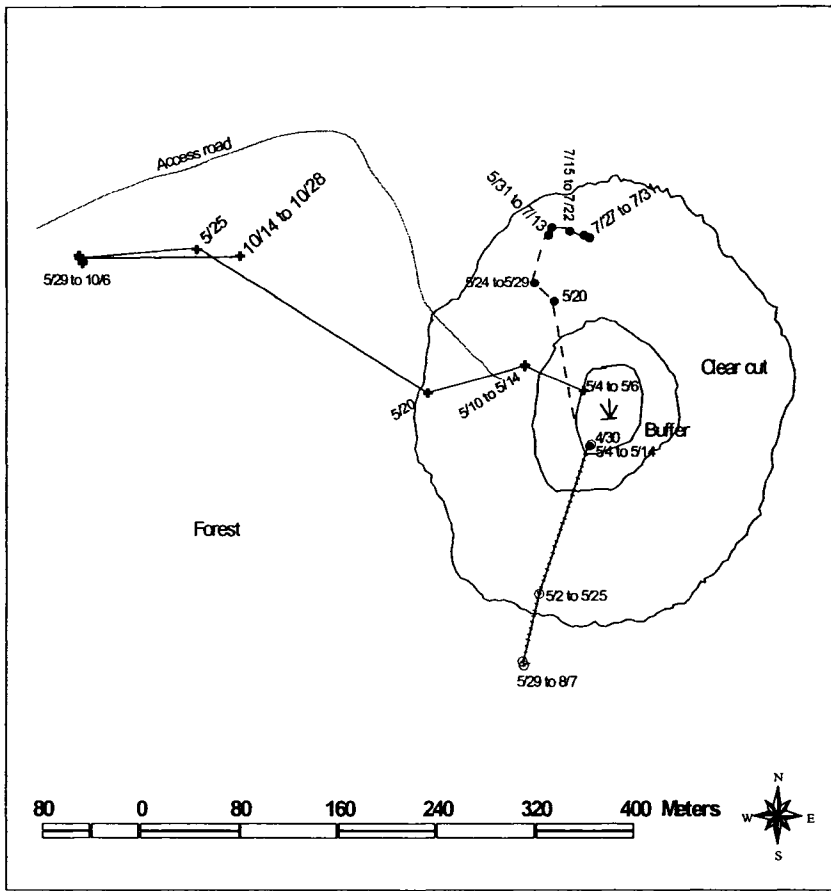


Figure 2. Migratory paths of three salamanders tracked at a 30-m buffer treatment pool in 2005.

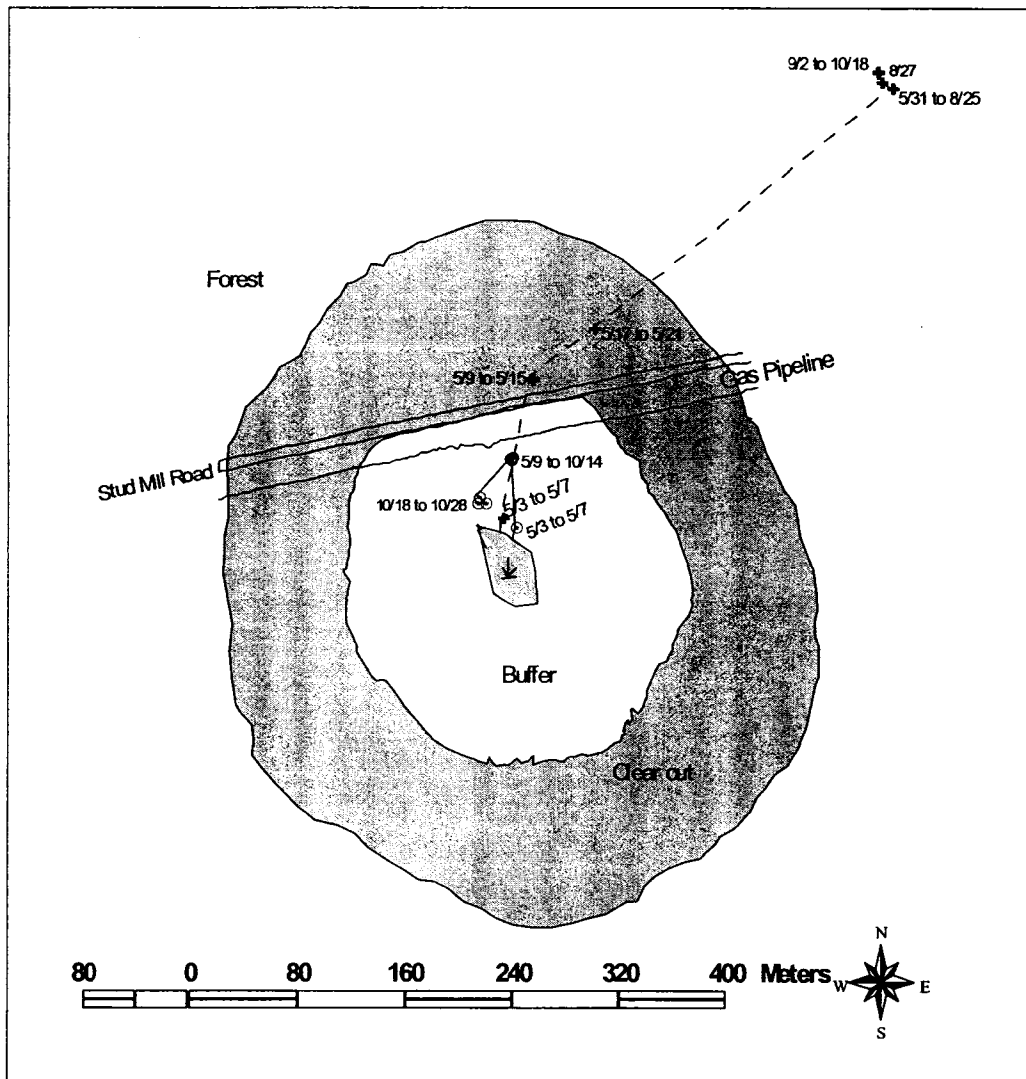


Figure 3. Migratory paths of two salamanders tracked at a 100-m buffer treatment pool in 2005. A gas pipe line and a major dirt road intersected the buffer and clear cut at this site.

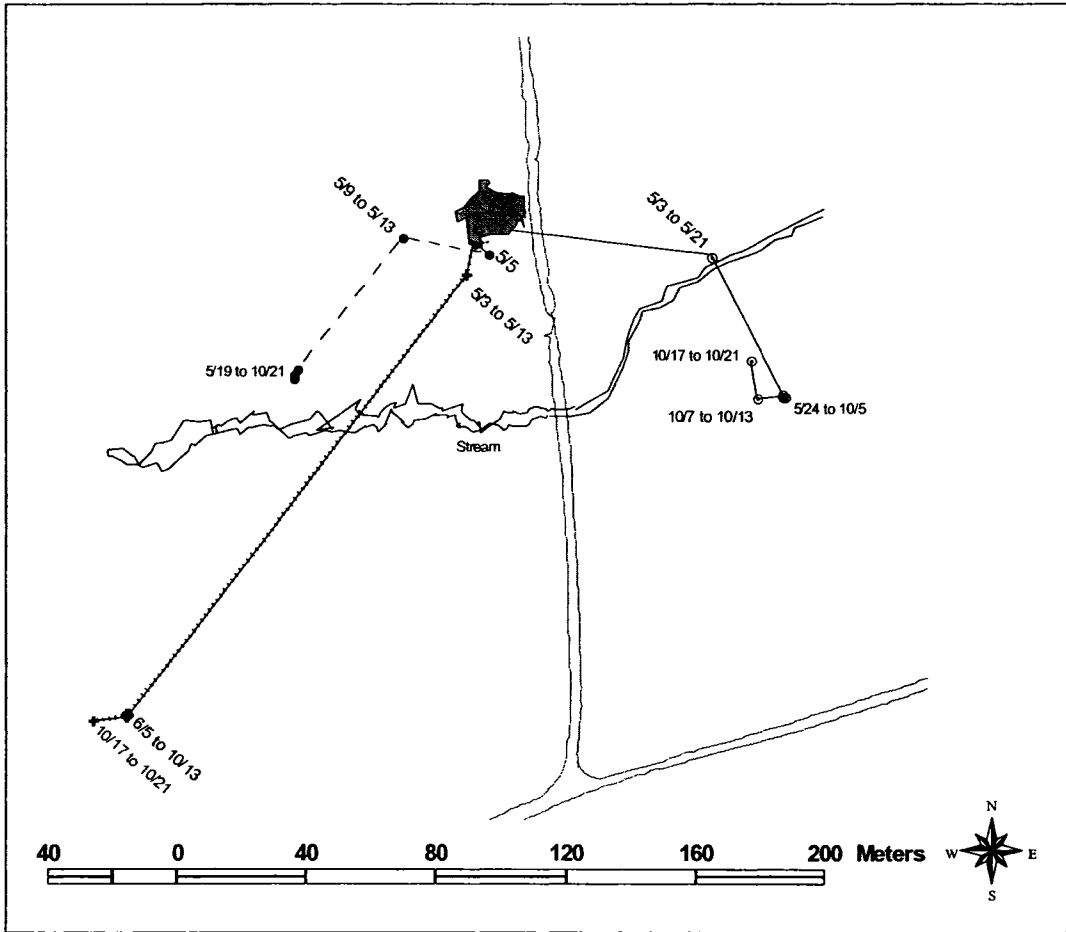


Figure 4. Migratory paths of three spotted salamanders tracked at a reference wetland in 2005. The wetland abutted a small, dirt access road.

Of the 27 salamanders that bred in clear cut-treatment pools, 14 (51.9%) entered the clear cut, while 6 (22.2%) crossed the clear cut and entered forest on the far side of the clear cut (Figure 5). Of the 14 clear cut-treatment salamanders tracked in 2004, 10 never ventured from the buffer into the clear cut; while 4 entered, but did not cross the clear cut. Of the 13 clear cut-treatment salamanders, tracked in 2005, 3 never left the buffer; 4 entered, but did not cross the clear cut; while 6 entered and completely crossed the clear cut. Of the 27 clear cut-treatment salamanders, 15, dropped out of the study before mid-October. I do not know how these salamanders would have moved with respect to the clear cut were they tracked throughout the whole season. Nonetheless, it is notable that no salamanders crossed, and far fewer even entered the clear cut in 2004, compared to 2005.

Mean percent of time spent in the clear cut by salamanders at the clear cut-treatment pools was $27.2 \pm 7.2\%$ (range = 0 to 99%). Mean duration spent in the clear cut, among clear cut-treatment salamanders, was 30.7 ± 9.1 d (range = 0 to 167 d; Figure 6).

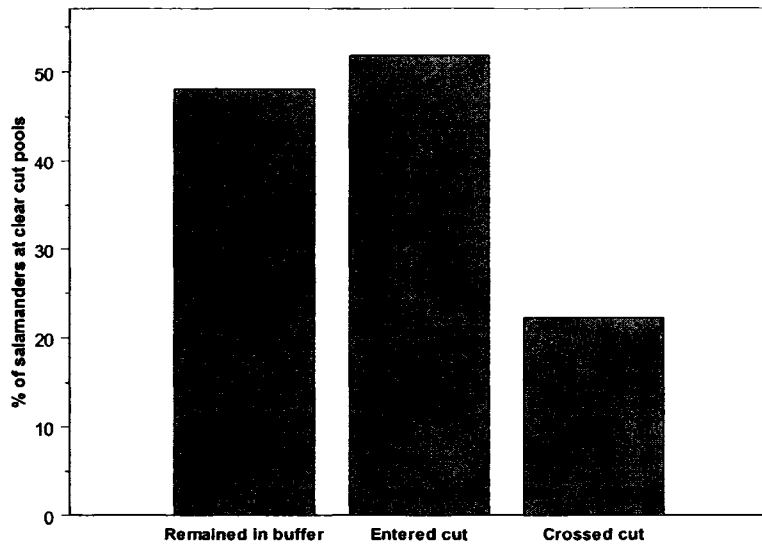


Figure 5. Percent of salamanders at clear-cut treatments pools that, respectively, remained in the buffer (48%); entered the cut (52%); and crossed through the cut into adjacent forest (22%). The 52% of salamanders that entered the cut includes both salamanders that entered, but did not cross, and salamanders that entered and crossed the cut.

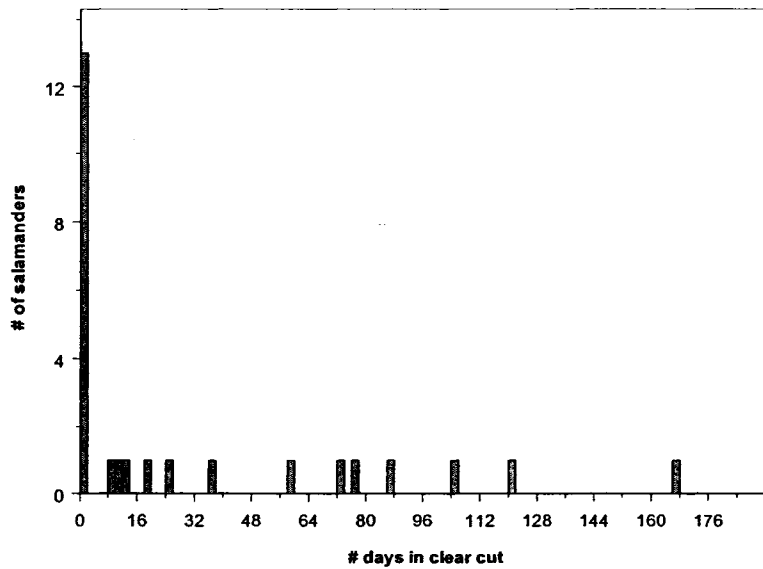


Figure 6. Distribution for the number of days that salamanders at clear cut-treatment pools spent in the clear cut. Mean duration in the clear cut was 31 ± 9 days (range = 0 to 167 days).

Probability of Salamander Movement

I used a mixed-effects logistic regression to model the daily probability of spotted salamander movement (coded: 0 = did not move or moved < 1 m, and 1 = moved \geq 1 m, on a given day). A total of 1243 observations, representing repeated fixes for 33 salamanders were used in developing this regression model. I was unable to use the full data set of 40 salamanders for this regression because snout-vent length (SVL) was significantly predictive of movement probability (through an interactive effect with cumulative precipitation), and I only had SVL measurements for 33 of the 40 salamanders.

In the early stages of the regression, data screening confirmed the need to specifically model the correlation structure of the data. Plots of the autocorrelation function showed serial correlation between radio-fixes within individual salamanders. I modeled the correlation using an autoregressive process of order 1, in which fixes adjacent in time were most highly correlated, while those distant in time were least correlated. Cumulative number of days tracked was used to indicate the passage of time in the correlation function. For the random effects, a separate random intercept was assigned to each salamander.

Results of the best-fit regression are summarized in Table 4. A marginal ANOVA was used to assess the contributions of individual predictors to the regression. Individual predictors most strongly associated with the probability of salamander movement were: cumulative precipitation fallen since tracking of that salamander began (mm; $cumppt$; $F_{1, 1200} = 25.8, p < 0.0001$); and number of days since the salamander was last located (d;

no.days; $F_{1, 1200} = 13.8, p = 0.0002$). Three interactions were also included in the final model: cumppt X SVL ($F_{1, 1200} = 26.2, p < 0.0001$); season X day of the year ($F_{2, 1200} = 26.2, p < 0.0001$); and season X no.days ($F_{2, 1200} = 9.9, p = 0.0001$). SVL, season, and day of the year, which would not have been included in the model were their respective interactions not included, were also significant (respectively, $F_{1, 1200} = 18.0, p = 0.0002$; $F_{2, 1200} = 19.4, p < 0.0001$; $F_{1, 1200} = 35.8, p < 0.0001$).

50

Table 4. Summary of Mixed-effects Logistic Regression Predicting Logit of Odds of Salamander Movement

	move ^a	cumppt (mm)	no.days (d)	svl (mm)	season – summer ^b	season – fall ^c	day of year (d)	Coefficient	SE	
cumppt	-0.15							0.028***	0.005	
no.days	0.09	-0.10						0.248**	0.067	
svl	0.04	-0.13	0.37					0.090**	0.021	
season-summer ^b								-3.077***	0.676	
season-fall ^c								-7.545***	1.672	
day of the year	-0.13	0.92	0.06	0.04				-0.088***	0.015	
cumppt X svl								-0.0003***	0.00006	
season-summer								0.091***	0.014	
X day of the year										
season-fall								0.108***	0.016	
X day of the year										
season-summer								-0.217*	0.079	
X no.days										
season-fall								0.134	0.109	
X no.days										
								Intercept =	-6.690***	1.701
Mean	0.21	318.2	3.5	80.4			81.8			
SE	0.01	5.4	0.1	0.2			1.4			
Range	0 - 1	0 – 943	1 - 29	66 - 94			1 – 195			

Notes: * p < 0.05, ** p < 0.001, *** p ≤ 0.0001.

^a Outcome variable. Coded: 0 = did not move or moved less than 1 m; 1 = moved ≥ 1 m.

^b Dummy variable. Coded: 0 = spring; 1 = summer.

^c Dummy variable. Coded: 0 = spring; 1 = fall.

Three additional interactions (total precipitation fallen during the previous week X maximum temperature during the previous week; total precipitation fallen during the previous 48 hours [2dppt] X habitat [forest or clear cut]; and cumpppt X 2dppt) were also highly significant when added to the model. Inclusion of all or some of these additional interactions improved the model fit, but not enough to justify the increased complexity associated with their addition to the model. If I speculate, however, that these additional interactions should be included (i.e., their significance is not a result of Type I error), then salamander movement becomes a very complex behavior. In this case, salamander movement would better be described by the time-dependent interplays of precipitation and temperature of the complicated model, than by the more parsimonious model described throughout the rest of the analysis.

Neither buffer treatment, nor any of tested interactions involving buffer treatment were among the best predictors of probability of salamander movement. The nature of the relationships between significant individual predictors and probability of salamander movement are described below.

The interaction between season and day of the year was the strongest predictor of probability of movement, and is best described by Figure 7. In general, probability of movement was higher in the spring than in both summer and fall ($t_{1200} = -4.5, p < 0.0001$, for summer vs. spring; $t_{1200} = -4.5, p < 0.0001$, for fall vs. spring). Fifty-seven percent of all movements occurred in May; the next most common month for movements was June with 12.5% of movements. Probability of movement varied with day of the year. Variation was greater in the spring than the summer ($t_{1200} = 6.4, p < 0.0001$), but was less in the spring than the fall ($t_{1200} = 6.8, p < 0.0001$). Movement probability

decreased from the beginning to the end of the spring (i.e., from end April to mid-June); was relatively constant throughout the summer, and increased (due to high variability) from the beginning to the end of the fall (i.e., from early September to early November).

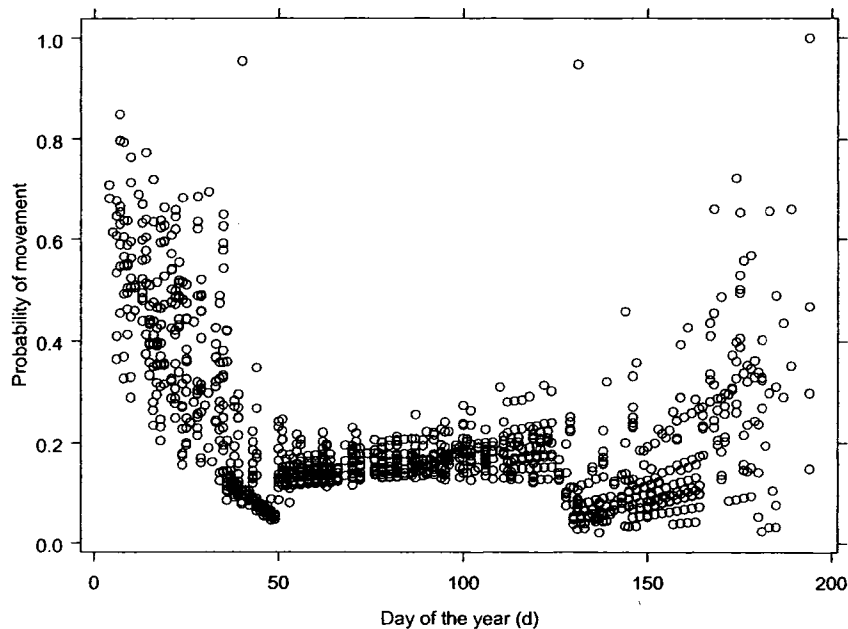


Figure 7. Probability of salamander movement versus day of the year. Seasonal differences in probability of movement are dramatically apparent. Spring = days 0 to 49; summer = days 50 to 127; fall = days 128 to 195.

The main effect of each additional day of the year was to decrease salamander movement probability. However, the negative impact of each additional day was softened by the positive interaction effects between day of the year and season. In the summer and fall, the negative impacts of day of the year were partially offset by the relatively strong coefficients of their respective season X day of the year interaction coefficients.

In general, as the number of days between radio-fixes increased, the probability of salamander movement increased. Due to a negative interaction between summer (versus

spring) and no.days, this pattern was least strong, but still evident, during the summer. On average (i.e., if other variables were held constant, at seasonal, mean levels), the inter-fix interval after which a salamander was more likely than not to have moved, was 6 d, 7d, and 11 d, in the spring, summer, and fall, respectively.

The main effect of increasing cumppt was to increase the probability of salamander movement. However, this positive association was dampened by the interaction of cumppt with SVL (Figure 8). When SVL was less than 84 mm, a 1mm increase in cumppt was associated with an increasing probability of salamander movement. At an SVL of 84 mm, the negative interaction effect with SVL exactly counteracted the unit effect of cumppt, such that the probability of movement was 0.5, when all other variables were statistically controlled. At SVLs greater than 84 mm, a 1 unit increase in cumppt was actually associated with a decrease in the probability of salamander movement. Overall, cumppt exerted a relatively weak influence on the probability of salamander movement. In the spring, when salamanders were most likely to move, if cumppt were to increase from 50 to 600 mm, the probability of movement would only increase from 0.33 to 0.49. This effect would be even less in the summer and fall, when salamanders were less likely to move.

The main effect of SVL was also to increase the probability of salamander movement. As with cumppt, however, the interaction between SVL and cumppt tended to decrease the strength of the positive association between SVL and the probability of movement. The switching point between a positive and negative unit impact of SVL on the probability of movement was 274.7 mm cumppt. For the 2 years of this study, 274.7 mm of cumppt had fallen by sometime in June or July. When cumppt was < 274.7 mm, a

1 mm increase in SVL was associated with an increase in the probability of movement. When $cumppt \geq 274.7$, a 1 mm increase in SVL was associated with a decrease in the probability of movement. Thus, longer salamanders are more likely to move when $cumppt$ is low (i.e., in the spring) than when $cumppt$ is high (i.e., in the fall). For shorter salamanders, the probability of movement was less restricted by $cumppt$.

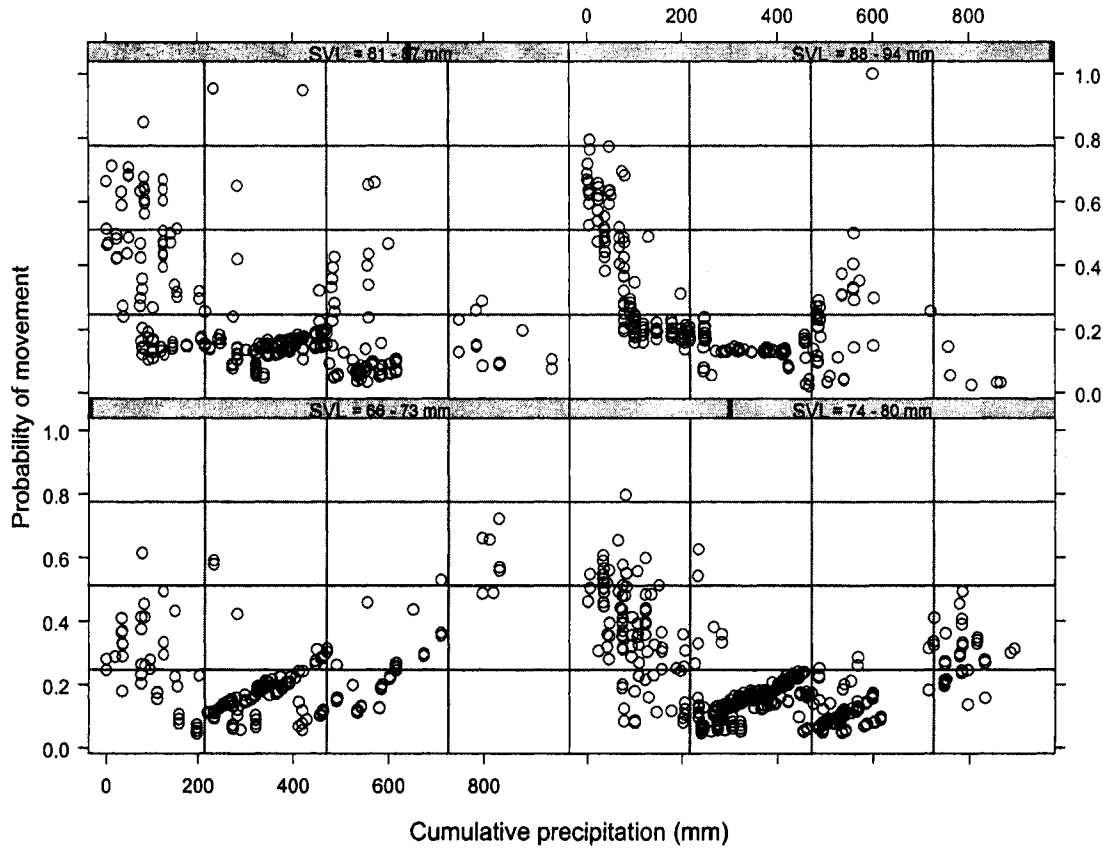


Figure 8. Predicted probability of salamander movement versus cumulative precipitation fallen since tracking of a salamander started (mm), grouped by snout-vent lengths (mm). Among shorter salamanders, increased cumulative precipitation led to increased probability of movement. Among longer salamanders, increased probability led to decreased probability of movement.

Migration Rate

Daily adult spotted salamander migration rate was modeled using a mixed-effects Poisson regression. This regression applies for those days when salamander movements were ≥ 1 m. Exact distance moved since the previous radio-fix was the outcome variable. Natural log of the number of days since the previous radio-fix was the offset variable (i.e., number of days since previous radio-fix was statistically controlled; exact distance moved / number of days since previous fix = migration rate). The log link function was used to mathematically relate the Poisson distribution and the predictors. A total of 287 observations, representing repeated fixes for 40 salamanders were used in developing this regression model.

Early data screening confirmed the need to specify the variance / covariance structure of the data. The correlation was modeled with an autoregressive process of order 1, in which cumulative number of days tracked was the time variable. Highly patterned residual plots indicated heterogeneous variance with respect to within-group error. A “fixed” variance structure, in which variance was modeled as a linear function of maximum temperature during the week preceding the radio fix, was selected. For the random effects, random intercepts were assigned to each salamander.

Results of the best-fit regression are summarized in Table 5. A marginal ANOVA was used to assess the contributions of individual predictors to the regression. Predictors most strongly associated with migration rate were: straight-line distance of a salamander from the nearest edge of the vernal pool (m; distvp ; $F_{1,242} = 62.1, p < 0.0001$); cumppt ($F_{1,242} = 65.5, p < 0.0001$); and total precipitation fallen during the week preceding the

fix (mm; weekppt; $F_{1, 242} = 27.6, p < 0.0001$). One interaction was also included in the final model: distvp X minimum temperature during the week preceding the fix ($^{\circ}\text{C}$; prevweekTmin; $F_{1, 242} = 16.7, p = 0.0001$). PrevweekTmin, which was only included in the model as part of the interaction, was not significant ($F_{1, 242} = 0.00238, p = 0.9612$). To ensure that the distvp X prevweekTmin interaction was significant in its own right (i.e., not just because of the specific variance partition obtained when prevweekTmin was included as a main effect in the model), I removed the main effect of prevweekTmin and examined the resulting modified regression. Results of this modified regression confirmed that the interaction was significant. Consequently, the interaction and the main effect of prevweekTmin were included in the final model.

Table 5. Summary of Mixed-effects Poisson Regression Predicting Migration Rate. 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.

	distance moved (m)	no.days (d)	distance from pool (m)	cumppt (mm)	weeklyppt (mm)	prevweekTmin (°C)	Coefficient	SE
distance from pool	0.28	0.09					0.010***	0.001
cumppt	-0.19	0.08	0.24				-0.003***	0.0004
weeklyppt	0.27	0.03	0.09	0.13			0.010***	0.002
prevweekTmin	-0.15	0.05	0.28	0.29	-0.18		0.002	0.032
distvp X prevweekTmin							-0.001***	0.0003
						Intercept =	1.347***	0.163
Mean	19.4	3.8	85.7	270.2	35.3	4.4		
SE	2.2	0.2	5.4	13.3	2.0	0.3		
Range	0.5 -271	1 - 29	0 - 428	0 - 943	0 - 181	-5 - 14		

Notes: * p < 0.05, ** p < 0.001, *** p ≤ 0.0001.

58

Neither buffer treatment nor any of the tested interactions involving treatment were significantly predictive of migration rate. The nature of the relationships between significant individual predictors and migration rate are described below.

In general, as a salamander's distance from the vernal pool increased, the salamander's migration rate increased. However, this effect was dampened by the interaction between *distvp* and *prevweekTmin* (Figure 9). In general, as the minimum temperature increased, salamander migration rates decreased. Further, although every 1 m increase in *distvp* was consistently associated with an increase in migration rate, the magnitude of that increase in migration rate decreased as minimum temperatures increased. For example, if *prevweekTmin* increased from 2 to 10 °C, while all other covariates were held at 0, a 1 m increase in *distvp* would result in a 0.0396 m/d versus a 0.0393 m/d increase in migration rate at 2 ° vs. 10 ° C, respectively.

The effects of cumulative precipitation and weekly precipitation were less complicated. For every 1 mm increase in cumulative precipitation, salamander migration rate decreased by 0.3% (Figure 10). For instance, if all other covariates were equal to zero, and *cumppt* increased from 0 to 1 mm, migration rate would decrease from 3.85 to 3.84 m/d. For every 1 mm increase in weekly precipitation, salamander migration rate increased by 1.0% (Figure 11). For instance, if all other covariates were equal to zero, and *weeklyppt* increased from 0 to 1 mm, migration rate would increase from 3.85 to 3.89 m/d.

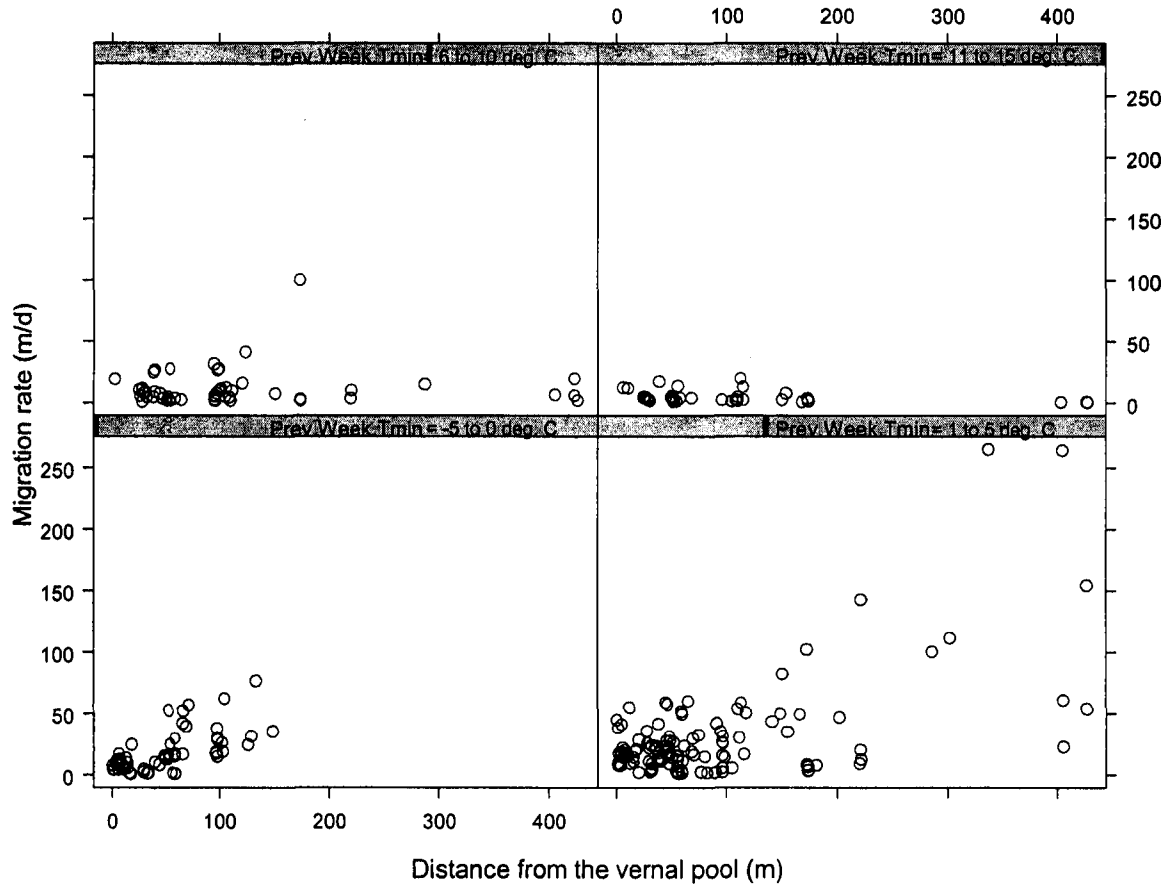


Figure 9. Predicted migration rate as a function of distance of a salamander from the vernal pool (m), grouped by the minimum temperature ($^{\circ}\text{C}$) recorded during the week preceding a radio-fix. In general, increasing distance from the vernal pool was associated with an increase in migration rate, but the magnitude of this increase was significantly dampened by increasing minimum temperatures.

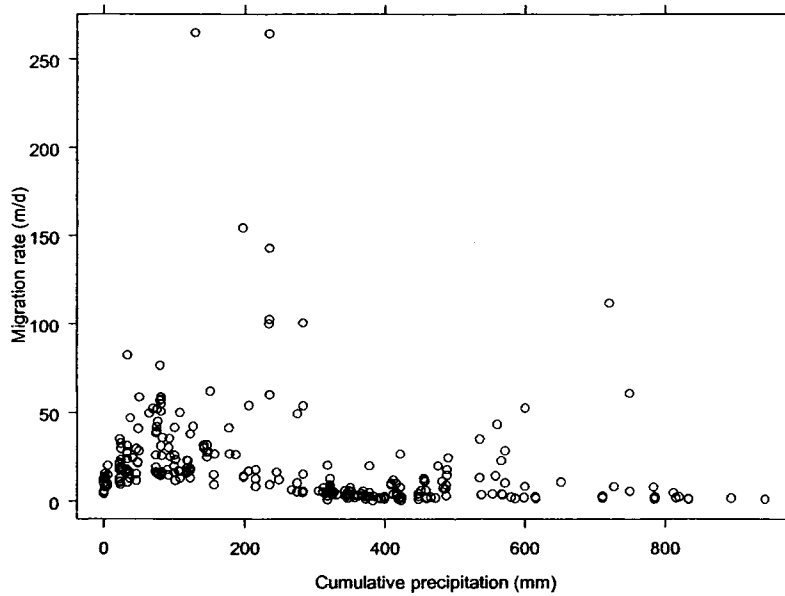


Figure 10. Predicted migration rate as a function of cumulative precipitation fallen since tracking of a salamander started (mm). Increasing cumulative precipitation was associated with decreasing migration rates.

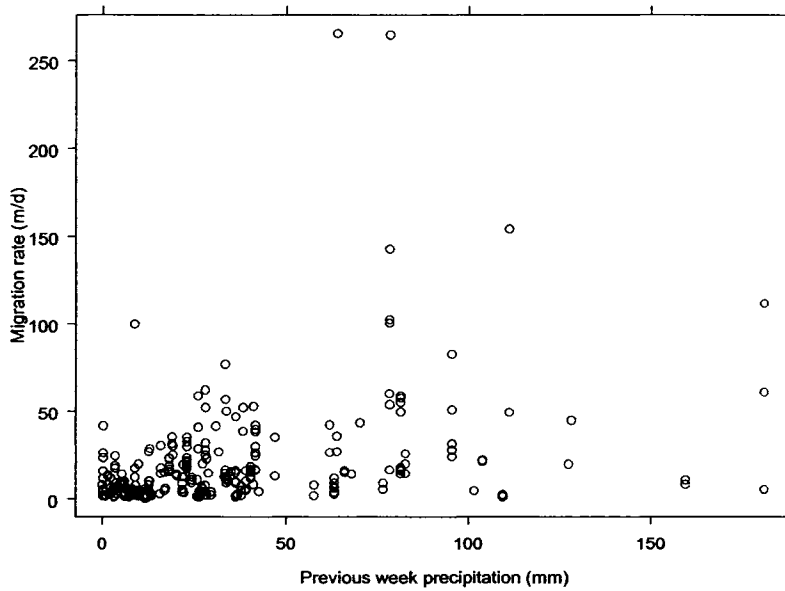


Figure 11. Predicted migration rate as a function of the volume of precipitation that fell during the week preceding a radio-fix (mm). Increases in weekly precipitation were associated with increased migration rates.

Distance from the Vernal Pool

The straight-line distance of a salamander from the vernal pool was modeled using linear, mixed-effects regression. Log (distvp) was used as the outcome variable, since distvp was not normally distributed. A total of 1345 observations, representing repeated fixes for 40 salamanders were used in developing this regression model.

Early data screening confirmed the need for a specifically-modeled variance/covariance structure. The correlation was modeled using an autoregressive process of order 1, in which cumulative number of days tracked was the time variable. Variance was modeled as an exponential function of 2dppt; with separate variances calculated for each of the 2 years in the study. For random effects, a separate random intercept was assigned to each salamander.

Results of the best-fit regression are summarized in Table 6. A marginal ANOVA was used to assess the contribution of individual predictors to the regression. Predictors most strongly associated with log (distvp) were: log (cumulative number of days tracked) (log (CumDays), $F_{1, 1300} = 252.4, p < 0.0001$); and cumppt ($F_{1, 1300} = 154.7, p < 0.0001$). I used log (CumDays) rather than CumDays as the predictor because I suspected that distance from the vernal pool tended to increase quickly early in the tracking period, and asymptotically approach some maximum distance later in the tracking period. Two interactions were also significantly predictive of log (distvp): log (CumDays) X cumppt ($F_{1, 1300} = 153.7, p < 0.0001$); and log (CumDays) X habitat (coded 0 = forest, 1 = clear cut; $F_{1, 1300} = 119.0, p < 0.0001$). Both cumppt and habitat, which would not have been included in the model were they not part of an interaction, were significant (respectively,

$F_{1,1300} = 154.7, p < 0.0001; F_{1,1300} = 251.4, p < 0.0001$). Although habitat type was important in predicting $\log(\text{distvp})$, buffer treatment was not significantly predictive of $\log(\text{distvp})$. The nature of the relationship between significant individual predictors and $\log(\text{distvp})$ are described below.

Table 6. Summary of Mixed-effects Linear Regression Predicting Distance From the Vernal Pool.

	log (distance from vernal pool [m])	log (cumulative days tracked)	cumppt (mm)	habitat ^a	Coefficient	SE
log (cumulative days tracked)	0.48				0.493***	0.031
cumppt	0.40	0.87			0.008***	0.0006
habitat ^a					1.200***	0.076
log (cumulative days tracked) X cumppt					-0.003***	0.0003
log (cumulative days tracked) X habitat					-0.563***	0.052
				Intercept =	0.511***	0.074
Mean	1.79	1.71	318.2			
SE	0.01	0.01	5.4			
Range	-0.42 – 2.63	0 – 2.26	0 - 943			

Notes: * p < 0.05, ** p < 0.001, *** p ≤ 0.0001.

^a Coded 0 = forested habitat; 1 = clear cut habitat.

In general, the longer a salamander was tracked, the further it was from the vernal pool. The main effect of log (CumDays), however, was tempered by the interactions of log (CumDays) with cumppt and with habitat, respectively (Figure 12). In both forest and clear cut, as cumppt increased, the positive effect of log(CumDays) on log(distvp) decreased (i.e., when cumulative precipitation was high, more tracking days were needed for a salamander to reach a certain distance from the vernal pool).

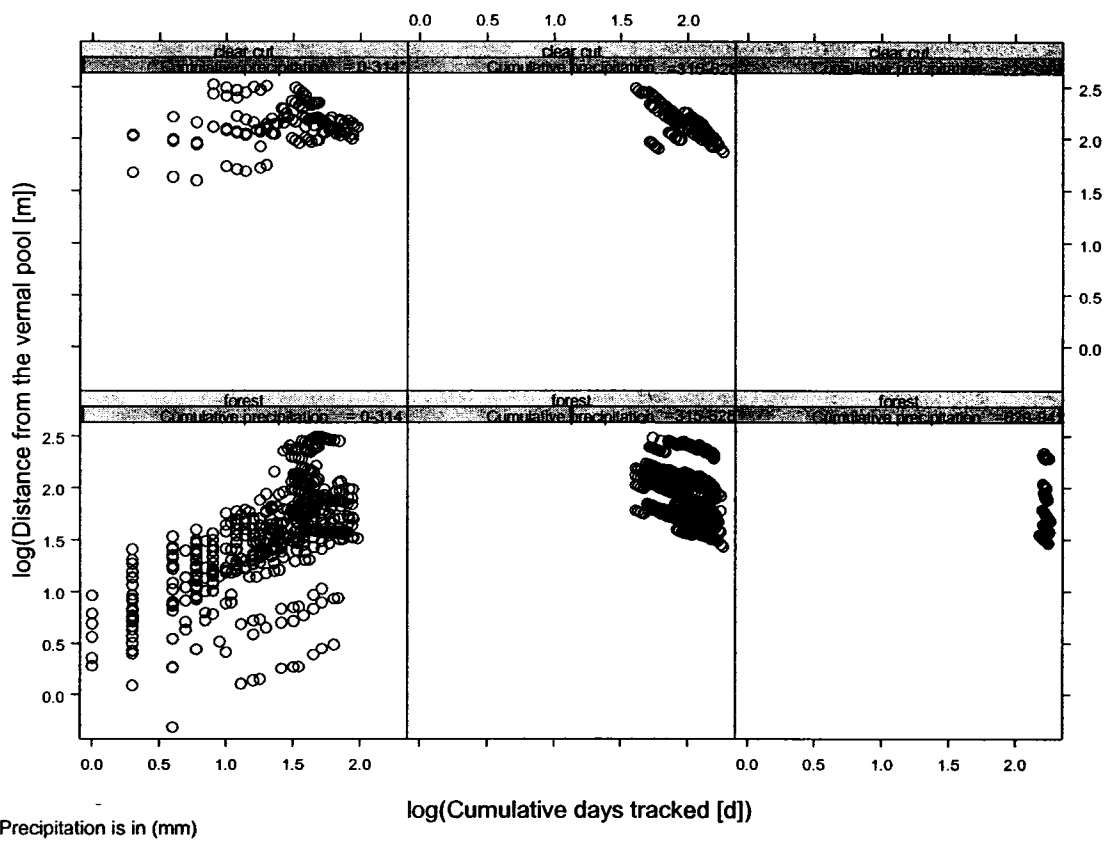


Figure 12. Predicted log (distance from the vernal pool [m]) as a function of the log (cumulative number of days a salamander has been tracked), grouped by both habitat (forest or clear cut), and cumulative precipitation fallen since tracking of a salamander started (mm). Habitat refers to a salamander’s location for a given radio-fix, regardless of cutting treatment (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). In general, as log (cumulative days) increased, distance from the vernal pool increased, but this effect was dampened by increasing cumulative precipitation. The relationship between 3 variables was more pronounced in the forest than in the clear cut.

As a main effect, cumulative precipitation was positively associated with distance of a salamander from the vernal pool. This effect was dampened by the interaction between cumppt and log (CumDays). As the number of days a salamander was tracked increased, less cumulative precipitation was needed for that salamander to reach a certain distance from the pool. On average, however, every 1 mm increase in cumppt resulted in a 1.004 m increase in distance from the vernal pool.

The positive effect of log (CumDays) was stronger in the forest than in the clear cut. On average, a 1 day increase in the number of days tracked was associated with a 0.025 m versus a 0.007 m increase in distance from the vernal pool, in forest versus clear cut habitat.

The main effect of habitat indicated that a salamander was likely to be further from the vernal pool when in the clear cut than when in the forest. However, the interaction between habitat and log(CumDays), counteracted this pattern. For each additional day a salamander was tracked, it was likely to be farther from the pool if in the forest, than if in the clear cut. These seemingly contradictory results are partly an artifact of the experimental design: clear cuts were 100 m wide, and implemented at 1 of only 2 possible distances (i.e., either at 30 m or 100 m). Forested habitat at clear cut-treatment pools, however, included both the small amount of forest in the buffer, and a vast area of forest beyond the outer edge of the clear cut. Thus, most available forest at the clear cut treatment pools was further from the pool than clear cut habitat. At the beginning of the year, when a salamander in forested habitat was more likely to be in the buffer than in forest on the far side of the clear cut, it is not surprising that that the model would classify that salamander as closer to the pool than a salamander in the clear cut. However, as the

year progressed, and a salamander in forested habitat was more likely to be on the far side of the clear cut than in the buffer, it is logical that the salamander in the clear cut would be closer to the pool than the salamander in the forest.

There appears to be more to the log (CumDays) X habitat interaction than just artifact, however. First, the difference in distance from the pool, between salamanders in the clear cut and salamanders in the forest, increased, as the number of days tracked increased.

Second, the interaction indicates that over the course of an entire tracking season (i.e., late April to early November), if a salamander did not have to travel through a clear cut (e.g., at a reference pool), it would be further from the pool than if it had to travel through a clear cut (e.g., at a clear cut-treatment pool). Imagine two salamanders, one that encountered a clear cut, and one that encountered only forest. Early in the year, the salamander that encountered the clear cut may have been further from the pool than the salamander that encountered only forest (i.e., as indicated by the positive main effect of habitat). As the year progressed, however, the movements of the salamander in the clear cut would have been hindered by its being in the clear cut. Consequently, at the end of the year, the salamander that encountered only forest would have surpassed the other salamander in distance from the pool (i.e., as indicated by the negative log (CumDays) X habitat interaction). This pattern was not confirmed by a significant effect of buffer treatment, suggesting that this last interpretation of the interaction may be wrong. However, the interpretation might well be valid, and simply not expressed as a significant effect of treatment because of the particular interplay of clear cut configuration and cumulative days tracked in my study.

CHAPTER IV

DISCUSSION

Buffer treatment was not a significant predictor of adult spotted salamander migratory movement. Adult spotted salamanders were able to spend substantial periods of time in, and migrate through 100-m clear cuts. Nevertheless, over the course of the year, the presence of a clear cut was associated with lesser mean distances migrated from the vernal pool. The 3 salamanders that emigrated furthest, however, bred at clear cut-treatment pools.

These results are contrary to what I expected, but perhaps should not be surprising. Previous research suggested spotted salamanders would be averse to crossing the forest – clear cut edge, but would likely cross into the clear cut if insufficient habitat were available directly adjacent to the pool (e.g., deMaynadier and Hunter 1999; Regosin et al 2005; Windmiller 1996). I expected that a 30-m wide buffer might be insufficient adjacent habitat, while a 100-m wide buffer, while less than ideal, might suffice for adjacent habitat (Semlitsch 1998, Semlitsch and Bodie 2003). Thus, I expected that salamanders would be more likely to enter the clear cut in the 30-m buffer treatment; would more likely remain in the buffer in the 100-m buffer treatment, and would migrate a variety of distances from the pool at the reference pools. Further, I expected that a 100-m-wide clear cut would likely be too wide for salamanders to successfully cross (Windmiller 1996; Montieth and Paton 2006; Rothermel 2004).

Not only was there no significant difference in migration behavior with respect to buffer treatment, and not only were salamanders capable of entering and tarrying in clear cuts, but just over 50% of salamanders at clear cut-treatment pools entered the clear cut, 22% crossed the clear cut, and on average, salamanders at clear cut-treatment pools spent 27% of their time in clear cuts.

We tend to think of clear cuts as habitats that are largely inhospitable to salamanders, due to the high temperatures and low moisture associated with canopy loss in the clear cut (Finkler 2006; Rothermel and Semlitsch 2002; Feder and Burggren 1992). While this is true, relative to intact forests, the reality is that salamanders travel during rainy nights when clear cuts are relatively cool and moist. In New England, where root raking and other mechanical soil preparation techniques are uncommon forestry practices (Ducey, pers. comm.), several structural features of clear cuts also facilitate salamander migration through cuts. First, the essential soil structure of a mature forest is maintained throughout much of the clear cut. Thus, cues derived from forest soil that may guide salamander migration (Rittenhouse et al. 2004) would still be intact. Second, clear cuts retain micro-habitats that are suitable as subterranean salamander refugia. Beneath the surface in clear cuts, a substantial leaf layer is often present, if buried (pers. obs.), which provides insulation and traps moisture near the surface. Additionally, tree stumps remain rooted after clear cutting. The burrows that trace tree roots, formed by small rodents and other phenomena, especially those burrows near the base of the tree, are commonly used by salamanders for terrestrial refuge (pers obs; Faccio 2003). Though the heavy machinery used for clear cutting compacts soil in parts of the cut, the burrows closest to tree boles are most likely to remain uncompacted, as the machinery does not usually

approach within several meters of the tree it is cutting (pers. obs.). These burrows are used by salamanders in clear cuts. Finally, after the initial cut, the vegetative structure in clear cuts changes rapidly with time. By the end of the first summer following my clear cuts, portions of the cuts were covered with grasses, young raspberries (*Rubus idaeus*), and regenerating red maple (*Acer rubrum*). By the end of the second summer post-cut, large areas of the cuts were revegetated with a variety of herbs, shrubs, and regenerating tree species (some of which reached nearly 2 m in height), all of which produced substantial leaf litter when the leaves dropped. If a salamander migrating through the clear cut is able to locate one of the suitable refuges which are present in the clear cut before the higher temperatures of day return and / or precipitation ceases, then this salamander is likely to survive while in the clear cut. With each growing season that passes post-cut, as shade and leaf litter increase, the probability of that salamander finding a suitable refuge before desiccation likely increases.

Although I demonstrated that adult spotted salamanders can survive in and traverse clear cuts, I do not know the long-term effects of occupying a clear cut versus forest. Rothermel and Semlitsch (2006) for instance, found that metamorphic spotted salamanders experienced greatly reduced survival in old fields compared to forests. But Chazal and Niewiarowski (1998) found no difference in growth rate or fecundity between mole salamanders (*A. talpoideum*) raised in clear cuts versus mature forest. Differences in food availability, refuge abundance and quality, and other biotic and abiotic conditions may translate into differential survival and/or fecundity for salamanders in clear cut versus forested habitat.

My results offer some insight into the effects of clear cuts on adult spotted salamanders. Though sample sizes were too small for statistical comparisons, salamanders that crossed the clear cut experienced predation and were healthy (at the end of the tracking period), in proportions similar to the entire set of 40 tracked salamanders. Predation accounted for 17% of clear-cut crossers and 17.5% of all salamanders; 33% of clear-cut crossers and 35% of all salamanders were classified as healthy at the end of the study. In fact, the salamander that moved furthest in my study, who was from a clear-cut treatment pool, had already started to generate an egg mass internally by the time she was excavated for the mid-summer transmitter replacement surgery. After spending most of the year at about 428 m from the vernal pool, she moved 128 m back towards the pool in mid-October. When her transmitter was removed in late fall, her eggs were still clearly visible, and apparently healthy.

Among salamanders that entered the clear cut, 7% were predated and 14% were classified as healthy. These lower percents, as compared to all salamanders, were offset by a greater percent of salamanders that entered the clear cut who were missing at the end of the tracking period (43%; missing due to battery failure, undetected movement, or predation). Only 35% of all salamanders and 0% of clear cut crossers were classified as missing. Although no clear cut crossers were missing, 1 (17%) was too light for a replacement transmitter during the mid-summer surgeries; and 1 (17%) was the salamander found dying, above-ground, with its incision split open in the forest on the far side of the clear cut. I don't know the fate of missing salamanders; they could equally as well have moved beyond the tracking area and remained healthy, lost body-mass or died. I do know, however, that the 6 salamanders who crossed the clear cut experienced a

range of fates, some of which (e.g., apparent health at the end of the year) were observed, and some of which (e.g., decreased body mass; split incision) were not observed among salamanders that entered, but did not cross, and salamanders that never entered the clear cut.

The interaction between log (CumDays) and habitat offers a second insight into possible impacts to salamanders of time spent in clear cuts. Over the course of an entire year (i.e., from late April to early November), my models indicate that a typical salamander who encounters a clear cut will move less far from the vernal pool than a salamander who travels only through forest. This suggests there is something about life in the clear cut that impacts a typical salamander's instinct or decisions about how far from the pool to migrate. Based on existing knowledge of salamander physiology and clear cut conditions (Feder and Burggren 1992; Freidenfelds and Babbitt, unpub. data), it is likely that the clear cut negatively impacts a salamander's capacity to travel greater distances.

Numerous other questions about the relationship between spotted salamander movement and clear cuts remain. My study documents salamander migration when exposed to 3 possible buffer treatments (i.e., reference, 30-m buffer, 100-m buffer). All clear cuts in my study were 100-m wide. Forested habitat was left adjacent to all pools, and was available on the far side of all clear cuts. All of my clear cuts and forest were configured in concentric rings centered on a pool. I do not know how salamander would react to different-sized or shaped clear cuts; to non-concentric configurations of forest-clear cut; if no forest was left between the cut and the pool; or if some land use / habitat other than forest was available on the far side of the clear cut. (During my field work, however, I did observe one vernal pool whose adjacent upland was clear cut right to the

edge of the pool as part of a balsam wooly adelgid control measure. This clear cut [which is estimated at over 100-m wide] and my cuts were conducted during the same winter. I observed spotted salamander egg masses in this vernal pool during the first 3 springs post-cut [data for additional springs is not yet available]; indicating that adult salamanders were able to both immigrate to and emigrate from this pool, though no buffer was intact). I also do not know whether salamanders might preferentially use a forest corridor if one were available that connected pool-to-intact forest across some less-than-permeable habitat. Nor do I quantitatively know how the permeability of clear cuts changes with time as the vegetation in the cut regenerates.

My analysis also does not address the capacity of metamorphic and juvenile spotted salamanders to cross and dwell in a clear cut. Though I observed both metamorphs and juveniles in and crossing clear cuts as part of the larger study, I do not currently have sufficient data to analyze movement of these age classes with respect to clear cuts. Metamorphs and/or juveniles may be the primary dispersers for this species, but these age classes may also be more limited in their movements due to greater susceptibility to desiccation (Rothermel and Semlitsch 2002) and/or by dispersal capabilities that differ from adults. In the context of logging, spotted salamander regional persistence may be most disturbed by interference of metamorph and/or juvenile dispersal.

Finally, forested upland – vernal pool communities are complicated systems comprised of numerous species interlinked by a variety of abiotic and biotic processes. We do not know the effects of clear cutting on most of these other species and processes. In particular, while we may partially understand the effects of clear cutting on adult

spotted salamander migration, we do not know the impact of clear cutting on local salamander population persistence. The ability of a salamander to migrate through a clear cut may be moot, if its local population collapses.

A second major result of my study is the long distances salamanders migrated from the vernal pools. The mean maximum migration distances salamanders in my study moved (106 ± 15.4 m for all salamanders; 118 ± 25.9 m for salamanders tracked through mid-October) were comparable to those of previous studies (Madison 1997; Faccio 2003; see review in Semlitsch 1998). Except for recent work by Montieth and Paton (2006) however, no other studies have documented spotted salamanders moving such great distances from their breeding wetlands. Prior to Montieth and Paton (2006), the maximum distances spotted salamander had been observed from their breeding wetlands were between 200 and 250 m (Kleeberger and Werner 1983, Faccio 2003, Madison 1997). Montieth and Paton observed individual salamanders that moved 259 m, 358 m, and 467 m. Noting that these 3 salamanders were all at a disturbed site, they suggested that disturbance might cause salamanders to migrate further than they would migrate in undisturbed conditions.

I also documented 3 salamanders that moved greater than 250 m (i.e., 427.6 m, 405.9 m, and 287.5 m), and 2 salamanders that moved between 200 and 250 m (i.e., 201.9 m and 221.6 m). All but one of these (i.e., the salamander that moved 201.9 m) was from a clear-cut treatment pool. Although these observations also hint that salamanders at disturbed sites might move further distances from breeding wetlands than those at undisturbed sites, my statistical analyses contradict this pattern. My analyses indicated that salamanders encountering a clear cut disturbance would, over the course of the year,

be likely to move less far than salamanders in undisturbed forest. Montieth and Paton (2006) only tracked their salamanders in the spring and summer. Some spotted salamanders apparently undertake major emigration movements in the fall (Madison 1997). If Montieth and Paton (2006) had tracked their animals through the fall, they might have observed greater maximum migration distances for the salamanders that tracked at undisturbed sites.

The third major contribution of my study is the novel statistical approach I applied to amphibian radio-tracking data. This approach incorporates random effects, accounts for serial correlation among repeated measures, and allows for heteroscedastic variance, within the context of multiple regression. This technique has been applied to longitudinal data sets in a variety of other contexts (e.g., industrial, medical), but is an area of active statistical exploration, and has only recently been incorporated into ecological analyses (Venables and Dichmont 2004). I believe that mixed-effects regression is a preferred technique for analyzing radio-tracking data, and that previous tracking studies may not have sufficiently accounted for serial correlation. I offer the following critique of my implementation of the method, however.

I used mixed-effects regression to describe mean salamander migration behavior on a multi-day scale. This approach limits me to describing general patterns of salamander migration over multiple-day periods. My models, therefore, poorly describe rare, long-distance movements that occur in short time periods. This deficiency was compounded by the fact that salamanders were often lost for periods of several days to several weeks, when they undertook these long-distance movements. In my models, I assumed that a salamander required the whole period during which it was lost, to move

the long distance. However, the salamander likely covered that distance in bursts during which it moved very quickly, rested for a couple days, then moved quickly again. Thus, my assumption likely led to an underestimation of migration rate, and introduced error into my probability of movement model.

Additionally, the rare, long-distance movements are of great biological interest. Alternative analytic techniques might be used to better understand the factors that drive these rare, extreme movements. I used a mixture that first assessed the probability of salamander movement, and then predicted its migration rate, given that it moved. Another possibility would be to use a 3-part mixture, which first assessed the probability of salamander movement, then described the conditions under which a salamander would be likely to undertake a rare, long-distance movement, and finally examined the factors that best predict the common, shorter movements. Finally, while linear regression is a suitable technique for describing mean movements, salamanders do not move in a linear fashion. Their movement is characterized by a long migration, early in the year, followed by a period of rest. They might undertake smaller migratory movements before or after the major migration; or even a relatively large movement in the fall, in search of an overwintering refuge; but more or less, salamanders settle into one location by the end of spring. A non-linear process might describe spotted salamander migration better than a linear process.

The migratory behavior of adult spotted salamanders in my study was highly dependent on precipitation patterns. Volume of cumulative precipitation fallen since tracking of a salamander started was the only predictor common to all 3 models. Increasing cumulative precipitation was associated with: increased probability of

movement, but only up to a certain SVL; decreased migration rate; and increased distance from the vernal pool, but only when cumulative days tracked was relatively low.

Fortunately, the 2 years during which I tracked salamanders varied substantially in both the timing and volume of rainfall, allowing me to document how drastically salamander migratory behavior can change with precipitation. In 2004, 125 mm, 318 mm, and 182 mm of cumulative precipitation fell in the spring, summer, and fall, for a total of 625 mm cumulative precipitation during the tracking season. In 2005, 338 mm, 172 mm, and 435 mm of cumulative precipitation fell in the spring, summer, and fall, for a total of 944 mm of total cumulative precipitation. In 2004, no salamanders crossed the clear cut, and only 4 entered the clear cut. In 2005, 6 salamanders crossed the clear cut, while 4 additional salamanders entered, but did not cross the clear cut. Whether a salamander crosses the clear cut or not, may depend mostly on the amount of precipitation and the time of year at which it falls.

Because migratory behavior is so highly dependent on precipitation patterns, and precipitation varies widely from year to year, migratory behavior is likely to differ greatly between years, even within a local salamander population. To fully understand the upland habitat needs of a local population, one would have to study that population over a period of several years of varying precipitation patterns.

Beyond precipitation, however, my models indicated that several other factors were strongly associated with salamander movement. For instance, migratory rate was significantly influenced by the distance of a salamander from the vernal pool. Generally, the further the salamander from the pool, the faster it was likely to move. Once a salamander is far from the pool, it is likely to move really far from the pool. Whereas, the

salamander that lingers near the pool, is likely to stay relatively close to the pool. That is, a salamander's tendency to move far from the pool in some years (i.e., due to greater precipitation), is compounded by behavior that makes it move faster when it is further from the pool.

Several other important predictors of migratory behavior relate to study design. Season, cumulative days tracked, and number of days between fixes were all strongly related to migration patterns. The design choices made, as to timing and duration of a study, and frequency of observations, will influence the particular partial lens through which a researcher perceives the complicated and dynamic process of salamander migration. I tracked salamanders during 2 years that differed dramatically in precipitation, but increased my likelihood of observing the different migratory responses to precipitation by tracking salamanders from spring through fall, and at regular, short intervals (i.e., every few days). Short-term studies, especially those that last only a couple of weeks during the breeding season, will not provide even close to a complete understanding of the upland habitat requirements of the spotted salamander.

This study and the Montieth and Paton (2006) study demonstrate that adult spotted salamanders can emigrate even greater distances (i.e., over 400 m) than previously supposed. It would be impractical to suggest that private-land managers preserve all upland within a 400+ m radius of a pool. In a forestry setting, my research suggests that preservation of this entire 400+ m-radius area might not be necessary. Adult spotted salamanders are more resilient than I expected, and are able to cross and dwell in clear cuts configured like those of my study. However, a salamander's ability to cross and survive in a clear cut may depend directly on precipitation patterns, which are highly

unpredictable and variable. A management plan based on migratory behavior in rainy years, which assumes that salamanders can cross clear cuts to access distant forest patches, might cause devastation if a local population were subject to a series of drought years and its salamanders were unable to access that distant forest patch.

Perhaps though, clear cuts are just sub-optimal spotted salamander habitat: salamanders can live in and cross clear cuts, but at the risk of long-term negative fitness effects. If an appropriate percent (e.g., 30 to 50%) of intact forest is left both within some core upland area (e.g., within 200-m of the pool) and within the larger landscape context (i.e., within 1 km; Porej et al. 2004; Homan et al. 2004; Gibbs 1998b; Herman et al 2005; Mattfeldt 2004), it might be that details, such as buffer width, clear cut width, and configuration of clear cut to forest are not particularly important. (For water quality protection, and as a staging area for adult and metamorphic salamanders that are preparing to emigrate from the pool, however, some minimal buffer is likely advisable [Semlitsch and Bodie 2003]).

In the forestry context, where clear cuts are semi-permeable to adult spotted salamander migratory movements, the buffer / life zone model might not be most appropriate. A different template, modeled after the shifting mosaic steady state of northern hardwoods forests (Bormann and Likens 1979), might be more appropriate. According to the shifting mosaic model, under natural conditions, northern hardwoods forests tend to evolve into a mosaic of forest patches that are in different successional stages. The forest reaches a steady-state when the % of patches in each successional stage remains constant over time. If this model is accurate, it may describe the disturbance regime to which spotted salamanders are optimally adapted (Hunter 1990; Bunnell 1995;

McGee 1999). A logging plan that mimics the steady-state of the shifting mosaic model, would allow smaller clear cuts in different configurations and at all distances from the vernal pool, but would rotate cutting across the landscape such that most areas are clear cut at some time, and allowed to develop into fully mature stands at other times.

Much remains unknown with respect to the relation between spotted salamanders and upland habitat alteration, however. The conclusions and suggestions drawn from this study of migratory movement may contradict data from future studies that examine other aspects of spotted salamander ecology and management. In particular, clear cuts are impermanent disturbances that are semi-permeable to spotted salamanders. Suburban sprawl is a process permanently altering the landscape over much of the spotted salamander's range. Sprawl may be less permeable to salamander migration than forest clear cuts, and salamanders may behave quite differently in the context of sprawl. As human populations continue to grow in number and geographic extent, it becomes increasingly important to determine the differences in salamander behavior in undisturbed, temporarily disturbed (e.g., logging), and permanently disturbed landscapes.

REFERENCES

- Andreozzi, V.L., T.C., Bailey, F.F. Nobre, C.J. Struchiner, M.L. Barreto, A.M.O. Assis, and L.M.P. Santos. 2006. Random-effects models in investigating the effect of vitamin A in childhood diarrhea. *Annals of Epidemiology* **16**(4): 241-247.
- 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.
- _____. 1988. Disappearance of salamanders from clear cut plots. *Journal of the Elisha Mitchell Scientific Society* **104**: 116-122.
- Babbitt, K.J. Unpublished data. 215 James Hall, University of New Hampshire, Durham,
- Baldauf, R.J. 1952. Climatic factors influencing the breeding migration of the spotted salamander, *Ambystoma maculatum* (Shaw). *Copeia* **1952**:178-181.
- Bishop, J., W.N. Venables, and Y. Wang. 2004. Analysing commercial catch and effort data form a Penaeid trawl fisher – A comparison of linear models, mixed models, and generalised estimating equations approaches. *Fisheries Research* **70**(2-3): 179-193.
- Bormann, F.H., and G.E. Likens. 1979. Patterns and process in a forested ecosystem. Springer-Verlag, New York, New York, 253 pp.
- Boyd, L. 2001. Buffer zones and beyond: wildlife use of wetland buffer zones and their protection under the Massachusetts wetland protection act. Massachusetts, Amherst, University of Massachusetts, Wetland Conservation Professional Program.
- Breunig, Kevin. 2003. Losing ground: at what cost? Third edition. Advocacy Department, MassAudubon.
- Bunnell, F.L. 1995. Forest-dwelling vertebrate faunas and natural fire regimes in British Columbia: patterns and implications for conservation. *Conservation Biology* **9**(3): 636-644.
- Calhoun, A.J.K., and P.G. deMaynadier. 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.

- Chazal, A.C., and P.H. Niewiarowski. 1998. Responses of mole salamanders to clearcutting: using field experiments in forest management. *Ecological Applications* 8(4): 1133-1143.
- Connecticut. Wetlands and Watercourses. General Statutes of Connecticut. Chapter 440, Title 22a, Rev. 2005.
- Cooper, A.B., J.C. Pinheiro, J.W. Unsworth, and R Hilborn. 2002. Predicting hunter success rates from elk and hunter abundance, season structure, and habitat. *Wildlife Society Bulletin* 30(4): 1068-1077.
- Cromer, R.B., J.D. Lanham, and H.H. Hanlin. 2002. Herpetofaunal response to gap and skidder-rut wetland creation in a southern bottomland hardwood forest. *For. Sci.* 48: 407-413.
- Davic, R.D., and H.H. Welsh, Jr. 2004. On the ecological roles of salamanders. *Annual Review of Ecology, Evolution, and Systematics* 35: 405-434.
- DeGraaf, R.M., and M. Yamasaki. 2001. New England wildlife: habitat, natural history, and distribution. New Hampshire, Hanover, University Press of New England.
- deMaynadier, P.G., and M.L. Hunter. 1999. Forest canopy closure and juvenile emigration by pool-breeding amphibians in Maine. *Journal of Wildlife Management* 63(2): 441-450.
- _____. 1998. Effects of silvicultural edges on the distribution and abundance of amphibians in Maine. *Conservation Biology* 12(2): 340-352.
- den Boer, P.J. 1970. On the significance of dispersal power for populations of carabid beetles (Coleoptera: Carabidae). *Oecologia (Berl.)* 4: 1-28.
- Dodd, C.K., and B.S. Cade. 1998. Movement patterns and the conservation of amphibians breeding in small, temporary wetlands. *Conservation Biology* 12: 331-339.
- Douglas, M.E., and B.L. Monroe. 1981. A comparative study of topographical orientation in *Ambystoma* (Amphibia: Caudata). *Copeia* 1981(2): 460-463.
- Duellman, W.E. 1954. Observations on autumn movements of the salamander *Ambystoma tigrinum tigrinum* in southeastern Michigan. *Copeia* 1954(2): 156-157.

- Duellman, W.E., and L. Trueb. 1986. Biology of amphibians. Maryland, Baltimore, The Johns Hopkins University Press, 670 pp.
- Dupuis, L.A., J.N.M. Smith, and F. Bunnell. 1995. Relation of terrestrial-breeding amphibian abundance to tree-stand age. *Conservation Biology* 9(3): 645-653.
- Enge, K.M., and W.R. Marion. 1986. Effects of clearcutting and site preparation on herpetofauna of a north Florida flatwoods. *Forest Ecology Management* 14: 177-192.
- Faccio, S.D. 2003. Postbreeding emigration and habitat use by Jefferson and Spotted Salamanders in Vermont. *Journal of Herpetology* 37(3): 479-489.
- Feder, M.E., and W.W. Burggren. 1992. Environmental physiology of the amphibians. University of Chicago Press, Chicago, Illinois, 472 pp.
- Flageole, S., and R. LeClair, Jr. 1992. Étude démographique d'une population de salamanders (*Ambystoma maculatum*) à l'aide de la méthode squeletto-chronologique. *Canadian Journal of Zoology* 70: 740-749.
- 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(1): 103-106.
- Finkler, M.S., M.T. Sugalski, and D.L. Claussen. 2003. Sex-related differences in metabolic rate and locomotor performance in breeding spotted salamanders (*Ambystoma maculatum*). *Copeia* 2003(4): 887-893.
- Ford, W.M., M.A. Menzel, T.S. McCay, J.W. Gassett, and J. Laerm. 2000. Woodland salamander and small mammal responses to alternative silvicultural practices in the southern Appalachians of North Carolina. *Proceedings of the Annual Conference of the Southeast Association of Fish and Wildlife Agencies* 54: 241-250.
- Freidenfelds, N.A., and K.J. Babbitt. Unpublished data. 215 James Hall, University of New Hampshire, Durham, NH.
- Gamble, L.R., K. McGarigal, C.L. Jenkins, and B.C. Timm. 2006. Limitations of regulated "buffer zones" for the conservation of marbled salamanders. *Wetlands* 26(2): 298-306.
- Gibbons, J.W. 2003. Terrestrial habitat: a vital component for herpetofauna of isolated wetlands. *Wetlands* 23(3): 630-635.

- Gibbs, J.P. 2005. Can mortality limit populations of pool-breeding amphibians? *Wetlands Ecology and Management* 13: 281-289.
- _____. 1998a. Amphibian movements in response to forest edges, roads, and streambeds in southern New England. *Journal of Wildlife Management* 62(2): 584-589.
- _____. 1998b. Distribution of woodland amphibians along a forest fragmentation gradient. *Landscape Ecology* 13: 263-268.
- _____. 1993. Importance of small wetlands for the persistence of local populations of wetland-associated animals. *Wetlands* 13: 25-31.
- Golet, W.J., D.A. Scopel, A.B. Cooper, and W.H. Watson. In press. Daily patterns of locomotion expressed by American lobsters (*Homarus americanus*) in their natural habitat. *Journal of Crustacean Biology*.
- Hall, D.B. 2000. Zero-inflated Poisson and binomial regression with random effects: a case study. *Biometrics* 56(4): 1030-1039.
- Hansen, A.J., T.A. Spies, F.J. Swanson, and J.L. Ohmann. 1991. Conserving biodiversity in managed forests: lessons from natural forests. *BioScience* 41: 382-392.
- Hanski, I. 1997. Predictive and practical metapopulation models: the incidence function approach. Pages 21-45 in D. Tilman and P. Kareiva (eds.). *Spatial Ecology: The Role of Space in Population Dynamics and Interspecific Interactions*, New Jersey, Princeton, Princeton University Press.
- Hanski, I., and M. Gilpin. 1991. Metapopulation dynamics: brief history and conceptual domain. *Biological Journal of the Linnaean Society* 42(1 & 2): 3-16.
- Hansson, L. 1991. Dispersal and connectivity in metapopulations. *Biological Journal of the Linnaean Society* 42(1 & 2): 89-103.
- Hecnar, S.J., and R.T. M'Closkey. 1996. Regional dynamics and the status of amphibians. *Ecology* 77(7): 2091-2097.
- Herbeck, L.A., and D.R. Larsen. 1999. Plethodontid salamander response to silvicultural practices in Missouri Ozark forests. *Conservation Biology* 13(3): 623-632.
- Hermann, H.L., K.J. Babbitt, M.J. Baber, and R.G. Congalton. 2005. Effects of landscape characteristics on amphibian distribution in a forest-dominated landscape. *Biological Conservation* 123: 139-149.

- Homan, R.N., J.V. Regosin, J.M. Reed, and B.S. Windmiller, Unpublished data. Department of Biology, Denison University, Granville, OH
- Homan, R.N., J.V. Regosin, D.M. Rodrigues, J.M. Reed, B.S. Windmiller, and L.M. Romero. 2003. Impacts of varying habitat quality on the physiological stress of spotted salamanders (*Ambystoma maculatum*). *Animal Conservation* 6: 11-18.
- Homan, R.N., B.S. Windmiller, and J.M. Reed. 2004. Critical thresholds associated with habitat loss for two vernal pool-breeding amphibians. *Ecological Applications* 14(5): 1547-1553.
- Hunter, M.L. Jr. 1990. Wildlife, forests, and forestry. Principles of managing forests for biological diversity. Prentice Hall, Englewood Cliffs, New Jersey.
- Hunter, M.L., A. Calhoun, and M. McCollough (eds.). 1999. Maine Amphibians and Reptiles. Maine, Orono, University of Maine Press, 256 pp.
- Husting, E.L. 1965. Survival and breeding structure in a population of *Ambystoma maculatum*. *Copeia* 1965(3): 352-362.
- Jackson, S.D. 1990. Demography, migratory patterns and effects of pond chemistry on two syntopic mole salamanders, *Ambystoma jeffersonianum* and *maculatum*. *Master's thesis*, University of Massachusetts, Amherst, MA, 96 pp.
- Joly, O., C. Miaud, A. Lehmann, and O. Grolet. 2001. Habitat matrix effects on pond occupancy in newts. *Conservation Biology* 15: 239-248.
- Kleeberger, S.R., and J.K. Werner. 1983. Post-breeding migration and summer movement of *Ambystoma maculatum*. *Journal of Herpetology* 17(2): 176-177.
- Klemens, M.W. 1993. Amphibians and reptiles of Connecticut and adjacent regions. State Geological and Natural History Survey of Connecticut, Bulletin 112, Connecticut, Hartford, DEP Maps and Publication Office.
- Knapp, S.M., C.A. Haas, and D.N. Harpole. 2003. Initial effects of clearcutting and alternative silvicultural practices on terrestrial salamander abundance. *Conservation Biology* 17(3): 752-762.
- Knox, C.B. 1999. Blue-spotted salamander. In M.L. Hunter, A. Calhoun, and M. McCollough (eds.), Maine Amphibians and Reptiles. Maine, Orono, University of Maine Press, 256 pp.

- Knutson, M.G., J.R. Sauer, D.A. Olsen, M.J. Mossman, L.M. Hemesath, and M.J. Lannoo. 1999. Effects of landscape composition and wetland fragmentation on frog and toad abundance and species richness in Iowa and Wisconsin, U.S.A. *Conservation Biology* 13: 1437-1446.
- Lambert, D. 1992. Zero-inflated Poisson regression, with an application to defects in manufacturing. *Technometrics* 34(1): 1-14.
- Madison, D.M. 1997. The emigration of radio-implanted spotted salamanders, *Ambystoma maculatum*. *Journal of Herpetology* 31: 542-551.
- Maine. Maine revised statues. Public Law Chapter 618, 2002.
- Maine. Maine revised statues. Title 38, Chapter 3, Section 480, Rev. 1993.
- Marsh, D.M., and P.C. Trenham. 2001. Metapopulation dynamics and amphibian conservation. *Conservation Biology* 15(1): 40-49.
- Massachusetts. Wetlands protection act regulations. Code of Massachusetts Regulations, Title 310, Section 10, Rev. 2005.
- Mattfeldt, S. 2004. Effects of wetland isolation and surrounding landscape characteristics on vernal-pool dependent amphibians. *Master's Thesis*, University of New Hampshire, Durham, NH.
- Mazerolle, M.J. 2004. Amphibian road mortality in response to nightly variations in traffic intensity. *Herpetologica* 60(1): 45-53.
- Means, D.B., J.G. Palis, and M. Baggett. 1996. Effects of slash pine silviculture on a Florida population of flatwoods salamander. *Conservation Biology* 10(2): 426-437.
- McGee, G.G., D.J. Leopold, and R.D. Nyland. 1999. Structural characteristics of old growth, maturing, and partially cut northern hardwood forests. *Ecological Applications* 9(4): 1316-1329.
- McLeod, R.F., and J.E. Gates. 1998. Response of herpetofaunal communities to forest cutting and burning at Chesapeake Farms, Maryland. *The American Midland Naturalist* 139(1): 164-177.
- Millar, R.B., and M.J. Anderson. 2004. Remedies for pseudoreplication. *Fisheries Research* 70(2-3): 397-407.
- Moilanen, A., and I Hanski. 1998. Metapopulation dynamics: effects of habitat quality and landscape structure. *Ecology* 79: 2503-2515.

- Montieth, K.E., and P.W.C. Paton. 2006. Emigration Behavior of Spotted Salamanders on Golf Courses in Southern Rhode Island. *Journal of Herpetology* 40(2): 195-205.
- Moseley, K.R., S.D. Castleberry, and S.H. Schweitzer. 2003. Effects of prescribed fire on herpetofauna in bottomland hardwood forests. *Southeastern Naturalist* 2(4): 475-486.
- Naughton, G.P., C.B. Henderson, K.R. Foresman, and R.L. McGraw. 2000. Long-toed salamanders in harvested and intact Douglas-fir forests of western Montana. *Ecological Applications* 10: 1681-1689.
- New Hampshire. Water Management and Protection. Revised Statutes, Title L, Chapter 482-A, Rev. 1996.
- Noss, R.F., and A.Y. Cooperrider. 1994. Saving nature's legacy. Washington D.C., Island Press, 416 pp.
- Patrick, D.A., M.L. Hunter Jr., and A.J.K. Calhoun. 2006. Effects of experimental forestry treatments on a Maine amphibian community. *Forest Ecology and Management* 234: 323-332.
- Petranka, J.W. 2004. Identifying the minimal demographic unit for monitoring pond-breeding amphibians. *Ecological Applications* 14(4): 1065-1078.
- _____. 1999. Recovery of salamanders after clearcutting in the southern Appalachians: a critique of Ash's estimates. *Conservation Biology* 13(1): 203-205.
- _____. 1998. Salamanders of the United States and Canada. Washington D.C., Smithsonian Institution Press, 387 pp.
- Petranka, J.W., M.P. Brannon, M.E. Hopey, and C.K. Smith. 1994. Effects of timber harvesting on low elevation populations of southern Appalachian salamanders. *Forest Ecology and Management* 67: 135-147.
- Petranka, J.W., M.E. Eldridge, K.E. Haley. 1993. Effects of timber harvesting on Southern Appalachian salamanders. *Conservation Biology* 7: 363-370.
- Phelps, J.P., and R.A. Lancia. 1995. Effects of a clear cut on the herpetofauna of a South Carolina bottomland swamp. *Brimley* 22: 31-45.
- Pinheiro, J.C., and D.M. Bates. 2000. Mixed-Effects Models in S and S-PLUS. New York, Springer, 528 pp.

- Porej, D., M. Micacchion, and T.E. Hetherington. 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., and R.E. Wilson. 1970. Natural daily temperature stress, dehydration, and acclimation in juvenile *Ambystoma maculatum* (Shaw) (Amphibia: Caudata). *Physiological Zoology* **43**: 194-205.
- Raymond, L.R., and L.M. Hardy. 1990. Demography of a population of *Ambystoma talpoideum* (Caudata: *Ambystomatidae*) in north-western Louisiana. *Herpetologica* **46**: 371-382.
- Regester, K.J., K.R. Lips, and M.R. Whiles. 2006. Energy flow and subsidies associated with the complex life cycle of ambystomatid salamanders in ponds and adjacent forest in southern Illinois. *Oecologia* **147**: 303-314.
- Regosin, J.V., B.S. Windmiller, R.N. Homan, and J.M. Reed. 2005. Variation in terrestrial habitat use by four pool-breeding amphibian species. *Journal of Wildlife Management* **69**(4): 1481-1493.
- Regosin, J.V., B.S. Windmiller, and J.M. Reed. 2003. Influence of abundance of small-mammal burrows and conspecifics on the density and distribution of spotted salamanders (*Ambystoma maculatum*) in terrestrial habitats. *Canadian Journal of Zoology* **81**: 596-605.
- Renken, R.B., W.K. Gram, D.K. Fantz, S.C. Richter, T.J. Miller, K.B. Ricke, B. Russell, and X. Wang. 2004. Effects of forest management on amphibians and reptiles in Missouri Ozark forests. *Conservation Biology* **18**(1): 174-188.
- Rhode Island. Rules and regulations governing the administration and enforcement of the freshwater wetlands act. 1998.
- Rittenhouse, T.A.G., M.C. Doyle, C.R. Mank, B.B. Rothermel, and R.D. Semlitsch. 2004. Substrate cues influence habitat selection by spotted salamanders. *Journal of Wildlife Management* **68**(4): 1151-1158.
- Rittenhouse, T.A.G., and R.D. Semlitsch. 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.
- Rothermel, B.B., 2004. Migratory success of juveniles: a potential constraint on connectivity for pond-breeding amphibians. *Ecological Applications* **14**(5): 1535-1546.

- Rothermel, B.B. and R.D. Semlitsch. 2006. Consequences of forest fragmentation for juvenile survival in spotted (*Ambystoma maculatum*) and marbled (*Ambystoma opacum*) salamanders. *Canadian Journal of Zoology* **84**: 797-807.
- _____. 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**(5): 1324.
- Sakamoto, Y., M. Ishiguro, and G. Kitagawa. 1986. Akaike Information Criterion statistics. Reidel, Dordrecht, Netherlands.
- Semlitsch, R.D. 2000. Principles for management of aquatic-breeding amphibians. *Journal of Wildlife Management* **64**(3): 615-631.
- _____. 1998. Biological delineation of terrestrial buffer zones for pond-breeding salamanders. *Conservation Biology* **12**(5):1113-1119
- _____. 1981. Terrestrial activity and summer home range of the mole salamander (*Ambystoma talpoideum*). *Canadian Journal of Zoology* **59**: 315-322.
- Semlitsch, R.D., and J.R. Bodie. 2003. Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. *Conservation Biology* **17**(5): 1219-1228.
- Sexton, O.J., C. Phillips, and J.E. Bramble. 1990. The effects of temperature and precipitation on the breeding migration of the spotted salamander (*Ambystoma maculatum*). *Copeia* **1990**(3): 781-787.
- Shoop, R.C. 1974. Yearly variation in larval survival of *Ambystoma maculatum*. *Ecology* **55**: 440-444.
- Sjogren, U. 1991. Extinction and isolation gradients in metapopulations: the case of the pool frog (*Rana lessonae*). *Biological Journal of the Linnaean Society* **42**(1 & 2): 135-147.
- Sundquist, D., and M. Stevens. 1999. New Hampshire's changing landscape: population growth, land use conversion, and resource fragmentation in the Granite State. The Society for the Protection of New Hampshire Forests, Concord, NH, 159 pp.
- Vasconcelos, D., and A.J.K. Calhoun. 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**(4): 551-561.
- Venables, W.N., and C.M. Dichmont. 2004. GLMs, GAMs, and GLMMs: an overview of theory for applications in fisheries research. *Fisheries Research* **70**: 319-337.

- Vermont. Vermont Wetlands Rules. Water Resources Board, 2002.
- Veysey, J.S., and K.J. Babbitt. Unpublished data. 215 James Hall, University of New Hampshire, Durham, NH.
- Wacasey, J.W. 1961. An ecological study of two sympatric species of salamanders, *Ambystoma maculatum* and *Ambystoma jeffersonianum*, in southern Michigan. *Ph.D. thesis*, University of Michigan, Ann Arbor, MI.
- Wassersug, R. 1984. Why tadpoles love fast food. *Natural History* **93**(4): 60-69.
- Wiens, J.A. 1997. Metapopulation dynamics and landscape ecology. Pages 43-68 in I. Hanski and M.E. Gilpin (eds.). *Metapopulation biology*. California, San Diego, Academic Press.
- Williams, P.K. 1973. Seasonal movements and population dynamics of four sympatric mole salamanders, genus *Ambystoma*. *Doctoral thesis*, Indiana University, Indiana.
- Whitford, W.G., and A. Vinegar. 1966. Homing, survivorship, and overwintering of larvae in spotted salamanders, *Ambystoma maculatum*. *Copeia* **1966**(3): 515-519.
- 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.
- Windmiller, B.S., R.N. Homan, J.V. Regosin, L.A. Willitts, D.L. Wells, and J.M. Reed. In press. Breeding amphibian population declines following loss of upland forest habitat around vernal pools in Massachusetts, USA. *Herpetological Conservation*.

APPENDIX A

Institutional Animal Care and Use Committee Approval Letters



UNIVERSITY of NEW HAMPSHIRE

June 1, 2004

Babbitt, Kimberly J
Natural Resources
James Hall
Durham, NH 03824

IACUC #: 020601
Approval Date: 06/26/2002
Review Level: C

Project: Experimental testing of buffer requirements for amphibians inhabiting vernal pools in a forested landscape

The Institutional Animal Care and Use Committee (IACUC) reviewed and approved the protocol submitted for this study under Category C on Page 4 of the Application for Review of Vertebrate Animal Use in Research or Instruction - *the research potentially involves minor short-term pain, discomfort or distress which will be treated with appropriate anesthetics/analgesics or other assessments.*

Approval is granted for a period of three years from the approval date above. Continued approval throughout the three year period is contingent upon completion of annual reports on the use of animals. At the end of the three year approval period you may submit a new application and request for extension to continue this study. Requests for extension must be filed prior to the expiration of the original approval.

Please Note:

1. All cage, pen, or other animal identification records must include your IACUC # listed above.
2. Use of animals in research and instruction is approved contingent upon participation in the UNH Occupational Health Program for persons handling animals. Participation is mandatory for all principal investigators and their affiliated personnel, employees of the University and students alike. A Medical History Questionnaire accompanies this approval; please copy and distribute to all listed project staff who have not completed this form already. Completed questionnaires should be sent to Dr. Gladi Porsche, UNH Health Services.

If you have any questions, please contact either Van Gould at 862-4629 or Julie Simpson at 862-2003.

For the IACUC,



Roger E. Wells, D.V.M.
Vice Chair

cc: File

Research Conduct and Compliance Services, Office of Sponsored Research, Service Building,
51 College Road, Durham, NH 03824-3585 * Fax: 603-862-3564



UNIVERSITY of NEW HAMPSHIRE

June 30, 2005

Babbitt, Kimberly J
Natural Resources, Nesmith 206
Durham, NH 03824

IACUC #: 050604
Approval Date: 06/29/2005
Review Level: C
Project: Experimental Testing of Buffer Requirements for Amphibians Inhabiting Vernal Pools in a Forested Landscape

The Institutional Animal Care and Use Committee (IACUC) reviewed and approved the protocol submitted for this study under Category C on Page 4 of the Application for Review of Vertebrate Animal Use in Research or Instruction - *the research potentially involves minor short-term pain, discomfort or distress which will be treated with appropriate anesthetics/analgesics or other assessments.* The IACUC made the following comments on this protocol:

1. *The Committee suggested that the investigator might consider using surgical glue/tissue cement instead of sutures.*
2. *In the future, the investigator should include references for any citations included in the protocol.*

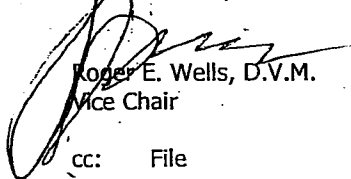
Approval is granted for a period of three years from the approval date above. Continued approval throughout the three year period is contingent upon completion of annual reports on the use of animals. At the end of the three year approval period you may submit a new application and request for extension to continue this project. Requests for extension must be filed prior to the expiration of the original approval.

Please Note:

1. All cage, pen, or other animal identification records must include your IACUC # listed above.
2. Use of animals in research and instruction is approved contingent upon participation in the UNH Occupational Health Program for persons handling animals. Participation is mandatory for all principal investigators and their affiliated personnel, employees of the University and students alike. A Medical History Questionnaire accompanies this approval; please copy and distribute to all listed project staff who have not completed this form already. Completed questionnaires should be sent to Dr. Gladi Porsche, UNH Health Services.

If you have any questions, please contact either Van Gould at 862-4629 or Julie Simpson at 862-2003.

For the IACUC,


Roger E. Wells, D.V.M.
Vice Chair

cc: File

Research Conduct and Compliance Services, Office of Sponsored Research, Service Building,
51 College Road, Durham, NH 03824-3585 * Fax: 603-862-3564