

## ABSTRACT

Title of Document:                   DISPERSAL AND POPULATION ECOLOGY  
OF THE RED-BACKED SALAMANDER  
(*PLETHODON CINEREUS*)

Kyle Miller Hesed, Doctor of Philosophy, 2015

Directed By:                         Professor Gerald S. Wilkinson,  
Department of Biology

Terrestrial salamanders are major components of ecosystems in eastern North America. One species, the Red-backed Salamander (*Plethodon cinereus*), may be the most abundant vertebrate throughout its range. Red-backed Salamanders are commonly monitored as indicators of ecosystem health and to assess the effects of forest management practices. In order to address poorly understood aspects of the ecology of Red-backed Salamanders, I conducted a 4-y mark-recapture study of a population in Maryland, resulting in 2,745 records of 752 marked salamanders, along with a complementary genetic analysis of six microsatellite loci.

I estimated growth rates and age at sexual maturity using a hierarchical Bayesian model fitted by mark-recapture measurements, then measured home range size and seasonal and annual movement distances by immatures and adults, before and after the experimental removal of 98 conspecifics. Males grow and mature more slowly than females, despite reaching slightly larger asymptotic sizes; they may also

face greater competition for space: adult males occupy the largest home ranges and show the largest increase in home range size after the removal of conspecifics. The largest between-year movements were made by individuals as they transitioned from immaturity to maturity.

Using mark-recapture population models, I found that estimates of survival, detection, and abundance varied temporally along with the age and sex of the individuals present, both within and among seasons. Encounter probability varied among weekly sampling occasions, and models with separate parameters for each sex were strongly preferred. Survival was approximately the same over winters and summers, and lower for males than for females; this may be an artifact of sex-biased dispersal, as the majority of encountered immature individuals were estimated to be males, with models indicating a pulse of emigration in the fall and an influx of immature males onto the study site in the spring.

An  $F_{ST}$  randomization test of multilocus genotypes showed a significant male bias in dispersal. Of salamanders captured repeatedly as both immatures and adults, males moved significantly farther before maturity than females did. Together, these results provide a comprehensive assessment of sex-biased dispersal at fine spatial and temporal scales in a terrestrial ectothermic vertebrate.

DISPERSAL AND POPULATION ECOLOGY OF THE RED-BACKED  
SALAMANDER (*PLETHODON CINEREUS*)

By

Kyle Miller Hesed

Dissertation submitted to the Faculty of the Graduate School of the  
University of Maryland, College Park, in partial fulfillment  
of the requirements for the degree of  
Doctor of Philosophy  
2015

Advisory Committee:  
Professor Gerald S. Wilkinson, Chair  
Professor Bill Fagan  
Professor Emeritus David W. Inouye  
Adjunct Professor Robert C. Fleischer  
Associate Professor Maile C. Neel

© Copyright by  
Kyle Miller Hesed  
2015

## Dedication

To my parents, Larry (1945–2011) and Laurie Hesed; to Linda Trueb; and to Kraig Adler.

## Acknowledgments

For assistance with various aspects of fieldwork, I thank Nicole Angeli, Andrew Dietrich, Grace DiRenzo, Gerry Carter, Krysta Hawkey, Luke Horner, Cora Johnston, Nathan Jud, Ray Kessler, Carolyn Marzke, Magnus McCaffery, Rebecca McCaffery, Kyle Melin, Abbe Miller, David Miller, Ed Miller, Christy Miller Heses, Ernie Osburn, Brianna Schumaker, Stephanie Wein, Amber Wiewel, Tom Williams, and Jen Wollman. For guidance on specific aspects of this project, I thank Sam Droege, Evan Campbell Grant, Richard Highton, William Link, William Kendall, James Hines, and Kimberly Paczolt.

Funding was provided by the University of Maryland Department of Biology (Eugenie Clark Fellowship, Summer Research Fellowship); the UMD College of Computer, Mathematical, and Natural Sciences (Drs. Wayne T. and Mary T. Hockmeyer Endowed Fellowship); the UMD Graduate School (Flagship Fellowship, Ann G. Wylie Dissertation Fellowship); the National Science Foundation (Graduate Research Fellowship: Grant No. DGE-0750616); the Explorers Club Washington Group (Exploration and Field Research Grant); the Cosmos Club Foundation (Cosmos Scholars Award); the American Philosophical Society (Lewis and Clark Fund for Exploration and Field Research); a Washington Biologists Field Club Research Award; and an International Herpetological Symposium Grant in Herpetology. I thank the Society for the Study of Amphibians and Reptiles for permission to reprint Chapter 2, previously published in the *Journal of Herpetology* (Vol. 46, No. 4, 442–450, 2012). Protocols were approved by the University of Maryland IACUC (R-12-40) and Patuxent Wildlife Research Center (NSR-CT-0910).

# Table of Contents

Dedication .....	ii
Acknowledgments.....	iii
Table of Contents .....	iv
List of Tables .....	vi
List of Figures .....	vii
Introduction.....	1
Chapter 1: A Review of Coverboard Design for Ecological Studies of Salamanders..	5
Abstract .....	5
Introduction.....	6
Coverboard Design .....	7
<i>Material</i> .....	7
<i>Dimensions</i> .....	9
<i>Age and weathering</i> .....	10
<i>Placement with respect to ground</i> .....	11
<i>Sampling frequency</i> .....	12
<i>Number and spacing of boards</i> .....	13
<i>Preventing disturbance to arrays</i> .....	13
Potential Concerns for Salamander Coverboard Studies .....	14
<i>Disproportionate usage by different size or age classes</i> .....	14
<i>Applicability to diverse species</i> .....	15
Summary .....	16
<i>Design</i> .....	16
<i>Potential concerns</i> .....	18
<i>Comparison with other techniques</i> .....	19
Chapter 2: Differential Growth, Age at Maturation, and Movement Patterns by Male and Female Red-Backed Salamanders ( <i>Plethodon cinereus</i> ) .....	20
Abstract .....	20
Introduction.....	21
Materials and Methods.....	24
<i>Study site</i> .....	24
<i>Data collection</i> .....	25
<i>Modeling growth and maturation</i> .....	26
<i>Field study and removal experiment</i> .....	29
Results.....	30
<i>Growth</i> .....	30
<i>Movement patterns</i> .....	31
Discussion.....	32
Chapter 2 Figures .....	39
Chapter 2 Tables .....	49

Chapter 3: Variation in Population Parameters of Red-Backed Salamanders ( <i>Plethodon cinereus</i> ) Due to Season, Sampling Occasion, Sex, and Life Stage .....	50
Abstract .....	50
Introduction.....	51
Materials and Methods.....	54
<i>Study site and data collection</i> .....	54
<i>Mark-recapture modeling: across-season analysis</i> .....	54
<i>Mark-recapture modeling: within-season analysis</i> .....	58
Results.....	59
Discussion.....	61
<i>Encounter probability within seasons</i> .....	61
<i>Survival probability between seasons</i> .....	62
<i>Sex differences in state-uncertainty parameters and emigration</i> .....	63
Chapter 3 Figures .....	66
Chapter 3 Tables .....	70
 Chapter 4: Male-Biased Dispersal in a Terrestrial Amphibian ( <i>Plethodon cinereus</i> ): Kin Competition & Inbreeding Avoidance.....	77
Abstract .....	77
Introduction.....	78
Materials and Methods.....	84
<i>Study site and data collection</i> .....	84
<i>Genetic analyses</i> .....	85
<i>Movement analyses</i> .....	87
Results.....	88
<i>Genetic analyses</i> .....	88
<i>Movement analyses</i> .....	89
Discussion.....	89
Chapter 4 Tables .....	95
 Appendices.....	96
Appendix 1.1. Materials used as coverboards in studies of salamanders. ....	96
Appendix 1.2. Salamander species encountered in studies using coverboards. ....	99
Appendix 2.1. Numbers of points used to generate MCPs. ....	114
Appendix 3.1. Model-averaged CJS parameter estimates, Fall 2009. ....	115
Appendix 3.2. Model-averaged CJS parameter estimates, Spring 2010.....	116
Appendix 3.3. Model-averaged CJS parameter estimates, Fall 2010.....	117
Appendix 3.4. Model-averaged CJS parameter estimates, Spring 2011.....	118
Appendix 3.5. Model-averaged CJS parameter estimates, Fall 2011. ....	119
Appendix 3.6. Model-averaged CJS parameter estimates, Spring 2012.....	120
Appendix 3.7. Model-averaged CJS parameter estimates, Fall 2012. ....	121
Appendix 3.8. Model-averaged CJS parameter estimates, Spring 2013.....	122
Appendix 3.9. Goodness-of-fit tests for CJS models.....	123
Appendix 4.1. Frequencies of estimated kinship values: Fall 2010, Spring 2011.....	125
 Bibliography .....	128



## List of Tables

Table 2.1. Growth and development parameters .....	49
Table 3.1. Multistate open robust design models with state uncertainty .....	70
Table 3.2. Summary statistics for sampling periods .....	71
Table 3.3. Top multistate open robust models .....	72
Table 3.4. Parameter estimates from multistate open robust design analysis.....	73
Table 3.5. Top Cormack-Jolly-Seber models .....	75
Table 4.1. Summary statistics of microsatellite loci .....	95

## List of Figures

Figure 2.1. Schematic of study site .....	39
Figure 2.2. Asymptotic body sizes .....	40
Figure 2.3. Growth rates .....	41
Figure 2.4. Individual heterogeneity in growth .....	42
Figure 2.5. Age at sexual maturity.....	43
Figure 2.6. Individual heterogeneity in age at sexual maturity.....	44
Figure 2.7. Simulated growth curves .....	45
Figure 2.8. Home range areas in natural population.....	46
Figure 2.9. Home range areas in experimentally manipulated population .....	47
Figure 2.10. Distances moved between successive years .....	48
Figure 3.1. Survival probabilities.....	66
Figure 3.2. Encounter probabilities.....	67
Figure 3.3. Probability of sex classification.....	68
Figure 3.4. Derived population estimates .....	69

## Introduction

Over the past several decades, the development of microsatellite markers has revolutionized the study of the genetics, behavior, and ecology of wild populations (Jarne and Lagoda, 1996; Selkoe and Toonen, 2006; Pemberton, 2008). Concurrent with this technical development has been a paradigmatic shift in the understanding of spatial structuring in both ecology (Legendre, 1993) and behavioral ecology (Valcu and Kempenaers, 2010). Together, these advances have ushered in a new focus within ecology and population genetics on fine spatial and temporal scales (Manel et al., 2003; Manel et al., 2005). In addition, it is increasingly recognized that some of the most important questions in ecology and evolution must be addressed with long-term studies of individual animals, not just populations (Clutton-Brock and Sheldon, 2010).

Although the study of dispersal has made great advances through the incorporation of new molecular approaches (Broquet and Petit, 2009), empirical results have lagged behind the production of sex-biased dispersal theory due both to a preoccupation with methodological advances in modeling and the difficulty in measuring dispersal in nature (Ronce, 2007). The causes and patterns of sex-biased dispersal remain an area of active interest in ecology and evolution, but our understanding of this process is still dominated by data from a few taxonomic groups (Mossman and Waser, 1999). An understanding of the evolutionary pressures and ecological and genetic results of sex-biased dispersal will depend on measures of its prevalence and magnitude in natural populations (Prugnolle and de Meeus, 2002).

In this dissertation, I assess the existence of sex-biased dispersal in the Red-backed Salamander (*Plethodon cinereus*) through a study of its population ecology. The Red-backed Salamander was described early in the nineteenth century (Green, 1818) and was already considered a well-studied species by the early twentieth century (Blanchard, 1928b; Burger, 1935). Cope (1889) called it the most abundant salamander in the eastern United States; Burton and Likens (1975) estimated that its biomass exceeded that of both birds and small mammals at a site in New Hampshire; and Semlitsch et al. (2014) concluded that this estimate of abundance may have been low by an order of magnitude. Over the past four decades, extensive laboratory research has addressed territorial interactions in this species (reviewed by Mathis et al., 1995).

Despite nearly two centuries of attention, however, many aspects of Red-backed Salamander biology are poorly understood. Particularly lacking are long-term studies of the ecology of natural populations. To address this deficit, I conducted a four-year mark-recapture study in which I collected 2,745 records of 752 marked salamanders; each record included spatial coordinates, two measurements of body length, and the maturity state of the individual. By collecting a tissue sample from each individual in the study, I was able to genotype them at six microsatellite loci and complement the spatial analyses with genetic tests for sex-biased dispersal.

In Chapter 1, I begin by reviewing the use of coverboards for ecological studies of salamanders. Although they have been used for decades in research on amphibians and reptiles, the characteristics of coverboards have varied widely. In order to facilitate comparisons among studies and to help improve the effectiveness of

coverboards in field studies, I summarize and evaluate information relating to coverboard design (e.g., material, dimensions, placement, location, and spacing) as they relate to salamanders. This chapter was previously published (Miller Hesed, K. [2012]. "Uncovering salamander ecology: a review of coverboard design." *Journal of Herpetology* 46[4]: 442–450.).

In Chapter 2, I provide the first estimates of these salamanders' growth rates and ages at sexual maturity with a hierarchical Bayesian model; within-population variation in these important life-history traits is poorly understood for many species, including most amphibians. To provide ecological context for these analyses, I investigated home range sizes along with seasonal and annual movement distances by immatures and adults; I then compared home range sizes before and after a removal experiment in order to evaluate how these spatial patterns may be influenced by the presence of conspecifics.

In Chapter 3, I compare mark-recapture models to estimate population parameters including survival and detection probabilities, including the effects of temporary emigration and transience. Terrestrial salamanders are major components of eastern North America's forested ecosystems, and as one of the most abundant vertebrates throughout its range, the Red-backed Salamander is commonly monitored as an indicator of ecosystem health and to assess the effects of forest management practices. However, the many studies generating counts of this species do not accurately measure true abundance, hampering interpretation of their results; here I report the first estimates of these parameters for the Red-backed Salamander.

In Chapter 4, I conduct spatial and genetic tests for sex-biased dispersal in the Red-backed Salamander, using six microsatellite loci and several recently developed genetic approaches that evaluate dispersal on contemporary timescales. Sex-biased dispersal has been widely observed in many species of birds and mammals, but little is known about patterns of dispersal in other taxa. In order to evaluate the generality of theories for sex-biased dispersal, allow *a priori* testing of predictions, and avoid the confounding effects of phylogeny, additional studies are needed in a variety of ectothermic taxa (Perrin and Mazalov, 1999; Lawson Handley and Perrin, 2007).

Long-distance dispersal is a rare process with important biogeographic consequences (Gillespie et al., 2012), and it can be studied with a variety of approaches, including tracking devices, stable isotopes, and mechanistic models (reviewed by Nathan et al., 2003). However, the distances required to avoid interactions with relatives are expected to be smaller than those required to colonize new habitat (Ronce et al., 2001). As a result, sex-biased dispersal may be apparent at the scale at which kin interactions take place, but not at larger spatial scales (Goudet et al., 2002; Fontanillas et al., 2004; Gauffre et al., 2009; Hatchwell, 2010). For this reason, I chose to study dispersal at fine spatial and temporal scales within a population of Red-backed salamanders. Together, these chapters represent a new and comprehensive assessment of the ecology of sex-biased dispersal in one of the most widely studied and abundant vertebrates in eastern North America.

# Chapter 1: A Review of Coverboard Design for Ecological Studies of Salamanders

## Abstract

Coverboards have been used for decades in research on amphibians and reptiles, but their characteristics have varied widely. This diversity in design may both complicate comparisons among studies and preclude assessment of how coverboards could be deliberately tailored to specific study objectives. Although numerous studies have evaluated the effectiveness of various aspects of coverboards, a general synthesis of these results as they relate to salamanders is lacking. Here, I summarize and evaluate information relating to coverboard design and potential concerns for using coverboards in studies of salamanders. Although many salamander species have been encountered under coverboards, coverboard design may have been optimized for the Red-backed Salamander (*Plethodon cinereus*), a terrestrial species found in eastern North America. Altered designs (e.g., material, dimensions, placement, location, or spacing) may prove more effective for other species. With reported declines in salamander populations at both of their global centers of diversity, now may be a crucial time to expand the use of coverboards for studies of a wider variety of species. Further work also should evaluate the ability of a given design to address specific hypotheses and study objectives. In future studies, it should be possible to better tailor coverboard designs to the species, site, and study questions at hand.

## Introduction

Many techniques exist for amphibian ecology, monitoring, and conservation (reviewed by Heyer et al., 1994; Dodd, 2010). Coverboards have been used in salamander surveys for over half a century (Stebbins, 1954; Taub, 1961), and their use has risen in frequency since reports of their advantages in the early 1990s. Coverboards require a relatively small investment of time and resources to establish and maintain, induce little risk to the animals being monitored, require relatively limited training to implement and monitor (although species identification may require additional training), reduce between-observer variability in data collection, result in low levels of disturbance to habitats, and allow cover objects to be standardized in number and size (DeGraaf and Yamasaki, 1992; Grant et al., 1992; Fellers and Drost, 1994).

Interest in monitoring amphibian populations has also risen following their noted declines worldwide (e.g., Wake, 1991). Salamanders in particular have been promoted as especially good candidates for monitoring ecosystem health and assessing silvicultural practices (e.g., Corn and Bury, 1989; Welsh and Droege, 2001; Davic and Welsh, 2004; Welsh and Hodgson, 2008; but see Kroll et al., 2009; Corn, 2010; Kerby et al., 2010). In comparison with other monitoring methods, coverboards have generally been shown to be comparable or superior. Relative to leaf litter quadrat searches and transects, censuses of coverboards produced greater numbers of captures and lower sampling variability (Monti et al., 2000; Hyde and Simons, 2001). Coverboards also yielded a similar diversity of species in comparison with drift



fence/pitfall trap arrays (Bonin and Bachand, 1997), transect searches (Harpole and Haas, 1999), and grids of natural cover (Houze and Chandler, 2002).

Although coverboards may be an important tool in continued studies of salamanders, the variation in coverboard design in published studies may pose a problem for two reasons. First, if salamanders respond differentially to different designs, comparisons among studies may be complicated. Second, variation in design makes evaluation of those potential effects difficult. Without data on the effects of characteristics such as material, spacing, and weathering time, specialized guidelines for addressing specific research questions (e.g., movement, territoriality, activity patterns, occupancy, population genetics) are not possible. The aim of this review is to summarize the available information on the use of coverboards with salamanders, highlighting recommended methods, gaps in knowledge, potential concerns, and directions for further research.

### Coverboard Design

#### *Material*

Of the 11 identified materials used in published salamander coverboard studies (Appendix 1), less than half have been used in more than one study: engineered wood (hereafter collectively referred to as plywood), pine, tin, hemlock, and sugar maple. Available data on numbers of salamanders encountered beneath different materials suggest that salamanders may not use all materials equivalently.

Plywood coverboards yielded significantly fewer *Plethodon ocmulgee* and *Eurycea cirrigera* than natural cover in one study (Houze and Chandler, 2002), and no salamanders at all in another (McDade and Maguire, 2005); both authors noted that the soil beneath the plywood coverboards was usually dry, even after several inches of rain. In a study comparing pine and plywood coverboards, Carfioli et al. (2000) reported that the latter tended to create a patch of warm, dry soil in the center of the covered area (although the effects of material and size were confounded in that study). In comparison with tin coverboards, plywood was used to a greater extent by *Ambystoma talpoideum*, *A. opacum*, *P. glutinosus*, and *E. quadridigitata*, although the boards rotted within 3 y (Grant et al., 1992).

The use of treated wood for coverboards has generally been avoided, probably due to concerns about the effects of chemicals on amphibians and their prey (e.g., Davis, 1997). The only study to have reported using treated wood (Hampton, 2007) found that treated plywood coverboards were used by three species of pond-breeding salamanders (*A. opacum*, *A. texanum*, and *Notophthalmus viridescens*) with about the same frequency as corrugated tin coverboards.

Pine coverboards yielded numbers of *P. cinereus* approximately twice as high as natural cover (Taub, 1961), and mean numbers of *P. cinereus* under pine coverboards and natural cover were correlated across 3 different ages of forest stands (DeGraaf and Yamasaki, 1992). Hemlock coverboards yielded significantly higher encounter rates of *P. cinereus* than asphalt shingles only in stands dominated by Eastern Hemlock (*Tsuga canadensis*); there was no difference in mixed deciduous stands (Mathewson, 2009). The use of native Sugar Maple (*Acer saccharum*)

coverboards has also been reported to yield high encounter rates of *P. cinereus* (Moore, 2005).

Counts of *P. cinereus* were lower under cedar shingles than natural cover (Monti et al., 2000). Marsh and Goicochea (2003) suggested that cedar may repel arthropods, and thus cedar coverboards might be avoided by salamanders seeking cover objects as foraging sites. Squares of carpet provided lower encounter rates of *P. albagula* than wood and degraded within 2 years (Scheffers et al., 2009). Bonin and Bachand (1997) suggested the use of plastic coverboards and artificial sponges to reduce variability in the aging and microclimate characteristics of coverboards, but to my knowledge this design has not been tested.

### *Dimensions*

It has long been noted that the size of a cover object may influence the microhabitat conditions available beneath it (e.g., Test and Bingham, 1948). Most salamanders are dependent on cool, moist conditions (Spotila, 1972; Feder, 1983; Grover, 2000), and so the effect of coverboard dimensions on microhabitat conditions is an important consideration in coverboard design.

Pine or fir at 5-cm thickness is reported to retain moisture better and provide a more stable thermal environment than 0.5-cm plywood, with no additional advantages from 10-cm-thick boards (Fellers and Drost, 1994). Daily temperature fluctuations are also greater under 2-cm plywood coverboards (10° C) than natural cover objects (3° C) (Houze and Chandler, 2002). Soil temperatures beneath small (11 x 11 cm) 2-cm pine boards did not differ from the surrounding leaf litter, while larger (23 x 24 cm)

boards were significantly cooler than both; *P. cinereus* were found only under the larger boards (Mathis, 1990). In a comparison of pine and plywood (Carfioli et al., 2000), the coolest and wettest microhabitats were found under large pine boards (106.7 x 17.8 cm), and the warmest and driest microhabitats were found under extra-large plywood boards (121.9 x 61.0 cm). However, board size was not significant as a main effect in a linear model of encounter rates of *P. cinereus*; which size had higher encounter rates varied with both transect and season.

#### *Age and weathering*

The effects of array age and coverboard weathering are difficult to distinguish in many studies. Boards may be weathered for a period of time (or not at all) prior to being deployed, and once deployed, the arrays may be left to weather in place for a period of time before data collection is initiated. Although it has been suggested that older, weathered boards are preferred by salamanders (e.g., Bonin and Bachand, 1997), the only available data indicate no difference in encounter rates for either *P. cinereus* or *Desmognathus fuscus* under new boards (weathered 2 weeks) and old boards (weathered 2–3 y) (Carlson and Szuch, 2007).

Several multi-year studies report different numbers of salamanders encountered each year (Grant et al., 1992; Davis, 1997; Brooks, 1999; Brooks, 2001), while others show no change in salamander numbers over time (Monti et al., 2000; Houze and Chandler, 2002; Moore, 2005). In such studies it is generally not possible to determine if differences in weather conditions, aging of boards, or the duration of coverboard deployment are responsible for the differences in salamander numbers.

Environmental conditions may have a strong influence on counts of salamanders (e.g., Fellers and Drost, 1994) and should not be overlooked in studies comparing multiple years. A larger point is that counts of salamanders (index values) are potentially biased by variation in detection probabilities (Hyde and Simons, 2001; Corn, 2010); the use of analytical frameworks that explicitly incorporate detection has been a recent and rarely employed development in studies of salamanders (e.g., Bailey et al., 2004; Dodd and Dorazio, 2004; Mazerolle et al., 2007).

#### *Placement with respect to ground*

Carlson and Szuch (2007) reported significantly higher encounter rates of *P. cinereus* under boards placed on bare soil, in comparison with boards placed on leaf litter. Board age was confounded with placement in that comparison, and a second study showed no difference in encounter rates when boards of different ages were placed directly on the soil. Placing coverboards on leveled ground reduces moisture loss during repeated sampling, as they are more easily repositioned flush with ground (Marsh and Goicochea, 2003).

Several studies have placed coverboards in or over holes in the ground, either to provide better access to moister soil (Monti et al., 2000; Jaeger et al., 2001; Gillette, 2003) or to attempt to sample fossorial species (Bonin and Bachand, 1997). The latter study compared single raised coverboards and stacks of 2, 3, or 4 coverboards placed in holes. The greatest numbers of *P. cinereus* were found in installations with 4 coverboards stacked in a hole, but single raised boards on the surface yielded more than twice as many captures as stacks of 3 coverboards in a

hole. The results of Bonin and Bachand (1997) are difficult to interpret, and as yet there has been no direct evaluation of salamander encounter rates for coverboards in or over holes in comparison with coverboards placed flat on the ground.

A few studies in addition to Bonin and Bachand (1997) have used boards that were raised off of the surface, either alone (Carfioli et al., 2000) or in stacks (Davis, 1997; McDade and Maguire, 2005). In comparison with coverboards that were placed flat on the leaf litter, those raised on one edge yielded 14.6% fewer encounters of *P. cinereus* (Carfioli et al., 2000). Stacks of 2 coverboards, propped up by 2-cm pieces of wood, yielded no salamanders over the duration of a 7-month study (McDade and Maguire, 2005). However, the effectiveness of raised boards may depend both on design and target species. The coverboards used by Davis (1997) created wedge-shaped spaces between pieces of lumber; all *Ensatina eschscholtzii* and most *P. vehiculum* and *Taricha granulosa* were found underneath the boards, while nearly all *Aneides ferreus* were found between the pieces of wood.

#### *Sampling frequency*

Marsh and Goicochea (2003) found no difference in numbers of *P. cinereus* under coverboards checked weekly and triweekly, but significantly fewer under boards checked daily. Similarly, encounter rates of *P. cinereus* declined with each census when coverboards were surveyed three times in one week (Bonin and Bachand, 1997).

### *Number and spacing of boards*

Little research has been done on the effects of array size and coverboard density on salamander encounters. If coverboards are to be used for gathering movement data, spacing of boards gains extra importance. Fellers and Drost (1994) suggested that large grids (100 or more boards) would be necessary for reliable data on individual movements; Willson and Gibbons (2010) suggest conducting a power analysis to determine the number of coverboards necessary to achieve the appropriate sample size (based on preliminary counts of salamander abundance) for a given statistical analysis.

Coverboard placement may also influence the social dynamics of salamanders that use them due to differences in individual movement distances. Gillette (2003) reported that it was not uncommon for individual *P. cinereus* in Virginia to move between boards separated by 1 m, but only 1.9% of adults moved between boards separated by 4 m or further. *P. cinereus* also showed no difference in movement between boards with finer-scale spacing (adjacent, 5 cm, or 1 m) (Schieltz et al., 2010). However, male salamanders did not co-occur beneath adjacent boards in that study, and male-female pairs shared the same board more often when board pairs were closer.

### *Preventing disturbance to arrays*

Several different designs have been used to keep boards immobile: placing a rock on each board after positioning it (Stewart and Bellis, 1970), holding boards in place with aluminum tent stakes (Carlson and Szuch, 2007), and securing boards to

the ground by pounding metal rods through holes drilled in the corners of the boards and fastening them with wingnuts (Gillette, 2003). No study has experimentally compared the effectiveness of these techniques.

### Potential Concerns for Salamander Coverboard Studies

#### *Disproportionate usage by different size or age classes*

One concern over the use of coverboards is whether individuals found beneath artificial cover are a representative sample of the larger population. Hyde and Simons (2001) determined that members of the *D. imitator* complex under small boards (26 x 13 cm) were significantly smaller than individuals under large boards (26 x 26 cm). Similarly, permanently removed *P. cinereus* were replaced by significantly smaller individuals (suggesting exclusion by the larger individuals) (Mathis, 1990), and the proportions of adult, hatchling, and juvenile *P. cinereus* under coverboards and natural cover varied among seasons (Marsh and Goicochea, 2003).

By contrast, no significant size differences (mass, snout–vent length, or relative tail length, depending on the study) were found for *P. cinereus* relative to the area of coverboards (Moore, 2005), age of coverboards (Carlson and Szuch, 2007), or between coverboards and natural cover (Monti et al., 2000). Similarly, body size did not differ between *P. albagula* under wood or carpet pieces (Scheffers et al., 2009), or between *P. ocmulgee* under natural and artificial cover (Houze and Chandler, 2002).

Given the lack of natural history information (including age structure, site fidelity, detectability, natal dispersal, and associations among kin) for many



populations, some caution should be used in interpreting causality when different sizes of salamanders are encountered beneath cover objects. Further studies, particularly addressing the availability of natural and artificial cover when using coverboards, could help determine the extent of differential usage patterns across sites, seasons, and species.

#### *Applicability to diverse species*

Published studies using coverboards have resulted in encounters of 44 species of salamanders in 3 families (Appendix 2). The most common species in these studies is the Red-backed Salamander, *Plethodon cinereus*. This taxonomic focus is likely due in part to the abundance and broad geographic range of the species, which includes much of eastern North America (Petranka, 1998). Many studies report that *P. cinereus* is the most common species encountered in herpetofaunal surveys, and often the only species providing enough data for analysis (e.g., Bonin and Bachand, 1997; Brooks, 1999; Harpole and Haas, 1999; Carfioli et al., 2000; Ross et al., 2000; Brooks, 2001; Morneault et al., 2004; Carlson and Szuch, 2007; Maerz et al., 2009).

Although the available data on coverboard design may be skewed toward the biology of *P. cinereus*, other species of salamander may be very rarely encountered under coverboards or very common depending on the details of the study (Appendix 2). The effort to optimize coverboard design, location, and placement for additional species may prove very fruitful. Examples include structurally complex coverboards that create a variety of microhabitats (Davis, 1997) and a hybrid coverboard design

incorporating halved PVC pipe that was developed for use with semi-aquatic salamanders (Luhring and Young, 2006).

Salamander diversity is extremely high in Mexico, Central America, and the southern Appalachians of the eastern United States (Petranka, 1998). However, studies using coverboards to monitor many species are lacking from the literature, and coverboards are absent from the protocol manual *Amphibian Monitoring in Latin America* (Lips et al., 2001). In light of recent declines of salamander populations in both of their centers of diversity (Highton, 2005; Rovito et al., 2009) and the anticipated effects of future climate change (Buckley and Jetz, 2007), much stands to be gained by evaluating the use of coverboards for a greater variety of salamander species.

Abundances of different species may vary markedly from site to site (e.g., Grant et al., 1992; Davis, 1997), and careful site selection may be necessary to effectively sample diverse species. As the data on coverboard design summarized here may be biased by the dominance of *P. cinereus* in the literature, different coverboard characteristics may be more suitable for monitoring other species, and further research is needed to determine what coverboard design features are most appropriate for a greater variety of species.

## Summary

### *Design*

Cedar and plywood may be avoided by salamanders, while pine and other solid woods appear to be generally superior. Wood is more effective than tin and

carpet; both carpet and plywood may degrade within 2–3 yr. Treated plywood was shown to be used by salamanders with the same frequency as was tin, and asphalt shingles appear to be effective, although further studies should assess whether chemicals present in these materials have any adverse effect on salamanders or their prey. Though different forms of engineered wood (e.g., plywood, chipboard, and Masonite) may behave differently from one other, the poor performance of those types that have been tested may suggest that engineered woods should be avoided in general. Use of native dominant native wood may be more effective than other materials in certain forest types. To determine the best material to use for a given species and site, further studies should use arrays with multiple materials (e.g., pine, plywood, cedar, and native wood) across different habitat types and seasons.

Plywood coverboards up to 2 cm in thickness exhibit much larger daily temperature fluctuations than natural cover; 5-cm pine or fir boards provide more thermal stability than does plywood; and 10-cm boards provide no additional advantages. The coolest and wettest conditions can be achieved under appropriately sized boards: temperatures under smaller boards (e.g., 10 x 10 cm) may not differ from the surrounding leaf litter, and larger plywood boards (e.g., 120 x 60 cm) may create warm, dry conditions. Different sizes of boards may affect the age or size classes of salamanders that use them. Further studies should address this possibility with coverboard arrays of differently sized boards, tested over multiple seasons with several different species.

The age of arrays appears to be more important than the age of coverboards themselves. There may be a delay in occupancy by salamanders immediately after

boards are placed, but capture rates are likely to vary from year to year even after boards have been weathered in place. The age of a coverboard itself may or may not matter if it is deployed simultaneously with boards of other ages. The effect of coverboard and array age may be very difficult to determine in multiple-year studies due to the confounding influences of array age, board age, changes in microhabitat, and differences in weather. Carefully designed studies and the use of mark-recapture models could help distinguish among these different variables.

Coverboards placed on bare, leveled ground generally result in the highest encounter rates of salamanders, followed by boards placed on existing leaf litter, and then by raised boards (although encounter rates may differ among species). Further studies should evaluate the usefulness of stacking coverboards for different species and the effect of placing coverboards in or over holes.

Sampling boards more often than once per week may reduce the number of captures. Apparently very little research has been done on the effects of array size and board density on salamander encounters; available data suggest that movements between boards separated by more than 1 m may be limited, and the spacing of boards may influence which salamanders are encountered due to social dynamics. A few methods have been used to minimize disturbance to arrays, but their effectiveness has not been evaluated.

#### *Potential concerns*

Coverboards may be used disproportionately by larger or older salamanders of some species, although studies have found conflicting results. Researchers should

consider this possible bias when planning a study, and further research should address temporal and taxonomic patterns in the segregation of available cover (both natural and artificial) by salamanders, as well as evaluating the behavioral and ecological bases for these patterns.

#### *Comparison with other techniques*

Coverboard arrays appear to provide comparable numbers, lower variability, and a similar diversity of species when compared with alternative approaches such as drift fence/pitfall arrays, natural cover transects, quadrats, and leaf litter surveys. Coverboards may under-sample some species, but adjusted designs could improve their effectiveness for those species. The effect of available natural cover on the usage of coverboards by salamanders should be studied further. Additional studies comparing efficacy, ease of use, and observer bias among different methods would be valuable.

Although many salamander species have been encountered under coverboards, coverboard design may have been optimized for *Plethodon cinereus*, a terrestrial species found in eastern North America. Altered designs (e.g., material, dimensions, placement, location, or spacing) may prove superior for other species. With reported declines in salamander populations at both of their global centers of diversity, now may be a crucial time to expand the use of coverboards for studies of a wider variety of species. Further work also should evaluate the ability of a given design to address specific hypotheses and study objectives. In future studies, it should be possible to tailor coverboard designs for specific taxa, sites, and study questions.

## Chapter 2: Differential Growth, Age at Maturation, and Movement Patterns by Male and Female Red-Backed Salamanders (*Plethodon cinereus*)

### Abstract

Growth and maturation are important aspects of organisms' life histories, but within-population variation in these traits is poorly understood for many species, including most amphibians. Here I provide estimates of growth and age at sexual maturity for a population of terrestrial salamanders, using a hierarchical Bayesian model fitted by four years of mark-recapture measurements; to complement these analyses, I investigated home range sizes along with seasonal and annual movement distances by immatures and adults. To evaluate how these spatial patterns may be influenced by the presence of conspecifics, I then compared home range sizes before and after a removal experiment. Results of this study reveal that males grow and mature more slowly than females, despite reaching slightly larger asymptotic sizes. An explanation for this difference is provided by evidence of competition for space: adult males occupy the largest home ranges and show the largest increase in home range size after the removal of conspecifics; in addition, the largest between-year movements are made by individuals as they transition from immaturity to maturity.

## Introduction

The growth and development of individual organisms are subject to a wide variety of selective pressures and potential tradeoffs (reviewed by Arendt, 1997), with variation in these life-history traits generally considered to reflect interactions between an organism's physiology and the environment it experiences (reviewed by Ricklefs and Wikelski, 2002). Large-scale patterns in growth and development across taxa have been suggested, such as Bergmann's rule that species of endotherms in colder climates are larger than their relatives in warmer climates (Blackburn et al., 1999).

Although ectotherms have not been studied as intensively as endotherms (Adams and Church, 2008), many amphibians appear to exhibit consistent geographic variation across populations within a species (reviewed by Morrison and Hero, 2003) or across the species within larger clades, such as frogs and salamanders (e.g., Olalla-Tarraga and Rodriguez, 2007; Olalla-Tarraga et al., 2010). These analyses consider the average body size of a species or a population; however, variation within populations is a subject of increasing interest (e.g., Roff, 2000; Berner and Blanckenhorn, 2007), and there is growing evidence of widespread individual variation in growth rates (Vitt and Caldwell, 2014).

In studies of amphibians and reptiles, three main methods have been widely used to estimate growth (Halliday and Verrell, 1988): skeletochronology, extrapolation from size-frequency data, and recapture of known individuals. Each method has certain disadvantages. Skeletochronology requires destructive sampling to obtain cross-sections of long bones, and sacrificing large numbers of animals may

not be desirable for many studies. In addition, growth marks on bones can be difficult to read accurately, and assumptions about the durability and creation rate of these marks are not always reliable.

Size frequency data come from using concurrent measurements of large numbers of individuals to create a size-frequency histogram, which can then be inspected for discontinuities. This approach assumes a relationship between age and size, which is often unknown, and is made unreliable by variation in size within age classes. Mark-recapture measurements may require large amounts of time and effort, but they are regarded as the only wholly reliable approach for measuring growth rates (Tilley, 1977; Halliday and Verrell, 1988).

Even for amphibian species as intensively studied as the Red-backed Salamander (*Plethodon cinereus*), growth and development are incompletely understood. One previous study used skeletochronology (Leclair et al., 2006), an approach with questionable accuracy (Halliday and Verrell, 1988) and known difficulties when applied to plethodontid salamanders (Castanet et al., 1996). That study used the graphic method of Walford (1946) for parameterization and did not attempt statistical comparison of growth parameters between males and females.

All other previous reports of growth or age in Red-backed Salamanders (Blanchard, 1928a, b; Bishop, 1941; Test and Bingham, 1948; Saylor, 1966; Nagel, 1977; Pflingsten, 1989) have relied on extrapolation from size-frequency data of preserved specimens. In addition to changes in size that occur during preservation (5–6% shrinkage; Bruce, 2000) and the inability to distinguish age classes of adults due to the slowing of growth around reproductive maturity (Nagel, 1977), the major



problem inherent in this approach was noted over a century ago (Piersol, 1910, p. 478):

The rate of growth in *Plethodon* must vary enormously in different individuals, for at this season [early October] it is easy to collect a series beginning with young accompanying the mother and ending with full grown specimens, the increase in size being so gradual that it is impossible to draw with certainty a line between this year's and last year's broods.

To date, the most thorough analysis of the life history of Red-backed Salamanders is the study by Sayler (1966); this paper continues to be cited as the standard reference for age and size in this species (e.g., Homyack and Haas, 2009; Caceres-Charneco and Ransom, 2010; Liebgold and Dibble, 2011). Although this study has provided a wealth of information, it was somewhat limited by methodology—a “polymodal frequency analysis” developed by Harding (1949). This approach involved plotting the distribution of sizes onto graph paper and connecting the points to yield a straight line (representing a single normal distribution) or a polysigmoid curve (with inflection points representing the boundary between two normal distributions). No published study has measured the growth of Red-backed Salamanders over time in a natural population, leaving the extent of individual variation in growth and development unknown.

Hierarchical structuring of parameters and Bayesian inference methods used in recently developed models (e.g., Eaton and Link, 2011) represent a methodological improvement over previous approaches in allowing growth curves to vary as

individual-specific stochastic processes. In this study, I estimate growth parameters and age at maturity for a population of Red-backed Salamanders using a hierarchical Bayesian growth and maturation model fitted with mark-recapture data, to evaluate whether males and females differ in asymptotic size, growth rate, age at maturity, or degree of individual heterogeneity.

To provide ecological context for these patterns of growth and development, I compared patterns of space use by immatures, adult females, and adult males, including home range size with seasons, movement distances between successive seasons, and movement distances between successive years. In order to experimentally examine the influence of conspecific interactions on space use, I removed 98 adult males and females from the study plots and compared the home range sizes of individuals on the plots before and after the removals.

### Materials and Methods

#### *Study site*

I conducted this study in mature bottomland hardwood forest at Patuxent Wildlife Research Center (PWRC) in Laurel, Maryland (39.054376°N, 76.817206°W). Forest composition at the site (Hotchkiss and Stewart, 1947) is dominated by American Beech (*Fagus grandifolia*), with smaller numbers of Tulip Tree (*Liriodendron tulipifera*), Northern Red Oak (*Quercus rubra*), and American Sweetgum (*Liquidambar styraciflua*). Within a section of continuous forest, I established three study plots (Fig. 2.1), separated from one another by 30–40 m and >50 m from the forest edge (Demaynadier and Hunter, 1998).

Red-backed Salamanders have been reported to commonly move between cover objects separated by 1 m, but rarely to move between covers separated by 4 m or more (Gillette, 2003). In order to standardize the availability of shelter objects (Marsh and Goicochea, 2003), I removed natural cover (downed wood) and arranged coverboards in a 1-m grid on each plot. Boards were pine, with dimensions of 30 cm  $\times$  30 cm  $\times$  2.5 cm, placed flush with bare ground (Miller Hesed, 2012). One plot consisted of a 20  $\times$  20 array of boards (400 boards in an area of 625 m<sup>2</sup>; monitored for 2 y), and the other two plots each consisted of a 10  $\times$  10 array of boards (100 boards in an area of 156 m<sup>2</sup>; monitored for 4 y).

#### *Data collection*

In Maryland, Red-backed Salamanders exhibit seasonal activity patterns: a prolonged mating season lasts from October–April, with oviposition occurring the following June; brooding females remain with their clutches for the 6–8 weeks of development and reemerge in August, while hatchlings remain in the nest for 1–3 weeks and appear on the surface in September (Sayler, 1966). At PWRC, salamanders are active on the surface only in the fall (approximately October–December) and spring (approximately March–May). To minimize disturbance to animals and plots, I conducted searches at weekly intervals (Marsh and Goicochea, 2003) during these periods.

During each sampling occasion, I overturned each coverboard and captured any salamanders present. I placed each salamander in an individual plastic sandwich bag with a spray of spring water and held all captured salamanders in a plastic cooler

with ice packs; once I completed sampling, I transported the salamanders < 1 km to a laboratory for processing. I measured each individual's body length (snout–vent length [SVL], the length from the tip of the snout to the posterior of the vent) and total length (the length from the tip of the snout to the tip of the tail) twice to the nearest 0.1 mm with dial calipers (Swiss Precision Instruments, Inc.; Garden Grove, CA). I determined sex by candling each salamander with an LED headlamp to visualize testes and developing ova (Piersol, 1910; Gillette and Peterson, 2001); I could not determine sex prior to maturity, the point at which gonads become pigmented (Sayler, 1966). In this paper, I refer to unsexable individuals as “immatures,” while “males” and “females” refer to sexually mature adults.

I marked each newly captured individual with Visible Implant Elastomer (VIE; Northwest Marine Technology; Shaw Island, WA), sterilizing the needle with 95% ethyl alcohol between uses. VIE has been shown to have no effect on weight gain, growth, or survival of several plethodontid species including *P. cinereus* (Davis and Ovaska, 2001; Gillette, 2003; Bailey, 2004; Phillips and Fries, 2009) and no change in readability over a year-long study (Heemeyer et al., 2007). I checked marks twice to reduce error (Campbell Grant, 2008). After processing, I returned each individual to its site of capture, releasing it at the edge of the coverboard.

### *Modeling growth and maturation*

To relate the body size of individual salamanders to their age, I modeled growth with a Gamma process von Bertalanffy model similar to that in Eaton and

Link (2011). In this analysis, the population mean size of individuals of age  $A$  is modeled as a von Bertalanffy curve (Fabens, 1965) given by the following equation:

$$S(A) = a(1 - be^{-kA}).$$

In this parameterization,  $a$  is the asymptotic body length such that  $S(\infty) = a$ ; birth size is related to asymptotic size by the parameter  $b$  such that  $S(0) = a(1 - b)$ ; and  $k > 0$  is a growth rate coefficient.

Individual-specific growth curves,  $L_i(\cdot)$ , describe the length of animal  $i$  of unknown age  $A_{ij}$  on each capture occasion  $j$ , represented as  $L_i(A_{ij})$ . The paired measurements taken on each occasion,  $l_{ij1}$  and  $l_{ij2}$ , are modeled as independent normal random variables having mean  $L_i(A_{ij})$  and variance  $\sigma_e^2$ , allowing measurement error to be estimated. The individual growth curves are related to the population mean by the following equation:

$$L_i(A) = S(0) + \eta_i (S(A) - S(0)).$$

The  $\eta_i(\cdot)$  are individual-specific, independent, identically distributed Gamma processes defined on the positive real numbers;  $\eta_i(x)$  has a Gamma distribution with mean  $x$  and variance  $x/\lambda$ , for  $\lambda > 0$ .  $S(A)$  is then the population mean value of  $L_i(A)$ , with population variance of  $(S(A) - S(0))/\lambda$ .

The individual-specific and population parameters in this model can be fitted with mark-recapture data for animals of unknown age, with the exception of the parameter  $b$  relating birth size and asymptotic size. Based on the average hatchling size of Red-backed Salamanders throughout the Atlantic Coastal Plain (R. Highton, pers. comm.), I set  $S(0) = 15$  mm. This value is similar to snout-vent lengths reported for hatchlings in Ohio (13.5 mm; Pflingsten, 1989) and the consistently similar total

lengths (18.5–20 mm) of hatchlings in Massachusetts (Cochran, 1911), New York (Bishop, 1941), and Wisconsin (Vogt, 1981). Any variation in size at hatching of salamanders in this study would be accounted for by the incorporation of individual heterogeneity in the model.

Predominantly mid- to late-August hatching dates are reported for Red-backed Salamanders in Massachusetts (Cochran, 1911; Lynn and Dent, 1941), Pennsylvania (Burger, 1935; Bishop, 1941), New Jersey (Burger, 1935), New York (Bishop, 1941), Michigan (Test, 1955; Davidson and Heatwole, 1960), Virginia (Highton, 1959), Ohio (Pfungsten, 1989), and Wisconsin (Vogt, 1981); a late-August hatching date is also likely for populations on the Atlantic Coastal Plain (R. Highton, pers. comm.). Based on these dates, the model was parameterized to calculate age from August 20 of the unknown birthyear of each individual. Growth rate appears to be slow for the first several weeks after hatching (Burger, 1935; Saylor, 1966), so variation around hatching date should have little effect on the model.

I classified individuals as immature or mature at each capture occasion based on the presence of pigmented testes and ova; age at maturity ( $G_i$ ) was then modeled as a normal random variable with mean  $\mu_G$  and variance  $\sigma_G^2$ . In the combined Bayesian analysis,  $a$  was modeled with a uniform prior; birthyear over the 10 years prior to first capture was modeled with a discrete uniform prior; and other parameters were modeled with vague (i.e., noninformative) Gamma priors. Sex was modeled with a 50% prior probability that an individual was male, and model parameters were estimated separately for females and for males. The model was fitted using Markov chain Monte Carlo implemented in OpenBUGS version 3.1.1 (Lunn et al., 2009) with

the results of six chains of length 421,000 (the first 60,000 discarded as burn-in) compared to ensure adequate mixing. The model is described in more detail in a separate manuscript (Link and Miller Hesed, in review).

### *Field study and removal experiment*

To compare the spatial ecology of immatures, adult females, and adult males, I monitored three study plots for 2 y (October 2009–April 2011), marking 428 salamanders over that period. The following 2 y (October 2011–May 2013), I conducted a removal experiment on two of the plots to evaluate whether home range sizes would change in the absence of resident individuals. For this study, I marked an additional 328 salamanders. In the spring and fall of 2012, I removed a total of 49 adult male and 49 adult female salamanders (all previously marked and recaptured) from the plots, resulting in pre-removal and post-removal periods of equal length.

I used ArcGIS 9.3.1 (Esri; Redlands, CA) and HawthTools (Beyer, 2004) to calculate an average location for each individual in each season and the distance between average locations in successive seasons and years. I also calculated a minimum convex polygon (MCP for each salamander captured three or more times within a season. I used the “car” package (Fox and Weisberg, 2011) in the software environment R (R Core Team, 2014) to conduct Type II analyses of variance comparing the resulting areas and distances.

For some multiply captured individuals, it was possible to calculate more than one seasonal or annual distance over the duration of the study; to avoid pseudoreplication, values for those individuals were averaged so that each individual

salamander is represented in the dataset only once. Although the initial field study and the removal experiment largely comprise separate groups of salamanders, there were 37 individuals with records in both datasets; excluding them from the analysis did not affect results. Because MCP areas may be dependent on the number of points used for estimation (Powell, 2000), I repeated analyses, successively removing MCPs by number of captures (Appendix 2.1). The results remained consistent and significant after removal of MCPs based on 3 points and after removal of MPCs based on 3 points or 4 points; after removal of MCPs based on 3, 4, or 5 points, the dataset was depauperate of immature individuals and results were only marginally significant.

## Results

### *Growth*

I marked 752 salamanders over the course of the study and captured them a total of 2,745 times; 479 individuals (64%) were measured on more than one occasion, allowing estimates of growth increments. Parameter estimates (Table 1) reported in the text are given as posterior medians with 95% credible intervals (CIs).

The estimated asymptotic body sizes of males and females had non-overlapping credible intervals, with males slightly larger: 50.69 mm (48.96, 53.22) compared with 47.62 mm (46.84, 48.48) for females (Fig. 2.2). Despite reaching a slightly smaller maximum size, females grew more quickly than males: the growth rate coefficient  $k$  was estimated to be 0.73 (0.69, 0.77) for females and 0.34 (0.29,



0.39) for males (Fig. 2.3). These values of  $k$  indicate that females would reach 90% of their growth in 3.15 y, while males would take on average 6.7 y to grow to an equivalent proportion of their asymptotic size. Individual heterogeneity in growth (Fig. 2.4) was greater for males (0.91 [0.85, 0.97]) than for females (0.72 [0.67, 0.77]).

The pattern for maturation was similar to that for growth: males reached maturity later than females (3.05 y [2.82, 3.32] vs. 2.04 y [1.91, 2.11]; Fig. 2.5) and with a substantially larger standard deviation (0.915 y [0.757, 1.121] vs. 0.079 y [0.033, 0.163]; Fig. 2.6). Measurement errors were minor, with a standard deviation of  $\sigma_\epsilon = 1.044$  mm (1.016, 1.170). Simulated growth curves based on posterior median parameter values show the slower and more variable growth by males (Fig. 2.7).

### *Movement patterns*

In the initial field study, home range sizes differed significantly among immatures, females, and males ( $F_{2,147} = 4.9172$ ;  $p = 0.009$ ). Males occupied areas significantly larger than those of immatures (Tukey's HSD test with 95% family-wise confidence level:  $p = 0.007$ ); female home ranges were intermediate and statistically indistinguishable from those of immatures and males (Fig. 2.8).

Results of the removal experiment are depicted in Fig. 2.9. As in the previous field study, home range size differed among immatures, females, and males ( $F_{2,110} = 6.14$ ;  $p = 0.003$ ), with males occupying significantly larger areas than immatures (Tukey's HSD test with 95% family-wise confidence level:  $p = 0.01$ ). Home range areas were significantly larger after removals than before ( $F_{1,110} = 12.68$ ;  $p = 0.0005$ ).

Stage and removal also had a significant interaction ( $F_{2,110} = 5.3$ ;  $p = 0.006$ ), due to the relatively greater response to removals by adult males.

There was no significant difference in the distance moved by females, males, and immatures between the seasons of a year ( $F_{2, 143} = 1.577$ ;  $p = 0.2102$ ). The distance moved between successive years differed significantly due to maturation state ( $F_{1, 78} = 12.1802$ ;  $p = 0.0008$ ): the shortest distances were moved by individuals that were mature in both years, while individuals that matured over the course of the year (i.e., were immature in the first year and mature in the second year) moved significantly greater distances (Tukey's HSD test with 95% family-wise confidence level:  $p = 0.002$ ). Individuals that were immature in both years moved intermediate and statistically indistinguishable distances (Fig. 2.10).

### Discussion

The results of this study indicate that female Red-backed Salamanders in this population grow more quickly and with less variation than do males. It has been known for more than a century that there must be extensive individual heterogeneity in growth rates in this species (Piersol, 1910); however, subsequent studies have only compared size distributions of collected specimens or reconstructed population average growth rates with skeletochronology. As a result, growth rates have never been measured in a natural population of Red-backed Salamanders, and this is the first report of sex differences in the growth rates of this species prior to maturity; one previous study suggested that in a northern population, the growth rate of females may be higher than that of males several years after maturity (Leclair et al., 2006).

Despite growing more slowly, males in this study eventually reach slightly larger asymptotic body sizes than females. Previous studies have anecdotally suggested greater body lengths for males (Cochran, 1911) or for females (Bishop, 1941), and three analyses using *t*-tests (Sayler, 1966; Quinn and Graves, 1999; Leclair et al., 2006) failed to detect a difference between the sexes. The nearly identical asymptotic sizes and the extensive individual heterogeneity revealed in this study suggest why it would be difficult to detect a statistical difference between two distributions of adult body sizes as measured in previous studies.

In addition to their faster and less variable growth rates, females also reach maturity more quickly and with substantially less variation than do males. On average, females mature just after their second birthday, at the beginning of their third year, while maturity occurs for males one year later on average. However, the large variability in this date for males (a standard deviation of nearly 1 y) indicates that some males mature at the same time as most females.

Many previous studies have observed three size groups in collections of Red-backed Salamanders and concluded that maturity must occur after two years of growth (Blanchard, 1928a, b; Burger, 1935; Bishop, 1941; Test and Bingham, 1948; Sayler, 1966); without measuring the size of individuals over time, it has not been possible to detect this heterogeneity in maturation. Interestingly, this result is contrary to the apparent trend of later maturity by females among plethodontids (Houck, 1977; Tilley, 1977; Marvin, 1996; Bruce, 2000).

Male and female Red-backed Salamanders may reach similar maximum sizes in this population due to different selection pressures. The rapid growth by females

until maturity (Fig. 2.7) suggests selection for fecundity; a tradeoff between growth and reproduction has been shown for several species of plethodontids (e.g., Maiorana, 1976; Harris and Ludwig, 2004). Although Blanchard (1928b) determined that small female Red-backed Salamanders will lay as many eggs as large females, the production of greater amounts of yolk—which is important for provisioning young for several weeks after hatching (Burger, 1935; Bishop, 1941)—is a likely advantage for a larger body size in females. At two of four sites in a population in Quebec, females were larger than males, and males appeared to mature at a smaller body size than females (Leclair et al., 2006); although results were not consistent across sites in that study, females at higher latitudes on average take two years to yolk a clutch of eggs (Petranka, 1998), potentially reflecting selection pressure for later maturity and larger body size.

Males in this study showed greater variation both in how quickly they are able to grow and in how quickly they reach maturity; this result suggests that males may face greater intrasexual competition for resources than females do. Variation among males may reflect condition-dependence and/or alternative male reproductive strategies (Emlen and Oring, 1977). Patterns of long-term pairing are virtually unknown in amphibians (Wells, 2007). However, several studies have offered intriguing speculation about social interactions in Red-backed Salamanders, and social monogamy has been repeatedly asserted for this species.

Mathis (1991) found greater overlap in the distributions of individual Red-backed Salamanders between the sexes than within each sex. Over an 11-day survey of random transects in Virginia, Jaeger et al. (1995) found approximately 28% of

adult salamanders in male-female pairs under cover objects, but no female-female pairs and only one male-male pair. Based on these observations and their finding that members of a pair are more aggressive toward novel individuals of the same sex, Lang and Jaeger (2000) suggested that males and females form long-term affiliations and co-defend territories as “quasi-monogamous” pairs.

A variety of laboratory studies have indicated that Red-backed Salamanders display reduced aggression toward familiar individuals, relative to unfamiliar individuals (e.g., Jaeger, 1981; Jaeger et al., 1995; Guffey et al., 1998; Joseph et al., 2005). Lacking from all of these studies, however, is evidence of long-term spatial associations and resulting reproductive success. Decades of lab-based behavioral studies have addressed territoriality by Red-backed Salamanders (reviewed by Mathis et al., 1995; Wells, 2007), but the results of the present field study and removal experiment provide some of the first evidence of apparent territorial differences by males and females in a natural population.

Males but not females occupy home ranges that are significantly larger than those of immature individuals. This pattern was evident in both the 2-y field study and the 2-y removal experiment detailed here. A previous study in Virginia (Mathis, 1991) found no difference in home range areas of juveniles, adult males, and adult females; because that study was conducted on 9 m<sup>2</sup> study plots and calculated home range areas of 0.162–0.335 m<sup>2</sup>, the study area may not have been large enough to encompass entire home ranges. In the present study, home range sizes were larger for all three groups after the removal of 98 resident adults; however, males showed a

larger increase than either females or immatures, which resulted in a significant interaction with the removal effect.

A comparison of individual salamanders' average locations in successive years indicates that resident adults (by definition, individuals repeatedly captured in successive years) shift their center of activity very little. Along with the removal results discussed above, this finding is consistent with the "dear-enemy" relationships hypothesized by Jaeger (1981; 971–972):

If these experiments reflect the behavior of *P. cinereus* in natural forest habitats, the following competitive interactions can be envisioned. The salamanders establish territories in prey-depauperate patches of moisture on the forest floor and mark them with individual-specific pheromones, thereby protecting a scarce food resource. Neighbors are relatively immune from attack because their pheromones are familiar to one another, and agonistic displays are probably sufficient to maintain territorial spacing. However, strangers are more likely to be attacked, with the consequence that the intruder (and perhaps the occupant of the territory) risks the loss of its tail, and thus much of its fat reserves, or risks injury to its chemosensory structures. The latter case can lead to a long-term decrease in foraging efficiency and perhaps to a decreased ability to locate mates and competitors. It appears, then, that although these salamanders lack conspicuous weapons for fighting and are incapable of inflicting mortal wounds, they use their small premaxillary and vomerine teeth to attack the most vulnerable parts of an opponent's body; i.e.,

they inflict injuries that have the most potential for reducing the future fitness of opponents.

The results of this study indicate that competition for space among these salamanders occurs primarily among sexually mature adults, consistent with evidence that adults display reduced aggression toward juveniles (Jaeger et al., 1995; Liebgold and Cabe, 2008). Individuals that were immature in the first year of the study and mature in the second year, in contrast to individuals that were immature in both years, shifted significantly greater distances than the adults (Fig. 2.10). There was no significant sex effect in this analysis, indicating that both males and females face strong competition for space as they mature; a difference between the sexes, as suggested by their growth and maturation differences, might be apparent with larger sample sizes.

If they face less competition for space, immature females could invest energy primarily in growth and reproductive development; as a result, they would grow quickly and mature early, with little variation. If males face more intense competition for space, they may need to invest disproportionate energy into securing resources; as a result, they would grow and mature more slowly on average, but with much greater variation in their success, a pattern associated with reproductive traits of many male animals (Bateman, 1948).

Future work should address differential competition for space by males and females and the possibility of alternative male reproductive strategies. Multiple paternity has been shown for Red-backed Salamanders (Liebgold et al., 2006), and additional studies should attempt to distinguish the social and genetic mating systems that exist in wild populations (Hughes, 1998; Griffith et al., 2002). In contrast to well-

studied aggregate-breeding salamanders (Gabor et al., 2000; Jones et al., 2002; Garner and Schmidt, 2003; Myers and Zamudio, 2004; Gopurenko et al., 2006; Steinfartz et al., 2006), the long breeding season and terrestrial life history of Red-backed Salamanders offers a unique opportunity to evaluate spatial proximity and physical factors affecting reproductive success.

The results of this study indicate several previously unknown aspects of the biology of Red-backed Salamanders: slightly larger asymptotic size for males; faster growth and maturation by females; greater individual heterogeneity in growth and age at maturation for males; larger home range sizes of males; greater male expansion of home range size after reduced competition; and the largest movements between years by individuals transitioning from immaturity to maturity. However, these results should be extrapolated with care: life history characteristics of plethodontid salamanders are expected to vary both among populations and among years (reviewed by Houck, 1977; Tilley and Bernardo, 1993; Marvin, 1996)—further work should attempt to address the extent of this variation.



*Chapter 2 Figures*

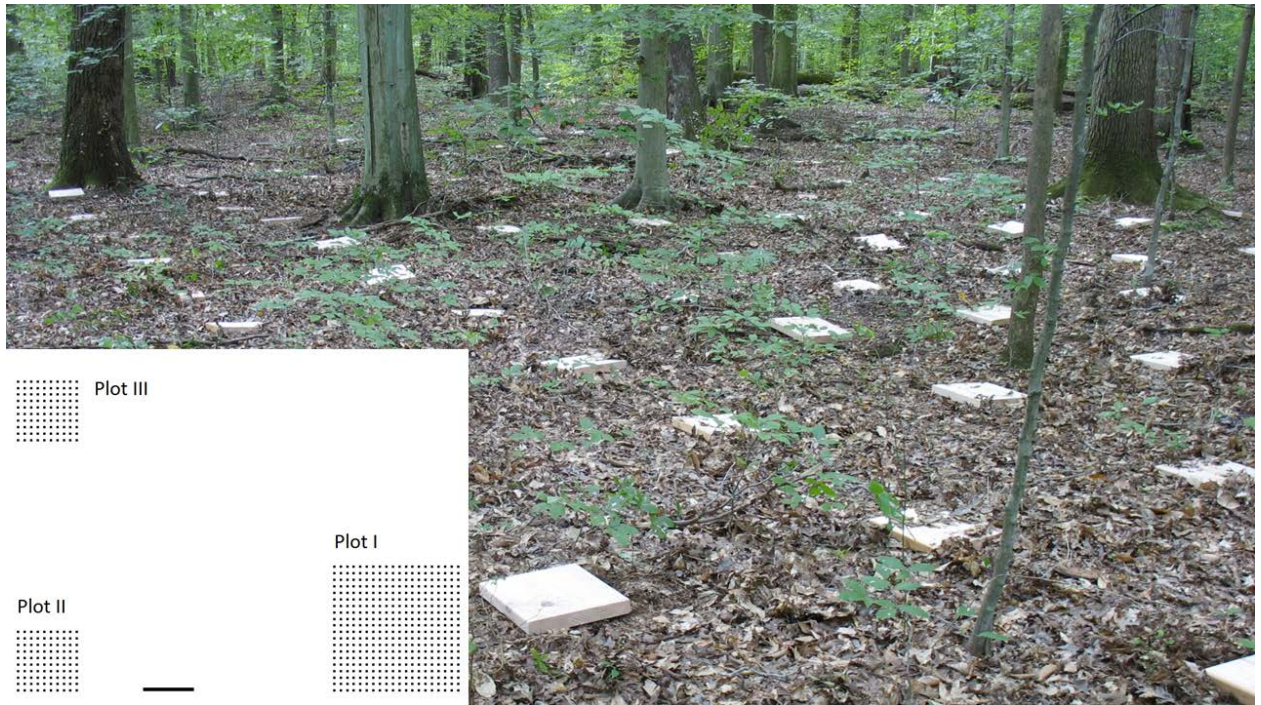


Figure 2.1. View of one study plot of coverboards used to monitor a population of Red-backed Salamanders (*Plethodon cinereus*) in mature bottomland hardwood forest at Patuxent Wildlife Research Center (PWRC) in Laurel, Maryland (39.054376°N, 76.817206°W). Photograph taken in early September 2009. Inset: schematic of the three plots of coverboards used in this study (scale bar = 10 m). Plots II and III are 156 m<sup>2</sup>, each with 100 pine coverboards (30 cm × 30 cm × 2.5 cm) arranged in a 1-m square grid. Plot I, 625 m<sup>2</sup>, contains 400 coverboards. All plots are located within a section of continuous forest.

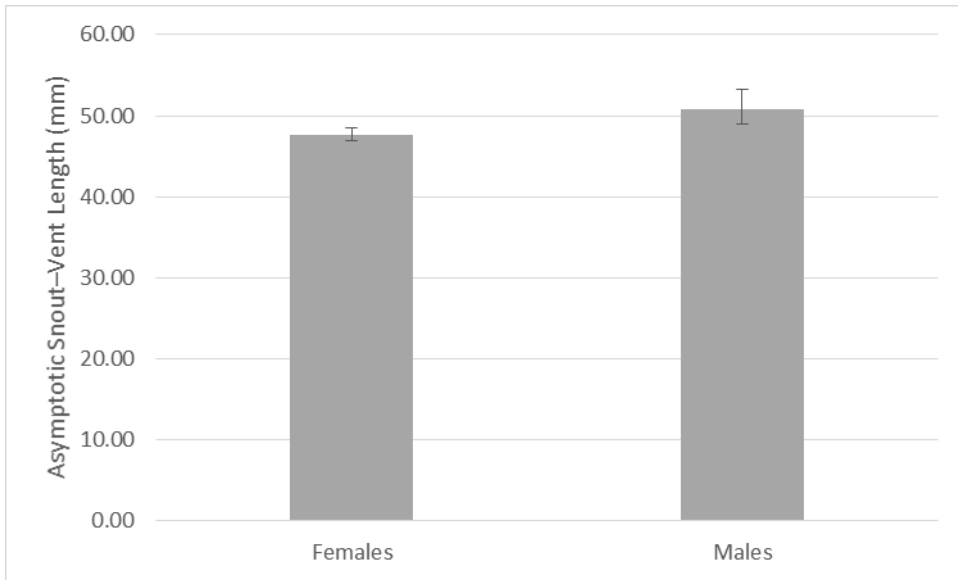


Figure 2.2. Medians of the posterior distributions of asymptotic body size for female and male Red-backed Salamanders, modeled by a Gamma process von Bertalanffy growth model fitted by repeated measurements from 4 y of mark-recapture data. Error bars represent 95% credible intervals, which do not overlap between the sexes.

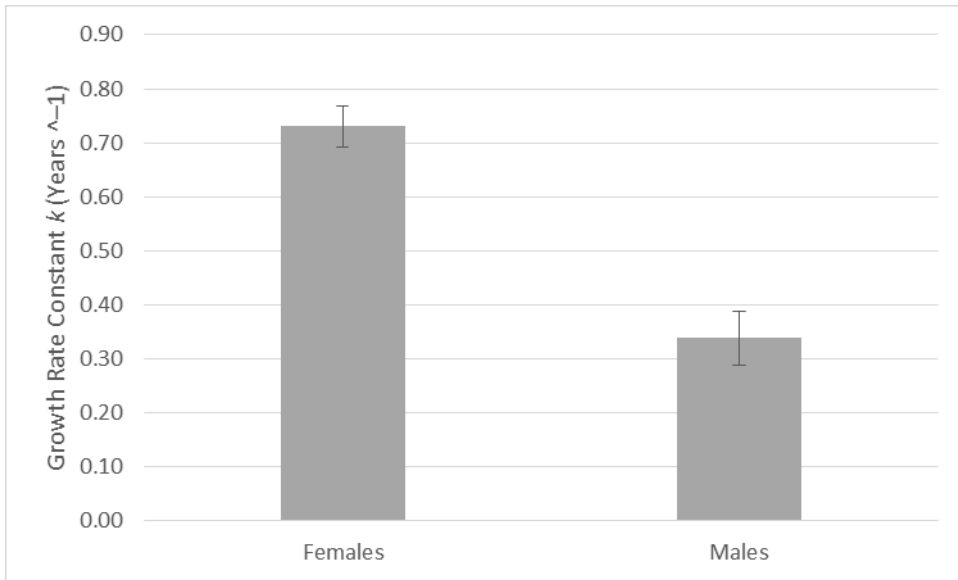


Figure 2.3. Medians of the posterior distributions of the growth rate parameter  $k$  for female and male Red-backed Salamanders, modeled by a Gamma process von Bertalanffy growth model fitted by repeated measurements from 4 y of mark-recapture data. Error bars represent 95% credible intervals, which do not overlap between the sexes.

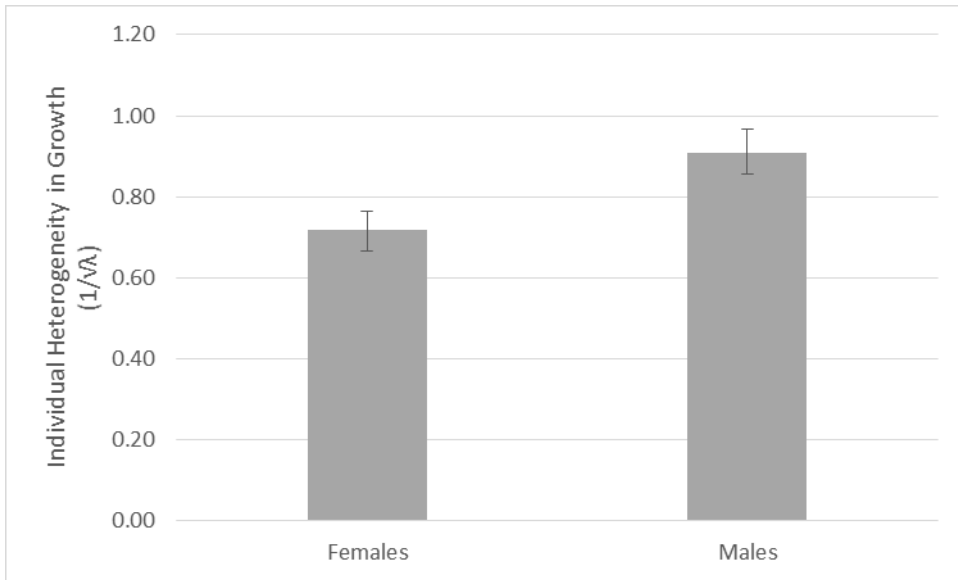


Figure 2.4. Medians of the posterior distributions of individual heterogeneity in growth (estimated as  $1/\sqrt{\lambda}$ ) for female and male Red-backed Salamanders, modeled by a Gamma process von Bertalanffy growth model fitted by repeated measurements from 4 y of mark-recapture data. Error bars represent 95% credible intervals, which do not overlap between the sexes.

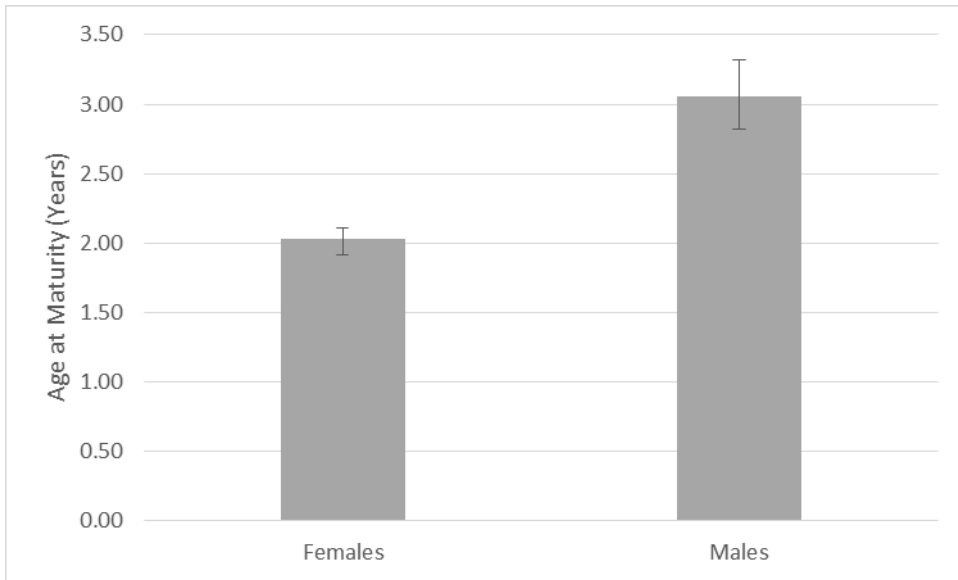


Figure 2.5. Medians of the posterior distributions of mean age at sexual maturity for female and male Red-backed Salamanders, modeled by a Gamma process von Bertalanffy growth model fitted by repeated measurements from 4 y of mark-recapture data. Error bars represent 95% credible intervals, which do not overlap between the sexes.

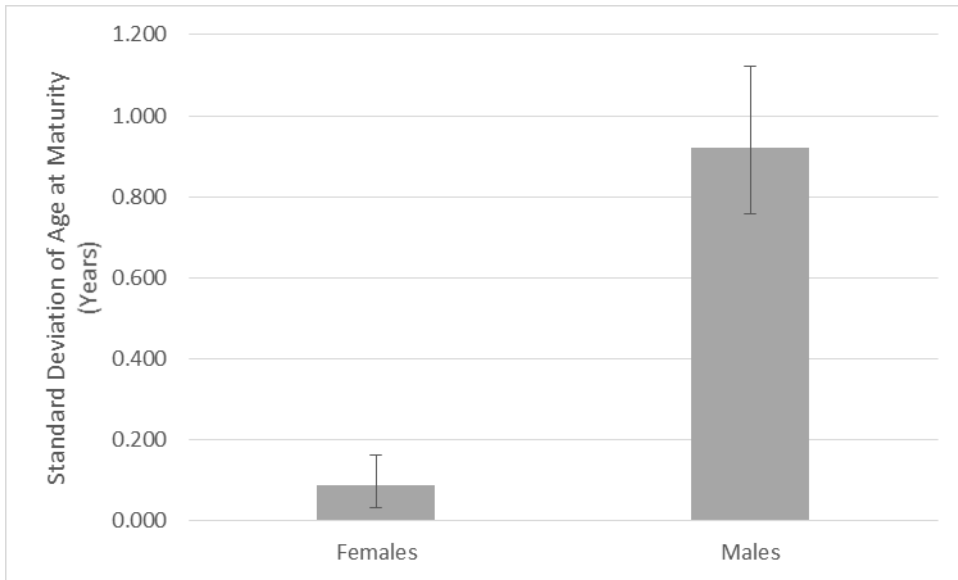


Figure 2.6. Medians of the posterior distributions of standard deviation in age at sexual maturity for female and male Red-backed Salamanders, modeled by a Gamma process von Bertalanffy growth model fitted by repeated measurements from 4 y of mark-recapture data. Error bars represent 95% credible intervals, which do not overlap between the sexes.

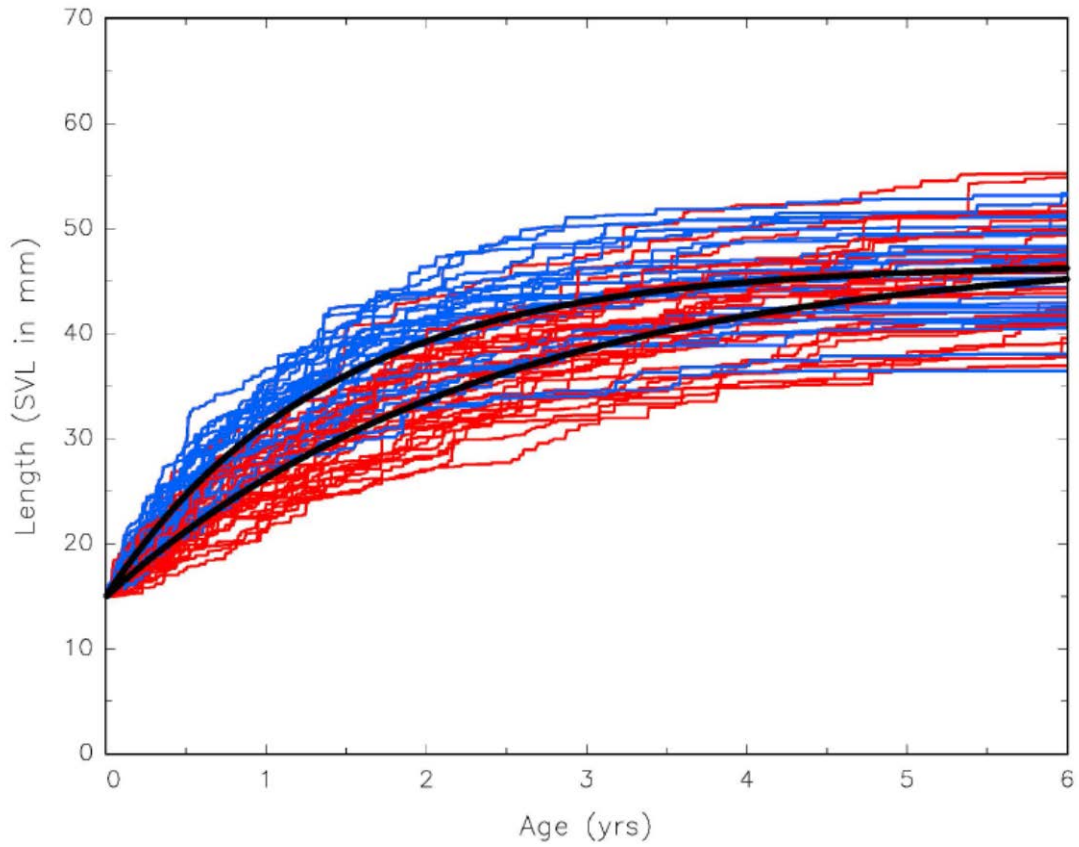


Figure 2.7. Simulated growth curves for 15 male (red lines) and 15 female (blue lines) Red-backed Salamanders, using posterior median values as parameter estimates for Gamma von Bertalanffy growth model. Solid curves are population means for females and males.

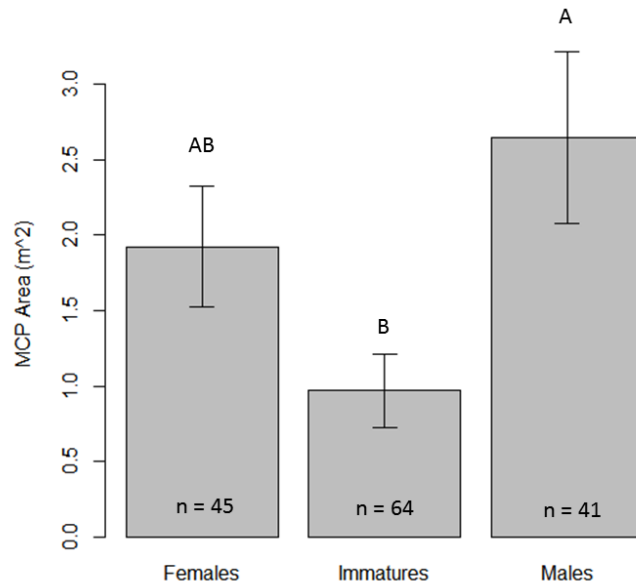


Figure 2.8. Home range areas (minimum convex polygons) of a population of Red-backed Salamanders in Maryland, Fall 2009–Spring 2011. Error bars represent one standard error of the mean. Letters indicate significantly different means (Tukey's HSD test with 95% family-wise confidence level:  $p = 0.007$ ).



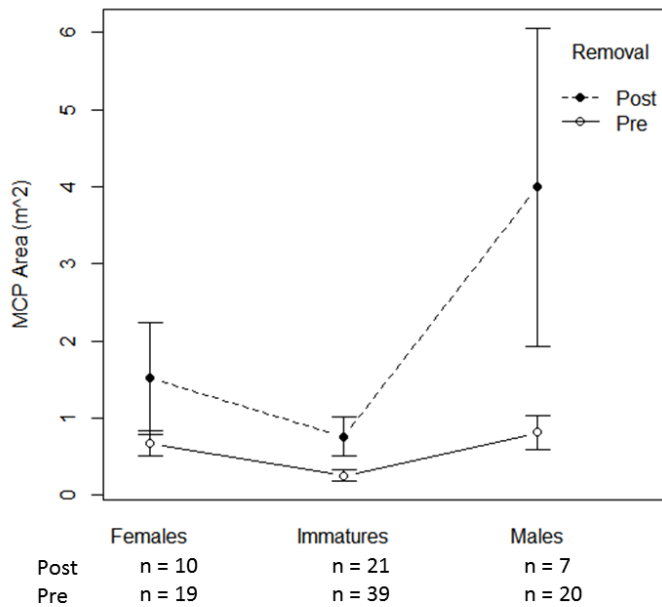


Figure 2.9. Home range areas (minimum convex polygons) of an experimentally manipulated population of Red-backed Salamanders in Maryland, Fall 2011–Spring 2013. Stage and removal were both significant factors, along with a significant interaction between the two. Error bars represent one standard error of the mean.

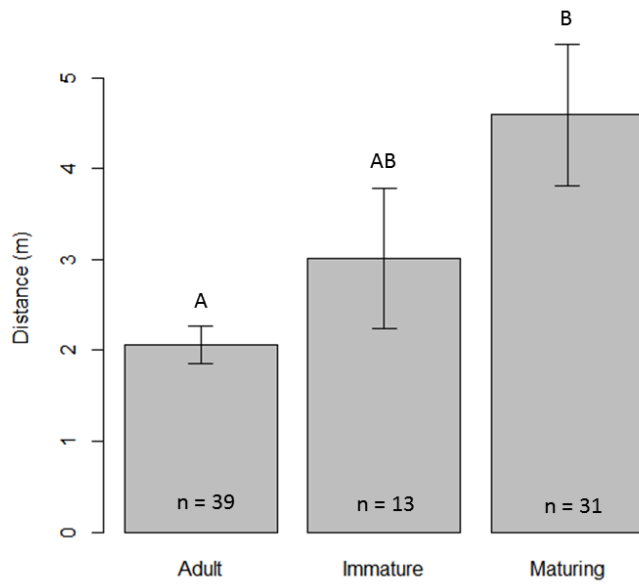


Figure 2.10. Distances moved between successive years by Red-backed Salamanders in Maryland, Fall 2009–Spring 2011. Adults were mature in both years; immatures were immature in both years; and maturing individuals were immature the first year and mature the second year. Error bars represent one standard error of the mean. Letters indicate significantly different means ( $p = 0.002$ ).

Chapter 2 Tables

Table 2.1. Growth and development parameters for Red-backed Salamanders, modeled by a Gamma process von Bertalanffy growth model fitted by repeated measurements from 4 y of mark-recapture data.

Parameter	Mean	SD	Posterior Percentiles		
			2.5%	50%	97.5%
$a$ [Females]	47.63	0.66	46.84	47.62	48.48
$a$ [Males]	50.80	1.16	48.96	50.69	53.22
$k$ [Females]	0.73	0.02	0.69	0.73	0.77
$k$ [Males]	0.34	0.03	0.29	0.34	0.39
$1/\sqrt{\lambda}$ [Females]	0.72	0.03	0.67	0.72	0.77
$1/\sqrt{\lambda}$ [Males]	0.91	0.03	0.85	0.91	0.97
$\mu_G$ [Females]	2.03	0.06	1.91	2.04	2.11
$\mu_G$ [Males]	3.06	0.13	2.82	3.05	3.32
$\sigma_G$ [Females]	0.088	0.040	0.033	0.079	0.163
$\sigma_G$ [Males]	0.921	0.093	0.757	0.915	1.121
$\sigma_\varepsilon$	1.054	0.047	1.016	1.044	1.170

*Notes:* Parameters are  $a$ : asymptotic body size;  $k$ : yearly growth-rate coefficient;  $1/\sqrt{\lambda}$ : estimate of individual heterogeneity in growth;  $\mu_G$ : average age at sexual maturity;  $\sigma_G$ : standard deviation of age at sexual maturity; and  $\sigma_\varepsilon$ : standard deviation of measurement error.

# Chapter 3: Variation in Population Parameters of Red-Backed Salamanders (*Plethodon cinereus*) Due to Season, Sampling Occasion, Sex, and Life Stage

## Abstract

Terrestrial salamanders are major components of ecosystems in eastern North America. One species, the Red-backed Salamander (*Plethodon cinereus*), may be the most abundant vertebrate throughout its range. Red-backed Salamanders are commonly monitored as indicators of ecosystem health and to assess the effects of forest management practices. However, the many studies generating counts of this species do not accurately measure true abundance, hampering interpretation of their results. I compared mark-recapture models using 2,745 records of 752 marked salamanders gathered over a 4-year field study in Maryland; the results indicate that estimates of survival, detection, and abundance of Red-backed Salamanders varied temporally along with the age and sex of the individuals present, both within and among seasons. Encounter probability (reflecting availability and temporary emigration) varied among weekly sampling occasions and was similar for males and females for much of each season, although models with separate parameters for each sex were strongly preferred. Survival was approximately the same over winters and summers and higher than previous experimental estimates, and also differed between the sexes (~ 65% for males vs. ~ 78% for females). The lower inter-seasonal survival of males may be an artifact of sex-biased dispersal: the majority of encountered

immature individuals were estimated to be males, with transience models indicating a pulse of emigration in the fall and an influx of immature males onto the study site in the spring. Studies of terrestrial salamander populations should consider the effect of these behavioral differences between the sexes on estimated abundances.

### Introduction

Terrestrial salamanders play important functional roles in the forested ecosystems of North America (reviewed by Davic and Welsh, 2004), with ecosystem effects that are likely to be highly context-dependent (Hocking and Babbitt, 2014). The ecological impact of terrestrial salamanders is amplified by their abundance: due to low metabolic energy demands (Feder, 1983), terrestrial salamanders may reach tremendous population densities. At Hubbard Brook Experimental Forest in New Hampshire, the biomass of terrestrial salamanders was estimated to be approximately equal to that of small mammals and double that of birds (Burton and Likens, 1975). A recent analysis indicates that this classic study may have underestimated population densities by an order of magnitude, suggesting that terrestrial salamanders are even more important components of their ecosystems than generally believed (Semlitsch et al., 2014).

Despite disagreement about the susceptibility of amphibians to environmental change (Kroll et al., 2009; Kerby et al., 2010), terrestrial salamanders are widely used as indicators of ecosystem health (reviewed by Welsh and Droege, 2001) and the effects of forest management practices (reviewed by Demaynadier and Hunter, 1995). The need to monitor salamander populations has become increasingly important

given population declines at their major centers of diversity—eastern North America (Highton, 2005) and Mesoamerica (Rovito et al., 2009)—and concern that many populations may be susceptible to local extinction as a result of habitat fragmentation (e.g., Ash, 1997; Gibbs, 1998).

The most commonly monitored species of terrestrial salamander in North America is the Red-backed Salamander (*Plethodon cinereus*), a small species found in well-drained deciduous and coniferous forests of the eastern United States and Canada (Petranka, 1998). This species has long been recognized as the most abundant salamander throughout its range (e.g., Cope, 1889), and it is often the most abundant species of amphibian or reptile documented in herpetofaunal surveys in this region (Miller Hesel, 2012). In Burton and Likens' (1975) study at Hubbard Brook, Red-backed Salamanders accounted for 93.5% of the total salamander biomass at the site. Most of the species' current distribution represents post-glacial range expansion (Highton and Webster, 1976), and its ecological dominance may result in part from competitive interactions; Red-backed Salamanders have been shown to exclude other species of terrestrial salamander from preferred habitat and food resources (Jaeger, 1971, 1972).

Due to their commonness, abundance, and broad distribution, there has been a long history of attempts to estimate the abundance of Red-backed Salamanders (e.g., references reviewed in Demaynadier and Hunter, 1995; Welsh and Droege, 2001; Tilghman et al., 2012). Invariably, these estimates use population estimates based on count data. Because counts and other population indices do not adjust for the effect of detection probability, they may not reliably provide accurate estimates of actual

population sizes (Jung et al., 2000). To date, there is no published information on temporal variation in survival and detectability in Red-backed Salamanders, which makes it difficult to draw inference from the extensive literature comparing relative abundances of this species.

Fitting models to mark-recapture data is important both for making parameter estimates and for identifying important biological processes in natural populations (Lebreton et al., 1992). In this paper, I use 2,745 records of 752 marked salamanders monitored over a 4-year field study within a mark-recapture modeling framework to determine whether a variety of population parameters vary by capture occasion or sampling season, and to estimate differences in parameters due to the age and sex of the salamanders. In particular, I use a multistate open robust design, treating immature individuals as state-uncertain, to evaluate survival between seasons, detectability within seasons, and probability of correct assignment to sex. To further evaluate differences in survival and detectability for adults and immatures within seasons, I conduct separate analyses using Cormack-Jolly-Seber open models.

In addition to the above parameters, I also consider the existence of two biological processes with relevance to estimating salamander abundance. Over a century of research on terrestrial salamanders (particularly *P. cinereus*) indicate that large portions of the population may be underground at any given time (e.g., Piersol, 1910; Test and Bingham, 1948; Taub, 1961; Bailey et al., 2004). I implicitly modeled temporary emigration between the surface and underground retreats by allowing encounter probabilities to vary over sampling occasions modeled in the multistate open robust design analysis. The existence of transient individuals, which are caught

once and then permanently emigrate from the study area (Pradel et al., 1997), may also affect mark-recapture parameter estimates. I considered the effect of transience in Cormack-Jolly-Seber open models of each season.

### *Materials and Methods*

#### *Study site and data collection*

This study took place in mature bottomland hardwood forest at Patuxent Wildlife Research Center (PWRC) in Laurel, Maryland (39.054376°N, 76.817206°W), from October 2009–May 2013. During the fall and spring, I conducted weekly searches of three plots of pine coverboards in a 1-m grid and separated from one another by 30–40 m (Fig. 2.1): two 156 m<sup>2</sup> plots with 100 boards each and one 625 m<sup>2</sup> plot with 400 boards. On each capture, I measured snout–vent length, determined sex by candling, marked new individuals with VIE, and returned each individual to its site of capture. Individuals in the removal experiment described in Chapter 2 were explicitly coded as removals in the mark-recapture dataset and were not included in parameter estimates after the occasion of their removal.

For more details, see Chapter 2 above.

#### *Mark-recapture modeling: across-season analysis*

To test for differences in population parameters over time and between the sexes, I conducted mark-recapture analyses using the multistate open robust design with state uncertainty (Kendall et al., 2012). The sampling framework of this model is



based on Pollock's (1982) robust design, which consists of multiple secondary sampling periods within primary periods of interest; in this study, each fall or spring season represented a primary period, with weekly coverboard surveys representing the secondary sampling periods. Refinements to the robust design have allowed for improved estimation of parameters both within and between primary periods (Kendall and Nichols, 1995; Kendall et al., 1995; Kendall et al., 1997).

In contrast to the "classic" robust design described above, the open robust design (Kendall and Bjorkland, 2001; Kendall and Nichols, 2002) does not require the assumption of closure within primary periods (i.e., that there are no births, deaths, immigration, or emigration in the population); relaxing these assumptions allows for changes in population size due to mortality or transient individuals moving in and out of the study site during primary periods. Because the salamanders in this study could not be sexed before they reached maturity, I treated sex as an uncertain state (Kendall et al., 2004; Kendall et al., 2012).

For this analysis, I considered the models presented in Table 3.1; multiplicative models include both stated factors along with a term for their interaction. Here I briefly describe the rationale for model choice. Each salamander on each capture exists in one of two states, female or male. Adults by definition are of known sex and are coded as "F" or "M"; immature individuals by definition are of uncertain sex and are coded as "u." Survival from one season to the next occurs with probability  $S$ ; I compared models in which  $S$  varied as a function of the following factors: 1) constant (no difference between sexes or seasons); 2) sex; 3) seasonal interval (fall–spring or spring–fall); 4) sex + season; or 5) sex \* season.

Within each season, individuals enter the study area with probability  $p_{ent}$ , remain there between weekly sampling occasions with probability  $\phi$ , and are encountered with probability  $p$ . In order to reduce computation time and the number of possible candidate models, I eliminated explicit within-season temporary emigration by fixing  $p_{ent}$  to 1 for the first sampling occasion of each season and to 0 for the following occasions and then fixing  $\phi$  to 1 for all possible occasions.

Modeled in this way, all individuals captured on a plot within a season are considered to be present from the first sampling occasion onward and to remain there for the subsequent sampling occasions. Temporary emigration, should it occur, is then reflected in the apparent encounter probability  $p$ . Apparent encounter probability is actually the product of two parameters: availability and true encounter probability. Due to the use of coverboards for sampling, true encounter probability ( $p^*$ ) in this study is expected to approximately equal 1; given that a salamander survived, remained on the plot, and was available for capture (i.e., present under the board), it was always detected.

With  $p^* = 1$ , the parameter  $p$  then represents availability; I compared models with the  $p$  parameterized as a function of the following functions: 1) constant (no difference between sexes, occasions, or seasons); 2) sex; 3) weekly sampling occasion; 4) fall or spring season; 5) sex + occasion; 6) sex + season; 7) sex \* occasion; or 8) sex \* season. I explicitly modeled temporary emigration in within-season models, described below. For the models in which  $p$  varied by sampling occasion, the parameters were allowed to differ among the weekly sampling occasions but constrained to be the same across seasons.

Three additional parameters in the multistate open robust design relate to state uncertainty. The probability of correctly identifying the state of an encountered animal, given its true state, is estimated as  $\delta$ ; I considered models in which this probability varied as a function of the following factors: 1) constant (no difference between sexes or seasons); 2) sex; 3) fall or spring season; 4) sex + season; or 5) sex \* season. Sexing adult males and females by visualization of testes and ova was unambiguous, so this parameter indicates knowledge about immature individuals that could not be assigned to a sex.

Two mixtures relating to these uncertain individuals are estimable for each primary period: the proportion of individuals released in a given state ( $\pi$ , a nuisance parameter) and the proportion of the population in that state ( $\omega$ , the parameter of interest). Transition between states occurs with probability  $\psi$ ; transition from one sex to the other is biologically impossible in this system, and this parameter was fixed to 0 in all models. Population sizes for each state at each primary sampling period were estimated as derived parameters, not explicitly modeled in the likelihood.

A balanced design, equally representing each level of each parameter under consideration, resulted in 200 candidate models. Due to the generality of the multistate open robust modeling framework, this candidate model set represents a small fraction of the number of models that would be possible by allowing  $S$ ,  $pent$ ,  $\phi$ ,  $p$ ,  $\delta$ ,  $\pi$ , and  $\omega$  to vary in all possible combinations over all 8 primary periods, 7 intervals between primary periods, and 70 total secondary periods of this study.

*Mark-recapture modeling: within-season analysis*

In order to test for differences between immatures and adults within seasons and to consider the importance of transience, I conducted separate analyses within each primary period using the Cormack-Jolly-Seber open model (Cormack, 1964; Jolly, 1965; Seber, 1965). I treated immatures and adults as separate groups and considered 16 candidate models, allowing  $\phi$  (apparent survival probability between successive weekly sampling occasions) and  $p$  (apparent encounter probability during each sampling occasion) each to vary according to the following factors: 1) constant (no difference between groups or occasions); 2) group; 3) sampling occasion; or 4) group \* occasion.

The presence of transients (individuals that are captured only once and then permanently emigrate from the study site) results in negatively biased survival estimates; when newly marked individuals are released, the transients will emigrate and appear “dead” in the model. To account for this possibility, I modified the top model in each season ( $\Delta AIC_C = 0$ ) by adding time-since-marking structure to the  $\phi$  parameters: survival was then estimated separately for the newly marked individuals on each sampling occasion (potentially a mixture of residents and transients) and the recaptured individuals that had been marked on previous occasions (who by virtue of being recaptured are by definition not transients). In the presence of transients, this parameterization would become the new top model; otherwise, the cost of the additional parameters would decrease support for the modified model.

I constructed models and conducted model selection using AIC (Akaike, 1973) in Program MARK (White and Burnham, 1999), using the package “RMark”

(Laake and Rexstad, 2008) in R (R Core Team, 2014) to set up the multistate models. I conducted goodness-of-fit tests for the CJS models in Program RELEASE (Burnham et al., 1987), which produces two chi-square tests for violation of mark-recapture assumptions; there is no goodness-of-fit test available for the multistate open robust design.

### Results

Sample sizes for each of the primary sampling periods are reported in Table 3.2, including numbers of secondary sampling occasions, numbers of marked individuals, total captures, and tests for deviation from a 1:1 sex ratio. I captured 752 salamanders (163 females, 158 males, and 431 immatures) a total of 2,745 times over 70 weekly sampling periods in 8 spring and fall seasons of 4 years. The sex ratio of captured individuals did not differ from 1:1 in any season or in the overall sample.

In the multistate open robust across-season analysis, all model weight was concentrated in the top nine models (Table 3.3). Three models were within  $\Delta\text{AIC}_C \leq 2$  of the top model, indicating substantial support (Burnham and Anderson, 2004). These four models, representing 82% of the model weight, show strong temporal differences and effects of sex (model-averaged parameter estimates reported in Table 3.4).

Survival between seasons,  $S$ , was slightly higher for females than males and approximately equal over winter and summer periods for both sexes (Fig 3.1). Apparent encounter probability  $p$  varied for both sexes across each weekly sampling occasion (Fig. 3.2). Probability of correct sex classification  $\delta$  was higher for females

than for males, and lower for males in the spring than in the fall (Fig 3.3). Estimated numbers of males were higher than numbers of females in every season of the study (Fig 3.4).

Top season-specific CJS models are reported in Table 3.5, including all models within  $\Delta AIC_C \leq 2$  of the top model for each season. Simpler models tended to be preferred in seasons with relatively sparse data (Fall 2009, Spring 2010, and Spring 2013; Table 3.2); for other seasons, apparent encounter probability  $p$  varied across sampling occasions, and apparent survival  $\phi$  differed for adults and immatures.

Two seasons (Fall 2011 and Fall 2012) showed a strong effect of transience; in those seasons, the addition of time-since-marking structure to the top model increased model weight substantially (to 0.869 and 0.999, respectively) and made each the sole top model. In four other seasons, the TSM-modified model remained within  $\Delta AIC_C \leq 2$  of the top model but did not replace it (Spring 2010, Fall 2010, Spring 2012, and Spring 2013).

Model-averaged parameter estimates for each season are reported in Appendices 3.1–3.8. Standard errors and confidence intervals are large for many estimates due to data sparseness, but when estimates of apparent survival differ, they are usually higher for adults than for immatures. Goodness-of-fit of the most general (time-dependent) CJS model was rejected for only one test of one group: immatures showed some evidence of heterogeneity in apparent encounter probability on two sampling occasions in Spring 2012 (Appendix 3.9). This effect of this heterogeneity was apparently minimal; although homogeneity in apparent encounter probability

between immatures and adults was rejected in the goodness-of-fit test, an age effect did not appear in the top models for that season (Table 3.5).

### Discussion

The results of this study indicate that estimates of encounter probabilities, survival, and abundance of Red-backed Salamanders (*Plethodon cinereus*) varied both within and among the 8 spring and fall seasons of a 4-y field study, with many parameters differing between the sexes or between mature and immature individuals. The top four across-season multistate open robust models had strong support from  $\Delta AIC_C$  values and represented 82% of the total model weight.

#### *Encounter probability within seasons*

In all four top models, apparent encounter probability  $p$  differed by both sex and weekly sampling occasion. Apparent encounter probability is the product of availability for capture and true encounter probability given that the animal is available. In this study, true encounter probability was approximately equal to 1—given that a salamander was alive and available for capture by being on the surface under the coverboard, it was always detected.

Therefore, the apparent encounter probability  $p$  estimated in this study largely reflect availability; i.e., some salamanders temporarily emigrated from the study site: they were alive but not available for capture and thus not detected. Previous work (Bailey et al., 2004) has shown that temporary emigration from the surface is an

important process in populations of terrestrial salamanders, but differences between the sexes have not been previously shown. In this study, models with a shared encounter parameter for males and females received no support; however, encounter probability was not consistently higher for one sex than the other (Fig 3.2). Future studies should pursue the behavioral or ecological factors that lead male and female terrestrial salamanders to differ in their availability for capture.

#### *Survival probability between seasons*

In the top four across-season models, survival between successive seasons  $S$  showed a strong difference between the sexes; the top two models also featured an additive seasonal effect. Survival for both sexes appears to be slightly lower over the summer than over the winter, although not significantly so (Fig 3.1). At the study site in Laurel, Maryland, the summer inactive period is on average slightly longer than the winter inactive period (late May to late September vs. late November to late February), which may explain the slight dip in estimated survival over the summer.

Previous field experiments with artificial underground cages have suggested high mortality levels for overwintering Red-backed Salamanders—e.g., 57% mortality (Vernberg, 1953) or 50–100% mortality (Taub, 1961). Relatively high overwinter survival rates in this study are consistent with opportunistic observations of Red-backed Salamanders continuing to feed on invertebrates up to 1 m below the surface during the winter (Caldwell and Jones, 1973; Caldwell, 1975), suggesting that the experimental cages in previous studies led to abnormally high mortality.



In mark-recapture studies, permanent emigration is indistinguishable from death; due to either cause, attrition between seasons is apparently greater for male than for female Red-backed Salamanders (~ 65% survival vs. ~ 78%) in this study.

*Sex differences in state-uncertainty parameters and emigration*

A comparison of sex ratios throughout this study suggests that the lower estimated survival of males may be due to emigration from the study site; in no season was the sex ratio of captured individuals significantly different from 1:1, and the total numbers of males and females captured and marked over the course of the study also did not deviate from 1:1 (Table 3.2). Other published accounts also indicate a 1:1 sex ratio of adults (e.g., Burger, 1935), although summer surveys often fail to encounter many females, who are likely ensconced in nest chambers with their recently laid clutches (e.g., Test, 1955).

Modeling sex as an uncertain state with robust-design mark-recapture data allowed the proportion of individuals of each sex in the population ( $\omega$ ) to be estimated. That estimate (Table 3.4) suggest that females represent only 24% of the overall population (Fig. 3.4). Because adult males and females were sexed unambiguously in this study, state uncertainty applies entirely to the unsexed immature individuals. These results indicate that the majority of those 431 immatures, whose sex was never determined over the course of the study, were males.

This abundance of immature males helps explain the difference between the sexes in  $\delta$ , the probability of correct assignment to state (Table 3.4; Fig. 3.3). The majority of males encountered in the study were immature and never recaptured as

mature adults; the probability of being able to (eventually) correctly classify an immature individual as male varied from ~ 40% in the fall to only ~ 25% in the spring, apparently reflecting an influx of immature males in the spring that would not be encountered again the following fall. In support of this interpretation, season-specific models showed a strong effect of transience in two fall seasons, with a smaller effect in three spring seasons and an additional fall. In addition, most seasons had a top models with an age effect for apparent survival (Table 3.5), which was consistently higher for adults (Appendices 3.1–3.8), consistent with greater emigration by immatures.

Estimates of the numbers of males in this study were significantly higher than estimates of the numbers of females (Fig. 3.4); although a greater number of immature males than immature females may have been encountered over the course of the study, this result seems to be due to different patterns of movement between the sexes rather than different underlying sex ratios (Table 3.2). Notably, the survey plots in this study (156–625 m<sup>2</sup>) were substantially larger than those commonly used in field studies of Red-backed Salamanders—e.g., 9 m<sup>2</sup> (Mathis, 1991); 15, 20 or 35 m<sup>2</sup> (Jung et al., 2000). With a greater chance for emigrating individuals to leave the study site, smaller plots would be expected to lead to negatively biased estimates of juvenile and/or male survival.

Although they are commonly regarded as having small home ranges and making only short-distance movements (e.g., Welsh and Droege, 2001; Wells, 2007), a few studies have suggested that Red-backed Salamanders are not only capable of long-distance exploratory movements (Heatwole, 1962), but may regularly undertake

them (Marsh et al., 2004). The results of this study indicate that dispersal in this species may be predominantly undertaken by immature males. Future studies should explicitly test for this possibility.

Finally, given concern over the impact of forest management practices on salamander abundances (e.g., Demaynadier and Hunter, 1995; Ash, 1997; Messere and Ducey, 1998; Brooks, 1999; Morneault et al., 2004; Homyack and Haas, 2009) and the potential of terrestrial salamanders to affect ecosystem dynamics such as carbon sequestration (e.g., Wyman, 1998; Best and Welsh, 2014), future studies should carefully consider the effects of temporal variation and sex and age-specific differences when estimating population parameters of terrestrial salamanders—particularly the widely studied Red-backed Salamander, perhaps the most abundant vertebrate in eastern North America.

*Chapter 3 Figures*

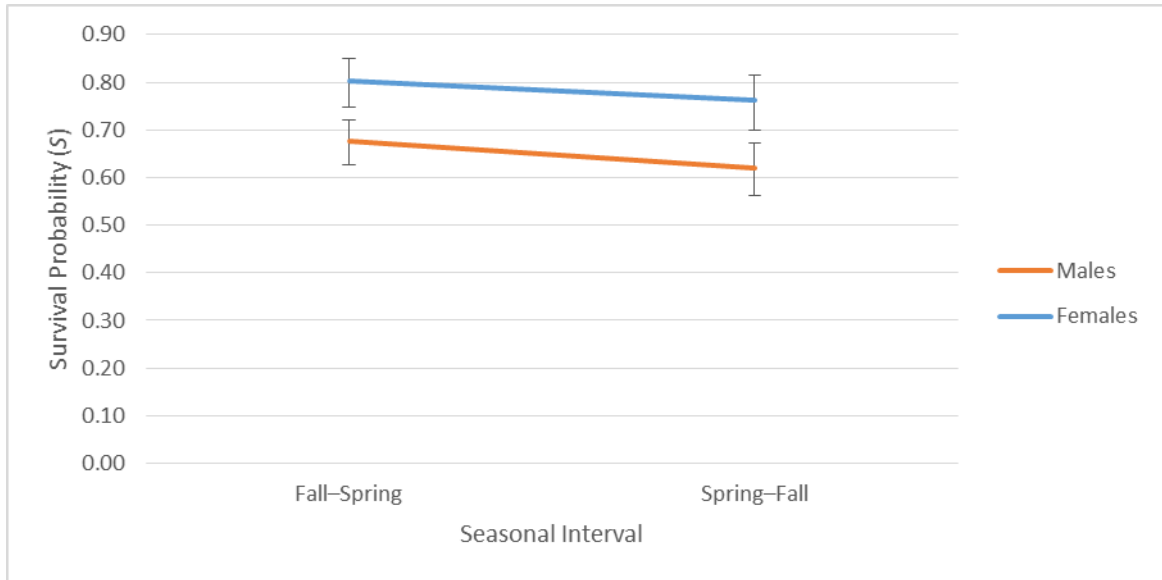


Figure 3.1. Survival probability ( $S$ ) of Red-backed Salamanders in Maryland 2009–2013 varying by sex and between two possible seasonal intervals: winter (Fall–Spring) and summer (Spring–Fall). Error bars represent 95% confidence intervals.

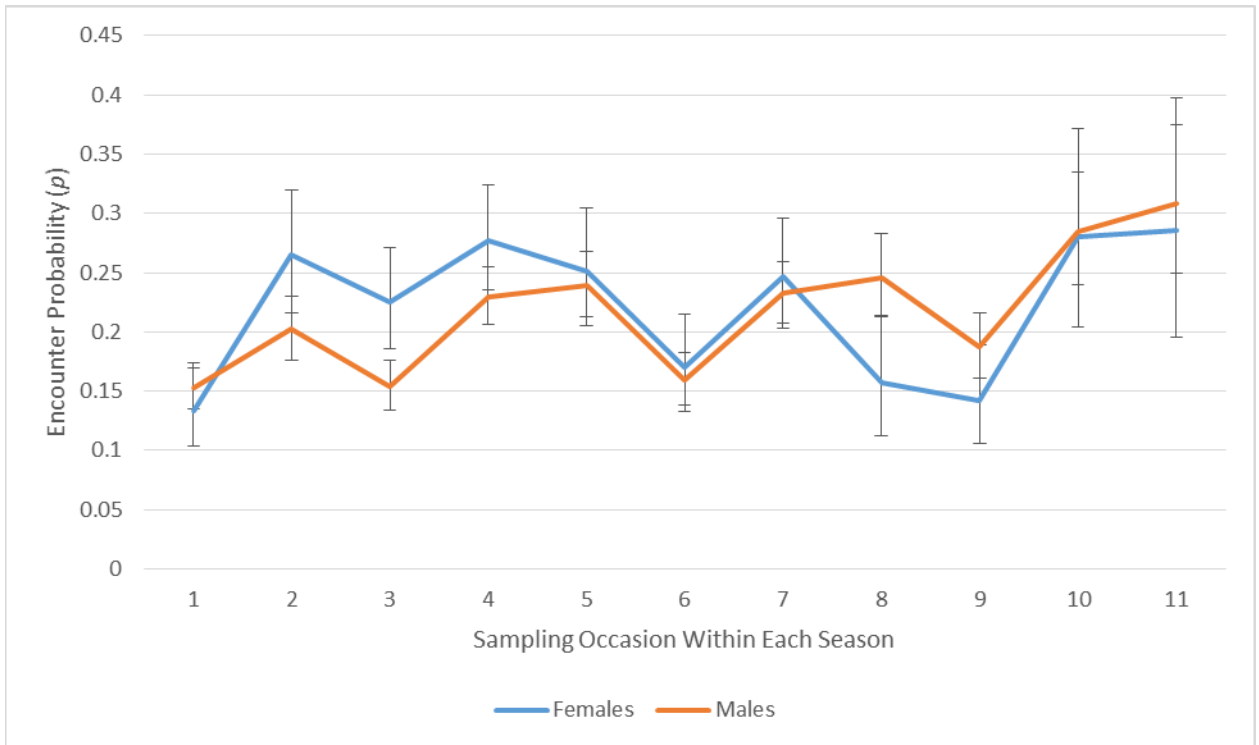


Figure 3.2. Encounter probability ( $p$ ) of Red-backed Salamanders in Maryland varying by sex and across the weekly sampling occasions within eight spring or fall sampling seasons, 2009–2013. Error bars represent 95% confidence intervals.

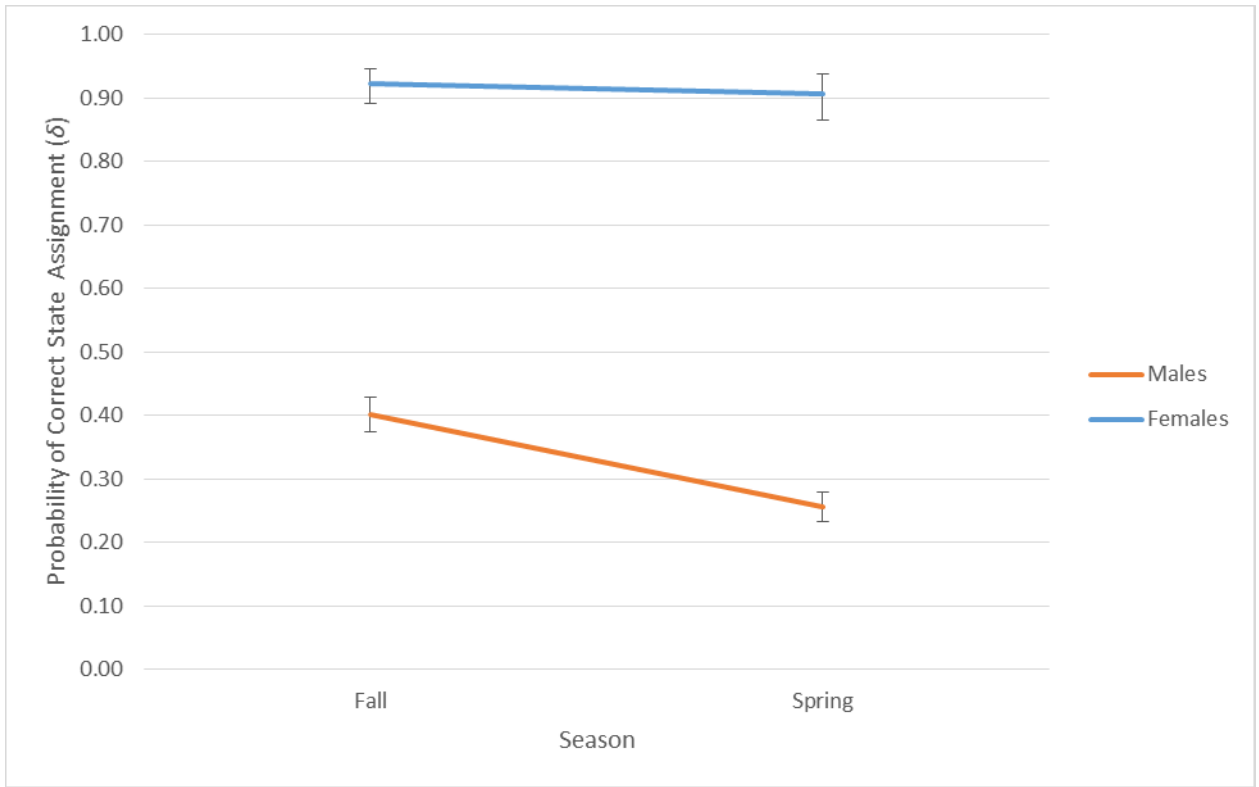


Figure 3.3. Probability of correct state (sex) assignment ( $\delta$ ) of Red-backed Salamanders in Maryland varying by sex and sampling season, 2009–2013. Error bars represent 95% confidence intervals.

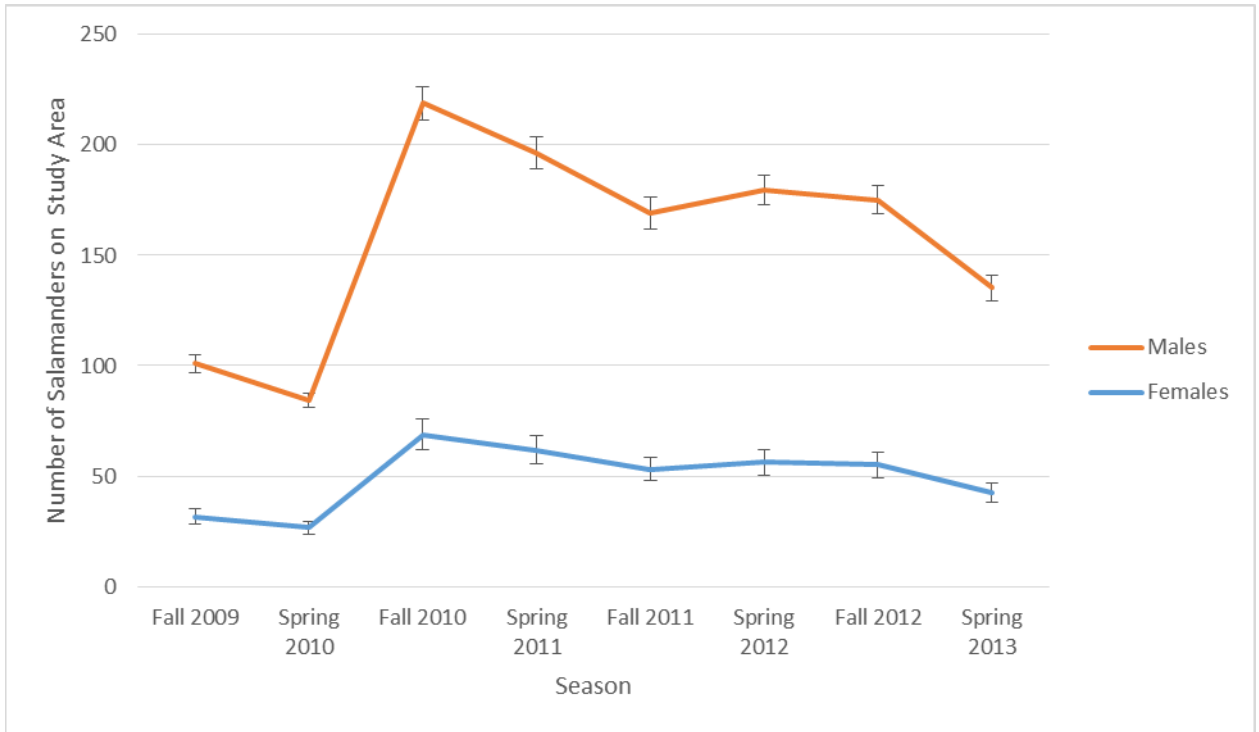


Figure 3.4. Derived population estimates for male and female Red-backed Salamanders in Maryland across eight sampling seasons. Error bars represent 95% confidence intervals.

Chapter 3 Tables

Table 3.1. Candidate parameterizations for multistate open robust design models with state uncertainty, modeling population parameters of Red-backed Salamanders over 4 years.

<i>S</i>	<i>pent</i>	$\phi$	<i>p</i>	$\delta$	$\pi$	$\omega$	$\psi$
(.)	(.)	(.)	(.)	(.)	(.)	(.)	(.)
sex			sex	sex			
season			occasion	season			
sex + season			season	sex + season			
sex * season			sex + occasion	sex * season			
			sex + season				
			sex * occasion				
			sex * season				

*Notes:* *S* is the probability of survival between successive fall and spring primary sampling periods of the study; *pent* and  $\phi$  respectively represent the probability of entering the study site and remaining there within a primary period; *p* is the probability that an individual in the study area is detected during a weekly secondary sampling period;  $\delta$  is the probability of correctly identifying the sex of an encountered animal;  $\pi$  is the proportion of the population released as a given sex;  $\omega$  is the proportion of that sex in the population; and  $\psi$  represents the probability of transition between the sexes (biologically impossible and fixed to 0 for all models). Parameters were allowed to vary by sex (female or male, with immature individuals treated as being state-uncertain), season (fall or spring sampling period), or occasion (weekly sampling period within a season); dot models (.) are constant. See text for more details.



Table 3.2. Number of weekly secondary sampling periods, captured individual Red-backed Salamanders, total captures, and chi-square tests evaluating deviation from a sex ratio of 1:1 for each primary period (season) in the study.

Primary Period	Secondary Periods	Sample Size (Number of Salamanders Captured)				Total Captures	Sex Ratio $\neq$ 1:1
		Females	Males	Immat.	Total		
Fall 2009	8	31	28	50	109	142	$\chi^2 = 0.153$ , df = 1, p = 0.6961
Spring 2010	9	27	32	36	95	110	$\chi^2 = 0.424$ , df = 1, p = 0.5151
Fall 2010	11	82	79	106	267	635	$\chi^2 = 0.056$ , df = 1, p = 0.8131
Spring 2011	9	71	74	75	220	551	$\chi^2 = 0.062$ , df = 1, p = 0.8033
Fall 2011	7	58	56	55	169	304	$\chi^2 = 0.035$ , df = 1, p = 0.8514
Spring 2012	9	61	55	84	200	431	$\chi^2 = 0.310$ , df = 1, p = 0.5775
Fall 2012	10	53	54	98	205	357	$\chi^2 = 0.009$ , df = 1, p = 0.9230
Spring 2013	7	17	16	102	135	215	$\chi^2 = 0.030$ , df = 1, p = 0.8618
Totals	70	163	158	431	752	2,745	$\chi^2 = 0.078$ , df = 1, p = 0.7802

*Notes:* The total numbers of marked individuals (bottom row) are smaller than the sums of each season's sample sizes because some individuals were caught in multiple seasons.

Table 3.3. Top models for multistate open robust analysis of Red-backed Salamanders in Maryland, depicting sex differences and temporal variation among 70 weekly sampling occasions and 8 sampling seasons (fall and spring seasons over four years, October 2009–May 2013).

<i>S</i>	Model		AICc	$\Delta$ AICc	<i>w</i>	<i>K</i>	Deviance
	<i>p</i>	$\delta$					
sex + season	sex * occasion	sex * season	18627.18	0.000	0.230	31	18564.44
sex + season	sex * occasion	sex + season	18627.34	0.161	0.212	30	18566.65
sex	sex * occasion	sex * season	18627.49	0.312	0.197	30	18566.80
sex	sex * occasion	sex + season	18627.65	0.472	0.182	29	18569.00
sex * season	sex * occasion	sex * season	18629.18	2.008	0.084	32	18564.40
sex * season	sex * occasion	sex + season	18629.33	2.155	0.078	31	18566.60
sex + season	occasion	sex + season	18634.41	7.229	0.006	19	18596.12
sex	occasion	sex + season	18634.72	7.545	0.005	18	18598.47
sex + season	sex + occasion	sex * season	18634.91	7.734	0.005	21	18592.57

Notes: *S* is survival between successive seasons; *p* is detection probability for the weekly sampling occasions;  $\delta$  is the probability of correctly classifying the sex of an individual. Other parameters (*pent*,  $\phi$ ,  $\pi$ ,  $\omega$ , and  $\psi$ ) were constant for all models. AICc is Akaike’s Information Criterion corrected for finite sample sizes;  $\Delta$ AICc is the difference in AICc from the top model; *w* is the AICc model weight; *K* is the number of estimated parameters in the model; Deviance is  $-2\ln(L)$ .

Table 3.4. Model-averaged parameter estimates from multistate open robust design analysis with state uncertainty, describing population parameters for Red-backed Salamanders.

Parameter	Interpretation	Estimate	SE	95% CI	
				Lower	Upper
<i>S</i> (F) 1	Survival Fall–Spring (Females)	0.80	0.03	0.75	0.85
<i>S</i> (F) 2	Survival Spring–Fall (Females)	0.76	0.03	0.70	0.81
<i>S</i> (M) 1	Survival Fall–Spring (Males)	0.68	0.02	0.63	0.72
<i>S</i> (M) 2	Survival Spring–Fall (Males)	0.62	0.03	0.56	0.67
<i>p</i> (F) 1	Detection on 1st occasion of each season (Females)	0.13	0.02	0.10	0.17
<i>p</i> (F) 2	Detection on 2nd occasion of each season (Females)	0.26	0.03	0.22	0.32
<i>p</i> (F) 3	Detection on 3rd occasion of each season (Females)	0.23	0.02	0.19	0.27
<i>p</i> (F) 4	Detection on 4th occasion of each season (Females)	0.28	0.02	0.24	0.32
<i>p</i> (F) 5	Detection on 5th occasion of each season (Females)	0.25	0.03	0.20	0.31
<i>p</i> (F) 6	Detection on 6th occasion of each season (Females)	0.17	0.02	0.13	0.22
<i>p</i> (F) 7	Detection on 7th occasion of each season (Females)	0.25	0.02	0.20	0.30
<i>p</i> (F) 8	Detection on 8th occasion of each season (Females)	0.16	0.03	0.11	0.21
<i>p</i> (F) 9	Detection on 9th occasion of each season (Females)	0.14	0.02	0.11	0.19
<i>p</i> (F) 10	Detection on 10th occasion of each season (Females)	0.28	0.04	0.20	0.37
<i>p</i> (F) 11	Detection on 11th occasion of each season (Females)	0.29	0.05	0.20	0.40
<i>p</i> (M) 1	Detection on 1st occasion of each season (Males)	0.15	0.01	0.13	0.17
<i>p</i> (M) 2	Detection on 2nd occasion of each season (Males)	0.20	0.01	0.18	0.23
<i>p</i> (M) 3	Detection on 3rd occasion of each season (Males)	0.15	0.01	0.13	0.18
<i>p</i> (M) 4	Detection on 4th occasion of each season (Males)	0.23	0.01	0.21	0.26
<i>p</i> (M) 5	Detection on 5th occasion of each season (Males)	0.24	0.01	0.21	0.27
<i>p</i> (M) 6	Detection on 6th occasion of each season (Males)	0.16	0.01	0.14	0.18

$p$ (M) 7	Detection on 7th occasion of each season (Males)	0.23	0.01	0.21	0.26
$p$ (M) 8	Detection on 8th occasion of each season (Males)	0.25	0.02	0.21	0.28
$p$ (M) 9	Detection on 9th occasion of each season (Males)	0.19	0.01	0.16	0.22
$p$ (M) 10	Detection on 10th occasion of each season (Males)	0.28	0.02	0.24	0.33
$p$ (M) 11	Detection on 11th occasion of each season (Males)	0.31	0.03	0.25	0.37
$\delta$ (F) 1	Correct Classification in Fall (Females)	0.92	0.01	0.89	0.95
$\delta$ (F) 2	Correct classification in Spring (Females)	0.91	0.02	0.86	0.94
$\delta$ (M) 1	Correct classification Fall (Males)	0.40	0.01	0.37	0.43
$\delta$ (M) 2	Correct classification Spring (Males)	0.26	0.01	0.23	0.28
$\pi$	Proportion of individuals released as F each season	0.13	0.02	0.09	0.18
$\omega$	Proportion of F in population each season	0.24	0.01	0.22	0.26

Table 3.5. Top models for Cormack-Jolly-Seber open analysis of Red-backed Salamanders in Maryland over eight sampling seasons, depicting differences between immatures and adults (age) and temporal variation among weekly sampling occasions (occasion).

Season	Model		AICc	$\Delta$ AICc	<i>w</i>	<i>K</i>	Deviance
	$\phi$	$p$					
Fall 2009	age	(.)	143.7586	0.0000	0.6100	3	137.5808
Spring 2010	(.)	(.)	94.1763	0.0000	0.3450	2	90.0597
	(.)	age	95.6354	1.4591	0.1663	3	89.4001
	age	(.)	96.0532	1.8769	0.1350	3	89.8180
	TSM	(.)	96.0920	1.9157	0.1324	3	89.8567
Fall 2010	age	occasion	1261.5511	0.0000	0.5803	11	1239.0558
	age * TSM	occasion	1262.5264	0.9753	0.3563	13	1235.8409
Spring 2011	occasion	(.)	1178.9072	0.0000	0.6639	9	1160.5682
Fall 2011	age * TSM	occasion	483.5602	0.0000	0.8691	10	462.5273
Spring 2012	age	occasion	950.3022	0.0000	0.5232	10	929.7453
	age * TSM	occasion	951.3445	1.0423	0.3107	12	926.5506
Fall 2012	age * TSM	occasion	586.2777	0.0000	0.9989	13	559.0225
Spring 2013	(.)	(.)	439.9190	0.0000	0.36584	2	435.8590
	(.)	age	441.1190	1.2000	0.20077	3	434.9984
	TSM	(.)	441.1474	1.2284	0.19794	3	435.0268

*Notes:* TSM represents time-since-marking structure, reflecting the existence of transience (see text for details). Dot models (.) are constant. All models within  $\Delta\text{AIC}_c \leq 2$  of the top model are listed for each season:  $\phi$  is apparent survival between successive weekly sampling occasions;  $p$  is apparent detection probability for each occasions. AICc is Akaike's Information Criterion corrected for finite sample sizes;  $\Delta\text{AIC}_c$  is the difference in AICc from the top model;  $w$  is the AICc model weight;  $K$  is the number of estimated parameters in the model; Deviance is  $-2\ln(L)$ .

## Chapter 4: Male-Biased Dispersal in a Terrestrial Amphibian (*Plethodon cinereus*): Kin Competition & Inbreeding Avoidance

### Abstract

Sex-biased dispersal has been widely observed in many species of birds and mammals, but little is known about patterns of dispersal in other taxa. Associations among kin are expected to play a role in dispersal, and genetic methods have recently allowed the detection of fine-scale population structure. Here I use spatial data from 2,745 records of 752 individually marked Red-backed Salamanders in a Maryland population to compare movement distances by females and males before maturity; in addition, I conduct tests for sex-biased dispersal and spatial genetic structure using six microsatellite loci. Relatively few salamanders were repeatedly captured as both immatures and adults, but of those, males moved significantly farther before maturity (3.80 m) than females did (2.36 m); an  $F_{ST}$  randomization test likewise detected a significant male bias in dispersal. Spatial genetic analyses detected clustering of female-immature pairs with significantly positive kinship at distances of 2–4 m in the fall but not in the spring; a negative relationship between kinship and geographic distance for immatures was likewise significant in the fall and only marginally so in the spring. Significant but low estimates of inbreeding coefficients in the spring may reflect a Wahlund effect of sampling immigrants. These results suggest a role for both inbreeding avoidance and kin competition in leading to male-biased dispersal at fine spatial scales in this terrestrial ectothermic vertebrate.

## Introduction

Dispersal is a fundamental topic in ecology and evolutionary biology, interconnected with diverse processes including population dynamics, species distributions, community structure, and the evolution of life-history traits (Dieckmann et al., 1999). The causes and consequences of dispersal have also recently drawn attention for their role in management and conservation concerns such as habitat fragmentation, climate change, and the effects of invasive species (Bowler and Benton, 2005; Cote et al., 2007; Ronce, 2007). Because the concept of dispersal incorporates multiple related processes, the definition of terms has been a source of confusion in the literature (Bowler and Benton, 2005).

Dispersal may be categorized according to the age and life history stage of the dispersing individual (natal and breeding dispersal) or by whether dispersal results in reproductive success, i.e., gross and effective dispersal (Greenwood, 1980) or ecological and genetic dispersal (Johnson and Gaines, 1990). In addressing natal dispersal, I will use the definition of Howard (1960: 152): “Dispersal of an individual vertebrate is the movement the animal makes from its point of origin to the place where it reproduces or would have reproduced if it had survived and found a mate.”

Extensive empirical studies of dispersal in the 20<sup>th</sup> century (Waser and Jones, 1983) revealed a tendency in many species for one sex to disperse greater distances or at a greater rate than the other sex. Which sex disperses and which remains philopatric varies taxonomically, with female-biased dispersal in most birds and male-biased dispersal in most mammals (Greenwood, 1980). Greenwood related patterns of sex-biased dispersal in birds and mammals to their mating systems (Emlen



and Oring, 1977) and the differential costs and benefits that philopatry and dispersal provided to each sex. In this framework, a resource-defense mating system (in which one sex defends resources to attract the opposite sex) favors monogamy, philopatry of the resource-defending sex, and greater dispersal by the attracted sex; by contrast, a mate-defense mating system (in which one sex controls access to members of the limiting sex) favors polygamy, philopatry of the limiting sex, and greater dispersal by the limited sex.

Subsequent to Greenwood's seminal paper, multiple reviews have addressed how dispersal may be affected by competition for mates (Dobson, 1982), factors leading to philopatry (Waser and Jones, 1983), inbreeding avoidance (Pusey, 1987), optimal dispersal rates (Johnson and Gaines, 1990), taxonomy (Clarke et al., 1997), and social systems (Lawson Handley and Perrin, 2007; Clutton-Brock and Lukas, 2012). However, each of these reviews focused exclusively on birds or mammals, despite repeated calls—beginning with Greenwood (1980)—for data from additional taxa.

In marked contrast to the extensive empirical data available for endotherms, patterns of sex-biased dispersal have only recently been investigated in amphibians. Overall, these studies have not yielded a consistent pattern. Mark-recapture studies showed no sex differences in dispersal in populations of the Wood Frog *Rana sylvatica* (Berven and Grudzien, 1990), Columbia Spotted Frog *Rana luteiventris* (Pilliod et al., 2002), or Fowler's Toad *Bufo fowleri* (Smith and Green, 2006), while male-biased dispersal was suggested for the Alpine Newt *Triturus alpestris* (Joly and Grolet, 1996).

Genetic tests of sex-biased dispersal in amphibians have also yielded mixed results. Dispersal was shown to be female-biased in the Bullfrog (*Rana catesbeiana*), as predicted based on mating benefits to philopatric, territorial males (Austin et al., 2003). The Common Frog, *Rana temporaria* (Palo et al., 2004) also exhibited genetic patterns of female-biased dispersal, although no *a priori* hypothesis was proposed for this species. Lampert et al. (2003) predicted male-biased dispersal in the Túngara Frog (*Physalaemus pustulosus*) due to its mammal-like polygynous mating system; they found tentative support from genetic data. By contrast to the above studies, no genetic signature of sex-biased dispersal was found in studies of the Cascades Frog, *Rana cascadae* (Monsen and Blouin, 2003) or the Moor Frog, *Rana arvalis* (Knopp and Merila, 2009).

As with amphibians overall, the evidence for sex-biased dispersal in the Red-backed Salamander (*Plethodon cinereus*) is conflicting. Of multiple population genetics studies of this species (Marsh et al., 2007; Noel et al., 2007; Marsh et al., 2008; Jordan et al., 2009; Noel and Lapointe, 2010; Fisher-Reid et al., 2013), only one (Cabe et al., 2007) tested for sex-biased dispersal, and they were unable to detect any evidence of it. Given the expected short dispersal distances for this species, and the importance of spatial scale on dispersal evolution (Ronce et al., 2001), that analysis may have been conducted at distances too large (200–2,000 m) to detect sex-biased dispersal. Another study recently reported low levels of positive spatial-genetic autocorrelation among both female and male Red-backed Salamanders over distances of 0–14 m (Liebgold et al., 2011). No study of this species has yet used the

two most powerful genetic tests for detecting sex bias in dispersal: assignment indices and post-dispersal  $F_{ST}$  tests (Goudet et al., 2002).

Until recently, genetic assessments of dispersal consisted solely of estimates of the effective number of migrants into a population ( $Nm$ ) calculated from Wright's (1931) island model (Broquet and Petit, 2009). However, recent work has revealed several problems with this approach. Violations of the simplifying assumptions of the island model can significantly affect the interpretation of results; the effective number of migrants per generation ( $Nm$ ) estimated by this method may have little biological relevance; and estimates have high statistical uncertainty (Whitlock and McCauley, 1999). As a result of these issues, a variety of new techniques have been developed recently to measure dispersal in natural populations (reviewed by Broquet and Petit, 2009).

The  $F_{ST}$  test of Goudet et al. (2002) compares the difference between female and male subpopulation structure to a null distribution formed by randomly assigning a sex to each multilocus genotype. After dispersal, the dispersing sex should share more similar allele frequencies among subpopulations, reflected in a lower  $F_{ST}$ . The incorporation of only post-dispersal individuals means that this test reflects contemporary dispersal, and thus differs from most uses of  $F$ -statistics (Goudet et al., 2002); by contrasting  $F_{ST}$  values among sex and age classes, rather than on evaluating absolute  $F_{ST}$  values, this approach is less sensitive to departures from island assumptions than are traditional methods (Fontanillas et al., 2004).

Assignment tests (AIC tests) were originally developed to evaluate genetic differentiation among populations (Paetkau et al., 1995); it was then shown that

individuals with low probabilities of assignment to their population of capture were likely to be immigrants (Favre et al., 1997), and further that differences between male and female likelihood distributions reflect sex-biased dispersal (Waser and Strobeck, 1998). An individual's assignment index is the expected frequency of its multilocus genotype in the population in which it is encountered (Mossman and Waser, 1999). By subtracting the average probability of the sample, the distribution of individual multilocus probabilities is centered on 0 (Goudet et al., 2002)—positive values represent resident individuals, and negative values represent immigrants; the dispersing sex is expected to exhibit a lower mean assignment index ( $mAIc$ ) and greater variance ( $vAIc$ ).

Genetic approaches for detecting sex-biased dispersal have been evaluated with both empirical data and simulations. The assignment test was effective in detecting a sex bias in the White Footed Mouse (*Peromyscus leucopus*), a species in which both sexes disperse (Mossman and Waser, 1999). Similarly, estimates of dispersal rates from assignment tests were similar to those from a long-term mark-recapture dataset of the Grand Skink *Oligosoma grande* (Berry et al., 2004). Through simulations, Goudet et al. (2002) showed that the  $vAIc$  test performs best at dispersal rates  $< 10\%$ , the  $F_{ST}$  test performs best at dispersal rates  $> 10\%$ , and the performance of the  $mAIc$  test is intermediate to those two tests.

Hypotheses for the evolutionary cause of sex-biased dispersal (Johnson and Gaines, 1990; Perrin and Mazalov, 2000) have centered on interactions among kin: local mate competition (Hamilton, 1967), local resource competition (Clark, 1978), inbreeding avoidance (Bengtsson, 1978), and local resource enhancement (Perrin and

Mazalov, 2000). Methodology to address population genetic structure can be divided into two complementary approaches (Palsboll et al., 2010). In population-based approaches, individual genotypes are assigned to a population of samples. These methods (including the most common population genetics inference methods, such as Wright's  $F_{ST}$  and coalescent-based inference methods) generally assume panmictic populations with no reproductive skew, discrete generations, and constant population sizes and migration rates. They perform best when the degree of structure is high between populations; with low genetic divergence, confidence in assignments is low because a given genotype will have similar likelihood among populations.

By contrast, kinship-based approaches detect genetic structure by comparing individual multilocus genotypes to other individual multilocus genotypes rather than populations (Palsboll et al., 2010). The advantage of these methods is that their statistical power derives from the overall level of genetic variation but not the degree of divergence among populations. As a result, they can perform well with low levels of genetic structure and provide estimates of current (rather than equilibrium) population structure; this is important because the fine-scale kin structure within which kin selection acts may not be apparent at the population level (Hatchwell, 2010). The use of these kinship-based genetic inference methods is a relatively new and comparatively unexplored area of research (Palsboll et al., 2010).

In this study, I conduct AIC and  $F_{ST}$  tests for sex-biased dispersal in a population of Red-backed Salamanders in Maryland. To complement these genetic analyses, I calculate movement distances for male and female salamanders prior to maturity, using 4 y of mark-recapture data. In addition, I test for spatial genetic

structure by calculating inbreeding coefficients and pairwise kinship coefficients based on the averaged location of each individual in spring and fall seasons, binned into seven distance categories. I also regress these kinship statistics on geographic distances separately for immatures, adult females, and adult males, in order to measure the strength of spatial structuring in each of these groups.

### Materials and Methods

#### *Study site and data collection*

This study took place in mature bottomland hardwood forest at Patuxent Wildlife Research Center (PWRC) in Laurel, Maryland (39.054376°N, 76.817206°W), from October 2009–May 2013. During the fall and spring, I conducted weekly searches of three plots of pine coverboards in a 1-m grid and separated from one another by 30–40 m (Fig. 2.1): two 156 m<sup>2</sup> plots with 100 boards each and one 625 m<sup>2</sup> plot with 400 boards.

On each capture, I measured snout–vent length and determined sex by candling. Individuals captured for the first time were marked with VIE and had approximately 10 mm of tissue removed from the tip of the tail for genetic analysis (Sites et al., 2004; Cabe et al., 2007); I sterilized the VIE needle and the tissue forceps with 95% ethyl alcohol between uses. After processing, I returned each individual to its site of capture.

For more details, see Chapter 2 above.

### *Genetic analyses*

I extracted DNA from tail-tip tissue samples using DNeasy Blood & Tissue Kits (Qiagen; Valencia, CA). I attempted to amplify nine microsatellite loci (PcLX16, PcLX23, PcI16, PcCCO4, PcJX24, PcII14, PcJX05, PcFXO8, PcJX06) in 12.5  $\mu$ l multiplex reactions (1  $\mu$ l template, 4.5  $\mu$ l H<sub>2</sub>O, 0.125  $\mu$ l each primer, 6.25  $\mu$ l EconoTaq PLUS 2X Master Mix [Lucigen Corporation; Middleton, WI]) following the protocols in Connors and Cabe (2003): 94°C for 2 min, 30x (94°C for 30 s, annealing temperature [61.8°C or 58.9°C] for 45 s, 72°C for 30 s), and 72°C for 5 min. I genotyped samples on an ABI 3730xl DNA Analyzer and manually called alleles using GeneMapper 4.0 (Life Technologies; Carlsbad, CA). I was able to genotype 750 salamanders at seven microsatellite loci; the markers PcCCO4 and PcJX05 did not amplify for any individuals, and I have not found any studies reporting the use of these markers since their description (Connors and Cabe, 2003).

I used the program GENEPOP v. 4.2 (Raymond and Rousset, 1995; Rousset, 2008) to calculate summary statistics (number of alleles per locus, observed and expected heterozygosities) and to test for linkage disequilibrium and deviation from Hardy-Weinberg equilibrium. I compared immatures, females and males separately and adjusted for multiple testing with a Bonferroni correction for an experiment-wise alpha value of 0.05 (Weir, 1990). Summary statistics for the loci are reported in Table 4.1.

Linkage equilibrium was rejected for a different pair of loci in each group (immatures: PcLX16 and PcXFO8; females: PcLX16 and PcII14; males: PcI16 and PcXFO8). Several previous studies have found no evidence of linkage disequilibrium

among any of these markers (Liebgold et al., 2006; Cabe et al., 2007; Noel et al., 2007; Liebgold and Cabe, 2008; Jordan et al., 2009; Noel and Lapointe, 2010); one study (Marsh et al., 2007) reported linkage disequilibrium between PcI16 and PcJX06, loci which showed no evidence of linkage in any group in the current study. The lack of consistent disequilibrium between any single pair of loci in this or other studies suggests that none of these markers are physically linked (Selkoe and Toonen, 2006).

One locus (PcI16) deviated from Hardy-Weinberg equilibrium in all groups due to a deficit of heterozygotes, suggesting the presence of null alleles (Selkoe and Toonen, 2006). The frequency of null alleles has been found to vary across populations of Red-backed Salamanders in western Virginia and eastern West Virginia (R. Page, pers. comm.), and I did not include this locus in analyses. Two additional loci (PcLX23 and PcII14) were found to deviate from Hardy-Weinberg equilibrium in the sample of immatures; however, in neither case was a test for heterozygote deficit significant ( $p = 0.29$  and  $p = 0.11$ , respectively; Hardy-Weinberg Exact Tests in GENEPOP). The loci PcI16, PcJX06, PcLX16, and several others not used in the present study have previously been found to deviate from Hardy-Weinberg equilibrium in populations of Red-backed Salamanders at some localities, but never in a consistent pattern among or within studies (Liebgold and Cabe, 2008; Marsh et al., 2008; Noel and Lapointe, 2010; Liebgold et al., 2011).

I performed *mAIC*, *vAIC*, and post-dispersal  $F_{ST}$  tests in the program FSTAT (Goudet, 1995). Given the evidence that dispersal is undertaken prior to maturity in Red-backed Salamanders (see Chapters 2 and 3 above), I used only adults (163



females and 157 males) in these analyses. For these tests, I used 1,000 randomizations, Weir and Cockerham's (1984) estimator of  $F_{ST}$ , and two-tailed tests, analyzing the three study plots as subpopulations.

To test for spatial genetic structure, I analyzed the two seasons for which I had the most data (Fall 2010 and Spring 2011; Table 3.2) using the program SPAGEDI (Hardy and Vekemans, 2002). I used the kinship estimator ( $r$ ) of Ritland (1996), which has been shown to have lower sampling variance than other estimators and greater power to detect genetic structure (Vekemans and Hardy, 2004).

In order to measure the strength of spatial structuring in each season, I calculated pairwise kinship coefficients separately for the following groups: 1) immatures, 2) adult females, 3) adult males, 4) female-immature pairs, and 5) female-male pairs. To calculate these coefficients, I binned pairwise distances between individuals (using the season's average location for each individual) into seven distance categories: 0–2 m, 2–4 m, 4–8 m, 8–16 m, 16–32 m, 32–64 m, and 64–128 m. Inbreeding coefficients were estimated as intra-individual kinship coefficients. I also performed linear regression of pairwise kinship statistics on the natural logarithm of geographic distances. For these spatial tests, I calculated  $p$  values based on 1,000 permutations of genotype and location; this process is equivalent to a Mantel test (Mantel, 1967).

#### *Movement analyses*

I used ArcGIS 9.3.1 (Esri; Redlands, CA) and HawthTools (Beyer, 2004) to calculate an average location for each individual in each season; I then calculated the

distance between individuals' average locations in each season they were captured. For individuals captured repeatedly both before and after maturity, I averaged the distances for each individual before maturity, tested for equality of variances with an  $F$  test, and then compared female and male distances with a  $t$ -test.

## Results

### *Genetic analyses*

Dispersal was significantly male-biased based in the  $F_{ST}$  randomization test (female  $\Delta F_{ST} = 0.0062$ ; male  $\Delta F_{ST} = -0.0058$ ;  $p = 0.04$ ). Mean and variance assignment tests did not detect a significant difference between the sexes, although the result of the latter test was in the expected direction (mean assignment females:  $-0.07694$ , males:  $0.07937$ ,  $p = 0.684$ ; variance assignment females:  $11.19799$ , males:  $12.02916$ ,  $p = 0.245$ ).

The regression of kinship coefficient on the natural logarithm of geographic distance was significant for only two comparisons: immatures in the fall ( $\beta = -0.00114$ ,  $R^2 = 0.00063$ ,  $p = 0.02$ ) and female-immature pairs in the fall ( $\beta = -0.00152$ ,  $R^2 = 0.00114$ ,  $p = 0.003$ ); the relationship was marginally significant for immatures in the spring ( $\beta = -0.0009$ ,  $R^2 = 1.30E-05$ ,  $p = 0.09$ ). Estimated kinship coefficients were generally low (Appendices 4.1, 4.2). For female-immature pairs in the fall, kinship coefficients were significantly positive at distances of 2–4 m ( $r = 0.0057$ ,  $p = 0.005$ ) and negative with marginal significance at distances of 32–64 m ( $r = -0.003$ ,  $p = 0.05$ ). Inbreeding coefficients (intra-individual kinship coefficients)

were positive and significant for three groups only in the spring: immatures ( $F_{IS} = 0.024, p = 0.03$ ), females ( $F_{IS} = 0.031, p = 0.02$ ), and female-immature pairs ( $F_{IS} = 0.026, p = 0.01$ ).

### *Movement analyses*

Of 752 marked salamanders in the study, I recorded movements between two or more seasons both before and after maturity for 25 females and 24 males.

Variances did not differ between the sexes ( $F_{24,23} = 0.57; p = 0.09$ ), and the mean distance moved between seasons prior to maturity ( $\pm$  SD) was significantly higher for males ( $3.80 \pm 2.40$  m) than for females ( $2.36 \pm 1.88$  m):  $t = -2.30, df = 47, p = 0.03$ .

### *Discussion*

The signature of male-biased dispersal in Red-backed Salamanders from the post-dispersal  $F_{ST}$  test is consistent with the results of Chapters 2 and 3, which indicated via growth and maturation rates, home range sizes, and mark-recapture analyses that immature males are the predominant dispersers in this species. Mean and variance assignment tests for sex-biased dispersal were both nonsignificant in this analysis; however, the latter was in the expected direction (males with greater  $vAIC$ ). Based on simulations (Goudet et al., 2002), the  $vAIC$  test performs best when dispersal is very low ( $< 10\%$ ); in all other cases, the most powerful test is the post-dispersal  $F_{ST}$  randomization test.

Of 431 immature salamanders marked over 4 y in this study, only 25 females and 24 males were captured repeatedly both before and after maturity, indicating successful establishment as resident individuals; the majority were never recaptured as adults. This result is consistent with the evidence of strong competition for space among Red-backed Salamanders (Chapter 2 above); in addition, the duration of the study may not have been sufficient to allow some of those individuals to mature, due to individual heterogeneity in age at maturation (Chapter 2). Of the individuals that matured and remained on the study plots, males moved significantly greater distances prior to maturity than females did.

One previous study (Cabe et al., 2007) found no genetic evidence of sex-biased dispersal in Red-backed Salamanders on plots separated by 200–2,000 m, while another found some positive spatial-genetic autocorrelation at distances of 0–14 m (Liebgold et al., 2011). Theory indicates that both the causes and consequences of dispersal may vary greatly with spatial scale. Although long-distance dispersal has important biogeographical consequences (Gillespie et al., 2012), the distances required to avoid interactions with relatives are expected to be smaller than those required to colonize new habitat (Ronce et al., 2001). For this reason, sex-biased dispersal may be apparent at the scale at which kin interactions take place, but not at larger spatial scales (Goudet et al., 2002; Fontanillas et al., 2004; Gauffre et al., 2009).

The spatial genetic analyses in the present study indicate significant positive kinship coefficients between female-immature pairs at distances of 2–4 m in the fall, when young-of-the-year first appear on the surface (Sayler, 1966); the relationship

between kinship and the natural logarithm of geographic distance was significantly negative for immatures in the fall and only marginally so in the spring. These results are consistent with the results in Chapter 3 indicating an influx of dispersing immature males in the spring relative to the fall. It has been suggested that adult Red-backed Salamanders may provide foraging benefits to related juveniles by allowing them to remain within defended territories (Jaeger et al., 1995); that hypothesis is not supported by the results of this genetic study.

This analysis may have lacked sufficient power to detect a stronger spatial genetic signal due to the number and variability of microsatellite loci used; estimators of relatedness are known to exhibit large variances (Blouin, 2003). Only one previous study has addressed relatedness and spatial associations of Red-backed Salamanders at the individual level, finding some evidence of positive spatial-genetic autocorrelation for both females and males at distances of 0–14 m (Liebgold et al., 2011). The signal of spatial structure was also weak in that study (which used six of the same microsatellite loci as in the present study, along with one additional locus); confidence intervals of relatedness estimates always overlapped confidence intervals of the null distribution.

Overall, the present analysis indicated a lack of strong spatial genetic structure over distances of 0–128 m in this population. Even significant spatial relationships explained very little of the genetic variation. Several previous studies have assessed genetic structure of Red-backed Salamanders at the population level. Plots of salamanders separated by 200 m to 2 km in continuous forest exhibited low levels of divergence (Cabe et al., 2007), while barriers such as second-order streams (Marsh et

al., 2007), urban fragmentation (Noel et al., 2007), and interstate highways (Marsh et al., 2008) appear to contribute slightly to divergence of salamanders on plots separated by 200 m to 4 km. Collectively, these studies indicate only marginally limited gene flow in populations of Red-backed Salamanders, even those intersected by dispersal-limiting barriers, a fact that limits the ability to detect within-population genetic structure.

Hypotheses for sex-biased dispersal in birds and mammals have often focused on mating systems. For more than a decade, laboratory studies have suggested that Red-backed Salamanders are socially monogamous (e.g., Gillette et al., 2000; Lang and Jaeger, 2000; Jaeger et al., 2001; Jaeger et al., 2002; Prosen et al., 2004; Joseph et al., 2005) and that both males and females defend territories (e.g., Mathis, 1990; Gabor and Jaeger, 1995; Simons et al., 1997; Toll et al., 2000).

The evidence of male-biased dispersal in Red-backed Salamanders in this study is inconsistent with the association of monogamy, resource defense, and female dispersal in birds, and polygamy, mate defense, and male dispersal in mammals (Greenwood, 1980); however, resource defense and mate defense may not be easily distinguished or exclusive categories in all situations (Waser and Jones, 1983; Dobson and Jones, 1985), and dispersal is often likely to result from multiple ultimate causes (Ronce et al., 2001; Bowler and Benton, 2005; Ronce, 2007).

Competition among kin (Hamilton and May, 1977) or inbreeding depression (Pusey and Wolf, 1996; Keller and Waller, 2002) are widely considered to be important processes leading to the evolution of dispersal. Mathematical models have shown that if inbreeding avoidance were the only cause of dispersal, complete

philopatry by one sex would be expected; as a result, inbreeding alone cannot be the sole selective pressure in situations in which some dispersal is exhibited by both sexes, as is the case in most species studied to date (Perrin and Mazalov, 1999).

If males are more likely to exhibit local mate competition and females are more likely to show local resource competition in promiscuous or polygynous systems, dispersal patterns are predicted to depend on a balance between these two factors, with the bias predicted for the sex with greater costs due to local competition, whether for mates or resources (Perrin and Mazalov, 2000). However, no framework yet fully accounts for the interaction among inbreeding avoidance, kin competition, and cooperation to explain the variety of dispersal patterns and social systems observed in nature (Lawson Handley and Perrin, 2007).

In the present study, I detected low but significant inbreeding coefficients (0.024–0.031) for immatures, females, and female-immature pairs in the spring but not in the fall. This apparent inbreeding may be a result of sampling increased numbers of dispersing individuals in the spring, representing a broader area and more rare alleles (Wahlund, 1928). This Wahlund effect would be consistent with the mark-recapture results of Chapter 3, indicating an influx of dispersing immature males in the spring moving through the study area. The low inbreeding coefficients seem to indicate that the salamanders are generally avoiding close inbreeding; a lack of evidence for close inbreeding was also found in a previous population genetic study of this species (Cabe et al., 2007).

The lack of significant pairwise kinship coefficients between adult females and adult males, and the overall lack of spatial genetic structure at distances of 0–128

m in this population, together indicate that both females and males are dispersing large enough distances to avoid creating clusters of kin. Together with results from previous chapters, this suggests that both immature females and immature males face competition for space (consistent with empirical evidence indicating that kin competition is most prevalent between parents and offspring; Lambin, 1994; Gundersen and Andreassen, 1998; Lena et al., 1998; Clobert et al., 2001), but greater competition among males leads to a level of male-biased dispersal detectible through both spatial and genetic tests.



Chapter 4 Tables

Table 4.1. Summary statistics of microsatellite loci used in a study of Red-backed Salamanders in Maryland.

<b>Locus</b>	<b>Size Range (bp)</b>	<b>Alleles</b>	<b><math>H_O</math></b>	<b><math>H_E</math></b>
<i>Females (n = 163)</i>				
PcLX16	183–235	11	0.76	0.79
PcLX23	160–176	4	0.58	0.60
PcI16	134–155	6	0.29	0.63
PcJX24	160–212	15	0.45	0.43
PcII14	127–237	38	0.83	0.87
PcXFO8	175–202	11	0.79	0.72
PcJX06	100–108	5	0.55	0.58
<i>Males (n = 158)</i>				
PcLX16	183–235	10	0.71	0.77
PcLX23	160–176	4	0.56	0.59
PcI16	134–155	6	0.17	0.56
PcJX24	160–212	16	0.49	0.48
PcII14	118–241	33	0.85	0.86
PcXFO8	175–202	11	0.64	0.69
PcJX06	100–110	5	0.59	0.55
<i>Immatures (n = 429)</i>				
PcLX16	183–235	12	0.71	0.78
PcLX23	160–176	5	0.57	0.60
PcI16	134–155	6	0.23	0.57
PcJX24	160–212	18	0.48	0.49
PcII14	118–241	38	0.85	0.88
PcXFO8	175–202	14	0.75	0.77
PcJX06	100–110	5	0.62	0.58

## Appendices

*Appendix 1.1. Materials used as coverboards in studies of salamanders.*

Material	No. of studies	Source
unidentified	1	Hyde and Simons, 2001
unidentified lumber	6	Hendrickson, 1954; Stebbins, 1954; Davis, 1997; Ford and Hampton, 2005; Semlitsch et al., 2007; Scheffers et al., 2009
Pine ( <i>Pinus</i> spp.)	8	Taub, 1961; Stewart and Bellis, 1970; Mathis, 1990; Degraaf and Yamasaki, 1992; Carfioli et al., 2000; Jaeger et al., 2001; Gillette, 2003; Morneault et al., 2004
tar paper	1	Taub, 1961
asphalt shingle	1	Mathewson, 2009
plywood chipboard; plywood; chipboard; CDX pine plywood; particle board; treated plywood	9	Grant et al., 1992; Bonin and Bachand, 1997; Carfioli et al., 2000; Houze and Chandler, 2002; Ryan et al. 2002; McDade and Maguire, 2005; Luhring and Young, 2006; Carlson and Szuch, 2007; Hampton, 2007
galvanized tin; tin; corrugated tin	3	Grant et al., 1992; Ford and Hampton, 2005; Hampton, 2007

---

Eastern Hemlock ( <i>Tsuga canadensis</i> )	4	Brooks, 1999; Brooks, 2001; DeGraaf and Yamasaki, 2002; Mathewson, 2009
Tulip Poplar ( <i>Liriodendron tulipifera</i> )	1	Harpole and Haas, 1999
cedar shingle ( <i>Thuja plicata?</i> )	1	Monti et al., 2000
White Oak ( <i>Quercus alba</i> )	1	Marsh and Goicochea, 2003
Sugar Maple ( <i>Acer saccharum</i> )	2	Moore, 2005; Maerz et al., 2009
carpet	1	Scheffers et al., 2009

---

Appendix 1.2. Salamander species encountered in studies using coverboards.

Species	Study location	No. of encounters	Total salamander encounters	Proportion of species in total salamander encounters	Source
<hr/>					
Family Ambystomatidae					
<i>Ambystoma annulatum</i>	Daniel Boone Conservation Area, Missouri	4	310	1.29%	Scheffers et al., 2009
<i>Ambystoma laterale</i>	Mont Orford Park, Quebec	9	134	6.72%	Bonin and Bachand, 1997
<i>A. laterale</i>	Ontario	24	2208	1.09%	Morneault et al., 2004
<i>A. laterale</i>	Kresge Environmental Education Center, Michigan	17	154	11.04%	Carlson and Szuch, 2007
<i>A. laterale</i>	Murphy Lake State Game Area, Michigan	3	352	0.85%	Carlson and Szuch, 2007
<i>Ambystoma macrodactylum</i>	Greater Victoria Watershed, Vancouver Island (forested sites)	3	—	0–2.4%	Davis, 1997

<i>Ambystoma maculatum</i>	Mont Orford Park, Quebec	1	75	1.33%	Bonin and Bachand, 1997
<i>A. maculatum</i>	Quabbin Reservation, Massachusetts	10	2387	0.42%	Brooks, 1999
<i>A. maculatum</i>	Barkhamsted Reservoir, Connecticut/Massachusetts	8	592	1.35%	Brooks, 2001
<i>A. maculatum</i>	Ontario	33	2208	1.49%	Morneault et al., 2004
<i>A. maculatum</i>	Camp Maxey, Texas	1	2	50.00%	Ford and Hampton, 2005
<i>A. maculatum</i>	Lapeer County, Michigan	3	154	1.95%	Carlson and Szuch, 2007
<i>A. maculatum</i>	Murphy Lake State Game Area, Michigan	6	352	1.70%	Carlson and Szuch, 2007
<i>A. maculatum</i>	Nantahala National Forest, North Carolina	1	199	0.50%	Semlitsch et al., 2007
<i>A. maculatum</i>	central New York; northeastern Pennsylvania	—	—	—	Maerz et al., 2009
<i>Ambystoma opacum</i>	Savannah River Site (SRS), South Carolina	25	844	2.96%	Grant et al., 1992
<i>A. opacum</i>	Camp Maxey, Texas	1	2	50.00%	Ford and Hampton, 2005

---

<i>A. opacum</i>	Old Sabine Bottom Wildlife Management Area, Texas	1	33	3.03%	Hampton, 2007
<i>A. opacum</i>	Daniel Boone Conservation Area, Missouri	1	310	0.32%	Scheffers et al., 2009
<i>Ambystoma texanum</i>	Old Sabine Bottom Wildlife Management Area, Texas	30	33	90.91%	Hampton, 2007
<i>Ambystoma talpoideum</i>	Savannah River Site (SRS), South Carolina	21	844	2.49%	Grant et al., 1992
Family Plethodontidae					
<i>Aneides ferreus</i>	Greater Victoria Watershed, Vancouver Island (forested sites)	5	—	0–2.4%	Davis, 1997
<i>A. ferreus</i>	Rosewall Creek Provincial Park, Vancouver Island	64	—	68.9–87.1%	Davis, 1997
<i>Aneides lugubris</i>	Pinehurst Madrone Grove Park, California	—	—	—	Stebbins, 1954
<i>Batrachoseps attenuatus</i>	Pinehurst Madrone Grove Park,	327	—	—	Hendrickson, 1954

---



---

	California				
<i>B. attenuatus</i>	Pinehurst Madrone Grove Park,	—	—	87.50%	Stebbins, 1954
	California				
<i>Batrachoseps pacificus</i>	Channel Islands, California	—	—	—	Fellers and Drost, 1994
<i>Desmognathus auriculatus</i>	Richmond County, Georgia	1	30	3.33%	Luhring and Young, 2006
<i>Desmognathus conanti</i>	Richmond County, Georgia	5	30	16.67%	Luhring and Young, 2006
<i>Desmognathus fuscus</i>	Centre County, Pennsylvania	294	399	73.68%	Stewart and Bellis, 1970
<i>D. fuscus</i>	Centre County, Pennsylvania	65	130	50.00%	Stewart and Bellis, 1970
<i>D. fuscus</i>	White Mountain National Forest,	1	110	0.91%	DeGraaf and Yamasaki,
	New Hampshire				1992
<i>D. fuscus</i>	Mont Orford Park, Quebec	3	75	4.00%	Bonin and Bachand, 1997
<i>D. fuscus</i>	Quabbin Reservation, Massachusetts	6	2387	0.25%	Brooks, 1999
<i>D. fuscus</i> complex	Great Smoky Mountains National	—	1224	—	Hyde and Simons, 2001
	Park, Tennessee/North Carolina				
<i>D. fuscus</i>	White Mountain National Forest,	1	4050	0.02%	Degraaf and Yamasaki,
	New Hampshire				2002

---

---

<i>D. fuscus</i>	Murphy Lake State Game Area, Michigan	116	352	32.95%	Carlson and Szuch, 2007
<i>Desmognathus imitator</i> complex	Great Smoky Mountains National Park, Tennessee/North Carolina	—	1224	—	Hyde and Simons, 2001
<i>Desmognathus monticola</i>	Great Smoky Mountains National Park, Tennessee/North Carolina	—	1224	—	Hyde and Simons, 2001
<i>Desmognathus ocoee</i>	Nantahala National Forest, North Carolina	3	199	1.51%	Semlitsch et al., 2007
<i>Desmognathus ocrophaeus</i>	Centre County, Pennsylvania	77	399	19.30%	Stewart and Bellis, 1970
<i>D. ocrophaeus</i>	Centre County, Pennsylvania	25	130	19.23%	Stewart and Bellis, 1970
<i>D. ochrophaeus</i>	central New York; northeastern Pennsylvania	—	—	—	Maerz et al., 2009
<i>Desmognathus</i> <i>quadramaculatus</i>	Great Smoky Mountains National Park, Tennessee/North Carolina	—	1224	—	Hyde and Simons, 2001
<i>Desmognathus wrighti</i>	Great Smoky Mountains National Park, Tennessee/North Carolina	—	1224	—	Hyde and Simons, 2001

---

---

<i>Ensatina eschscholtzii</i>	Pinehurst Madrone Grove Park, California	527	—	—	Stebbins, 1954
<i>E. eschscholtzii</i>	Greater Victoria Watershed, Vancouver Island (forested sites)	22	—	4.9–11.9%	Davis, 1997
<i>E. eschscholtzii</i>	Rosewall Creek Provincial Park, Vancouver Island	2	—	0–2.1%	Davis, 1997
<i>Eurycea bislineata</i>	Somerset County, New Jersey	118	266	44.36%	Taub, 1961
<i>E. bislineata</i>	Centre County, Pennsylvania	25	399	6.27%	Stewart and Bellis, 1970
<i>E. bislineata</i>	Centre County, Pennsylvania	31	130	23.85%	Stewart and Bellis, 1970
<i>E. bislineata</i>	Mont Orford Park, Quebec	15	75	20.00%	Bonin and Bachand, 1997
<i>E. bislineata</i>	Mont Orford Park, Quebec	12	134	8.96%	Bonin and Bachand, 1997
<i>E. bislineata</i>	Quabbin Reservation, Massachusetts	6	2387	0.25%	Brooks, 1999
<i>E. bislineata</i>	Valley Forge National Historical Park, Pennsylvania	2	952	0.21%	Carfioli et al., 2000
<i>E. bislineata</i>	White Mountain National Forest, New Hampshire	7	4050	0.17%	Degraaf and Yamasaki, 2002

---

<i>E. bislineata</i>	Barkhamsted Reservoir, Connecticut/Massachusetts	6	592	1.01%	Brooks, 2001
<i>E. bislineata</i>	Lake Clair Watershed, Quebec	23	309	7.44%	Moore, 2005
<i>E. bislineata</i>	central New York; northeastern Pennsylvania	—	—	—	Maerz et al., 2009
<i>Eurycea cirrigera</i>	Jenkins County, Georgia	9	43	20.93%	Houze and Chandler, 2002
<i>E. cirrigera</i>	Richmond County, Georgia	2	30	6.67%	Luhring and Young, 2006
<i>Eurycea guttolineata</i>	Jenkins County, Georgia	1	43	2.33%	Houze and Chandler, 2002
<i>E. guttolineata</i>	Richmond County, Georgia	1	30	3.33%	Luhring and Young, 2006
<i>Eurycea longicaudata</i>	Centre County, Pennsylvania	1	130	0.77%	Stewart and Bellis, 1970
<i>Eurycea quadridigitata</i>	Savannah River Site (SRS), South Carolina	133	844	15.76%	Grant et al., 1992
<i>E. quadridigitata</i>	Jenkins County, Georgia	1	43	2.33%	Houze and Chandler, 2002
<i>Eurycea wilderae</i>	Great Smoky Mountains National Park, Tennessee/North Carolina	—	1224	—	Hyde and Simons, 2001
<i>E. wilderae</i>	Nantahala National Forest, North	2	199	1.01%	Semlitsch et al., 2007

---

	Carolina				
<i>Gyrinophilus porphyriticus</i>	Centre County, Pennsylvania	1	399	0.25%	Stewart and Bellis, 1970
<i>G. porphyriticus</i>	Centre County, Pennsylvania	3	130	2.31%	Stewart and Bellis, 1970
<i>G. porphyriticus</i>	Great Smoky Mountains National Park, Tennessee/North Carolina	—	1224	—	Hyde and Simons, 2001
<i>G. porphyriticus</i>	White Mountain National Forest, New Hampshire	4	4050	0.10%	Degraaf and Yamasaki, 2002
<i>G. porphyriticus</i>	central New York; northeastern Pennsylvania	—	—	—	Maerz et al., 2009
<i>Hemidactylium scutatum</i>	Quabbin Reservation, Massachusetts	1	2387	0.04%	Brooks, 1999
<i>H. scutatum</i>	Murphy Lake State Game Area, Michigan	6	352	1.70%	Carlson and Szuch, 2007
<i>H. scutatum</i>	central New York; northeastern Pennsylvania	—	—	—	Maerz et al., 2009
<i>Plethodon albagula</i>	Daniel Boone Conservation Area, Missouri	303	310	97.74%	Scheffers et al., 2009

---

---

<i>Plethodon cinereus</i>	Somerset County, New Jersey	145	266	54.51%	Taub, 1961
<i>P. cinereus</i>	Centre County, Pennsylvania	1	130	0.77%	Stewart and Bellis, 1970
<i>P. cinereus</i>	Mountain Lake Biological Station, Virginia	7	7	100.00%	Mathis, 1990
<i>P. cinereus</i>	White Mountain National Forest, New Hampshire	109	110	99.09%	Degraaf and Yamasaki, 1992
<i>P. cinereus</i>	Mont Orford Park, Quebec	56	75	74.67%	Bonin and Bachand, 1997
<i>P. cinereus</i>	Mont Orford Park, Quebec	113	134	84.33%	Bonin and Bachand, 1997
<i>P. cinereus</i>	Quabbin Reservation, Massachusetts	2280	2387	95.52%	Brooks, 1999
<i>P. cinereus</i>	George Washington and Jefferson National Forest, Virginia	—	—	—	Harpole and Haas, 1999
<i>P. cinereus</i>	Valley Forge National Historical Park, Pennsylvania	947	952	99.47%	Carfioli et al., 2000
<i>P. cinereus</i>	Holt Research Forest, Maine	1235	1235	100.00%	Monti et al., 2000
<i>P. cinereus</i>	Barkhamsted Reservoir, Connecticut/Massachusetts	556	592	93.92%	Brooks, 2001

---

---

<i>P. cinereus</i>	Mountain Lake Biological Station, Virginia	67	—	—	Jaeger et al., 2001
<i>P. cinereus</i>	White Mountain National Forest, New Hampshire	4038	4050	99.70%	Degraaf and Yamasaki, 2002
<i>P. cinereus</i>	Mountain Lake Biological Station, Virginia	3733	—	—	Gillette, 2003
<i>P. cinereus</i>	Washington and Lee University, Virginia	—	—	—	Marsh and Goicochea, 2003
<i>P. cinereus</i>	Ontario	2144	2208	97.10%	Morneault et al., 2004
<i>P. cinereus</i>	Lake Clair Watershed, Quebec	285	309	92.23%	Moore, 2005
<i>P. cinereus</i>	Lapeer County, Michigan	130	154	84.42%	Carlson and Szuch, 2007
<i>P. cinereus</i>	Murphy Lake State Game Area, Michigan	221	352	62.78%	Carlson and Szuch, 2007
<i>P. cinereus</i>	central New York; northeastern Pennsylvania	—	—	—	Maerz et al., 2009
<i>P. cinereus</i>	Harvard Forest, Massachusetts	444	—	—	Mathewson, 2009

---

---

<i>Plethodon cylindraceus</i>	George Washington and Jefferson National Forest, Virginia	1	—	—	Harpole and Haas, 1999
<i>Plethodon glutinosus</i>	Savannah River Site (SRS), South Carolina	665	844	78.79%	Grant et al., 1992
<i>P. glutinosus</i>	central New York; northeastern Pennsylvania	—	—	—	Maerz et al., 2009
<i>P. glutinosus</i> complex	Great Smoky Mountains National Park, Tennessee/North Carolina	—	1224	—	Hyde and Simons, 2001
<i>Plethodon jordani</i>	Great Smoky Mountains National Park, Tennessee/North Carolina	—	1224	—	Hyde and Simons, 2001
<i>Plethodon metcalfi</i>	Nantahala National Forest, North Carolina	153	199	76.88%	Semlitsch et al., 2007
<i>Plethodon ocmulgee</i>	Jenkins County, Georgia	32	43	74.42%	Houze and Chandler, 2002
<i>Plethodon oconaluftee</i>	Nantahala National Forest, North Carolina	23	199	11.56%	Semlitsch et al., 2007
<i>Plethodon richmondi</i>	Centre County, Pennsylvania	4	130	3.08%	Stewart and Bellis, 1970

---



---

<i>Plethodon serratus</i>	Great Smoky Mountains National Park, Tennessee/North Carolina	—	1224	—	Hyde and Simons, 2001
<i>P. serratus</i>	Nantahala National Forest, North Carolina	13	199	6.53%	Semlitsch et al., 2007
<i>Plethodon vehiculum</i>	Goldstream Provincial Park, Vancouver Island	—	—	100%	Davis, 1997
<i>P. vehiculum</i>	Lake Cowichan, Vancouver Island	168	—	69.70%	Davis, 1997
<i>P. vehiculum</i>	Greater Victoria Watershed, Vancouver Island (forested sites)	217	—	72.6–81.3%	Davis, 1997
<i>P. vehiculum</i>	Greater Victoria Watershed, Vancouver Island (clearcut site)	15	—	100%	Davis, 1997
<i>P. vehiculum</i>	Rosewall Creek Provincial Park, Vancouver Island	17	—	0–29.17%	Davis, 1997
<i>Pseudotriton ruber</i>	Somerset County, New Jersey	3	266	1.13%	Taub, 1961
<i>P. ruber</i>	Centre County, Pennsylvania	2	399	0.50%	Stewart and Bellis, 1970
<i>P. ruber</i>	Great Smoky Mountains National	—	1224	—	Hyde and Simons, 2001

---

---

	Park, Tennessee/North Carolina				
<i>P. ruber</i>	Valley Forge National Historical Park, Pennsylvania	3	952	0.32%	Carfioli et al., 2000
<i>P. ruber</i>	Richmond County, Georgia	19	30	63.33%	Luhring and Young, 2006
<i>P. ruber</i>	central New York; northeastern Pennsylvania	—	—	—	Maerz et al., 2009
Family Salamandridae					
<i>Notophthalmus viridescens</i>	Quabbin Reservation, Massachusetts	84	2387	3.52%	Brooks, 1999
<i>N. viridescens</i>	Barkhamsted Reservoir, Connecticut/Massachusetts	22	592	3.72%	Brooks, 2001
<i>N. viridescens</i>	Ontario	24	2208	1.09%	Morneault et al., 2004
<i>N. viridescens</i>	Lake Clair Watershed, Quebec	1	309	0.32%	Moore, 2005
<i>N. viridescens</i>	Old Sabine Bottom Wildlife Management Area, Texas	2	33	6.06%	Hampton, 2007
<i>N. viridescens</i>	Lapeer County, Michigan	4	154	2.60%	Carlson and Szuch, 2007

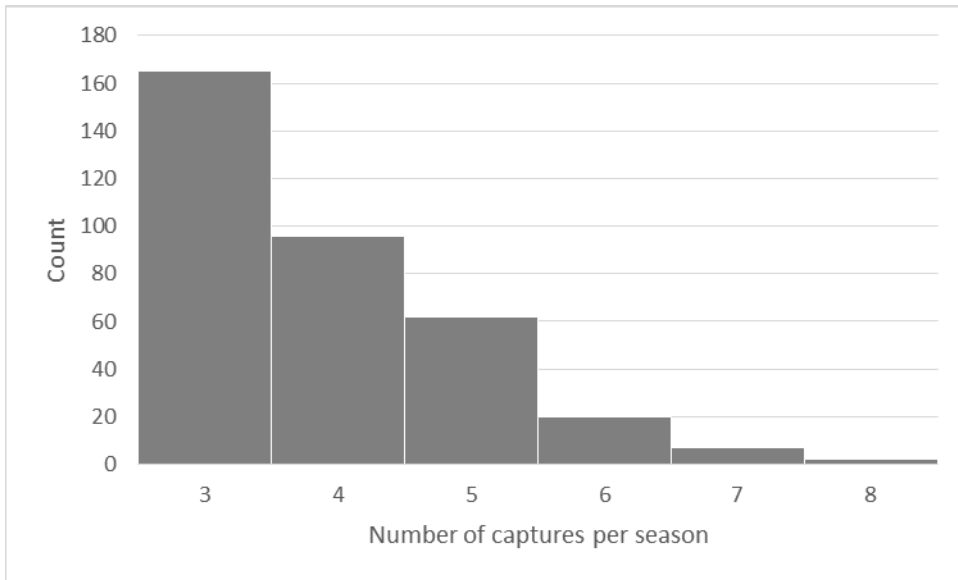
---

---

<i>N. viridescens</i>	Nantahala National Forest, North Carolina	3	199	1.51%	Semlitsch et al., 2007
<i>N. viridescens</i>	central New York; northeastern Pennsylvania	—	—	—	Maerz et al., 2009
<i>N. viridescens</i>	Daniel Boone Conservation Area, Missouri	2	310	0.65%	Scheffers et al., 2009
<i>Taricha granulosa</i>	Lake Cowichan, Vancouver Island	73	—	30.30%	Davis, 1997
<i>T. granulosa</i>	Greater Victoria Watershed, Vancouver Island (forested sites)	30	—	7.7–13.1%	Davis, 1997
<i>T. granulosa</i>	Rosewall Creek Provincial Park, Vancouver Island	1	—	0–3.2%	Davis, 1997
<i>Taricha torosa</i>	Pinehurst Madrone Grove Park, California	—	—	—	Stebbins, 1954

---

*Appendix 2.1. Numbers of points used to generate MCPs.*



*Appendix 3.1. Model-averaged CJS parameter estimates, Fall 2009.*

Parameter	Estimate	SE	95% Confidence Interval	
			Lower	Upper
$\phi$ Immatures, Interval 1	0.633	0.115	0.395	0.820
$\phi$ Immatures, Interval 2	0.649	0.093	0.454	0.805
$\phi$ Immatures, Interval 3	0.650	0.093	0.454	0.805
$\phi$ Immatures, Interval 4	0.649	0.093	0.453	0.805
$\phi$ Immatures, Interval 5	0.649	0.640	0.007	0.998
$\phi$ Immatures, Interval 6	0.649	7.887	0.000	1.000
$\phi$ Immatures, Interval 7	0.649	7.799	0.000	1.000
$\phi$ Adults, Interval 1	0.982	0.094	0.001	1.000
$\phi$ Adults, Interval 2	0.977	0.101	0.006	1.000
$\phi$ Adults, Interval 3	0.977	0.101	0.006	1.000
$\phi$ Adults, Interval 4	0.977	0.101	0.006	1.000
$\phi$ Adults, Interval 5	0.977	0.640	0.000	1.000
$\phi$ Adults, Interval 6	0.977	7.800	0.000	1.000
$\phi$ Adults, Interval 7	0.977	7.800	0.000	1.000
$\rho$ Immatures, Occasion 2	0.496	0.188	0.184	0.811
$\rho$ Immatures, Occasion 3	0.472	0.162	0.199	0.762
$\rho$ Immatures, Occasion 4	0.468	0.155	0.206	0.749
$\rho$ Immatures, Occasion 5	0.461	0.162	0.193	0.754
$\rho$ Immatures, Occasion 6	0.466	0.562	0.010	0.986
$\rho$ Immatures, Occasion 7	0.469	0.150	0.214	0.742
$\rho$ Immatures, Occasion 8	0.455	1.271	0.000	1.000
$\rho$ Adults, Occasion 2	0.494	0.181	0.191	0.801
$\rho$ Adults, Occasion 3	0.473	0.154	0.210	0.751
$\rho$ Adults, Occasion 4	0.467	0.143	0.220	0.730
$\rho$ Adults, Occasion 5	0.462	0.150	0.208	0.737
$\rho$ Adults, Occasion 6	0.464	1.184	0.000	1.000
$\rho$ Adults, Occasion 7	0.466	0.138	0.227	0.722
$\rho$ Adults, Occasion 8	0.452	0.158	0.192	0.742

*Appendix 3.2. Model-averaged CJS parameter estimates, Spring 2010.*

Parameter	Estimate	SE	95% Confidence Interval	
			Lower	Upper
$\phi$ Immatures, Interval 1	0.682	109.969	0.000	1.000
$\phi$ Immatures, Interval 2	0.682	104.192	0.000	1.000
$\phi$ Immatures, Interval 3	0.682	124.146	0.000	1.000
$\phi$ Immatures, Interval 4	0.610	0.205	0.225	0.894
$\phi$ Immatures, Interval 5	0.712	0.152	0.367	0.914
$\phi$ Immatures, Interval 6	0.712	0.152	0.367	0.913
$\phi$ Immatures, Interval 7	0.625	138.324	0.000	1.000
$\phi$ Immatures, Interval 8	0.625	138.324	0.000	1.000
$\phi$ Adults, Interval 1	0.663	109.998	0.000	1.000
$\phi$ Adults, Interval 2	0.680	104.212	0.000	1.000
$\phi$ Adults, Interval 3	0.680	124.148	0.000	1.000
$\phi$ Adults, Interval 4	0.607	0.294	0.121	0.946
$\phi$ Adults, Interval 5	0.710	0.261	0.169	0.967
$\phi$ Adults, Interval 6	0.710	0.261	0.169	0.967
$\phi$ Adults, Interval 7	0.623	138.318	0.000	1.000
$\phi$ Adults, Interval 8	0.623	138.318	0.000	1.000
$p$ Immatures, Occasion 2	0.463	0.275	0.089	0.883
$p$ Immatures, Occasion 3	0.463	0.275	0.089	0.883
$p$ Immatures, Occasion 4	0.486	0.296	0.085	0.906
$p$ Immatures, Occasion 5	0.451	0.283	0.080	0.885
$p$ Immatures, Occasion 6	0.457	0.279	0.085	0.884
$p$ Immatures, Occasion 7	0.459	0.282	0.084	0.887
$p$ Immatures, Occasion 8	0.463	0.275	0.089	0.883
$p$ Immatures, Occasion 9	0.449	5.141	0.000	1.000
$p$ Adults, Occasion 2	0.422	0.269	0.078	0.864
$p$ Adults, Occasion 3	0.422	0.269	0.078	0.864
$p$ Adults, Occasion 4	0.445	0.789	0.002	0.998
$p$ Adults, Occasion 5	0.410	0.275	0.070	0.866
$p$ Adults, Occasion 6	0.417	0.301	0.059	0.890
$p$ Adults, Occasion 7	0.419	0.275	0.073	0.869
$p$ Adults, Occasion 8	0.422	0.269	0.078	0.864
$p$ Adults, Occasion 9	0.409	5.140	0.000	1.000

*Appendix 3.3. Model-averaged CJS parameter estimates, Fall 2010.*

Parameter	Estimate	SE	95% Confidence Interval	
			Lower	Upper
$\phi$ Immatures, Interval 1	0.741	0.050	0.632	0.827
$\phi$ Immatures, Interval 2	0.768	0.051	0.654	0.853
$\phi$ Immatures, Interval 3	0.770	0.038	0.686	0.836
$\phi$ Immatures, Interval 4	0.770	0.038	0.686	0.836
$\phi$ Immatures, Interval 5	0.769	0.037	0.689	0.834
$\phi$ Immatures, Interval 6	0.770	0.038	0.687	0.836
$\phi$ Immatures, Interval 7	0.769	0.038	0.686	0.835
$\phi$ Immatures, Interval 8	0.769	0.037	0.688	0.834
$\phi$ Immatures, Interval 9	0.769	0.777	0.001	1.000
$\phi$ Adults, Interval 1	0.863	0.044	0.754	0.929
$\phi$ Adults, Interval 2	0.895	0.028	0.826	0.939
$\phi$ Adults, Interval 3	0.895	0.027	0.828	0.938
$\phi$ Adults, Interval 4	0.895	0.027	0.830	0.937
$\phi$ Adults, Interval 5	0.895	0.027	0.830	0.937
$\phi$ Adults, Interval 6	0.895	0.027	0.831	0.937
$\phi$ Adults, Interval 7	0.895	0.027	0.830	0.937
$\phi$ Adults, Interval 8	0.895	0.027	0.830	0.937
$\phi$ Adults, Interval 9	0.895	0.776	0.000	1.000
$p$ Immatures, Occasion 2	0.032	0.126	0.000	0.990
$p$ Immatures, Occasion 3	0.032	0.126	0.000	0.990
$p$ Immatures, Occasion 4	0.611	0.139	0.333	0.832
$p$ Immatures, Occasion 5	0.388	0.067	0.267	0.525
$p$ Immatures, Occasion 6	0.525	0.056	0.416	0.632
$p$ Immatures, Occasion 7	0.544	0.050	0.446	0.638
$p$ Immatures, Occasion 8	0.665	0.060	0.539	0.771
$p$ Immatures, Occasion 9	0.533	0.051	0.433	0.631
$p$ Immatures, Occasion 10	0.627	0.777	0.002	0.999
$p$ Adults, Occasion 2	0.033	0.129	0.000	0.990
$p$ Adults, Occasion 3	0.033	0.129	0.000	0.990
$p$ Adults, Occasion 4	0.612	0.139	0.334	0.832
$p$ Adults, Occasion 5	0.389	0.069	0.265	0.529
$p$ Adults, Occasion 6	0.526	0.056	0.417	0.632
$p$ Adults, Occasion 7	0.545	0.049	0.448	0.638
$p$ Adults, Occasion 8	0.666	0.058	0.544	0.768
$p$ Adults, Occasion 9	0.534	0.051	0.434	0.631
$p$ Adults, Occasion 10	0.628	0.779	0.002	0.999

*Appendix 3.4. Model-averaged CJS parameter estimates, Spring 2011.*

Parameter	Estimate	SE	95% Confidence Interval	
			Lower	Upper
$\phi$ Immatures, Interval 1	0.827	0.093	0.571	0.945
$\phi$ Immatures, Interval 2	0.865	0.056	0.716	0.942
$\phi$ Immatures, Interval 3	0.993	0.053	0.888	1.098
$\phi$ Immatures, Interval 4	0.861	0.065	0.681	0.948
$\phi$ Immatures, Interval 5	0.769	0.072	0.601	0.880
$\phi$ Immatures, Interval 6	0.704	0.088	0.510	0.845
$\phi$ Immatures, Interval 7	0.400	0.081	0.257	0.563
$\phi$ Immatures, Interval 8	0.310	10.061	0.000	1.000
$\phi$ Adults, Interval 1	0.842	0.092	0.581	0.954
$\phi$ Adults, Interval 2	0.867	0.053	0.727	0.941
$\phi$ Adults, Interval 3	0.997	0.047	0.904	1.089
$\phi$ Adults, Interval 4	0.850	0.061	0.689	0.935
$\phi$ Adults, Interval 5	0.760	0.071	0.596	0.872
$\phi$ Adults, Interval 6	0.682	0.090	0.488	0.829
$\phi$ Adults, Interval 7	0.387	0.084	0.239	0.559
$\phi$ Adults, Interval 8	0.306	10.061	0.000	1.000
$p$ Immatures, Occasion 2	0.561	0.032	0.499	0.622
$p$ Immatures, Occasion 3	0.561	0.031	0.499	0.621
$p$ Immatures, Occasion 4	0.561	0.031	0.500	0.621
$p$ Immatures, Occasion 5	0.561	0.031	0.500	0.621
$p$ Immatures, Occasion 6	0.561	0.031	0.500	0.621
$p$ Immatures, Occasion 7	0.561	0.031	0.499	0.622
$p$ Immatures, Occasion 8	0.562	0.034	0.494	0.627
$p$ Immatures, Occasion 9	0.561	10.060	0.000	1.000
$p$ Adults, Occasion 2	0.563	0.031	0.501	0.623
$p$ Adults, Occasion 3	0.563	0.031	0.502	0.622
$p$ Adults, Occasion 4	0.563	0.031	0.502	0.622
$p$ Adults, Occasion 5	0.563	0.031	0.502	0.622
$p$ Adults, Occasion 6	0.563	0.031	0.502	0.622
$p$ Adults, Occasion 7	0.563	0.031	0.501	0.623
$p$ Adults, Occasion 8	0.563	0.034	0.496	0.628
$p$ Adults, Occasion 9	0.562	10.060	0.000	1.000



*Appendix 3.5. Model-averaged CJS parameter estimates, Fall 2011.*

Parameter	Estimate	SE	95% Confidence Interval	
			Lower	Upper
$\phi$ Immatures, Interval 1	0.590	0.120	0.353	0.792
$\phi$ Immatures, Interval 2	0.860	0.078	0.633	0.957
$\phi$ Immatures, Interval 3	0.860	0.078	0.633	0.956
$\phi$ Immatures, Interval 4	0.861	2.301	0.000	1.000
$\phi$ Immatures, Interval 5	0.861	2.629	0.000	1.000
$\phi$ Immatures, Interval 6	0.861	2.539	0.000	1.000
$\phi$ Adults, Interval 1	0.750	0.082	0.559	0.876
$\phi$ Adults, Interval 2	0.986	0.041	0.166	1.000
$\phi$ Adults, Interval 3	0.986	0.041	0.164	1.000
$\phi$ Adults, Interval 4	0.986	1.230	0.000	1.000
$\phi$ Adults, Interval 5	0.986	1.309	0.000	1.000
$\phi$ Adults, Interval 6	0.986	1.325	0.000	1.000
$p$ Immatures, Occasion 2	0.408	0.088	0.252	0.584
$p$ Immatures, Occasion 3	0.468	0.076	0.326	0.616
$p$ Immatures, Occasion 4	0.583	0.084	0.416	0.734
$p$ Immatures, Occasion 5	0.447	0.026	0.396	0.499
$p$ Immatures, Occasion 6	0.447	0.026	0.396	0.499
$p$ Immatures, Occasion 7	0.604	1.017	0.000	1.000
$p$ Adults, Occasion 2	0.412	0.087	0.258	0.585
$p$ Adults, Occasion 3	0.473	0.070	0.341	0.610
$p$ Adults, Occasion 4	0.589	0.071	0.447	0.718
$p$ Adults, Occasion 5	0.451	0.013	0.427	0.476
$p$ Adults, Occasion 6	0.451	0.013	0.427	0.476
$p$ Adults, Occasion 7	0.608	0.982	0.000	1.000

*Appendix 3.6. Model-averaged CJS parameter estimates, Spring 2012.*

Parameter	Estimate	SE	95% Confidence Interval	
			Lower	Upper
$\phi$ Immatures, Interval 1	0.849	0.054	0.711	0.928
$\phi$ Immatures, Interval 2	0.886	0.031	0.812	0.934
$\phi$ Immatures, Interval 3	0.887	0.030	0.813	0.934
$\phi$ Immatures, Interval 4	0.887	0.031	0.812	0.934
$\phi$ Immatures, Interval 5	0.886	0.031	0.811	0.934
$\phi$ Immatures, Interval 6	0.887	0.031	0.811	0.934
$\phi$ Immatures, Interval 7	0.887	0.031	0.811	0.934
$\phi$ Immatures, Interval 8	0.886	2.109	0.000	1.000
$\phi$ Adults, Interval 1	0.800	0.057	0.666	0.889
$\phi$ Adults, Interval 2	0.811	0.042	0.716	0.879
$\phi$ Adults, Interval 3	0.811	0.042	0.716	0.880
$\phi$ Adults, Interval 4	0.811	0.042	0.715	0.880
$\phi$ Adults, Interval 5	0.811	0.042	0.716	0.880
$\phi$ Adults, Interval 6	0.811	0.042	0.715	0.880
$\phi$ Adults, Interval 7	0.811	0.042	0.714	0.881
$\phi$ Adults, Interval 8	0.810	1.862	0.000	1.000
$p$ Immatures, Occasion 2	0.722	0.078	0.548	0.847
$p$ Immatures, Occasion 3	0.472	0.059	0.360	0.588
$p$ Immatures, Occasion 4	0.385	0.057	0.281	0.501
$p$ Immatures, Occasion 5	0.390	0.061	0.279	0.513
$p$ Immatures, Occasion 6	0.238	0.055	0.147	0.361
$p$ Immatures, Occasion 7	0.339	0.068	0.221	0.480
$p$ Immatures, Occasion 8	0.622	0.090	0.437	0.777
$p$ Immatures, Occasion 9	0.346	2.413	0.000	1.000
$p$ Adults, Occasion 2	0.735	0.073	0.572	0.852
$p$ Adults, Occasion 3	0.462	0.063	0.344	0.584
$p$ Adults, Occasion 4	0.380	0.060	0.271	0.503
$p$ Adults, Occasion 5	0.379	0.069	0.255	0.521
$p$ Adults, Occasion 6	0.230	0.060	0.134	0.368
$p$ Adults, Occasion 7	0.328	0.077	0.198	0.491
$p$ Adults, Occasion 8	0.590	0.132	0.331	0.807
$p$ Adults, Occasion 9	0.321	1.814	0.000	1.000

*Appendix 3.7. Model-averaged CJS parameter estimates, Fall 2012.*

Parameter	Estimate	SE	95% Confidence Interval	
			Lower	Upper
$\phi$ Immatures, Interval 1	0.530	0.064	0.406	0.650
$\phi$ Immatures, Interval 2	0.922	0.038	0.806	0.971
$\phi$ Immatures, Interval 3	0.922	0.038	0.805	0.971
$\phi$ Immatures, Interval 4	0.922	0.038	0.806	0.971
$\phi$ Immatures, Interval 5	0.922	0.039	0.805	0.971
$\phi$ Immatures, Interval 6	0.922	0.038	0.806	0.971
$\phi$ Immatures, Interval 7	0.922	0.144	0.189	0.998
$\phi$ Immatures, Interval 8	0.922	0.144	0.189	0.998
$\phi$ Immatures, Interval 9	0.922	0.495	0.000	1.000
$\phi$ Adults, Interval 1	0.735	0.076	0.564	0.856
$\phi$ Adults, Interval 2	0.947	0.045	0.758	0.990
$\phi$ Adults, Interval 3	0.947	0.045	0.757	0.990
$\phi$ Adults, Interval 4	0.947	0.045	0.758	0.990
$\phi$ Adults, Interval 5	0.947	0.045	0.757	0.990
$\phi$ Adults, Interval 6	0.947	0.045	0.758	0.990
$\phi$ Adults, Interval 7	0.947	0.146	0.058	1.000
$\phi$ Adults, Interval 8	0.947	0.146	0.058	1.000
$\phi$ Adults, Interval 9	0.947	0.495	0.000	1.000
$p$ Immatures, Occasion 2	0.999	0.022	0.956	1.043
$p$ Immatures, Occasion 3	0.167	0.152	0.023	0.631
$p$ Immatures, Occasion 4	0.429	0.126	0.215	0.673
$p$ Immatures, Occasion 5	0.671	0.073	0.515	0.797
$p$ Immatures, Occasion 6	0.307	0.066	0.195	0.448
$p$ Immatures, Occasion 7	0.692	0.069	0.545	0.809
$p$ Immatures, Occasion 8	0.450	0.000	0.449	0.451
$p$ Immatures, Occasion 9	0.464	0.082	0.312	0.623
$p$ Immatures, Occasion 10	0.551	0.524	0.019	0.987
$p$ Adults, Occasion 2	0.999	0.022	0.957	1.042
$p$ Adults, Occasion 3	0.167	0.152	0.023	0.631
$p$ Adults, Occasion 4	0.429	0.126	0.215	0.673
$p$ Adults, Occasion 5	0.671	0.073	0.515	0.796
$p$ Adults, Occasion 6	0.307	0.066	0.195	0.448
$p$ Adults, Occasion 7	0.692	0.069	0.545	0.809
$p$ Adults, Occasion 8	0.450	0.001	0.449	0.451
$p$ Adults, Occasion 9	0.464	0.082	0.312	0.623
$p$ Adults, Occasion 10	0.551	0.539	0.017	0.989

*Appendix 3.8. Model-averaged CJS parameter estimates, Spring 2013.*

Parameter	Estimate	SE	95% Confidence Interval	
			Lower	Upper
$\phi$ Immatures, Interval 1	0.696	0.045	0.601	0.777
$\phi$ Immatures, Interval 2	0.697	0.049	0.595	0.783
$\phi$ Immatures, Interval 3	0.696	0.047	0.597	0.779
$\phi$ Immatures, Interval 4	0.694	0.049	0.591	0.780
$\phi$ Immatures, Interval 5	0.696	0.049	0.593	0.782
$\phi$ Immatures, Interval 6	0.695	4.163	0.000	1.000
$\phi$ Adults, Interval 1	0.727	0.106	0.484	0.883
$\phi$ Adults, Interval 2	0.698	0.057	0.576	0.797
$\phi$ Adults, Interval 3	0.697	0.056	0.578	0.794
$\phi$ Adults, Interval 4	0.695	0.058	0.572	0.795
$\phi$ Adults, Interval 5	0.696	0.058	0.573	0.797
$\phi$ Adults, Interval 6	0.696	4.198	0.000	1.000
$p$ Immatures, Occasion 2	0.336	0.051	0.245	0.441
$p$ Immatures, Occasion 3	0.336	0.051	0.245	0.442
$p$ Immatures, Occasion 4	0.338	0.053	0.243	0.448
$p$ Immatures, Occasion 5	0.336	0.051	0.244	0.442
$p$ Immatures, Occasion 6	0.337	0.052	0.243	0.445
$p$ Immatures, Occasion 7	0.336	4.166	0.000	1.000
$p$ Adults, Occasion 2	0.312	0.064	0.202	0.448
$p$ Adults, Occasion 3	0.312	0.064	0.201	0.449
$p$ Adults, Occasion 4	0.314	0.066	0.200	0.455
$p$ Adults, Occasion 5	0.312	0.064	0.201	0.449
$p$ Adults, Occasion 6	0.313	0.066	0.200	0.453
$p$ Adults, Occasion 7	0.312	4.190	0.000	1.000

*Appendix 3.9. Goodness-of-fit tests for CJS models.*

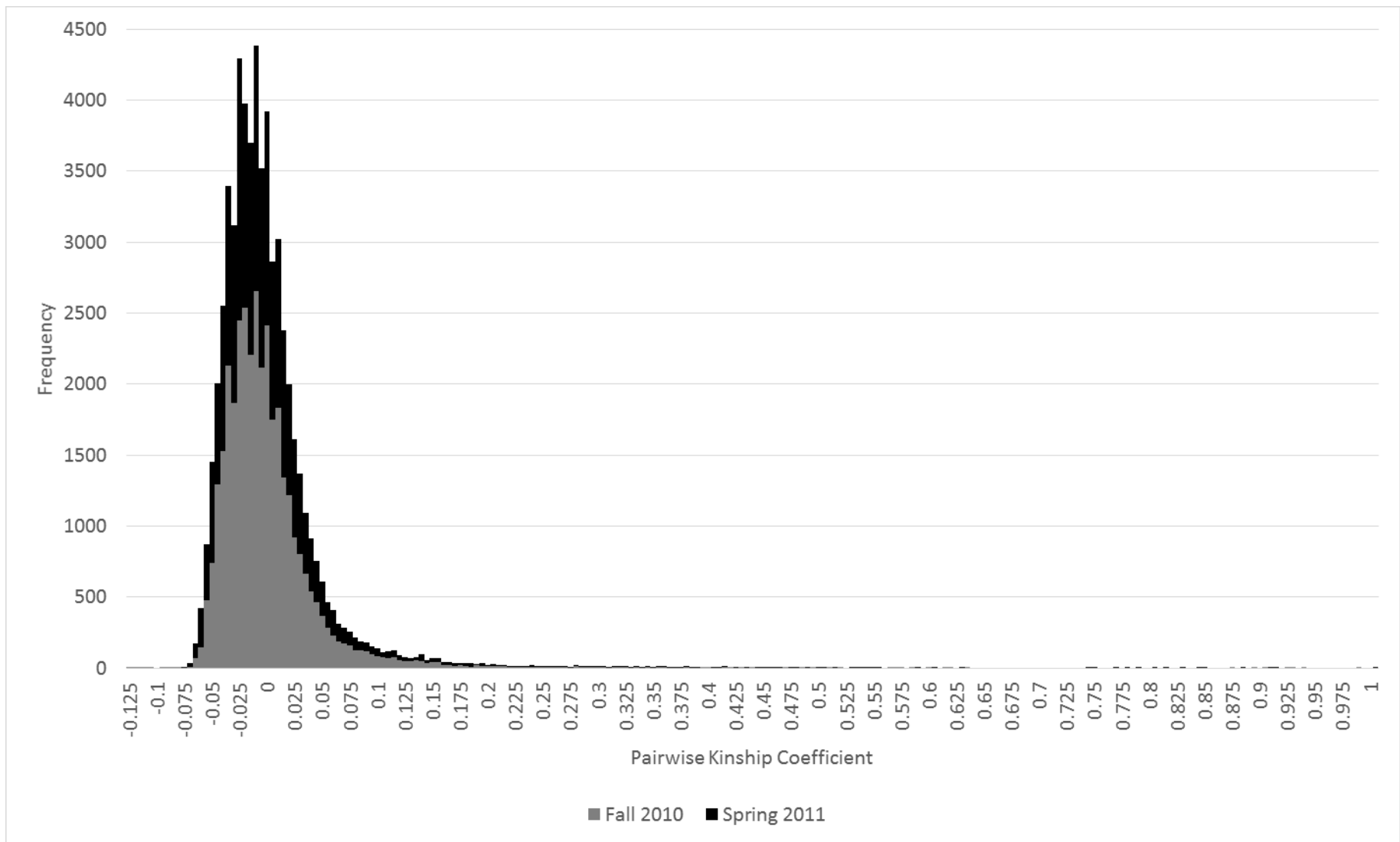
<b>Season</b>	<b>Group</b>	<b>Component</b>	<b>Chi-Square</b>	<b>df</b>	<b>P-Level</b>
Fall 2009	Group 1	Test 2	1.466	3	0.6901
Fall 2009	Group 2	Test 2	5.9147	3	0.1158
Fall 2009	All Groups	Test 2	7.3806	6	0.2871
Spring 2010	Group 1	Test 2	1.3233	2	0.5160
Spring 2010	Group 2	Test 2	0	0	1.0000
Spring 2010	All Groups	Test 2	1.3233	2	0.5160
Fall 2010	Group 1	Test 3	6.7333	11	0.8203
Fall 2010	Group 2	Test 3	3.7652	11	0.9763
Fall 2010	All Groups	Test 3	10.4985	22	0.9812
Fall 2010	Group 1	Test 2	4.5438	6	0.6035
Fall 2010	Group 2	Test 2	10.2621	8	0.2471
Fall 2010	All Groups	Test 2	14.8059	14	0.3916
Fall 2010	Group 1	Test 2 + Test 3	11.2771	17	0.8418
Fall 2010	Group 2	Test 2 + Test 3	14.0273	19	0.7821
Fall 2010	All Groups	Test 2 + Test 3	25.3044	36	0.9086
Spring 2011	Group 1	Test 3	7.5822	13	0.8697
Spring 2011	Group 2	Test 3	5.5564	11	0.9013
Spring 2011	All Groups	Test 3	13.1386	24	0.9638
Spring 2011	Group 1	Test 2	11.2979	6	0.0796
Spring 2011	Group 2	Test 2	0	5	1.0000
Spring 2011	All Groups	Test 2	11.2979	11	0.4187
Spring 2011	Group 1	Test 2 + Test 3	18.8801	19	0.4646
Spring 2011	Group 2	Test 2 + Test 3	5.5564	16	0.9922
Spring 2011	All Groups	Test 2 + Test 3	24.4365	35	0.9092
Fall 2011	Group 1	Test 3	1.3116	5	0.9337
Fall 2011	Group 2	Test 3	9.3007	5	0.0977
Fall 2011	All Groups	Test 3	10.6123	10	0.3885
Fall 2011	Group 1	Test 2	0.5846	2	0.7465
Fall 2011	Group 2	Test 2	4.1043	3	0.2504
Fall 2011	All Groups	Test 2	4.6889	5	0.4550
Fall 2011	Group 1	Test 2 + Test 3	1.8962	7	0.9654
Fall 2011	Group 2	Test 2 + Test 3	13.405	8	0.0987
Fall 2011	All Groups	Test 2 + Test 3	15.3012	15	0.4299
Spring 2012	Group 1	Test 3	5.7509	11	0.8895
Spring 2012	Group 2	Test 3	2.6657	10	0.9882
Spring 2012	All Groups	Test 3	8.4167	21	0.9931
Spring 2012	Group 1	Test 2	24.3817	9	0.0037
Spring 2012	Group 2	Test 2	12.0092	7	0.1003
Spring 2012	All Groups	Test 2	36.3909	16	0.0026

Spring 2012	Group 1	Test 2 + Test 3	30.1326	20	0.0677
Spring 2012	Group 2	Test 2 + Test 3	14.6749	17	0.6189
Spring 2012	All Groups	Test 2 + Test 3	44.8075	37	0.1770
Fall 2012	Group 1	Test 3	9.6192	10	0.4745
Fall 2012	Group 2	Test 3	13.958	8	0.0829
Fall 2012	All Groups	Test 3	23.5772	18	0.1694
Fall 2012	Group 1	Test 2	2.9218	5	0.7120
Fall 2012	Group 2	Test 2	5.252	5	0.3859
Fall 2012	All Groups	Test 2	8.1738	10	0.6119
Fall 2012	Group 1	Test 2 + Test 3	12.541	15	0.6377
Fall 2012	Group 2	Test 2 + Test 3	19.2099	13	0.1167
Fall 2012	All Groups	Test 2 + Test 3	31.751	28	0.2848
Spring 2013	Group 1	Test 3	2.5357	8	0.9600
Spring 2013	Group 2	Test 3	2.1474	3	0.5424
Spring 2013	All Groups	Test 3	4.6832	11	0.9455
Spring 2013	Group 1	Test 2	5.2899	5	0.3815
Spring 2013	Group 2	Test 2	0.4064	2	0.8161
Spring 2013	All Groups	Test 2	5.6963	7	0.5756
Spring 2013	Group 1	Test 2 + Test 3	7.8257	13	0.8548
Spring 2013	Group 2	Test 2 + Test 3	2.5538	5	0.7684
Spring 2013	All Groups	Test 2 + Test 3	10.3795	18	0.9188

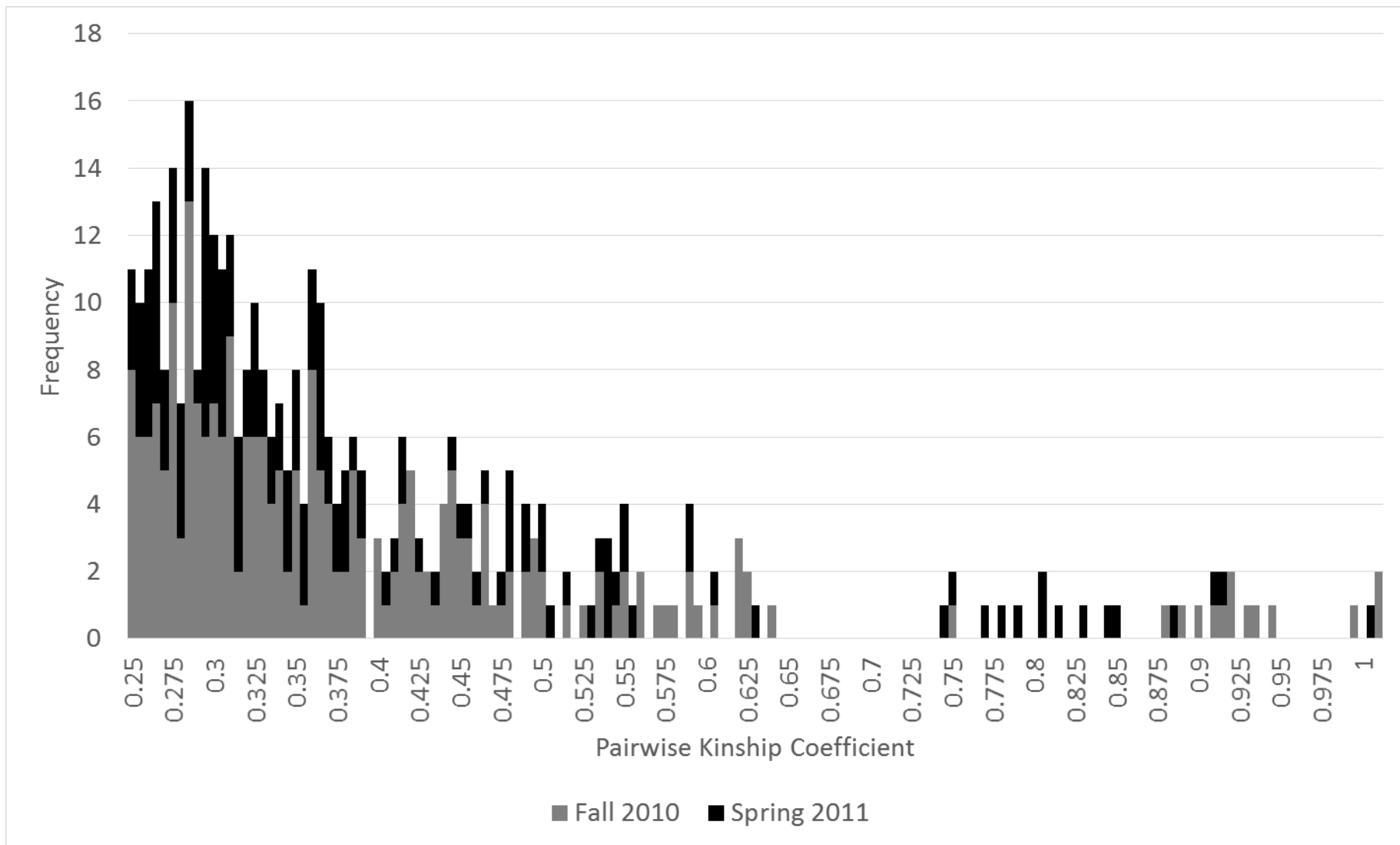
*Notes:* Groups 1 and 2 are immatures and adults, respectively. Test 2 evaluates whether the probability of being detected at occasion  $i + 1$  is a function of being detected at occasion  $i$ , given survival from  $i$  to  $i + 1$ ; rejection of Test 2 thus reflects heterogeneity in detection probability. Test 3 evaluates whether marked animals alive at occasion  $i$  have the same probability of surviving to  $i + 1$ ; rejection of Test 3 thus reflects heterogeneity in survival probability.

Appendix 4.1. Frequencies of estimated kinship values: Fall 2010, Spring 2011.

Top panel: all kinship values. Bottom panel: the subset of kinship values from 0.25–1.







## Bibliography

- ADAMS, D. C., and J. O. CHURCH. 2008. Amphibians do not follow Bergmann's rule. *Evolution* 62:413–420.
- AKAIKE, H. 1973. Information theory as an extension of the maximum likelihood principle. In B. N. Petrov and F. Csak (eds.), *Second International Symposium on Information Theory*, pp. 267–281. Akademiai Kiado, Budapest.
- ARENDR, J. D. 1997. Adaptive intrinsic growth rates: An integration across taxa. *Quarterly Review of Biology* 72:149–177.
- ASH, A. N. 1997. Disappearance and return of plethodontid salamanders to clearcut plots in the southern Blue Ridge Mountains. *Conservation Biology* 11:983–989.
- AUSTIN, J. D., J. A. DAVILA, S. C. LOUGHEED, and P. T. BOAG. 2003. Genetic evidence for female-biased dispersal in the bullfrog, *Rana catesbeiana* (Ranidae). *Molecular Ecology* 12:3165–3172.
- BAILEY, L. L. 2004. Evaluating elastomer marking and photo identification methods for terrestrial salamanders: Marking effects and observer bias. *Herpetological Review* 35:38–41.
- BAILEY, L. L., T. R. SIMONS, and K. H. POLLOCK. 2004. Estimating detection probability parameters for *Plethodon* salamanders using the robust capture-recapture design. *Journal of Wildlife Management* 68:1–13.
- BATEMAN, A. J. 1948. Intra-sexual selection in *Drosophila*. *Heredity* 2:349–368.
- BENGTSSON, B. O. 1978. Avoiding inbreeding: at what cost? *Journal of Theoretical Biology* 73:439–444.
- BERNER, D., and W. U. BLANCKENHORN. 2007. An ontogenetic perspective on the relationship between age and size at maturity. *Functional Ecology* 21:505–512.
- BERRY, O., M. D. TOCHER, and S. D. SARRE. 2004. Can assignment tests measure dispersal? *Molecular Ecology* 13:551–561.
- BERVEN, K. A., and T. A. GRUDZIEN. 1990. Dispersal in the wood frog (*Rana sylvatica*): implications for genetic population structure. *Evolution* 44:2047–2056.
- BEST, M. L., and J. H. H. WELSH. 2014. The trophic role of a forest salamander: impacts on invertebrates, leaf litter retention, and the humification process. *Ecosphere* 5:art16.
- BEYER, H. L. 2004. Hawth's Analysis Tools for ArcGIS. Available at <http://www.spatial ecology.com/htools>.
- BISHOP, S. C. 1941. The salamanders of New York. *New York State Museum Bulletin*:1–365.
- BLACKBURN, T. M., K. J. GASTON, and N. LODER. 1999. Geographic gradients in body size: A clarification of Bergmann's rule. *Diversity and Distributions* 5:165–174.
- BLANCHARD, F. N. 1928a. Amphibians and reptiles of the Douglas Lake region in northern Michigan. *Copeia* 1928:42–51.

- . 1928b. Topics from the life history and habits of the red-backed salamander in southern Michigan. *The American Naturalist* 62:156–164.
- BLOUIN, M. S. 2003. DNA-based methods for pedigree reconstruction and kinship analysis in natural populations. *Trends in Ecology & Evolution* 18:503–511.
- BONIN, J., and Y. BACHAND. 1997. The use of artificial covers to survey terrestrial salamanders in Québec. *In* D. M. Green (ed.), *Amphibians in Decline: Canadian Studies of a Global Problem*, pp. 175–179. Society for the Study of Amphibians and Reptiles, St. Louis, Missouri, USA.
- BOWLER, D. E., and T. G. BENTON. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Reviews* 80:205–225.
- BROOKS, R. T. 1999. Residual effects of thinning and high white-tailed deer densities on northern redback salamanders in southern New England oak forests. *Journal of Wildlife Management* 63:1172–1180.
- BROOKS, R. T. 2001. Effects of the removal of overstory hemlock from hemlock-dominated forests on eastern redback salamanders. *Forest Ecology and Management* 149:197–204.
- BROQUET, T., and E. J. PETIT. 2009. Molecular estimation of dispersal for ecology and population genetics. *Annual Review of Ecology Evolution and Systematics* 40:193–216.
- BRUCE, R. C. 2000. Sexual size dimorphism in the Plethodontidae. *In* R. C. Bruce, R. G. Jaeger, and L. D. Houck (eds.), *The Biology of Plethodontid Salamanders*, pp. 243–260. Kluwer Academic/Plenum Publishers, New York.
- BUCKLEY, L. B., and W. JETZ. 2007. Environmental and historical constraints on global patterns of amphibian richness. *Proceedings of the Royal Society B: Biological Sciences* 274:1167–1173.
- BURGER, J. W. 1935. *Plethodon cinereus* (Green) in Eastern Pennsylvania and New Jersey. *The American Naturalist* 69:578–586.
- BURNHAM, K. P., and D. R. ANDERSON. 2004. Multimodel inference - understanding AIC and BIC in model selection. *Sociological Methods & Research* 33:261–304.
- BURNHAM, K. P., D. R. ANDERSON, G. C. WHITE, C. BROWNIE, and K. H. POLLOCK. 1987. Design and analysis methods for fish survival experiments based on release-recapture. *American Fisheries Society Monograph* 5:1–437.
- BURTON, T. M., and G. E. LIKENS. 1975. Salamander populations and biomass in the Hubbard Brook Experimental Forest, New Hampshire. *Copeia* 1975:541–546.
- CABE, P. R., R. B. PAGE, T. J. HANLON, M. E. ALDRICH, L. CONNORS, and D. M. MARSH. 2007. Fine-scale population differentiation and gene flow in a terrestrial salamander (*Plethodon cinereus*) living in continuous habitat. *Heredity* 98:53–60.
- CACERES-CHARNECO, R. I., and T. S. RANSOM. 2010. The influence of habitat provisioning: use of earthworm burrows by the terrestrial salamander, *Plethodon cinereus*. *Population Ecology* 52:517–526.
- CALDWELL, R. S. 1975. Observations on the winter activity of the red-backed salamander *Plethodon cinereus* in Indiana, USA. *Herpetologica* 31:21–22.

- CALDWELL, R. S., and G. S. JONES. 1973. Winter congregations of *Plethodon cinereus* in ant mounds, with notes on their food habits. *American Midland Naturalist* 90:482–485.
- CAMPBELL GRANT, E. H. 2008. Visual implant elastomer mark retention through metamorphosis in amphibian larvae. *Journal of Wildlife Management* 72:1247–1252.
- CARFIOLI, M. A., H. M. TIEBOUT, III, S. A. PAGANO, K. M. HEISTER, and F. C. LUTCHER. 2000. Monitoring *Plethodon cinereus* populations: field tests of experimental coverboard designs. In R. C. Bruce, R. G. Jaeger, and L. D. Houck (eds.), *The Biology of Plethodontid Salamanders*, pp. 463–475. Kluwer Academic/Plenum Publishers, New York, New York, USA.
- CARLSON, T. A. Y., and E. J. SZUCH. 2007. Un-weathered (new) artificial cover objects effectively sample plethodontid salamanders in Michigan. *Herpetological Review* 38:412–415.
- CASTANET, J., H. FRANCILLONVIEILLOT, and R. C. BRUCE. 1996. Age estimation in desmognathine salamanders assessed by skeletochronology. *Herpetologica* 52:160–171.
- CLARK, A. B. 1978. Sex ratio and local resource competition in a prosimian primate. *Science* 201:163–165.
- CLARKE, A. L., B. E. SAETHER, and E. ROSKIFT. 1997. Sex biases in avian dispersal: A reappraisal. *Oikos* 79:429–438.
- CLOBERT, J., E. DANCHIN, A. A. DHONDT, and J. D. NICHOLS (eds.). 2001. *Dispersal*. Oxford University Press, New York.
- CLUTTON-BROCK, T., and B. C. SHELDON. 2010. Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Trends in Ecology & Evolution* 25:562–573.
- CLUTTON-BROCK, T. H., and D. LUKAS. 2012. The evolution of social philopatry and dispersal in female mammals. *Molecular Ecology* 21:472–492.
- COCHRAN, M. E. 1911. The biology of the red-backed salamander (*Plethodon cinereus erythronotus* Green). *Biological Bulletin* 20:332–349.
- CONNORS, L. M., and P. R. CABE. 2003. Isolation of dinucleotide microsatellite loci from red-backed salamander (*Plethodon cinereus*). *Molecular Ecology Notes* 3:131–133.
- COPE, E. D. 1889. *The Batrachia of North America*. Bulletin of the United States National Museum.
- CORMACK, R. M. 1964. Estimates of survival from sighting of marked animals. *Biometrika* 51:429–438.
- CORN, P. S. 2010. Selection of species and sampling areas: the importance to inference. In C. K. Dodd, Jr. (ed.), *Amphibian Ecology and Conservation: A Handbook of Techniques*, pp. 431–446. Oxford University Press, New York, New York, USA.
- CORN, P. S., and R. B. BURY. 1989. Logging in western Oregon: responses of headwater habitats and stream amphibians. *Forest Ecology and Management* 29:39–57.

- COTE, J., J. CLOBERT, and P. S. FITZE. 2007. Mother-offspring competition promotes colonization success. *Proceedings of the National Academy of Sciences of the United States of America* 104:9703–9708.
- DAVIC, R. D., and H. H. WELSH. 2004. On the ecological roles of salamanders. *Annual Review of Ecology, Evolution, and Systematics* 35:405–434.
- DAVIDSON, M., and H. HEATWOLE. 1960. Late summer oviposition in the salamander, *Plethodon cinereus*. *Herpetologica* 16:141–142.
- DAVIS, T. M. 1997. Non-disruptive monitoring of terrestrial salamanders with artificial cover objects on southern Vancouver Island, British Columbia. In D. M. Green (ed.), *Amphibians in Decline: Canadian Studies of a Global Problem*, pp. 161–174. Society for the Study of Amphibians and Reptiles, St. Louis, Missouri, USA.
- DAVIS, T. M., and K. OVASKA. 2001. Individual recognition of amphibians: Effects of toe clipping and fluorescent tagging on the salamander *Plethodon vehiculum*. *Journal of Herpetology* 35:217–225.
- DEGRAAF, R. M., and M. YAMASAKI. 1992. A nondestructive technique to monitor the relative abundance of terrestrial salamanders. *Wildlife Society Bulletin* 20:260–264.
- DEMAYNADIER, P. G., and M. L. HUNTER. 1998. Effects of silvicultural edges on the distribution and abundance of amphibians in Maine. *Conservation Biology* 12:340–352.
- DEMAYNADIER, P. G., and M. L. HUNTER, JR. 1995. The relationship between forest management and amphibian ecology: A review of the North American literature. *Environmental Reviews* 3:230–261.
- DIECKMANN, U., B. O'HARA, and W. WEISSER. 1999. The evolutionary ecology of dispersal. *Trends in Ecology & Evolution* 14:88–90.
- DOBSON, F. S. 1982. Competition for mates and predominant juvenile male dispersal in mammals. *Animal Behaviour* 30:1183–1192.
- DOBSON, F. S., and W. T. JONES. 1985. Multiple causes of dispersal. *American Naturalist* 126:855–858.
- DODD, C. K., and R. M. DORAZIO. 2004. Using counts to simultaneously estimate abundance and detection probabilities in a salamander community. *Herpetologica* 60:468–478.
- DODD, C. K., JR. (ed.). 2010. *Amphibian Ecology and Conservation: A Handbook of Techniques*. Oxford University Press, New York, New York, USA.
- EATON, M. J., and W. A. LINK. 2011. Estimating age from recapture data: integrating incremental growth measures with ancillary data to infer age-at-length. *Ecological Applications* 21:2487–2497.
- EMLEN, S. T., and L. W. ORING. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215–223.
- FABENS, A. J. 1965. Properties and fitting of the von Bertalanffy growth curve. *Growth* 29:265–289.
- FAVRE, L., F. BALLOUX, J. GOUDET, and N. PERRIN. 1997. Female-biased dispersal in the monogamous mammal *Crocodyrus russula*: Evidence from field data and microsatellite patterns. *Proceedings of the Royal Society of London Series B-Biological Sciences* 264:127–132.

- FEDER, M. E. 1983. Integrating the ecology and physiology of plethodontid salamanders. *Herpetologica* 39:291–310.
- FELLERS, G. M., and C. A. DROST. 1994. Sampling with artificial cover. In W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L.-A. C. Hayek, and M. S. Foster (eds.), *Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians*, pp. 146–150. Smithsonian Institution Press, Washington, DC, USA.
- FISHER-REID, M. C., T. N. ENGSTROM, C. A. KUCZYNSKI, P. R. STEPHENS, and J. J. WIENS. 2013. Parapatric divergence of sympatric morphs in a salamander: incipient speciation on Long Island? *Molecular Ecology* 22:4681–4694.
- FONTANILLAS, P., E. PETIT, and N. PERRIN. 2004. Estimating sex-specific dispersal rates with autosomal markers in hierarchically structured populations. *Evolution* 58:886–894.
- FOX, J., and S. WEISBERG. 2011. *An R Companion to Applied Regression*. Sage, Thousand Oaks, CA, USA.
- GABOR, C. R., and R. G. JAEGER. 1995. Resource quality affects the agonistic behaviour of territorial salamanders. *Animal Behaviour* 49:71–79.
- GABOR, C. R., J. D. KRENZ, and R. G. JAEGER. 2000. Female choice, male interference, and sperm precedence in the red-spotted newt. *Behavioral Ecology* 11:115–124.
- GARNER, T. W. J., and B. R. SCHMIDT. 2003. Relatedness, body size and paternity in the alpine newt, *Triturus alpestris*. *Proceedings of the Royal Society of London Series B-Biological Sciences* 270:619–624.
- GAUFFRE, B., E. PETIT, S. BRODIER, V. BRETAGNOLLE, and J. F. COSSON. 2009. Sex-biased dispersal patterns depend on the spatial scale in a social rodent. *Proceedings of the Royal Society B-Biological Sciences* 276:3487–3494.
- GIBBS, J. P. 1998. Distribution of woodland amphibians along a forest fragmentation gradient. *Landscape Ecology* 13:263–268.
- GILLESPIE, R. G., B. G. BALDWIN, J. M. WATERS, C. I. FRASER, R. NIKULA, and G. K. RODERICK. 2012. Long-distance dispersal: a framework for hypothesis testing. *Trends in Ecology & Evolution* 27:47–56.
- GILLETTE, J. R. 2003. Population ecology, social behavior, and intersexual differences in a natural population of red-backed salamanders: a long-term field study. Unpubl. Ph.D. Diss., University of Louisiana at Lafayette, Lafayette, Louisiana, USA.
- GILLETTE, J. R., R. G. JAEGER, and M. G. PETERSON. 2000. Social monogamy in a territorial salamander. *Animal Behaviour* 59:1241–1250.
- GILLETTE, J. R., and M. G. PETERSON. 2001. The benefits of transparency: Candling as a simple method for determining sex in red-backed salamanders (*Plethodon cinereus*). *Herpetological Review* 32:233–235.
- GOPURENKO, D., R. N. WILLIAMS, C. R. MCCORMICK, and J. A. DEWOODY. 2006. Insights into the mating habits of the tiger salamander (*Ambystoma tigrinum tigrinum*) as revealed by genetic parentage analyses. *Molecular Ecology* 15:1917–1928.
- GOUDET, J. 1995. FSTAT (Version 1.2): A computer program to calculate F-statistics. *Journal of Heredity* 86:485–486.

- GOUDET, J., N. PERRIN, and P. WASER. 2002. Tests for sex-biased dispersal using biparentally inherited genetic markers. *Molecular Ecology* 11:1103–1114.
- GRANT, B. W., A. D. TUCKER, J. E. LOVICH, A. M. MILLS, P. M. DIXON, and J. W. GIBBONS. 1992. The use of coverboards in estimating patterns of reptile and amphibian biodiversity. *In* D. R. McCullough and R. H. Barrett (eds.), *Wildlife 2001: Populations*, pp. 379–403. Elsevier Science Publishers Ltd., Essex, UK.
- GREEN, J. 1818. Descriptions of several species of North American Amphibia, accompanied with observations. *Journal of the Academy of Natural Sciences of Philadelphia* 1:348–359.
- GREENWOOD, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* 28:1140–1162.
- GRIFFITH, S. C., I. P. F. OWENS, and K. A. THUMAN. 2002. Extra pair paternity in birds: a review of interspecific variation and adaptive function. *Molecular Ecology* 11:2195–2212.
- GROVER, M. C. 2000. Determinants of salamander distributions along moisture gradients. *Copeia* 2000:156–168.
- GUFFEY, C., J. G. MAKINSTER, and R. G. JAEGER. 1998. Familiarity affects interactions between potentially courting territorial salamanders. *Copeia* 1998:205–208.
- GUNDERSEN, G., and H. P. ANDREASSEN. 1998. Causes and consequences of natal dispersal in root voles, *Microtus oeconomus*. *Animal Behaviour* 56:1355–1366.
- HALLIDAY, T. R., and P. A. VERRELL. 1988. Body size and age in amphibians and reptiles. *Journal of Herpetology* 22:253–265.
- HAMILTON, W. D. 1967. Extraordinary sex ratios. *Science* 156:477–488.
- HAMILTON, W. D., and R. M. MAY. 1977. Dispersal in stable habitats. *Nature* 269:578–581.
- HAMPTON, P. 2007. A comparison of the success of artificial cover types for capturing amphibians and reptiles. *Amphibia-Reptilia* 28:433–437.
- HARDING, J. P. 1949. The use of probability paper for the graphical analysis of polymodal frequency distributions. *Journal of the Marine Biological Association of the United Kingdom* 28:141–153.
- HARDY, O. J., and X. VEKEMANS. 2002. SPAGEDi: a versatile computer program to analyse spatial genetic structure at the individual or population levels. *Molecular Ecology Notes* 2:618–620.
- HARPOLE, D. N., and C. A. HAAS. 1999. Effects of seven silvicultural treatments on terrestrial salamanders. *Forest Ecology and Management* 114:349–356.
- HARRIS, R. N., and P. M. LUDWIG. 2004. Resource level and reproductive frequency in female four-toed salamanders, *Hemidactylium scutatum*. *Ecology* 85:1585–1590.
- HATCHWELL, B. J. 2010. Cryptic kin selection: kin structure in vertebrate populations and opportunities for kin-directed cooperation. *Ethology* 116:203–216.
- HEATWOLE, H. 1962. Environmental factors influencing local distribution and activity of the salamander, *Plethodon cinereus*. *Ecology* 43:460–472.

- HEEMEYER, J. L., J. A. HOMOYACK, and C. A. HAAS. 2007. Retention and readability of visible implant elastomer marks in eastern red-backed salamanders (*Plethodon cinereus*). *Herpetological Review* 38:425–428.
- HEYER, W. R., M. A. DONNELLY, R. W. MCDIARMID, L.-A. C. HAYEK, and M. S. FOSTER (eds.). 1994. *Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians*. Smithsonian Institution Press, Washington, DC, USA.
- HIGHTON, R. 1959. The inheritance of the color phases of *Plethodon cinereus*. *Copeia* 1959:33–37.
- HIGHTON, R. 2005. Declines of eastern North American woodland salamanders (*Plethodon*). In M. Lannoo (ed.), *Amphibian Declines: The Conservation Status of United States Species*, pp. 34–46. University of California Press, Berkeley, California, USA.
- HIGHTON, R., and T. P. WEBSTER. 1976. Geographic protein variation and divergence in populations of the salamander *Plethodon cinereus*. *Evolution* 30:33–45.
- HOCKING, D. J., and K. J. BABBITT. 2014. Effects of Red-Backed Salamanders on Ecosystem Functions. *Plos One* 9.
- HOMOYACK, J. A., and C. A. HAAS. 2009. Long-term effects of experimental forest harvesting on abundance and reproductive demography of terrestrial salamanders. *Biological Conservation* 142:110–121.
- HOTCHKISS, N., and R. E. STEWART. 1947. Vegetation of the Patuxent Research Refuge, Maryland. *American Midland Naturalist* 38:1–75.
- HOUCK, L. D. 1977. Life history patterns and reproductive biology of neotropical salamanders. In D. Taylor and S. Guttman (eds.), *The Reproductive Biology of Amphibians*, pp. 43–72. Plenum Press, New York, NY, USA.
- HOUZE, C. M., and C. R. CHANDLER. 2002. Evaluation of coverboards for sampling terrestrial salamanders in south Georgia. *Journal of Herpetology* 36:75–81.
- HOWARD, W. E. 1960. Innate and environmental dispersal of individual vertebrates. *American Midland Naturalist* 63:152–161.
- HUGHES, C. 1998. Integrating molecular techniques with field methods in studies of social behavior: A revolution results. *Ecology* 79:383–399.
- HYDE, E. J., and T. R. SIMONS. 2001. Sampling plethodontid salamanders: sources of variability. *Journal of Wildlife Management* 65:624–632.
- JAEGER, R. G. 1971. Competitive exclusion as a factor influencing distributions of two species of terrestrial salamanders. *Ecology* 52:632–637.
- . 1972. Food as a limited resource in competition between two species of terrestrial salamanders. *Ecology* 53:535–546.
- . 1981. Dear enemy recognition and costs of aggression between salamanders. *American Naturalist* 117:962–974.
- JAEGER, R. G., J. R. GILLETTE, and R. C. COOPER. 2002. Sexual coercion in a territorial salamander: males punish socially polyandrous female partners. *Animal Behaviour* 63:871–877.
- JAEGER, R. G., M. G. PETERSON, G. GOLLMANN, B. GOLLMANN, and V. R. TOWNSEND, JR. 2001. Salamander social strategies: living together in female-male pairs. *Journal of Herpetology* 35:335–338.



- JAEGER, R. G., J. A. WICKNICK, M. R. GRIFFIS, and C. D. ANTHONY. 1995. Socioecology of a terrestrial salamander: juveniles enter adult territories during stressful foraging periods. *Ecology* 76:533–543.
- JARNE, P., and P. J. L. LAGODA. 1996. Microsatellites, from molecules to populations and back. *Trends in Ecology & Evolution* 11:424–429.
- JOHNSON, M. L., and M. S. GAINES. 1990. Evolution of dispersal: Theoretical models and empirical tests using birds and mammals. *Annual Review of Ecology and Systematics* 21:449–480.
- JOLLY, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika* 52:225–247.
- JOLY, P., and O. GROLET. 1996. Colonization dynamics of new ponds, and the age structure of colonizing Alpine newts, *Triturus alpestris*. *Acta Oecologica-International Journal of Ecology* 17:599–608.
- JONES, A. G., E. M. ADAMS, and S. J. ARNOLD. 2002. Topping off: A mechanism of first-male sperm precedence in a vertebrate. *Proceedings of the National Academy of Sciences of the United States of America* 99:2078–2081.
- JORDAN, M. A., D. A. MORRIS, and S. E. GIBSON. 2009. The influence of historical landscape change on genetic variation and population structure of a terrestrial salamander (*Plethodon cinereus*). *Conservation Genetics* 10:1647–1658.
- JOSEPH, L. L., C. T. COPE, N. R. KOHN, and R. G. JAEGER. 2005. The influence of familiarity on socially monogamous behavior of red-backed salamanders. *Herpetologica* 61:343–348.
- JUNG, R. E., S. DROEGE, J. R. SAUER, and R. B. LANDY. 2000. Evaluation of terrestrial and streamside salamander monitoring techniques at Shenandoah National Park. *Environmental Monitoring and Assessment* 63:65–79.
- KELLER, L. F., and D. M. WALLER. 2002. Inbreeding effects in wild populations. *Trends in Ecology & Evolution* 17:230–241.
- KENDALL, W. L., and R. BJORKLAND. 2001. Using open robust design models to estimate temporary emigration from capture-recapture data. *Biometrics* 57:1113–1122.
- KENDALL, W. L., C. A. LANGTIMM, C. A. BECK, and M. C. RUNGE. 2004. Capture-recapture analysis for estimating manatee reproductive rates. *Marine Mammal Science* 20:424–437.
- KENDALL, W. L., and J. D. NICHOLS. 1995. On the use of secondary capture-recapture samples to estimate temporary emigration and breeding proportions. *Journal of Applied Statistics* 22:751–762.
- . 2002. Estimating state-transition probabilities for unobservable states using capture-recapture/resighting data. *Ecology* 83:3276–3284.
- KENDALL, W. L., J. D. NICHOLS, and J. E. HINES. 1997. Estimating temporary emigration using capture-recapture data with Pollock's robust design. *Ecology* 78:563–578.
- KENDALL, W. L., K. H. POLLOCK, and C. BROWNIE. 1995. A likelihood-based approach to capture-recapture estimation of demographic parameters under the robust design. *Biometrics* 51:293–308.

- KENDALL, W. L., G. C. WHITE, J. E. HINES, C. A. LANGTIMM, and J. YOSHIZAKI. 2012. Estimating parameters of hidden Markov models based on marked individuals: use of robust design data. *Ecology* 93:913–920.
- KERBY, J. L., K. L. RICHARDS-HRDLICKA, A. STORFER, and D. K. SKELLY. 2010. An examination of amphibian sensitivity to environmental contaminants: are amphibians poor canaries? *Ecology Letters* 13:60–67.
- KNOPP, T., and J. MERILA. 2009. Microsatellite variation and population structure of the moor frog (*Rana arvalis*) in Scandinavia. *Molecular Ecology* 18:2996–3005.
- KROLL, A. J., M. P. HAYES, and J. G. MACCRACKEN. 2009. Concerns regarding the use of amphibians as metrics of critical biological thresholds: a comment on Welsh & Hodgson (2008). *Freshwater Biology* 54:2364–2373.
- LAAKE, J., and E. REXSTAD. 2008. RMark: R code for MARK.
- LAMBIN, X. 1994. Natal philopatry, competition for resources, and inbreeding avoidance in Townsend's voles (*Microtus townsendii*). *Ecology* 75:224–235.
- LAMPERT, K. P., A. S. RAND, U. G. MUELLER, and M. J. RYAN. 2003. Fine-scale genetic pattern and evidence for sex-biased dispersal in the tungara frog, *Physalaemus pustulosus*. *Molecular Ecology* 12:3325–3334.
- LANG, C., and R. G. JAEGER. 2000. Defense of territories by male-female pairs in the red-backed salamander (*Plethodon cinereus*). *Copeia* 2000:169–177.
- LAWSON HANDLEY, L. J., and N. PERRIN. 2007. Advances in our understanding of mammalian sex-biased dispersal. *Molecular Ecology* 16:1559–1578.
- LEBRETON, J. D., K. P. BURNHAM, J. CLOBERT, and D. R. ANDERSON. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62:67–118.
- LECLAIR, M. H., M. LEVASSEUR, and R. LECLAIR. 2006. Life-history traits of *Plethodon cinereus* in the northern parts of its range: Variations in population structure, age and growth. *Herpetologica* 62:265–282.
- LEGENDRE, P. 1993. Spatial autocorrelation: trouble or new paradigm? *Ecology* 74:1659–1673.
- LENA, J. P., J. CLOBERT, M. DE FRAIPONT, J. LECOMTE, and G. GUYOT. 1998. The relative influence of density and kinship on dispersal in the common lizard. *Behavioral Ecology* 9:500–507.
- LIEBGOLD, E. B., E. D. BRODIE, and P. R. CABE. 2011. Female philopatry and male-biased dispersal in a direct-developing salamander, *Plethodon cinereus*. *Molecular Ecology* 20:249–257.
- LIEBGOLD, E. B., and P. R. CABE. 2008. Familiarity with adults, but not relatedness, affects the growth of juvenile red-backed salamanders (*Plethodon cinereus*). *Behavioral Ecology and Sociobiology* 63:277–284.
- LIEBGOLD, E. B., P. R. CABE, R. G. JAEGER, and P. L. LEBERG. 2006. Multiple paternity in a salamander with socially monogamous behaviour. *Molecular Ecology* 15:4153–4160.
- LIEBGOLD, E. B., and C. J. DIBBLE. 2011. Better the devil you know: familiarity affects foraging activity of red-backed salamanders, *Plethodon cinereus*. *Animal Behaviour* 82:1059–1066.

- LINK, W. A., and K. MILLER HESED. in review. Individual heterogeneity in growth and age of sexual maturity: a gamma process analysis of capture-mark-recapture data. *Journal of Agricultural, Biological, and Environmental Statistics*.
- LIPS, K. R., J. K. REASER, B. E. YOUNG, and R. IBÁÑEZ. 2001. *Amphibian Monitoring in Latin America: A Protocol Manual*. Society for the Study of Amphibians and Reptiles, Ithaca, NY.
- LUHRING, T. M., and C. A. YOUNG. 2006. Innovative techniques for sampling stream-inhabiting salamanders. *Herpetological Review* 37:181–183.
- LUNN, D., D. SPIEGELHALTER, A. THOMAS, and N. BEST. 2009. The BUGS project: Evolution, critique and future directions. *Statistics in Medicine* 28:3049–3067.
- LYNN, W. G., and J. N. DENT. 1941. Notes on *Plethodon cinereus* and *Hemidactylium scutatum* on Cape Cod. *Copeia* 1941:113–114.
- MAERZ, J. C., V. A. NUZZO, and B. BLOSSEY. 2009. Declines in woodland salamander abundance associated with non-native earthworm and plant invasions. *Conservation Biology* 23:975–981.
- MAIORANA, V. C. 1976. Size and environmental predictability for salamanders. *Evolution* 30:599–613.
- MANEL, S., O. E. GAGGIOTTI, and R. S. WAPLES. 2005. Assignment methods: Matching biological questions techniques with appropriate. *Trends in Ecology & Evolution* 20:136–142.
- MANEL, S., M. K. SCHWARTZ, G. LUIKART, and P. TABERLET. 2003. Landscape genetics: Combining landscape ecology and population genetics. *Trends in Ecology & Evolution* 18:189–197.
- MANTEL, N. 1967. Detection of disease clustering and a generalized regression approach. *Cancer Research* 27:209–220.
- MARSH, D. M., and M. A. GOICOCHEA. 2003. Monitoring terrestrial salamanders: biases caused by intense sampling and choice of cover objects. *Journal of Herpetology* 37:460–466.
- MARSH, D. M., R. B. PAGE, T. J. HANLON, H. BAREKE, R. CORRITONE, N. JETTER, N. G. BECKMAN, K. GARDNER, D. E. SEIFERT, and P. R. CABE. 2007. Ecological and genetic evidence that low-order streams inhibit dispersal by red-backed salamanders (*Plethodon cinereus*). *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 85:319–327.
- MARSH, D. M., R. B. PAGE, T. J. HANLON, R. CORRITONE, E. C. LITTLE, D. E. SEIFERT, and P. R. CABE. 2008. Effects of roads on patterns of genetic differentiation in red-backed salamanders, *Plethodon cinereus*. *Conservation Genetics* 9:603–613.
- MARSH, D. M., K. A. THAKUR, K. C. BULKA, and L. B. CLARKE. 2004. Dispersal and colonization through open fields by a terrestrial, woodland salamander. *Ecology* 85:3396–3405.
- MARVIN, G. A. 1996. Life history and population characteristics of the salamander *Plethodon kentucki* with a review of *Plethodon* life histories. *American Midland Naturalist* 136:385–400.

- MATHEWSON, B. 2009. The relative abundance of eastern red-backed salamanders in eastern hemlock-dominated and mixed deciduous forests at Harvard Forest. *Northeastern Naturalist* 16:1–12.
- MATHIS, A. 1990. Territoriality in a terrestrial salamander: the influence of resource quality and body size. *Behaviour* 112:162–175.
- . 1991. Territories of male and female terrestrial salamanders: Costs, benefits, and intersexual spatial associations. *Oecologia* 86:433–440.
- MATHIS, A., R. G. JAEGER, W. H. KEEN, P. K. DUCEY, S. C. WALLS, and B. W. BUCHANAN. 1995. Aggression and territoriality by salamanders and a comparison with the territorial behaviour of frogs. *In* H. Heatwole and B. K. Sullivan (eds.), *Amphibian Biology*, Vol. 2. *Social Behaviour*, pp. 633–676. Surrey Beatty and Sons, Chipping Norton, NSW, Australia.
- MAZEROLLE, M. J., L. L. BAILEY, W. L. KENDALL, J. A. ROYLE, S. J. CONVERSE, and J. D. NICHOLS. 2007. Making great leaps forward: accounting for detectability in herpetological field studies. *Journal of Herpetology* 41:672–689.
- MCDADE, K. A., and C. C. MAGUIRE. 2005. Comparative effectiveness of three techniques for salamander and gastropod land surveys. *American Midland Naturalist* 153:309–320.
- MESSERE, M., and P. K. DUCEY. 1998. Forest floor distribution of northern redback salamanders, *Plethodon cinereus*, in relation to canopy gaps: first year following selective logging. *Forest Ecology and Management* 107:319–324.
- MILLER HESED, K. 2012. Uncovering salamander ecology: a review of coverboard design. *Journal of Herpetology* 46:442–450.
- MONSEN, K. J., and M. S. BLOUIN. 2003. Genetic structure in a montane ranid frog: restricted gene flow and nuclear-mitochondrial discordance. *Molecular Ecology* 12:3275–3286.
- MONTI, L., M. HUNTER, and J. WITHAM. 2000. An evaluation of the artificial cover object (ACO) method for monitoring populations of the redback salamander *Plethodon cinereus*. *Journal of Herpetology* 34:624–629.
- MOORE, J.-D. 2005. Use of native dominant wood as a new coverboard type for monitoring eastern red-backed salamanders. *Herpetological Review* 36:268–271.
- MORNEAULT, A. E., B. J. NAYLOR, L. S. SCHAEFFER, and D. C. OTHMER. 2004. The effect of shelterwood harvesting and site preparation on eastern red-backed salamanders in white pine stands. *Forest Ecology and Management* 199:1–10.
- MORRISON, C., and J. M. HERO. 2003. Geographic variation in life-history characteristics of amphibians: a review. *Journal of Animal Ecology* 72:270–279.
- MOSSMAN, C. A., and P. M. WASER. 1999. Genetic detection of sex-biased dispersal. *Molecular Ecology* 8:1063–1067.
- MYERS, E. M., and K. R. ZAMUDIO. 2004. Multiple paternity in an aggregate breeding amphibian: the effect of reproductive skew on estimates of male reproductive success. *Molecular Ecology* 13:1951–1963.
- NAGEL, J. W. 1977. Life history of the red-backed salamander *Plethodon cinereus* in northeastern Tennessee, USA. *Herpetologica* 33:13–18.

- NATHAN, R., G. PERRY, J. T. CRONIN, A. E. STRAND, and M. L. CAIN. 2003. Methods for estimating long-distance dispersal. *Oikos* 103:261–273.
- NOEL, S., and F. J. LAPOINTE. 2010. Urban conservation genetics: Study of a terrestrial salamander in the city. *Biological Conservation* 143:2823–2831.
- NOEL, S., M. OUELLET, P. GALOIS, and F. J. LAPOINTE. 2007. Impact of urban fragmentation on the genetic structure of the eastern red-backed salamander. *Conservation Genetics* 8:599–606.
- OLALLA-TARRAGA, M. A., L. M. BINI, J. A. F. DINIZ, and M. A. RODRIGUEZ. 2010. Cross-species and assemblage-based approaches to Bergmann's rule and the biogeography of body size in *Plethodon* salamanders of eastern North America. *Ecography* 33:362–368.
- OLALLA-TARRAGA, M. A., and M. A. RODRIGUEZ. 2007. Energy and interspecific body size patterns of amphibian faunas in Europe and North America: anurans follow Bergmann's rule, urodeles its converse. *Global Ecology and Biogeography* 16:606–617.
- PAETKAU, D., W. CALVERT, I. STIRLING, and C. STROBECK. 1995. Microsatellite analysis of population structure in Canadian polar bears. *Molecular Ecology* 4:347–354.
- PALO, J. U., D. LESBARRERES, D. S. SCHMELLER, C. R. PRIMMER, and J. MERILA. 2004. Microsatellite marker data suggest sex-biased dispersal in the common frog *Rana temporaria*. *Molecular Ecology* 13:2865–2869.
- PALSBOU, P. J., M. Z. PEERY, and M. BERUBE. 2010. Detecting populations in the 'ambiguous' zone: kinship-based estimation of population structure at low genetic divergence. *Molecular Ecology Resources* 10:797–805.
- PEMBERTON, J. M. 2008. Wild pedigrees: The way forward. *Proceedings of the Royal Society B-Biological Sciences* 275:613–621.
- PERRIN, N., and V. MAZALOV. 1999. Dispersal and inbreeding avoidance. *American Naturalist* 154:282–292.
- . 2000. Local competition, inbreeding, and the evolution of sex-biased dispersal. *American Naturalist* 155:116–127.
- PETRANKA, J. W. 1998. *Salamanders of the United States and Canada*. Smithsonian Institution Press, Washington, DC, USA.
- PFINGSTEN, R. A. 1989. *Plethodon cinereus* (Green), redback salamander. In R. A. Pflingsten and F. L. Downs (eds.), *Salamanders of Ohio*, pp. 229–242. College of Biological Sciences, Ohio State University, Columbus, OH.
- PHILLIPS, C. T., and J. N. FRIES. 2009. An evaluation of visible implant elastomer for marking the federally listed fountain darter and the San Marcos salamander. *North American Journal of Fisheries Management* 29:529–532.
- PIERSOL, W. H. 1910. The habits and larval state of *Plethodon cinereus erythronotus*. *Transactions of the Canadian Institute* 8:469–493.
- PILLIOD, D. S., C. R. PETERSON, and P. I. RITSON. 2002. Seasonal migration of Columbia spotted frogs (*Rana luteiventris*) among complementary resources in a high mountain basin. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 80:1849–1862.
- POLLOCK, K. H. 1982. A capture-recapture design robust to unequal probability of capture. *Journal of Wildlife Management* 46:752–757.

- POWELL, R. A. 2000. Animal home ranges and territories and home range estimators. *In* L. Boitani and T. K. Fuller (eds.), *Research Techniques in Animal Ecology: Controversies and Consequences*, pp. 65–110. Columbia University Press, New York, New York, USA.
- PRADEL, R., J. E. HINES, J. D. LEBRETON, and J. D. NICHOLS. 1997. Capture-recapture survival models taking account of transients. *Biometrics* 53:60–72.
- PROSEN, E. D., R. G. JAEGER, and D. R. LEE. 2004. Sexual coercion in a territorial salamander: females punish socially polygynous male partners. *Animal Behaviour* 67:85–92.
- PRUGNOLLE, F., and T. DE MEEUS. 2002. Inferring sex-biased dispersal from population genetic tools: a review. *Heredity* 88:161–165.
- PUSEY, A., and M. WOLF. 1996. Inbreeding avoidance in animals. *Trends in Ecology & Evolution* 11:201–206.
- PUSEY, A. E. 1987. Sex-biased dispersal and inbreeding avoidance in birds and mammals. *Trends in Ecology & Evolution* 2:295–299.
- QUINN, V. S., and B. M. GRAVES. 1999. A technique for sexing red-backed salamanders (*Plethodon cinereus*). *Herpetological Review* 30:32.
- R CORE TEAM. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- RAYMOND, M., and F. ROUSSET. 1995. GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. *Journal of Heredity* 86:248–249.
- RICKLEFS, R. E., and M. WIKELSKI. 2002. The physiology/life-history nexus. *Trends in Ecology & Evolution* 17:462–468.
- RITLAND, K. 1996. Estimators for pairwise relatedness and individual inbreeding coefficients. *Genetical Research* 67:175–185.
- ROFF, D. A. 2000. Trade-offs between growth and reproduction: an analysis of the quantitative genetic evidence. *Journal of Evolutionary Biology* 13:434–445.
- RONCE, O. 2007. How does it feel to be like a rolling stone? Ten questions about dispersal evolution. *Annual Review of Ecology Evolution and Systematics* 38:231–253.
- RONCE, O., I. OLIVIERI, J. CLOBERT, and E. DANCHIN. 2001. Perspectives on the study of dispersal evolution. *In* J. Clobert, E. Danchin, A. A. Dhondt, and J. D. Nichols (eds.), *Dispersal*, pp. 341–357. Oxford University Press, New York.
- ROSS, B., T. FREDERICKSEN, E. ROSS, W. HOFFMAN, M. L. MORRISON, J. BEYEA, M. B. LESTER, B. N. JOHNSON, and N. J. FREDERICKSEN. 2000. Relative abundance and species richness of herpetofauna in forest stands in Pennsylvania. *Forest Science* 46:139–146.
- ROUSSET, F. 2008. GENEPOP '007: a complete re-implementation of the GENEPOP software for Windows and Linux. *Molecular Ecology Resources* 8:103–106.
- ROVITO, S. M., G. PARRA-OLEA, C. R. VASQUEZ-ALMAZAN, T. J. PAPENFUSS, and D. B. WAKE. 2009. Dramatic declines in neotropical salamander populations are an important part of the global amphibian crisis. *Proceedings of the National Academy of Sciences of the United States of America* 106:3231–3236.
- SAYLER, A. 1966. The reproductive ecology of the red-backed salamander, *Plethodon cinereus*, in Maryland. *Copeia*:183–193.

- SCHEFFERS, B., E. McDONALD, D. J. HOCKING, C. A. CONNER, and R. D. SEMLITSCH. 2009. Comparison of two artificial cover objects for sampling herpetofaunal communities in Missouri. *Herpetological Review* 40:419–421.
- SCHIELTZ, J. M., L. M. B. HAYWOOD, and D. M. MARSH. 2010. Effects of cover object spacing on the socioecology of the red-backed salamander, *Plethodon cinereus*. *Herpetologica* 66:276–282.
- SEBER, G. A. F. 1965. A note on the multiple-recapture census. *Biometrika* 52:249–259.
- SELKOE, K. A., and R. J. TOONEN. 2006. Microsatellites for ecologists: A practical guide to using and evaluating microsatellite markers. *Ecology Letters* 9:615–629.
- SEMLITSCH, R. D., K. M. O'DONNELL, and F. R. THOMPSON. 2014. Abundance, biomass production, nutrient content, and the possible role of terrestrial salamanders in Missouri Ozark forest ecosystems. *Canadian Journal of Zoology* 92:997–1004.
- SIMONS, R. R., R. G. JAEGER, and B. E. FELGENHAUER. 1997. Competitor assessment and area defense by territorial salamanders. *Copeia*:70–76.
- SITES, J. W., M. MORANDO, R. HIGHTON, F. HUBER, and R. E. JUNG. 2004. Phylogenetic relationships of the endangered Shenandoah Salamander (*Plethodon shenandoah*) and other salamanders of the *Plethodon cinereus* group (Caudata: Plethodontidae). *Journal of Herpetology* 38:96–105.
- SMITH, M. A., and D. M. GREEN. 2006. Sex, isolation and fidelity: unbiased long-distance dispersal in a terrestrial amphibian. *Ecography* 29:649–658.
- SPOTILA, J. R. 1972. Role of temperature and water in ecology of lungless salamanders. *Ecological Monographs* 42:95–125.
- STEBBINS, R. C. 1954. Natural history of the salamanders of the plethodontid genus *Ensatina*. University of California Publications in Zoology 54:47–123.
- STEINFARTZ, S., K. STEMSHORN, D. KUESTERS, and D. TAUTZ. 2006. Patterns of multiple paternity within and between annual reproduction cycles of the fire salamander (*Salamandra salamandra*) under natural conditions. *Journal of Zoology* 268:1–8.
- STEWART, G. D., and E. D. BELLIS. 1970. Dispersion patterns of salamanders along a brook. *Copeia* 1970:86–89.
- TAUB, F. B. 1961. The distribution of the red-backed salamander, *Plethodon c. cinereus*, within the soil. *Ecology* 42:681–698.
- TEST, F. H. 1955. Seasonal differences in populations of the red-backed salamander in southeastern Michigan. *Papers of the Michigan Academy of Science, Arts, and Letters* 40:137–153.
- TEST, F. H., and B. A. BINGHAM. 1948. Census of a population of the red-backed salamander (*Plethodon cinereus*). *American Midland Naturalist* 39:362–372.
- TILGHMAN, J. M., S. W. RAMEE, and D. M. MARSH. 2012. Meta-analysis of the effects of canopy removal on terrestrial salamander populations in North America. *Biological Conservation* 152:1–9.
- TILLEY, S. G. 1977. Studies of the life histories and reproduction in North American plethodontid salamanders. In D. Taylor and S. Guttman (eds.), *The*

- Reproductive Biology of Amphibians, pp. 1–41. Plenum Press, New York, NY, USA.
- TILLEY, S. G., and J. BERNARDO. 1993. Life-history evolution in plethodontid salamanders. *Herpetologica* 49:154–163.
- TOLL, S. J., R. G. JAEGER, and J. R. GILLETTE. 2000. Socioecology of a terrestrial salamander: Females and males as territorial residents and invaders. *Copeia*:276–281.
- VALCU, M., and B. KEMPENAERS. 2010. Spatial autocorrelation: an overlooked concept in behavioral ecology. *Behavioral Ecology* 21:902–905.
- VEKEMANS, X., and O. J. HARDY. 2004. New insights from fine-scale spatial genetic structure analyses in plant populations. *Molecular Ecology* 13:921–935.
- VERNBERG, F. J. 1953. Hibernation studies of two species of salamanders, *Plethodon cinereus cinereus* and *Eurycea bislineata bislineata*. *Ecology* 34:55–62.
- VITT, L. J., and J. P. CALDWELL. 2014. *Herpetology: An Introductory Biology of Amphibians and Reptiles*. Academic Press, Waltham, MA, USA.
- VOGT, R. C. 1981. *Natural History of Amphibians and Reptiles in Wisconsin*. Milwaukee Public Museum, Milwaukee, WI, USA.
- WAHLUND, S. 1928. The constitution of populations and correlation phenomena regarded from a genetic viewpoint. *Hereditas* 11:65–106.
- WAKE, D. B. 1991. Declining amphibian populations. *Science* 253:860.
- WALFORD, L. A. 1946. A new graphic method of describing the growth of animals. *Biological Bulletin* 90:141–147.
- WASER, P. M., and W. T. JONES. 1983. Natal philopatry among solitary mammals. *Quarterly Review of Biology* 58:355–390.
- WASER, P. M., and C. STROBECK. 1998. Genetic signatures of interpopulation dispersal. *Trends in Ecology & Evolution* 13:43–44.
- WEIR, B. S. 1990. *Genetic Data Analysis: Methods for Discrete Population Genetic Data*. Sinauer Associates, Inc., Sunderland, MA, USA.
- WEIR, B. S., and C. C. COCKERHAM. 1984. Estimating *F*-statistics for the analysis of population structure. *Evolution* 38:1358–1370.
- WELLS, K. D. 2007. *The Ecology and Behavior of Amphibians*. University of Chicago Press, Chicago, IL.
- WELSH, H. H., and S. DROEGE. 2001. A case for using plethodontid salamanders for monitoring biodiversity and ecosystem integrity of North American forests. *Conservation Biology* 15:558–569.
- WELSH, H. H., and G. R. HODGSON. 2008. Amphibians as metrics of critical biological thresholds in forested headwater streams of the Pacific Northwest, USA. *Freshwater Biology* 53:1470–1488.
- WHITE, G. C., and K. P. BURNHAM. 1999. Program MARK: Survival estimation from populations of marked animals. *Bird Study* 46:120–139.
- WHITLOCK, M. C., and D. E. MCCAULEY. 1999. Indirect measures of gene flow and migration:  $F_{ST} \approx 1/(4Nm+1)$ . *Heredity* 82:117–125.
- WILLSON, J. D., and J. W. GIBBONS. 2010. Drift fences, coverboards, and other traps. In C. K. Dodd, Jr. (ed.), *Amphibian Ecology and Conservation: A Handbook of Techniques*, pp. 229–245. Oxford University Press, New York, New York, USA.



- WRIGHT, S. 1931. Evolution in Mendelian populations. *Genetics* 16:97–159.
- WYMAN, R. L. 1998. Experimental assessment of salamanders as predators of detrital food webs: effects on invertebrates, decomposition and the carbon cycle. *Biodiversity and Conservation* 7:641–650.