EFFECTS OF PRESCRIBED FIRE AND TIMBER HARVEST ON TERRESTRIAL SALAMANDER ABUNDANCE, BEHAVIOR, AND MICROHABITAT USE

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by

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The undersigned, appointed by the dean of the Graduate School,
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"It takes a whole village to raise a child"

– African proverb

I dedicate this to each and every "villager"
who has helped me on this journey—

my kinfolk,
my Mizzou family,
and my Runaways.

This would not have been remotely achievable
without your guidance, love, and support.

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ABSTRACT

Forest-associated wildlife populations are commonly exposed to anthropogenic disturbances such as prescribed fire and timber harvest. Forest managers use prescribed fire to decrease wildfire risk, reduce fuel loads, and restore fire-adapted ecosystems; however, many fire management decisions are weighted toward vegetation responses, as wildlife responses to prescribed fire remain unclear. To fully evaluate the effects of fire management on wildlife, both population-level studies and individual-level mechanistic studies are necessary. Individual animals may respond to altered habitats in physiological, behavioral, or ecological ways that subsequently influence population-level dynamics such as survival rate and spatial distribution.

Terrestrial woodland salamanders (family Plethodontidae) are ecologically important animals that comprise large amounts of biomass, are important for nutrient cycling, and are key predators in forest-floor ecosystems. However, terrestrial salamanders are highly moisture-dependent, have small home ranges, and have limited movement capacity – all of which increase their sensitivity to habitat changes. My dissertation research has focused on how terrestrial salamanders respond to forest management practices at the population and individual levels. Specifically, I investigated (1) whether terrestrial salamander abundance and microhabitat use changed after timber harvest or prescribed fire, and (2) how individual salamanders respond behaviorally to prescribed fire.

In pre-treatment surveys, I found most salamanders within leaf litter (rather than under cover objects), but the proportion of leaf litter captures varied with time-since-rainfall. I also found that salamander capture frequency varied greatly with rainfall, which illustrates the importance of accounting for imperfect detection when estimating population metrics such as abundance. To estimate salamander abundance before and after treatments, I used a hierarchical modeling approach that allowed me to correct for imperfect detection. Modeling results indicated that terrestrial salamanders reduced their surface activity in response to both prescribed burn and timber harvest, but abundance did not change drastically in the short term. Using PIT-telemetry to relocate terrestrial salamanders in prescription-burned and unburned areas, I again found a substantial decrease in salamander surface activity in burned areas, but found no evidence of direct salamander mortality.

Results from these studies indicate that terrestrial salamanders respond to post-fire and post-harvest conditions by spending more time belowground to avoid increased physiological stress. Though it appears that terrestrial salamanders can generally avoid direct consequences of prescribed fire, behavioral responses to post-fire micro-environmental conditions could affect salamander populations in ways that are not yet apparent.

CHAPTER 1 • ADVANCING TERRESTRIAL SALAMANDER POPULATION ECOLOGY: THE CENTRAL ROLE OF IMPERFECT DETECTION

ABSTRACT

Terrestrial salamanders are increasingly cited as important surrogates for monitoring forest ecosystem health and biodiversity. To accurately assess the role of salamanders in ecosystems, total population size is more relevant than the size of the population available for sampling. Thus, estimating detectability is important if unbiased population metrics are of primary interest. The past two decades have seen a tremendous increase in analytical methods that account for imperfect detection. Terrestrial salamanders have unique physiological requirements and surface activity patterns that contribute to their inherently low detection levels, and variable terminology makes it difficult to compare detectability parameter values across species, geographic regions, survey methods, and species. It is important to use consistent terminology and be explicit about what specific components of detectability are being presented in a study. Availability for sampling is governed by the presence of individuals in the sampling area and the capacity of the survey method to detect the targeted animals. Conditional capture probability is affected by survey methodology, observer experience level, habitat complexity, and species crypsis. Imperfect detection is an issue when estimating all population-related

metrics, including abundance, occupancy, and species richness. Population analysis via hierarchical modeling is a more recently developed approach that can be used to account for imperfect detection. Hierarchical models enable researchers to partition complex ecological systems into two or more simpler component models and focus on the mechanisms underlying the observed data. With improved population analyses of terrestrial salamanders, monitoring and conservation efforts can become more precise and effective.

INTRODUCTION

Terrestrial salamanders are increasingly cited as important surrogates for monitoring forest ecosystem health and biodiversity (e.g., Davic and Welsh, 2004; Welsh and Droege, 2001). In addition to their environmental sensitivity, terrestrial salamanders comprise great amounts of biomass, and are thought to help regulate invertebrate community composition and density, leaf litter decomposition, and forest nutrient cycles (Burton and Likens, 1975; Wyman, 1998; Davic and Welsh, 2004; Walton, 2005, 2013; Best and Welsh, 2014; Semlitsch et al., 2014). However, terrestrial salamanders are primarily subterranean (Taub, 1961; Heatwole, 1962), so field surveys generally sample only a small portion of total salamander populations (Jung et al., 2000; Bailey et al., 2004a). To accurately assess the role of salamanders in ecosystems, the true, total population size is more relevant than the size of the population available for sampling (Kendall, 1999). Therefore, estimating detectability is important if unbiased population metrics are of primary interest. Fortunately, the past two decades have seen a tremendous increase in analytical methods that account for imperfect detection, including capture-mark-recapture (CMR) models (see Nichols, 1992; Williams et al., 2002), site occupancy models (e.g., Mackenzie et al., 2002), and abundance models not requiring marked individuals (e.g., Royle, 2004; Kéry and Schaub, 2012).

Terrestrial salamanders have unique physiological requirements and surface activity patterns that contribute to their inherently low detection levels (Hyde and Simons, 2001; Bailey et al., 2004a). Heterogeneity of various environmental factors causes terrestrial salamanders' already low detectability levels to vary spatially and temporally. However, many herpetological surveys do not explicitly account for imperfect detection, but use counts as indices of abundance (see overview in Mazerolle et al., 2007). Because counts (C) = true abundance (N) x effective detection probability (P), such studies make an inherent assumption that detection probabilities are equal among survey sites and occasions. If counts differ between populations, it is not certain if the true population sizes are indeed different ($N_1 \neq N_2$), or if the probabilities of detection are different ($P_1 \neq P_2$). If counts are equal between populations ($C_1 = C_2$), it is not guaranteed that the population sizes are equal – differing detection probabilities could cause unequal populations to appear equivalent (Hyde and Simons, 2001; Schmidt, 2003; Dodd Jr. and Dorazio, 2004; Mazerolle et al., 2007). In short, count data only guarantee a "minimum estimate of unknown quality" if they are not adjusted for imperfect detection (Schmidt, 2003). In this paper, we will provide an overview of detectability terminology, consider factors that affect detectability, outline methods for accounting for imperfect detection of terrestrial salamanders, and provide examples of studies that have done so. We hope to foster cross-study comparisons by increasing the consistency of detectability-related terminology in the literature and underscore the importance of considering heterogeneity in the detectability of terrestrial salamanders.

PITFALLS: INCONSISTENT TERMINOLOGY AND COUNT DATA

Inconsistent terminology

Herpetologists consider a wide range of factors that affect detectability, but detection-related terminology tends to vary among studies (see Table 1). For example, Bailey et al. (2004a) use the term "effective capture probability" for the overall detection probability, "conditional capture probability" as the probability of capture, given a salamander is available for sampling, and "temporary emigration probability" for the probability that an animal is not available for capture, but is still alive. Buderman and Liebgold (2012) use different terms – "encounter probability" for the overall detection probability, which they define as "a function of an individual being available for sampling, and the 'true' encounter probability, or, given availability, the probability an individual is encountered." Both studies rightly acknowledge that the overall detection probability is a function of at least two distinct probabilities – (1) availability, and (2) capture (given availability). However, the use of different terminology creates ambiguity when comparing parameter values from various studies.

Many other abundance studies report a single detection probability value, which may differ in definition from study to study. For example, McKenny et al. (2006) define detection probability as the probability of a salamander being detected, given it is present; however, that definition corresponds to Bailey et al.'s "conditional capture probability" term, rather than overall capture probability. McKenny et al. (2006) may have intended their estimates to represent joint probabilities of salamanders being detected *and* being available, which differs slightly but importantly from being detected *given* being available (Table 1). In many abundance studies that report detection probability estimates, *P* represents the effective capture probability, which depends on both availability and conditional capture probability (Kendall, 1999; Bailey et al., 2004a). In these cases, availability and conditional capture probability are confounded (Kendall et al., 1997), and the studies are reporting a joint probability of animals being detected and being present (e.g., Dodd Jr. and Dorazio, 2004; Mazerolle et al., 2007). Contrary to studies of abundance, detection probability values from occupancy models seem to agree on a definition: the probability of detecting a species at a site, given it is present (Mackenzie et al., 2002).

Variable terminology makes it difficult to compare detectability parameter values across species, geographic regions, survey methods, and studies. We think it is important to be explicit about what specific components of detectability are being presented in a study, along with definitions of the probabilities being reported. Here, we suggest terms that would increase congruence among studies if used consistently (Table 1), and propose that ambiguous terms such as "encounter probability" be avoided unless explicitly defined when used.

Count data

While standardization of sampling protocols can increase consistency of detection probability, unpredictable factors such as weather prevent detectability from remaining constant across space or time (Hyde and Simons, 2001; Schmidt, 2003; Dodd Jr. and Dorazio, 2004; Mazerolle et al., 2007). Several studies have demonstrated spatial and temporal heterogeneity in capture probabilities, especially for terrestrial salamanders (Pollock et al., 1990; Jung et al., 2000; Hyde and Simons, 2001; Salvidio, 2001; Bailey et al., 2004a; Buderman and Liebgold, 2012). Schmidt (2004) showed that correlations between count data and true population estimates were lower for terrestrial salamanders (0.27 for *Plethodon cinereus* in Jung et al. 2000) than for anurans (correlations between 0.59 and 0.99). Hyde and Simons (2001) demonstrated that abundance estimates generated from four different "standard" sampling methods were not strongly correlated, and that all methods showed "extremely high" spatiotemporal variability of capture probability. Taken together, these studies confirm that even count data collected using standardized sampling protocols is inadequate for reliably monitoring terrestrial salamanders.

FACTORS AFFECTING COMPONENTS OF DETECTABILITY

Availability

Terrestrial salamanders' surface activity is restricted to moist conditions because they lack lungs and respire cutaneously (Spotila, 1972; Gatz et al., 1975; Feder, 1983; Jørgensen, 1997). Surface cover objects provide moisture for some time following rain events, but terrestrial salamanders eventually retreat underground when surface conditions become too dry (Jaeger, 1980; Grover, 1998; O'Donnell et al., 2014a). Availability for sampling is governed by the presence of individuals in the sampling area, as well as the capacity of the survey method to detect the targeted animals (Pollock et al., 2004). Thus, most methods of surveying terrestrial salamanders require individuals to be surface-active to be considered available.

Processes known to drive terrestrial salamander surface activity include elevation, disturbance, topography, season, climate (temperature, humidity, rainfall, wind speed), and breeding phenology (Hyde and Simons, 2001; Bailey et al., 2004a,b; Dodd Jr. and Dorazio, 2004; Mazerolle et al., 2007). For example, our study of southern red-backed salamander microhabitat use illustrated the effects of several of these factors. We found that time since last rainfall was the strongest predictor of salamander surface activity, explaining > 60% of the variation in survey counts (O'Donnell et al., 2014a). Bailey et al. (2004a) showed that terrestrial salamanders were less surface-active in disturbed, low-elevation habitats than in undisturbed, high-elevation sites. Generally, terrestrial salamanders are likely to exhibit high levels of surface activity in areas of minimally variable, moist, cool microhabitat conditions (Bailey et al., 2004a).

Surface activity (and thus, availability) has long been known to be very low for terrestrial salamanders (2-32%; Taub, 1961), and this has been confirmed by CMR studies (e.g., Bailey et al., 2004a,c). Vertical temporary emigration of terrestrial salamanders can be estimated and accounted for using a CMR robust design (Bailey et al., 2004a; Buderman and Liebgold, 2012); we have also incorporated temporary emigration into binomial mixture models (O'Donnell et al., 2014b). These methods help account for the frequent temporary emigration exhibited by terrestrial salamanders.

Conditional capture probability

Factors that affect terrestrial salamanders' conditional capture probability likely include survey methodology, observer experience level, habitat complexity, and species crypsis. Because this detectability component applies to animals that are available for capture, factors that affect surface activity are not considered influential. The concept of conditional capture probability is illustrated by considering surveys of red-backed salamanders (*Plethodon cinereus*) in areas where both striped and unstriped (leadback) morphs are present. Assuming no difference in surface availability between the morphs, if the red striped morphs are easier to spot against a dark soil surface than the unstriped morphs, the striped morphs would have a higher conditional capture probability. Behavioral differences among species or individuals could also lead to variation in conditional capture probabilities. More complex habitats, such as areas with substantial herbaceous vegetation versus only leaf litter, could decrease conditional capture probability. Observer experience is another relevant factor, with more experienced observers having higher success spotting and capturing available salamanders. Even observer motivation has been reported to affect capture probabilities (Hairston and Wiley, 1993).

An additional influence on conditional capture probability is the sampling method used in a study, which largely determines the biological parameter being measured. For example, using pitfall traps to sample terrestrial salamanders will only capture the roaming, non-territorial portion of the surface-active population. Artificial cover objects, on the other hand, may only sample territorial individuals. Disturbance such as timber harvest, prescribed fire, or wildland fire may alter terrestrial salamander's habitat use and, consequently, both availability and conditional capture probability. For example, using cover boards to sample areas after prescribed burns or wildfire that removes leaf litter and fine-woody debris might positively bias captures because cover boards represent the best or only cover objects available. The interaction of disturbances and sampling methodology could have substantial effects on the validity of inferences drawn from otherwise well-designed studies (Hyde and Simons, 2001; Chelgren et al., 2011). Terrestrial salamanders inhabit spatially and temporally variable microhabitats (e.g., leaf litter, rocks, downed wood); this variability greatly influences detectability, and may interact with disturbances. In a recent study, we found that relative microhabitat use by red-backed salamanders differed among disturbance treatments, which could have biased our inferences had we not accounted for it (Fig. 2).

Including both availability and conditional capture probability in a population model allows researchers to partition the overall detectability in a biologically meaningful way, and increases congruence between the model and reality. If availability is low, as is intrinsically the case with terrestrial salamanders, interpreting abundance and density estimates may be difficult (Kendall et al., 1997; Pollock et al., 2004; Kéry and Schmidt, 2008). Choosing sampling methods that maximize both availability and conditional capture probability is key, as low capture probabilities can result in large confidence intervals around population parameter estimates (Dodd Jr. and Dorazio, 2004; Kéry and Schmidt, 2008; Buderman and Liebgold, 2012).

Several studies have compared different methods for surveying terrestrial salamanders, and have shown that detectability can differ greatly among survey techniques (e.g., Hyde and Simons, 2001; Bailey et al., 2004b; Williams and Berkson, 2004; Otto and Roloff, 2011; Buderman and Liebgold, 2012). Clearly, researchers need to carefully consider which survey technique(s) are most appropriate to answer their questions. Regardless of sampling method, researchers should collect data that may later inform the detectability parameters in a population model, including observer characteristics and weather conditions (Kéry and Schaub, 2012). Additionally, designing sampling protocols that maximize both availability and conditional capture probability helps by eliminating extraneous variation in the data.

STATISTICAL METHODS ACCOUNTING FOR IMPERFECT DETECTION

Imperfect detection is an issue when estimating all population-related metrics, including abundance, occupancy, and species richness. In each case, there are several approaches for accounting for detection probabilities < 1. For estimating abundance, CMR is a common, well-tested approach that has been applied to terrestrial salamanders in a number of cases (Mathis, 1991; Marvin, 1996; Jung et al., 2000; Petranka and Murray, 2001; Bailey et al., 2004c; Marsh et al., 2004; Maerz et al., 2009; Buderman and Liebgold, 2012). Many extensions of CMR exist, and have been applied to closed populations (abundance within a season or year), open populations (population parameters change among seasons or years), and in combination (robust design models). As the name suggests, CMR analyses are based on recapture patterns of previously caught and marked individuals. While this approach is reliable for monitoring populations over time (provided assumptions are met), there are some potential drawbacks. The methods involved are often labor and time intensive, and can be logistically difficult (Mazerolle et al., 2007). Recapture rates for terrestrial salamanders are often low (Taub, 1961; Jung et al., 2000; Smith and Petranka, 2000), so analyses require a large number of marked individuals, which is often difficult to obtain and expensive in terms of time and funding (Pollock et al., 1990; Donnelly and Guyer, 1994; Dodd Jr. and Dorazio, 2004). A number of software packages for analyzing CMR data exist, including Program MARK (White and Burnham, 1999). CMR methods in general have been discussed more thoroughly in other locations (e.g., Nichols, 1992; Williams et al., 2002; Mazerolle et al., 2007), so we will not expand on them further here.

Population analysis via hierarchical modeling is a more recently developed approach that can be used to account for imperfect detection when estimating occupancy, abundance, or species richness. Hierarchical models enable researchers to partition complex ecological systems into two or more simpler component models and focus on the mechanisms underlying the observed data (Royle and Dorazio, 2008; Kéry and Schaub, 2012). Hierarchical models distinguish between ecological processes, which are often the subject of study, and observation processes that affect how researchers perceive the ecological state variable of interest. This hierarchical structure increases congruency between the ecological system of interest and the analytical methods, and forces researchers to think critically about what environmental and survey-related factors are operating at various levels of the hierarchy (see Fig. 1; Royle and Dorazio, 2008; Kéry and Schaub, 2012). The structure of hierarchical models is fairly conserved across these population metrics (occupancy, abundance, species richness), which decreases the difficulty of understanding the entire class of models (Kéry and Schaub, 2012).

Occupancy models were developed to estimate the proportion of sites occupied by a species while accounting for imperfect detection (Mackenzie et al., 2002). Occupancy (or occurrence) refers to the true ecological state of a site – a given species is either present or absent (Royle and Dorazio, 2008). The occupancy probability is the percent chance that a randomly selected site within the study area is occupied by the species (Mackenzie et al., 2006; Royle and Dorazio, 2008). Occupancy is the ecological parameter of interest for several fields, including species distribution modeling, disease modeling, and metapopulation dynamics (Mackenzie et al., 2006; Royle and Dorazio, 2008; Kéry and Schaub, 2012). Imperfect detectability is a concern in distributional analyses, as ignoring detectability leads to underestimation of true species distributions and misjudgment of the strength of habitat-related factors that affect distributions (Tyre et al., 2003; Kéry, 2011; Kéry and Schaub, 2012). If detectability is not accounted for, researchers may confound factors that affect the difficulty of finding a species with the true distribution of the species (Kéry, 2011; Kéry and Schaub, 2012). For instance, terrestrial salamanders may be difficult to detect in areas of dense herbaceous vegetation; if unaccounted for in statistical analyses, one could mistakenly interpret differences in detectability between sites as differences in true occupancy. A species distribution map from this example analysis (uncorrected for imperfect detection) would reflect the distribution of herbaceous vegetation (a detectability factor), rather than the true distribution of terrestrial salamanders.

Occupancy models are appealing because they require less information than abundance models – detection/nondetection data rather than counts of individuals. As with other hierarchical models, occupancy models do not require marked individuals, but do require repeated surveys at multiple study sites. The models consist of two linked submodels: one logistic regression representing the ecological process (occupancy) and another logistic regression describing the observation process (detectability, Fig. 1). Occupancy models can be applied to single species over one or more seasons, or extended to model species richness by simultaneously modeling the occurrence of multiple species. They can also be expanded into multistate occupancy models when there is more than one category of occurrence. For example, a site could be occupied by (1) juveniles only, (2) adults only, or (3) a combination of juveniles and adults. While false negative observations are of primary concern, false-positive observations also pose a detectability issue; multistate occupancy models are one approach for jointly addressing these two types of observation error (Miller et al., 2011).

Hierarchical models of abundance, known as binomial mixture models (or N-mixture models), were developed to simultaneously estimate true abundance (population size) and detectability from spatially and temporally replicated counts (Royle, 2004). Binomial mixture models, like occupancy models, consist of two (or more) linked submodels (Fig. 1). The state process (abundance) is typically described using a Poisson or negative binomial distribution, while the observation process (detectability) is represented as a binomial distribution. Site-level factors that affect abundance, such as canopy cover and aspect, are incorporated into the ecological process model via a log-link function; site- or survey-specific covariates such as rainfall and weather conditions that affect the observation process are included using a logit-link function. Binomial mixture models have been applied to both demographically closed and open populations over single and multiple seasons.

Occupancy models have been applied to amphibians in general (e.g., Miller et al., 2012; Adams et al., 2013; Hossack et al., 2013), whereas abundance models have been used more frequently for terrestrial salamanders (Dodd Jr. and Dorazio, 2004; McKenny et al., 2006; Chelgren et al., 2011; Connette and Semlitsch, 2013; Peterman and Semlitsch, 2013; Otto et al., 2014). Several statistical packages exist to analyze detection/nondetection data and count data for occupancy and abundance analyses, respectively. Program PRESENCE (Hines, 2006) and the R package unmarked (Fiske and Chandler, 2011) are frequentist software packages that include many extensions of hierarchical occupancy and abundance models, and work well for standard applications of such models. There are also many examples of Bayesian approaches to hierarchical modeling (see Kéry and Schaub, 2012 for overview) that can be executed using programs such as WinBUGS or JAGS (Plummer, 2003).

CONCLUSIONS

In addition to correcting for heterogeneity in detectability, methods that account for imperfect detection give a more complete picture of the ecological role of terrestrial salamanders. In a review of studies on small plethodontid salamanders, we found that density estimates corrected for imperfect detection were nearly an order of magnitude greater than density estimates from surface counts (Semlitsch et al., 2014). Because terrestrial salamanders spend much of their time underground, they surely have ecological impacts deeper than the forest floor (Taub, 1961; Davic and Welsh, 2004). Thus, it is appropriate to include both surface-active and underground individuals in population estimates. These “superpopulation” (Kendall, 1999; Bailey et al., 2004a,b) estimates will aid researchers in determining the ecological role of terrestrial salamanders, managing their populations, and conserving their biodiversity.

Accounting for detectability is essential for accurate studies of terrestrial salamander abundance, occupancy, species richness, and demography. With improved population analyses of terrestrial salamanders, monitoring and conservation efforts can become more precise and effective. The past decade has seen an increase in the use of new analytical methods, and we hope to see the trend continue and terrestrial salamander population ecology continue to advance.

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TABLE 1. Variety of terms used to describe aspects of detectability and suggestions for unifying language.

Suggested term	**Definition**	**Previously used alternatives**	**Example**
Effective detection probability	Joint probability of an individual being available for sampling AND actually being captured	Encounter probability[c], detection probability[d,e], effective capture probability[e,f]	= (availability) * (conditional capture probability)
Availability[a]	Probability that an animal is alive and available for capture (e.g., salamander is part of surface population)	Exposure to sampling[g]	= 1 – (temporary emigration)
Temporary emigration[b]	Probability that an animal is alive but unavailable for capture (e.g., salamander is part of superpopulation, but not surface population)		= 1 – (availability)
Conditional capture probability	Probability of capture, given (i.e., conditional on) a salamander is available for capture	True encounter probability[c], detection probability[h], detection given availability[g]	= (capture prob)|(availability)

[a,b] these terms are antonyms; availability = (1 – temporary emigration)

[c] Buderman and Liebgold 2012

[d] Dodd and Dorazio 2004

[e] Mazerolle et al 2007

[f] Bailey et al 2004(a)

[g] Kery and Schmidt 2008

[h] McKenny et al 2006

FIGURE 1. Structure of hierarchical models, consisting of an ecological process generating the parameter of interest (e.g. abundance) and an observation process through which the ecological process is filtered. Factors affecting state parameters are often related to site/habitat. Factors affecting detectability are related to site/habitat and/or survey conditions. Observable components in solid lines, imperfectly observable or unobservable components in dashed lines.

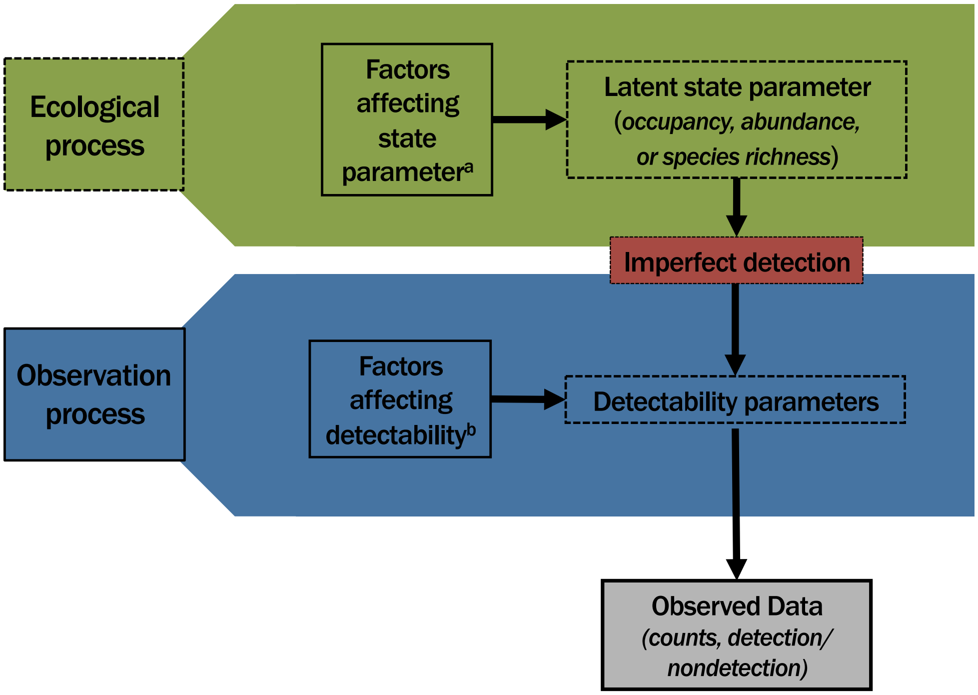
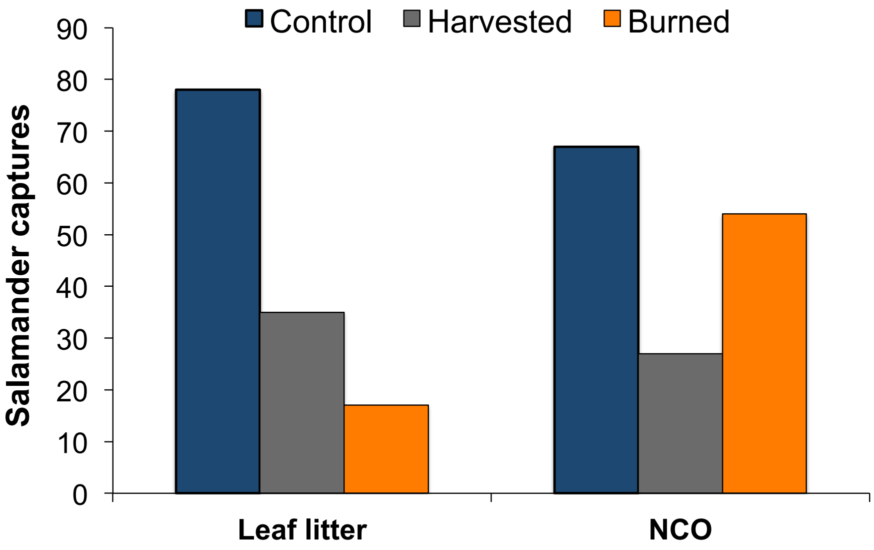


FIGURE 2. Captures of *Plethodon serratus* from seasons following timber harvest and prescribed burn treatments (spring and fall 2013). Relative capture frequencies differed between leaf litter and natural cover objects (NCO), reflecting potential bias related to sampling method when imperfect detection is unaccounted for.



CHAPTER 2 • PREDICTING VARIATION IN MICROHABITAT UTILIZATION OF TERRESTRIAL SALAMANDERS

ABSTRACT

Understanding patterns of microhabitat use among terrestrial salamanders is important for predicting their responses to natural and anthropogenic disturbances. The dependence of terrestrial salamanders on cutaneous respiration limits their spatial distribution to moist, humid areas. Although many studies have shown negative effects of canopy removal on terrestrial salamander abundance, some have shown potential ameliorating effects of retaining coarse woody debris (CWD) as moist refugia (critical resources in the landscape). Because cover objects like CWD retain moisture longer than fine debris, terrestrial salamanders are often more locally abundant in areas of dense cover. Temporally variable environmental conditions could affect microhabitat quality and influence the fine scale spatial distributions of salamanders. Spatial and temporal variability in microhabitat use greatly influence individual detectability, which is always a challenge for terrestrial salamanders. We conducted repeated area-constrained surveys to examine variation in salamander microhabitat use of terrestrial salamanders in relation to season, year, and weather conditions. We found that time since rain (TSR) was the best predictor of relative salamander microhabitat use, but the strength of this relationship varied among years. TSR was also the best predictor of salamander surface activity. We captured most salamanders within leaf litter, but the proportion of leaf litter captures varied with TSR. Our results illustrate the importance of accounting for variable detectability when sampling for terrestrial salamanders. Disturbances which affect leaf litter depth and decomposition rates could influence the availability and quality of microhabitats, and potentially increase competition among individuals for natural cover objects.

INTRODUCTION

Understanding patterns of woodland salamander microhabitat use is important for predicting their response to natural and anthropogenic disturbances, such as land use and climate change. Although many studies have shown negative effects of anthropogenic disturbances such as timber harvest and tree canopy removal on woodland salamanders (Petranka, Eldridge & Haley 1993; Ash & Bruce 1994; Ash 1997; Herbeck & Larsen 1999; Hocking *et al.* 2013), some research has shown the potential ameliorating effects of retaining coarse woody debris (CWD) that functions as moist refugia (Moseley, Castleberry & Ford 2004; Patrick, Hunter Jr & Calhoun 2006; Rittenhouse *et al.* 2008; Kluber, Olson & Puettmann 2009). At fine spatial scales, woodland salamanders occupy spatially and temporally variable microhabitats, such as leaf litter, rocks, and downed wood. This variability in microhabitat availability and use greatly influences individual detectability, which is notoriously low for woodland salamanders (Bailey, Simons & Pollock 2004a), and thereby affects our ability to discern changes in habitat use and abundance.

Lungless salamanders require moisture to sustain cutaneous respiration (Gatz et al., 1975); thus, their ranges are limited to moist, humid areas (Spotila 1972; Feder 1983). Because cover objects like CWD retain moisture longer than fine debris (e.g., leaf litter, fine woody debris), woodland salamanders are often more abundant and surface active in areas of higher CWD density (Mathis, 1990; Petranka et al., 1994; DeMaynadier and Hunter, 1995; Grover, 1998; McKenny et al., 2006). They are also more active under moist conditions (Heatwole 1962; Jaeger 1980; Grover 1998). Heatwole (1962) showed that terrestrial salamanders move to areas of higher humidity, especially after desiccation. This often means moving under cover objects as the forest floor dries after rain events (Heatwole 1962; Fraser 1976; Jaeger 1980).

Moisture and cover availability might also influence the foraging success of terrestrial salamanders. The volume of prey ingested by salamanders is negatively correlated with the time since the last heavy rainfall (Jaeger, 1972). Salamander foraging success is dependent on cover availability (Fraser, 1976; Jaeger, 1980) and the mass of salamanders is positively related to cover density (Grover, 1998).

We sought to elucidate the patterns of microhabitat use of woodland salamanders in relation to variation across seasons, years, and weather patterns. We predicted that salamanders would utilize cover objects during periods of low rainfall and high temperature, when they offer an important refuge. We sampled for

Southern Red-backed Salamanders (*Plethodon serratus*) in seasons of high surface activity, and tested how salamander activity varied in relation to habitat and weather conditions.

MATERIALS AND METHODS

Study Site

We conducted our study at the US Forest Service Sinkin Experimental Forest within the Mark Twain National Forest, Dent County, Missouri, USA. The site is located in the Ozark Plateau, and consists of mature (80-100 year old), fully stocked, oak-dominated stands (primarily white, black, scarlet, and post oak, *Quercus* spp.); other species include hickory, maple, dogwood, shortleaf pine, blackgum, and sassafras (Kabrick *et al.* 2014). We conducted surveys for terrestrial salamanders on 20 experimental units that were each 5 ha in size and separated by ≥10 m, and were oriented on a slope encompassing a mesic-to-xeric moisture gradient. There is little variation in forest cover among sites – they are all within a mature, oak-hickory forest in the same landscape.

Field Methods

We surveyed two 9-m^2 plots within each unit, yielding 40 survey plots. Plots were selected at the top (dry) and bottom (moist) of the slope to encompass the moisture gradient within each unit. We surveyed each of the 40 plots 3-5 times in each Spring and Autumn 2010-2012; surveys were separated by an average (±1 SD) of 7

± 3.7 d. We conducted diurnal area-constrained searches by raking through leaf litter and turning over natural cover objects. Each round of sampling lasted until each plot was surveyed once (2-4 d per round); the search order of plots was randomly determined. We recorded the life-history stage and snout-vent length (SVL, ±1 mm) of each salamander captured (juveniles were categorized as any individual ≤31 mm SVL [Herbeck and Semlitsch, 2000]). We also recorded the capture location of each individual (e.g., leaf litter, rock, woody cover object [WCO]), the total number of rocks (≥5 cm in size) and WCOs encountered in each plot, soil temperature using Raytek Mini Temp non-contact thermometer gun (a mean of 3 measurements), and leaf litter depth (±0.5 cm; a mean of 3 points in each plot). Individuals were returned to their point of capture upon survey completion. Daily rainfall and temperature data were obtained from the Sinkin Experimental Forest weather station.

Statistical analysis

We used multinomial logistic regression to assess the effects of (1) season (Spring vs. Autumn), (2) year, and (3) time since rainfall ≥0.25 cm (TSR, in days) on the probability of salamanders using various microhabitats. We fitted seven a priori models (3 single variable [season, year, TSR], 4 multiple variable [combinations of season, year, TSR]) using the multinom function in the nnet package (Venables & Ripley 2002) of program R (R Core Team 2013), and compared these models using AIC. Using the top-ranking model, we calculated the predicted probabilities of finding an active salamander within each microhabitat type. We also tested for additive effects of life-history stage (juvenile vs. adult) and SVL in post-hoc modeling. We assessed model fit using a likelihood ratio test.

We analyzed the effects of seven environmental variables on salamander surface activity (counts per plot) using a Poisson generalized linear model (Table 1). We scaled all covariates using a z-score procedure prior to analysis to promote model convergence, fitted models using the glm function in R, and performed a likelihood ratio test to assess goodness-of-fit. We accounted for overdispersion in the Poisson distribution by calculating robust standard errors and 95% confidence intervals via the sandwich package in R (Zeileis 2006).

RESULTS

We searched 1080 9-m^2 plots during 27 sampling rounds from 9 April 2010 to 26 October 2012, and captured 2309 *P. serratus*. Sampling was conducted from April to May (Spring) and September to October (Autumn), which corresponded with periods of greatest salamander surface activity (Herbeck & Semlitsch 2000). We captured 1018 individuals in 2010 (10 rounds), 856 in 2011 (10 rounds), and 435 in 2012 (7 rounds). Across all years, 72.1% of captured salamanders were in leaf litter; the remaining salamanders were under WCO (13.4%), rocks (13.9%), or other locations (0.6%; Fig. 1).

Of the seven a priori multinomial regression models, the best prediction of salamander microhabitat use probability contained TSR, year, and an interaction between TSR and year. The day following a rain event, the most likely capture location in each year was leaf litter (Fig. 2). As TSR increased, the probability of capturing a salamander within the leaf litter decreased, while the probability of capture under a cover object increased. The lowest initial probability of being captured in leaf litter was in 2012; that year also had the lowest precipitation total (82.5 cm) during the approximate salamander active season (1 April – 31 October; for comparison, 2010 = 94.6 cm, 2011 = 115.6 cm). In each year, the predicted probability of capturing a salamander in leaf litter was greater than under a cover object (WCO or rock) for a period of at least seven days following rainfall (Fig. 2). We incorporated additive effects of life-history stage (juvenile vs. adult) and SVL into the top three models (ΔAIC < 15) in a post hoc analysis. The model consisting of life stage, season, TSR, year, and the TSR*year interaction outranked the previous top model (ΔAIC = 24.3); however, it was not more likely than the same model with season excluded (ΔAIC = 0.3). A X^2 likelihood ratio test of the top model versus an intercept-only model suggested adequate model fit ($P < 0.001$).

Variation in the surface activity (counts per plot) of *P. serratus* was most strongly related to TSR and year (Table 1). Rock and WCO abundances were also significant predictors of surface activity (Table 1). Surface activity decreased steadily as TSR increased (Fig. 3); this corresponded with the decline in the proportion of salamanders captured within the leaf litter (Fig. 4). A X^2 likelihood ratio test comparing the full model to an intercept-only model indicated adequate goodness-of-fit ($P < 0.001$).

DISCUSSION

We observed a clear shift in salamander microhabitat use from leaf litter to surface cover objects and subterranean areas as TSR increased. Our observation that *P. serratus* decreased surface activity as the forest floor dried is consistent with previous studies of woodland salamanders (Heatwole, 1962; Grover, 1998). However, our finding contrasts with what Jaeger (1980) observed in *P. cinereus* (Eastern Red-backed Salamander), a close relative of *P. serratus*. Whereas Jaeger (1980) observed a shift in microhabitat use in drier conditions from leaf litter to cover objects, his measure of surface activity did not change as a function of recent rainfall. Because surface activity decreased as TSR increased in our study system, it appears that the concurrent decline in proportion of leaf litter captures is partially caused by salamanders retreating underground into burrows rather than shifting to surface cover objects. It is possible that this difference between the studies could be caused by species differences in moisture preference or the geographic differences in rainfall and rate of soil moisture decline. Mean annual precipitation at Jaeger's (1980) study area is 35 cm greater than ours (138 vs. 103 cm); soils in the Missouri Ozarks are shallow, rocky, and dry rapidly.

There were minimal differences between life-history stages for predicted microhabitat location. Changes in predicted leaf litter captures did not differ between juveniles and adults; however, we predicted slightly more juveniles than adults using WCO as TSR increased, but more adults than juveniles using rocks. This effect is likely caused by juveniles' higher susceptibility to desiccation (compared to adults; Spotila, 1972), and the greater moisture-holding capacity of WCO versus rocks.

We have documented a difference in salamander surface activity among years. The reason for the drop in leaf litter capture proportion in 2012 is not clear. It is possible that the 2012 drought in Missouri (Nixon 2013) caused soil and leaf litter moisture to be lower than average; however, rainfall amounts over longer time spans (1-3 months prior to sampling) were not strongly predictive of surface activity. Interestingly, the within-year decline in leaf litter use as TSR elapsed was not as severe in 2012 as in the previous two years (Fig. 2). We suspect that conditions were harsh in 2012 no matter how recently it had rained, even under cover objects that would normally provide suitable refuge. Thus, the few salamanders that were surface active were more evenly distributed among the leaf litter and cover objects when surface active and foraging.

Our study focused on the salamanders' relative use of available microhabitats, but our results further support the prevalence of variable detectability within an amphibian species and the importance of accounting for changes in detectability when estimating woodland salamander abundance, occupancy, or density (Mazerolle *et al.* 2007). Even when moisture conditions were ostensibly similar (TSR = 1), the proportion of captures within the leaf litter varied from ≈50% to 90% (Fig. 4). This shows that even if efforts are made to standardize sampling design, other factors that influence detectability must be acknowledged when estimating population density. Using area-constrained searches—rather than cover boards, natural cover searches, or pitfall traps—allows for a complete account of salamander microhabitat use (Marsh & Goicochea 2003). This is especially important when distinguishing natural variation in microhabitat use from that caused by factors such as forest management or climate change.

In a companion study (Chapter 3), we have developed a model that accounts for distinct components of detectability in light of variable salamander surface activity (i.e., availability for sampling/capture). We found that salamander availability probability varied widely among sites and surveys (range: 5–70%), but conditional capture probability (given salamander availability) was more stable (mean: 83%) due to our survey method. TSR was the strongest predictor of salamander availability, while cover object density best predicted conditional capture probability.

There is considerable evidence that CWD can offset some of the negative effects of disturbances that reduce leaf litter availability (Moseley, Castleberry & Ford 2004; Patrick, Hunter Jr & Calhoun 2006; Rittenhouse *et al.* 2008; Kluber, Olson & Puettmann 2009). It is clear that in our study system, however, terrestrial salamanders frequently occupy leaf litter microhabitat. Forest management practices (e.g., timber harvest, prescribed burns, etc.) that decrease leaf litter depth, increase decomposition rate, or alter soil or leaf litter moisture could substantially alter the distribution of microhabitats available to salamanders (Semlitsch *et al.* 2009). This could lead to decreased foraging opportunities and greater competition for remaining natural cover objects. Climate change could also alter patterns of microhabitat quality and utilization, as salamanders cope with increased temperatures, more variable rainfall, and potentially longer periods between rainfall events (IPCC 2013). Ultimately, understanding patterns of microhabitat use will enable us to better assess changes in the abundance and behavior of organisms in relation to either natural or anthropogenic disturbance events.

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TABLE 1. Effect sizes of environmental variables on *Plethodon serratus* counts per plot (salamander surface activity) within the Mark Twain National Forest, Missouri, from 2010–2012. Significant parameters (95% CI not overlapping zero) are indicated in bold.

Parameter	Estimate	Robust SE[b]	LL[c]	UL[c]
(Intercept)	**0.963**	**0.173**	**0.624**	**1.301**
Soil temp[a]	-0.010	0.006	-0.022	0.002
Litter depth[a]	0.044	0.035	-0.025	0.113
# Rocks[a]	**0.008**	**0.002**	**0.004**	**0.012**
# Woody COs[a]	**0.052**	**0.008**	**0.037**	**0.066**
TSR (days)[a]	**-0.575**	**0.047**	**-0.666**	**-0.483**
Season	-0.052	0.058	-0.166	0.063
Year	**-0.303**	**0.040**	**-0.381**	**-0.226**

[a] parameter standardized using z-score method prior to analysis

[b] Robust SE obtained via sandwich covariance matrix estimator

[c] LL and UL are 95% confidence limits

FIGURE 1. Percent of *Plethodon serratus* captures within the Mark Twain National Forest, Missouri, from 2010–2012, in each of four microhabitat types. Numbers of captures are indicated above each bar.

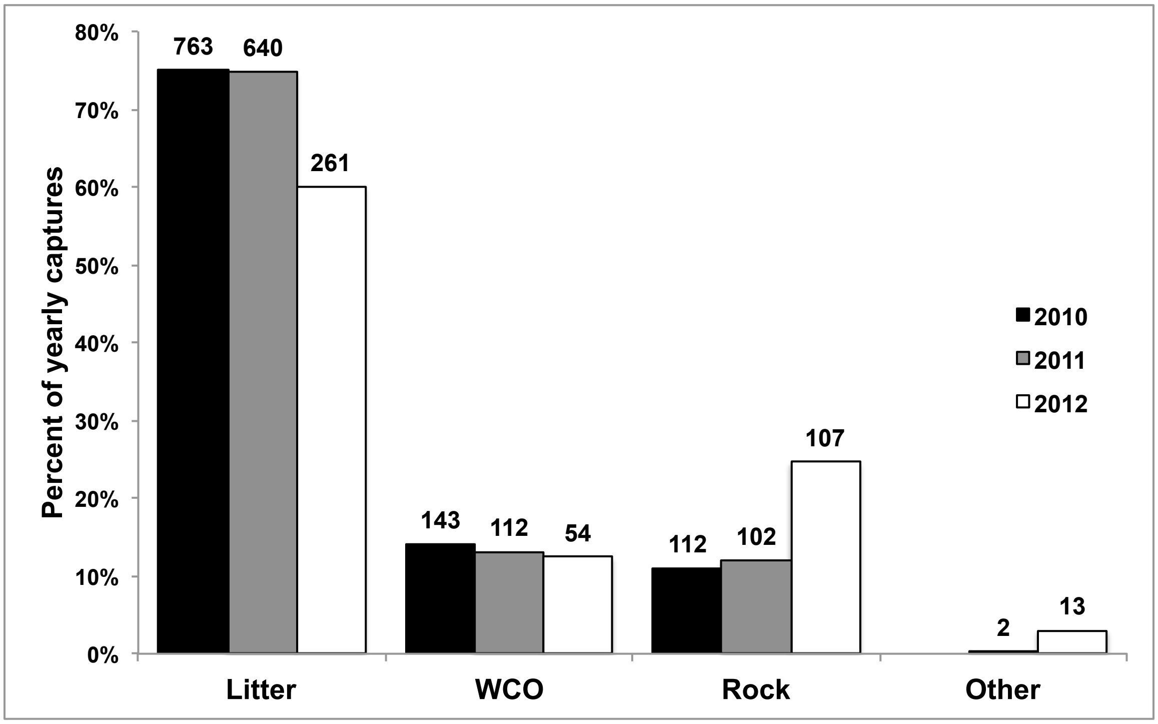


FIGURE 2. Predicted probabilities of *Plethodon serratus* occurrence within the Mark Twain National Forest, Missouri, from 2010–2012, in each of three microhabitat types (leaf litter, woody cover objects, rocks) relative to time since last rainfall.

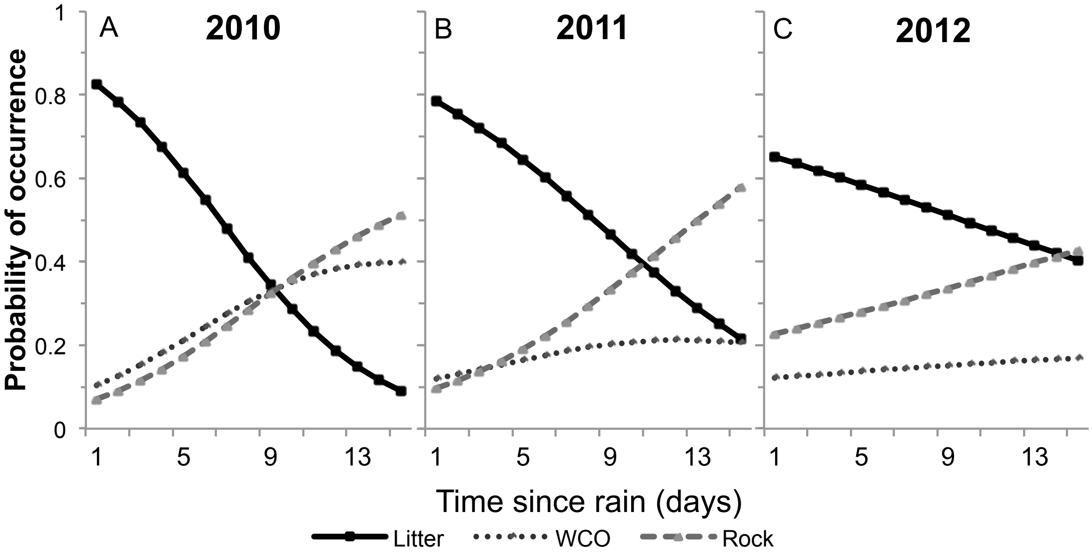


FIGURE 3. Relationship between *Plethodon serratus* surface activity and recent rainfall across three years in the Mark Twain National Forest, Missouri. Lines indicate predicted relationships for each year (solid=2010, dashed=2011, dotted=2012).

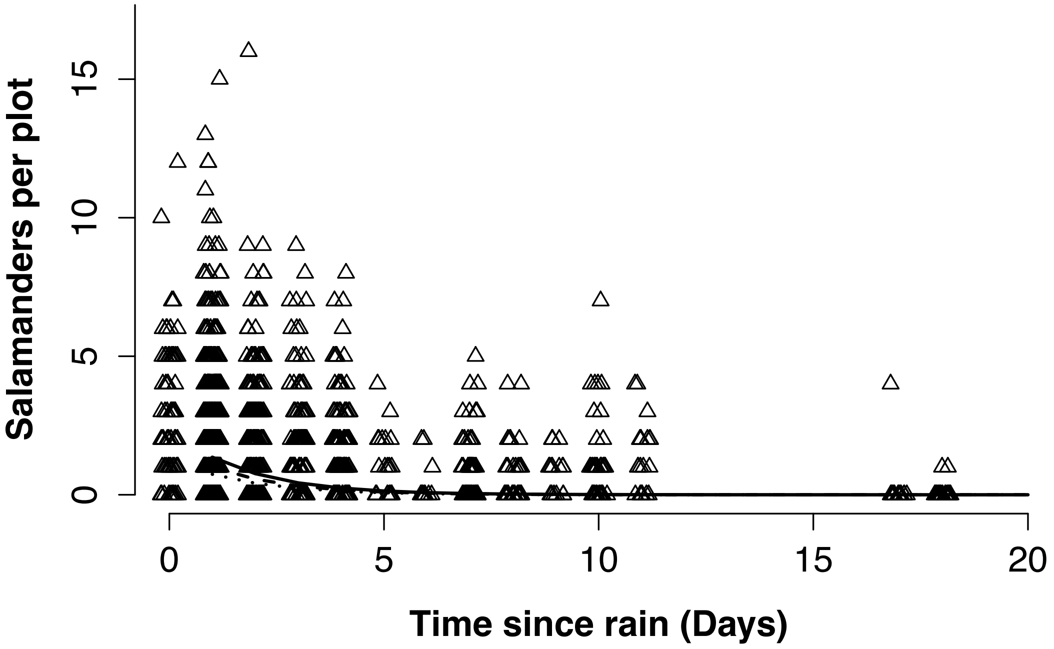
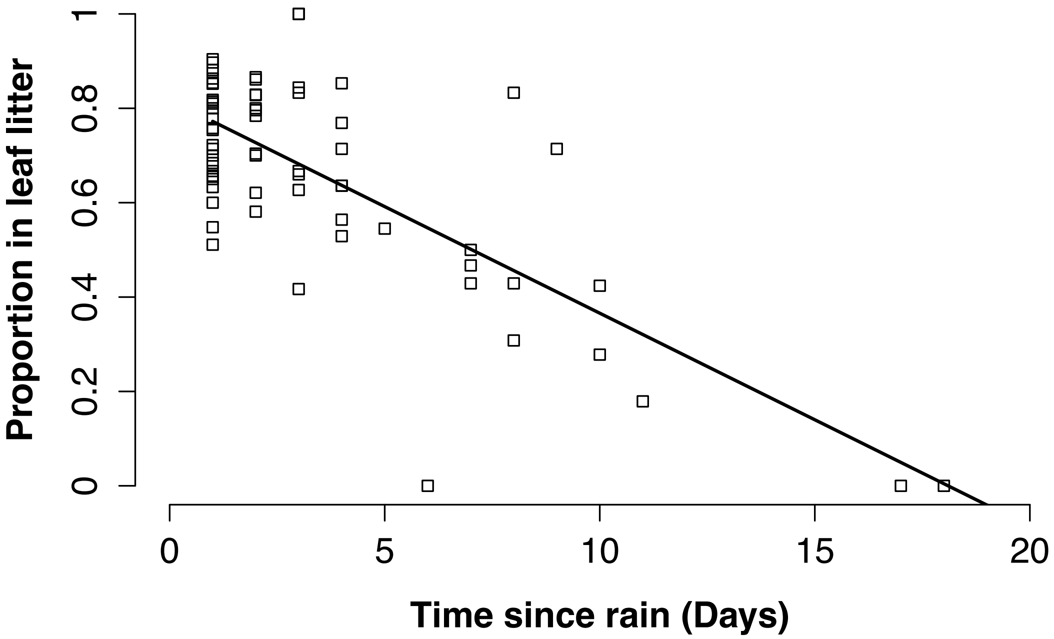


FIGURE 4. Effect of recent rainfall on *Plethodon serratus* use of leaf litter within the Mark Twain National Forest, Missouri, from 2010–2012.



CHAPTER 3 • PARTITIONING DETECTABILITY COMPONENTS IN POPULATIONS SUBJECT TO WITHIN-SEASON TEMPORARY EMIGRATION USING BINOMIAL MIXTURE MODELS

ABSTRACT

Detectability of individual animals is highly variable and nearly always < 1; imperfect detection must be accounted for to reliably estimate population sizes and trends. Hierarchical models can simultaneously estimate abundance and effective detection probability, but there are several different mechanisms that cause variation in detectability. Neglecting temporary emigration can lead to biased population estimates because availability and conditional detection probability are confounded. In this study, we extend previous hierarchical binomial mixture models to account for multiple sources of variation in detectability. The state process of the hierarchical model describes ecological mechanisms that generate spatial and temporal patterns in abundance, while the observation model accounts for the imperfect nature of counting individuals due to temporary emigration and false absences. We illustrate our model's potential advantages – including the allowance of temporary emigration between sampling periods – with a case study of southern red-backed salamanders *Plethodon serratus*. We fit our model and a standard binomial mixture model to counts of terrestrial salamanders surveyed at 40 sites during 3-5 surveys each spring and fall 2010-2012.

Our models generated similar parameter estimates to standard binomial mixture models. Aspect was the best predictor of salamander abundance in our case study; abundance increased as aspect became more northeasterly. Increased time-since-rainfall strongly decreased salamander surface activity (i.e. availability for sampling), while higher amounts of woody cover objects and rocks increased conditional detection probability (i.e. probability of capture, given an animal is exposed to sampling).

By explicitly accounting for both components of detectability, we increased congruence between our statistical modeling and our ecological understanding of the system. We stress the importance of choosing survey locations and protocols that maximize species availability and conditional detection probability to increase population parameter estimate reliability.

INTRODUCTION

Ecologists have long recognized that population dynamics form the foundation of ecology (Andrewartha & Birch 1954; Slobodkin 1980). Estimating how many individuals occupy various habitats is also fundamental for management and conservation. Understanding the mechanisms of population dynamics is essential for assessing the conditions of populations, predicting changes due to land use and climate change, and managing habitats in which populations live. Generating unbiased estimates of demographic parameters is crucial for such endeavors, yet parameters like abundance (*N*) are not easily measured because of imperfect detectability; detection probability (*p*) fluctuates and is nearly always < 1 (Royle *et al*. 2007; Royle & Dorazio 2008; Kéry & Royle 2010; Kéry & Schaub 2012). Studies that ignore the imperfectness of the observation process may underestimate true *N* (Royle & Dorazio 2008), report biased abundance-covariate relationships (Tyre, Tenhumberg & Field 2003; Kéry 2008), or misidentify population trends (Kéry & Schmidt 2008) by implicitly assuming that the relationship between *p* and *N* is constant across time, space, and other factors of the study (Pollock *et al.* 2002; Bailey, Simons & Pollock 2004b; Kéry & Schmidt 2008). This assumption is rarely (if ever) true because observed counts vary spatially and temporally with changes in *p* and *N*; thus, using naïve counts for estimating *N* is precarious (Pollock *et al.* 2002; Kéry & Schmidt 2008; Royle & Dorazio 2008; Kéry 2008; Kéry & Royle 2010). Abundance and detection probabilities must be modeled distinctly (yet simultaneously) if unbiased estimates are required (Mackenzie & Kendall 2002; Kéry & Schmidt 2008).

Many population analysis methods that account for imperfect detection are labor or cost intensive (overview in (Williams, Nichols & Conroy 2002)), but recently-developed hierarchical models allow for simultaneous estimation of population parameters and detection probability without requiring marked individuals (Mackenzie, Nichols & Lachman 2002; Royle 2004; Royle & Dorazio

2008; Kéry & Schaub 2012; Halstead *et al.* 2012). A strategic benefit of the hierarchical approach is the ability to partition a complicated system into two or more simpler, linked, stochastic models that accurately represent the mechanisms generating the parameters and observations (Royle 2004; Royle & Dorazio 2008; Kéry & Schaub 2012; Halstead *et al.* 2012). One such model – the binomial mixture model – was developed to estimate *N* and *p* from spatially and temporally replicated counts (Royle 2004). Extensions of the binomial mixture model have incorporated environmental covariates (Dodd Jr. & Dorazio 2004; Peterman & Semlitsch 2013), correlated behavior of individuals (Martin *et al.* 2011), and temporal trends in open populations (Royle & Dorazio 2008; Kéry *et al.* 2009; Kéry & Royle 2010). The model's hierarchical structure involves (1) a state process, which describes spatial and temporal variation in *N*, and (2) a dependent observation process that represents the filter through which we see the latent state process (Royle 2004).

The observation process can be further divided into two components of detectability – availability and conditional capture probability (Pollock *et al.* 2004; Kéry & Schmidt 2008). Availability is determined by the presence/absence of individuals in an area, the capacity of the survey technique to detect animals of interest, and environmental factors that influence animal locations (Pollock *et al.* 2004). The counterpart of availability is temporary emigration, which is the probability that an individual is alive, yet unavailable to be detected during a survey (Kendall, Nichols & Hines 1997; Bailey, Simons & Pollock 2004b); thus, we consider temporary emigration = 1 – (probability of availability for capture). Conditional capture probability is the probability that an organism is detected, given that it is available for sampling (Kéry & Schmidt 2008). Conditional capture probability can be affected by factors such as survey methodology, observer experience level, habitat complexity, and species crypsis.

In most studies, *p* represents an overall or effective detection probability, which encompasses both availability and conditional capture probability (Kendall 1999; Bailey, Simons & Pollock 2004b). However, neglecting temporary emigration can lead to biased density estimates because availability and conditional capture probability are confounded (Kendall, Nichols & Hines 1997). Problems with interpreting abundance estimates also occur, particularly when availability is low or varies spatiotemporally (Pollock *et al.* 2004; Kéry & Schmidt 2008). Many population models do not explicitly include availability, as it is not often recognized as a possible concern for many taxa (Kéry & Schmidt 2008). Availability can be affected by the behavior or physiology or both, and by survey methods (Pollock *et al.* 2004). For instance, the availability of birds or frogs being counted via calls may be affected by behavioral differences between individuals or weather-related factors. Aquatic animals may be unavailable during visual surveys because they are too far below the surface or water clarity is poor. Small mammals may be unavailable for surveys due to temporary emigration into burrows, tree cavities, or other refugia. Including availability is useful in these cases, as it enables researchers to partition and model the effective detection probability in a quantitatively and biologically meaningful way.

Terrestrial woodland salamanders (family Plethodontidae) are ideal for examining the components of detectability using binomial mixture models for several reasons. First, capture-mark-recapture (CMR) is not always an option for amphibians; its labor-intensive nature means that marking enough amphibians to satisfy CMR assumptions is difficult and expensive (Pollock *et al.* 1990; Donnelly & Guyer 1994; Dodd Jr. & Dorazio 2004). Additionally, recapture rates are often very low for amphibians (Taub 1961; Jung *et al.* 2000; Smith & Petranka 2000). Second, terrestrial salamanders' 3-dimensional use of forest litter and soil is fairly unique among vertebrates. Because they lack lungs, they require moist substrate to sustain cutaneous respiration (Spotila 1972; Feder 1983). This high moisture requirement, coupled with terrestrial salamanders' limited mobility, means that they exhibit limited activity on the ground surface and have small home ranges (Kleeberger & Werner 1982; Liebgold, Brodie & Cabe 2011). Terrestrial woodland salamanders often remain under surface cover objects to retain moisture, but retreat to underground burrows to prevent desiccation when surface conditions become too dry (Jaeger 1980; Grover 1998; O'Donnell, Thompson III & Semlitsch 2014). Therefore, unlike many other animals, terrestrial woodland salamanders' primary direction of movement is vertical rather than horizontal, which causes high levels of daily and seasonal temporary emigration underground (Taub 1961; Bailey, Simons & Pollock 2004b; Price *et al.* 2012).

Terrestrial salamanders undoubtedly have ecological impacts deeper than the forest floor (Taub 1961; Davic & Welsh 2004a); accordingly, when estimating abundance, we are interested in the total number of salamanders in an area – both at the surface and belowground. This quantity has been termed "superpopulation," as opposed to the "surface population" consisting of salamanders available for capture (Kendall 1999; Bailey, Simons & Pollock 2004b; c). As with other organisms, terrestrial salamanders' detectability varies in two major ways: (1) spatially, because of local habitat characteristics, and (2) temporally, due to changing environmental conditions and seasonal activity patterns (Bailey, Simons & Pollock 2004b).

Our objectives were to: (1) develop a binomial mixture model that explicitly accounts for the distinct components of effective detection probability – conditional capture probability and availability and (2) compare our model to a standard binomial mixture model. For our terrestrial salamander case study, we sought to (3) identify landscape factors that best predict abundance, and (4) identify weather and habitat-related factors that best predict availability and conditional capture probability. We present our modeling approach and results of our case study using Southern red-backed salamanders *Plethodon serratus*.

MATERIALS AND METHODS

Model development

STATE PROCESS—The state process describes the ecological mechanisms that generate spatial and temporal patterns in abundance. If sampling adheres to a metapopulation design with repeated counts of unmarked individuals (y_{ijk}) occurring at $i = 1, 2, \ldots, R$ sites over $j = 1, 2, \ldots, T$ surveys (secondary periods) and $k = 1, 2, \ldots, K$ seasons (primary periods), then we may presume the abundance at each site (N_{ik}) follows a Poisson distribution with mean λ_{ik} (eqn. 1; (Royle 2004; Royle & Dorazio 2008; Kéry *et al.* 2009)).

$$N_{ik} \mid \lambda_{ik} \sim Poisson(\lambda_{ik}) \qquad \text{eqn 1}$$

$$\log(\lambda_{ik}) = \alpha_{\lambda(ik)} + \sum_{l=1}^{m} x_{\lambda(ikl)}\, \beta_{\lambda(ikl)} + \delta_{\lambda(ik)} \qquad \text{eqn 2}$$

The parameter λ_{ik} represents the mean abundance of animals at site i in season k. We can account for spatial heterogeneity in abundance by including m site and/or season-specific covariates on the log-transformed λ_{ik}, as well as site-specific random effects ($\delta_{\lambda(ik)}$; eqn 2). We assume N at each site remains constant during each primary period, but abundance may change via births, deaths, immigration, or emigration between primary periods.

OBSERVATION PROCESS—The observation model reflects the imperfect process of counting individuals. Repeated counts (y_{ijk}) follow a binomial distribution, with index N_{ik} (per-site abundance) and success probability p_{ijk} (per-individual detection probability; eqn 3). Implicitly, p represents the effective detection probability, which is the product of the conditional capture probability ω and availability probability v (eqn 4).

$$y_{ijk} \mid N_{ik} \sim Binomial(N_{ik}, p_{ijk}) \qquad \text{eqn 3}$$

$$p_{ijk} = v_{ijk} * \omega_{ijk} \qquad \text{eqn 4}$$

We distinctly modeled the two components of p to more accurately reflect the separate processes that generated our observations. It is difficult to make inferences about both components of p without relevant explanatory variables; v and ω remain confounded and the effective detection probability is reported (Kendall, Nichols & Hines 1997). However, if covariates are available that explain variation in each of the two components, then distinct parameter estimates may be identifiable. We logit-transformed v and ω to constrain the probabilities between 0 and 1 and to incorporate covariates, which can be site, season, and/or survey-specific (eqns 5, 6). Site or survey-specific random effects (δ) can also be included.

$$\text{logit}(v_{ijk}) = \alpha_{v(ijk)} + \sum_{l=1}^{d} \beta_{v(ijkl)} x_{v(ijkl)} + \delta_{v(ijk)} \qquad \text{eqn 5}$$

$$\text{logit}(\omega_{ijk}) = \alpha_{\omega(ijk)} + \sum_{l=1}^{z} \beta_{\omega(ijkl)} x_{\omega(ijkl)} + \delta_{\omega(ijk)} \qquad \text{eqn 6}$$

Simulation study

To test the validity of our temporary emigration (TE) model, we evaluated its performance on simulated data for 6 different scenarios – each combination of low, moderate, and high availability intercepts (α_v = 0.2, 0.5, 0.8) with moderate and high conditional capture probability intercepts (α_ω = 0.5, 0.9). All simulated data sets included 6 primary periods, 5 secondary periods per primary period, and 40 study sites. We simulated data using R (R Core Team 2013) and performed analyses using JAGS (Plummer 2003) via the package R2jags (Su & Yajima 2013). For each simulation, we ran 3 chains for 10000 iterations, discarded the first 5000 as burn-in, and specified random starting values. We assessed convergence of all parameters using the Gelman-Rubin statistic (*R-hat* < 1.1; (Gelman & Hill 2007)), and conducted enough simulations to accrue 100 replicates for each scenario. We computed the bias and coverage rate (proportion of posterior 95% credible intervals [CRI] that contained true value) from the posterior means of α_ν, α_ω, α_λ, and total abundance.

Case study: Southern red-backed salamanders

Plethodon serratus can be found in four isolated regions in the US, including the southeastern portion of Missouri (Petranka 1998). Like other terrestrial woodland salamanders, they spend much of their lives underground, but surface during favorable conditions to forage and mate. In Missouri, red-backed salamanders exhibit a seasonal activity pattern, with highest surface activity from March to May and September to October. Females oviposit during May and June, and eggs hatch between July and August (Herbeck & Semlitsch 2000). These physiological constraints and life-history traits generate daily and seasonal patterns of surface activity.

We conducted surveys for *P. serratus* at the US Forest Service Sinkin Experimental Forest (Dent County, Missouri, USA; Fig. 1). The study site – within the Ozark Plateau – consists of mature (80-100 year old) oak and oak-pine stands (*Quercus* spp., *Pinus echinata*) that had not been harvested or thinned for ≥ 40 years (Kabrick *et al.* 2014). We established two 10m x 10m plots within each of twenty 5-ha experimental units, yielding $i = 40$ survey sites (Fig. 1). We surveyed a different 3m x 3m section of each plot 3-5 times (j) in each spring and fall 2010-2012 ($k = 6$ seasons); surveys were separated by an average (±1 SD) of 7 ± 3.7 days. We completed all surveys within each season in a short enough time span (32.1 ± 5.7 days) to assume the population was demographically closed. Terrestrial salamanders do not experience large population fluctuations over the course of a few months, so we did not expect substantial turnover or permanent emigration (Dodd Jr. & Dorazio 2004).

We conducted diurnal area-constrained searches; each of two observers searched 1m-wide transects by crawling through the 3m x 3m plot while hand-raking leaf litter and duff. Natural cover objects were flipped when encountered. Surveys continued until entire quadrat was thoroughly searched (average 9.1 ± 2.8 min); we continually replaced leaf litter and cover objects and ensured plots were reconstructed upon completion. Each round of sampling lasted until each plot was surveyed once (2-4 days); we randomly determined search order of plots each round. For each plot, we recorded total salamanders captured, rocks (≥ 5 cm), woody cover objects (WCOs), mean soil temperature, and mean leaf litter depth (as in (O'Donnell, Thompson III & Semlitsch 2014)). We obtained rainfall and temperature data from the Sinkin Experimental Forest weather station (MSINM7).

Site-specific variables of slope, Beers-transformed aspect (linear scale; southwest=0, northeast=2), soil water-holding capacity (AW), terrain shape index (TSI), and landform index (LFI) were determined from the Regional Oak Study (Kabrick *et al.* 2014).

We expected variation in landscape features to drive variation in abundance among sites; thus, we included aspect, slope, AW, TSI, and LFI as abundance covariates. We let the abundance intercept vary by season ($\alpha_{\lambda(k)}$; model TE[season]) and site-by-season ($\alpha_{\lambda(ik)}$; model TE[site x season]), and included a site-level random effect to account for overdispersion. For comparison, we also fit a standard binomial-mixture model (NE) that does not partition detectability. We again included a random site-level effect, let the abundance intercept vary by season (model NE[season]) and site-by-season (model NE[site x season]), and included the same covariates.

Because our survey technique targeted aboveground salamanders, we assumed availability probability v was strongly associated with climatic and temporal factors that drive terrestrial salamander surface activity. Previous work suggested that time since rainfall explained over 60% of the variation among raw survey counts, which approximate salamander surface activity (O'Donnell, Thompson III & Semlitsch 2014). Thus, we included days-since-rainfall, soil temperature, time-of-day, and a quadratic time-of-day term as availability covariates. We also included a site-by-season random effect to account for unexplained variation in availability.

Conditional capture probability, by definition, is only applicable to animals that are available for capture. For our study, ω can be thought to represent the likelihood of an observer capturing a surface-active (i.e., available) salamander. Area-constrained searches have inherently higher capture likelihoods because of their comprehensive nature and the proximity of the observer to the target organisms (Jaeger & Inger 1994). Thus, we assumed the intercept α_ω to be relatively high, and that differences in conditional capture probability among plots were primarily influenced by the structural complexity of the quadrat. Therefore, we included the covariates leaf litter depth, rocks, and WCO to reflect plot complexity.

As in the simulation study, we fit our models using JAGS (Plummer 2003) via the R2jags library (Su & Yajima 2013) within R (R Core Team 2013). Prior to analysis, all covariates were standardized to promote Markov chain Monte Carlo convergence. We chose a vague normal prior for α_λ (mean = 0, SD = 10), weakly informative uniform priors for all coefficient terms (-3, 3) and the intercept α_v (-4.6, 4.6), and an informative normal prior for α_ω (mean = 2.2 [= 0.9 on probability scale], SD = 0.4). Informative priors promote model convergence by excluding unreasonably extreme values and stabilizing the logit function. For both site-by-season abundance models, we ran 3 chains with 500000 iterations each, discarded the first 250000 as burn-in, and thinned the remaining samples by 1 in 150 to obtain 5001 samples for analysis. The season-specific abundance models required fewer iterations to achieve convergence; we ran 3 chains for 50000 iterations, discarded the initial 25000, and thinned the remainder by 1 in 15 to obtain 5001 posterior samples. We confirmed convergence using the Gelman-Rubin statistic (*R-hat* < 1.01; (Gelman & Hill 2007)) and assessed model fit using posterior predictive checks – we calculated a Bayesian *P*-value by comparing Chi-squared discrepancy statistics of observed to simulated data (Kéry & Schaub 2012).

RESULTS

Simulation study

The absolute bias of α_{ν} ranged from -1 to +3% on the probability scale; coverage rate was 93-98% (Appendix A, Table 1). The width of the 95% CRI decreased as the availability and conditional capture probabilities increased (Appendix A, Table 1). The absolute bias of α_{ω} ranged from 0 to +3% on the probability scale; coverage rate was 91-99% (Appendix A, Table 2). The width of the 95% CRI decreased among scenarios as the availability probability increased, but did not differ between moderate and high conditional capture probability scenarios (Appendix A, Table 2). The mean relative bias of α_{λ} (on raw scale) was -1.5% (range: -8.5% to +1.1%); coverage rate ranged from 92-97% (Appendix A, Table 3). The width of the 95% CRI again decreased as availability probability increased, but did not differ with conditional capture probability (Appendix A, Table 3). The relative bias of total abundance ranged from -2.4% to +6.3% (Appendix A, Table 4). The coverage rate for correctly estimating the abundance in all 6 seasons ranged from 72 to 94%, while the coverage rate for estimating at least 5 seasons correctly was between 90 and 97% (Appendix A, Table 4).

Case study: Southern red-backed salamanders

We captured 2309 *P. serratus* during 27 sampling rounds over six seasons between 9 April 2010 and 26 October 2012. Posterior predictive checks indicated adequate fit for each of our four models (Bayesian *P*-values, fit-ratios: TE[season] = 0.338, 1.03; TE[site x season] = 0.285, 1.04; NE[season] = 0.443, 1.01; NE[site x season] = 0.373, 1.03). Estimates of per-season abundance totals differed under each of the four models (Fig. 2, Table 1). Both the TE and NE models with site-by-season abundance intercepts had higher abundance estimates than their counterparts with season-specific intercepts (Fig. 2). The mean TE[season] abundance was 53.5% of the TE[site x season] abundance; similarly, the mean NE[season] abundance was 54.5% of the NE[site x season] mean abundance. Both [site x season] models had wider 95% CRIs for all abundance-related parameters than [season] models (Tables 1 & 2). Standard deviations of site-specific random effects (abundance) and site-by-survey random effects (detection process) were significant for all models (Table 2).

TEMPORARY EMIGRATION MODELS—After correcting for imperfect detection, aspect had a greater effect on salamander abundance than other landscape factors (Table 2). Abundance increased as the aspect approaches northeast, and deceased toward southwest (Fig. 4). The estimates of total abundance per season varied between temporary emigration models, but some CRIs overlapped slightly (Table 1). Fall 2010 had the highest abundance estimate under model TE[season], while Spring

2010 had the highest estimate under model TE[site x season]. Spring 2012 had the lowest abundance estimate under model TE[season], while model TE[site x season] estimated the lowest abundance in Fall 2011 (Table 1). We calculated salamander density by dividing the predicted abundance per plot by the area searched ($9m^2$). Mean seasonal per-plot abundance ranged from 3.6 to 7.8 salamanders under model TE[season] and 8.2 to 14.1 under TE[site x season]; thus, mean density ranged from 0.40 to 0.87 salamanders/m^2 under TE[season] and 0.91 to 1.57 under TE[site x season].

Time-since-rainfall was the strongest predictor of salamander availability (v); the CRI for the quadratic effect of time-of-day also did not overlap zero in the TE[site x season] model (Table 2). Availability steadily decreased as time-since-rainfall increased (Fig 5a). Per-season availability averaged 0.47 (range: 0.39 to 0.56) under model TE[season] (Fig. 3) and 0.43 (range: 0.36 to 0.50) under TE[site x season]. Per-survey availability varied widely, with an overall range of 0.05 to 0.70 under TE[season] and 0.05 to 0.61 under TE[site x season].

Rock density had the greatest effect on conditional capture probability (ω), followed by WCO abundance (Table 2). The conditional capture probability increased as the number of WCO and rocks increased (Figs 5b & 5c). Overall, conditional capture probability was fairly steady across seasons (Fig. 3); it averaged 0.83 under model TE[season] and 0.84 under model TE[site x season].

STANDARD BINOMIAL MIXTURE MODELS—Parameter estimates for both NE models were similar to their TE counterparts. Aspect had the greatest effect on abundance under model NE[season] (Table 2); salamander abundance increased as aspect approached northeast. Seasonal abundance estimates also varied between NE models, with slight overlap in CRI for a few seasons (Table 1). Fall 2010 had the highest abundance estimate under model NE[season], while Spring 2010 had the highest estimate under model NE[site x season]. Spring 2012 had the lowest abundance estimate under both NE models (Table 1). Mean seasonal per-plot salamander abundance ranged from 3.4 to 7.2 (density = 0.38 to 0.80/m^2) under model NE[season] and 8.2 to 13.0 (density = 0.91 to 1.4/m^2) under NE[site x season].

Time-since-rainfall had the greatest effect on effective detection probability (*p*) in both NE models (Table 2). Rocks and WCO abundance per plot had moderate positive effects on detection probability (Table 2). The quadratic of time-of-day was also important for detection probability under both models (Table 2). The mean effective detection probability per season averaged 0.42 under NE[season] and 0.39 under NE[site x season]. The per-survey detection probability was highly variable, ranging from 0.06 to 0.66 under NE[season] and 0.06 to 0.59 under NE[site x season].

DISCUSSION

We built an explicit description of a two-component observation process into a binomial mixture model to distinguish between two pertinent components of detectability: availability (or lack of temporary emigration) and conditional capture probability. By explicitly considering two components of the observation process, we increased congruence between our statistical model and our ecological understanding of the system. Many animals exhibit behaviors that affect their availability to be detected; examples include terrestrial mammals and invertebrates that periodically use underground burrows, aquatic animals that are not close enough to the surface to be seen, and populations in which only breeding individuals are available for capture. Our model framework is flexible, making it possible to apply to many different taxa and survey methods. Our simulation study indicates that the model is valid over a range of reasonable availability and conditional capture probability values.

Other models accounting for temporary emigration have been developed (Kendall, Nichols & Hines 1997; Kendall 1999; Bailey, Simons & Pollock 2004b; c), but many involve CMR, which can be time-intensive and prohibitively expensive for amphibians (Dodd Jr. 2003; Mazerolle *et al.* 2007) and other taxa. Chandler et al. (2011) developed a single-season generalized binomial/multinomial-mixture model accounting for temporary emigration in unmarked organisms; however, their model is set in a maximum-likelihood framework, and is not open to changes in demographic parameters. Like CMR methods, temporary emigration is only allowed between primary periods, so the model cannot accommodate temporary emigration that occurs between secondary periods. In systems like ours, it makes biological sense for availability to vary among surveys (secondary periods) because terrestrial salamanders respond so strongly to changing moisture levels and temperature (O'Donnell, Thompson III & Semlitsch 2014). Our model allows for temporary emigration between secondary periods, which enables estimation of survey-specific values of availability. Like other models, it also allows fitting of site and/or season-specific covariates to both components of detection probability.

Overall, parameter estimates from our TE models did not differ greatly from the NE models. Corresponding 95% CRIs overlapped for all covariate parameter estimates. The difference between posterior mean estimates from models TE[season] and NE[season] ranged from 3.5 to 38.6% for abundance covariates, 11.5 to 52.4% for availability covariates, and 18.1 to 87.0% for conditional detection covariates. The starkest differences between models were between those with an abundance intercept varying by season versus site-by-season (Tables 2 & 3). We believe the observation that we can partition detectability into its components – and still generate similar abundance estimates to a standard binomial mixture model – is evidence of the usefulness of our model.

We used a terrestrial salamander for our study because they are known to exhibit high levels of temporary emigration that is largely vertical, unlike many animals that wander horizontally on the landscape (Bailey, Simons & Pollock

2004b; Mazerolle *et al.* 2007; Price *et al.* 2012; Buderman & Liebgold 2012). Our study further illustrated the prevalence of infrequent surface activity in terrestrial salamanders, and the importance of choosing a sampling method appropriate for the desired level of inference about a population. We estimated site and season-specific abundance, which represents the superpopulation of surface-active and belowground salamanders. We saw considerable variation in abundance among sites, but overall the most informative predictor of abundance was aspect. Highest salamander abundance is predicted on northeast slopes, while southwest slopes have the lowest predicted abundance. Northeast slopes are generally the coolest and wettest areas, which may be ideal for terrestrial salamanders that require moisture for cutaneous respiration (Spotila 1972; Feder 1983). Site-specific random effects on abundance encompassed overdispersion; these terms explained variation in abundance otherwise unaccounted for in the model.

We found levels of temporary emigration somewhat lower than previous studies of terrestrial salamanders that used CMR: our per-survey range was 30% to 95% (mean 47%). Buderman and Liebgold (2012) found per-season temporary emigration ranged from 65% to 83%, while Bailey et al. (2004b; c) reported a range of 61% to 98% (mean 87%) per season. Bailey et al. (2004c) found that temporary emigration varied across the landscape; undisturbed/high-elevation sites had greater salamander surface activity than disturbed/low-elevation sites. They attributed the difference to decreased microhabitat variability in higher quality sites, leading to lower levels of belowground salamander emigration. In our study, salamander surface activity was primarily driven by temporally variable factors such as recent rainfall, which we used to inform the availability parameter. This allowed us to estimate a survey-specific value for availability, unlike other temporary emigration models. Variation in availability not explained by specified covariates was captured in the random survey effect.

Conditional capture probability is highly influenced by spatially variable factors such as rock and cover object density. Bailey et al. (2004c) reported higher conditional capture probabilities on disturbed/low-elevation sites than undisturbed/high-elevation sites. They suspected that higher conditional capture probabilities resulted from higher densities of cover objects, which may concentrate surface-active salamanders and make them easier to catch. We think that our result of conditional capture probability increasing with rock and WCO density also illustrates this point. We believe this is because the chance of capturing a salamander, given it is available, decreases as plot complexity increases; sites that have higher cover object density tend to have less vegetation, and are therefore easier to search. Search protocols also have a substantial impact on capture probability of terrestrial salamanders (Williams & Berkson 2004; Buderman & Liebgold 2012). It is critical to choose methods that maximize the capture probability of available individuals; low capture probabilities often result in large confidence intervals in population parameter estimates and can make detecting population trends difficult (Dodd Jr. & Dorazio 2004; Kéry & Schmidt 2008; Buderman & Liebgold 2012).

The models we compared are designed to fit data collected in a metapopulation design – with replicate surveys over time at a number of replicate sites (Royle 2004). Previous studies have applied binomial mixture models in terrestrial salamander research (Dodd Jr. & Dorazio 2004; McKenny, Keeton & Donovan 2006; Peterman & Semlitsch 2013), but none explicitly incorporated temporary emigration. Our temporary emigration model requires more information than the standard binomial-mixture model in order to partition the observation process into its two components. We collected data on spatial covariates that we believe influence conditional capture probability, and we relied on expert opinion and field experience to determine its prior distribution. In other situations, this information could be gleaned from preliminary data or a more intensive sampling regime on a subset of sites (*sensu* (Pollock *et al.* 2002)). This ability to use pilot data or expert knowledge of a study system to set informative priors (and encourage model fitting) is a major advantage of the flexible Bayesian framework (Kéry *et al.* 2009; Halstead *et al.* 2012; Bolker *et al.* 2013).

Understanding the distinction between detectability components, as well as how they are differentially affected by natural or anthropogenic disturbances, could be key in certain management decisions. Some disturbances may increase conditional detection probability by clearing survey areas and making it easier to spot organisms of interest. However, if availability is not accounted for, a false increase in effective detection probability could be perceived, leading to spurious conclusions about population estimates. For example, suppose we are interested in bird responses to wildfire, and are studying two different forest species – one green, the other brown. Before a fire, we presume the species would have similar conditional detection probabilities because they both have some camouflaging. After an intense fire that burns through the canopy, the green species would lose its camouflage and be easier for researchers to spot against the black and brown landscape. If we counted the same number of green and brown birds after the fire, but did not account for the increase in conditional capture probability of the green species, our green population estimate would be biased high, and we could miss a true population decline in the species.

Both parameters – availability and conditional detection probability – are required to fully describe the observation process that we use to make inferences about the ecological process. For robust, long-term monitoring programs, managers should select sites and survey protocols that maximize both species availability and conditional detection probability to increase precision of population parameter estimates and predictability of population trends.

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TABLE 1. Per-season estimates of *P. serratus* abundance over 40 9-m^2 plots. Lower and upper values represent 95% Bayesian credible intervals. Estimated from temporary emigration (TE) and standard binomial mixture (NE) models with abundance intercepts varying by season or site-by-season.

	TE[season]		**TE[site x season]**		**NE[season]**		**NE[site x season]**	
	Mean (SD)	95% CRI	Mean (SD)	95% CRI	Mean (SD)	95% CRI	Mean (SD)	95% CRI
S10	306.4 (23.6)	266, 358	562.6 (177.1)	350, 1016	281.3 (19.1)	249, 324	520.4 (169.3)	321, 944
F10	313.6 (19.0)	281, 355	547.7 (192.8)	337, 1055	288.5 (14.9)	263, 321	503.7 (181.4)	318, 1000
S11	252.2 (14.7)	228, 284	419.9 (135.8)	274, 774	233.0 (11.0)	215, 258	399.2 (137.9)	260, 746
F11	182.0 (11.9)	162, 207	326.9 (110.3)	204, 606	168.9 (9.9)	153, 191	317.5 (110.4)	194, 609
S12	143.0 (13.7)	120, 173	363.8 (253.9)	167, 967	136.5 (12.5)	115, 163	308.4 (169.0)	154, 736
F12	197.0 (13.4)	175, 227	384.2 (135.0)	232, 739	186.3 (11.5)	167, 211	329.7 (99.2)	211, 564

TABLE 2. Comparison of posterior means and 95% Bayesian credible intervals of model parameters for four binomial mixture models. NE models include effective detection probability. TE models partition effective detection probability into availability (lack of temporary emigration) and conditional detection probability. Abundance intercepts varied by season or site-by-season. Parameters with CRI not overlapping zero indicated in bold.

		TE[season]			**TE[site x season]**		
Parameter		Mean	SD	95% CRI	Mean	SD	95% CRI
Abundance	LFI	-0.057	0.121	-0.290, 0.180	-0.002	1.324	-2.529, 2.490
	TSI	0.085	0.085	-0.081, 0.255	0.181	0.951	-1.721, 2.101
	Aspect	**0.155**	**0.062**	**0.035, 0.281**	0.094	0.758	-1.428, 1.559
	AW	0.055	0.059	-0.060, 0.172	0.230	0.748	-1.248, 1.649
	Slope	0.066	0.091	-0.114, 0.249	-0.076	1.056	-2.176, 1.940
Availability	**Rain**	**-1.255**	**0.108**	**-1.476,-1.054**	**-1.076**	**0.094**	**-1.268, -0.900**
	Time	-0.151	0.090	-0.328, 0.027	-0.116	0.075	-0.262, 0.031
	Time^2	-0.149	0.078	-0.300, 0.006	**-0.205**	**0.069**	**-0.341, -0.068**
	Temp	-0.122	0.096	-0.307, 0.071	-0.131	0.085	-0.297, 0.039
P|availability	Litter	0.077	0.223	-0.355, 0.516	0.117	0.275	-0.384, 0.701
	Rocks	**1.506**	**0.449**	**0.461, 2.228**	**1.241**	**0.505**	**0.316, 2.191**
	WCO	**0.474**	**0.227**	**0.135, 1.014**	**0.743**	**0.287**	**0.261, 1.343**
Random effects	**SD(site)**	**0.244**	**0.065**	**0.125, 0.378**	**0.597**	**0.447**	**0.025, 1.690**
	SD(v)	**1.730**	**0.130**	**1.494, 1.995**	**1.369**	**0.117**	**1.515, 1.612**
		NE[season]			**NE[site x season]**		
Parameter		Mean	SD	95% CRI	Mean	SD	95% CRI
Abundance	LFI	-0.079	0.114	-0.301, 0.144	-0.311	1.300	-2.619, 2.395
	TSI	0.100	0.081	-0.054, 0.262	0.465	0.966	-1.444, 2.170
	Aspect	**0.136**	**0.060**	**0.019, 0.255**	0.245	0.735	-1.206, 1.710
	AW	0.061	0.055	-0.046, 0.172	0.332	0.693	-0.915, 1.754
	Slope	0.089	0.084	-0.075, 0.254	0.117	1.060	-2.119, 2.085
Effective *P*	**Rain**	**-1.101**	**0.088**	**-1.279, -0.931**	**-0.985**	**0.080**	**-1.143, -0.832**
	Time	-0.121	0.074	-0.265, 0.027	-0.101	0.067	-0.232, 0.027
	Time^2	**-0.227**	**0.068**	**-0.359, -0.096**	**-0.255**	**0.063**	**-0.381, -0.136**
	Temp	-0.136	0.082	-0.296, 0.023	-0.139	0.075	-0.287, 0.008
	Litter	0.010	0.082	-0.149, 0.170	0.006	0.073	-0.134, 0.153
	Rocks	**0.424**	**0.092**	**0.245, 0.610**	**0.376**	**0.087**	**0.215, 0.547**
	WCO	**0.388**	**0.075**	**0.239, 0.534**	**0.330**	**0.066**	**0.203, 0.462**
Random effects	**SD(site)**	**0.218**	**0.069**	**0.079, 0.351**	**0.620**	**0.497**	**0.021, 1.852**
	SD(*p*)	**1.515**	**0.101**	**1.326, 1.723**	**1.277**	**0.096**	**1.098, 1.475**

TABLE 3. Summary of differences between temporary emigration (TE) models and standard binomial mixture (NE) models with either season-specific or site-by-season abundance intercept.

	Abundance intercept specification	
Model	**Season**	**Site-by-season**
TE	• Lower abundance than TE[site x season] • More precise estimates (tighter CRI) • Partitions detectability components	• Higher abundance estimates • Less precise estimates (wider CRI) • Partitions detectability components
NE	• Lower abundance than NE[site x season] • More precise estimates (tighter CRI) • Detectability not partitioned	• Higher abundance estimates • Less precise estimates (wider CRI) • Detectability not partitioned

FIGURE 1. Location of study site in Dent County, Missouri, USA (inset) and relief map of 20 experimental units.

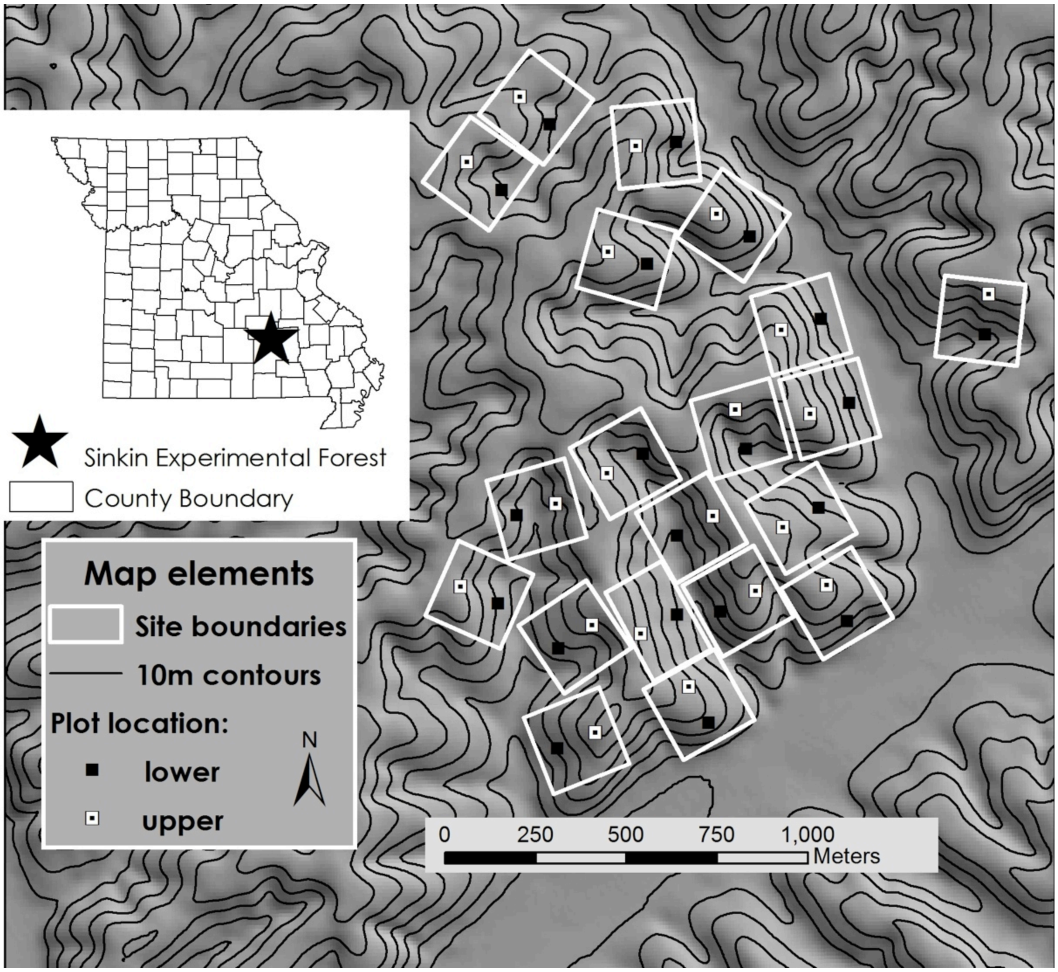


FIGURE 2. Estimates of total per-season abundance from temporary emigration models (TE) and standard binomial-mixture models (NE) versus uncorrected counts. Vertical lines represent 95% Bayesian credible intervals. “Max counts” = uncorrected estimates; sum of maximum counts per site per season.

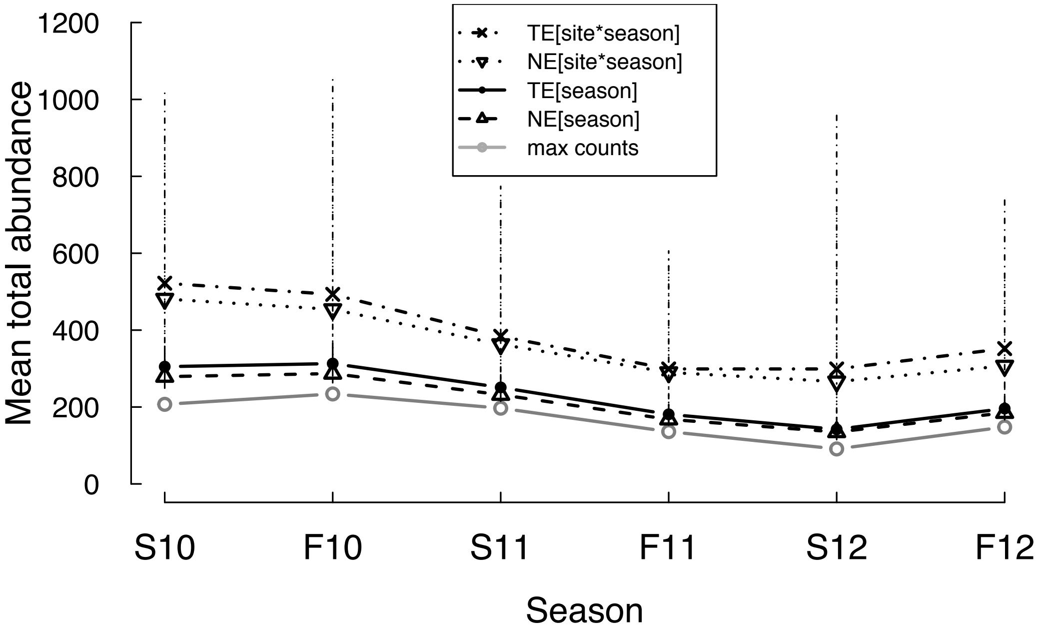


FIGURE 3. Estimates of mean per-season detection parameters. Conditional detection and availability probability estimates from model TE[season]. Effective detection probability (NE) estimates from model NE[season]. Effective detection probability (TE) values calculated from model TE[season]. Vertical lines represent 95% Bayesian credible intervals.

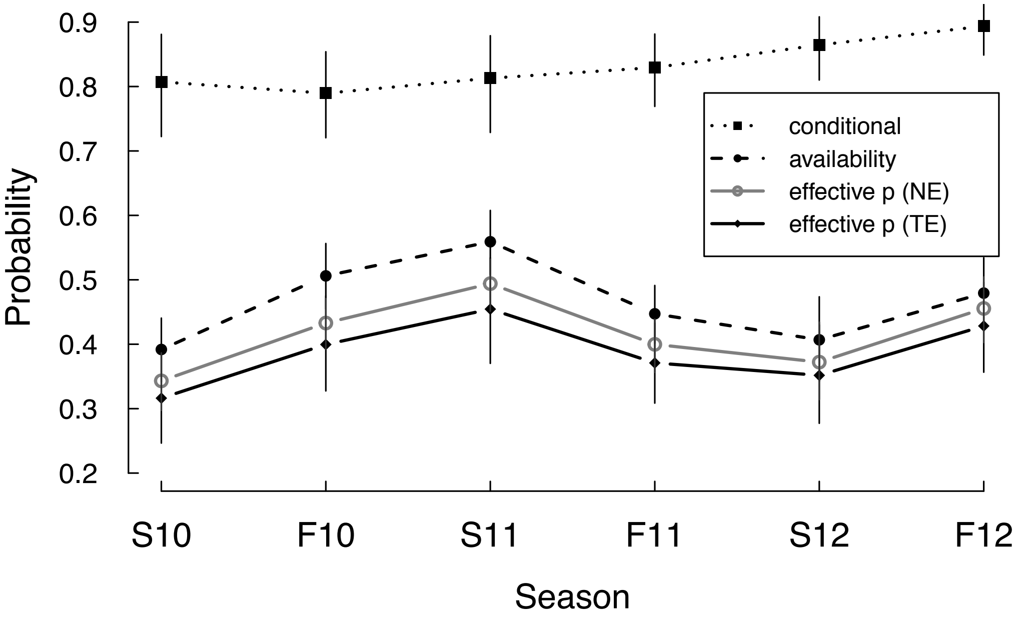


FIGURE 4. Relationship between salamander abundance and aspect, calculated using model TE[season]. Dashed lines represent 95% CRI.

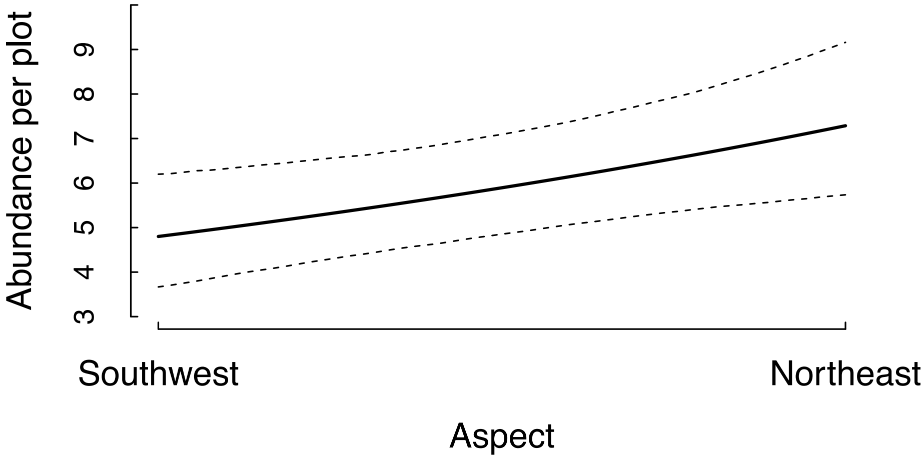
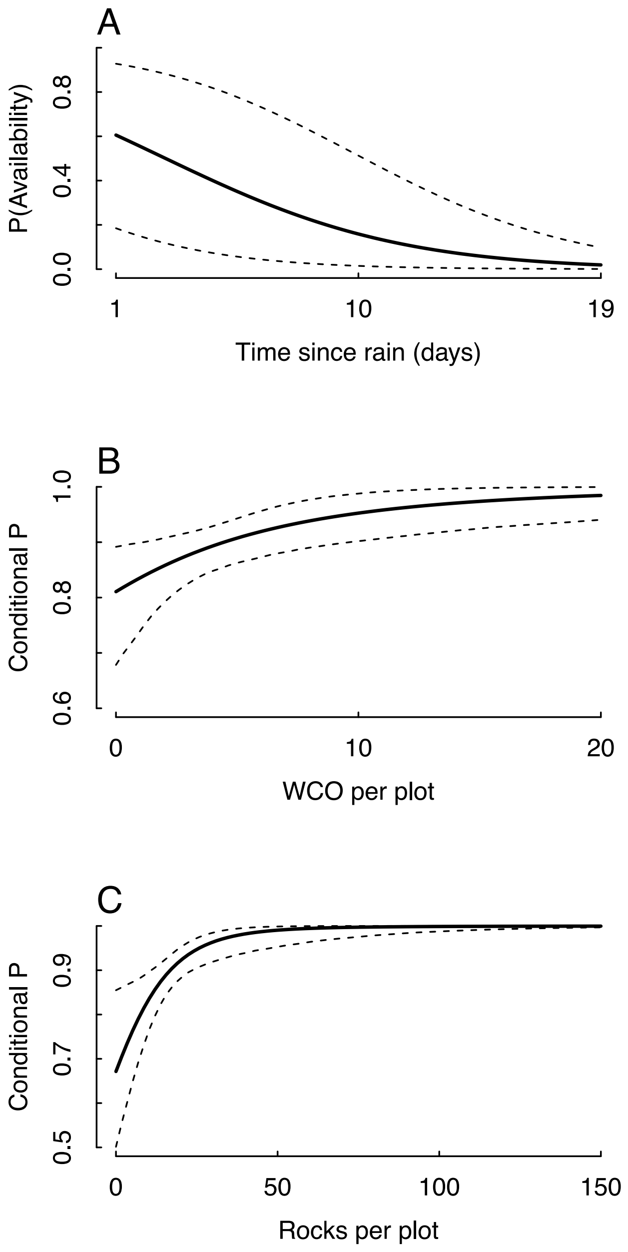


FIGURE 5. Relationships between availability (A), conditional detection probability (B, C), and important covariates. Dashed lines indicate 95% CRI.



CHAPTER 4 • PRESCRIBED FIRE AND TIMBER HARVEST EFFECTS ON TERRESTRIAL SALAMANDER ABUNDANCE, DETECTABILITY, AND MICROHABITAT USE

ABSTRACT

Prescribed fire and timber harvest are anthropogenic disturbances that modify resource availability and ecosystem structure, and can affect wildlife both directly and indirectly. Terrestrial salamanders are effective indicators of forest health due to their high abundance and sensitivity to climate. Given their ecological importance, it is critical to understand how these salamanders respond to management-related disturbances. We predicted that timber harvest and prescribed fire would decrease salamander abundance and availability, and increase salamander cover object use. We surveyed for southern red-backed salamanders (*Plethodon serratus*) from 2010–2014 in a Missouri Ozark (USA) forest, and used binomial mixture models to estimate abundance and detectability in a large-scale Before-After, Control-Impact (BACI) experiment. Five replicate 5-ha units were randomly assigned to each treatment (prescribed burn, shelterwood harvest, midstory herbicide) and control. We compared abundance, surface activity, detectability, and microhabitat use among treatments. Abundance and surface activity decreased post-treatment in shelterwood, midstory, and burn units.

Abundance estimates in midstory and burn units rebounded in the second post-treatment year, but declined further in shelterwood harvest units. Overall, treatments had stronger effects on salamander availability than on abundance. We also found a higher proportion of salamanders under cover objects after prescribed fire, further illustrating the importance of accounting for imperfect detectability. Our findings foster a more robust understanding of the mechanisms underlying population-level responses to management practices, ultimately increasing our ability to effectively manage terrestrial salamanders.

INTRODUCTION

Natural and anthropogenic disturbances affect ecosystems by modifying resource availability and community structure (Pickett and White 1985). The size, severity, and timing of disturbances greatly influence how wildlife populations are affected (Karr and Freemark 1985, White and Pickett 1985). Forest-associated wildlife populations are commonly exposed to management-related disturbances such as prescribed fire and timber harvest, which are used to achieve a variety of objectives. Prescribed fire is increasingly being employed to reintroduce fire as an ecosystem process, particularly in response to a century of fire suppression policies that led to increased fuel loads, more frequent and extensive wildfires in the western United States, and altered forest composition across the country (Pyne et al. 1996, Nowacki and Abrams 2008, Hanberry et al. 2013). Prescribed fire can decrease wildfire risk, reduce fuel loads, and restore fire-adapted ecosystems (Pilliod et al. 2003, Hanberry et al. 2013, Pausas and Keeley 2014). Commercial timber harvests are often implemented for the economic and practical benefits of wood, but trees are also cut for non-extractive purposes, such as ecosystem restoration, reducing the probability of wildfires, and creating wildlife habitat.

Amphibians and other wildlife can be affected by disturbances both directly (i.e., injury, mortality) and indirectly (i.e., disturbance-induced habitat changes). Animals may respond at an individual level to altered habitats in physiological, behavioral, or ecological ways that subsequently influence population-level dynamics such as survival rate and spatial distribution (Karr and Freemark 1985, Sutton et al. 2014). The relative impact of a disturbance is mediated by many factors, including the type, spatial extent, frequency, and timing of the disturbance, as well as the natural history and habitat of the affected organisms (Karr and Freemark 1985). Salamander responses to forest management practices are greatly influenced by their unique life-history characteristics. Terrestrial salamanders respire cutaneously, which makes them dependent on moisture (Spotila 1972, Gatz et al. 1975, Kleeberger and Werner 1982, Feder 1983) and limits their surface activity (Jaeger 1980, O'Donnell et al. 2014*a*). Terrestrial salamanders have small home ranges – typically just a few square meters – because of their limited movement capacity and high site fidelity (Kleeberger and Werner 1982, Ousterhout and Liebgold 2010). Salamanders are top vertebrate predators in forest-floor ecosystems and may have substantial effects on nutrient cycling and leaf litter decomposition (Burton and Likens 1975, Wyman 1998, Davic and Welsh 2004, Walton 2013, Semlitsch et al. 2014). These life history characteristics make terrestrial salamanders effective indicators of overall ecosystem health, and thus, ideal organisms for examining the impacts of forest disturbances (Welsh and Droege 2001, Davic and Welsh 2004).

Early investigations of wildlife responses to prescribed fire largely focused on terrestrial megafauna (Bendell 1974, Lyon et al. 1978, 2000). Much less is known about effects on amphibians, but available studies indicate that responses vary greatly among individuals, species, life-history strategies, and geographic regions (Russell et al. 1999, Bury et al. 2002, Pilliod et al. 2003). With prescribed fire, direct mortality of terrestrial salamanders is thought to be limited because they spend most of their time underground out of fire's path (Taub 1961, Russell et al. 1999, Petranka and Murray 2001, Bailey et al. 2004). However, many prescribed burns are conducted in spring and late fall, when terrestrial salamanders in many regions are most surface-active (Russell et al. 1999, Pilliod et al. 2003); thus, rates of direct mortality may vary with burn seasonality and geographic region. Indirect fire effects are thought to have more influence on terrestrial salamanders, as they do not have the capability to emigrate as quickly or as far as many other terrestrial vertebrates (Kleeberger and Werner 1982, Ousterhout and Liebgold 2010). Salamanders may effectively become trapped in a fire-disturbed landscape, which could involve reduced prey availability, fewer cover objects, and decreased soil moisture (Russell et al. 1999, Pilliod et al. 2003). Prescribed fires generally decrease leaf litter and duff (i.e., decomposed organic material) depths, can combust or desiccate downed wood that salamanders use as refugia, and may lead to higher ground temperatures (Lyon et al. 1978, Harmon and Franklin 1986, Ford et al. 1999, Bury et al. 2002, Moseley et al. 2003, Pilliod et al. 2003, Major 2005, Cummer and Painter 2007, Matthews et al. 2010). Salamanders may respond by spending more time underground, which could reduce foraging and breeding opportunities and lead to decreased survival.

The relative importance of direct and indirect effects of prescribed fire on terrestrial salamanders is likely influenced by several factors, including seasonality, burn frequency, fire intensity, and historical fire regime (Pilliod et al. 2003). Several studies have found no effect of prescribed burns on terrestrial salamanders (e.g., Ford et al. 1999, 2010, Moseley et al. 2003, Schurbon and Fauth 2003, Keyser and Sausville 2004, Greenberg and Waldrop 2008). However, these conclusions are based on relative abundance measures (i.e., catch-per-unit-effort) and do not account for potential differences in detectability between burned and unburned areas, which has been shown to change following wildland fires (Hossack and Corn 2007, Chelgren et al. 2011, Hossack et al. 2013). Additionally, prescribed fires differ in severity, which can greatly affect the magnitude of post-fire changes in the environment (Pilliod et al. 2003, Hossack and Pilliod 2011). In fact, Major (2005) found a negative relationship between fire severity and terrestrial salamander occupancy. Unfortunately, however, fire severity is often not reported in wildlife studies (Renken 2006). For instance, Keyser et al. (2004) and Greenberg and Waldrop (2008) found no difference in terrestrial salamander captures after prescribed fire; in both cases, the fire did not consume the duff layer, which could have ameliorated negative effects of the burn.

In contrast to prescribed fire, impacts of timber harvest on amphibians have been more thoroughly studied – they are predominantly negative, but the degrees vary by amphibian species and harvest severity (Petranka et al. 1993, 1994, DeMaynadier and Hunter Jr 1995, Semlitsch et al. 2009, Tilghman et al. 2012). Most adverse effects of timber harvest are due to post-harvest changes in salamanders' environments (i.e., indirect effects), not directly due to the harvest activity (DeMaynadier and Hunter Jr 1995). Indirect effects of harvests can reduce survival of salamanders (Petranka et al. 1993, 1994, Homyack and Haas 2009), limit surface activity (Johnston and Frid 2002, Homyack et al. 2011, Hocking et al. 2013), and induce emigration from the harvested area (Ash and Bruce 1994, Semlitsch et al. 2008, Peterman et al. 2011) – summarized as the mortality, retreat, and evacuation hypotheses (Semlitsch et al. 2009). Many studies that have reported terrestrial salamander declines after timber harvest implicate higher ground temperatures and decreased soil moisture due to canopy cover removal (e.g., Petranka et al. 1993, 1994, DeMaynadier and Hunter Jr 1995, Harpole and Haas 1999, Semlitsch et al. 2009, Tilghman et al. 2012, Homyack and Haas 2013). Several studies have shown potential to lessen or prevent salamander declines by limiting canopy cover removal via partial timber harvests (Pough et al. 1987, Harpole and Haas 1999, McKenny et al. 2006, Semlitsch et al. 2009, Hocking et al. 2013, Homyack and Haas 2013) or retaining favorable microhabitats such as coarse woody debris (Rittenhouse et al. 2008, Kluber et al. 2009, Semlitsch et al. 2009). Generally, timber harvests can cause drier soil, loss and drying of leaf litter, and loss of fine woody debris – changes that decrease forests' ability to sustain salamander populations (Welsh and Droege 2001).

Discerning terrestrial salamander responses to forest management practices is essential for informing amphibian conservation and management strategies. Prescribed fire and timber harvest are used to accomplish many forest management objectives; in the eastern United States, they are often employed to encourage oak or pine (*Quercus, Pinus* spp.) regeneration. However, we do not have sufficient information about the effects of these disturbances on terrestrial salamander population dynamics and habitat use – especially in the Midwestern United States (but see Herbeck and Larsen 1999, Hocking et al. 2013). Considering the potential importance of terrestrial salamanders in ecosystems, it is critical to understand how they respond to disturbances. Our objective was to determine responses of southern red-backed salamanders (*Plethodon serratus*) to prescribed fire and timber harvest in a central hardwood forest. We examined salamander responses to three forest management practices in a randomized, large-scale Before-After, Control-Impact (BACI) experiment. We investigated changes in salamander abundance over nine seasons, and explicitly accounted for potential differences in salamander detectability among the treatments. We also examined the effects of timber harvest and prescribed fire on terrestrial salamander microhabitat use. We expected salamander populations to decrease following timber harvest and prescribed fire treatments, but hypothesized that our ability to detect salamanders would increase after treatments were implemented. We predicted that salamanders would increase their use of cover objects such as rocks and coarse woody debris in burned and harvested areas, and would decrease surface activity. We expected this combination of evidence to foster a more robust understanding of the mechanisms underlying population-level responses to forest management practices, ultimately increasing our ability to effectively manage terrestrial salamander populations.

STUDY AREA

We conducted our study at the Sinkin Experimental Forest (Dent County, Missouri, USA; Fig. 1), located within the Current River Hills Subsection of the Ozark Highlands (Nigh and Schroeder 2002). The overstory was dominated by oaks – primarily white (*Quercus alba)*, black (*Q. velutina*), scarlet (*Q. coccinea*), and northern red oak (*Q. rubra*) – as well as shortleaf pine (*Pinus echinata*) and hickory (*Carya spp.;* Kabrick et al. 2014). Understory species included spice bush (*Lindera benzoin*) and Carolina buckthorn (*Frangula caroliniana*). The mature (80-100 year old) stands had not been harvested or thinned for at least 40 years.

Twenty 5-ha experimental units, each oriented on a slope covering a mesic-to-xeric moisture gradient, were separated by ≥ 10 m and delineated across our study area (Fig. 1). Five replicate units were randomly assigned to each treatment: (1) prescription burn, (2) shelterwood harvest, (3) midstory herbicide, or (4) control.

These are part of the USDA Forest Service Regional Oak Study (ROS), which is investigating oak regeneration dynamics.

Treatments

The midstory herbicide treatment was intended to decrease competition for young oak trees by reducing basal area by 25-30%; Garlon 3A herbicide at 50% strength was applied to non-oak midstory trees (5-25 cm dbh) via the “hack-and-squirt” method in fall 2011 (Loftis 1990). The initial application did not effectively kill all tree species, so a second application at full strength was applied in fall 2012. Midstory units will also be shelterwood-harvested in 8-10 years. The shelterwood treatment commercially harvested a portion of overstory trees, retaining 30-40% of original basal area to provide shadier conditions for oak seedlings (Brose et al. 1999). Harvesting was conducted in December 2011 and January 2012 (2 units), September and October 2012 (2 units), and January 2013 (1 unit); slash was left on site. All shelterwood-harvested units will also be prescription burned 3-5 years after harvest. All 5 units in the prescribed burn treatment were burned on 13 December 2012 via ground ignition. Fire temperatures were measured at ground level and 30 cm above ground using temperature-sensitive paint (getting details/brand from Tex). Mean maximum fire temperature at ground level was 291 °C (range 232-315 °C) at lower slope positions and 312 °C (range 232-371 °C) at upper slope plots. At 30 cm above ground, lower slope mean maximum temperature was 168 °C (range 93-

537+ ºC); upper slope was 178 ºC (range 93-315 ºC). Five units were left untreated and served as controls.

METHODS

Sampling Design

We established two 10-m x 10-m survey plots on each of the 20 5-ha experimental units (N = 40 survey sites, Fig. 1). We conducted repeated surveys for southern red-backed salamanders 3 to 5 times each spring and fall from April 2010 to June 2014 (9 seasons, 39 surveys, N = 1560 plots sampled). We thoroughly searched a 3m x 3m quadrat of each plot; two observers crawled through the quadrat, searching 1m-wide transects with a small hand rake and flipping all natural cover objects encountered. We continually replaced leaf litter and cover objects, and ensured plots were reconstructed upon completion of each survey. Each round of sampling lasted until each plot was surveyed once (2–4 days); we randomly determined search order of plots each round. For each plot, we recorded total salamanders captured, rocks (≥ 5 cm), woody cover objects, mean soil temperature, and mean leaf litter depth. We measured and recorded size (snout-vent length; SVL) and capture location (leaf litter, rock, woody cover) of each individual. We obtained rainfall and temperature data from the Sinkin Experimental Forest weather station (MSINM7). Site-specific variables of slope and Beers-transformed aspect (linear scale; southwest=0, northeast=2) were determined from the ROS. We handled all animals in accordance with the University of Missouri Animal Care and Use Committee (protocol no. 7403) and the Missouri Department of Conservation.

Analyses

We compared red-backed salamander raw counts (captures per plot) among treatments using a Poisson-distributed generalized linear mixed model (function glmer, package lme4, R version 3.1.1, www.r-project.org) as a measure of salamander surface activity. We assessed treatment effects on leaf litter depth and soil temperature using linear mixed models (function lmer, package lme4, R version 3.1.1, www.r-project.org). We specified separate models for pre-treatment and post-treatment seasons to facilitate interpretation of results. For each model, we included treatment, season, and a treatment*season interaction as fixed effects and plot as a random effect. We tested for differences in counts, leaf litter depth, and soil temperature among treatments and seasons using Wald χ^2 tests (function Anova, package car, R version 3.1.1, www.r-project.org).

We calculated the proportion of salamander captures per microhabitat type (leaf litter, rock, woody cover) within each treatment and season. We fit analysis of variance models to pre- and post-treatment log-transformed captures per microhabitat with treatment, microhabitat type, and a treatment*microhabitat interaction as fixed effects (function lm, package stats, R version 3.1.1, www.r-project.org).

We estimated red-backed salamander abundance by correcting for imperfect detection using a binomial mixture model (see O'Donnell et al. 2014*b* for model details). We used a Bayesian approach to fit our model using JAGS (Plummer 2003; function jags, package R2jags, R version 3.1.1, www.r-project.org). We included covariates of slope, aspect, and treatments on abundance; time-since-rainfall, time of day, temperature, and treatments on availability; and leaf litter depth, woody cover object density, rock density, and treatments on conditional capture probability. We specified a normal prior (mean = 0.9, SD = 0.25) for the conditional capture probability intercept, and uninformative prior distributions for all other parameters. We standardized all covariates to promote Markov chain Monte Carlo convergence. We ran 3 chains for 200000 iterations, discarded the first 150000 as "burn-in," and thinned the remaining samples by 1 in 10 to obtain 5000 simulations for analysis. We confirmed convergence using the Gelman-Rubin statistic (*R-hat* < 1.01; (Gelman and Hill 2007)) and performed posterior predictive checks (Bayesian *P*-value) to assess model fit adequacy (Kéry and Schaub 2012).

RESULTS

Surface Activity and Abundance

Prior to treatments, salamander surface activity (mean counts) varied among seasons, from 1.59 (fall 2011) to 2.93 (spring 2010) salamanders per 9m^2 plot (χ_5^2 = 169.18, $P \leq 0.001$; Fig. 2). The average difference between the highest and lowest per-treatment mean counts was 26.8% for the first four seasons, but there was no consistent relationship among the treatments (χ_3^2 = 1.30, P = 0.73; Fig. 2). After all treatments were implemented, the mean difference between the highest and lowest mean counts was 62.0%, with controls consistently higher than the other treatments. Relative to controls, counts decreased by 58.4% in shelterwood, 49.0% in prescribed burn, and 36.7% in midstory herbicide units after treatments. In addition to differences among treatments (χ_3^2 = 14.34, P = 0.002), surface activity continued to vary among seasons (χ_2^2 = 25.30, $P \leq$ 0.001) but the relationship among treatments did not vary seasonally (treatment*season, χ_6^2 = 4.12, P = 0.66).

Mean per-plot abundance (accounting for imperfect detection) varied among seasons, but did not vary consistently among treatments prior to implementation (Table 1). Each of the four treatments had the highest mean abundance in one of the first four seasons. Following treatments, mean abundance was lowest in shelterwood harvest units and highest in control units (Table 1). Bayesian 95% credible intervals (CRI) overlapped in most pairwise contrasts, but the extent varied among treatments (Table 1). The greatest difference between control and a treatment occurred in spring 2014; mean abundance in shelterwood harvests was 50.2% lower than controls (Table 1). Mean abundance in midstory herbicide and prescribed burn units treatments was lower than controls in fall 2013 (30.4% and 24.3%, respectively), but the differences lessened by spring 2014 (Table 1). Treatments had stronger effects on salamander availability (i.e., probability of being exposed to sampling) than they did on abundance (Table 2).

Aspect was also a strong predictor of abundance (mean [CRI]; 0.181 [0.079, 0.282]), while time-since-rainfall (-0.345 [-0.616, -0.082]), soil temperature (-1.603 [-1.891, -1.333]), and time of day (-0.203 [-0.438, 0.028]) highly influenced availability.

Habitat Conditions and Use

Mean soil temperature varied among seasons from a low of 14.9 ºC (spring 2010) to a high of 20.0 ºC (fall 2010) before treatments were implemented (Fig. 3; $\chi_5^2 = 184.60$, $P \leq 0.001$). In the first four seasons, the mean difference between the lowest and highest temperature per treatment was 5.7%; in the last three seasons (after all treatments implemented), the mean difference was 16.6%. Soil temperature differed among both treatments ($\chi_3^2 = 10.24$, $P = 0.017$) and seasons ($\chi_2^2 = 22.47$, $P \leq 0.001$) following treatment. Mean post-treatment soil temperature was higher in both shelterwood harvest (+2.58 ºC) and midstory herbicide (+1.62 ºC) treatments relative to controls; mean soil temperature in prescribed burn units did not differ from controls.

Mean leaf litter depth ranged from 1.98 cm (fall 2011) to 2.52 cm (spring 2011) prior to treatments (season: $\chi_5^2 = 129.49$, $P \leq 0.001$; Fig. 4), but did not differ among treatments. Post-burn leaf litter depth decreased in prescribed burn units for 2 seasons following prescribed burn, averaging 0.57 cm in spring 2013 (63.7% lower than other treatments) and 0.58 cm in fall 2013 (57.7% lower than other treatments). In spring 2014, mean leaf litter depth in prescribed burn plots was only

8.7% lower than controls (Fig. 4). Statistically, the treatment*season interaction ($\chi_6^2 = 42.15$, $P \leq 0.001$) explained differences in mean leaf litter depth post-treatments.

We found higher proportions of salamanders in leaf litter than under rocks or woody cover prior to treatments ($F_{2,60} = 43.02$, $P \leq 0.001$; Fig. 5), but relative microhabitat use did not differ among treatments (treatment*microhabitat, $F_{6,60} = 0.540$, $P = 0.78$). Following treatment implementation, captures differed among treatments ($F_{3,24} = 8.08$, $P \leq 0.001$) and microhabitats ($F_{2,24} = 14.18$, $P \leq 0.001$). Additionally, the relative use of microhabitat differed among treatments ($F_{6,24} = 2.12$, $P = 0.088$); relative capture frequency in prescribed burn units was higher under cover objects (73.8% of captures) than within leaf litter (26.3% of captures), while capture frequency remained highest in leaf litter in shelterwood harvest, midstory herbicide, and control treatments (mean = 56.5%; Fig. 5).

DISCUSSION

Our findings indicate that red-backed salamanders were most adversely affected by shelterwood harvests, but were also negatively affected by midstory herbicide and prescribed burn treatments. Lower post-treatment capture rates in shelterwood, midstory, and burn units reflect reduced surface activity in response to these forest management practices (Fig. 2). Abundance estimates corrected for imperfect detection also generally decreased in all treatments the year following implementation; estimates in midstory herbicide and prescribed burn units recovered slightly in the second year, but estimates in shelterwood harvest units decreased further (Table 1).

In shelterwood harvest units, lower salamander surface activity was likely due to higher soil temperatures and drier leaf litter. Although some overstory trees remained after harvest, substantial canopy gaps were created, which led to harsher salamander microhabitat conditions overall. We saw the largest control vs. treatment discrepancy in abundance in shelterwood harvest units in the third season after harvests were completed, which indicates that microhabitat conditions likely worsened over time. In contrast, the shrinking differences between control and both midstory herbicide and prescribed burn unit estimated abundances in spring 2014 (Table 1) suggest quicker recovery of favorable microhabitat conditions in those treatments.

Decreased surface activity in the prescribed burn treatment may have reflected the drastic decline in leaf litter depth following the burn (Fig. 4). Leaf litter is an important resource for terrestrial salamanders – it affords cover from predators, reduces soil desiccation, and provides ideal foraging opportunities due to prey abundance in leaf litter (Fraser 1976, Jaeger 1980). Notably, salamanders were still less active in leaf litter in spring 2014 after leaf litter depth had seemingly recovered. We suspect this is partly due to the condition of the leaf litter layer – though it was present, it did not appear to retain moisture as well as litter that was further fragmented and decomposed.

We did not expect the decrease in surface activity in midstory herbicide plots, as microhabitat conditions did not appear to differ greatly from control plots. However, soil temperatures were slightly higher in midstory plots, which may explain the difference in activity. Higher temperatures increase the amount of energy needed for salamanders to maintain homeostasis (Gifford and Kozak 2012). Therefore, salamanders may retreat further underground to avoid high temperatures and the associated increase in energetic demand (Homyack et al. 2011).

The changes in salamander microhabitat use we observed after the prescribed fire illustrated the importance of accounting for variable and imperfect detectability of wildlife. Several studies have found differences in capture probabilities after fire (Bury et al. 2002, Chelgren et al. 2011, Hossack et al. 2013). We did not find a substantial effect of treatment on conditional capture probability – that is, given a salamander was exposed to sampling, our probability of capturing it did not differ among treatments. This was likely due to the comprehensive nature of our survey method, but we posit that conditional capture probability could vary greatly between treatments if the survey method was less intensive. Tilghman et al. (2012) found that studies using passive sampling techniques (e.g., pitfall traps) were likely to report weaker effects of timber harvest than those using active sampling methods. We also stress that sampling method can influence conclusions; for instance, finding more salamanders in pitfall traps in a given area may not truly reflect higher abundance. Rather, it may indicate that salamanders are attempting to evacuate or disperse from an area to escape poor habitat conditions (Semlitsch et al. 2008, Peterman et al. 2011).

Accounting for imperfect detection allowed us to increase understanding of the mechanisms behind the broad patterns we observed. Our modeling results indicated that terrestrial salamanders reduced their activity in response to both prescribed burn and timber harvest, but their abundance did not change drastically in the short term. We observed a trend of abundance progressively decreasing in harvested areas, which may become a stronger trend with longer-term data. Reduced availability probability – presumably due to salamanders spending more time underground – could cause a lag in detecting population trends. Lower levels of surface activity could indicate a behavioral avoidance of increased physiological stress, which also reduces potential foraging time. These indirect consequences of disturbance could take time to manifest into detectable changes in abundance.

MANAGEMENT IMPLICATIONS

We encourage forest managers to consider management practices that limit canopy removal where there is interest in minimizing impacts on salamanders, as it is likely the ultimate cause of increased temperatures and decreased moisture in harvested areas. Increased temperatures and decreased moisture may limit the ability of salamanders to be surface-active, which reduces foraging and breeding opportunities. Retaining coarse woody debris in harvested areas could also provide important microhabitat for salamanders, perhaps increasing their capacity to remain surface-active. Managers may also want to consider limiting prescribed burns during periods of high salamander surface activity to minimize direct mortality. While timber harvest more adversely affected terrestrial salamanders in our study than prescribed burning, we note that all prescribed burns occurred in December, which is a period of low salamander activity. Burns that occur during breeding events or emergence from hibernation could be more detrimental and cause higher direct mortality. Additionally, burns that promote herbaceous understory vegetation could help ameliorate the drier and more variable environmental conditions that typically follow prescribed burns. We suggest post-disturbance terrestrial salamander monitoring surveys sample in leaf litter and not just cover objects. We found minimal differences in salamander use of woody cover objects between treatments, but large differences in leaf litter use. Including all potential microhabitats in sampling protocols yields a more complete understanding of microhabitat use and limits potential post-management observation biases.

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FIGURE 1. Arrangement of Regional Oak Study experimental units within the Sinkin Experimental Forest, Mark Twain National Forest, Dent County, Missouri, USA. Five replicate units were randomly assigned to each of four treatments: shelterwood harvest, prescribed burn, midstory herbicide, or control. Southern red-backed salamanders were surveyed from 2010–2014.

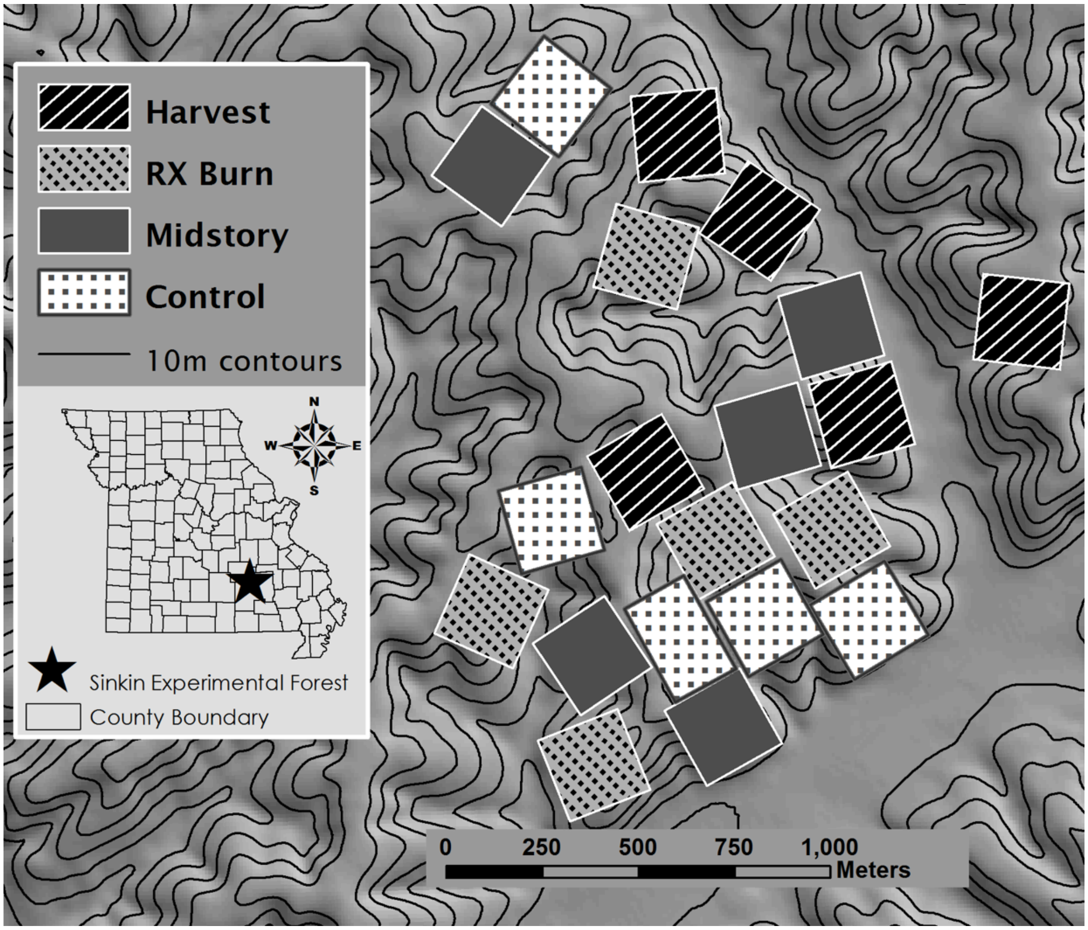

FIGURE 2. Variation among seasons in mean captures of southern red-backed salamanders per plot (± SE) across four treatments in Dent County, Missouri, USA from 2010–2014. First arrow represents harvest of initial two units; second arrow represents timing of prescribed burn, midstory herbicide, and harvest of three remaining units.

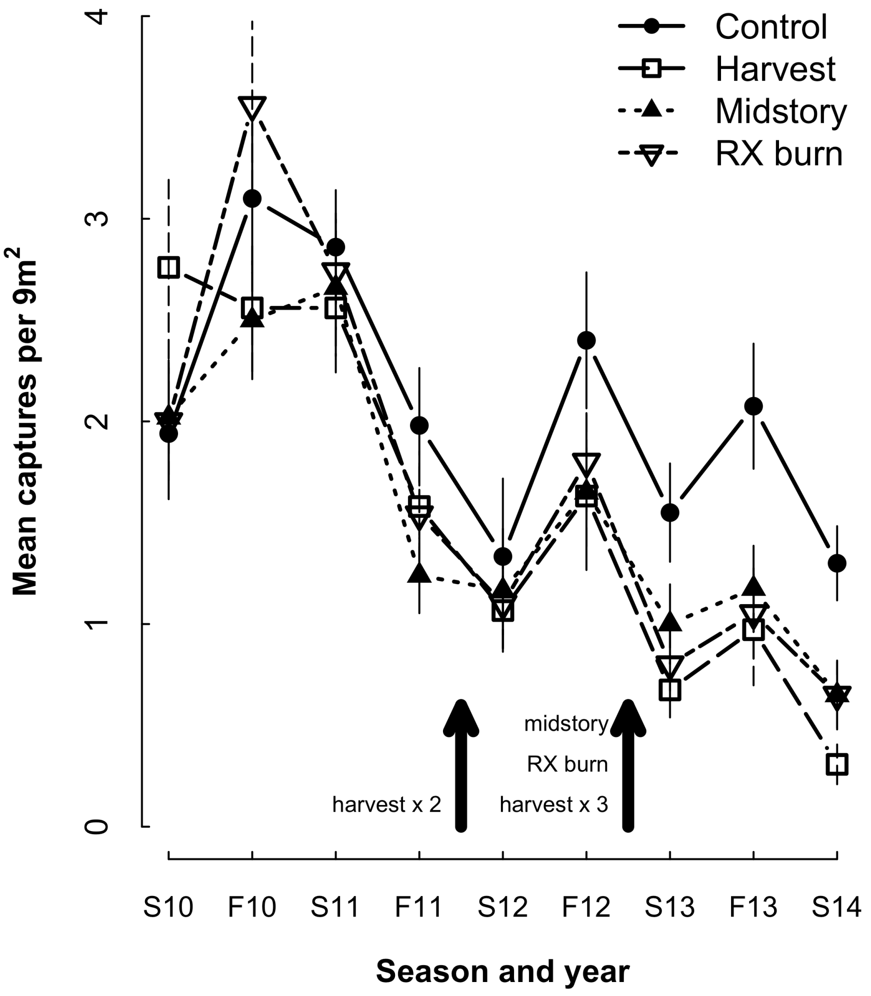

FIGURE 3. Mean (± SE) soil temperature of sampling plots per season across four treatments in Dent County, Missouri, USA from 2010–2014. First arrow represents harvest of initial two units; second arrow represents timing of prescribed burn, midstory herbicide, and harvest of three remaining units.

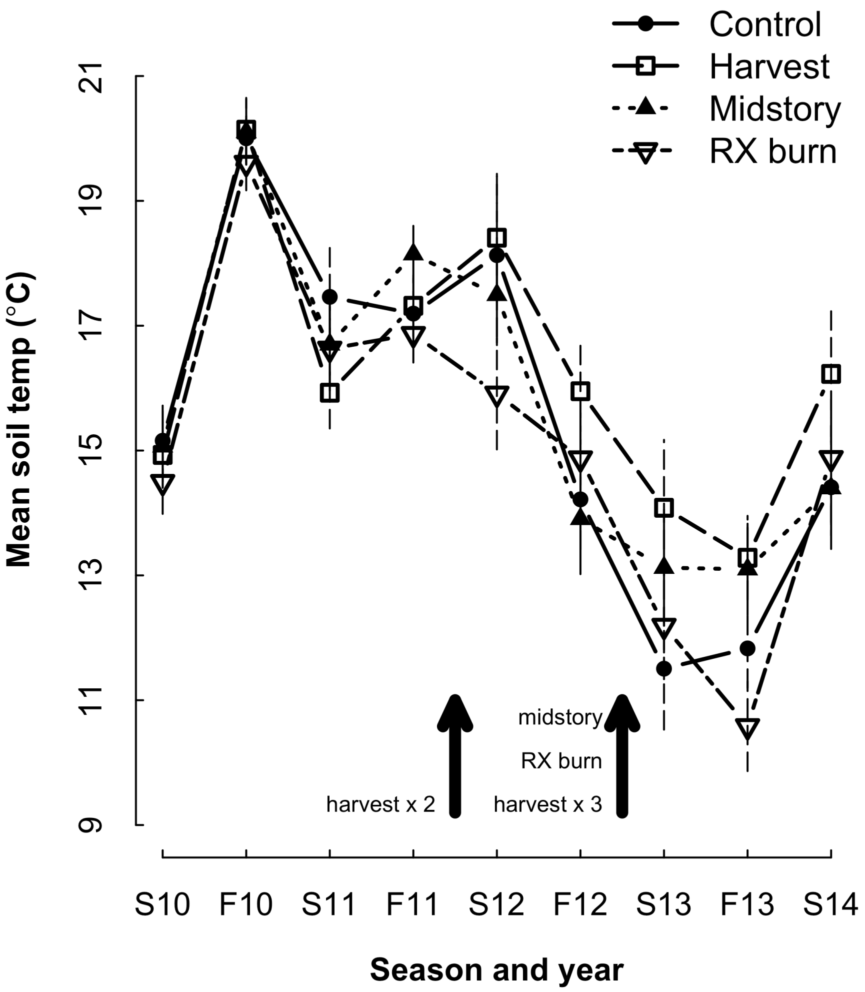

FIGURE 4. Mean leaf litter depth (± SE) within sampling plots across four treatments in Dent County, Missouri, USA from 2010–2014. First arrow represents harvest of initial two units; second arrow represents timing of prescribed burn, midstory herbicide, and harvest of three remaining units.

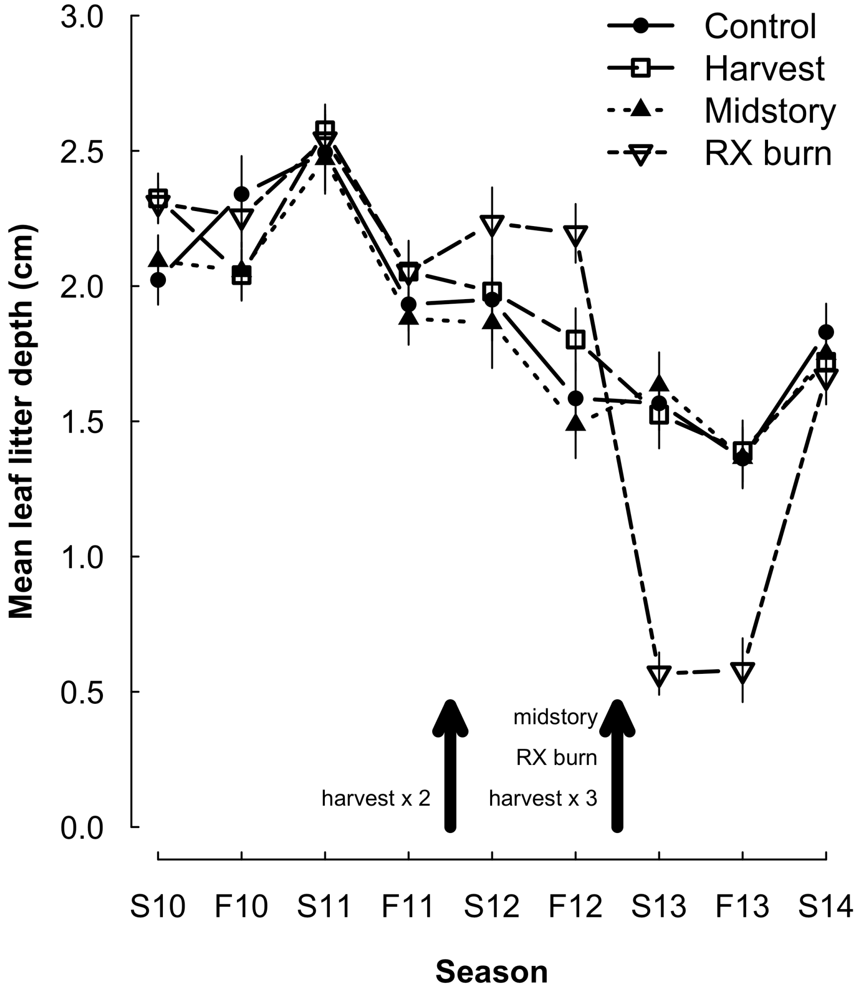

FIGURE 5. Frequency of southern red-backed salamander captures per treatment in three microhabitat types – leaf litter, rocks, and woody cover objects (WCO) in Missouri, 2010–2014. Bars represent percent of pre- or post-treatment captures within each microhabitat. Mean capture rate also differed between treatments (see Fig. 2).

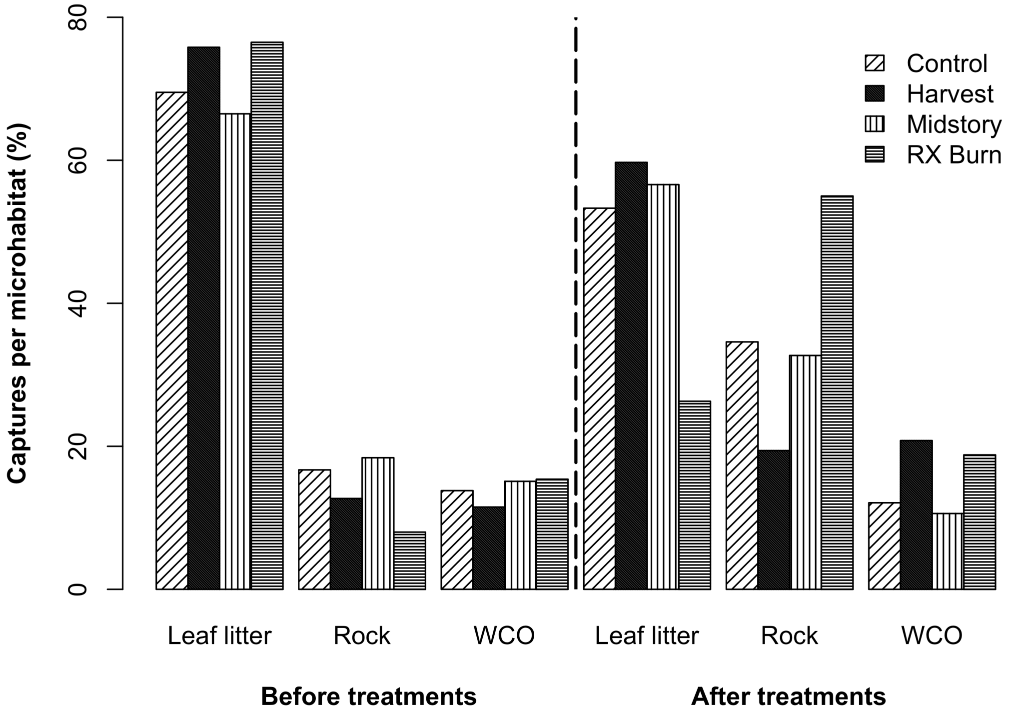

TABLE 1. Mean abundance (per 9-m^2 plot) and percent difference (vs. control) of southern red-backed salamanders per treatment in Sinkin Experimental Forest, Dent County, Missouri, 2010-2014.

	Treatment			
Season	**Control**	**Shelterwood harvest**	**Midstory herbicide**	**Prescribed burn**
Spring 2010	7.71 (4.9, 13.2)[a]	8.62 (6.8, 12.9)	7.11 (5.0, 12.2)	7.16 (4.2, 12.2)
		+11.8	-7.8	-7.1
Fall 2010	7.36 (6.0, 10.7)	7.34 (5.2, 11.9)	6.68 (4.9, 11.1)	8.96 (7.5, 12.3)
		-0.3	-9.2	21.7
Spring 2011	5.4 (4.6, 8.3)	6.11 (4.7, 9.3)	6.76 (5.5, 10.3)	6.37 (5.0, 9.4)
		13.1	25.2	18.0
Fall 2011[b]	4.87 (4.2, 7.5)	4.07 (3.2, 7.2)	3.88 (2.7, 7.0)	4.74 (3.5, 7.8)
		-16.4	-20.3	-2.7
Spring 2012[c]	4.05 (2.9, 7.4)	3.01 (2.0, 6.9)	3.48 (2.2, 7.2)	3.21 (2.0, 6.8)
		-25.7	-14.1	-20.7
Fall 2012[d]	5.29 (4.4, 8.5)	4.47 (3.3, 8.4)	5.2 (3.9, 9.0)	4.03 (3.2, 7.4)
		-15.5	-1.7	-23.8
Spring 2013[e]	3.04 (2.5, 5.6)	2.17 (1.5, 5.2)	3.30 (2.3, 7.0)	2.56 (1.6, 5.9)
		-28.6	+8.6	-15.8
Fall 2013	5.75 (4.2, 10.0)	4.85 (2.3, 10.4)	4.00 (2.6, 8.2)	4.35 (2.7, 9.0)
		-15.7	-30.4	-24.3
Spring 2014	3.21 (2.7, 5.7)	1.6 (0.9, 4.5)	2.71 (1.6, 6.4)	2.98 (1.6, 6.9)
		-50.2	-15.6	-7.2

[a] values in parentheses represent 95% Bayesian credible intervals
[b] first midstory herbicide application applied during fall 2011 season
[c] two of five shelterwood units harvested
[d] four of five shelterwood units harvested; second midstory herbicide application
[e] all treatments fully implemented

TABLE 2. Mean effect (95% CRI) of treatments on red-backed salamander availability and abundance in Sinkin Experimental Forest, Dent County, Missouri, 2013-2014.

	Effect on availability				Effect on abundance			
	Control	Shelterwood harvest	Midstory herbicide	Prescribed burn	Control	Shelterwood harvest	Midstory herbicide	Prescribed burn
Spring 2013	-0.39	-1.02	-1.21	-1.47	0.23	-0.09	0.36	0.078
	(-2.6, 2.2)	(-2.9, 1.6)	(-2.9, 1.1)	(-2.9, 1.3)	(-2.5, 2.7)	(-2.8, 2.4)	(-2.4, 2.8)	(-2.7, 2.6)
Fall 2013	-0.27	-1.86	-1.18	-1.33	0.45	0.29	0.13	0.20
	(-2.6, 2.2)	(-2.9, 0.30)	(-2.9, 1.1)	(-2.9, 0.8)	(-2.4, 2.8)	(-2.6, 2.7)	(-2.7, 2.6)	(-2.7, 2.6)
Spring 2014	0.30	-1.4	-1.73	-1.79	0.41	-0.32	0.25	0.34
	(-2.1, 2.5)	(-2.9, 1.6)	(-2.9, 0.7)	(-2.9, 0.4)	(-2.2, 2.8)	(-2.8, 2.2)	(-2.4, 2.7)	(-2.3, 2.7)

CHAPTER 5 • PRESCRIBED FIRE ALTERS SURFACE ACTIVITY AND MOVEMENT BEHAVIOR OF A TERRESTRIAL SALAMANDER

INTRODUCTION

Fire is a key driver of ecosystem composition and function, but fire regimes have shifted over the last century due to human population growth and changes in forest management practices (Pyne, Andrews & Laven 1996; Pausas & Keeley 2009). These changes – particularly fire suppression policies – have caused combustible forest material ("fuel") buildups that have increased wildfire frequency and extent, and have produced continental-scale changes in forest composition (e.g., increased tree density, shifts in species dominance, and reduced diversity; Pyne, Andrews & Laven 1996; Nowacki & Abrams 2008; Hanberry, Kabrick & He 2013). In response, prescribed fire has become a commonly used forest management tool for reducing the occurrence of catastrophic wildfires, decreasing fuel loads, and reestablishing the historic ecological influences of fire (Pilliod *et al*. 2003; Hanberry, Kabrick & He 2013; Pausas & Keeley 2014).

Despite the importance of wildlife to ecosystem health, there is a considerable lack of information about faunal responses to prescribed fire – especially relative to the comparable literature on plants. Because the effects of prescribed fire on wildlife remain unclear (and likely differ considerably among taxa), many decisions about fire management are weighted toward predicted vegetation responses (Lyon *et al.* 2000; Driscoll *et al.* 2010). Investigating population-level wildlife responses to prescribed fire is important for evaluating the effects of fire management on animals. However, to increase our ability to predict wildlife responses to potential management actions, mechanistic studies that elucidate individual-level responses are essential (Driscoll *et al.* 2010).

Amphibians are ideal for examining effects of prescribed fire – they are especially sensitive to changes in microhabitat, yet the diversity of life-history strategies within this taxon yields a variety of responses to fire (Russell, Lear & Guynn 1999; Bury, Major & Pilliod 2000; Pilliod *et al.* 2003). Terrestrial woodland salamanders (family Plethodontidae) are ecologically important animals that comprise large amounts of biomass (Burton & Likens 1975b; Semlitsch, O'Donnell & Thompson 2014), are important for nutrient cycling (Burton & Likens 1975a; Davic & Welsh 2004b; Semlitsch, O'Donnell & Thompson 2014), and are key predators in forest-floor ecosystems (Wyman 1998; Walton 2013; Best & Welsh 2014).

Because terrestrial salamanders are largely fossorial, direct mortality and injury of these organisms due to fire is likely rare (Taub 1961; Bailey, Simons & Pollock 2004b). However, plethodontid salamanders may be especially sensitive to fire-induced habitat changes, including consumption of woody debris and leaf litter that provide refugia and foraging opportunities, respectively (Fraser 1976; Russell, Lear & Guynn 1999; Pilliod *et al.* 2003). Terrestrial salamanders lack the physical capacity to disperse long distances to find new habitats (Ousterhout & Liebgold 2010; Liebgold, Brodie & Cabe 2011); thus, their persistence is closely linked with immediate microclimatic conditions and microhabitat availability (Peterman and Semlitsch 2013; O'Donnell et al. 2014a,b). Plethodontid salamanders also have particularly small home ranges relative to most vertebrates; they often spend their entire lives in areas <15 m^2 (Merchant 1972; Kleeberger & Werner 1982). In contrast to more mobile vertebrates that can easily disperse from altered habitats, terrestrial salamanders may exhibit subtler behavioral responses to prescribed fire. They may spend more time belowground due to drier surface conditions and reduced cover object abundance, or may expand foraging areas because of decreased prey availability (due to leaf litter reductions) and increased energetic requirements (e.g., Homyack et al. 2011). These seemingly minor changes in salamander activity can substantially affect overall population dynamics, thus warranting further investigation.

We used radio-frequency identification (RFID) to investigate individual-level responses of western slimy salamanders (*Plethodon albagula*) to prescribed fire. Using a portable reader/antenna system, we could locate salamanders implanted with uniquely coded passive integrated transponder (PIT) tags ≤ 30 cm belowground and minimize habitat disturbance from repeated surveys ("PIT-telemetry"; Connette & Semlitsch 2012). We compared salamander home range sizes, movement behaviors, and activity levels before and after prescribed fire using a randomized block experiment. We predicted that salamanders would decrease surface activity following prescribed fire, but would expand their home ranges if reduced prey availability forced them to increase foraging distances. We also expected salamanders in burned areas to move to control areas if they were close to the burn periphery. We did not expect to see substantial (if any) mortality or injury of salamanders directly due to the prescribed fire. We suggest that individual salamander behavioral responses to prescribed fire would improve our understanding of more frequently observed population-level patterns.

METHODS

Study site

We conducted our study within the 1425-ha Daniel Boone Conservation Area (DBCA), Warren County, in east-central Missouri, USA (Fig. 1). DBCA lies in the Outer Ozark Border subsection of the Ozark Highlands, and consists of rugged hills covered with mature (80–100 years old) oak-hickory (*Quercus*-*Carya*) forest (Nigh & Schroeder 2002). Annually, temperatures range from −5.6–29.8º C (mean = 12.2 ºC), and mean precipitation is 105.8 cm.

Field methods

We initiated a pilot study at three replicate plots (PR2, CN2, and EGG) in May 2011, and added two new plots (CN5 and CHK) in April 2012 (Fig. 1). In March 2013, we split each plot into two subplots that contained approximately equal numbers of previously recaptured salamanders. We randomly assigned one subplot per replicate plot to the prescribed burn treatment, and left the other subplot in each replicate as a control. On 4–5 April 2013, we conducted prescribed burns on all plots via ground ignition. At ignition, air temperatures ranged from 10.6–14.4 ºC, relative humidity was 30–42%, and winds were very light. Flame heights were ≤ 0.3 m, except in a few patches of accumulated leaf litter, and ≥ 95% of the area of each plot was burned. Fine fuel (leaf litter, fine woody debris) consumption was ≥ 75% in all plots.

We used PIT-tag telemetry to compare salamander home ranges and activity patterns before and after prescribed fire. To conduct telemetry observations, we first collected adult and large juvenile western slimy salamanders (*Plethodon albagula*) by searching under rocks and woody cover objects – including some remnant coverboards from a previous study (Hocking *et al.* 2013). We captured, tagged, and released at least 38 *P. albagula* at each of the five sites from 21 May 2011–13 May 2012 (total *N* = 205; Table 1).

We flagged initial capture locations, placed salamanders in individual containers containing wet leaf litter, and transported animals to the University of Missouri for PIT-tag implantation. We anesthetized salamanders in a 1% solution of tricaine methanesulfonate (MS-222) buffered with sodium bicarbonate (as in Peterman & Semlitsch 2006). Once salamanders were anesthetized (5–10 min), we measured them (snout-vent length [SVL]) and used a sterile scalpel to make a 3-mm incision ~5 mm anterior to the right hind limb. We then inserted a PIT tag just under the skin and gently pushed it forward ~5 mm from the incision. Salamanders with snout-vent length (SVL) 41–51 mm received an HPT9 PIT tag (9.0 x 2.12 mm, 0.08 g; Biomark, Boise, ID); those measuring 52–75 mm SVL received an HPT12 PIT tag (12.5 x 2.03 mm, 0.115 g; Biomark). HPT9 and HPT12 tags do not substantially differ in maximum detection distance (Ousterhout & Semlitsch 2013). Salamanders' skin secretions immediately sealed incisions shut, so sutures were not needed. We rinsed salamanders in deionized water and allowed them to recover on wet leaf litter. We returned each salamander to its point of capture within 3 days.

We conducted 29 surveys in the 2011 pilot season (3 June–1 November) to identify peak detection periods. The detection rate dropped below 5% from mid-July to mid-September; thus, we maximized our survey efforts from April–June in subsequent years. We completed 12–16 surveys per site from 17 April–8 September 2012, 7–13 per site from 7 April–31 July 2013, and 8–10 per site from 15 April–9 July 2014. We attempted to conduct surveys in optimal detection conditions – following rain events and in morning hours. For each individual, we searched an ~30 m^2 area centered on the point-of-capture flag (and the most recent relocation flag, when applicable). We performed these searches by slowly walking in three 1-m wide concentric circles while scanning the ground with a portable RFID system (FS-2001F-ISO reader, BP portable antenna; Biomark). We placed a marked flag at each new detection location, and noted whether the salamander was underground, within the leaf litter, or under a cover object.

Analysis

For each relocated individual, we measured the distance and bearing from the point-of-capture flag to each recapture flag. We converted these points to X and Y coordinates (relative to point-of-capture), which we used to determine utilized spatial area and distance between successive detections. For each individual, we divided each inter-capture distance by time (days) since the last relocation to determine mean daily displacement. We defined "maximum daily displacement" as the highest rate per individual. We calculated minimum convex polygons (MCP) for individuals with ≥5 detections using the "adehabitatHR" package in R (Calenge 2006; R Core Team 2014). If the final position of an individual was the same location as ≥1 consecutive previous detections, we only included the first detection in that location in our analyses. We compared MCP area, maximum daily displacement, recapture frequency, and recapture status (underground vs. surface-active) between treatments (burn vs. control) and treatment stages (pre vs. post) by fitting linear mixed models in the "lme4" package in R (R Core Team 2014) and testing differences via Wald χ^2 tests (Anova function, "car" package in R). We compared post-treatment proportions of known-alive salamanders in burn and control using an analysis of variance model in R (R Core Team 2014).

RESULTS

We recorded 918 total recaptures of 142 *Plethodon albagula*; 63 *P. albagula* (31%) were never recaptured (Table 1). The proportion of salamanders recaptured ranged from 42–88% per site (mean = 69%; Table 1). Nearly half of all recaptures (n = 422; 46%) occurred at a single site – EGG. Overall, we visually confirmed that 14% of detected salamanders were surface-active (Table 1). Prior to prescribed burns, the proportion of surface-active salamander recaptures did not differ between treatments ($\chi_1^2 = 0.12$, $P = 0.73$; Table 2). Following prescribed burns, the surface-active proportion of recaptures was nearly 7 times higher in control areas than burned areas ($\chi_1^2 = 3.55$, $P = 0.06$; Table 2). The total number of recaptures did not substantially differ between treatments before or after prescribed burns (Table 2).

Following prescribed burns, we found no difference between treatments in the proportion of salamanders known alive ($F_{1,8} = 0.24$, $P = 0.64$). We relocated 28 unique salamanders in burned areas in 2013, which represented 50.1% of a possible 55 that were detected in 2012 (year prior to burns). In control areas, we relocated 26 salamanders in 2013 – 44.8% of the 58 we recaptured in 2012.

The pre-burn maximum daily displacement was 13.1% higher among control salamanders (mean ± SE; 50.4 ± 7.9 $\text{cm}\bullet\text{d}^{-1}$) than burn salamanders (43.8 ± 5.2 $\text{cm}\bullet\text{d}^{-1}$; Fig. 2). Following prescribed burns, the maximum daily displacement was 43.3% higher among burn-area (30.2 ± 8.6 $\text{cm}\bullet\text{d}^{-1}$) than control-area salamanders (17.1 ± 4.3 $\text{cm}\bullet\text{d}^{-1}$; Fig. 2). Statistically, maximum daily displacement differed between pre- and post-treatment stages ($\chi_2^2 = 10.7$, $P = 0.001$), but did not differ between treatments ($\chi_2^2 = 0.009$, $P = 0.92$) or the treatment•stage interaction ($\chi_2^2 = 2.47$, $P = 0.116$).

Overall, the mean MCP was 1.81 m^2 (N = 89; Table 3), and 90% of MCPs were ≤ 3.8 m^2 (Fig. 3). We had relatively few salamanders with ≥ 5 pre- and post-burn recaptures (N_{burn} = 9; $N_{control}$ = 7), but we found that MCP varied among treatments and stages in a similar pattern to maximum daily displacements. In burned plots, the pre- and post-burn MCP means were 1.16 m^2 and 1.58 m^2, respectively; however, the median MCP decreased after prescribed burn (Table 3). In control plots, both mean and median MCP values decreased from pre-treatment to post-treatment (Table 3).

DISCUSSION

Following prescribed fire, we found a substantial decrease in surface activity among salamanders in burned areas, which indicates that *Plethodon albagula* respond to post-prescribed fire conditions by spending more time belowground. Forest floor conditions following the prescribed fires were rarely suitable for terrestrial salamanders to actively forage due to leaf litter combustion. Leaf litter is critical for terrestrial salamanders, as it buffers soil from desiccation and contains abundant invertebrate food resources (Fraser 1976; Jaeger 1980). We did not find evidence of direct mortality of salamanders from prescribed fires, as the post-burn proportion of known-alive individuals did not differ between treatments. The lack of direct mortality was unsurprising – the early April timing of the burns coincides with a period of low salamander surface activity. Together, these individual-level observations corroborate our findings from a population-level study of a congeneric terrestrial salamander, *Plethodon serratus* (O'Donnell, Thompson III & Semlitsch 2014c). In that study, we found that availability probability (i.e., surface activity) decreased following prescribed burns, but abundance (corrected for imperfect detection) did not decrease, indicating that salamanders are responding behaviorally rather than dying.

Though it appears that terrestrial salamanders can largely avoid direct consequences of prescribed fire, behavioral responses to post-fire micro-environmental conditions could affect salamander populations in ways that are not yet apparent. Terrestrial salamanders have narrow moisture and temperature tolerances; they primarily forage on the forest floor, but must retreat below ground when surface conditions are sub-optimal to conserve water and energy (Spotila 1972; Homyack, Haas & Hopkins 2011; Peterman & Semlitsch 2013, 2014). If salamanders substantially decrease their surface activity, populations may decline due to reductions in foraging and breeding opportunities (Homyack, Haas & Hopkins 2011).

We detected longer maximum daily displacements in burned areas, which may indicate attempts by salamanders to search for more hospitable microenvironments. Increased movement could also be a response to an overall reduction of invertebrate prey, though we did not measure prey availability in this study. While we observed increases in movement metrics among salamanders in burned areas, neither the total number of recaptures nor minimum number of known-alive salamanders decreased in burned areas. Thus, we do not believe that salamanders made extensive efforts to disperse from burned areas. It is possible that some salamanders emigrated horizontally out of survey areas, but we believe that most non-detections occurred because salamanders were deep enough underground that the portable RFID system could not detect them.

We used a PIT-telemetry approach to relocate terrestrial salamanders in prescription-burned and unburned areas. Overall, we relocated 69% of PIT-tagged salamanders by searching a circular area of 3-m radius around each individual's point of capture. Only 14% of all relocations were surface-active salamanders, which is consistent with many other studies of plethodontid salamander surface availability (Taub 1961; Bailey, Simons & Pollock 2004b; O'Donnell, Thompson III & Semlitsch 2014a). PIT-telemetry allowed us to confirm that most salamanders did not emigrate from their pre-burn home area. This approach is well-suited for long-term tracking of fossorial plethodontid salamanders with small home ranges, as PIT tags last ≥10 years, can be detected underground, and allow movement estimation at finer scales. The individual-level data contribute to our understanding of mechanisms underlying population dynamics measured at larger scales, which is critical for managers to effectively predict outcomes of various management scenarios. Currently, fire regime design is influenced more by predicted vegetation responses than by predicted wildlife responses, as the former has been more widely studied (Driscoll et al. 2010). We found that an early-season prescribed fire conducted prior to peak salamander surface activity did not seem to cause direct salamander mortality. When minimizing adverse effects of fire on terrestrial salamanders or other amphibians is important, we encourage avoiding prescribed burn applications during seasons of peak surface activity (terrestrial salamanders) or breeding migrations of pond-breeding amphibians. We saw evidence of salamander behavioral responses to post-fire conditions – particularly in reduced surface activity. Prescribed burns that foster rapid regeneration of herbaceous vegetation could provide a mechanism for moisture retention near the forest floor, which is a crucial requirement for terrestrial salamanders that often depend on leaf litter and duff layers for foraging and moisture.

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TABLE 1. Total captures and recapture frequency of *Plethodon albagula* at Daniel Boone Conservation Area from 2011–2014.

	Plots					
	PR2	**CN2**	**EGG**	**CN5**	**CHK**	**Total**
Total *P. albagula* tagged	39	38	49	39	40	**205**
No. not recaptured	14	22	6	8	13	**63**
Percent not recaptured	36%	58%	12%	21%	32%	**31%**
No. with ≥1 recapture	25	16	43	31	27	**142**
Percent with ≥ 1 recapture	64%	42%	88%	79%	68%	**69%**
Total recaptures	110	69	422	149	168	**918**
No. visually confirmed	14	31	42	32	5	**124**
Percent visually confirmed	13%	45%	10%	21%	3%	**14%**

TABLE 2. Position of *Plethodon albagula* relocations within each treatment before (2011–2012) and after (2013–2014) prescribed fire.

	2011–2012		**2013–2014**	
	(pre)Burn	**Control**	**(post)Burn**	**Control**
No. surface-active	47	40	5	32
Percent surface-active	12.9%	12.2%	4.3%	28.8%
No. underground	317	288	110	79
Total no. relocations	364	328	115	111

TABLE 3. Minimum convex polygon (MCP) measurements (m^2) across treatments and stages.

		Minimum	Median	Mean	Maximum
Burn (n = 9)	Pre	0.06	0.38	1.16	4.63
	Post	0.0	0.29	1.58	10.25
Control (n = 7)	Pre	0.0	0.31	0.54	2.17
	Post	0.0	0.035	0.24	1.11

FIGURE 1. Location of study plots within Daniel Boone Conservation Area, Warren County, Missouri, USA.

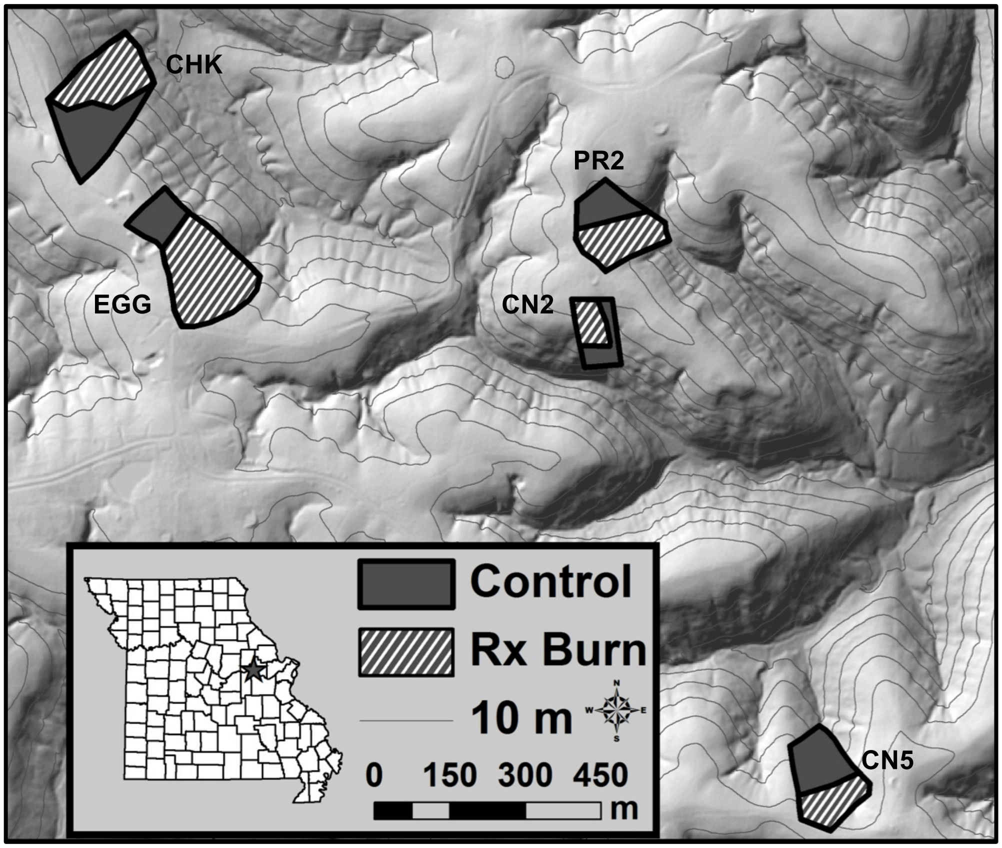


FIGURE 2. Pre- and post-treatment comparison of maximum daily displacement (± SE) of salamanders in burned and control plots.

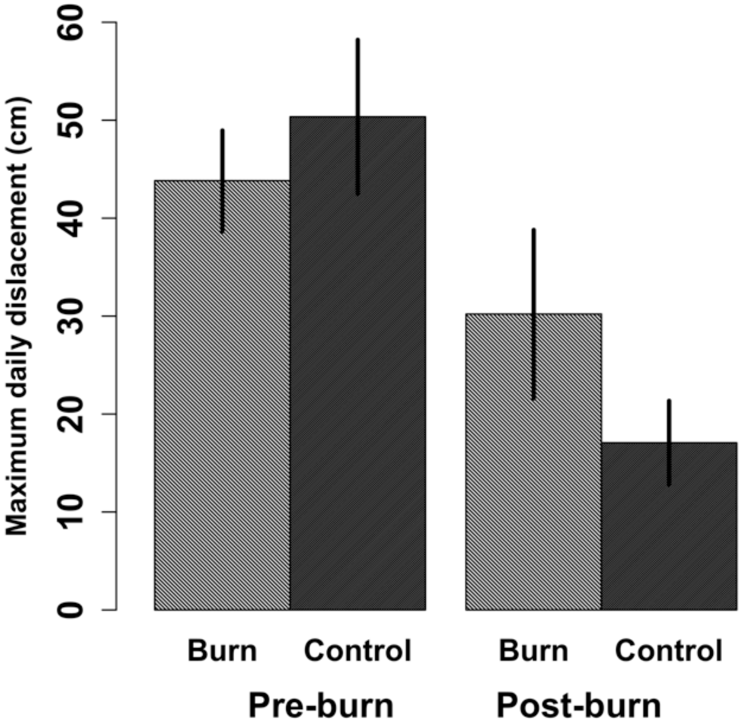


FIGURE 3. Frequency distribution of *Plethodon albagula* minimum convex polygon values.

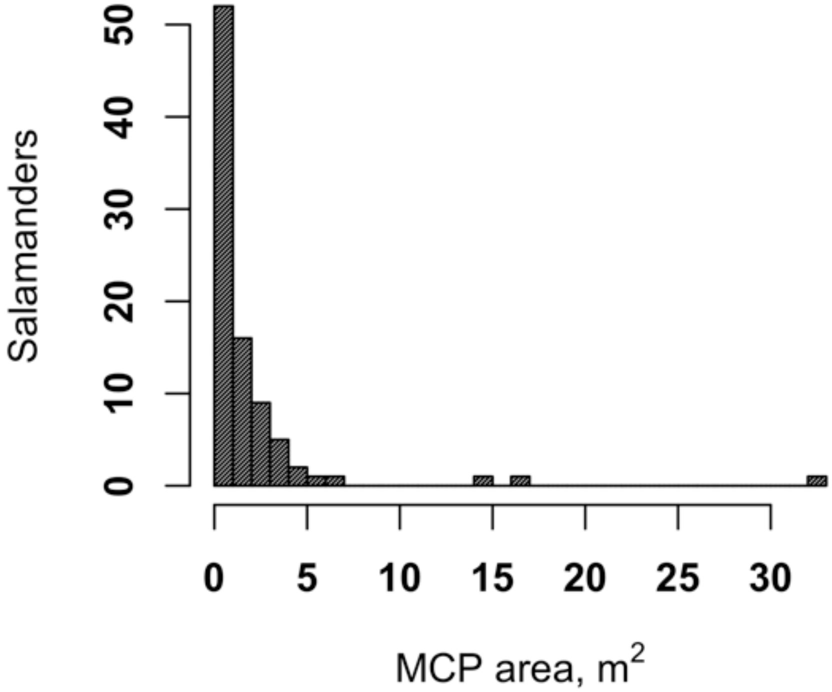
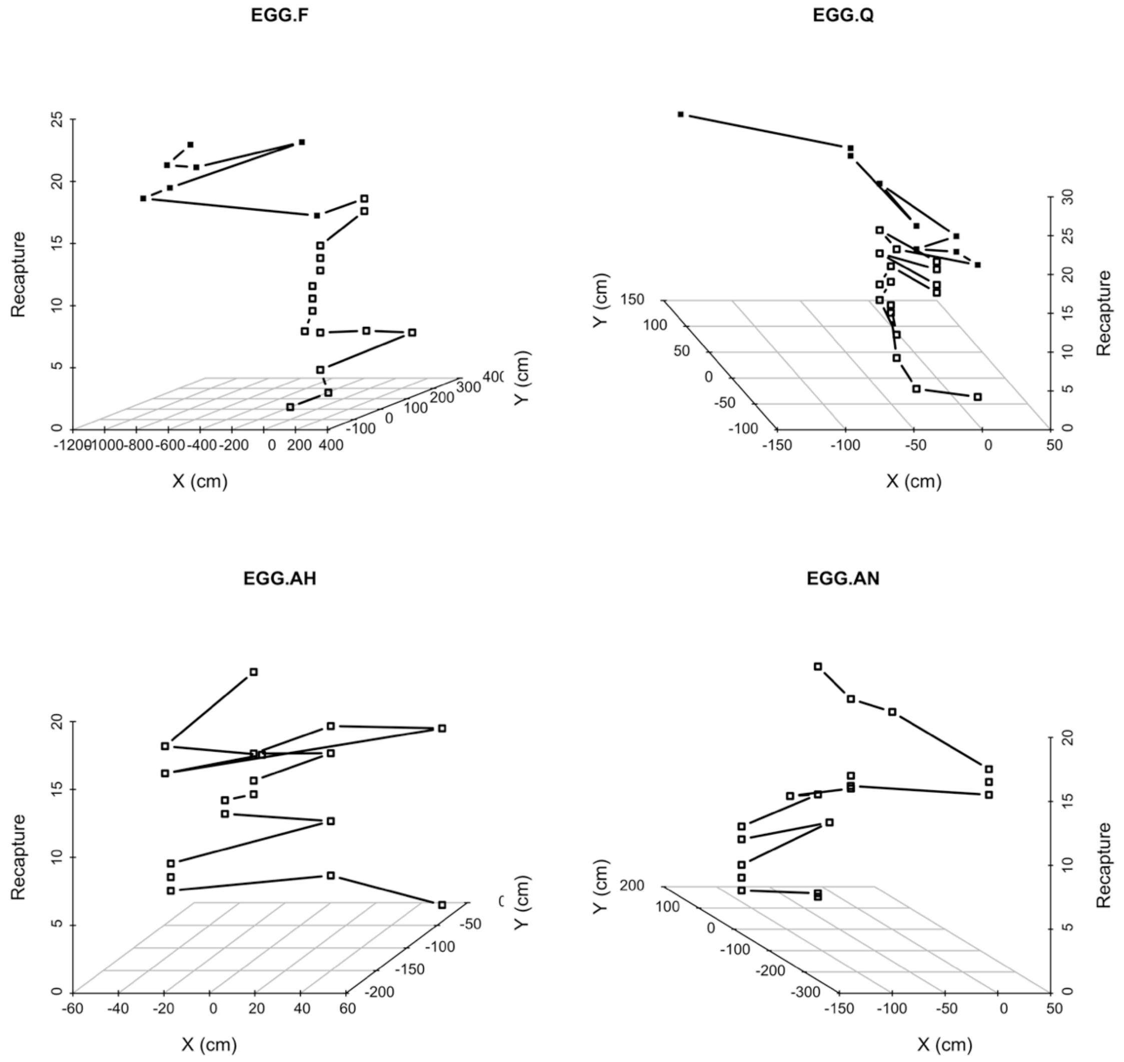


FIGURE 4. 3-dimensional representations of select individual salamander movements over time. Individuals “EGG.F” and “EGG.Q” were from burn treatments; open squares represent pre-burn captures, closed squares represent post-burn captures. Individuals “EGG.AH” and “EGG.AN” were in unburned areas.



CHAPTER 6 • CONCLUSIONS AND SUMMARY OF RESULTS

Individual animals may respond to habitat alteration in physiological, behavioral, or ecological ways that subsequently influence population-level dynamics such as survival rate and spatial distribution. Therefore, to fully evaluate the effects of forest management on wildlife, both population-level studies and individual-level mechanistic studies are necessary. For my dissertation research, I investigated (1) whether terrestrial salamander abundance and microhabitat use changed after timber harvest or prescribed fire, and (2) how individual salamanders respond behaviorally to prescribed fire.

Chapter 1 – Advancing Terrestrial Salamander Population Ecology: The Central Role of Imperfect Detection

» Accounting for imperfect detection is essential when estimating terrestrial salamander abundance or occupancy. Capture-mark-recapture and hierarchical population modeling are two of the common ways to simultaneously estimate population parameters and detection probabilities.

» Consistent terminology is needed to compare detectability parameter estimates among species, geographic regions, survey methods, and studies. *Effective detection probability* is the product of (1) *availability* – the probability of an individual being present in the survey area – and (2) *conditional capture probability* – the probability of detecting an individual, given it is available for sampling.

» With improved population analyses of terrestrial salamanders, monitoring and conservation efforts can become more precise and effective.

Chapter 2 – Predicting Variation in Microhabitat Utilization of Terrestrial Salamanders

» Terrestrial salamanders are limited to moist, humid habitats due to their dependence on cutaneous respiration. Thus, cover objects that retain moisture, such as coarse woody debris, are critical resources.

» We observed a shift in salamander microhabitat use from leaf litter to surface cover objects and subterranean refugia as time-since-rain elapsed. We captured most salamanders within leaf litter, but the proportion of leaf litter captures decreased with increased time-since-rain. These patterns of spatial and temporal variability of salamander microhabitat use illustrate the importance of accounting for imperfect detection.

Chapter 3 – Partitioning Detectability Components in Populations Subject to Within-season Temporary Emigration Using Binomial Mixture Models

» Hierarchical models can simultaneously estimate abundance and effective detection probability. We developed a binomial mixture model extension that estimates two pertinent components of detectability. Our model performed comparably to standard binomial mixture models. By explicitly considering both availability and conditional capture probability, we increased congruence between our statistical model and our ecological understanding of terrestrial salamander systems.

» At our Missouri Ozark study site, we estimated a density of 0.4 to 1.6 red-backed salamanders per m^2. Aspect best predicted red-backed salamander abundance, which increased as aspect became more northeasterly. Time-since-rainfall most strongly affected availability probability, while cover object density affected conditional capture probability.

» For robust, long-term monitoring programs, managers should select study sites and survey protocols that maximize both species availability and conditional detection probability; this would increase precision of population parameter estimates and accuracy of population trend predictions.

Chapter 4 – Prescribed Fire and Timber Harvest Effects on Terrestrial Salamander Abundance, Detectability, and Microhabitat Use

» We compared abundance, surface activity, detectability, and microhabitat use among three treatments – prescribed burn, shelterwood harvest, and midstory herbicide – and untreated controls. Abundance decreased following each of the three treatments. Abundance estimates in midstory and burn units rebounded in the second post-treatment year, but further declined in shelterwood harvest units; this could become a stronger trend with longer-term data.

» Treatments affected salamander availability more strongly than salamander abundance. Reduced availability probability – presumably due to salamanders spending more time underground – could cause a lag in detecting population trends. Lower levels of surface activity may indicate a behavioral avoidance of increased physiological stress, which may also reduce foraging and breeding opportunities. These indirect consequences of disturbance could take time to manifest into detectable changes in abundance.

Chapter 5 – Prescribed Fire Alters Surface Activity and Movement Behavior of a Terrestrial Salamander

» Prescribed fire is commonly used to reduce the risk of catastrophic wildfires, decrease fuel loads, and reestablish historic ecological influences of fire. Investigating population-level wildlife responses to prescribed fire is important for evaluating the effects of fire management on animals (Chapter 4). However, to increase our ability to predict wildlife responses to potential management actions, mechanistic studies that elucidate individual-level responses are also needed.

» We used PIT-telemetry to relocate terrestrial salamanders in prescription-burned and unburned areas. Following fire, we found a substantial decrease in surface activity among salamanders in burned areas, but found no evidence of direct salamander mortality. These results indicate that terrestrial salamanders respond to post-prescribed fire conditions by spending more time belowground, which is consistent with our results from our population-level study (Chapter 4).

» It appears that terrestrial salamanders can largely avoid direct consequences of prescribed fire, behavioral responses to post-fire micro-environmental conditions could affect salamander populations in ways that are not yet apparent. If salamander surface activity is depressed for a long enough period, populations may decline due to reductions in foraging and breeding opportunities.

APPENDIX A • SIMULATION STUDY DESCRIPTION AND RESULTS

We conducted a simulation study to evaluate the temporary emigration model over a range of availability and conditional capture probabilities. We simulated data in program R under 6 scenarios: all combinations of low, moderate, and high availability intercepts (α_ν = 0.2, 0.5, 0.8) with both moderate and high conditional capture probability intercepts (α_ϖ = 0.5, 0.9). For all scenarios, we generated data sets of observed counts over 6 seasons with 5 surveys per season at 40 study sites. We included a site-level covariate on abundance, a survey-specific covariate on availability, and a site-by-survey covariate on conditional capture probability. Covariate values were randomly generated for each simulation, but were all based on the same parameter values. The values of covariate effects (slope parameters) were also identical for all simulations.

We analyzed data under the temporary emigration model using JAGS via the package R2jags. For each simulation, we ran 3 chains for 10000 iterations and discarded the first 5000 as burn-in. We specified random starting values from the prior distributions of each parameter. We ran simulations under each scenario until we accumulated 100 converged model runs, assessed using the Gelman-Rubin statistic (R-hat < 1.1; Gelman & Hill 2007). Full results from simulation study are summarized in the tables below.

Data were simulated under the temporary emigration (TE) model for 6 scenarios. Parameters common to all data sets: alpha.lam = 1.5; beta.om = 1; beta.lam = 0.8; beta.nu = –0.5; R = 40 sites; K = 6 seasons; Tr = 5 surveys per season. α_{nu} = availability probability intercept, α_{omega} = conditional capture probability intercept.

TABLE 1. Posterior mean estimates and 95% Bayesian credible intervals of *alpha.nu* (availability probability intercept) from 100 simulated data sets. Coverage rate indicates the frequency with which the true parameter value was within the posterior 95% credible interval.

			$\alpha_{omega} = 0.5$		$\alpha_{omega} = 0.9$	
	Scale	**Truth**	**Mean (95% CRI)**	**Coverage**	**Mean (95% CRI)**	**Coverage**
$\alpha_{nu} = 0.2$	Probability	0.20	0.23 (0.12, 0.39)	0.93	0.21 (0.12, 0.33)	0.98
	Logit	-1.39	-1.22 (-1.96, -0.46)		-1.35 (-2.04, -0.71)	
$\alpha_{nu} = 0.5$	Probability	0.50	0.49 (0.39, 0.59)	0.94	0.50 (0.42, 0.58)	0.97
	Logit	0.00	-0.05 (-0.45, 0.35)		0.01 (-0.31, 0.33)	
$\alpha_{nu} = 0.8$	Probability	0.80	0.80 (0.75, 0.85)	0.95	0.79 (0.76, 0.83)	0.96
	Logit	1.39	1.40 (1.08, 1.75)		1.35 (1.14, 1.59)	

TABLE 2. Posterior mean estimates and 95% Bayesian credible intervals of *alpha.om* (conditional capture probability intercept) from 100 simulated data sets. Coverage rate indicates the frequency with which the true parameter value was within the posterior 95% credible interval.

		$\alpha_{omega} = 0.5$			$\alpha_{omega} = 0.9$		
	Scale	**Truth**	**Mean (95% CRI)**	**Coverage**	**Truth**	**Mean (95% CRI)**	**Coverage**
$\alpha_{nu} = 0.2$	Probability	0.5	0.50 (0.32, 0.72)	0.93	0.9	0.92 (0.67, 0.99)	0.99
	Logit	0.0	0.00 (-0.74, 0.95)		2.2	2.51 (0.70, 4.38)	
$\alpha_{nu} = 0.5$	Probability	0.5	0.50 (0.42, 0.59)	0.93	0.9	0.92 (0.79, 0.98)	0.97
	Logit	0.0	0.00 (-0.33, 0.38)		2.2	2.50 (1.30, 4.07)	
$\alpha_{nu} = 0.8$	Probability	0.5	0.50 (0.45, 0.55)	0.99	0.9	0.93 (0.86, 0.98)	0.91
	Logit	0.0	-0.01 (-0.21, 0.19)		2.2	2.59 (1.78, 3.79)	

TABLE 3. Posterior mean estimates and 95% Bayesian credible intervals of *alpha.lam* (abundance intercept) from 100 simulated data sets. Coverage rate indicates the frequency with which the true parameter value was within the posterior 95% credible interval.

			$\alpha_{omega} = 0.5$		$\alpha_{omega} = 0.9$	
	Scale	**Truth**	**Mean (95% CRI)**	**Coverage**	**Mean (95% CRI)**	**Coverage**
$\alpha_{nu} = 0.2$	Raw	4.48	4.10 (2.59, 7.17)	0.92	4.44 (2.89, 7.85)	0.97
	Log	1.50	1.40 (0.95, 1.97)		1.49 (1.06, 2.06)	
$\alpha_{nu} = 0.5$	Raw	4.48	4.53 (3.74, 5.58)	0.93	4.44 (3.82, 5.31)	0.95
	Log	1.50	1.51 (1.32, 1.72)		1.49 (1.34, 1.67)	
$\alpha_{nu} = 0.8$	Raw	4.48	4.48 (4.10, 4.90)	0.96	4.48 (4.14, 4.85)	0.97
	Log	1.50	1.50 (1.41, 1.59)		1.50 (1.42, 1.58)	

TABLE 4. Coverage rate and relative bias for total abundance estimates from 100 simulated data sets. Coverage indicates proportion of posterior 95% credible intervals for estimated abundance that contained true total abundance value. Relative bias calculated as mean discrepancy of all 6 seasons.

	$\alpha_{omega} = 0.5$			$\alpha_{omega} = 0.9$		
	Relative bias	**Coverage rate**		**Relative bias**	**Coverage rate**	
		≥ 5 seasons	6 seasons		≥ 5 seasons	6 seasons
$\alpha_{nu} = 0.2$	-0.024	0.92	0.89	0.063	0.97	0.94
$\alpha_{nu} = 0.5$	0.028	0.92	0.85	0.0054	0.92	0.83
$\alpha_{nu} = 0.8$	0.0050	0.92	0.72	-0.0005	0.90	0.78

VITA

Katie O'Donnell was born on June 4, 1986 in Detroit, Michigan. She attended Oakland University for undergraduate studies in Biology from 2004 – 2008 where she took courses in field botany, evolutionary biology, and vertebrate zoology that fostered her interest in studying ecology. Katie traces her interest in amphibian conservation to her interactions with Dr. Keith Berven and his passion for amphibians. In 2009, Katie began graduate studies with Dr. Raymond Semlitsch at the University of Missouri. In 2015, she will be joining the United States Geological Survey in Gainesville, Florida as a postdoctoral wildlife biologist.