EFFECTS OF FIRE MANAGEMENT PRACTICES ON THE AMPHIBIANS AND REPTILES OF GREAT SMOKY MOUNTAINS NATIONAL PARK

by

KEVIN LINDSEY FOUTS

(Under the direction of John C. Maerz and Susan B. Wilde)

ABSTRACT

Information regarding the effects of fire management practices on reptiles and amphibians is important for sound management decisions. We examined those effects by conducting surveys of stream plethodontids and upland reptiles, as well as examining the influence of fire on microclimate and modeled reptile activity periods in the Southern Appalachians. The results suggest fire application is associated with decreased abundance of large desmognathine salamanders, resulting in an ecological release of *Euycea* spp. Abundance of forest floor lizards was positively correlated with fire application. Fire effects on microclimate and models of lizard thermal activity windows suggest a relationship between fire and increased daily activity periods for lizards, though we caution some parameters in that model were not directly measured in this study.

INDEX WORDS: Fire, Southern Appalachians, Herpetofauna, Abundance Estimation, Monitoring, *Plethodon*, Operative Temperature, Bayesian Inference, National Parks, *Sceloporus*

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CHAPTER1

INTRODUCTION AND LITERATURE REVIEW

General Context

Public lands, especially those of the federal government, play a critical role in conservation and management of biodiversity in the United States. Many of these properties were secured for reasons other than preservation and are managed by various agencies operating under different mandates—which greatly influence the objectives and constraints governing resource management. However, regardless of their objectives, all federal land management agencies are required to comply with federal environmental laws and regulations. As the nation's largest landowner, adherence to these environmental restrictions results in many lands not intended to serve biological purposes, such as those of the Department of Defense and Department of Energy, harboring a substantial proportion of our nation's biodiversity (Stein et al. 2008). Other federal procurements, such as those of the National Park Service (NPS), were acquired specifically to meet biological objectives and uphold mandates that focus on the protection and conservation of natural resources. Such objectives allow NPS Parks—such as Great Smoky Mountains National Park (GSMNP)—not only to expose the public to current conservation concerns, but also devote more agency resources to preservation of biodiversity.

The Southern Appalachians are a well-documented hotspot of reptile and amphibian diversity in the United States (Kiester 1971, Lannoo et al. 2005). Past studies have examined how disturbances such as wind damage and timber harvesting have influenced the composition of herpetological communities though the alteration of vegetative structure—with specific focus on relationships between the forest canopy and floor (Greenberg 2001, Petranka et al. 1993). Fire suppression in southern Appalachia, which became significantly more effective around 1940 due to management policy in GSMNP, has also altered forest characteristics in much of region (Harmon 1981, Harrod 1998).

The Southern Appalachians owes its richness, particular for amphibians, to the interactions of montane forests and wet climate. Though the region receives high precipitation, areas of open xeric pine-oak forests were historically maintained by fire (Van Lear and Waldrop 1989). In the southwestern portion of GSMNP, slopes below 1,000m in elevation were subjected to burning on about a 12.7 year rotation before suppression (Devivo 1991, Harmon 1982). Most of these fires appear to have an anthropogenic source, and Native American use of fire dates back such that this fire-adapted pine-oak community has been established for over 10,000 years (Harmon 1982, Delcourt et al. 1998). As such, some species of herpetofuana native to the region were adapted to this fire maintained system and relied on regular episodes of fire (Greenberg 2000).

Current knowledge of the effects of fire restoration on herpetofuana within oak forests of the eastern United States are equivocal (Renken 2005). Most studies report no effects of prescribed burning on reptiles and amphibians—

however a decrease in abundance of stream salamanders and/or moderate increases in abundance of forest floor lizards are sometimes documented (Greenberg 2001, Moseley et al. 2003, Keyser et al. 2004). Past studies have taken place in flatter topographies, limiting their application to high montane regions of southern Appalachia (Ford et al. 2010, Moseley et al. 2003). Prescribed burning is not widely practiced in this region because fire management is a greater logistical challenge than in regions with flatter topographies; hence true experiments using replicated, random assignment of fire management treatments are difficult to achieve. As such, inferences about prescribed burning in southern Appalachia must be based on retrospective analyses of historically burned areas and the strength of those inferences are limited by available data. In the region of this study, GSMNP began a program of controlled burning and exotic vegetation removal in 1996. Since that time, data on the size and effects of each prescribed burn and managed wildfire have been carefully collected by GSMNP personnel. The completeness of this data, along with the Park's recognition as a hub of herpetological diversity, make GSMNP an ideal site to study fire's effects on herpetofauna in a montane region.

Stream Salamanders and Fire

GSMNP is considered the "salamander capital of the world" and hosts a great diversity of species, most belonging to the family Plethodontidae (Graf 2002, Petranka 1998). Plethodontids within GSMNP include several fully terrestrial species, and a rich community of semi-aquatic, stream-associated species within the genera *Desmognathus*, *Eurycea*, *Gyrinophilus*, and

Pseudotriton (Petranka 1998). Each has a biphasic life history that consists of larval and adult stages, and the group can be easily bifurcated into those needing ≤1 year to metamorphose and those needing ≥3 years (Dodd 2004). Such bifurcation splits GSMNP's first order stream salamander community into a predatory guild (≥3 year larval period) and a prey guild (≤1 year larval period), from which most population dynamics arise. *Desmognathus* contains members of both guilds, *Eurycea* function as prey and both *Gyrinophilus* and *Pseudotriton* serve as predators in the latter stages of larval development—all newly hatched (small) larval salamanders are susceptible to aquatic predators (Davic and Welsh 2004). Past research has demonstrated modest reductions in abundance of predatory guilds—specifically *Desmognathus quadramaculatus*—in this region, to result in a substantial ecological release in prey guilds—specifically *Eurycea wilderae* (Milanovich 2010). Due to the influence of these interspecific relationships on community structure, management activities affecting just one group or species could have cascading effects on the entire stream salamander community.

Salamander richness in the Southern Appalachians is at least partly an artifact of climatic sensitivities that prevent many species from dispersing into lower elevations (Bernardo et al. 2006). All plethodontid species respire cutaneously, which not only requires moist skin, but becomes more physiologically challenging at warmer temperatures and with larger body sizes (Feder 1983). Higher elevations in montane habitats offer increased precipitation and cooler temperatures that can accommodate the larger species in this family of lungless salamanders. Thus, many of the larger *Desmognathus* species inhabiting lower elevations in southwestern GSMNP are already living near the limit of their physiological tolerances (Bernardo et al. 2006). Physiological adaptations allowing for dispersal into warmer and more desiccant conditions, likewise prevent many lower elevation species from inhabiting the highest elevations, resulting in highest species richness at intermediate elevations (Kozak and Wiens 2010). As such, microclimatic changes in montane environments—especially within mid-elevation zones—can result in significant restructuring of salamander communities (Bernardo et al. 2007).

Numerous studies show that forest management practices that reduce canopy coverage adversely affect salamander populations (e.g., Harpole and Haas 1999, Pough 1987, Matthews et al. 2010; Petranka et al. 1994, 1993). While most of those studies focused on fully terrestrial, woodland salamanders, a recent study found that some common stream-associated, woodland salamanders (e.g., *Desmognathus quadramaculatus*) are sensitive to loss of forest cover, particularly riparian cover, within stream catchments (Cecala and Maerz, in review). However, other species were found to be (e.g., *Eurycea wilderae*) less sensitive to decreases in riparian and adjacent forest cover.

Application of fire creates more open canopy conditions that reduce stream shading and increase water temperatures (Ice et al. 2004). Furthermore, burning can increase sediment and nutrient transport within streams, and has been observed to increase nitrate concentrations in a stream within the study region (Ice et al 2004, Knoepp et al. 1993). Therefore, the restoration of fire to

GSMNP may have local impacts on stream salamander abundance and community composition.   While GSMNP has large areas of mesophytic forests to sustain stream salamander populations, they have identified impacts of fire restoration on mesophylic amphibians as a concern for consideration in adopting a fire management program.

Reptiles and Fire

Thermoregulation is an extremely important behavior with regard to reptile fitness, and it has been suggested prescribed burning provides better thermoregulatory opportunities by removing overstory cover and increasing ground temperatures (Matthews et al. 2010, Mosely 2003). Occasionally, studies in comparable regions have reported increased reptile captures in fire-restored woodlands when compared to nearby unburned second-growth forest (Perry et al 2009, Mosely et al. 2003). However, most research in the Southern Appalachians report prescribed fire’s influence on reptile abundance to be negligible, with possible benefits limited to lizards inhabiting the forest floor (Ford et al. 1999, Greenberg and Waldrop 2008, Matthews 2010). In these local studies, the largest increases in reptile abundance were observed when prescribed burning was conducted in conjunction with other fuel-reduction treatments, such as mechanical removal of the understory (Matthews et al. 2010, Greenberg and Waldrop 2008). This suggests fires severe enough to generate large understory mortality may result in increases in reptilian abundance.

Mechanistic Models and Species Distribution

Predictions of organismal responses to environmental change are typically generated through either correlative or mechanistic approaches. Correlative models rely on occurrence to develop associations between the current range of a species and environmental characteristics contained within; thus biological processes are incorporated implicitly through correlative relationships. In contrast, mechanistic models link environmental conditions to organismal performance, independent of current distributions, and explicitly incorporate underlying biological processes via parameters derived from relationships between species fitness and environmental conditions (Buckley et al. 2010). Therefore, mechanistic models predict geographic range based on processes influencing survival and reproduction, rather than habitat associations (Kearny and Porter 2009). Although more commonly used in predictive context, emphasis on fitness as a driver of distributional change bestows mechanistic approaches with more explanatory power for retrospective investigation into influence of past management action on current wildlife distributions. Although the approach relies on relationships that can be hard to parameterize, its independence from current distributions allows better formulation of inferences about *how* fire management practices are influencing faunal distribution.

Most applications of biophysical (mechanistic) models revolve around physiological limitations of the organism of interest (Kearny and Porter 2004, Porter et al. 2000). Models of reptilian distribution often focus on thermal constraints, particularly the potential duration of activity (Angilletta 2001, Buckley et al. 2008 and 2010). The range of temperatures to which a reptile will voluntarily expose itself has great influence on the proportion of time that can be spent engaging in behaviors—such as foraging and breeding—that govern population dynamics. In order to model the spatial extent of such thermal constraints, one must calculate operative temperatures for the population(s) of interest. A formal definition of operative temperature is given in Campbell and Norman (2000), but it can be regarded as the temperature to which an organism would equilibrate without heat capacitance. The equation can be informally described as air temperature plus or minus some temperature increment determined by absorbed radiation, wind speed, and animal morphology (Buckley 2008). Spatial mapping of operative temperatures provides a method for relating microclimatic conditions to species fitness and thus population dynamics (Angilletta 2001, Buckley et al. 2008 and 2010).

The use of mechanistic models provides a mechanism for investigating the potential for fire to improve reptile habitat. An episode of fire can significantly reduce midstory and herbaceous vegetation, which allows increased solar penetration and warming of the forest floor. Lizards inhabiting the forest floor are likely subjected to warmer ambient diurnal temperatures and increased solar exposure, resulting in higher operative body temperatures. As lizard activity is restricted by operative temperature, so is their ability to acquire metabolizable energy. As such, temperature of a site can directly influence fitness of its reptile inhabitants and impact population dynamics. Due to this relationship, prescribed burning in GSMNP may positively affect reptile fitness and abundance.

Research Need/Justification

GSMNP's mandate requires resources be managed to promote Park use in ways that leave habitats relatively unaltered by humans. Under this doctrine, restoration of fire through natural forest fires and prescribed burning has become a relatively recent practice with the objective of restoring fire-adapted biological communities. GSMNP's *Statement for Management* and *General Management Plan* both express a desire to re-establish fire as an ecological force within the Park, and the *Management Plan* goes further to specifically mandate that "[r]esearch into the natural role of fire in the Park will be conducted…." While there has been extensive effort to measure vegetative responses to fire, data on faunal responses and tools for incorporating fire into other faunal management objectives is limited. On September 27th 2010, the Park addressed those deficiencies by producing a list of research needs that prioritized (1) evaluation of the roles of fire and its use in restoration of species and habitats, (2) evaluating the linkage between fire and reptile abundance and distribution, (3) evaluating the relationship between fire intensity/frequency and resource response, including the native animal community, and (4) means of assessing stream salamander populations with respect to stressors, including fire. This study was designed to satisfy (from a herpetological perspective) the four research needs outlined above, as well as generally inform fire management decisions that may affect GSMNP amphibian or reptile communities.

Research Objectives

1) Compare patch abundance of selected salamander species inhabiting first order stream zones contained within burned and paired matched-control areas to evaluate associations between fire application and species occurrence and abundance.

2) Establish a pilot reptile monitoring program, with emphasis on species expected to be regularly encountered throughout study sites and exhibit population-level responses to fire management. Estimate abundance and rates of detection for focal reptilian species on study sites representing a gradient of burn histories using methodologies repeatable by GSMNP's Citizen Science program.

3) Measure microclimatic variables at ample locations throughout burned and paired matched-control sites surveyed for reptiles, and use this data to calculate operative temperatures for focal reptilian species across a gradient of fire management histories. Compare potential duration of reptile activity in burned and unburned sites to evaluate influence of previous fire management actions on the current distribution of focal reptilian species within the Park.

CHAPTER 2

METHODS

Study Sites

General Study Area

This study was conducted in the southwestern portion of GSMNP, an area dominated by xeric pine-oak forests on steep slopes drained by tumbling creeks. It has an extensive history of fire—mostly from anthropogenic sources—until suppression began around 1931 (Harmon 1982). From GSMNP's inception in 1934 until the lightening-ignited Polecat Ridge burn of 1976, a strict fire suppression policy altered natural disturbance and succession patterns. Although the Polecat Ridge fire was considered the unofficial switch from a strict fire suppression policy (Harmon 1981), because it was monitored by Park officials and allowed to extinguish naturally, GSMNP did not implement a fire management plan until 1996. By that time, alterations to historical disturbance patterns had resulted in growth of dense forests and invasions by nonnative plant species. Data collection on fires within the Park began in the late seventies and became more detailed with the installment of a fire management plan in 1996.

The 24 research sites selected for this study were generally confined to the Abrams Creek and Panther Creek drainages (Fig. 2.1). Overall, nine burn units ranging from 188 to 960 hectares were investigated and fire effects data were available for each (Tables 2.1 and 2.2). Three burn units were examined for effects on both salamanders and reptiles, including microclimate characterization. Three others were investigated only for fire's effects on stream salamanders and, in the remaining three, uplands were surveyed for reptiles as wells as microclimates measured.

Stream Sites

In summer of 2012, twelve 150m transects of first order stream were surveyed for salamanders (Figures 2.2-2.4). Six of those transects had experienced recent (3-24 years prior) episodes of fire. Each recently burned transect was paired with an unburned matched-control transect to the extent possible on attributes such as slope, elevation, aspect, size, and spatial proximity. Streams ranged from approximately 311m to 721m in elevation (Table 2.1), and were sampled from June 12th to August 2nd. Overall, streams in this region of GSMNP contained up to 11 caudate species from four genera, all belonging to the family Plethodontidae. The eight most common stream plethodontids in southwestern GSMNP include *Desmognathus conanti, D. marmoratus, D. monticola, D. quadramaculatus, Eurycea longicauda, E. wilderae, Gyrinophilus porphyriticus,* and *Pseudotriton ruber*.

Terrestrial Sites

In 2013, sampling transects (range 367-700m, Table 2.2) were established on sections of western GSMNP trails for reptile surveys (Figures 2.5-2.7). Transect lengths were determined by the extent of Park trail encompassed by an associated 10.1 hectare circular habitat characterization plot, and thus were variable. Six 10.1 hectare plots with recent burn histories (3-27 years prior) were again matched with unburned paired-controls to the extent possible on relevant attributes. Transects ranged from approximately 427m to 900m in elevation and were sampled from June 20th through July 18th.

Survey Methods

Stream Transects

Salamanders were surveyed in research streams via the use of leaf litter bags stuffed with decaying organic debris from the stream bank at each transect. Bags were spaced roughly five meters apart, for a total of 30 bags per transect, and left in the stream undisturbed for 24-48hrs—depending on the starting moisture content and degradation state of the duff from which the debris was taken. At the start of each sample, general weather conditions were recorded for later use in detection models. The presence or absence of pluerocerid snails, which graze on algae present in streams receiving ample sunlight, was also recorded in an effort to identify effects of fire unrelated to increased sun exposure. The species and life stage of all salamanders encountered within .5m of the bag's center (approximately the area encompassed by a dipnet swipe around each bag) were identified and recorded. To determine life stage, all salamanders exhibiting a size or morph associated with larvae were placed in a transparent plastic bag with clean stream water and examined for the presence of gills. Adults requiring observation of discrete characteristics for species diagnosis were also observed in this manner. As smaller *Eurycea Junaluska* larvae are extremely diificult to differentiate from *E. wilderae*—and no *Eurycea* larvae with an SVL greater than 42mm (Dodd 2004) were encountered—larvae belonging to that genus were only diagnosed as either *E. wilderae* or *E. longicauda*. Each stream pair (N=6) was sampled for three consecutive days except for a 3-day delay at ‘stream pair 3’ (Sites B3 and R3^s) due to GSMNP road closures resulting from the July 5th derecho—a violent wind event felling many trees. All field data sheets and maps were digitized for archiving and data transcribed into excel workbooks.

Terrestrial Transects

Upland surveys were designed to focus on Northern Fence Lizards (*Sceloporus undulatus hyacinthinus*) and skinks (*Eumeces* spp.), as their ubiquity and ease of identification make them effective focal species for repeatable surveys by participants in GSMNP’s Citizen Science program. Survey transects were overlaid on existing GSMNP trails for a few reasons: 1) These surveys are intended to serve as the foundation for a monitoring program carried out by GSMNP Citizen Scientists, and it was the belief of both the researcher and members of the Citizen Science program that participation was more likely if the challenges of establishing, maintaining and navigating off-trail transects were avoided; and 2) GSMNP’s ‘Trails Crew’ actively maintains the openness of these transects; reducing noise created by the observer and maintaining trailside basking sites that are attractive to the focal species. I also hoped that lizards maintaining these trailside territories would be desensitized to anthropogenic traffic, allowing for higher detection rates—although I have no literary basis for that assumption. At the start of each sample, the time, general weather conditions, and temperature were recorded. Reptile surveys were not conducted during precipitation events. Each burn/reference pair of transects was walked twice on the same day from opposite directions (out-and-back surveys), and all reptile encounters recorded and georeferenced. Each animal's distance from the transect was also recorded for each observation. To standardize comparisons between transects of varying length, reptile encounters were recorded per 50m segment of transect. A five minute pause was taken between transect passes or if hikers were encountered within the transect during sampling. A count of hikers passing through the transect during sampling was recorded for each sample. Surveys took place over a maximum of 5 days to assume a closed population. Members of the focal *Eumeces* genus were simply recorded as "*Eumeces* spp." Original field data sheets and maps were digitized for archiving, and observations were transcribed into Excel workbooks.

Microclimate Measurements

An array of 20 stations to measure a suite of relevant microclimates variables was established within a 10.1 ha circular plot centered on each of the 12 upland transects (Fig. 2.8). Placement of each station was guided by a Principal Component Analysis sampling tool developed by Tom Prebyl in ArcMap 10.1, which placed a minimum distance of 50m between each array and ensured stations were dispersed across topographic gradients to representatively sample the site's microclimate. Topographic features input into the principal components algorithm included elevation, slope, surface curvature, and solar radiation. Within each plot, half (n=10, N=120) of the stations were randomly assigned to be located at patches free of understory or midstory cover (Fig. 2.9) and the remaining half (n=10, N=120) at patches with understory or midstory vegetation (Fig. 2.10). Whether sensors were located beneath understory vegetation or midstory vegetation depended simply on which of those structures was more prominent in the immediate vicinity. In the event the assigned vegetative cover condition could not be met in the immediate vicinity of the assigned location, a station assigned to the opposite vegetative cover condition was selected randomly, and cover assignments switched. Air temperature and ground surface temperature were measured via Ibuttons (maxim integrated) deployed at all stations (N=240) and data recovered from 210 and 212 sensors respectively. Ibuttons measuring ground surface temperatures were thinly coated with white rubber to reflect solar radiation and weather-proof the sensor (Fig. 2.9 and 2.10). Ibuttons are susceptible to damage when exposed to precipitation and this method has been demonstrated to provide accurate measurements while greatly reducing the likelihood of instrument failure (Roznik 2012). Ibuttons measuring air temperature (n=20, N=240) and air humidity (n=10, N=120) were placed inside PVC housings that allowed ample air flow but protected them from direct precipitation (Fig. 2.11), and were hung from vegetation two meters from the ground. Due to sensor failure in the field, humidity data was recovered from 88 stations (of 120 deployed), with a range of 5-10 per site. Overall, data from 422 of the 480 sensors deployed was retrieved with hourly measurements recorded for 49-58 complete days. At five stations (B7-11, R7-10, $R1^u$-13, B3-10, and $R5^u$-12), both sensors were either destroyed by wildlife or failed.

Statistical Analysis

Salamander Abundance

A binomial-Poisson mixture model fit to counts of salamanders was used to estimate first-order stream salamander abundance in response to site-level predictors (Appendix 2). This approach relies on Bayesian inference and was developed by Royle (2004) and extended by Dodd and Dorazio (2004), as well as Kéry et al. (2005) to allow for simultaneous estimation of both abundance and detection. Thus, the model consists of two parts: a linear logit model for detection probability (p) at the sample/day level and a log-linear model for mean abundance (m) at the trap level. Abundance (N) is treated as a random unobserved variable sampled from a Poisson distribution with mean (m). The observed count is assumed to arise from a binomial distribution with parameters p and N. Markov chain Monte Carlo (MCMC) sampling in OpenBUGS was used to estimate posterior distributions of model parameters.

The detection probability model consisted of two linear terms: (1) an intercept and (2) a three-level effect of general weather condition [precipitation/overcast/partly to fully sunny]. Initially, random effects for trap, sample, site, and site pair were considered for the detection portion of the model, but they were ultimately removed over concerns about ability of the MCMC sampler to converge on reasonable estimates. Similarly, the random effects of sample, site, and site pairing were excluded from the abundance model. The effect of pluerocerid snail presence, originally included in the abundance model to investigate the possibility of fire effects unrelated to canopy, was also removed after its influence was consistently found to be in the same direction as that of fire. After exclusion of these parameters, the linear terms of the abundance model include: 1) an intercept, 2) a burn effect [burn or reference site], 3) a slope parameter for years since burning [applied only to burn sites], 4) a slope parameter for site elevation, and 5) a trap-level random effect.

The burn effect parameter (2) was included to reveal whether abundance of the taxon of interest is estimated to increase or decrease in response to fire, and at what magnitude. In the most direct terms, it indicates how designating a site as burned or unburned in the model influences the resulting abundance estimation. The years since burn effect (3) is intended to capture the temporal relationship between fire and species abundance. In mathematical terms it is a slope value produced from correlating abundance with burn age and can be used to inform prescribed fire regimes and estimate abundance during unsampled time windows throughout burn histories. The elevation parameter (4) is included simply to avoid misattributing the explanatory power of elevation on salamander occurrence/abundance to effects unrelated to elevation, including burning. Values or summaries for salamanders presented in the next chapter of this manuscript were obtained by using the estimated posterior distributions of these parameters.

Due to the significant influence of competition and predation within amphibian communities (Sih 1985), changes in the occurrence or abundance of any one species can result in interspecific compensation. As such, response assessment began at the species-level and progressed to broader taxonomic groupings as patterns emerged relating to taxonomy and guild position. Thus, the eight species were first grouped based on plethodontid subfamily associations: members of the *Desmognathus* genus belong to the Plethodontinae subfamily and members of *Eurycea, Gyrinophilus*, and *Pseudotriton* to the Spelerpinae subfamily. The *Desmognathus* spp. are physiologically constrained to higher elevation areas with cooler climates (Bernardo et al. 2006, 2007); while the four Spelerpinae species are commonly found in warmer areas at lower elevation. Groups were then divided based on trophic roles (typically predator or prey), which resulted in analysis of four guilds, each with two species: (1) large *Desmognathus* that are potential predators on smaller salamander species [*D. quadramaculatus* + *D. marmoratus*], (2) small *Desmognathus* that are potential prey of larger salamanders [*D. conanti* + *D. monticola*], (3) large Spelerpinae that are potential predators on smaller salamander species [*Gyrinophilus porphyriticus* + *Pseudotriton ruber*], and (4) small Spelerpinae that are potential prey of larger salamanders (*Eurycea longicauda* + *E. wilderae*).

When selecting sites for this study, only five burn/reference pairs that matched well on desired attributes were identified. The sixth pair (Sites B6 and R6) exhibited a large spatial (Figure 2.2) and elevational (Table 2.1) separations. Site B6 had the lowest elevation of all study sites and Site R6 the highest. Elevation has a large effect on salamander composition and abundance (Cecala 2012), which likely confounded any effects related to fire. Therefore, I excluded this pair of sites from my analyses. The third site pair (Sites B3 and R3) was spatially separated from the remaining four pairs and its reference site (R3) exhibited different species composition than other reference sites. For discussion purposes, the model was run with Sites B3 and R3 excluded as well.

It should also be noted that a parameter accounting for the frequency of burns since fire restoration in 1996 was intended to be included in the model. However, both types of sampling units in this study—streams and trails—are frequently used by GSMNP's Fire Crew as breaks delimiting the boundaries of prescribed burns or wildfires. In the field, it appeared that burns did not made it all the way to stream banks or trail edges, but it this was difficult to judge for older or less severe burns. Therefore, I ultimately could not include fire frequency or intensity in models. All sampling units are firmly within the burn boundaries of the fire used to provide a burn age value for analysis. However, two of the six stream sites and one terrestrial site experienced an additional burn that fully encompassed the sample area: stream B1 experienced fire in 2003 as well as 2007; stream B2 experienced fire in 2005 and 2007; and terrestrial site B1 was burned in 2003 as well as 2007. Part of the transect in terrestial site B4 was burned in 1997 in addition to 2005.

Reptile Abundance

In a similar approach as that used for salamanders, a binomial-Poisson mixture model was fit to reptile counts to estimate abundance in response to site-level predictors (Appendix 3). As in the previous analysis, random effects that posed problems in model fitting were again excluded from the detection model. Surprisingly, two fixed effects assumed important to modeling detection were counter-intuitive. A ‘Pass B’ effect, a binary indicator of whether the count was observed on the outbound or the inbound walk of the transect, was introduced to account for increased likelihood of repeat detections due to observer bias when surveying a transect for the second time on the same sample. However, the effect was found to be very small with credibility intervals centered near zero for each taxon, so it was removed from the model. The ‘Trail Traffic’ effect represented survey disruption due to hikers passing through the transect during sampling; however, trail traffic was positively related to detection. This was most likely related to weather, with sunny conditions increasing hiker traffic and drawing out lizards—thus, the effect was also removed. After exclusion of these parameters, linear terms of the reptile detection model used for analysis were: 1) an intercept, 2) a two-level effect of weather condition [overcast/partly to fully sunny]. After removing unstable random effects from the abundance portion of the model, the terms were: 1) an intercept, 2) a burn effect, 3) a slope parameter for years since burn, 4) a slope parameter for site elevation, 5) a segment length effect [the last segment in a transect was often shorter than 50m], and 6) a segment-level random effect. Parameters in the reptile abundance model serve the same utilities as those in the salamander model, with the addition of segment length (5) to account for the reduced opportunity to encounter reptiles on segments less than 50m. Abundance estimates and other inferences presented for reptiles in the next chapter were generated based on forecasted posterior distributions of those parameters.

Operative Temperatures

Microclimatic variables measured were specifically chosen for use in the operative temperature equation outlined in Campbell and Norman (1998, p. 185-206) and applied to *S. undulatus* by Buckley et al. (2008 and 2010) and Angilletta et al. (2009). See the Appendix in Buckley (2008) for a thorough outline of the process used to calculate operative temperatures for lizards. One major difference between this study and those previously mentioned, is that inputs to the operative temperature model were derived from hourly measurements of known air (T_a) and surface (T_s) temperatures obtained at the scale of the site, rather than estimates of temperature averaged over a coarse spatial grain. However, sensor failure resulted in 26 stations with T_a measurements lacked associated T_s values and an additional 25 stations produced T_s values while lacking measurements of T_a. To maintain the spatial and temporal resolution of estimates for the missing values, equations relating T_s to T_a and vice versa were calculated by correlating hourly measurements at the 184 stations for which complete data on both variables was retrieved. This was conducted for both levels of understory assignment, resulting in four predictive equations (Appendix 1) permitting the imputation of estimates for the missing values of these 51 stations with only T_s or T_a. The smaller spatial extent also allowed for measurement of canopy openness above the sensors; as such an equation relating canopy openness to solar radiation derived from data presented in Zou (2007) was used to adjust direct irradiance (S_p), rather than calculating temperatures at the two extremes of full sun (100% S_p) and full shade (0% S_p).

Two variables influencing operative temperature estimations—wind and lizard SVL—were not measured during the study. Examination of fire's effect on operative temperature (inc/dec, more/less variable, ect.) was not sensitive to changes in these input values, however, estimated activity period was heavily influenced by wind velocity. As such, potential daily activity windows were calculated for a gradient of relevant wind speeds, while effects on operative temperature were calculated using a constant wind speed of 0.1m/s—selected because the focal lizard species inhabits the boundary layer where drag reduces wind velocity (Mike Sears, Clemson University, personal communication). The mean of the most proximal *S. undulatus* population with available data, 72mm, was used for SVL (Niewiarowski 1993). This value was only 1 millimeter different from the mean SVL used by Buckley (2008) and Angilletta et al. (2010). The modest influence of SVL is demonstrated in Appendix 1; where distribution of daily activity periods are given for an SVL of 62mm. Parameter values and their sources can also be found in Appendix 1. To examine fire's effect on activity during the month of May, 5°C (the difference between the combined mean for June/July and mean May temperatures for nearby Townsend, TN according to wheather.com) was subtracted from each air and soil surface temperature measurement and the model rerun.

Using the procedure outlined in Buckley (2008), station measurements were converted to hourly operative temperatures for an adult *S. undulatus* at that station during daylight hours. Means and standard deviations of operative temperatures at the station and site-level were compared and their influence on the resulting activity period estimations examined. *S. undulatus* were considered capable of activity when diurnal operative temperatures were at or within the 20% to 80% percentiles of observed body temperatures in the field, 32.0-35.6C (Angiletta et al. 2002). Counts of potential daylight activity hours were compared between burn and reference patches at day-level. Correlations between means and variance in operative temperature, canopy openness, and daily activity hours were also examined.

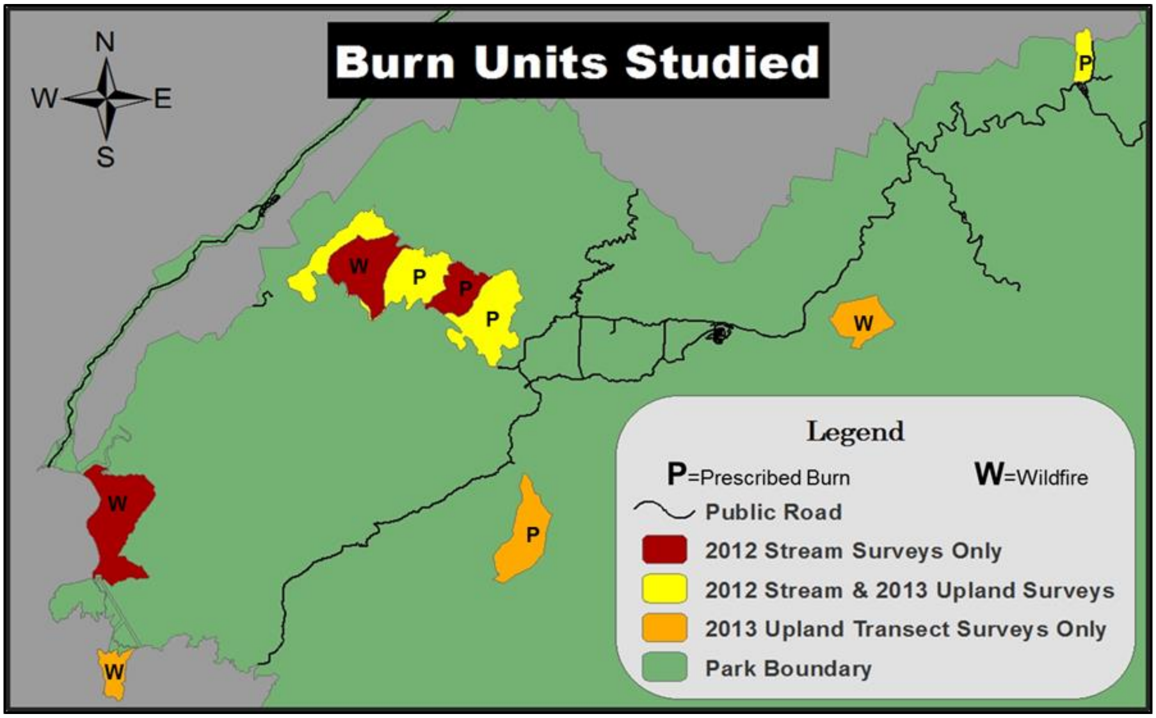


Figure 2.1: *Burn units studied.* This map shows the entire region of study. All nine burn units studied between 2012 and 2013 are included. Each fire polygon is indicated as being either a prescribed burn (P) or wildfire (W).

Table 2.1: *Stream transect attributes.* ‘Map Label’ corresponds to maps presented in Figures 2.3 and 2.4.

Stream Sampling Sites

Map Label	Burn Unit Name	Burn Unit Size (acres)	Fire Type	Years Since Burning	Stream Name	Elevation (m)	Transect Location (center)
B1	Arbutus	1,052	P	5	Arbutus Branch	669	-83.847W 35.614N
R1^{S}	N/A	N/A	N/A	>70	Arbutus Branch	624	-83.844W 35.611N
B2	Buckshank	943	W	5	Mill Branch	390	-83.906W 35.615N
R2	N/A	N/A	N/A	>70	Kingfisher Creek	366	-83.923W 35.619N
B3	Wear Cove Gap	224	P	3	Sweetwater Branch	542	-83.646W 35.689N
R3^{S}	N/A	N/A	N/A	>70	Sweetwater Branch	534	-83.644W 35.688N
B4	Stony Ridge	505	P	5	Stony Branch	493	-83.871W 35.607N
R4	N/A	N/A	N/A	>70	Morelicker Branch	608	-83.863W 35.586N
B5	Hatcher Mountain	2,372	P	7	Buckshank Branch	369	-83.914W 35.619N
R5^{S}	N/A	N/A	N/A	>70	Kingfisher Creek	366	-83.918W 35.626N
B6	Shop	1,305	W	24	Unnamed	311	-83.990W 35.541N
R6	N/A	N/A	N/A	>70	Parson’s Branch	721	-83.914W 35.531N

Table 2.2: *Trail transect attributes.* 'Map Label' corresponds to maps presented in figures 2.5 and 2.6.

Upland Sampling Sites								
Map Label	**Burn Unit Name**	**Burn Unit Size (acres)**	**Fire Type**	**Years Since Burning**	**Trail Name**	**Elevation (m)**	**Length (m)**	**Transect Location (center)**
B1	Arbutus	1,052	P	6	Cooper Road	701	700	-83.856W 35.612N
R1^{U}	N/A	N/A	N/A	>70	Rabbit Creek	594	565	-83.858W 35.588N
B3	Wear Cove Gap	224	P	4	Roundtop	610	606	-83.649W 35.692N
R3^{U}	N/A	N/A	N/A	>70	Greenbrier	610	690	-83.637W 35.694N
B5	Hatcher Mountain	2,372	P	8	Little Bottoms	427	533	-83.921W 35.619N
R5^{U}	N/A	N/A	N/A	>70	Goldmine	549	367	-83.909W 35.637N
B7	Hickory	535	W	27	Bote Mountain	846	443	-83.726W 35.608N
R7	N/A	N/A	N/A	>70	Bote Mtn & Finley Cane	640	633	-83.712W 35.619N
B8	Calderwood	291	W	3	Calderwood Fire Road	579	394	-83.985W 35.499N
R8	N/A	N/A	N/A	>70	Hannah Mountain	869	523	-83.903W 35.548N
B9	Gregory Ridge	820	P	6	Gregory Ridge	899	633	-83.837W 35.546N
R9	N/A	N/A	N/A	>70	Gregory Ridge	625	417	-83.845W 35.561N

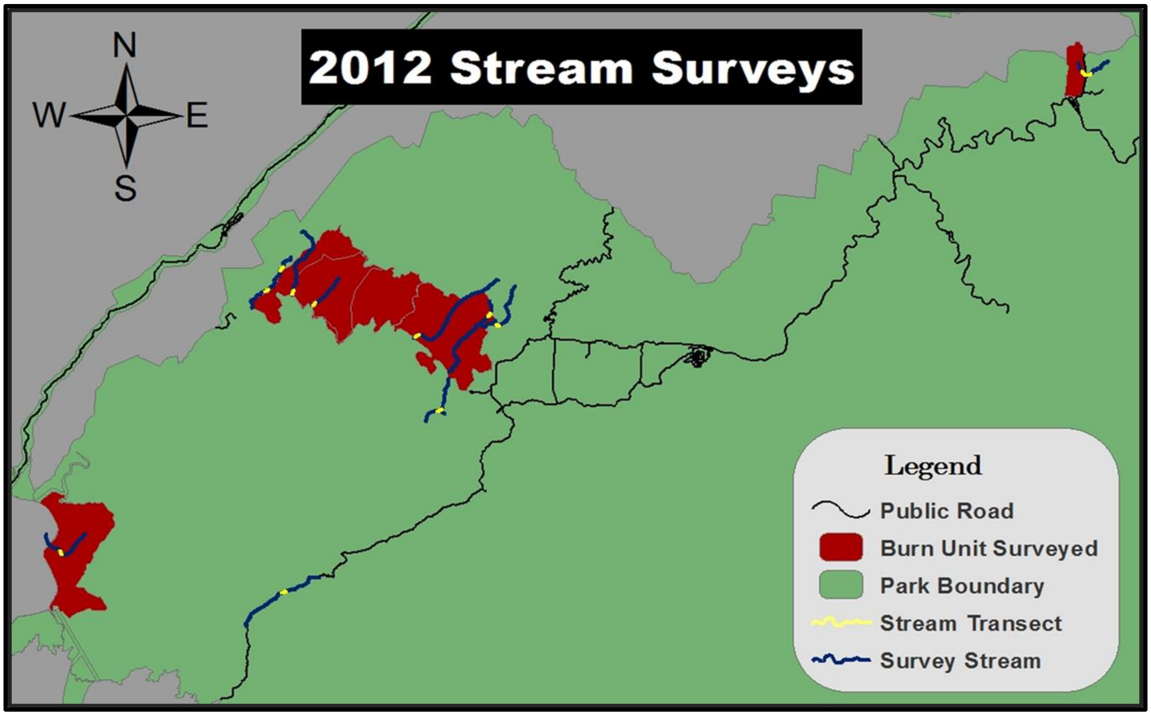


Figure 2.2: *Spatial arrangement of stream transects.* All 12 transects are shown.

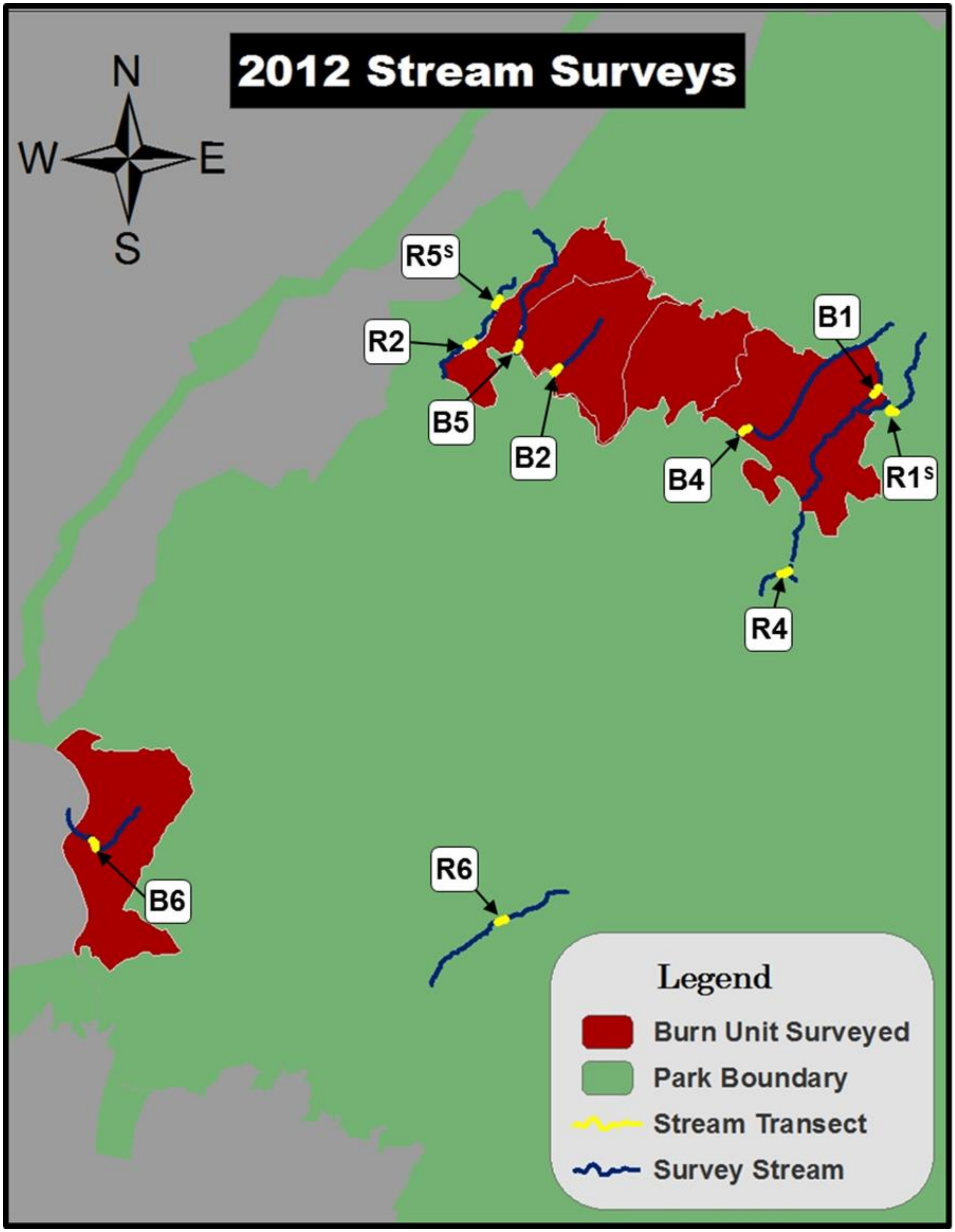


Figure 2.3: *Map A of 2012 stream transects.* 10 of 12 sites are included in this figure. Larger letters designate burn (B) or reference (R) transects. Numbers signify burn/reference pairs. Exponential letters differentiate reference stream transects (^{S}) from reference upland transects (^{U}) paired with the same burn unit, when viewing figures 2.1-2.4 in conjunction.

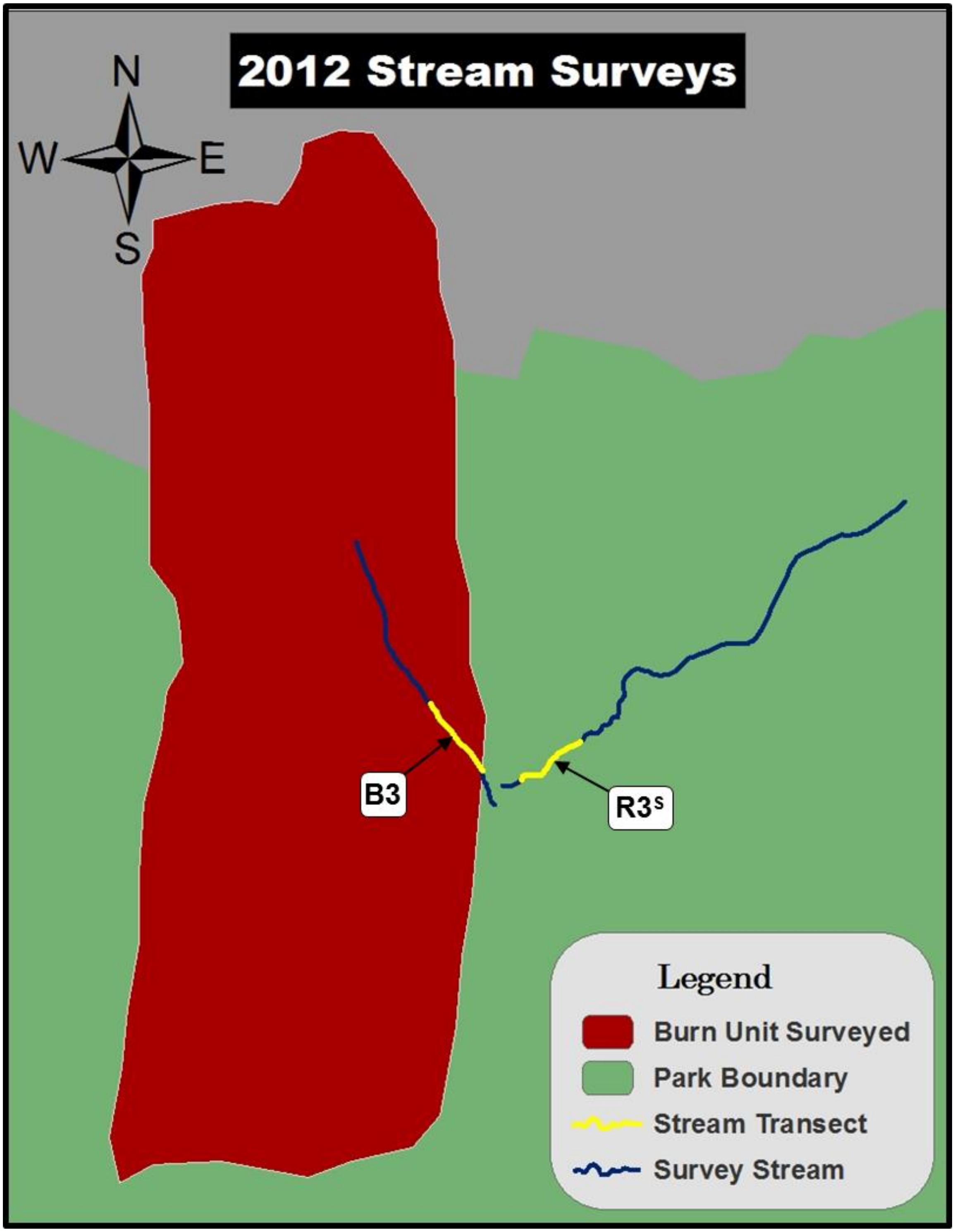


Figure 2.4: *Map B of 2012 stream transects.* 2 of 12 sites are included in this figure. Larger letters designate burn (B) or reference (R) transects. Numbers signify burn/reference pairs. Exponential letters differentiate reference stream transects (^{S}) from reference upland transects (^{U}) paired with the same burn unit, when viewing figures 2.1-2.4 in conjunction.

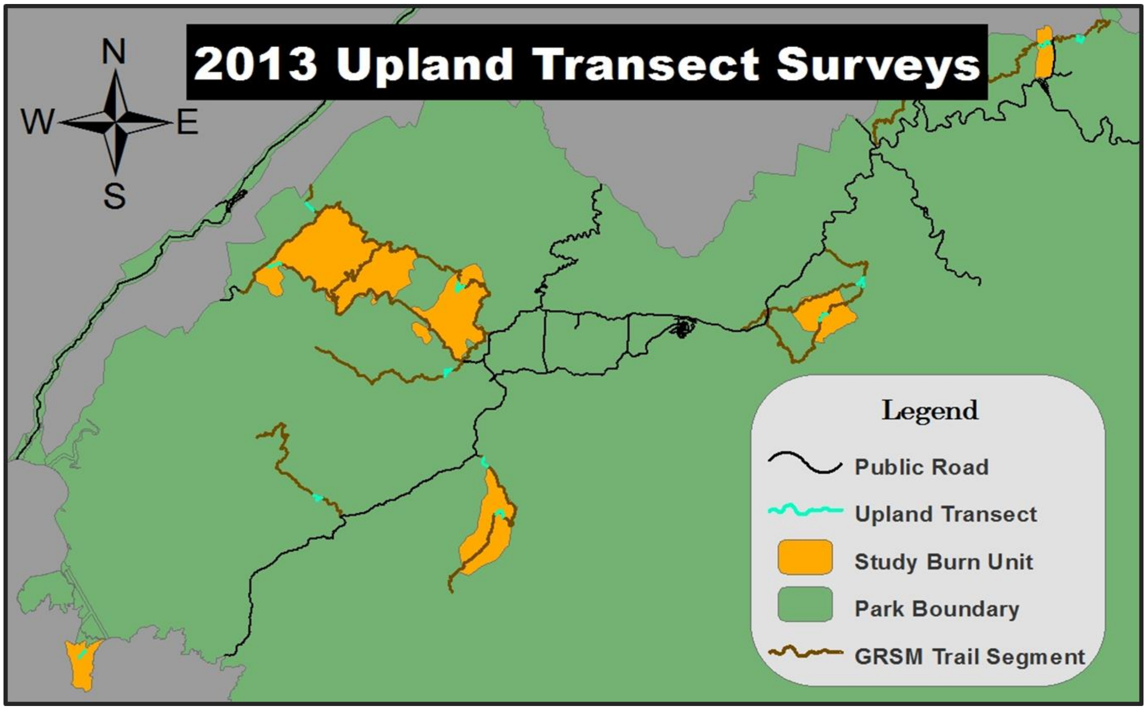


Figure 2.5: *Spatial arrangement of trail transects*. All 12 transects are shown.

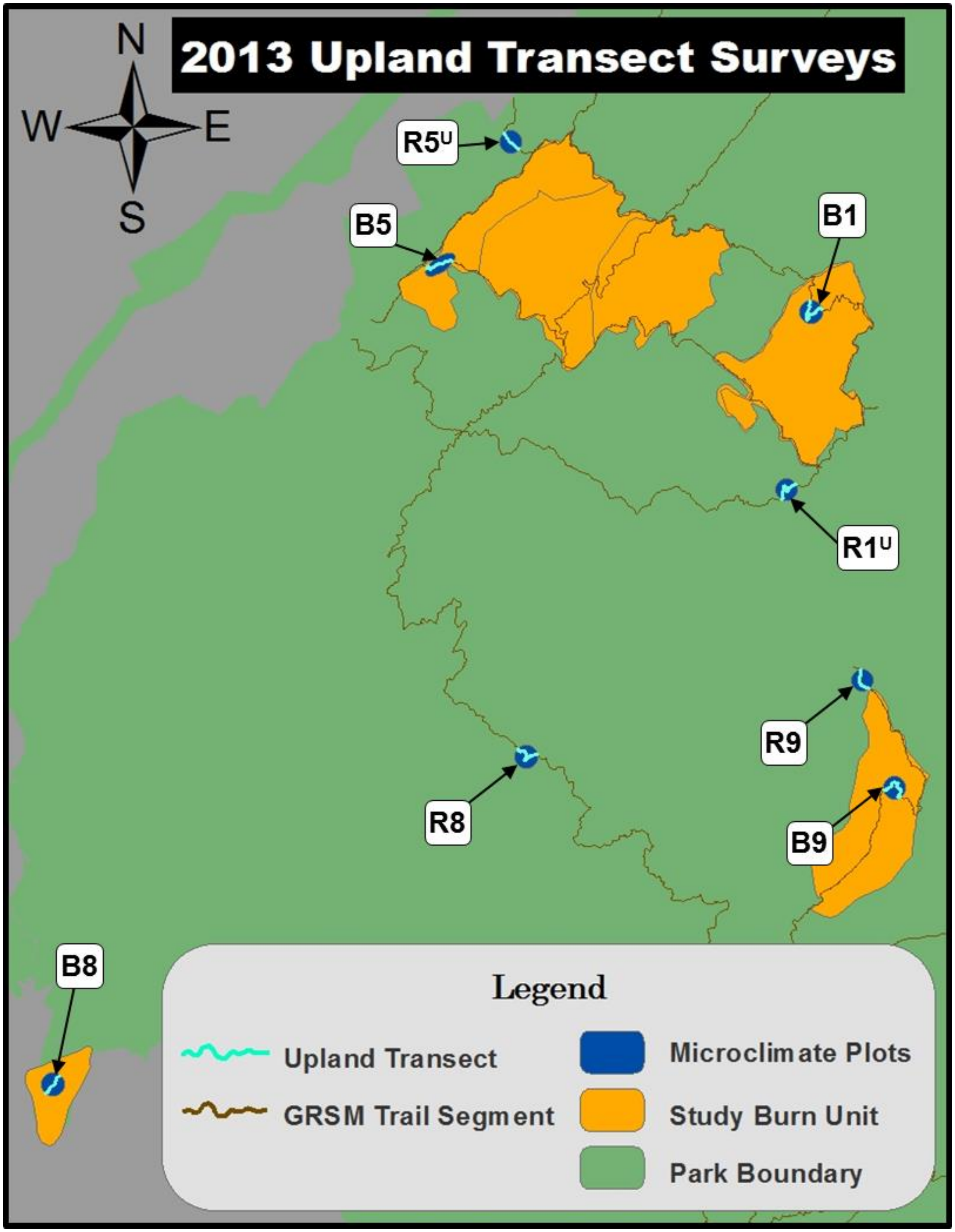


Figure 2.6: *Map A of 2013 trail transects.* 8 of 12 sites are included in this figure. Larger letters designate burn (B) or reference (R) transects. Numbers signify burn/reference pairs. Exponential letters differentiate reference stream transects (^{S}) from reference upland transects (^{U}) paired with the same burn unit, when viewing figures 2.1-2.4 in conjunction.

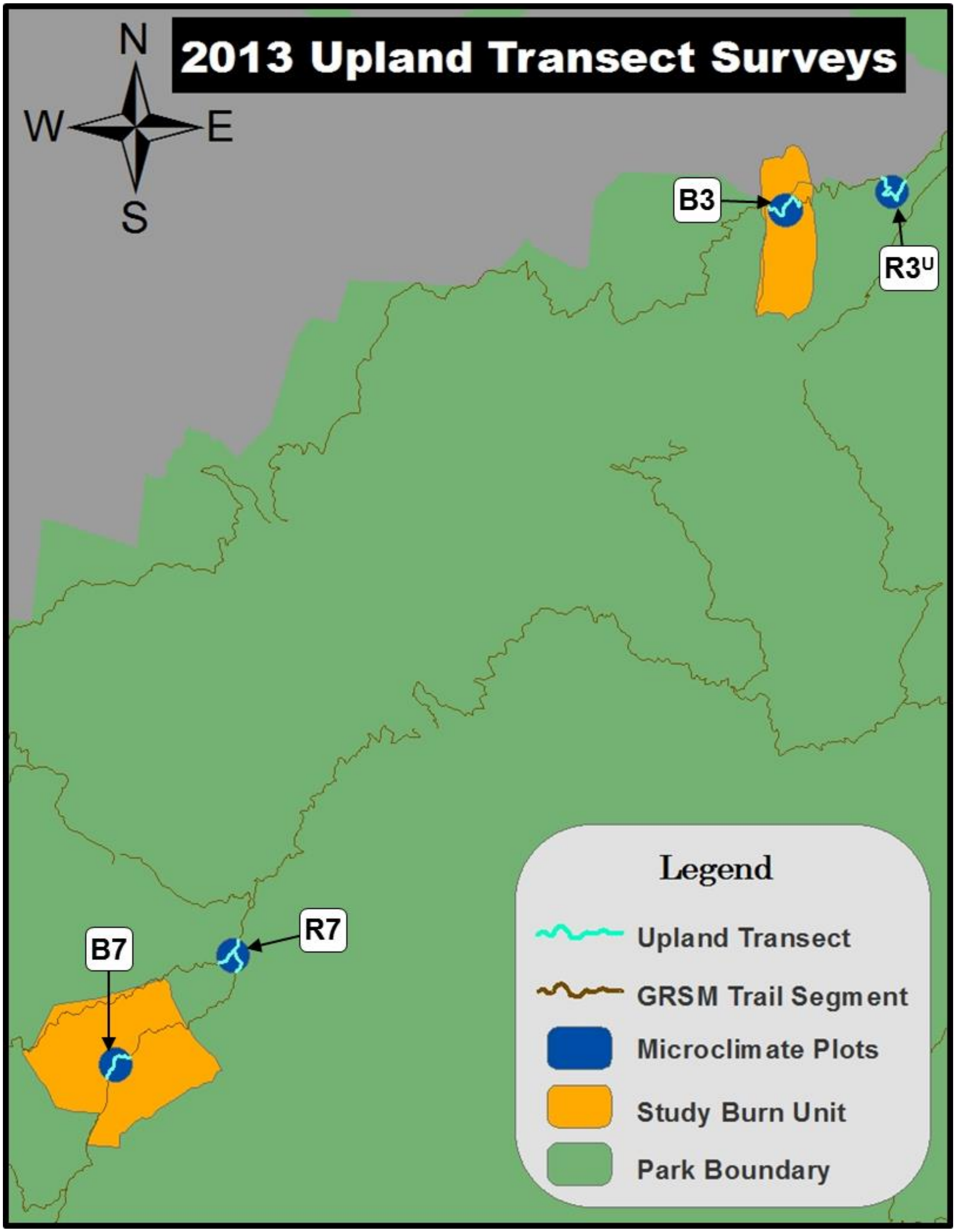


Figure 2.7: *Map B of 2013 trail transects.* 4 of 12 sites are included in this figure. Larger letters designate burn (B) or reference (R) transects. Numbers signify burn/reference pairs. Exponential letters differentiate reference stream transects (^{S}) from reference upland transects (^{U}) paired with the same burn unit, when viewing figures 2.1-2.4 in conjunction.

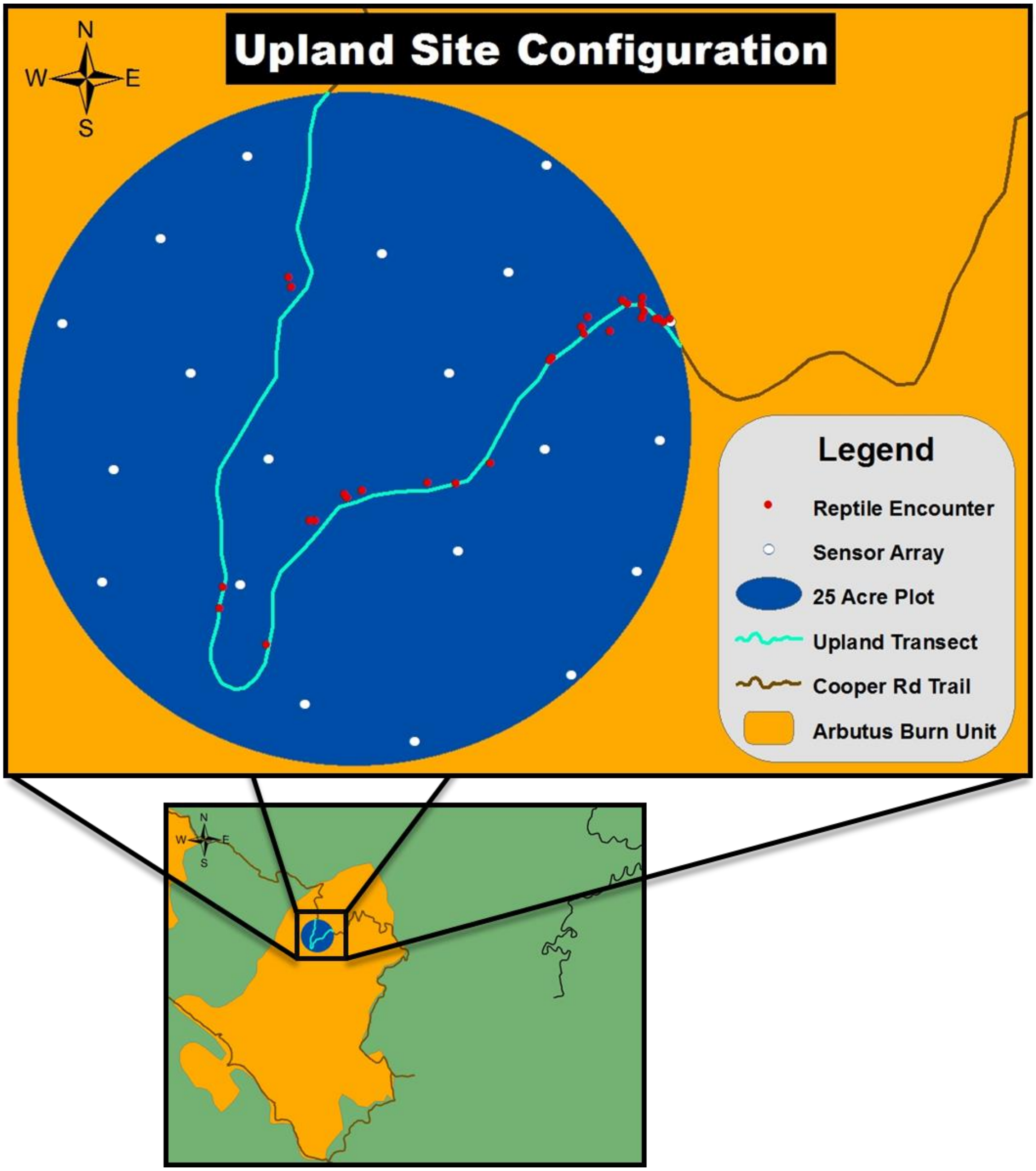


Figure 2.8: *Upland site configuration.* Reptile encounters are included to demonstrate the relationship between upland transects and microclimate characterization plots. The plot shown is within the Arbutus burn unit.

Figure 2.9: *Surface temp measurement - no understory cover.* Due to steep topography and curious wildlife, sensors (circled) were placed on a flat portion of woody debris stabilized by split twigs staked out around the periphery.

Figure 2.10: *Surface temp measurement - understory cover.* Due to steep topography and curious wildlife, sensors (circled) were placed on a flat portion of woody debris stabilized by split twigs staked out around the periphery.

Figure 2.11: *Air temp and humidity measurement.* The Ibutton (grey cylinder underhanging top of open PVC) is hung at 2m and receives ample atmospheric contact. The vertical PVC tube (white string attached) allows precipitation to pass through the housing without direct contact with the sensor. The white color reflects solar radiation, providing accurate readings of air temperature and humidity.

CHAPTER 3

RESULTS

Salamander Occurrence and Abundance

We estimated patch occupancy probability for burned and unburned sites at the trap level using our abundance model to calculate expected frequency of zero abundance. Since occupancy estimates were calculated based on a slope value produced by the model, once a species is projected to return to unburned (reference site) occurrence, the reference site value should be regarded as the occupancy estimate for all time periods thereafter. Of the species with sufficient observations for independent analysis, *D. quadramaculatus* on a site just burned (i.e. 0 years since burning) and *P. ruber* on a reference site had the lowest estimated patch occupancy (.012 and .018 respectively); no species had an estimated occupancy of zero for any combination of site attributes. Model output suggests *D. conanti* occurrence was unrelated to burning, while *Eurycea wilderae* was estimated to occupy more patches in streams that experienced recent fire (Figure 3.1). Consult Figure 3.2 to view survey data depicting species occurrence and abundance per site.

Fire was found to have species-specific effects on abundance. *D. quadramaculatus* abundance was estimated to be reduced 76.8% following fire, while *E. wilderae* and *P. ruber* were estimated to increase in abundance by 464%

and 19734%, respectively. Credibility intervals for fire's effect on *D. conanti* abundance were large and included zero (Figure 3.3).

Although there were not sufficient encounters of *D. marmoratus* for independent analysis, when grouped with *D. quadramaculatus,* the estimated negative effect of fire on abundance of these two sister taxa was larger than when *D. quadramaculatus* was analyzed alone (Figure 3.3)—indicating that *D. marmoratus* abundance was also negatively affected by fire. The estimated effect of fire on *D. monticola* + *D. conanti* was small and the credibility interval again centered about zero, further indicating a lack of effect on that guild. Fire had a positive but weaker relationship with the abundance of *G. porphyriticus* + *P. ruber,* suggesting the two members of this guild may respond differently to burning. Fire was positively associated with abundance of *E. longicauda* + *E. wilderae*. The model estimated *D. quadrmaculatus* abundance returned to that of an unburned site in 5.7 years (Figure 3.4). Similarly, members of Spelerpinae were projected to decline back to reference site abundance in 4.5-4.8 years.

Reptile Occurrence, Abundance, and Detection

Estimates of lizard occupancy per 50 m of trail, suggest a positive relationship between the restoration of fire and lizard occurrence (Figure 3.5). *S. undulatus* were estimated to occur 4.75 times more frequently at burned sites, but abundance was not strongly correlated with burn age. *S. undulatus* were only detected at one site that had not experienced recent burning (Figure 3.6). *Eumeces* spp. were estimated to occur more frequently overall than *S. undulatus*, as well as exhibit a higher rate of occupancy at burn sites. *Eumeces* spp. patch occupancy appeared to show a weak, negative correlation with burn age (Figure 3.7), but the credibility interval of the related parameter included zero. For all squamates, which included all lizard and snake encounters, burn sites were occupied at a much higher rate (Figure 3.5), but occupancy was unrelated to burn age.

Model output indicated an association between lizard abundance and fire, although there was still a lack of support relating abundance to burn age. Both Lacertilian groups are expected to be encountered in larger numbers at sites experiencing fire, with abundance of *Eumeces* spp. projected to be more than four times that of unburned sites (Figure 3.8). Abundance estimates produced for *Eumeces* spp. at 5 year increments after the application of fire are reduced by roughly 50% over each period (Figure 3.7), but—again—the credibility interval for that slope value includes zero. Abundance of *S. undulatus* on burn units is expected to be more than double that of reference sites (Figure 3.8). Although the only burn site not to produce *S. undulatus* encounters during surveys had experienced fire six years prior, plotting sites that did produce encounters by burn age suggests both lizard taxons peak in abundance around six years after burning (Figure 3.9). Analysis of all squamates resulted in an estimated abundance increase of just over 140%.

Estimated reptile detection rates were very high (Figure 3.10). Median values for *S. undulatus* and *Eumeces spp*. detection were 77% and 71% respectively. The overwhelming influence of these two groups, which accounted for 92% of encounters, is apparent by the estimated detection of all squamates squarely in the middle at 74%. Overcast weather was found to negatively impact detection (Figure 3.10).

Microclimate and Lizard Activity

Mean operative temperature for *S. undulatus* on GSMNP burn sites is approximately 1.4°C warmer than those on reference sites for the months of June and July, 30.61°C and 29.25°C respectively (Table 3.1). Day-to-day variability at a particular station was low and appeared to be relatively homogeneous among all sites, with standard deviations at burned stations being only 10% greater than those at reference stations. However, burn sites exhibited much more patch heterogeneity and the standard deviation of operative temperature means at each station within a given day was 32% greater within burn sites. Similarly, burn sites produced a mean daily site-wide operative range of 30.85°C, while reference sites produced an operative range of only 25.55°C over the same daylight period. There was also greater hour-to-hour variability at burn stations, which had a standard deviation of 6.26°C between hourly operative temperatures, compared to 5.69°C at reference stations. Individual stations within burns also exhibited daily operative ranges that averaged 1.95°C more than did discrete references stations (Table 3.1). The daily operative temperature range at a burn station was only 3.4 times the deviation between hourly operative temperatures over a 13 hour period—indicating that diurnal heating and cooling trends were less stable at burn stations, possibly due to increased influence of meteorological conditions. Hourly variability was strongly positively correlated to daily mean operating temperature, as well as canopy openness. Mean operating temperature was found to exhibit an even stronger positive association with canopy openness (Figure 3.11).

Burn sites averaged more canopy openness than reference sites (Table 3.1), and a greater proportion of the daylight period was estimated to produce an operative temperature too hot for activity, regardless of wind speed (Figure 3.12). In turn, reference stations were projected to induce body temperatures too cold for activity for longer periods each day. Burned stations were found to offer longer activity periods during June and July for all but the most stagnant wind conditions, under which lizard body temperatures quickly became too hot for activity as solar noon approached (Figure 3.13). In conjunction, canopy openness was found to have a curvilinear relationship with activity hours that became more pronounced at reduced wind speeds. Under an assumption of 0.1m/s wind velocity, over 76% of activity hours during June and July occurred at stations with 10-30% canopy openness (Figure 3.14). Rerunning the model using air and surface temperatures adjusted to simulate the month of May, resulted in more than 70% longer activity windows on burn sites (Figure 3.12).

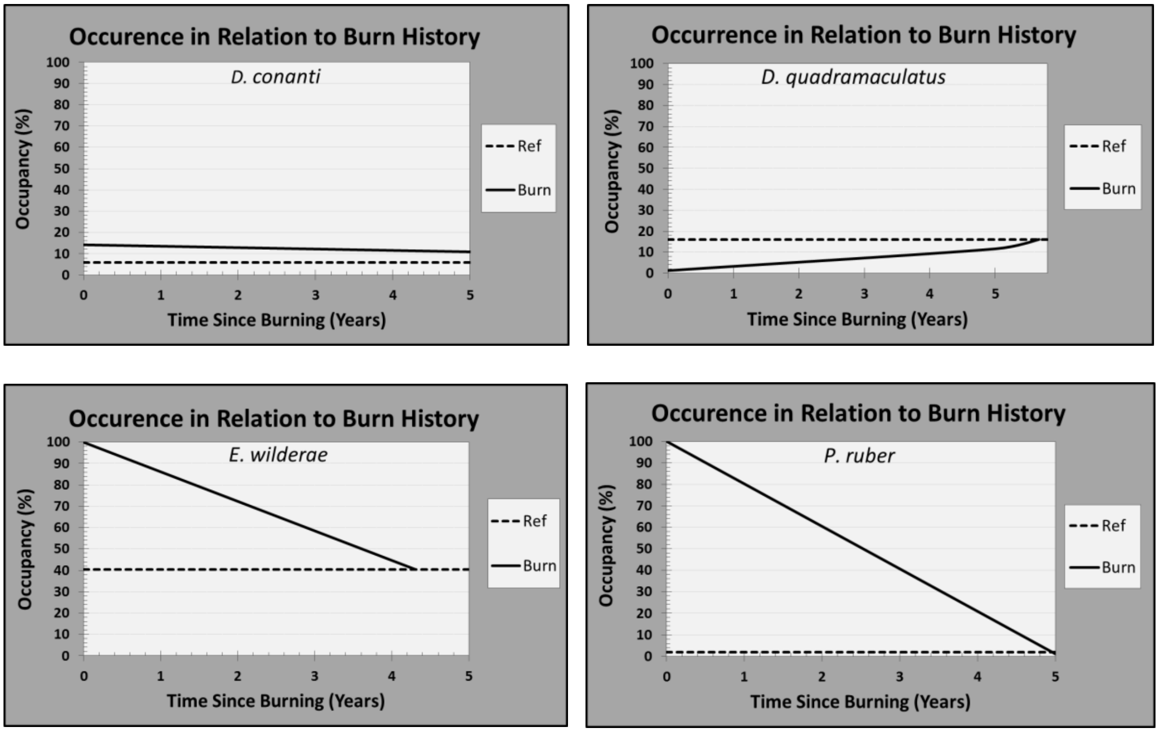


Figure 3.1: *Salamander occurrence in relation to burn history.* Estimated occupancy per trap is shown in relation to years since experiencing an episode of fire. Our models suggest *D. conanti* occurrence is unrelated to fire. Thus, the relationship between time since burning and *D. conanti* occurrence was not well determined. The very steep *P. ruber* trend is likely resulting from the influence of Site B3, where 81 *P. ruber* were observed in just 90 traps.

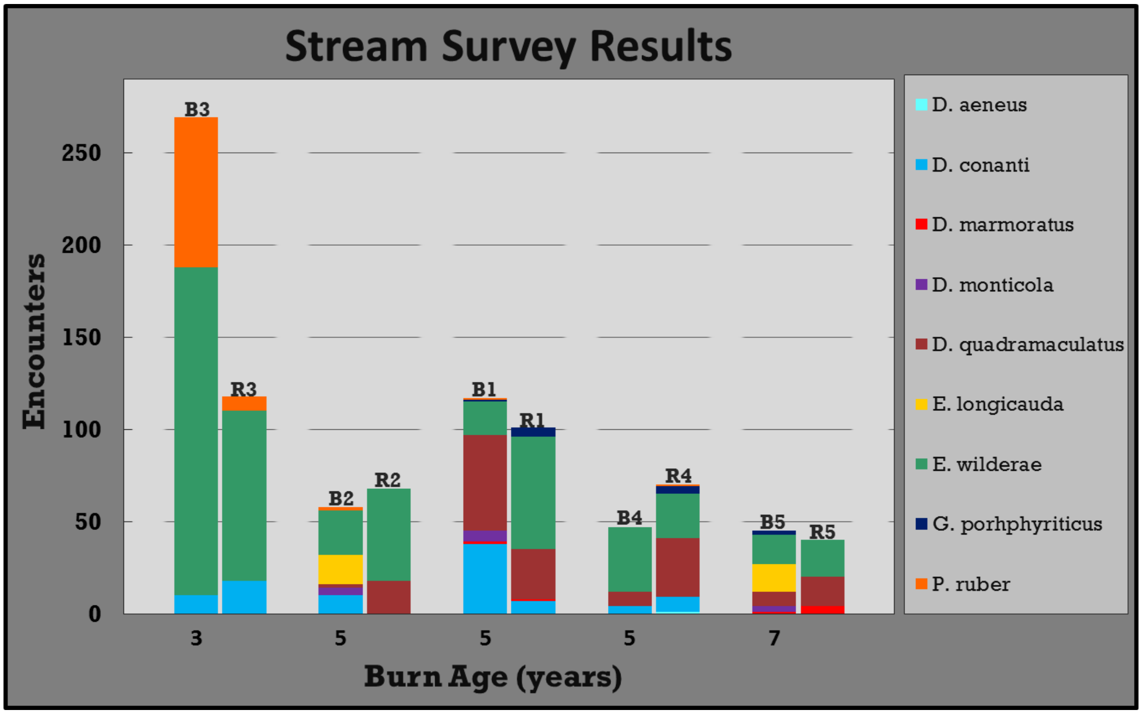
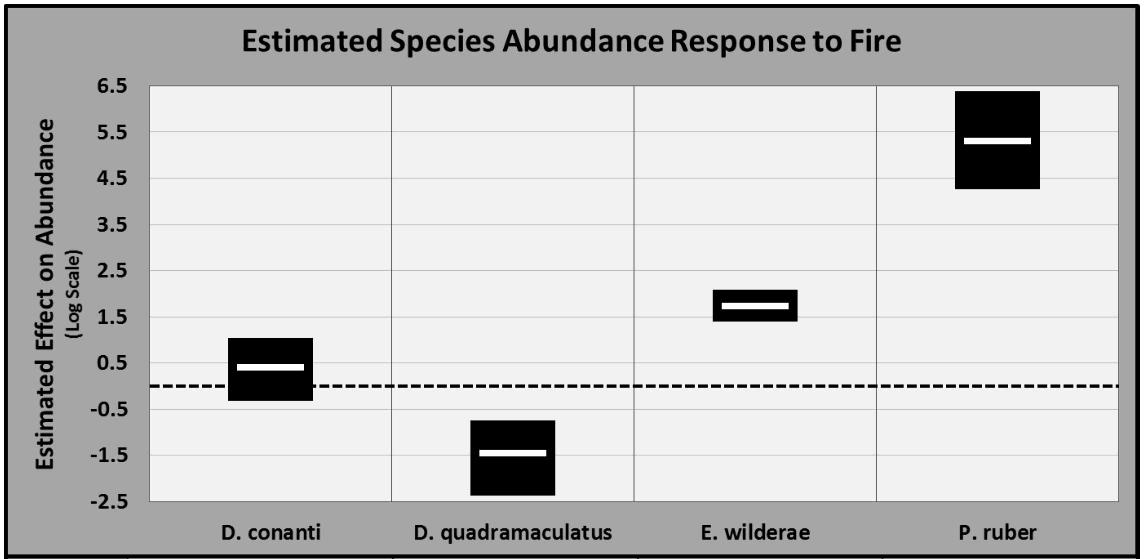
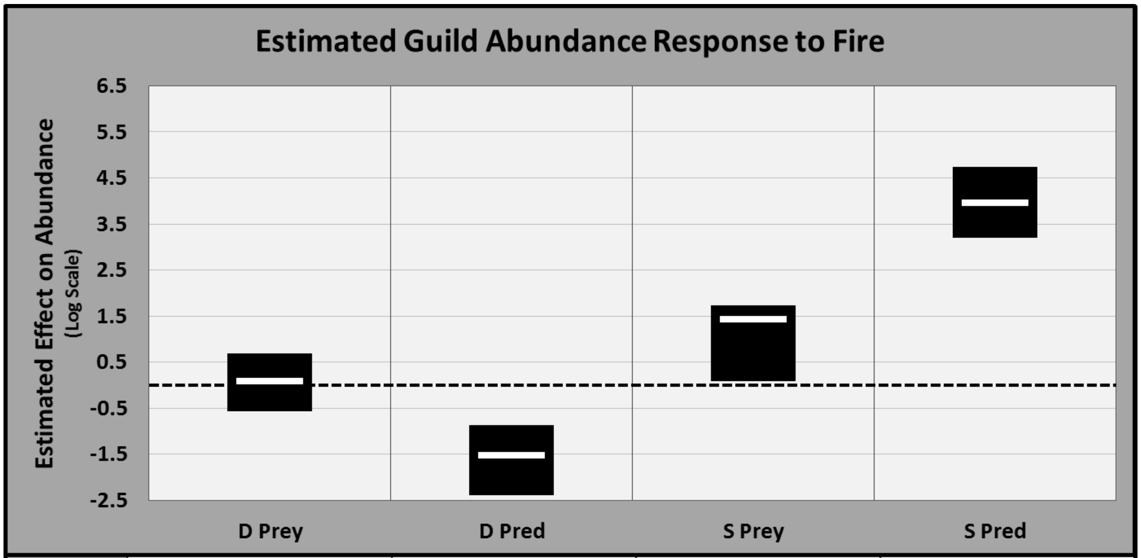


Figure 3.2: *Salamander survey results.* All species encountered during surveys are included. Burn/reference pairs are grouped and arranged along the x-axis by burn age. Site labels at the top of each bar correspond to maps presented in Figures 2.2 and 2.3.

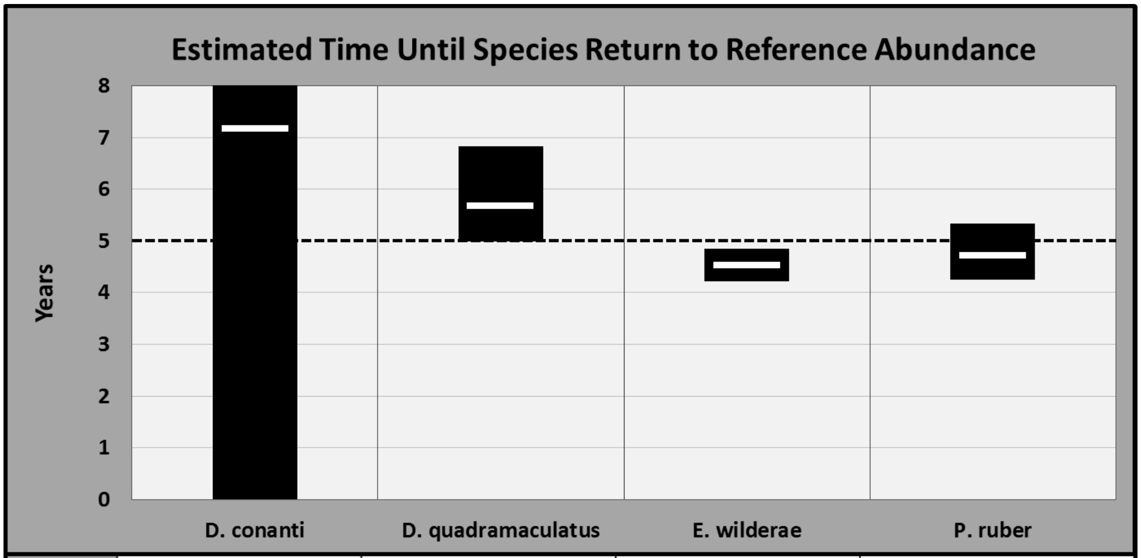


Mean	**+47.7%**	**-76.8%**	**+462.0%**	**+19734.3%**
95% CI	**-27%, +186%**	**-91%, -52%**	**+301%, +709%**	**+6981%, +58893%**

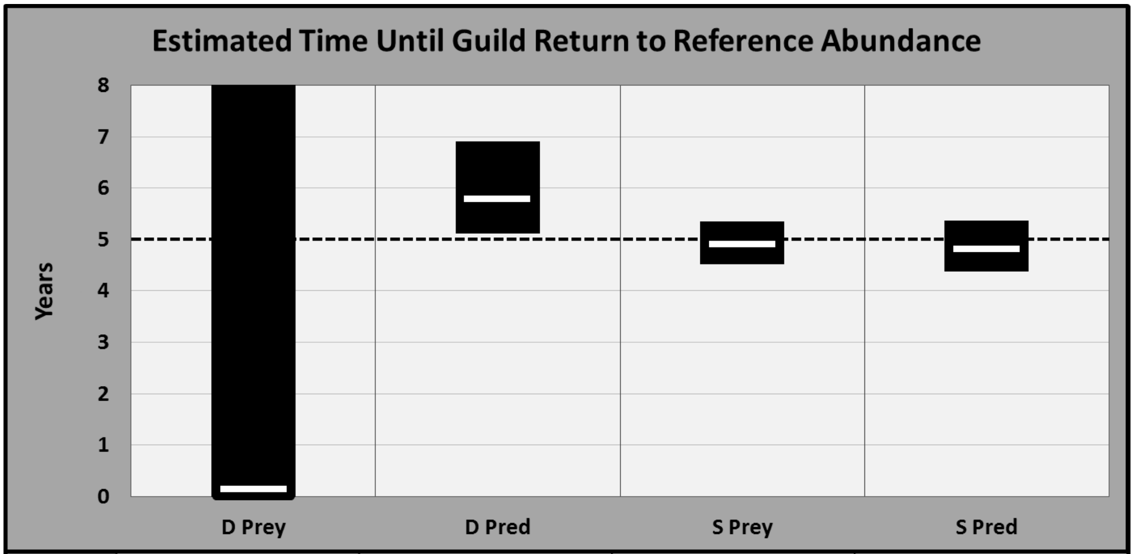


Mean	**+7.3%**	**-78.3%**	**+313.7%**	**+5093.5%**
95% CI	**-43%, +99%**	**-91%, -58%**	**+197%, +464%**	**+2329%, +11230%**

Figure 3.3: *Fire's effect on salamander abundance.* In the upper graph, white bars represent untransformed median values for the burn effect parameter and black boxes the extent of 95% credibility intervals. Values provided below are transformed rates of change; thus, +7% indicates abundance on burns is estimated to be 107% that of reference sites. 95% credibility intervals are also given as transformed rates of change. Intervals including zero indicate fire may have no effect on abundance of that taxon.



Mean	**7.17yrs**	**5.67yrs**	**4.52yrs**	**4.71yrs**
95% CI	**-62.34, 78.51**	**4.99, 6.83**	**4.22, 4.85**	**4.25,5.33**



Mean	**0.15yrs**	**5.79yrs**	**4.90yrs**	**4.81yrs**
95% CI	**-45.65, 44.50**	**5.11, 6.91**	**4.52, 5.34**	**4.87,5.87**

Figure 3.4: *Time until salamander return to reference abundance.* In the upper graph, white bars represent median values for the burn persistence parameter and black boxes the extent of 95% credibility intervals. Values provided below are in the same units, but reveal the extent of the credibility interval for *D. conanti*. Intervals including zero indicate fire may have no effect on abundance of that taxon.

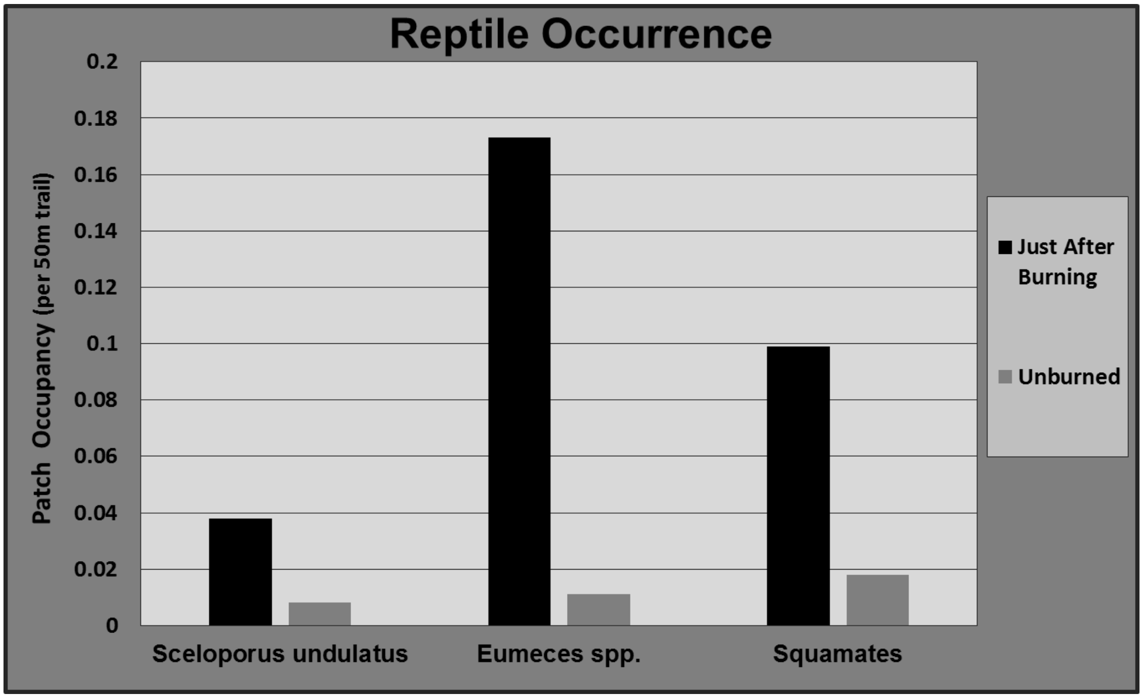


Figure 3.5: *Reptile occupancy following fire.* Estimated patch occupancy per 50m of GSMNP trail is shown. All reptiles are estimated to occur more frequently in burned areas. The relationship between occupancy and time since burning was not well determined for *S. undulatus* or squamates as a whole. See Figure 3.7 for the estimated relationship between *Eumeces Spp.* occupancy and burn age.

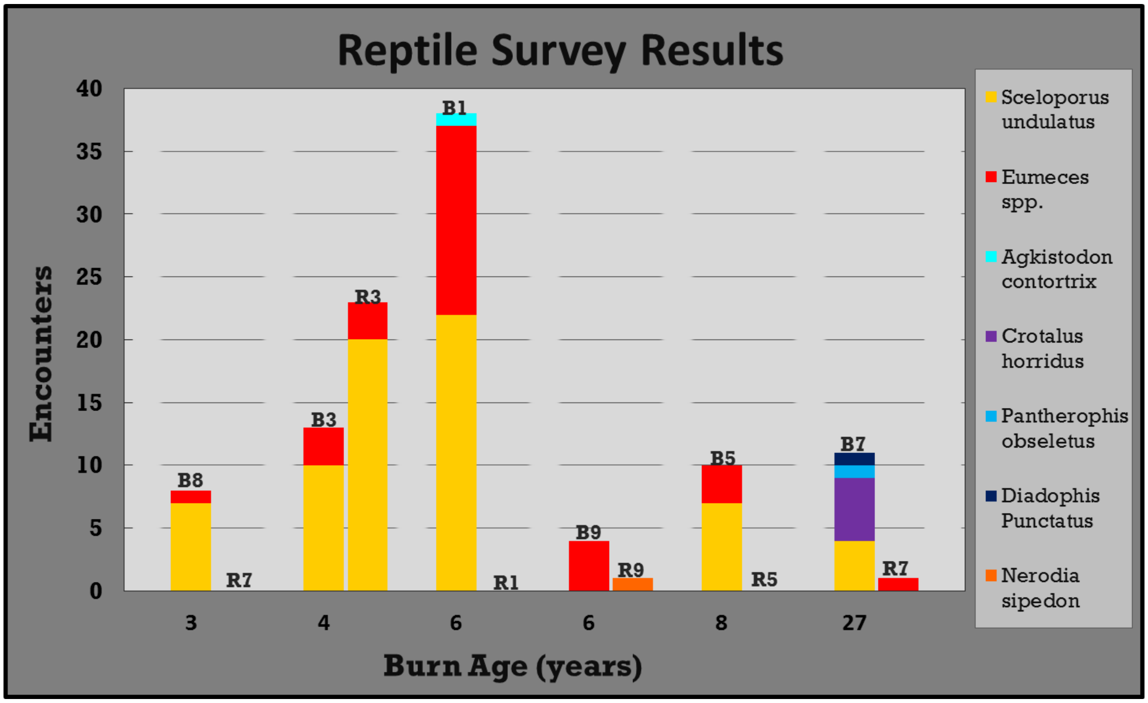


Figure 3.6: *Reptile survey results.* All species encountered during surveys are included. Burn/reference pairs are grouped and arranged along the x-axis by burn age. Site labels at the top of each bar correspond to maps presented in Figures 2.5 and 2.6.

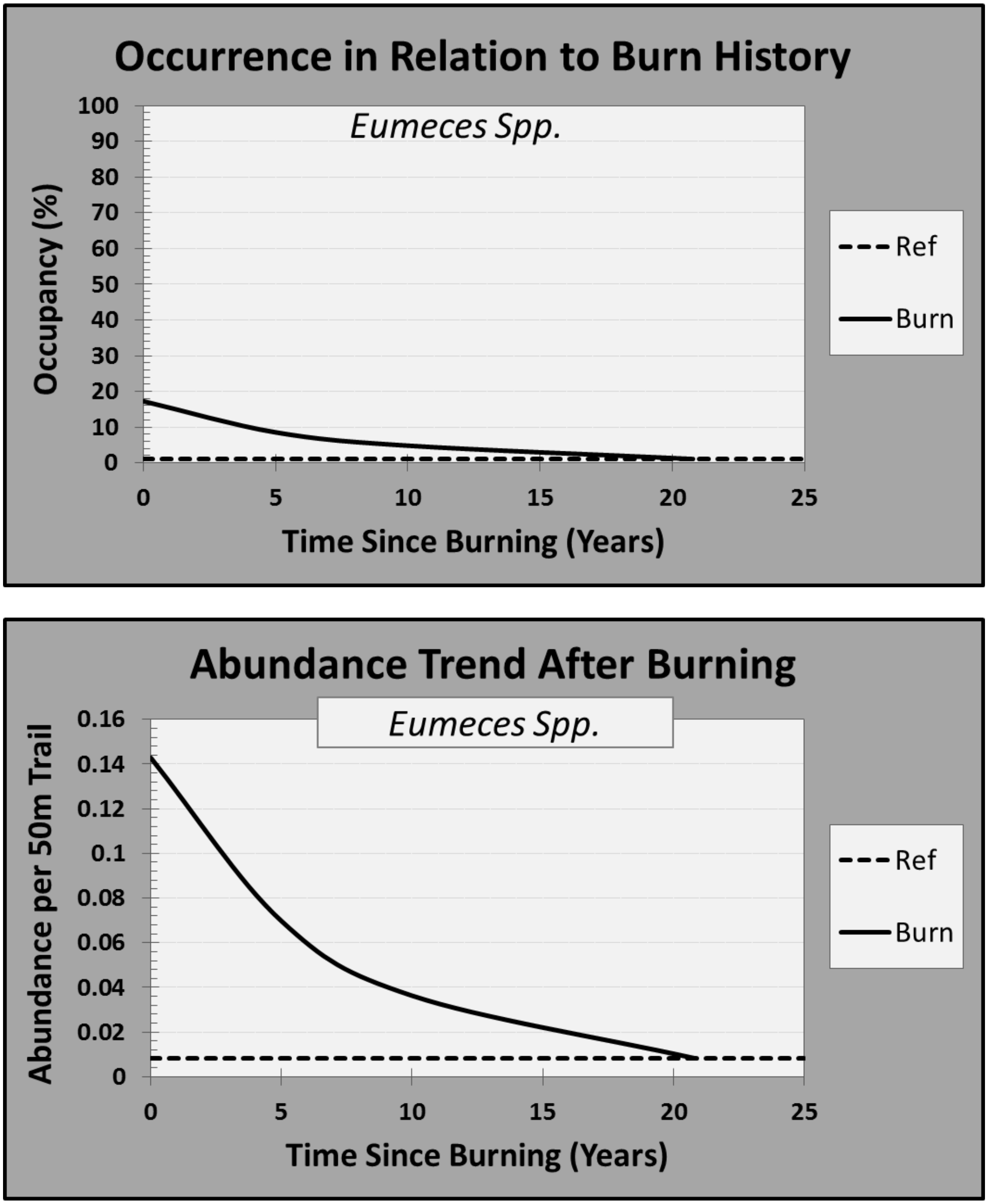
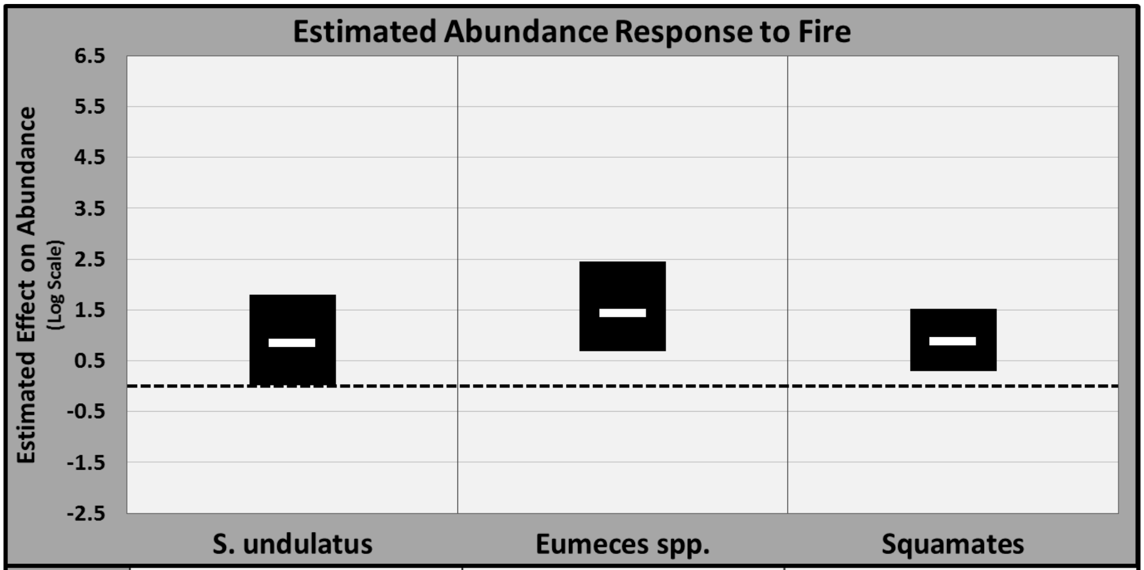


Figure 3.7: *Eumeces occurrence and abundance related to burn age.* It should be noted the slope value relating *Eumeces spp.* occurrence and abundance to burn age was not well determined by the model. Those parameter estimates were even less precise for *S. undulatus*, and as a result all squamates, thus graphs were not included for those taxons.



Mean	**+131.3%**	**+316.7%**	**+141.3%**
95% CI	+1%, +508%	+98%, +1,058%	+35%, +362%

Figure 3.8: *Fire's effect on reptile abundance.* In the upper graph, white bars represent untransformed median values for the burn effect parameter and black boxes the extent of 95% credibility intervals. Values provided below are transformed rates of change; thus, +131% indicates abundance on burns is estimated to be 231% that of reference sites. 95% credibility intervals are also given as transformed rates of change. Intervals including zero indicate fire may have no effect on abundance of that taxon.

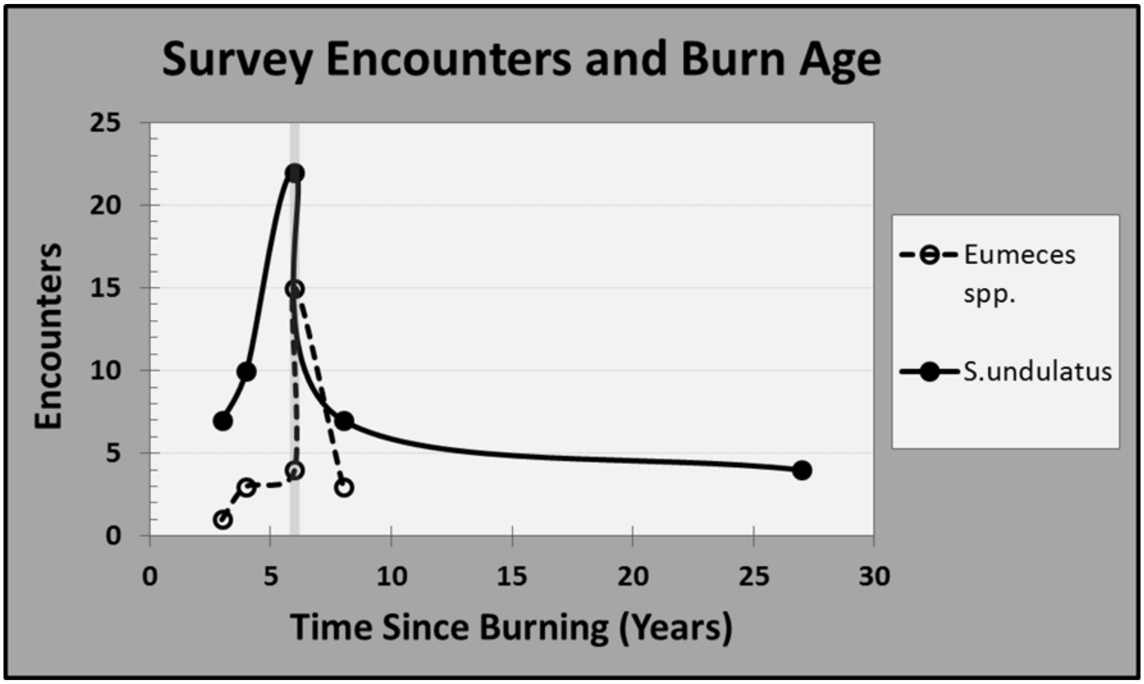
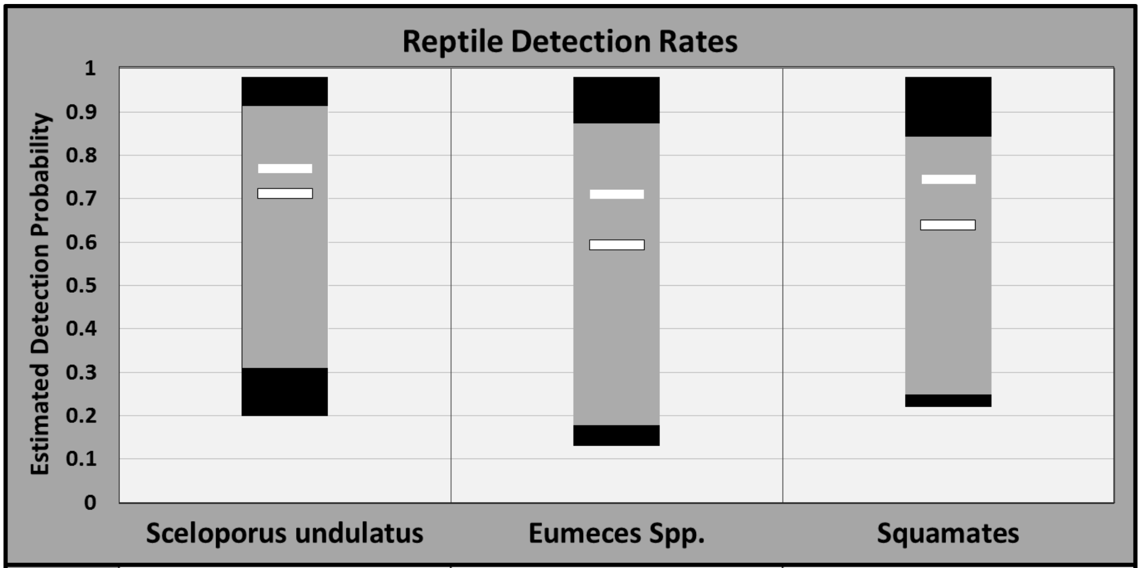


Figure 3.9: *Lizard survey encounters and burn age.* Although our model was unable to determine the relationship between burn age and lizard abundance, results of surveys suggest lizard abundance peaks at about six years (lightly pigmented vertical line) post fire.



Mean	**76.7%**	70.7%	**70.8%**	59.0%	**74.2%**	63.6%
95% CI	**20%,98%**	31%,91%	**13%,98%**	18%,87%	**22%,98%**	25%,84%

Figure 3.10: *Reptile detection rates.* In the upper graph, white bars represent median values for reptile detection rates; the marker with no outline represents median detection in sunny to partly sunny conditions, while the outlined marker represents median detection in overcast weather. Similarly, the black box indicates the 95% credibility interval for detection in sunny conditions and the grey box credibility intervals for overcast conditions. In the table below, values in bold (left) correspond to sunny conditions and values in regular width font (right) correspond with overcast conditions.

Table 3.1: *Daily diurnal operative temperature statistics.* Relevant statistics are given at the patch and site level. All values given are on the temporal scale of a single day. “Avg SD of Station Means” is the standard deviation of daily operative temperature means for all stations within a site; these values represents patch heterogeneity. “Avg Hourly SD” is the standard deviation of hourly operative temperatures at discrete stations within a site; it represents the hour-to-hour (within day) variability. “Avg SD of Daily Means” is the standard deviation of daily operative temperature means at a station and represents day-to-day (among day) variability with regard to operative temperatures.

Site-Level Daily Diurnal Operative Temperature Statistics

	Mean	Avg SD of Station Means	Avg Range	Mean Canopy Openness	Mean Activity Hours	Mean Hours Too Cold	Mean Hours Too Hot
Burn	30.61C	2.43C	30.85C	23.20%	2.92	7.33	2.75
Reference	29.25C	1.84C	25.55C	17.90%	3.26	8.29	1.45

Patch-Level Daily Diurnal Operative Temperature Statistics

	Avg Hourly SD	Avg SD of Daily Means	Average Range
Burn	6.26C	1.65C	20.72C
Reference	5.69C	1.51C	18.77C

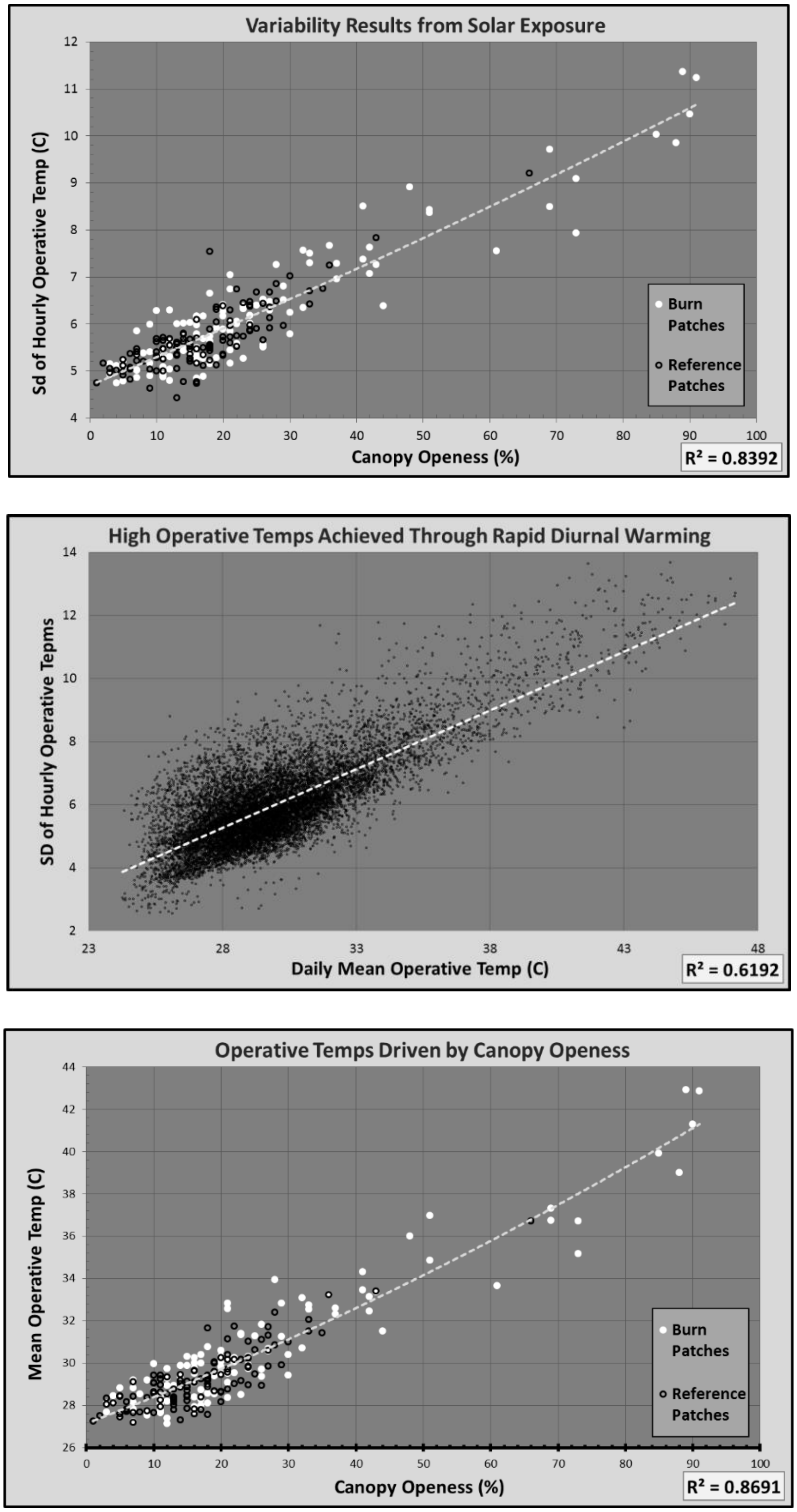


Figure 3.11: *Operative temp mean, variability, and canopy openness.* Study duration means are used for the top and bottom graphs, as canopy coverage was not recorded daily. The middle graph incorporates daily values for each station.

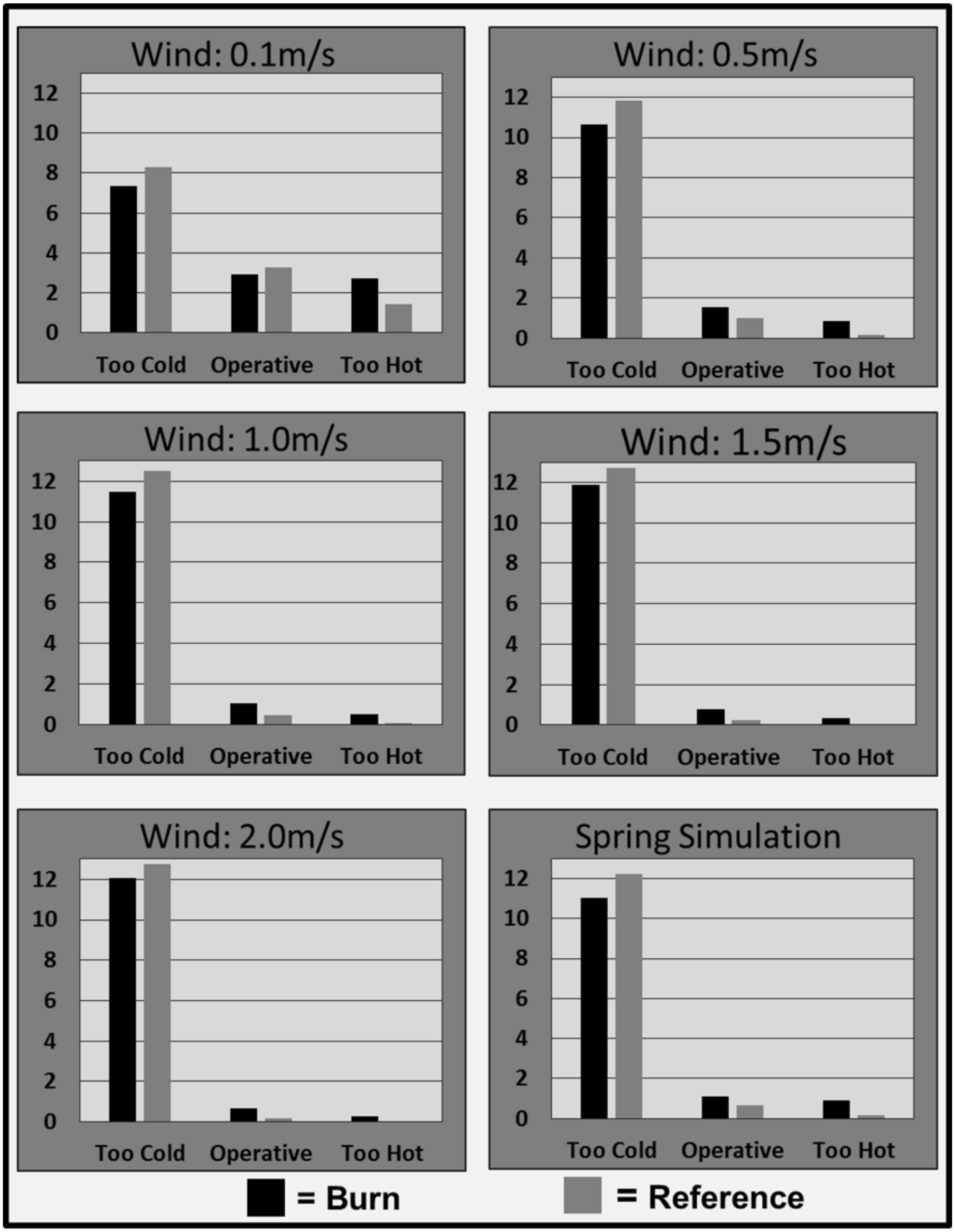


Figure 3.12: *Influence of wind and season on daily activity*. The distribution of daily activity on burn and reference sites is shown for various relevant wind velocities. To represent the month of May, distribution of daily activity is also given when 5°C is subtracted from each air and surface temperature measurement taken in the study.

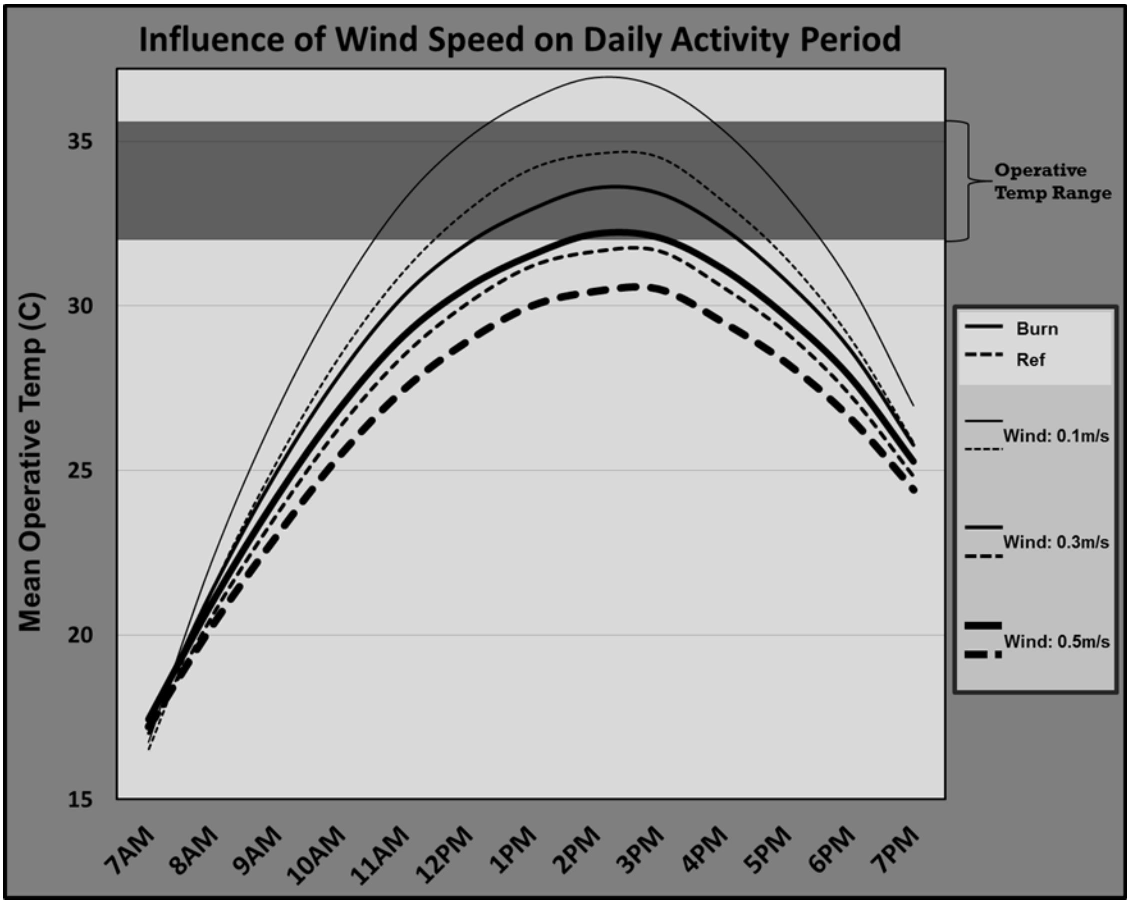


Figure 3.13: *Diurnal operative temp trajectories at different wind speeds*. Daily diurnal operative temperature trajectories are given for burn (solid line) and reference (dashed line) sites under various wind velocities. The thickness of trajectory lines increases with wind speed. *S. undulatus* operative range is represented by the dark grey band covering 32.0-35.6°C.

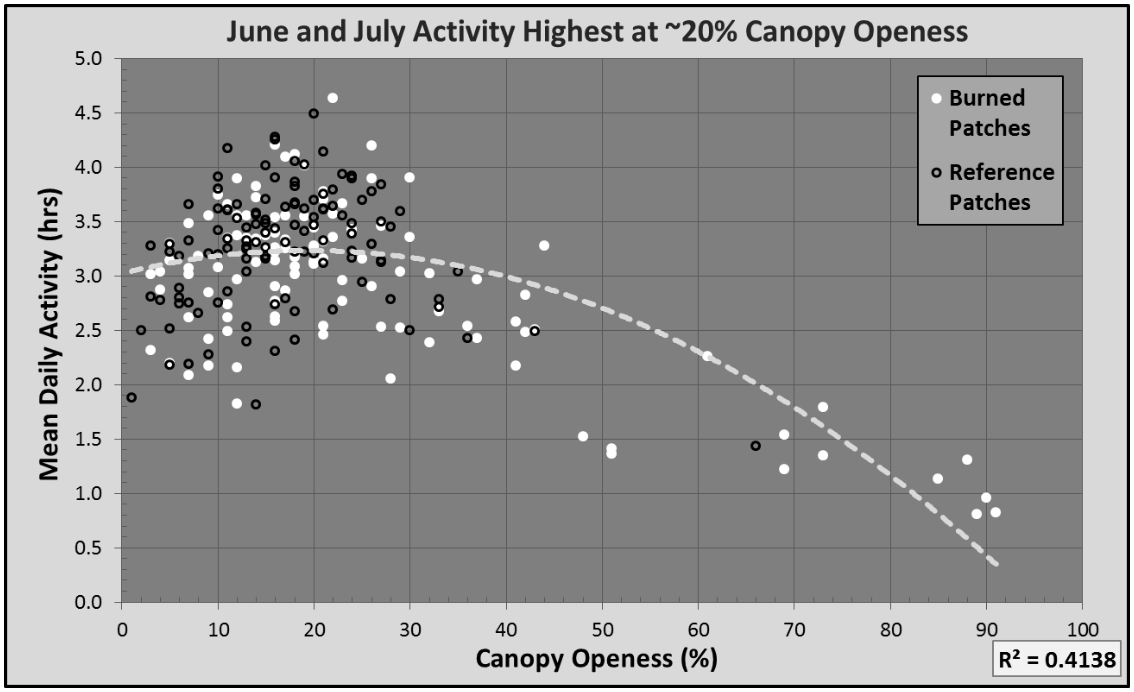


Figure 3.14: *Canopy's influence on activity hours.* Unlike many of the other canopy correlations examined, the relationship between canopy openness and activity period is curvilinear for the months of June and July.

CHAPTER 4

DISCUSSION

Stream Plethodontids

Like previous studies, our investigation suggests that fire's effects on salamanders are largely indirect, potentially small, and species specific. Nonetheless, our analysis provides evidence for declines in two species, *D. quadramaculatus* and *D. marmoratus*, known to be physiologically sensitive to warming in the region (Bernarod et al. 2006, 2007). The decline of these larger species may result in an ecological release among smaller salamander species that can tolerate warmer conditions on burned sites, notably *E. wilderae*. The opposing directional responses of these groups in our models provide evidence of such a release—which is consistent with current literature (Beachy 1994). Our models also indicate abundances of both groups return to pre-burn levels around the same time (5 years), providing further support for compensatory interspecific responses. Fire's estimated positive effect on *P. ruber* abundance might also result from a release attributable to declines in these large desmognathine species, as *P. ruber* competes with that group for stream resources at these intermediate elevations. However, it should be noted that our model estimates are heavily influenced by the youngest burn surveyed, Site B3. Neither *D. quadramaculatus* nor *D. marmoratus* were encountered at the reference stream (R3) for that burn, indicating the species may have been absent from the area before fire was applied to B3 in 2009. However, *D. quadramaculatus* was encountered in this stream during surveys conducted from 1998-2001 (Dodd 2004). Of further note, *E. wilderae* and *P. ruber* were most abundant on B3, with an astounding 87% of all *P. ruber* encounters occurring at that site. B3 is also the only site burned less than five years prior to being surveyed, thus temporal relationships between stream plethodontid abundance and fire rely heavily on fire acting as the mechanism extirpating *D. quadramaculatus* from that site. When site pair 3 is removed from analysis the effect of burning moves much closer to zero for all species.

Nevertheless, the climatic sensitivities of these large fully aquatic *Desmognathus* salamanders has been convincingly demonstrated, and investigations into the effects of global warming have predicted results similar to our own (Bernardo et al. 2007). Research by Issak et. al (2010) has shown montane stream temperatures within burn perimeters increase at two to three times the rate of surrounding forest, with approximately 50% of the increase attributable to gains in solar radiation. Such findings are consistent with the warming effects we found to occur in uplands following fire application, and would provide the mechanism promoting *D. quadramaculatus* and *D. marmoratus* declines. *D. conanti* presumably has the highest tolerance for warming of any desmognathine species within GSMNP; as it only inhabits lower elevations (Dodd 2004) and members of the complex (*D. fuscus*) from which it was recently separated can be found as far south as the Gulf of Mexico. The species moderate tolerance for climatic warming may contribute to the overall lack of response to fire by this species; any possible gains in abundance resulting from an ecological release could be tempered by the stress of a warmer environment. Much more tolerant of warmer conditions are the members of Spelerpinae—whom our models predict respond positively to an episode of fire. Hence there is a need to better determine the relationship between fire management practices and stream water temperatures within GSMNP.

However, if the management objective is to restore this ecosystem to its pre-fire suppression state, a reduction in the range of *D. quadramaculatus* and *D. marmoratus* within GSMNP may be consistent with that goal. Fires experienced by this system for more than 10,000 years were mostly initiated by anthropogenic sources (Harmon 1981) and would likely have affected stream plethodontid abundance similarly to modern fire management practices. As such, lineages of these climatically sensitive species may have been historically restricted to the wetter, eastern side of the Park. Thus, by including historical anthropogenic disturbance in its definition of the natural state of the system, it is unclear whether a reduction in species richness would be in accordance with or opposition to GSMNP's management goals.

Reptile Abundance and Fire's Effect on Lizard Activity

Surveys and subsequent analysis suggest a clear link between fire restoration and forest floor lizard abundance within GSMNP. Further, our model may be underestimating the magnitude of this effect, as 23 of 24 total lizard encounters on reference sites occurred at Site R3—which has a habitat structure analogous to burned sites, possibly due to previous wind damage. Anecdotally, it is also worth mentioning that eight of nine snake encounters, with the exception being one *Nerodia sipedon*, were on burned sites. Conditions on burned sites were warmer than reference sites as a result of more open canopy and increased direct solar radiation. This resulted in burn sites offering longer daily activity periods for all but the most stagnant wind conditions (any wind speed ≥0.2m/s favored burned sites). At very low wind velocities, lizard body temperatures become too hot for activity during peak solar hours for the months of June and July. However, although these lizards inhabit the forest floor, they are semi-arboreal when active—frequently climbing on the lower portions of woody vegetation. As such, they can select sites with wind velocities allowing them to be active for some or all of the diurnal period deemed too hot by models assuming a low constant wind speed. Conversely, behavioral selection of wind speed cannot increase activity periods on reference patches. Therefore, it is more likely that burn sites afford longer periods of activity during June and July, under all wind velocities. Further, during cooler months, the shift to warmer operating temperatures likely results in increased daily activity and prolonged activity season. *S. undulatus* is regularly observed basking on even cool spring and fall days, and mating takes place in late spring (Jensen 2008). Lending further support to this premise, our May simulation estimated activity periods to be significantly greater on burn sites. Thus our results suggest duration of daily activity is a viable mechanism for establishing the link between fire’s influence on habitat and reptile distribution within GSMNP. Such a link could be further confirmed by expanding the duration for which these measurements are collected and taking a more annual approach to assessing potential activity on burned and unburned sites.

Future Monitoring Recommendations

As the youngest burn during field work was three years old, continued monitoring of these transects as they progress through the burn cycle—including pre- and post-burn surveys—should better resolve robustness of inferences drawn from this investigation. The sites and methods we have selected, as well as the inferences provided on detection probability, ensure that endeavor is approachable by the Citizen Science program at GSMNP. To directly examine the link between fire and abundance of reptile species not easily observed via the methods employed in this study, drift fence arrays—which were beyond the scope of our two field seasons—would need to be established. However, our biophysical model was specifically designed to allow the morphological dimensions and solar absorptivity of other species to be input as a turn-key approach for crudely assessing the influence of fire management practices on their potential daily activity. Thus, we have provided GSMNP with the tools to inform fire management decisions and continue this investigation without requiring acquisition of additional resources.

REFERENCES

Angilletta Jr, Michael J. "Thermal and physiological constraints on energy assimilation in a widespread lizard (Sceloporus undulatus)." Ecology 82.11 (2001): 3044-3056.

Angilletta Jr, Michael J., Tracy Hill, and Michael A. Robson. "Is physiological performance optimized by thermoregulatory behavior?: a case study of the eastern fence lizard,< i> Sceloporus undulatus</i>." Journal of Thermal Biology 27.3 (2002): 199-204.

Beachy, C. K. 1994. Community ecology in streams: effects of two species of predatory salamanders on a prey species of salamander Herpetologica 50:129-136.

Bernardo, J. and J. Spotila (2006). "Physiological constraints on organismal response to global warming: mechanistic insights from clinally varying populations and implications for assessing endangerment." Biology Letters 2: 135-139.

Bernardo, J., R. J. Ossola, J. Spotila and K. A. Crandall (2007). "Interspecies physiological variation as a tool for cross-species assessments of global warming-induced endangerment: validation of an intrinsic determinant of macroecological and phylogeographic structure." Biology Letters 3: 695-698.

Buckley, Lauren B. "Linking traits to energetics and population dynamics to predict lizard ranges in changing environments." The American Naturalist 171.1 (2008): E1-E19.

Buckley, Lauren B., et al. "Can mechanism inform species’ distribution models?." Ecology letters 13.8 (2010): 1041-1054.

Cecala, Kristen K., and John C. Maerz. "COS 48-9: Consequences of ex-urban development: Evaluating the landscape, local, and sociological effects on salamander occupancy." The 95th ESA Annual Meeting. 2010.

Campbell, Gaylon S., and John M. Norman. An introduction to environmental biophysics. Springer, 1998.

Davic, Robert D., and Hartwell H. Welsh Jr. "On the ecological roles of salamanders." Annual Review of Ecology, Evolution, and Systematics (2004): 405-434.

Delcourt, P.A., Delcourt, H.R., Cridlebaugh, P.A., Chapman, J., 1998. Prehistoric human use of fire, the eastern agricultural complex, and Appalachian oakchestnut forests: paleoecology of Cliff Palace Pond, Kentucky. Am. Antiq. 63, 263–278.

Dodd, C. Kenneth. The amphibians of Great Smoky Mountains National Park. Univ. of Tennessee Press, 2004.

Dodd, C. Kenneth, and Robert M. Dorazio. "Using counts to simultaneously estimate abundance and detection probabilities in a salamander community." Herpetologica 60.4 (2004): 468-478.

Feder, M. E. (1983). "Integrating the ecology and physiology of plethodontid salamanders." Herpetologica 39(3): 291-310.

Graf, Mike. Great Smoky Mountains National Park. Capstone, 2002.

Greenberg, Cathryn H. "Fire, habitat structure and herpetofauna in the southeast." Proceedings of the Symposium ‘‘The Role of Fire for Nongame Wildlife Management and Community Restoration: Traditional Uses and New Directions.’’7th Annual Conference of the Wildlife Society. Vol. 15. 2000.

Greenberg, C.H., 2001. Response of reptile and amphibian communities to canopy gaps created by wind disturbance in the southern Appalachians. Forest Ecology and Management 148, 135–144.

Greenberg, Cathryn H., and Thomas A. Waldrop. "Short-term response of reptiles and amphibians to prescribed fire and mechanical fuel reduction in a southern Appalachian upland hardwood forest." Forest ecology and management 255.7 (2008): 2883-2893.

Harmon, M. E., 1981. Fire history of Great Smoky Mountains National Park. 1940–1979. Uplands Field Research Lab. Research/Resource Manag. Rep. No. 46

Harpole, D. N., and C. A. Haas. 1999. Effects of seven silvicultural treatments on terrestrial salamanders. Forest Ecology and Management 114:349–356.

Harrod, J., P S. White, and M. E. Harmon. 1998. Changes in xeric forests in western Great Smoky Mountains National Park, 1936-1995. Castanea 63: 346-360.

Heatwole, H. 1962. Environmental factors influencing local distribution and activity of the salamander, Plethodon cinereus. Ecology 43:460-472

Holt, Robert D., and Timothy H. Keitt. "Species’ borders: a unifying theme in ecology." Oikos 108.1 (2005): 3-6.

Ice, George G., Daniel G. Neary, and Paul W. Adams. "Effects of wildfire on soils and watershed processes." Journal of Forestry 102.6 (2004): 16-20.

Jensen, John B., ed. Amphibians and reptiles of Georgia. University of Georgia Press, 2008.

Johnson, Donald R. "Diet and estimated energy assimilation of three Colorado lizards." American Midland Naturalist (1966): 504-509.

Kearney, Michael, and Warren P. Porter. "Mapping the fundamental niche: physiology, climate, and the distribution of a nocturnal lizard." Ecology 85.11 (2004): 3119-3131.

Kearney, M. & Porter, W.P. (2009). Mechanistic niche modelling: combining physiological and spatial data to predict species ranges. Ecol. Lett., 12, 334–350.

Kéry, Marc, J. Andrew Royle, and Hans Schmid. "Modeling avian abundance from replicated counts using binomial mixture models." Ecological applications 15.4 (2005): 1450-1461.

Keyser, PD, DJ Sausville, WM Ford, DJ Schwab, and PH Brose. 2004. Prescribed fire impacts to amphibians and reptiles in shelterwood-harvested oak-dominated forests. Virginia Journal of Science 55: 159–168.

Kiester, A. R. 1971. Species density of North American amphibians and reptiles. Systematic Zoology 20:127–137.

Knoepp, Jennifer D., and Wayne T. Swank. "Site preparation burning to improve southern Appalachian pine-hardwood stands: nitrogen responses in soil, soil water, and streams." Canadian Journal of Forest Research 23.10 (1993): 2263-2270.

Kozak, K. H. and J. A. Wiens (2010). "Niche conservatism drives elevational diversity patterns in Appalachian salamanders." The Amercian Naturalist 176(1): 40-54.

Milanovich, Joseph Ross. "Modeling the current and future roles of stream salamanders in headwater streams." (2010).

Moseley, KR, SB Castleberry, and SH Schweitzer. 2003. Effects of prescribed fire on herptofauna in bottomland hardwood forests. Southeastern Naturalist 2: 475–486.

Niewiarowski, Peter H., Michael J. Angilletta, and Adam D. Leaché. "Phylogenetic comparative analysis of life-history variation among populations of the lizard Sceloporus undulatus: an example and prognosis." Evolution 58.3 (2004): 619-633.

Perry, Roger W., D. Craig Rudolph, and Ronald E. Thill. "Reptile and Amphibian Responses to Restoration of Fire-Maintained Pine Woodlands." Restoration ecology 17.6 (2009): 917-927.

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

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

Petranka, J. M. 1998. Salamanders of the United States and Canada. Smithsonian Institution Press, Washington, D.C.

Porter, W. P., S. Budaraju, W. E. Stewart, and N. Ramankutty. 2000. Physiology on a landscape scale: applications in ecological theory and conservation practice. American Zoologist 40:1175–1176.

Pough, F. H., E. M. Smith, D. H. Rhodes, and A. Collazo. 1987. The abundance of salamanders in forest stands with different histories of disturbance. Forest Ecology and Management 20:1–9.

Renken, RB 2005. Does fire affect amphibians and reptiles in eastern U.S. oak forests? Fire in Eastern Oak Forests: Delivering Science to Land Managers, Proceedings of a Conference, General Technical Report NRS-P-1: 158–166.

Royle, J. Andrew. "N-Mixture Models for Estimating Population Size from Spatially Replicated Counts." Biometrics 60.1 (2004): 108-115.

Roznik, Elizabeth A., and Ross A. Alford. "Does waterproofing Thermochron iButton dataloggers influence temperature readings?." Journal of Thermal Biology 37.4 (2012): 260-264.

Sih, Andrew, et al. "Predation, competition, and prey communities: a review of field experiments." Annual Review of Ecology and Systematics (1985): 269-311.

Stein, Bruce A., Cameron Scott, and Nancy Benton. "Federal lands and endangered species: the role of military and other federal lands in sustaining biodiversity." BioScience 58.4 (2008): 339-347.

Test, E H. 1946. Relations of the red-backed salamander (Plethodon cinereus) to light and contact. Ecology 27:246-254

Van Lear, D. H., and T. A. Waldrop. 1989. History, uses, and effects of fire in the Appalachians. U.S. Forest Service General Technical Report SE-54. Southeastern Forest Experiment Station, Asheville, North Carolina, USA.

Zou, C. B., G. A. Barron-Gafford, and D. D. Breshears (2007), Effects of topography and woody plant canopy cover on near-ground solar radiation: Relevant energy inputs for ecohydrology and hydropedology, Geophys. Res. Lett., 34, L24S21, doi:10.1029/2007GL031484.

APPENDIX

Appendix 1: *Operative temp parameters not measured*. Values and sources of parameter values not measured in this study are given, as well as the equations used to estimate missing air and surface temperatures.

Operative Temperature Model Parameterization Values Not Directly Measured		
Description	**Source**	**Value**
Albedo of mixed forest	EPA's AERSURFACE User's Guide	0.14
Wind Velocity	Dr. Mike Sears, pers comm.	0.1m/s
20% and 80% quartiles of field body temperature	Angiletta et. al 2002	32.0-35.6C
Solar absorptivity	Gates 1980	0.9
Thermal absorptivity	Bartlett and Gates 1967	0.965
Diffuse radiation view factor	Bartlett and Gates 1967	0.8
S. undulatus SVL	Niewiarowski 1993	72mm
Lizard Mass	Buckley 2008	$3.715*10^{-6}(SVL)^{3.49}$

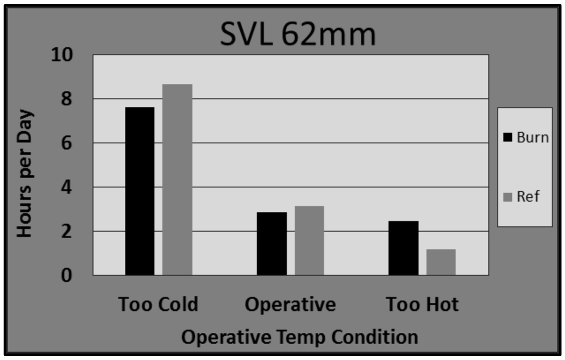
Equations Used to Estimate Missing Surface or Air Temp Measurements

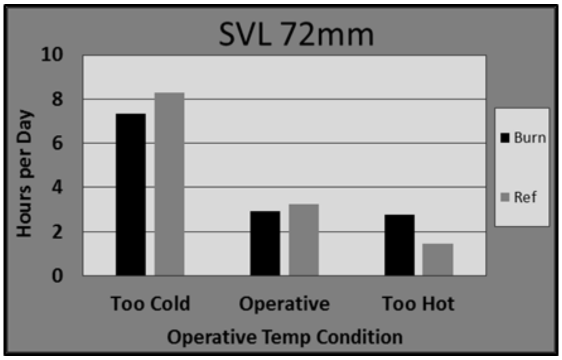
No Veg Cover, Ts → Ta: $T_a=19.669\ln(T_s)-38.045$

No Veg Cover, Ta → Ts: $T_s=9.2475e^{0.0377(T_a)}$

Veg Cover, Ts → Ta: $T_a=23.008\ln(T_s)-47.91$

Veg Cover, Ta → Ts: $T_s=9.6148e^{0.0353(T_a)}$





Appendix 2: *Salamander Abundance and Detection Model.*

```
model
    {

    ## Likelihood for observed counts

    for (i in 1:nobs)
        {

            ## Select species x stage of interest
            taxon[i] <-wilderae[i]

            ## Model for detection probability
            logitp[i] <- p.mu
#                                   + p.RE.pair[Pair[Site.T[i]]]
#                                   + p.RE.site[Site.T[i]]
                                + p.weather[Wcode[Sample.T[i]]]
#                               + p.RE.sample[Sample.T[i]]
#                                   + p.RE.trap[Trap[i]]

            ## Transform model result to a mean probability (p)
            p[i] <- 1 / (1 + exp(-logitp[i]))

            ## Model for abundance
            m0[i] <-        m.mu
#                                   + m.RE.pair[Pair[Site.T[i]]]
                                    + m.snail[Snail[Site.T[i]]+1]
                                    + m.elev*Elev[Site.T[i]]
                                    + m.burn[Burn[Site.T[i]]+1]
                        + m.ysburn[Burn[Site.T[i]]+1]*YSBurn[Site.T[i]]
#                                   + m.RE.site[Site.T[i]]
#                               + m.RE.sample[Sample.T[i]]
                                        + m.RE.trap[Trap[i]]

                ## Transform model result to a mean abundance (m)
                m[i] <- exp(m0[i])

            ## Abundance (N) at the trap is Poisson with mean m
            N[i] ~ dpois(m[i])

    ## Count at the trap per day is binomial with daily detection probability p
```

```
                        taxon[i] ~ dbin(p[i],N[i])

                }

        ## Priors

## Normal prior for logit(p) uses tau=0.37, yielding a flat prior on the (0,1) prob interval

        p.mu ~ dnorm(0.0, 0.37)
        m.mu ~ dnorm(0.0, 0.001)

        ## Random effects for site pairs
        for (i in 1:npairs)
                {
#                       p.RE.pair[i] ~ dnorm(0.0, p.RE.pair.tau)
#                       m.RE.pair[i] ~ dnorm(0.0, m.RE.pair.tau)
#                       m.RE.pair[i] ~ dnorm(m.mu, m.RE.pair.tau)
                }

#       p.RE.pair.tau <- 1/pow(p.RE.pair.sd,2)
#       p.RE.pair.sd ~ dunif(0, 100)
#       m.RE.pair.tau <- 1/pow(m.RE.pair.sd,2)
#       m.RE.pair.sd ~ dunif(0, 100)

        ## Random effects for sites
        for (i in 1:nsites)
                {
#                       p.RE.site[i] ~ dnorm(0.0, p.RE.site.tau)
#                       m.RE.site[i] ~ dnorm(0.0, m.RE.site.tau)
                }

#       p.RE.site.tau <- 1/pow(p.RE.site.sd,2)
#       p.RE.site.sd ~ dunif(0, 100)
#       m.RE.site.tau <- 1/pow(m.RE.site.sd,2)
#       m.RE.site.sd ~ dunif(0, 100)

        ## Random effects for samples
        for (i in 1:nsamples)
                {
#                       p.RE.sample[i] ~ dnorm(0.0, p.RE.sample.tau)
#                       m.RE.sample[i] ~ dnorm(0.0, m.RE.sample.tau)
                }

#       p.RE.sample.tau <- 1/pow(p.RE.sample.sd,2)
#       p.RE.sample.sd ~ dunif(0, 100)
```

```
#       m.RE.sample.tau <- 1/pow(m.RE.sample.sd,2)
#       m.RE.sample.sd ~ dunif(0, 100)

        ## Random effects for traps
        for (i in 1:ntraps)
                {
#                       p.RE.trap[i] ~ dnorm(0.0, p.RE.trap.tau)
                        m.RE.trap[i] ~ dnorm(0.0, m.RE.trap.tau)
#                       m.RE.trap[i] ~ dnorm(0.0, 0.37)
                }

#       p.RE.trap.tau <- 1/pow(p.RE.trap.sd,2)
#       p.RE.trap.sd ~ dunif(0, 100)
        m.RE.trap.tau <- 1/pow(m.RE.trap.sd,2)
        m.RE.trap.sd ~ dunif(0, 100)
#       m.RE.trap.sd ~ dunif(0, 10)

        ## Effect for weather on detection probability
        p.weather[1] ~ dnorm(0.0, 0.001)
        p.weather[2] ~ dnorm(0.0, 0.001)
p.weather[3] <- -(p.weather[1]+p.weather[2])     # Zero-sum constraint coding

        ## Effect for elevation
        m.elev ~ dnorm(0.0, 0.001)

        ## Effect of snail absent/present/abundant
        m.snail[1] ~ dnorm(0.0, 0.001)
        m.snail[2] <- -m.snail[1]               # Zero-sum constraint coding

        ## Effect for reference (no burn)
        m.burn[1] ~ dnorm(0.0, 0.001)
        m.burn[2] <- -m.burn[1]                         # Zero-sum constraint coding

        ## Covariate effect for years since burning (applies only to burn areas)
        m.ysburn[1] <- 0
        m.ysburn[2] ~ dnorm(0.0, 0.001)

        m.burnequiv <- (m.burn[1]-m.burn[2])/m.ysburn[2]

        p0 <- 1 / (1 + exp(-p.mu))
        a0 <- exp(m.mu)
        ## Mean occupancy (from poisson model assumption)
        occ ~ dpois(a0)
        psi0 <- step(occ-1)

        ## Estimation of mean abundance for reference and 3 levels of burn
```

```
a_ref <- exp(m.mu + m.burn[1])
a_burn00 <- exp(m.mu + m.burn[2])
a_burn05 <- exp(m.mu + m.burn[2] + m.ysburn[2]*5)
a_burn10 <- exp(m.mu + m.burn[2] + m.ysburn[2]*10)

## Estimation of mean occupancy rate for reference and 3 levels of burn
occ_ref ~ dpois(a_ref)
psi_ref <- step(occ_ref-1)
occ_burn00 ~ dpois(a_burn00)
psi_burn00 <- step(occ_burn00-1)
occ_burn05 ~ dpois(a_burn05)
psi_burn05 <- step(occ_burn05-1)
occ_burn10 ~ dpois(a_burn10)
psi_burn10 <- step(occ_burn10-1)

junk[1] <- Pair[1]
junk[2] <- Site[1]
junk[3] <- Burn[1]
junk[4] <- YSBurn[1]
junk[5] <- Snail[1]
junk[6] <- Fish[1]
junk[7] <- Elev[1]
junk[8] <- Site.S[1]
junk[9] <- Sample[1]
junk[10] <- CDay[1]
junk[11] <- Wcode[1]
junk[12] <- Site.T[1]
junk[13] <- Sample.T[1]
junk[14] <- Trap[1]
junk[15] <- DconL[1]
junk[16] <- DmarL[1]
junk[17] <- DmonL[1]
junk[18] <- DquaL[1]
junk[19] <- ElonL[1]
junk[20] <- EwilL[1]
junk[21] <- GporL[1]
junk[22] <- PrubL[1]
junk[23] <- PmonL[1]
junk[24] <- DaenA[1]
junk[25] <- DconA[1]
junk[26] <- DmarA[1]
junk[27] <- DmonA[1]
junk[28] <- DquaA[1]
junk[29] <- EwilA[1]
junk[30] <- GporA[1]
junk[31] <- PrubA[1]
```

```
junk[32] <- Quad[1]
junk[33] <- Desmogs[1]
junk[34] <- Spelerpinae[1]
junk[35] <- Larvae[1]
junk[36] <- Adults[1]
junk[37] <- nobs
junk[38] <- nsamples
junk[39] <- nsites
junk[40] <- npairs
junk[41] <- ntraps
junk[42] <- Pseudotriton[1]
junk[43] <- Caudates[1]
junk[44] <- conanti[1]
junk[45] <- Eurycea[1]
junk[46] <- ruberXgyro[1]
junk[47] <- quadXmarm[1]
junk[48] <- BigBoys[1]
junk[49] <- conantiXmonticola[1]
junk[50] <- wilderae[1]
}
```

Appendix 3: *Reptile Abundance and Detection Model.*

```
model
        {

        ## Likelihood for observed counts

        for (i in 1:nobs)
                {

                        ## Select species of interest
                        taxon[i] <- S_undulatus[i]

                        ## Treat Pass B Differently
                        PassB[i] <- step(Pass.seg[i]-2)

                  ## Account for Trail Traffic
                   TrlTraffic[i] <- step(Traffic[Site.seg[i]]-2)

                        ## Model for detection probability
                        logitp[i] <- p.mu
#                                       + p.RE.pair[Pair[Site.seg[i]]]
#                                       + p.RE.site[Site.seg[i]]
                                        + p.weather[Wcode[Sample.seg[i]]]
#                                       + p.RE.sample[Sample.seg[i]]
#                                       + p.RE.seg[SegmentIndex[i]]
                                        + p.PassBeffect * PassB[i]
#                                         +p.Traffic * TrlTraffic[i]

                                ## Transform model result to a mean probability (p)
                                p[i] <- 1 / (1 + exp(-logitp[i]))

                        ## Model for abundance
                        m0[i] <-        m.mu
#                                       + m.RE.pair[Pair[Site.seg[i]]]
                                        + m.elev*Elev[Site.seg[i]]
                                        + m.burn[Burn[Site.seg[i]]+1]
                                + m.ysburn[Burn[Site.seg[i]]+1]*YSBurn[Site.seg[i]]
#                                       + m.RE.site[Site.seg[i]]
                                          + m.RE.sample[Sample.seg[i]]
                                        + m.RE.seg[SegmentIndex[i]]
                                           + m.length * SegmentLength[i]
```

```
                                ## Transform model result to a mean abundance (m)
                                m[i] <- exp(m0[i])

                        ## Abundance (N) in each segment is Poisson with mean m
                        N[i] ~ dpois(m[i])

## Count at each segment per day is binomial with daily detection probability p
                        taxon[i] ~ dbin(p[i],N[i])

                }

        ## Priors

## Normal prior for logit(p) uses tau=0.37, yielding a flat prior on the (0,1) prob
interval

        p.mu ~ dnorm(0.0, 0.37)
        m.mu ~ dnorm(0.0, 0.001)

        ## Random effects for site pairs
#       for (i in 1:npairs)
#               {
#                       p.RE.pair[i] ~ dnorm(0.0, p.RE.pair.tau)
#                       m.RE.pair[i] ~ dnorm(0.0, m.RE.pair.tau)
#               }

#       p.RE.pair.tau <- 1/pow(p.RE.pair.sd,2)
#       p.RE.pair.sd ~ dunif(0, 100)
#       m.RE.pair.tau <- 1/pow(m.RE.pair.sd,2)
#       m.RE.pair.sd ~ dunif(0, 100)

        ## Random effects for sites
#       for (i in 1:nsites)
#               {
#                       p.RE.site[i] ~ dnorm(0.0, p.RE.site.tau)
#                       m.RE.site[i] ~ dnorm(0.0, m.RE.site.tau)
#               }

#       p.RE.site.tau <- 1/pow(p.RE.site.sd,2)
#       p.RE.site.sd ~ dunif(0, 100)
#       m.RE.site.tau <- 1/pow(m.RE.site.sd,2)
#       m.RE.site.sd ~ dunif(0, 100)

        ## Random effects for samples
#       for (i in 1:nsamples)
```

```
#               {
#                       p.RE.sample[i] ~ dnorm(0.0, p.RE.sample.tau)
#                       m.RE.sample[i] ~ dnorm(0.0, m.RE.sample.tau)
#               }

#       p.RE.sample.tau <- 1/pow(p.RE.sample.sd,2)
#       p.RE.sample.sd ~ dunif(0, 100)
#       m.RE.sample.tau <- 1/pow(m.RE.sample.sd,2)
#       m.RE.sample.sd ~ dunif(0, 100)

        ## Random effects for segments
        for (i in 1:nsegments)
                {
#                       p.RE.seg[i] ~ dnorm(0.0, p.RE.seg.tau)
                        m.RE.seg[i] ~ dnorm(0.0, m.RE.seg.tau)
#                       m.RE.seg[i] ~ dnorm(0.0, 0.37)
                }

#       p.RE.seg.tau <- 1/pow(p.RE.seg.sd,2)
#       p.RE.seg.sd ~ dunif(0, 100)
        m.RE.seg.tau <- 1/pow(m.RE.seg.sd,2)
        m.RE.seg.sd ~ dunif(0, 100)
#  m.RE.seg.sd ~ dunif(0, 10)

#        p.RE.pass.tau <- 1/pow(p.RE.pass.sd,2)
#        p.RE.pass.sd ~ dunif(0, 100)
          m.RE.pass.tau <- 1/pow(m.RE.pass.sd,2)
         m.RE.pass.sd ~ dunif(0, 100)

        ## Effect for weather on detection probability
        p.weather[1] ~ dnorm(0.0, 0.37)
        p.weather[2] <- -p.weather[1]                   # Zero-sum constraint coding

        ## Effect for elevation
        m.elev ~ dnorm(0.0, 0.001)

        ##Effect of Trail Traffic
        # p.Traffic ~ dnorm(0.0,0.37)

        ## Effect for Pass B
        # p.PassBeffect ~ dnorm(0.0, 0.37)

        ## Effect for segment length
        m.length ~ dnorm(0.0, 0.001)

        ## Effect for reference (no burn)
```

```
m.burn[1] ~ dnorm(0.0, 0.001)
m.burn[2] <- -m.burn[1]                    # Zero-sum constraint coding

## Covariate effect for years since burning (applies only to burn areas)
m.ysburn[1] <- 0
m.ysburn[2] ~ dnorm(0.0, 0.001)

m.burnequiv <- (m.burn[1]-m.burn[2])/m.ysburn[2]

p0 <- 1 / (1 + exp(-p.mu))
a0 <- exp(m.mu)
## Mean occupancy (from poisson model assumption)
occ ~ dpois(a0)
psi0 <- step(occ-1)

## Estimation of mean abundance for reference and 3 levels of burn
a_ref <- exp(m.mu + m.burn[1])
a_burn00 <- exp(m.mu + m.burn[2])
a_burn05 <- exp(m.mu + m.burn[2] + m.ysburn[2]*5)
a_burn10 <- exp(m.mu + m.burn[2] + m.ysburn[2]*10)

## Estimation of mean occupancy rate for reference and 3 levels of burn
occ_ref ~ dpois(a_ref)
psi_ref <- step(occ_ref-1)
occ_burn00 ~ dpois(a_burn00)
psi_burn00 <- step(occ_burn00-1)
occ_burn05 ~ dpois(a_burn05)
psi_burn05 <- step(occ_burn05-1)
occ_burn10 ~ dpois(a_burn10)
psi_burn10 <- step(occ_burn10-1)

junk[1] <- Pair[1]
junk[2] <- Site[1]
junk[3] <- Burn[1]
junk[4] <- YSBurn[1]
junk[5] <- Elev[1]
junk[6] <- Site.S[1]
junk[7] <- Sample[1]
junk[8] <- Wcode[1]
junk[9] <- Site.seg[1]
junk[10] <- Sample.seg[1]
junk[11] <- SegmentIndex[1]
junk[12] <- S_undulatus[1]
junk[13] <- E_spp[1]
junk[14] <- E_fasciatus[1]
junk[15] <- E_laticeps[1]
```

```
junk[17] <- A_contortrix[1]
junk[18] <- C_horridus[1]
junk[19] <- P_obsoletus[1]
junk[20] <- D_punctatus[1]
junk[21] <- N_sipedon[1]
junk[22] <- Lacertilia[1]
junk[23] <- Serpentes[1]
junk[24] <- Squamates[1]
junk[25] <- Scincidae[1]
junk[26] <- nobs
junk[27] <- nsamples
junk[28] <- nsites
junk[29] <- npairs
junk[30] <- nsegments
junk[31] <- PassB[1]
junk[16] <- TrlTraffic[1]

}
```