Articles

Lizard Activity and Abundance Greater in Burned Habitat of a Xeric Montane Forest

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Abstract

Restoring the natural or historical state of ecosystems is a common objective among resource managers, but determining whether desired system responses to management actions are occurring is often protracted and challenging. For wildlife, the integration of mechanistic habitat modeling with population monitoring may provide expedited measures of management effectiveness and improve understanding of how management actions succeed or fail to recover populations. Southern Appalachia is a region of high biodiversity that has undergone dramatic change as a result of human activities such as historic logging, exotic invasions, and alteration of disturbance regimes—including reduction in application of fire. Contemporary efforts to restore fire-maintained ecosystems within southern Appalachian forests require tools to assess the effects of fire management practices on individual animal fitness and relate them to corresponding influences on species abundance. Using automated sensing equipment, we investigated the effects of burned forests on reptile habitat suitability within the western portion of Great Smoky Mountains National Park, Tennessee. Specifically, we used microclimate measurements to model northern fence lizard *Sceloporus undulatus hyacinthinus* diurnal activity budgets in unburned and variable burn age (3–27-y) forest stands. We estimated northern fence lizard occurrence and abundance along transects through burned and unburned forests. Burned forest stands had microclimates that resulted in longer modeled daily activity periods under most conditions during summer. *S. undulatus* abundance was 4.75 times greater on burned stands compared to paired unburned stands, although the relationship between burn age and abundance was not well determined. Results suggest the more open habitat structure of burned areas within these xeric pine–oak forests may benefit *S. undulatus*.

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Introduction

Public lands, especially those managed by the Federal Government, play an important role in conservation and management of biodiversity in the United States. Some agencies, such as the National Park Service (NPS), procured lands specifically to meet biological objectives and uphold mandates that focus on the protection and conservation of natural resources. For many of these natural resource agencies, research into the mechanistic linkages between management strategies and resource response adds a valuable complement to their stewardship activities.

Although much of Great Smoky Mountains National Park (GSMNP; or park) in the southern Appalachian Mountains is appropriately described as temperate rain forest, the Tennessee portion of the park exhibits dry slopes and ridges historically maintained by fire applied by Indigenous Peoples (Delcourt and Delcourt 1998). Located in the southeastern United States—a region of substantial reptile diversity (Kiester 1971)—these relatively open xeric pine–oak forests in the western portion of GSMNP were capable of supporting reptiles that were much less common in the mixed-oak upland hardwood forests that cover much of the southern Appalachians. NPS and private landholder efforts to reduce application of fire and, to a lesser extent, quickly extinguish forest fires have since reduced the quality and extent of the drier pine–oak forests (Harrod et al. 1998).

Several studies have suggested periodic burning provides better thermoregulatory opportunities for reptiles by opening habitat structure and increasing ground temperatures (Moseley et al. 2003; Matthews et al. 2010). Greenberg (2001) similarly focused on increased solar exposure to the forest floor when investigating the effects of wind disturbance on reptile communities in southern Appalachia. Other studies in the southeastern United States have reported increased reptile captures in fire-restored woodlands compared to nearby unburned second-growth forest (Moseley et al. 2003; Perry et al. 2009). Yet, most research in southern Appalachia suggests the influence of prescribed fire 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 et al. 2010). Of the regional studies, the largest increases in reptile abundance were observed when prescribed burning was conducted in conjunction with other treatments, such as mechanical understory cuts, that provided fuels allowing for high-severity fires capable of reducing overstory cover (Greenberg and Waldrop 2008; Matthews et al. 2010). However, many of these studies took place in southern Appalachia's mixed-oak upland hardwood forests, and effects may differ within more open pine–oak forests.

A mechanistic modeling approach is appropriate to investigate thermoregulatory opportunities as a mechanism relating fire application and distribution of reptilian abundance. As opposed to correlative models, which rely on occurrence or abundance to develop associations between the current range of a species and environmental characteristics contained within, 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 directly, rather than implicitly through habitat associations (Kearney and Porter 2009). Biophysical (mechanistic) models of reptilian distribution often focus on thermal constraints, particularly the potential duration of activity (Angilletta 2001; Buckley 2008; Buckley et al. 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. To model the spatial extent of such thermal constraints, operative temperatures must be calculated for the population(s) of interest. A formal definition of operative temperature is given in Campbell and Norman (2012), but it can be regarded as the temperature to which an organism would equilibrate without heat capacitance. Informally, the relationship can be described quantitatively 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 for investigating microclimate as a driver of differences in relative abundance (Angilletta 2001; Buckley 2008; Buckley et al. 2010). Hence, although the approach relies on relationships that can be hard to parameterize, its independence from current distributions and emphasis on organismal fitness allow better formulation of inferences about how fire management practices have influenced lizard distribution.

In 1996, GSMNP implemented a fire management program intended to revitalize species or ecosystems that benefit from fire, as well as reduce fuel loads. Research needs identified by GSMNP in 2010 included "evaluation of the roles of fire and its use in restoration of species and habitats" and "evaluating the linkage between fire and reptile abundance and distribution." Our study was designed to satisfy those needs, resulting in two objectives. The first objective was to compare potential duration of lizard activity in burned and unburned plots to evaluate influence of previous fire management actions on the current distribution of northern fence lizard *Sceloporus undulatus hyacinthinus* and skinks *Plestiodon* spp. within GSMNP by measuring microclimatic variables throughout burned and paired matched-control plots and to subsequently make use of these data to calculate operative temperatures for these species across a gradient of fire management histories. The second objective was to establish a pilot reptile monitoring program for GSMNP's citizen science volunteers, with emphasis on these two focal lizard species

expected to be regularly encountered and exhibit population-level responses to fire management and to subsequently make use of survey data to estimate abundance on transects representing a gradient of burn histories.

Materials and Methods

Study area

Although GSMNP receives high levels of annual precipitation, indigenous use of fire dates back such that a fire-adapted pine–oak forest community had been established in the western region of the park for more than 10,000 y (Harmon 1981; Delcourt and Delcourt 1998). As such, some species of reptiles native to the area were adapted to this fire-maintained system and relied on regular episodes of fire to maintain robust populations (Greenberg 2002). From GSMNP's inception in 1934 until the lightning-ignited Polecat Ridge burn of 1976, a strict fire avoidance and suppression policy altered natural forest disturbance and successional patterns (Harmon 1981; Harrod et al. 1998). In 1996, the GSMNP began efforts to restore its fire-adapted forests by instituting a program of controlled burning and exotic vegetation removal.

The twelve 10.1-ha circular research plots selected for this study were generally confined to the Abrams Creek and Panther Creek drainages located in the western region of GSMNP (Figure 1). Our study focused on six units ranging from 91 to 960 ha last burned between 3 and 27 y before data collection (Table 1). We matched each burned unit with an unburned (no record of fire history since park inception) unit having similar attributes including elevation and aspect and belonging to the same pine–oak forest.

Microclimate measurements and mechanistic modeling

In summer 2013, we established an array of 20 stations—each with sensors measuring a suite of microclimate variables—within each of the research plots (Table S1, Workbook 1 and Workbook 2, *Supplemental Material*; Figure 2). We guided placement of each station through use of a principal component analysis sampling tool developed in ArcMap 10.1 (Esri, Redlands, CA) that placed a minimum distance of 50 m between each station and ensured measurements were dispersed across topographic gradients to representatively sample each plot's microclimate. Topographic features input into the principal components algorithm included elevation, slope, surface curvature, and solar radiation. Within each plot, we randomly assigned sensors at half of the stations to be placed within patches of understory or midstory vegetative cover and the remaining half at patches without understory or midstory cover. For stations randomly assigned to vegetative cover, we positioned sensors within either understory vegetation or midstory vegetation, depending simply on which structure was more prominent in the immediate vicinity

of the assigned location. In the event the designated vegetative cover condition could not be met in the proximity of the assigned location, we selected at random a station assigned to the opposite vegetative cover condition and switched the cover assignments. We used a spherical densiometer to measure canopy openness above each station at the time of deployment. We recorded air temperature and ground surface temperature hourly at each station ($n = 240$) throughout June and July 2013 via iButtons (Maxim Integrated, Inc., San Jose, CA) programmed to begin logging at midnight after deployment. We thinly coated sensors measuring ground surface temperatures with white rubber to reflect solar radiation and protect from moisture (Roznik and Alford 2012). We placed sensors measuring air temperature inside polyvinyl chloride housings that allowed ample air flow but protected sensors from direct precipitation (Appendix A), and we hung them from vegetation 2 m above the ground.

We specifically chose the microclimatic variables measured for use in the operative temperature equation outlined in Campbell and Norman (2012) and applied to *S. undulatus* by Buckley (2008), Angilletta et al. (2009), and Buckley et al. (2010). Buckley (2008; Appendix A) provides a thorough outline of the process for calculating operative temperatures for northern fence lizards. One major difference between this study and those previously mentioned is that our 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 research plot, rather than estimates of temperature averaged over a coarse spatial grain. However, sensor failure resulted in 26 stations with T_a measurements without associated T_s values and an additional 25 stations with T_s values that lacked corresponding measurements of T_a. To maintain the spatial and temporal resolution of estimates for the missing values, we calculated equations relating T_s and T_a by correlating hourly measurements at the 184 stations for which complete data on both variables were retrieved. We conducted this exercise for locations with and without midstory vegetation, resulting in four predictive equations used to estimate the missing values at 51 stations (Appendix A). The smaller spatial extent of our study plots also allowed for measurement of canopy openness above each sensor station. We derived an equation relating canopy openness to solar radiation from data presented in Zou et al. (2007) to directly estimate direct irradiance (Sp), rather than relying on an indirect approach of calculating temperatures at the two extremes of full sun (100% Sp) and full shade (0% Sp).

Wind speed and lizard body size are two important factors affecting operative temperatures that we did not measure directly as part of our study. Because these two factors were not measured, we conducted sensitivity analyses on our model to quantify their influence on operative temperature and activity period. The effect of burned habitat on mean operative temperature (and
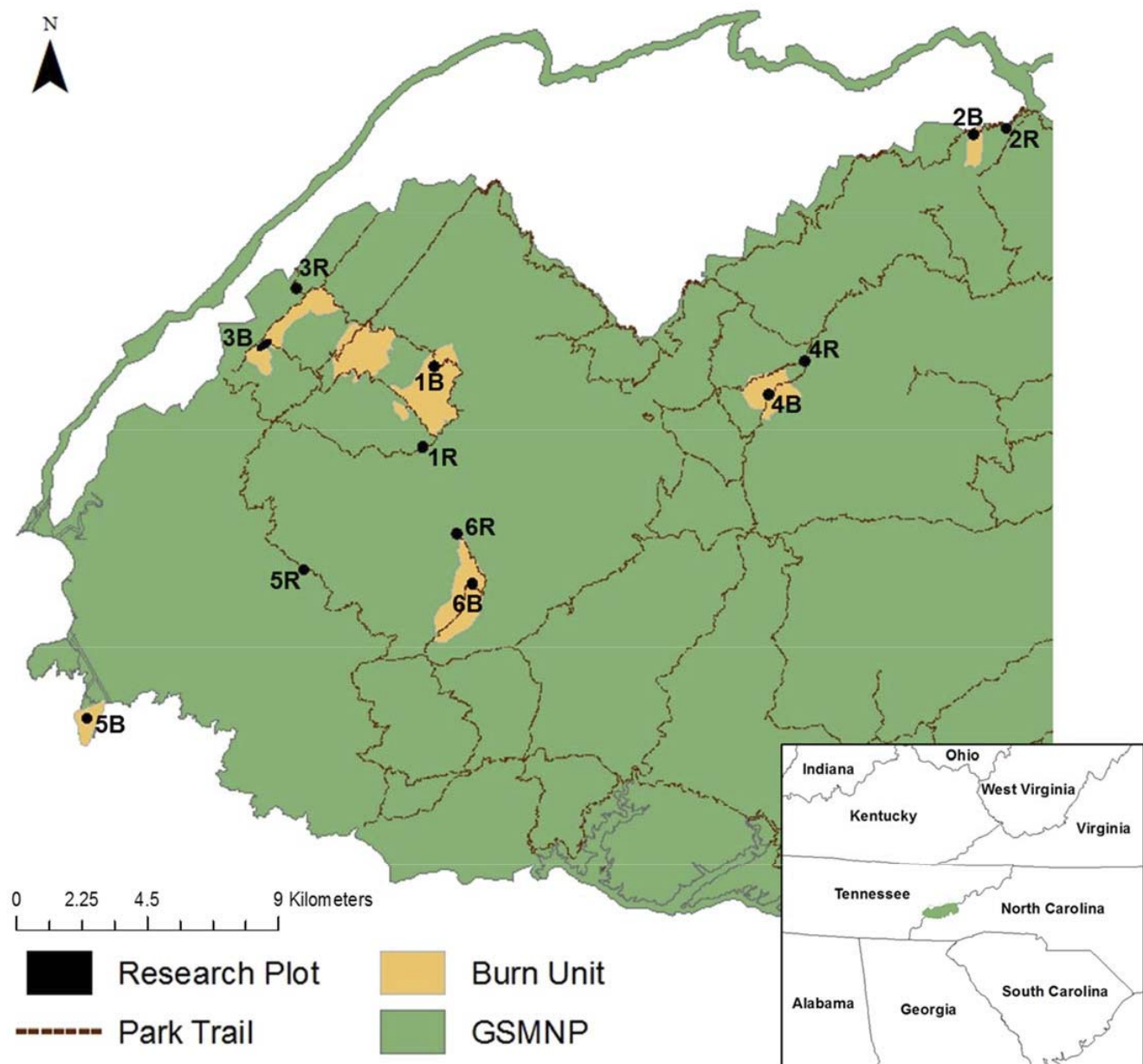
Figure 1. Locations of 10.1-ha burned (B) and matched-control/reference (R) plots within Great Smoky Mountains National Park (GSMNP), Tennessee, surveyed for reptiles and instrumented with microclimate loggers in 2013. Within research plots, GSMNP trails were used for transect surveys, with particular focus on northern fence lizard *Sceloporus undulatus hyacinthinus* and skinks *Plestiodon* spp. Inset map shows the location of GSMNP within the southeastern United States.

variance) was not sensitive to changes in these two variables; however, estimated activity period was highly sensitive to wind velocity. Therefore, we calculated potential daily activity windows for a range of relevant wind speeds. Because our selected focal northern fence lizard taxon inhabits the boundary layer where drag reduces wind velocity, we estimated effects of burned habitat on operative temperature by using a constant wind speed of 0.1 m/s (recommended by M. W. Sears, Clemson University, personal communication). We used a mean standard body length of 72 mm snout–vent length (SVL) based on the mean SVL for an *S. undulatus*

population studied in Blount County, Alabama (Niewiarowski et al. 2004). This was the closest population to our study population with a published estimate of mean *S. undulatus* body size. Parameter values for the operative temperature model and their sources are summarized in Appendix A. To examine the effect of burned habitat on northern fence lizard activity outside the period we sampled (e.g., May, which corresponds to the breeding season), we consulted *weather.com* to obtain mean temperatures for May, June, and July for nearby Townsend, Tennessee. On average, May temperatures were 5° C cooler than our study period of June and July. We

Table 1. Description of 12 study plots within Great Smoky Mountains National Park, Tennessee, where microclimate was characterized and reptile transect surveys were conducted in 2013. Study plots consist of six pairs of burned and unburned matched-control plots. Map labels correspond to Figure 1 of this article. A "P" in the Fire Type column indicates a planned prescribed burn, whereas a "W" indicates a controlled wildfire.

Map label	Burn unit name	Burn area (ha)	Fire type	Burn age (y)	Trail name	Transect elevation (m)	Transect length (m)	Transect location (center)
1B	Arbutus	425.7	P	6	Cooper Road	701	700	83.856°W, 35.612°N
1R	N/A[a]	N/A	N/A	>70	Rabbit Creek	594	565	83.858°W, 35.588°N
2B	Wear Cove Gap	90.6	P	4	Roundtop	610	606	83.649°W, 35.692°N
2R	N/A	N/A	N/A	>70	Greenbrier	610	690	83.637°W, 35.694°N
3B	Hatcher Mountain	959.9	P	8	Little Bottoms	427	533	83.921°W, 35.619°N
3R	N/A	N/A	N/A	>70	Goldmine	549	367	83.909°W, 35.637°N
4B	Hickory	216.5	W	27	Bote Mountain	846	443	83.726°W, 35.608°N
4R	N/A	N/A	N/A	>70	Bote Mountain & Finley Cane	640	633	83.712°W, 35.619°N
5B	Calderwood	117.8	W	3	Calderwood Fire Road	579	394	83.985°W, 35.499°N
5R	N/A	N/A	N/A	>70	Hannah Mountain	869	523	83.903°W, 35.548°N
6B	Gregory Ridge	331.8	P	6	Gregory Ridge	899	633	83.837°W, 35.546°N
6R	N/A	N/A	N/A	>70	Gregory Ridge	625	417	83.845°W, 35.561°N

[a] N/A = not applicable.

subtracted 5°C from each untransformed air and soil surface temperature we collected during June and July 2013, and we used the transformed temperatures as proxies for lizard operative temperatures in May 2013. We ran the model under these inputs to examine potential magnitude of northern fence lizard activity for the May 2013 breeding season.

Using the procedure outlined in Buckley (2008), we converted station measurements to hourly operative temperatures for an adult *S. undulatus* at that station during daylight hours (this species is strictly diurnal). We compared means and standard deviations of operative temperatures at the station level and plot level between burned and unburned forest, and we used regression to examine the influence of those parameter values on resulting activity period estimations. We considered *S. undulatus* capable of activity when diurnal operative temperatures were at or within the 20–80% percentiles of observed body temperatures in the field, 32.0–35.6°C (sensu Angiletta et al. 2002). We compared counts of potential daylight activity hours per day between burned and unburned stations, and we used regression to correlate canopy openness with mean operative temperature (and variance).

Reptile survey methods and analysis

During summer 2013, we established paired reptile monitoring transects (length range 367–700 m) along managed GMSNP trails within each burned and unburned microclimate characterization plot pair (Table S1, Workbook 3, *Supplemental Material*). We determined transect lengths by the extent of GSMNP trails encompassed by the associated 10.1-ha habitat characterization plots. We chose to use trails as transects for two reasons. First, we intended these surveys to serve as the foundation for a future monitoring program that could be carried out by GSMNP citizen scientists, and it was the belief of both researchers and directors of the citizen science program that participation was more likely if the

challenges of establishing, maintaining, and navigating off-trail transects were avoided; in addition, GSMNP's staff maintain trails, including the removal of obstructions that impede observer movement and northern fence lizard detection. We acknowledge that trails are not representative of off-trail conditions; however, we assume that such representation biases are the same on burned and unburned plots, allowing comparison between plot types. Furthermore, we note that the nonlinear characteristics of these trails allow for the repeat detection of individuals. Transects ranged between 427 and 899 m in elevation. Our transect surveys focused on *S. undulatus* and skinks in the genus *Plestiodon*, but we documented all reptile observations. *S. undulatus* was the focus of our mechanistic models of lizard activity and was easily identifiable, which made the species well suited for monitoring by citizen science volunteers. Lizards belonging to *Plestiodon* were easily identifiable to that genus at a distance, but they required hand capture for species level identification; thus, we limited observations to the resolution of *Plestiodon* spp.

At the start of each sample, an observer recorded time and general weather conditions, including temperature. We did not conduct surveys during rain. The observer walked each paired burned and unburned transect twice (out and back) on the same day. For each animal sighted, we recorded the location along the trail using a Garmin GPSMAP 64st and estimated the individual's perpendicular distance from the trail. To standardize comparisons between transects of varying length and satisfy the model's reliance on independent samples, we summed reptile encounters per 50-m segment of transect. In the event hikers passed during our survey, the observer paused 5 min before resuming and recorded the total number of hikers that passed during an entire transect sample. We sampled each transect three times within a 5-d period between June 20 and July 18; therefore, we assumed closed populations during our sampling period.
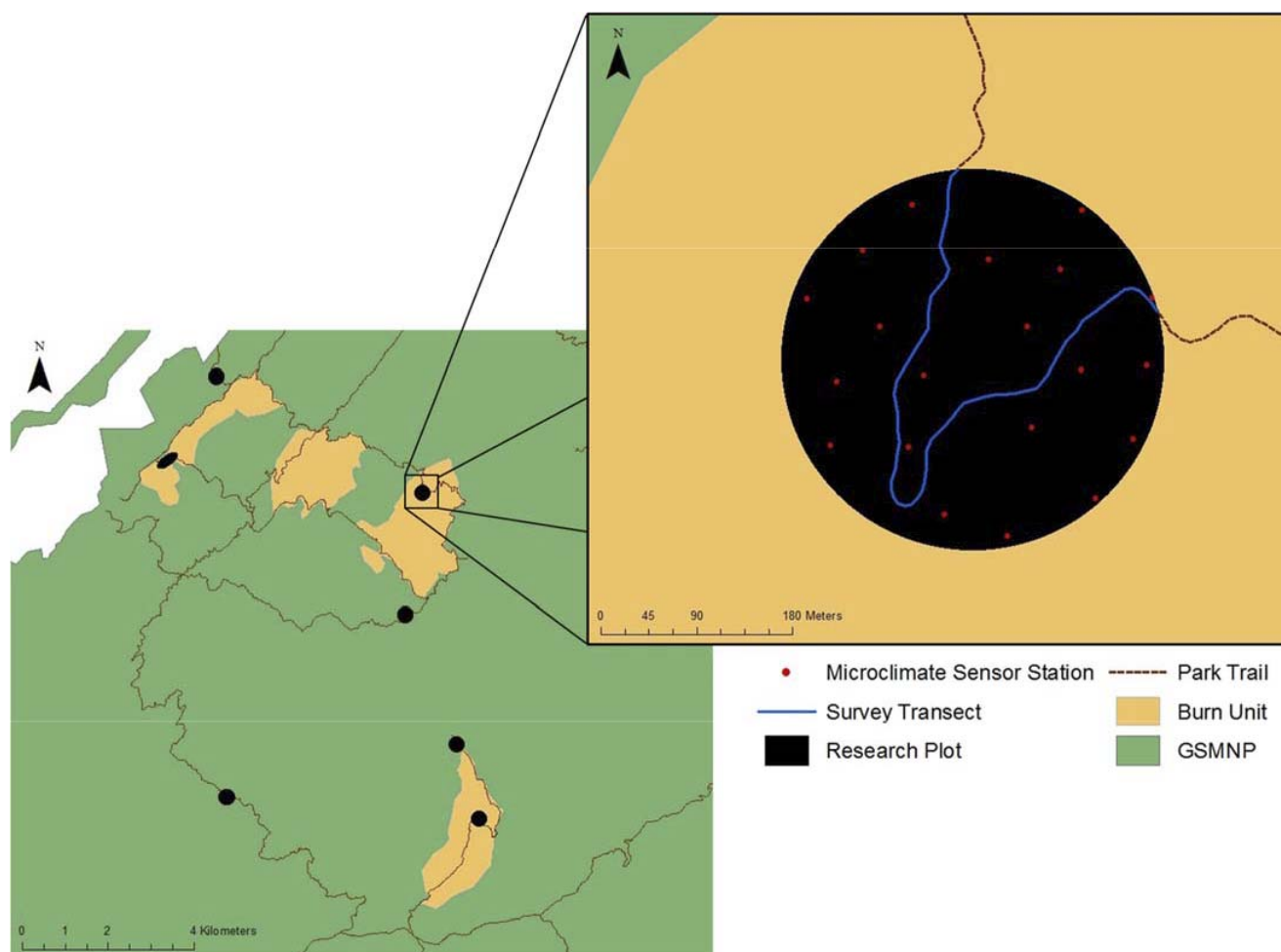
Figure 2. Spatial arrangement of survey transect and microclimate sensor stations in study plot B1 within the Arbutus burn unit in Great Smoky Mountains National Park (GSMNP), Tennessee. Microclimate data in the 10.1-ha plot were collected in 2013 before, during, and after reptile surveys were conducted along Cooper Road Trail, which served as a sampling transect (indicated in blue) within the plot boundaries. Plot B1 is representative of the other 11 plots from which data were collected in the study, and is displayed to conceptually depict the layout of all study plots. Transect surveys placed particular focus on northern fence lizard *Sceloporus undulatus hyacinthinus* and skinks *Plestiodon* spp.

All surveys were conducted by the same observer and all reptile encounters (including snakes) were recorded.

We used a binomial-Poisson mixture model (Dodd and Dorazio 2004; Royle 2004; Kéry et al. 2005) to estimate lizard abundance and occurrence (abundance > 0) based on counts of reptiles per 50 m. Under this model, the observed count was a binomial outcome of segment-level abundance (N) and detection probability (p), and N was itself an outcome of a Poisson distribution with mean (λ). Our model included sample (day) level factors as drivers of p and transect segment (50-m) level factors, including plot-level habitat variables, as drivers of λ. We used Bayesian inference to approximate posterior distributions of model parameters, applying Markov chain Monte Carlo sampling in OpenBUGS (Lunn et al. 2009).

In the detection part of the model, we initially included random effects for plot pairing, the plots and segments themselves, and sample day; but problems in sampler convergence led us to drop them from

consideration. We also initially included two fixed effects: a binary indicator of whether the observation was made on the outbound or inbound walk of the transect (to account for differential likelihood of detection due to observer familiarity with prior animal locations on the return trip) and a binary indicator of whether hikers were encountered during the survey (to account for differential detectability due to survey disruption). The outbound or inbound effect was small, with 95% credible intervals centered near zero for each taxon, so it was removed from the model. Hiker encounters were positively related to detection, likely explained by 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 detection part of the model were 1) an intercept and 2) a two-level effect of weather condition (overcast or partly to fully sunny).

In the abundance part of the model, we had difficulty fitting random effects for plot pairing, the plots and

Table 2. Estimated daily diurnal operative temperature statistics for *Sceloporus undulatus hyacinthinus* inhabiting burned and unburned forest within Great Smoky Mountains National Park, Tennessee, during summer 2013. Estimated mean operative temperature, hours in and out of activity range, and variability in daily operative temperature means among stations (SD) are given at the plot level of spatial resolution. Daily operative temperature range, daily variability (SD), and hourly variability (SD) are given at the station level of spatial resolution (20 stations per plot). All values are presented on a daily temporal scale, but result from averaging measurements from a 49–58-d collection period. Values were averaged for six burned and six unburned reference plots that were paired based on relevant attributes.

	Plot-level scale					Station-level scale		
	Body Temperature (°C)	Hours Active	Hours Too Cold	Hours Too Hot	Station SD (°C)	Daily Range (°C)	Daily SD (°C)	Hourly SD (°C)
Burn	30.61	2.92	7.33	2.75	2.43	20.72	1.65	6.26
Reference	29.25	3.26	8.29	1.45	1.84	18.77	1.51	5.69

segments themselves, and sample iteration; so, we removed these effects. The fixed effects in the resulting model were 1) an intercept, 2) a two-level burn effect (burned or unburned), 3) a slope parameter for burn age, 4) a slope parameter for site elevation, 5) a segment length effect (the last segment in a transect was typically shorter than 50 m), and 6) a segment-level random effect. We included the burn effect parameter (2) to reveal whether abundance of the taxon of interest was expected to differ with respect to the habitat having been burned and at what magnitude. We included the burn age effect (3) to capture the temporal relationship between fire application and species abundance. The parameter was a measure of linear correlation between log(abundance) and burn age and thus can be used to inform prescribed fire regimes and estimate abundance during unsampled time windows throughout burn histories. For unburned plots, we fixed the slope for burn age at 0 as burn age is undefined. Thus, the model permits abundance to differ overall with respect to burn status and—for burned plots—over time with respect to burn age. We included the elevation parameter (4) simply to avoid misattributing elevation-induced varia-tion in taxon abundance to effects unrelated to elevation, including burning. We included segment length (5) to account for the reduced opportunity to encounter reptiles on segments less than 50 m. As many structural characteristics of a burned forest are related to intensity of the burn, we intended to include a parameter for fire severity; however, data were not available in high enough resolution to maintain consis-tency with that of other parameters. Inferences and summaries for all of these parameters were based on their approximated posterior distributions.

Results

Microclimate and predicted lizard activity

We recovered air temperature and ground surface temperature data from 210 and 212 sensors (of 240 of each type), respectively (Table S2, *Supplemental Material*). The 422 sensors still functioning upon retrieval provided hourly measurements for 49–58 complete days. Five stations—each in separate plots—had to be excluded

from analysis because both sensors at those locations failed.

Mean operative temperature for *S. undulatus* in burned plots was approximately 1.36°C warmer than those on unburned plots for June and July (Table 2). Day-to-day variability at any particular station (20 per plot) was low and seemed to be relatively homogeneous, with standard deviations at burned stations only 10% greater than those at unburned stations. However, burned plots exhibited much more spatial heterogeneity and the standard deviation of operative temperature means between stations on a given day was 32% greater within burn plots (Table 2). Over the same daylight period, operative temperature estimations averaged a range of 30.85°C across stations within a burn plot compared to only 25.55°C within a reference plot.

There was greater hour-to-hour variability at burn stations, with a standard deviation of 6.26°C between hourly operative temperatures, compared to 5.69°C at unburned stations. Daily operative ranges at individual burn stations were 1.95°C greater than at stations in unburned plots (Table 2). Hourly variability and mean operative temperature were positively correlated with canopy openness (Figure 3). Mean canopy openness was 5.3% greater in burned than unburned plots (17.9% in unburned plots compared to 23.2% in burns), which resulted in greater estimated lizard diurnal body temperatures within burned plots. Stations within burned plots had longer estimated activity periods during June and July for all wind speeds ≥0.2 m/s (Figure 4). Under lower wind speeds, estimated lizard body temperatures were too hot for activity as solar noon approached (Figure 4). We found canopy openness to have a unimodal relationship with activity hours that became more peaked at reduced wind speeds. Stations under canopies with 10–30% openness yielded the longest activity periods, accounting for more than 76% of all hours estimated to be suited for lizard activity during June and July (Figure 5). Models using air and surface temperatures adjusted to simulate conditions during May resulted in more than 70% longer activity windows in burned plots (1.09 h/d on burned sites vs. 0.64 h/d on reference sites).
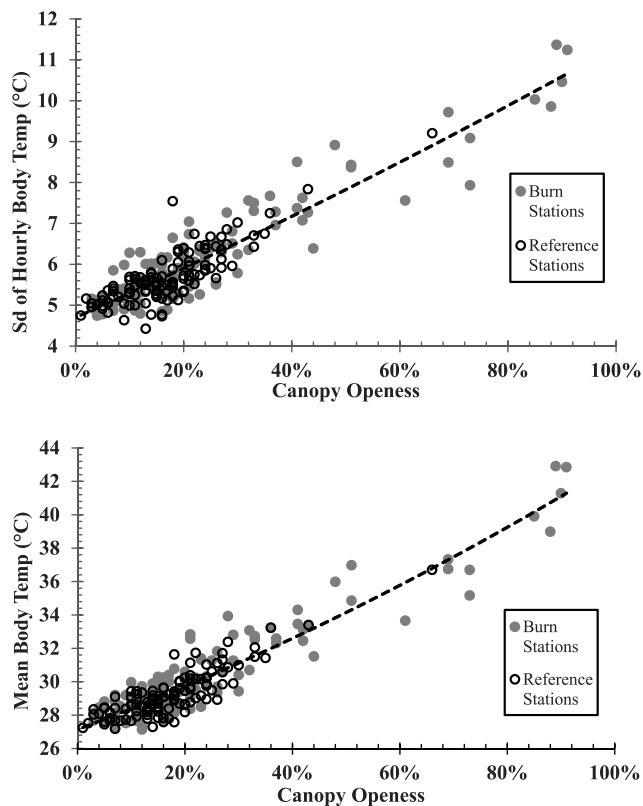
Figure 3. Correlations between estimated northern fence lizard *Sceloporus undulatus hyacinthinus* body temperature (as predicted by a biophysical model of operative temperatures) and canopy openness measurements taken from microclimate stations within six pairs of matched burned and unburned reference plots in Great Smoky Mountains National Park, Tennessee, during 2013. Rate of warming ($R^2 = 0.84$) and overall mean body temperature ($R^2 = 0.87$) of northern fence lizards are strongly positively correlated with canopy openness. The larger ranges and overall higher body temperatures under more open canopies indicates solar radiation as a likely driver of differences in body temperatures between northern fence lizards inhabiting burned and unburned patches of forest.

Fire and reptile detection, occupancy, and abundance

Over 36 passes of 12 transects, we recorded nine reptile taxa at least once (Table S1, Workbook 4, *Supplemental Material*). We recorded 70 encounters of *S. undulatus* and 18 encounters of *Plestiodon* spp. Three transects yielded no reptile encounters at all.

Estimates of lizard occupancy (derived from our abundance model as abundance > 0) per 50 m of trail suggest a positive relationship between burned forest and lizard occurrence. Estimated reptile detection rates were high. Median values of detection rate for *S. undulatus* and *Plestiodon* spp., which accounted for 92% of survey encounters, were 77 and 71%, respectively. We found overcast weather reduced *S. undulatus* detection probability by 6% and *Plestiodon* spp. by 12%. *Plestiodon* spp. occupancy of 50-m trail sections was greater than the occupancy of *S. undulatus* (4.2 and 1.6%

occupancy, respectively). Mobel-based estimates of *Plestiodon* spp. occupancy of trail sections within recently (<1 y) burned sites was 17.3%, compared to 1.1% on unburned sites. We detected *S. undulatus* on only one transect that had not been burned (since record keeping began). Overall, *S. undulatus* occupancy of trail sections in burned forests was 3.8%, which was 4.75 times greater than occupancy of trail sections through unburned forests (Figure 6). In total, 23 of 24 lizard encounters in unburned plots occurred along a single transect within Site 2R. In addition to lizards, we observed nine snakes during our transect surveys, eight of which occurred on transects through burned forests. Overall reptile occupancy of 50-m trail sections through burned forests was 9.9% compared to 1.8% through unburned forests.

Our model contained a linear time-since-burn relationship; thus, by setting burn age = 0, we found that overall reptile abundance would be expected to increase by slightly more than 140% after a burn. *Plestiodon* spp. showed the strongest positive response to fire (Figure 7). Our model results indicated that *Plestiodon* spp. abundance declines by roughly 50% for each 5-y increment after a fire. However, we note that the 95% credible interval for that rate of decline included zero. Although the temporal relationship between passage of time since fire and lizard abundance was not well determined by our model, anecdotally, it is worth noting that encounters of both lizard groups were greatest on sites experiencing fire around 6 y prior (Figure 8).

Discussion

Operative temperature modeling and subsequent surveys suggest a clear link between the microclimatic conditions in burned habitat and forest floor lizard abundance along trails within GSMNP. Our model may be underestimating the magnitude of this effect, as 23 of 24 lizard sightings on unburned sites occurred along a single transect within Site 2R. Site 2R had recently experienced significant wind throw of trees, resulting in open habitat structure similar to burned forests. Our lizard performance model indicates that average adult body temperatures of *S. undulatus* can become too hot for activity within burned forests during peak solar hours in summer, when wind velocities at the boundary layer are low. However, *S. undulatus* and *Plestiodon* spp. are scansorial, frequently perching on the exposed lower portions of woody vegetation where there is less frictional drag on wind speed. By perching above the forest floor, these lizards are likely able to select microsites with greater wind speeds that allow them to be active for some or all of the diurnal period we estimated as too hot at low wind speed. Conversely, behavioral selection to reduce wind exposure cannot increase activity periods within unburned sites where operative temperatures were estimated to be too cool for more of each day and never rise above the operative range.
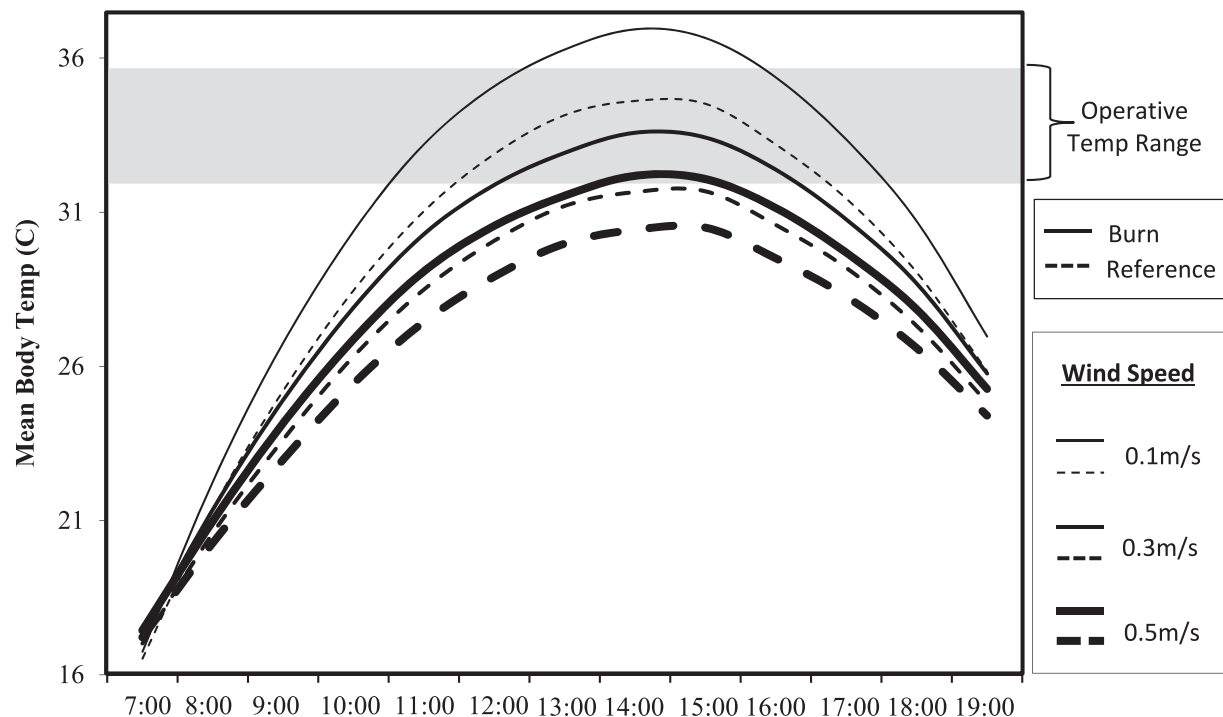
Figure 4. Estimated northern fence lizard *Sceloporus undulatus hyacinthinus* body temperatures within burned and unburned reference patches of forest within Great Smoky Mountains National Park, Tennessee, during summer 2013. *S. undulatus* body temperature trajectories are given for burn (solid line) and reference (dashed line) patches under various relevant wind speeds. *S. u. hyacinthinus* operative range is represented by the horizontal dark gray band covering 32.0–35.6°C.

Conclusions

We demonstrate that operative temperature modeling provides a complementary means to assess and monitor the effects of burned forests on reptile thermal habitat quality in southern Appalachia. Within the western slopes of GSMNP, xeric pine–oak forests experiencing

Figure 5. Mean daily hours of estimated northern fence lizard *Sceloporus undulatus hyacinthinus* activity displayed against canopy openness measured directly above microclimate stations within burned and unburned reference patches of forest in Great Smoky Mountains National Park, Tennessee, during the 2013 study period. Northern fence lizard activity was strongly correlated ($R^2 = 0.41$) with canopy openness. For the purpose of examining this relationship, a steady wind speed of 0.1 m/s was assumed.
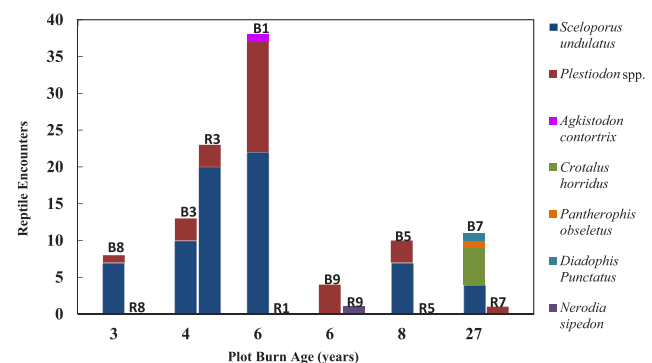
fire had more open structures that allowed for higher temperatures at the forest floor, resulting in higher estimated operative temperatures for lizards and longer periods of summer activity. Our models suggest that the positive effects of fire on lizard activity may be even

Figure 6. All reptile species encountered in 2013 during transect surveys of 12 study plots (numbers above bars correspond to identifiers in Figure 1) located in the Tennessee portion of Great Smoky Mountains National Park. During surveys particular emphasis was placed on northern fence lizard *Sceloporus undulatus hyacinthinus* and skinks *Plestiodon* spp. Burned and unburned reference plots were matched based on relevant attributes. Plot pairs are grouped and presented in ascending order of burn age along the x-axis. Common names for species given in the legend from top to bottom are as follows: northern fence lizard, skinks, copperhead, timber rattlesnake, black rat snake, ringneck snake, and northern water snake.
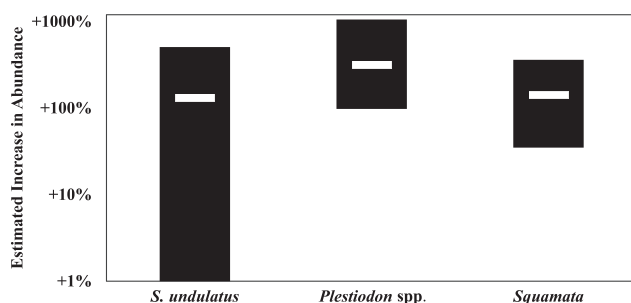
Figure 7. Estimate of immediate postburn effect in northern fence lizard *Sceloporus undulatus hyacinthinus*, skink *Plestiodon* spp., and general reptile *Squamata* spp. abundance within Great Smoky Mountains National Park, Tennessee. Estimated effect sizes are based on data collected in 2013 from previously burned habitats and reflect extrapolation of the time-since-burn relationship to the model's intercept (burn age = 0). Median values for each group are represented by white bars encompassed by black boxes corresponding to the range of 95% credible intervals. *Plestiodon* spp. was estimated to experience the largest increase with a median value of +317%, whereas the median for *S. undulatus* was +131%. Squamates in general were estimated to increase by 141%. The lower limit of the 95% credible interval for *S. undulatus* is at +1%.

greater during cooler months, although projections on the effects of burned habitat during cooler seasonal environments for lizards should be verified with field measurements from those periods. Conditions allowing for prolonged activity should translate to increased lizard fitness and ultimately abundance, which was consistent with our estimates of lizard occupancy and abundance within burned versus unburned forests. Because the fundamental principles regarding physiology, energy requirements, and insolation apply broadly to other ectotherms, the positive effects of fire on lizard thermal habitat quality may extend to other reptiles within GSMNP.

We see several implications for future research. The relationships proposed above can be further investigated by expanding the seasonal duration of these measurements, beyond the June–July investigation period. As the burn occurring most proximal to our fieldwork had occurred 3 y prior, continued monitoring of these transects as they progress through the burn cycle—including pre- and postburn surveys—should increase 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. Direct examination of the link between fire and abundance of reptile species not easily observed via the methods used in this study could be accomplished through deployment of drift fence arrays, which were beyond the scope of our time and labor resources. However, our biophysical model was specifically designed to allow the morphological dimensions and solar absorptivity of other species
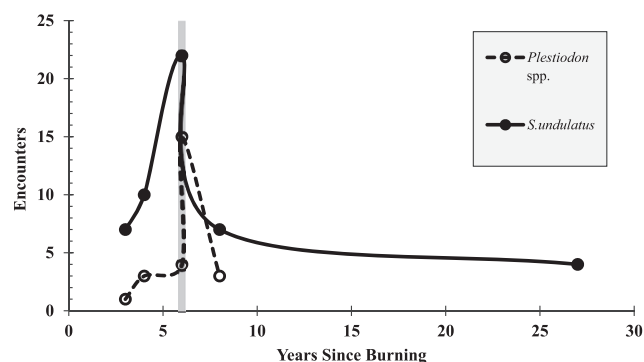

Figure 8. Total counts for encounters of northern fence lizard *Sceloporus undulatus hyacinthinus* and skinks *Plestiodon* spp. in six plots burned from 3 to 27 y before transect surveys conducted in Great Smoky Mountains National Park, Tennessee, in 2013. Each survey was repeated three times over a maximum of 5 d. A light gray vertical line denotes 6 y postburning.

to be input as a turn-key approach for crudely assessing the influence of fire management practices on the potential daily activity of other reptilian taxa in the park.

Supplemental Material

Please note: The *Journal of Fish and Wildlife Management* is not responsible for the content or functionality of any supplemental material. Queries should be directed to the corresponding author for the article.

Table S1. Excel Workbook 1. Description of field headings in Workbooks 2–4. Workbook 2. Deployment information and placement characteristics of microclimate stations established at study sites in Great Smoky Mountains National Park, Tennessee, June–July 2013. Workbook 3. Attributes of study sites, transects, and reptile sampling events associated with reptile monitoring in Great Smoky Mountains National Park, Tennessee, June–July 2013. Workbook 4. Reptile encounters and associated attributes during sampling of transects established on study plots within Great Smoky Mountains National Park, Tennessee, June–July 2013.

Found at DOI: http://dx.doi.org/10.3996/042016-JFWM-031.S1 (55 KB XLSX).

Table S2. Time series of environmental data collected from individual microclimate sensor devices (containing 510 subtables) deployed on study plots established within Great Smoky Mountains National Park, Tennessee, June–July 2013.

Found at DOI: http://dx.doi.org/10.3996/042016-JFWM-031.S2 (21770 KB XLSX).

Reference S1. Harmon ME. 1981. Fire history of the Great Smoky Mountains National Park – 1940 to 1979. Gatlinburg, TN: U.S. Department of the Interior, National Park Service, Great Smoky Mountains National Park, Uplands Field Research Laboratory. Research/Resources Management Report 46.

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Appendix A

Source of parameter values used to calculate operative temperature estimates, but not directly measured during the study.

Table A.1. Values and sources of operative temperature parameters not measured.

Parameter	Source	Value
Albedo of mixed forest	U.S. Environmental Protection Agency (2008)	0.14
Wind velocity	M.W. Sears, Clemson University, personal communication	0.1 m/s
Field body temperature (20–80th quantiles)	Angilletta et al. (2002)	32.0–35.6°C
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 et al. (2004)	72 mm
Lizard mass	Buckley (2008)	3.715×10^{-6} (SVL)$^{3.49}$

Table A.2. Equations used to estimate missing surface or air temperature measurements.

Equation	Description	Formula
A.1	Air temperature with no vegetative cover	$T_a = 19.669\ln(T_s) - 38.045$
A.2	Surface temperature with no vegetative cover	$T_s = 9.2475e^{0.0377(T_a)}$
A.3	Air temperature with vegetative cover	$T_a = 23.008\ln(T_s) - 47.91$
A.4	Surface temperature with vegetative cover	$T_s = 9.6148e^{0.0353(T_a)}$