

wildlife management

Lizard Microhabitat and Microclimate Relationships in Southeastern Pine-Hardwood Forests Managed With Prescribed Burning and Thinning

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Understanding the impacts of disturbances in forest ecosystems is essential for long-term biodiversity conservation. Many studies have evaluated wildlife responses to various disturbances but most generally do not use changes in microclimate features or microhabitat structure to explain these responses. We examined lizard responses to two common forest management practices (prescribed burning and thinning) in pine-hardwood forests of the Bankhead National Forest, Alabama, USA. Over 4 years, we captured 719 individual lizards representing seven species. Lizards exhibited species-specific responses to forest management: eastern fence lizard (*Sceloporus undulatus*) captures were positively associated with an increasing forest disturbance gradient and were greatest in thin with burn treatments, whereas little brown skink (*Scincella lateralis*) captures were positively associated with increasing litter depth and were greatest in control sites during the first year posttreatment. Green anole (*Anolis carolinensis*) captures increased in forest stands with concomitant increases in air temperature, whereas common five-lined skink (*Plestiodon fasciatus*) captures were related to coarse woody debris cover during posttreatment sampling. We were unable to detect a treatment response or microhabitat/microclimate associations for broad-headed skinks (*Plestiodon laticeps*). Through an information-theoretic approach, we were able to identify treatment effects along with changes in microclimate and microhabitat features potentially responsible for driving responses of southeastern lizard species to forest management.

Keywords: reptile, William B. Bankhead National Forest, disturbance, forest management, Akaike's information criterion

Forest disturbances such as fire and canopy gap creation are dynamic processes that can be used to by forest managers to emulate natural disturbance patterns and ultimately as a tool for ecosystem restoration (Elliott et al. 1999, Lafon et al. 2005, Long 2009). Although forests are primarily managed for timber resources, there is also a great need to manage for both ecosystem health (e.g., management practices to prevent the spread of forest pests) (Schowalter et al. 1981) and biological diversity (Simberloff 1999). For example, many management and conservation efforts are undertaken to benefit a single species, but it is important to consider the response of multiple species because different taxa may have varying responses to disturbance, largely due to disparities in natural history (Barrett and Guyer 2008). Overlooking these disparities may obscure assemblage level changes in response to management (Steen et al. 2010).

Beyond species responses, it is imperative to understand the impacts of different disturbances on the biological processes that operate within an ecosystem (Sousa 1984, Petraitis et al. 1989). Forest management often operates on a large scale, using a variety of management techniques (e.g., even-age, group selection, and thinning). However, wildlife may respond to subtle changes in the habitat that result from these management techniques. A better understanding of these fine-scale responses may permit refinement of forest management practices to facilitate the conservation of biodiversity without drastically changing current techniques. In addition, understanding the overall ecological response is essential because postdisturbance dynamics are important in allowing ecosystems to maintain function of biological processes (Keitt 2008).

Reptiles represent an important group for evaluating how forest management practices influence biodiversity (e.g., Litt et al. 2001,

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Todd and Andrews 2008, Steen et al. 2013a), because this group tends to demonstrate species-specific responses to habitat alteration (Greenberg et al. 1994, Vitt et al. 1998, Barrett and Guyer 2008). In addition, many once-common reptile species have become increasingly rare (Gibbons et al. 2000, Sinervo et al. 2010), and little is known about the relationships between reptile assemblages and habitat changes (Smith and Ballinger 2001, Gardner et al. 2007). Because lizards may be particularly sensitive to habitat disturbances (Steen et al. 2013a, 2013b), the focus of this study was to evaluate how forest restoration (i.e., preventing the spread of forest insect pests and reforestation of upland hardwood conditions) treatments in the form of prescribed burning and thinning, along with the associated changes in microhabitat and microclimate characteristics (e.g., Marzluff et al. 2000), influence a southeastern lizard assemblage. Although Sutton et al. (2013) previously examined lizard responses to forest management as part of the overall herpetofaunal assemblage response to prescribed burning and thinning at these sites, our current study explores the relationships between the changes in microhabitat and microclimate characteristics and species-specific lizard responses to forest management in a multiple hypothesis testing framework. We apply an information-theoretic approach to evaluate a set of a priori models developed based on our understanding of the biological requirements of southeastern lizards and used these models to identify specific microhabitat and microclimate characteristics important for predicting lizard abundance before and after forest management.

We hypothesized that burning and thinning practices would alter microhabitat and microclimate conditions, and lizards would show species-specific responses to these changes. For example, we expected that heliothermic lizard species (i.e., those with higher temperature tolerances) would be positively affected by management activities that alter microhabitats associated with thermoregulatory behavior, whereas species known to rely on the litter layer for foraging or refugia would be most negatively affected by forest management that caused disturbance to the forest litter layer.

Materials and Methods

Study Site Description

This study was conducted in the northern portion of the William B. Bankhead National Forest, Alabama, USA (BNF), which is a 72,900-ha multiuse forest located in Lawrence, Winston, and Franklin Counties of northwestern Alabama along the highly dissected portion of the southern Cumberland Plateau (Smalley 1982, Gaines and Creed 2003).

In the BNF, Southern pine beetle (*Dendroctonus frontalis* Zimmerman) infestations have led to large die-offs of loblolly pine (*Pinus taeda* L.), which was used to reforest abandoned agricultural and heavily timbered areas in the BNF (Gaines and Creed 2003, Sutton et al. 2013). These large-scale infestations have resulted in large numbers of standing dead trees and increased fuel loads, elevating the risk of damaging wildfires throughout the southeast. Fire disturbance events within the southeastern United States have historically occurred as low-intensity fires ignited by Native Americans and less commonly by lightning strikes (Delcourt and Delcourt 1997, 1998). Before the influence of Native Americans and early settlers, naturally occurring fires probably happened during early May and June when lightning strikes are most common and precipitation levels are relatively lower than during the midsummer months. Native Americans and early settlers are believed to have influenced fire histories greatly, with a majority of fires ignited during the dormant

and early growing season, mainly for land-clearing and hunting purposes (Knapp et al. 2009). Fire return intervals throughout the region have been estimated to be 1.7–11.1 years during the late 19th and early 20th centuries; naturally occurring fires were relatively nonexistent after 1940 mainly because of fire suppression activities and land use changes that reduced fire frequency at the landscape scale (McEwan et al. 2007).

As a means to reestablish native upland hardwood conditions and control the negative impacts associated with *D. frontalis* infestations, the BNF initiated a Forest Restoration Plan that included tree thinning and prescribed burning management activities; for additional study site information, please consult Sutton et al. (2013).

Experimental Design

Our experiment consisted of a before-after, control-impact (BACI), complete block 2×3 factorial design of two burning levels (no burn and burn), and three thinning levels (no thin, $11 \text{ m}^2 \text{ ha}^{-1}$ residual basal area [BA], and $17 \text{ m}^2 \text{ ha}^{-1}$ residual BA), resulting in six treatments (i.e., control, burn, light thin, heavy thin, light thin with burn, and heavy thin with burn); treatments were replicated three times across the landscape, resulting in 18 total experimental stands (Sutton et al. 2013). We blocked treatments temporally (i.e., year) because all forest treatments could not be implemented in the same year. Block 1 treatments were implemented during the summer of 2005, whereas block 2 and block 3 were implemented during the summer and fall of 2006. All harvesting was thin-from-below using feller bunchers with certain hardwood tree species, such as *Quercus* spp. and *Carya* spp. retained preferentially (Sutton et al. 2013). After treatment, residual coarse woody debris (CWD) were scattered throughout the harvested stand, and smaller diameter tree tops (i.e., slash) were piled in discrete locations within the boundary of the harvested area. Prescribed burns were generally completed during the dormant season (January–February), with backing fires initiated to ensure that burns were limited to understory and litter layers (Sutton et al. 2013). In thin with burn stands, prescribed burns were implemented after thinning operations were completed in a given stand.

Microclimate and Microhabitat Covariates

We installed one HOBO (Onset Computer Corp.) datalogger in each forest stand to record air and soil temperatures, relative humidity, and light intensity. Dataloggers were programmed to record every 12 hours starting at 1400 hours CST. Because the pretreatment sampling period was shorter in block 1, we used climate data collected from May 15 to June 15 during pre- and posttreatment sampling periods to make data comparable among years as described in Sutton et al. (2013). We quantified pre- and posttreatment microhabitat complexity and heterogeneity data via three yearly belt transect surveys in each treatment stand. We determined the habitat plot center a priori via a random compass bearing ($0\text{--}360^\circ$) and distance (30–50 m) from the center of each trapping array (see below) as described in Sutton et al. (2010, 2013). Each of the three microhabitat surveys within a particular stand consisted of four 10-m belt transects extending outward in the four cardinal directions from a randomly determined habitat plot center. We used a 2-m piece of 1.9-cm diameter polyvinyl chloride pipe centered on the transect line and recorded the presence or absence of a suite of microhabitat variables across the transect (Table 1). To determine percent litter, woody vegetation, CWD, and forest understory cover, we summed the total number present individually in each

Table 1. Microclimate and microhabitat variables collected at three habitat sampling locations within each forest stand in the BNF (2005–2008).

Habitat variable	Code	Variable description
Percent litter	%_litt	Presence (%) of ground cover such as leaves or small woody debris measured every 0.5 m along transect
Percent woody	%_woody	Presence of any woody stems (%) such as seedlings and large trees (living or dead) measured every 0.5 m along transect; woody stems taller than 1 m had to contact transects directly to be counted
Percent CWD	%_CWD	Presence of any fallen woody debris larger than 10 cm in diameter (must touch the ground somewhere along the length to be counted) measured every 0.5 m along transect
Litter depth	L_dep	Determined by measuring depth of the substrate to the nearest 0.5 cm with a metric ruler measured every 2 m along transect
Forest level 3	For_lev3	Percent coverage of forest levels >4–≤6 m (classified as midstory) measured every 5 m along transect
Air temperature	Air_temp	Average daily air temperature (° C) during the months of May and June recorded at 1400 hours CST; recorded with a climate datalogger
Treatment rank	Treat	Forest treatments ranked to represent increased basal area and vegetation removal (i.e., 1, control; 2, burn; 3, light thin; 4, heavy thin; 5, light thin with burn; and 6, heavy thin with burn)

Variables used to develop lizard predictive models.

habitat plot, divided this number by the total amount of possible survey locations, and multiplied by 100. We determined an overall stand estimate for each habitat variable by averaging the values from each of the three habitat plots. The microhabitat and microclimate data presented in this study represent individual metrics that were selected based on their biological importance for describing southeastern lizard responses to forest management. For more detailed information regarding microhabitat surveys including additional microhabitat and microclimate variables assessed, please refer to Sutton et al. (2010, 2013).

To evaluate the impacts of forest disturbances, we treated forest treatment as a rank variable (i.e., 1, control; 2, burn; 3, light thin; 4, heavy thin; 5, light thin with burn; and 6, heavy thin with burn) (Table 1) to represent increasing disturbance severity (i.e., overall impact of the disturbance to the ecosystem) (White and Pickett 1985). Although forest treatments did not represent an even and continuous gradient, each progressive rank corresponded with increased vegetation removal (i.e., tree basal area and surface vegetation).

Lizard Sampling

We used a trapping design consisting of three drift fences constructed from aluminum flashing (61 cm × 15 m) radiating 120° from a central triangular box trap; we also installed large box traps and paired pitfall traps at the terminus and midpoint of each fence, respectively (Sutton et al. 2010). To determine the location of a drift-fence array within a stand, we divided each stand into quadrants corresponding to the four cardinal directions and installed the drift-fence array into one of these randomly selected quadrants (Sutton et al. 2013). After the completion of pretreatment sampling, we removed all drift-fence arrays to avoid damage from tree harvesting and prescribed burning. Once treatments were completed, we reinstalled all traps in the same locations.

We sampled lizards (Order: Squamata; Suborder: Sauria) over a 4-year period (2005–2008). Because all treatments were not completed in the same year, we used 3 years of capture data from each treatment stand, representing 1 year of pretreatment data and 2 years of posttreatment data. Pretreatment data were collected from April to June 2005 for block 1 and from May 2005 to August 2005 and from March 2006 to May 2006 for blocks 2 and 3. We constrained all posttreatment sampling to seasons that were directly comparable to pretreatment data as described in Sutton et al. (2013). We sampled intermittently throughout early spring and began continuous sampling from the beginning of May until Sep-

tember of each year. During sampling periods, we opened traps by block(s) depending on weather conditions and availability of personnel, with the visiting order of block and stand determined randomly a priori. Traps were checked daily between 0700 to 1400 hours CST. We marked all newly captured lizards with a treatment-specific toe-clip and released all captures on the opposite side of the drift fence where they were captured.

Data Analysis

Microclimate and Microhabitat Analysis

We used mixed-models (PROC MIXED) analysis of variance (SAS version 9.1.3) to test for changes in microhabitat and microclimate conditions among pre- and posttreatment samples (within-subject factor) and among the treatments (between-subject factor), and their interactions. Before analysis, we transformed microhabitat and microclimate data using logistic, square root, and $1/x$ to satisfy normality assumptions. We declared significance at an α level ≤ 0.05 and used a Tukey test for post-hoc comparisons. We report means (\pm SE), unless otherwise indicated.

Species Detection

To determine whether species detection varied by treatment, we estimated detection probabilities for each lizard species using the program PRESENCE (version 3.0; Hines 2010). We used a single-season modeling approach in which each year was treated as a single sampling event (MacKenzie et al. 2002). This resulted in three total sampling events (i.e., pretreatment, posttreatment year 1, and posttreatment year 2). Because we were only interested in evaluating factors affecting detection, we kept occupancy constant across models. We evaluated two potential models for each species and species group, including a null model (no covariates and assuming a constant detection probability) and a model that included treatment covariates coded to represent the six treatments. To assess the fit of the resulting models, we calculated an overdispersion parameter (\hat{c}) and used this value to adjust the fit of the resulting models for each species or species group (MacKenzie et al. 2006).

Lizard Microclimate and Microhabitat Relationships

We standardized lizard captures by dividing total captures by the number of trap nights and multiplied this value by 100 to represent the number of captures over 100 trap nights (Greenberg and Waldrop 2008). We used an information-theoretic approach (Burnham

Table 2. A priori hypotheses to evaluate impacts of forest management and microclimate and microhabitat variables on southeastern lizard species in the BNF (2005–2008).

Model name	Model terms	Justification
Ground cover	%_litt + %_woody	Variability of litter, bare ground, and herbaceous groundcover will provide a variety of refuge sites for lizards (Mushinsky 1985, Greenburg 1994, Ruthven et al. 2008)
Structural	%_CWD + L_dep	Increased structural diversity will provide ground-level thermoregulation, nesting, and refuge sites for lizards (James and M'Closkey 2003, Owens et al. 2008)
Thermal	Air_temp + %_woody	Increased air temperature and habitat heterogeneity will present lizards with multiple thermoregulation opportunities (Vitt et al. 1998, Pianka and Vitt 2003)
Canopy	For_3 + L_dep	A stratified canopy and varying litter depth will collectively provide a variety of foraging, refuge, perching, and thermoregulation sites (Vitt et al. 1998, Greenberg 2001, Ruthven et al. 2008)
Global	%_litt + %_woody + %_CWD + L_dep + Air_temp + For_3	Global model

We also evaluated the influence of treatment and the treatment \times year interaction for each model set. See Table 1 for microclimate and microhabitat variable codes.

and Anderson 2002) to evaluate the relative importance of microhabitat and microclimate variables for explaining differences in lizard captures. We created a priori models (Peterman and Semlitsch 2009) based on our knowledge of lizard biology and the available literature (Table 2). To also determine the influence of forest treatments in a BACI framework, we evaluated the influence of both treatment and treatment \times year effects on lizard captures. We avoided an all-subsets modeling approach to avoid extraneous models that may not provide a biologically relevant explanation of the data (Burnham and Anderson 2002). We examined correlations among habitat variables and only included one variable from a correlated set when the correlation was >0.70 . For example, we originally intended to include basal area and canopy cover in the models but found that these variables were highly correlated with air temperature. We included air temperature in the models rather than basal area or percent canopy cover because thermal gradients are an important driver of activity patterns for most lizard species (Smith and Ballinger 2001, Pianka and Vitt 2003). We evaluated 15 total models for eastern fence lizards (*Sceloporus undulatus* Bosc and Daudin in Sonnini and Latreille), green anoles (*Anolis carolinensis* Voight), common five-lined skinks (*Plestiodon fasciatus* L.), broad-headed skinks (*Plestiodon laticeps* Schneider), and little brown skinks (*Scincella lateralis* Say in James). We excluded species with <60 captures from all analyses, which included coal skinks (*Plestiodon anthracinus* Baird) and southeastern five-lined skinks (*Plestiodon inexpectatus* Taylor).

We used Akaike's information criterion (AIC) to evaluate candidate models (Burnham and Anderson 2002) that best explained treatment and microhabitat and microclimate influences on lizard captures. We used linear mixed models (SPSS version 19.0) to create maximum-likelihood estimates for each model. We included block as a random effect; microhabitat and microclimate variables, treatment, and the treatment \times year interaction as fixed effects; and year as the repeated measure. Before analysis, lizard capture data were transformed with square root, logistic, and $1/x$ transformations to meet normality assumptions. We evaluated the same 15 candidate models for each lizard species using AIC adjusted for small sample sizes (AIC_c) (Burnham and Anderson 2002). We examined evidence ratios to evaluate the degree of difference between the highest supported and additional models. When there were several candidate models (evidence ratios <2.7), we averaged coefficients across the models and calculated SEs and 95% confidence intervals (CI) for the coefficients (Burnham and Anderson 2002). Last, we calculated R^2 values to evaluate the fit of variables with CIs that did not include 0.

Results

Microhabitat and Microclimate Response

We identified treatment-specific changes in the variables used to create lizard microclimate and microhabitat models. Pretreatment air temperatures ranged from 24.3 to 24.7° C and increased significantly in thinned stands ($F_{4, 34} = 12.11$, $P < 0.0001$; range, 32.4–33.7° C) (Table 3) after treatment. Litter depth ranged from 4.7 to 7.2 cm during pretreatment surveys and was reduced in thinned ($F_{4, 36} = 5.91$, $P = 0.009$) and burned stands ($F_{2, 36} = 11.14$, $P = 0.002$) to depths ranging from 4.8 to 5.5 and 3.7 to 3.8 cm in thin and thin with burn stands, respectively (Table 3). Pretreatment percent litter cover was consistently high (99.0–99.7% cover) in all stands and was reduced in burned stands ($F_{2, 34} = 4.17$, $P = 0.02$). Percent litter cover was reduced the greatest in stands receiving a thin with burn treatment (Table 3). Pretreatment CWD cover ranged from 0.7 to 2.4% and was not significantly affected by forest management practices. However, we did detect slight increases in CWD percent cover in thin and thin with burn stands after treatment (Table 3). Forest level 3 (understory) tree cover was highly variable during pretreatment sampling (40.2–76.4%) and was reduced in thinned ($F_{4, 34} = 4.7$, $P = 0.004$) stands to percent cover levels ranging from 12.5 to 19.5% (Table 3). We did not detect a treatment and year response for changes in woody vegetation cover; however, woody vegetation cover was significantly greater in light thin stands (32.9% cover) than in control stands (8.6% cover) in the second year posttreatment (Table 3).

Lizard Captures

We captured 719 individual lizards of seven species: *A. carolinensis* (261), *S. lateralis* (165), *S. undulatus* (129), *P. fasciatus* (97), *P. laticeps* (64), *P. anthracinus* (2), and *P. inexpectatus* (1) over 2,910 trap nights (block 1, 690 total trap nights; block 2, 1,146 total trap nights; and block 3, 1,074 total trap nights) (Appendix). Detection patterns for *A. carolinensis*, *P. fasciatus*, *P. laticeps*, *S. undulatus*, and *S. lateralis* were best described by the model with a constant detection probability, which provides support that changes in lizard captures were due to forest management rather than to unequal detection among treatments.

Lizard Responses to Forest Management

Of the seven lizard species encountered during this study, we recorded adequate captures of five lizard species (i.e., *A. carolinensis*, *P. fasciatus*, *P. laticeps*, *S. undulatus*, and *S. lateralis*) to examine forest treatment impacts. Overall, we found species-specific responses of lizards to forest management practices. Captures of *A.*

Table 3. Microclimate and microhabitat values by treatment before and after treatment in the BNF (2005–2008).

	C	B	LT	HT	LTB	HTB
Air temperature (° C)						
Pre	24.3 ± 0.2 ^A	24.3 ± 0.2 ^A	24.5 ± 0.4 ^A	24.5 ± 0.2 ^A	24.5 ± 0.2 ^A	24.7 ± 0.3 ^A
Post 1	28.5 ± 0.4 ^A	28.3 ± 0.5 ^A	34.2 ± 0.7 ^B	33.7 ± 1.2 ^{A,B}	34.5 ± 0.5 ^B	31.9 ± 0.7 ^B
Post 2	27.2 ± 0.1 ^A	27.6 ± 0.6 ^A	33.0 ± 2.1 ^B	33.7 ± 0.9 ^B	32.4 ± 1.1 ^B	33.7 ± 0.9 ^B
CWD cover (%)						
Pre	2.3 ± 1.0 ^A	0.7 ± 0.4 ^A	1.7 ± 0.6 ^A	1.7 ± 0.6 ^A	1.0 ± 0.1 ^A	2.4 ± 1.4 ^A
Post 1	1.4 ± 0.3 ^A	1.0 ± 0.5 ^A	2.3 ± 1.0 ^A	3.0 ± 0.1 ^A	2.3 ± 1.0 ^A	3.1 ± 1.0 ^A
Post 2	1.2 ± 0.2 ^A	0.9 ± 0.4 ^A	2.5 ± 0.8 ^A	2.0 ± 0.8 ^A	2.1 ± 0.8 ^A	3.3 ± 0.6 ^A
Forest level 3 cover (%)						
Pre	54.1 ± 11.0 ^A	72.3 ± 10.0 ^A	40.2 ± 2.8 ^A	73.7 ± 2.8 ^A	76.4 ± 19.5 ^A	69.4 ± 20.4 ^A
Post 1	43.0 ± 3.7 ^{A,B}	82.3 ± 7.9 ^A	22.2 ± 5.0 ^C	26.4 ± 2.8 ^C	22.2 ± 12.1 ^{B,C}	20.8 ± 9.6 ^{B,C}
Post 2	50.0 ± 12.7 ^{A,B}	70.8 ± 8.7 ^A	12.5 ± 4.8 ^C	19.4 ± 3.8 ^C	19.4 ± 11.4 ^{B,C}	19.5 ± 7.4 ^{B,C}
Litter depth (cm)						
Pre	6.9 ± 0.2 ^A	4.7 ± 0.4 ^B	6.6 ± 0.4 ^{AB}	5.6 ± 0.3 ^{AB}	7.2 ± 0.2 ^A	6.9 ± 0.4 ^A
Post 1	7.4 ± 0.4 ^A	3.7 ± 0.7 ^B	4.8 ± 0.5 ^{AB}	5.1 ± 0.1 ^B	3.7 ± 0.4 ^B	3.2 ± 0.4 ^B
Post 2	7.0 ± 0.3 ^A	4.3 ± 0.8 ^B	5.5 ± 0.5 ^{AB}	4.8 ± 0.2 ^B	3.8 ± 0.3 ^B	3.7 ± 0.3 ^B
Litter cover (%)						
Pre	99.0 ± 0.6 ^A	99.5 ± 0.1 ^A	99.2 ± 0.5 ^A	99.5 ± 0.4 ^A	99.4 ± 0.6 ^A	99.7 ± 0.3 ^A
Post 1	99.5 ± 0.3 ^A	97.5 ± 1.1 ^A	98.2 ± 0.4 ^A	97.7 ± 1.1 ^A	91.2 ± 3.5 ^A	90.7 ± 2.0 ^A
Post 2	98.8 ± 0.8 ^A	97.6 ± 1.6 ^A	98.5 ± 0.3 ^A	98.7 ± 0.7 ^A	97.9 ± 0.7 ^A	94.3 ± 2.3 ^A
Woody cover (%)						
Pre	4.1 ± 1.1 ^A	6.1 ± 2.1 ^A	14.3 ± 4.2 ^A	14.7 ± 8.1 ^A	7.0 ± 1.4 ^A	13.9 ± 4.2 ^A
Post 1	5.8 ± 1.1 ^A	7.6 ± 3.6 ^A	19.7 ± 4.7 ^A	16.5 ± 4.9 ^A	14.4 ± 3.4 ^A	18.4 ± 3.0 ^A
Post 2	8.6 ± 1.1 ^A	11.1 ± 2.9 ^{A,B}	32.9 ± 7.6 ^{B,C}	22.2 ± 7.5 ^{A,B}	24.4 ± 4.4 ^{A,B}	29.1 ± 8.4 ^{A,B}

Values are averages ± SE. Each treatment had three replications. Different superscript letters denote significant pairwise differences. Treatment designations are as follows: C, control; B, burn; LT, light thin; HT, heavy thin; LTB, light thin with burn; and HTB, heavy thin with burn. Sampling year abbreviations are as follows: Pre, pretreatment values, Post 1, posttreatment year 1 values, and Post 2, posttreatment year 2 values.

carolinensis during pretreatment surveys ranged from 0 to 9.3 individuals per 100 trap nights; posttreatment captures were greatest in thinned stands (range, 13.6–17.9 individuals per 100 trap nights). Although *A. carolinensis* captures tended to be highest in thinned stands during posttreatment surveys (Figure 1), the inclusion of the treatment model term ($\beta = 0.28 \pm 0.10$; 95% CI, 0.09–0.47) (Table 5) and not the treatment × year term in the highest supported models suggests that greater posttreatment captures in thinned stands were related to greater pretreatment abundance in these stands.

Pretreatment captures of *P. fasciatus* and *P. laticeps* ranged from 2.5–5.1 individuals per 100 trap nights and 0.8–5.0 individuals per 100 trap nights, respectively. Posttreatment captures for both species were neither negatively nor positively associated with the increasing forest disturbance gradient. Two of the top-ranked AIC models for *P. fasciatus* contained the treatment × year model term (Table 4); however, CIs included 0 ($\beta = 0.03 \pm 0.02$; 95% CI, –0.02 to 0.08), indicating that this term was not well supported (Table 5). We also did not detect a treatment effect for *P. laticeps*, as none of the highest supported models included the treatment or treatment × year model terms (Table 4).

Pretreatment captures of *S. undulatus* were relatively low (range, 0–5.6 individuals per 100 trap nights) but were greatest in thin with burn stands during the second year posttreatment sampling (range, 10.7–12.3 individuals per 100 trap nights) (Figure 1). This treatment × year response was included in the two highest supported models for *S. undulatus* (Table 4) and was supported based on CIs ($\beta = 0.08 \pm 0.02$; 95% CI, 0.04–0.12) (Table 5). The positive linear relationship between *S. undulatus* captures and increasing disturbance ($r^2 = 0.59$) (Figure 1) indicates that *S. undulatus* probably benefits from disturbed forest conditions (i.e., open canopy and reduced litter and vegetation).

Pretreatment captures of *S. lateralis* were highly variable (range, 4.3–20.5 individuals per 100 trap nights) across all treatments. Al-

though we observed large decreases in *S. lateralis* captures during the first year posttreatment in all stands excluding controls (range, 1.7–3.1 individuals per 100 trap nights), we observed an increase in captures during the second year of posttreatment in many of the stands whereas declines were noted previously (range, 2.7–9.0 individuals per 100 trap nights) (Figure 1). This treatment and year effect was supported in the top-ranked AIC model for *S. lateralis* (Table 4) and received support based on CIs ($\beta = 0.04 \pm 0.01$; 95% CI, 0.01–0.06) (Table 5). Interestingly, *S. lateralis* captures declined continuously in control stands throughout the study period (pretreatment, 18.8; posttreatment year 1, 8.0; and posttreatment year 2, 4.5 individuals per 100 trap nights), which suggests that *S. lateralis* may periodically exhibit population fluctuations independent of forest management.

Lizard Microclimate and Microhabitat Relationships

In addition to treatment-induced impacts, we aimed to evaluate the influence of environmental characteristics on lizard populations. Overall, the thermal model (Table 2) best explained *A. carolinensis* captures ($\omega_i = 0.48$) (Table 4), with the air temperature ($\beta = 11.87 \pm 2.36$; 95% CI, 7.25–16.49) (Table 5) model term positively associated with increased captures during first year ($r^2 = 0.42$) and second year ($r^2 = 0.60$) posttreatment surveys (Figure 1). Specifically, pretreatment captures of *A. carolinensis* were lower in stands with relatively lower air temperatures. After treatment, *A. carolinensis* captures increased linearly in forest stands with increasingly warmer air temperatures (Figure 1), suggesting that the thermal properties of harvested stands may have been the primary environmental characteristic driving the response of *A. carolinensis*. We also identified a weak positive relationship between *A. carolinensis* captures and woody vegetation cover during first ($r^2 = 0.33$) and second ($r^2 = 0.38$) year posttreatment surveys (Figure 1). The CWD model term ($\beta = 1.22 \pm 0.59$; 95% CI, 0.04–2.41) (Table 5) received support in the global model ($\omega_i = 0.30$) (Table 4) for

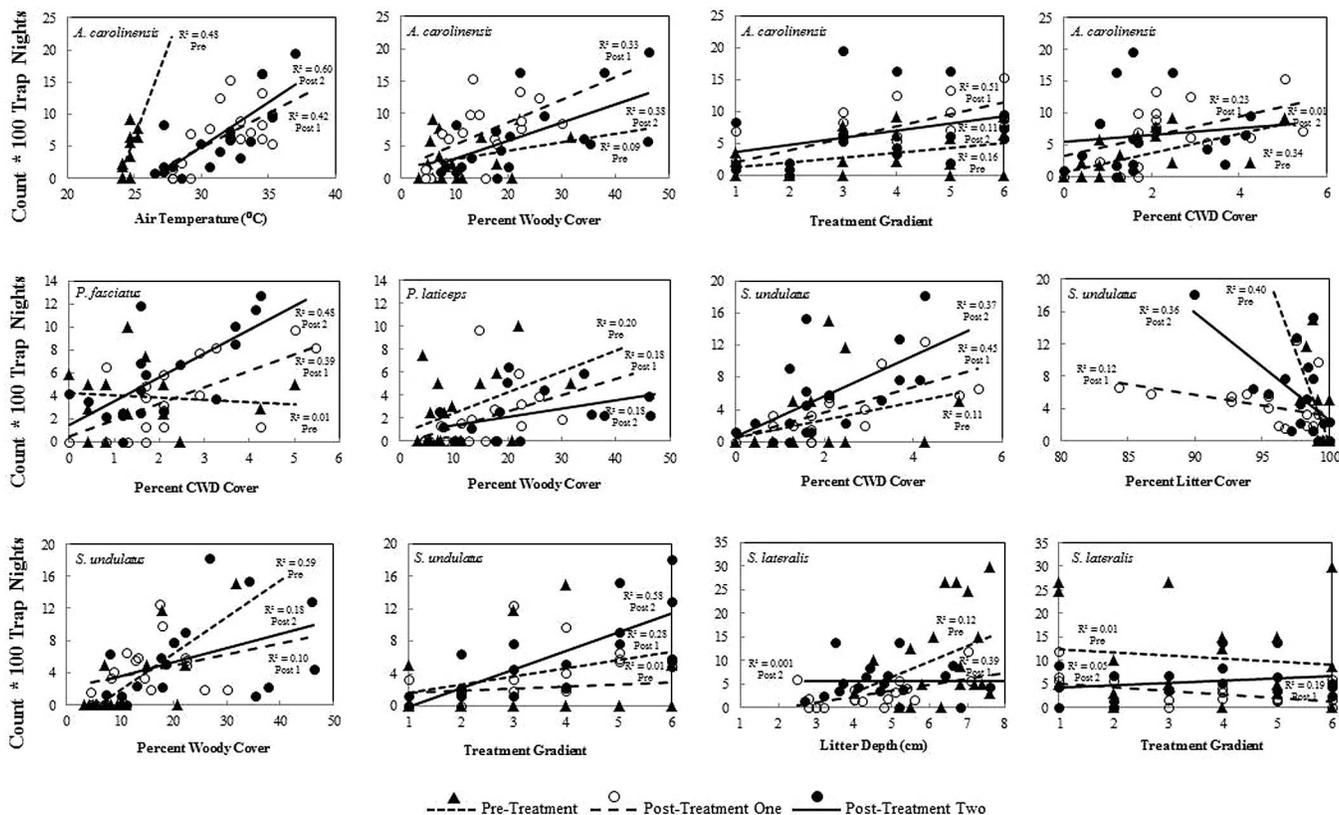


Figure 1. Univariate regressions relating lizard captures to treatment, microclimate, and microhabitat variables included in the highest ranked lizard predictive models. We only included figures depicting lizard and treatment, microclimate, and microhabitat relationships for variables that had CIs that did not include 0. Treatment designations were as follows: 1, control; 2, burn; 3, light thin; 4, heavy thin; 5, light thin with burn; and 6, heavy thin with burn.

Table 4. Highest supported ($\Delta AIC < 2.0$) predictive models describing lizard treatment, microclimate, and microhabitat relationships in the BNF (2005–2008).

Species	Model	$-2 \log$ likelihood ^a	K^b	AIC_c^c	ΔAIC_c^d	ω_i^e
<i>A. carolinensis</i>	Air_temp + %_woody + Treat + Treat*Year	122.33	10	147.44	0.00	0.48
	Air_temp + For_3 + %_CWD + %_litt + %_woody + L_dep + Treat + Treat*Year	109.64	14	148.41	0.96	0.30
<i>P. fasciatus</i>	%_CWD + L_dep + Treat*Year	107.12	9	129.21	0.00	0.23
	% CWD + L_dep	110.35	8	129.55	0.34	0.19
	% CWD + L_dep + Treat + Treat*Year	105.46	10	130.58	1.37	0.12
	Air_temp + %_woody	111.88	8	131.08	1.88	0.09
	For_3 + L_dep	111.91	8	131.11	1.90	0.09
<i>P. laticeps</i>	%_litt + %_woody	111.96	8	131.16	1.95	0.09
	Air_temp + %_woody	20.71	8	39.91	0.00	0.34
	%_litt + %_woody	21.52	8	40.72	0.81	0.23
<i>S. undulatus</i>	%_CWD + L_dep + Treat*Year	100.95	9	123.04	0.00	0.45
	%_litt + %_woody + Treat*Year	102.49	9	124.58	1.54	0.21
<i>S. lateralis</i>	%_CWD + L_dep + Treat*Year	37.58	9	59.67	0.00	0.70

See Table 1 for microclimate and microhabitat variable codes.

^a Value derived from the regression model.

^b Number of parameters in each model.

^c AIC adjusted for small samples.

^d The difference between the AIC of the highest supported model and each candidate model.

^e Akaike's weight value indicates relative support of each model. Higher values indicate models with better support.

describing increased captures of *A. carolinensis*. Specifically, CWD cover was most related to captures of this species during pretreatment ($r^2 = 0.34$) (Figure 1) surveys, which suggests that preexisting disturbances (i.e., *D. frontalis* infestations) probably resulted in increased CWD cover that may have positively influenced this species.

The structural model (Table 2) best described *P. fasciatus* captures ($\omega_i = 0.23$) (Table 4). In this model, the CWD model term

($\beta = 1.02 \pm 0.49$; 95% CI, 0.06–1.98) (Table 5) was associated with *P. fasciatus* captures. During pretreatment sampling, *P. fasciatus* captures were not associated with CWD cover ($r^2 = 0.01$). After treatment, *P. fasciatus* captures tended to increase in forest stands with greater CWD cover during first year ($r^2 = 0.39$) and second year ($r^2 = 0.54$) posttreatment surveys (Figure 1). Although *P. laticeps* captures were best explained by the thermal model, the

Table 5. Model-averaged parameter estimates, SEs, and 95% CIs for microclimate, microhabitat, and forest treatment variables in the AIC candidate models for each lizard species group in the BNF before and after implementation of thinning and prescribed burning treatments (2005–2008).

Species	Variable ^a	$\beta \pm SE$	95% CI
<i>A. carolinensis</i>	Air_temp ^a	12.09 ± 2.76	7.25 to 16.49
	For_3	0.02 ± 0.06	-0.11 to 0.15
	L_dep	0.25 ± 0.09	-0.01 to 0.44
	%_CWD ^a	1.22 ± 0.59	0.04 to 2.41
	%_litt	-0.12 ± 0.98	-1.11 to 0.84
	%_woody ^a	0.22 ± 0.11	0.01 to 0.32
	Treat ^a	0.28 ± 0.10	0.09 to 0.47
	Treat*Year	-0.08 ± 0.06	-0.04 to 0.16
<i>P. fasciatus</i>	Air_temp	0.69 ± 2.08	-3.49 to 4.87
	For_3	-0.09 ± 0.05	-0.18 to 0.00
	L_dep	0.07 ± 0.07	-0.07 to 0.21
	%_CWD ^a	1.02 ± 0.49	0.06 to 1.98
	%_litt	-0.04 ± 0.33	-0.70 to 0.61
	%_woody	0.13 ± 0.08	-0.03 to 0.29
	Treat*Year	0.03 ± 0.02	-0.02 to 0.08
	Air_temp	-0.90 ± 0.84	-2.60 to 0.79
<i>P. laticeps</i>	%_litt	-0.06 ± 0.15	-0.36 to 0.23
	%_woody ^a	0.16 ± 0.04	0.09 to 0.23
	L_Dep	-0.06 ± 0.07	-0.20 to 0.08
<i>S. undulatus</i>	%_CWD ^a	1.42 ± 0.68	0.09 to 2.75
	%_litt ^a	-1.18 ± 0.34	-1.85 to -0.51
	%_woody ^a	0.28 ± 0.09	0.10 to 0.46
	Treat*Year ^a	0.08 ± 0.02	0.04 to 0.12
	L_Dep ^a	0.16 ± 0.04	0.09 to 0.24
<i>S. lateralis</i>	%_CWD	-0.16 ± 0.25	-0.66 to 0.35
	Treat*Year ^a	0.04 ± 0.01	0.01 to 0.06

^aVariables with CIs that did not include 0.

woody vegetation cover model term ($\beta = 1.69 \pm 0.45$; 95% CI, 0.78–2.61) was weakly associated with captures of this species during all sampling years (Figure 1).

The habitat structure ($\omega_i = 0.45$) and groundcover models ($\omega_i = 0.21$) best described *S. undulatus* captures (Table 4). The CWD cover term ($\beta = 1.42 \pm 0.68$; 95% CI, 0.09–2.75) of the structural model and the litter cover term ($\beta = -1.18 \pm 0.34$; 95% CI, -1.85 to -0.51) in the ground cover model were positively ($r^2 = 0.58$) and negatively ($r^2 = 0.39$) associated with *S. undulatus* captures during second year posttreatment surveys, respectively (Figure 1). Pretreatment *S. undulatus* captures were weakly associated with sites possessing greater CWD cover (Figure 1). After treatment, *S. undulatus* captures increased linearly in forest stands with increased CWD cover (Figure 1). These results suggest that disturbances that decrease litter cover and increase CWD are probably beneficial for *S. undulatus* populations.

The structural model also best explained *S. lateralis* captures ($\omega_i = 0.70$) (Table 4), with the litter depth model term ($\beta = 0.16 \pm 0.04$; 95% CI, 0.01–0.06) (Table 5) primarily associated with *S. lateralis* captures. During pre- and posttreatment year 1 surveys, *S. lateralis* captures were greater in forest stands with greater litter depth. This relationship was relatively weak ($r^2 = 0.12$) during pretreatment surveys but received stronger support during first year posttreatment surveys ($r^2 = 0.39$) (Figure 1), indicating that changes in litter depth may be an important environmental characteristic regulating the response of *S. lateralis* to disturbance.

Discussion

Factors Affecting Lizard Responses to Forest Management

Our analyses revealed species-specific responses of southeastern lizard species to prescribed burning and thinning. In addition to

treatment effects, we observed diverse lizard species responses to changes in microhabitat and microclimate variables. Sutton et al. (2013) identified species-specific responses of southeastern lizards to forest management but did not explore the relative importance of the changes in microhabitat and microclimate characteristics for determining lizard responses to these disturbances. This current analysis identifies species-specific microhabitat and microclimate characteristics that drive responses of southeastern lizards to forest management in a multiple hypothesis framework. Specifically, *A. carolinensis* captures were greatest in forest stands with warmer air temperatures. Although captures for this species were not associated with the increasing forest disturbance gradient, the forest disturbances implemented in this study increased ambient air temperatures, suggesting that this species may benefit from forest canopy removal. Kilpatrick et al. (2010) similarly found that *A. carolinensis* responded positively to management practices that resulted in partial canopy removal. However, this species declined in abundance after removal of hardwood trees and reintroduction of fire in a longleaf pine forest, probably because this species is highly associated with hardwood habitats (Steen et al. 2013a). Herein, we corroborate this suggestion, finding that *A. carolinensis* benefits from removal of pine trees to facilitate restoration of hardwood forests. In addition, lizards with higher heliothermic tolerances (e.g., *Sceloporus*, *Anolis*, and *Aspidoscelis*) tend to colonize and inhabit open habitats with increased thermoregulation opportunities (Greenberg and Waldrop 2008, Ruthven et al. 2008, Kilpatrick et al. 2010). Our results for this species are consistent with previous research, suggesting that thermal gradients are important for determining lizard activity patterns (Du et al. 2006) and that the thermal landscape is of utmost importance for many lizard species (Smith and Ballinger 2001, Pianka and Vitt 2003). Furthermore, lizards are reliant on thermoregulation for a majority of life processes (e.g., foraging, breeding, growth, and predator avoidance) and many species have complex relationships with their surrounding habitat to maintain optimal body temperatures (Huey and Slatkin 1976, Pianka and Vitt 2003). The positive association of *A. carolinensis* captures with CWD cover during pretreatment surveys suggests that preexisting disturbances from *D. frontalis* infestations were important for determining the response of *A. carolinensis* to forest management. Forest stands with greater pretreatment captures of *A. carolinensis* tended to also have canopy disturbances due to *D. frontalis* infestations, which resulted in large canopy gaps with abundant downed woody debris (Sutton et al. 2010).

Neither *P. fasciatus* nor *P. laticeps* was directly affected by prescribed burning and thinning. This was indicated by the lack of support for the treatment and treatment \times year model terms in the highest supported models. Prior research suggests that *Plestiodon* species either respond positively (Kilpatrick et al. 2010) or show no measurable response to forest harvesting (Renken et al. 2004, Goldstein et al. 2005). Our sample size for *P. laticeps* was considerably less than that for the other species evaluated in this study, and it is likely that we may not have been able to detect a treatment response. However, both *P. fasciatus* and *P. laticeps* tend to inhabit more mesic, forest interior sites (Jensen et al. 2008, Kilpatrick et al. 2010) and probably do not have high thermal requirements compared with those of the other more heliothermic lizard species (Sutton et al. 2013). In the current study, *P. fasciatus* tended to be associated with forest stands possessing increased CWD cover. Specifically, treatment plots with greater amounts of downed woody debris

tended to have greater captures of *P. fasciatus*, especially during the second year of posttreatment sampling. The amount of residual CWD cover was highly variable at the individual forest stand, and the overall amount of residual CWD depended more on whether a stand was harvested rather than on the type of stand disturbance. *P. fasciatus* inhabit sites with an abundance of downed woody debris and are able to inhabit disturbed (i.e., urbanized) sites as long as CWD and refuge sites are maintained (Hecnar and M'Closkey 1998). In addition, studies of nest site selection have found that female *P. fasciatus* tend to select large, moderately decayed logs as nesting and brooding sites (Hecnar 1994).

Captures of *S. undulatus* increased in thin with burn stands up to 2 years posttreatment, indicating that disturbance practices resulting in canopy removal along with litter and groundcover vegetation reduction may be beneficial for this species. Our results are consistent with what others have found for *S. undulatus* elsewhere in the southeastern United States; for example, captures of this species increased in forest stands that have been managed with prescribed burning (Steen et al. 2013a) or a combination of prescribed burning and thinning (Greenberg and Waldrop 2008, Perry et al. 2009, Matthews et al. 2010). We found that *S. undulatus* captures increased in thin with burn stands after treatment as a result of the simultaneous reduction of canopy and litter cover and increased CWD cover. Past research has found that lizards in the genus *Sceloporus* occupy highly disturbed, open habitats with abundant CWD cover (Greenberg et al. 1994, Angert et al. 2002, James and M'Closkey 2003) and decreased canopy cover (Greenberg et al. 1994, Ruthven et al. 2008). Our findings provide support that thin with burn management creates environmental conditions that may lead to population increases of *S. undulatus*.

Scincella lateralis captures declined considerably during first year posttreatment surveys in all treated stands. Furthermore, the treatment \times year interaction term was supported in the top habitat model. However, when we compared *S. lateralis* captures by year, we found that some stands where declines were noted in the first posttreatment year recovered to pretreatment abundance during second year posttreatment surveys. This finding suggests that disturbance in the form of thinning and burning management may have short-term negative effects on *S. lateralis*. Greenberg et al. (1994) similarly found that *S. lateralis* in fire-prone, sandhill habitats were more abundant in unmanaged, control sites. However, Renken et al. (2004) found that *S. lateralis* captures increased after even-aged forest management and attributed these increases to possible recruitment from nearby undisturbed stands. Our habitat models provided evidence that the reduction of the litter layer may have led to declines in *S. lateralis* captures during the first posttreatment year. However, the steady decline of *S. lateralis* in control plots throughout all years makes it difficult to draw conclusions regarding the response of this species to thinning and burning forest management. Specifically, it is difficult to understand whether the changes in *S. lateralis* captures among years are due to perceived treatment impacts or stochastic population changes across all sites. Continued monitoring is necessary over periods of repeated disturbances to draw robust conclusions regarding the response of *S. lateralis* to prescribed burning and thinning forest management practices, especially considering that *S. lateralis* declined after long-term prescribed burning elsewhere (Steen et al. 2013a).

Anthropogenic Disturbances and Lizard Conservation

Most anthropogenic disturbances have the potential to affect the thermal environment, which in turn may positively influence certain lizard species residing in these habitats. However, the type and degree of the disturbances are important to consider because one of the major causes of worldwide reptile declines is anthropogenic habitat alteration (Gibbons et al. 2000, Sinervo et al. 2010). Although some lizard species adapt readily to human-altered landscapes, many species are sensitive to disturbances including urbanization or habitat conversion (Vega et al. 2000, Germaine and Wakeling 2001, Pianka and Vitt 2003). Overall, our study illustrates that thinning and thinning with prescribed burning created habitat conditions that led to changes in abundance for some southeastern lizard species; however, continued research examining how patterns of habitat heterogeneity and habitat succession affect lizard biodiversity patterns at the landscape scale are necessary to conserve lizard species assemblages that display a variety of responses to disturbance. Elmqvist et al. (2003) defines this disparity of species responses within a functional group to disturbance as response diversity; ecosystems with higher response diversity tend to maintain higher resiliency. Therefore, forest management that creates a mosaic of habitats may be more likely to increase lizard response diversity at the landscape scale and increase the overall resiliency of these ecosystems to environmental stressors (e.g., climate change and urbanization).

Large-scale ecosystem manipulation projects are invaluable to conservation because they permit a robust assessment of biodiversity responses to disturbance at the stand and landscape scale. Poiani et al. (2000) suggest that such multiscale approaches are necessary to account for rare species and ecosystems at local scales and relatively common species and habitats at larger spatial scales. Over the long-term, this approach will lead to the development of comprehensive management plans that contribute to the long-term conservation of forest biodiversity. Our study illustrates that a mosaic of managed forest habitats provides a suite of microhabitat and microclimate characteristics that leads to species-specific responses of a southeastern lizard assemblage.

Conclusions

Our results provide short-term information on the response of a southeastern lizard assemblage to prescribed burning and thinning forest management. Overall, we found that gradients in air temperature, CWD cover, litter cover, and litter depth were important drivers of lizard responses. Management considerations should include leaving behind large (>10-cm diameter) logs after completion of management practices to provide cover and thermoregulation sites for certain lizard species. Our results suggest that no single treatment will provide required habitat conditions for all lizard species. To maximize lizard abundance, it is important to provide a mosaic of habitat disturbance ranging from undisturbed, closed-canopy to heavily disturbed forest stands managed with prescribed burning and thinning. These management practices will provide greater habitat heterogeneity at the landscape scale and will create habitat for a wide range of species including litter-dwelling and disturbance-dependent lizard species. Our study highlights potential microhabitat and microclimate characteristics driving lizard responses in disturbed southeastern forests and evaluates the responses of multiple species to forest disturbances so management and conservation strategies can be developed to accommodate habitat requirements from a multispecies perspective.

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Appendix

Table A1. Total pre- and posttreatment lizard captures by forest treatment in the BNF (2005–2008).

	C			B			LT			HT			LTB			HTB			Year total	Species total
	B1	B2	B3	B1	B2	B3	B1	B2	B3	B1	B2	B3	B1	B2	B3	B1	B2	B3		
<i>Anolis carolinensis</i>																				
Pre	0	1	2	0	0	0	0	1	5	2	1	5	0	3	1	3	0	4	28	
Post 1	1	8	2	0	0	0	7	7	10	11	7	5	12	12	7	14	9	9	121	
Post 2	6	2	1	0	1	2	16	7	8	13	4	5	13	8	2	7	10	7	112	261
<i>Plestiodon anthracinus</i>																				
Pre	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Post 1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
Post 2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2
<i>Plestiodon fasciatus</i>																				
Pre	2	1	1	1	2	1	1	0	1	1	1	0	2	0	2	1	0	3	20	
Post 1	2	1	4	0	0	0	0	1	3	4	3	5	3	1	5	5	2	2	41	
Post 2	1	2	0	0	2	2	1	3	4	2	2	1	1	4	2	3	2	4	36	97
<i>Plestiodon inexpectatus</i>																				
Precaptures	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Post 1 captures	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Post 2 captures	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1
<i>Plestiodon laticeps</i>																				
Precaptures	0	0	2	0	0	3	0	2	0	1	1	1	0	0	1	2	0	2	15	
Post 1 captures	0	1	0	0	0	0	1	2	6	2	0	0	3	0	1	1	1	2	20	
Post 2 captures	0	0	2	0	0	1	1	2	5	1	1	2	0	5	4	2	0	3	29	64
<i>Sceloporus undulatus</i>																				
Precaptures	0	0	2	0	0	0	0	4	0	3	0	0	0	0	1	0	2		12	
Post 1 captures	0	0	2	1	0	1	1	9	2	1	3	6	3	4	4	3	4	3	47	
Post 2 captures	0	0	1	1	1	5	2	1	6	1	2	4	4	13	6	8	5	10	70	129
<i>Scincella lateralis</i>																				
Precaptures	1	9	10	0	1	4	1	9	2	0	5	5	1	1	6	0	3	12	70	
Post 1 captures	6	4	4	0	4	0	2	0	1	1	3	2	1	1	1	3	0	1	34	
Post 2 captures	2	0	7	3	0	1	3	3	3	6	7	4	6	3	5	2	2	4	61	165
Site total	22	30	40	6	11	20	36	52	56	49	40	45	49	55	47	55	38	68		
Treatment total		92			37			144			134			151		161			Total captures: 719	

Captures have not been corrected for sampling effort. Sites with the same block designation (e.g., B1) were from the same experimental block. Treatment designations are as follows: C, control; B, burn; LT, light thin; HT, heavy thin; LTB, light thin with burn; and HTB, heavy thin with burn. Sampling year abbreviations are as follows: Pre, pretreatment captures, Post 1, posttreatment year 1 captures, and Post 2, posttreatment year 2 captures.