

Response of Lizards to High-Severity Wildfires in a Southern United States Mixed Pine/Hardwood Forest

Adam Duarte¹, Donald J. Brown^{2,3}, and Michael R. J. Forstner⁴

High-severity forest fires are increasing in large areas of the southern and western United States as the climate becomes warmer and drier. Natural resource managers need a better understanding of the short- and long-term effects of wildfires on lizard populations, but there is a paucity of studies focused on lizard-wildfire relationships. We used a before-after, control-impact (BACI) sample design to assess the response of three lizard species—Six-lined Racerunner (*Aspidoscelis sexlineata*), Prairie Lizard (*Sceloporus consobrinus*), and Little Brown Skink (*Scincella lateralis*)—to high-severity wildfires that occurred in the Lost Pines Ecoregion, Texas, USA. Specifically, we analyzed monitoring data collected across 17 trapping sessions from spring 2008 to spring 2013 using stratified N-mixture models to estimate trends in lizard abundances, while accounting for environmental parameters that might influence lizard detectability. We found no evidence of a fire-induced change in abundance for any of the lizard species we studied, but there was an increase in detectability of *A. sexlineata* following the wildfires. Detectability of *A. sexlineata* and *S. lateralis* increased with air temperature, detectability of *S. consobrinus* decreased with precipitation, and detectability was related to Julian day for all three species. Mean detection probabilities were low (<0.1), suggesting capture-mark-recapture methods at a subset of sample units should be implemented to derive more accurate estimates in future monitoring efforts. Our results provide quantitative evidence of the short-term effects of high-severity wildfires on three widely distributed lizard species. Given the wildfires did not result in decreased lizard abundances, managers should minimize their vehicle footprints off of roads during post-wildfire habitat restoration to avoid soil compaction and the potential for direct mortality.

FUNDAMENTAL to wildlife management is the ability to forecast how species will respond to changes in the environment. Improved understanding of wildlife population-level responses to high-severity wildfires (i.e., wildfires that kill or top-kill the majority of live vegetation and consume the majority of dead organic matter) is needed to assist land managers with post-fire management decisions (Bisson et al., 2003; Beschta et al., 2004). This information is critical in much of the southern and western United States, especially in pine-dominated and mixed-pine forests (Miller et al., 2009; Miller and Safford, 2012) where climatic shifts toward warmer and drier conditions, coupled with long-standing and broad-scale fire suppression, have resulted in an escalation of high-severity wildfires (Litschert et al., 2012; Crotteau et al., 2013; Hurteau et al., 2014).

There is a paucity of information concerning the response of lizards to high-severity wildfires in the United States. In a chaparral dominated mountain range of the southwestern United States, lizard relative abundance, richness, and diversity was greater in a burned forest three years following a high-severity wildfire (Cunningham et al., 2002). Furthermore, there was no evidence high-severity wildfires resulted in direct mortality of Six-lined Racerunners (*Aspidoscelis sexlineata*) or Prairie Lizards (*Sceloporus consobrinus*) in a southern United States mixed pine/hardwood forest (Brown et al., 2014a). Additional studies in Australia found the direction and magnitude of reptile population-level responses to high-severity wildfires were species specific (e.g., Braithwaite, 1987; Driscoll and Henderson, 2008; Pianka and Goodyear, 2012; Doherty et al., 2015). Thus, there is a need for additional research on both short- and long-term effects of high-severity wildfires on lizards in the United

States. Furthermore, fires in Australia have been linked to increased movement rates of reptiles, which led to increased captures in pitfall traps (Driscoll et al., 2012). Therefore, accounting for heterogeneous detection probabilities is necessary to separate population-level responses of lizards and fluctuations in sample efficiency among habitat disturbance treatments.

In this study, we investigated population-level responses to high-severity wildfires and examined factors that might influence detection probabilities of *A. sexlineata*, *S. consobrinus*, and Little Brown Skink (*Scincella lateralis*). These species have large geographic ranges and differing habitat associations. *Aspidoscelis sexlineata* and *S. lateralis* are distributed throughout the southern and eastern United States, and *S. consobrinus* are distributed throughout much of the central United States (Jones and Lovich, 2009). *Aspidoscelis sexlineata* are associated with hot and dry environments, sandy soils, and open canopies (Bellis, 1964; Paulissen, 1988; Trauth and McAllister, 1996). In contrast, *S. consobrinus* are associated with open and edge habitats (Ferguson et al., 1980; Jones and Lovich, 2009). Furthermore, *S. consobrinus* are negatively associated with litter depth (Bateman et al., 2008) but positively associated with ground cover and downed woody debris (Perry et al., 2009). Lastly, *S. lateralis* are positively associated with interior forest habitats with deep litter (Fitch and von Achen, 1977; Watson, 2009; Sutton et al., 2010, 2014).

We monitored these lizard species in a southern United States mixed pine/hardwood forest for 17 trapping sessions across six years, a period that overlapped two high-severity wildfires. Our objectives were to (i) estimate trends in lizard abundance as part of the larger monitoring program, (ii)

¹ Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall, Corvallis, Oregon 97331; Email: adam.duarte@oregonstate.edu. Send reprint requests to this address.

² School of Natural Resources, West Virginia University, PO Box 6125, Morgantown, West Virginia 26506; Email: donald.brown1@mail.wvu.edu.

³ U.S. Forest Service, Northern Research Station, PO Box 404, Parsons, West Virginia 26287.

⁴ Department of Biology, Texas State University, 601 University Drive, San Marcos, Texas 78666; Email: mf@txstate.edu.

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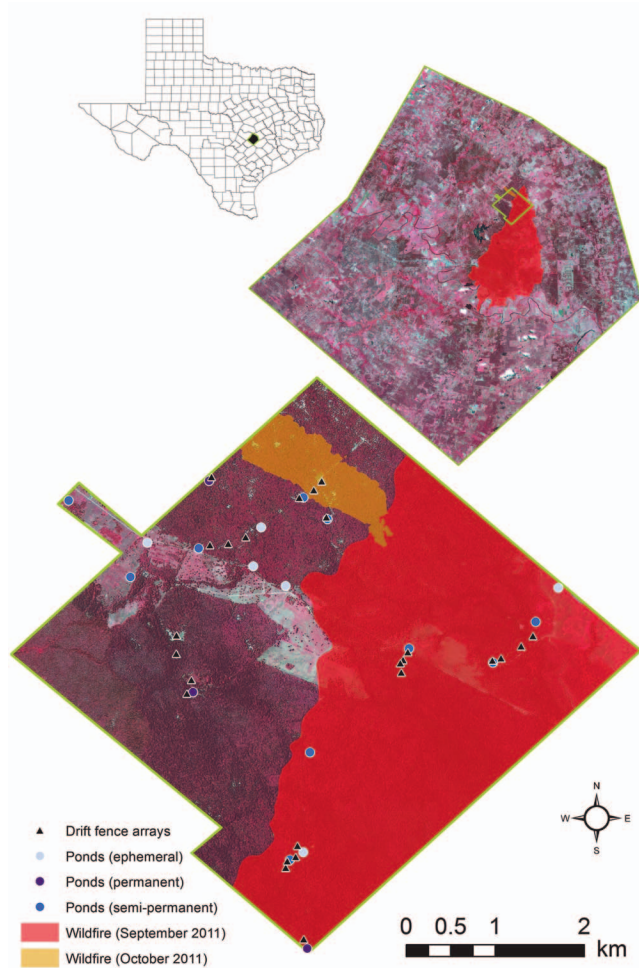


Fig. 1. Aerial image of the Griffith League Ranch (GLR), Bastrop County, Texas, USA and its location with respect to the high-severity wildfires that occurred in the Lost Pines Ecoregion in September and October 2011. Overlain on the image are the fires and the locations of the drift-fence arrays and ponds. On the right, images of the terrestrial habitat around a drift-fence array on the GLR before (A), shortly after (B), and ca. 1 y after (C) the fires.

examine the influence of environmental factors on lizard detection probabilities, and (iii) identify if burn treatments influenced lizard abundance and/or detectability. We analyzed three of the 17 trapping sessions as part of a previous study (e.g., Brown et al., 2014a). Here, we perform a more robust analysis to better understand the response of lizards to high-severity wildfires by incorporating a longer time series of monitoring data and studying the population dynamics of an additional species. Based on previous research and natural history characteristics that were described above, we hypothesized that the high-severity wildfires would lead to an increase in abundance of *A. sexlineata* and *S. consobrinus* and a decrease in abundance of *S. lateralis*. We also hypothesized lizard detection probabilities would be positively related to temperature and negatively related to precipitation based on our qualitative observations from six years of monitoring.

MATERIALS AND METHODS

Study area.—This study was conducted on the Griffith League Ranch (GLR), a 1,948 ha ranch owned by the Boy Scouts of America and located in the Lost Pines Ecoregion of Texas, USA. The property is primarily forested, with a pre-burn overstory dominated by Loblolly Pine (*Pinus taeda*), Post Oak (*Quercus stellata*), Blackjack Oak (*Q. marilandica*), and

Eastern Red Cedar (*Juniperus virginiana*), and an understory dominated by Yaupon Holly (*Ilex vomitoria*), American Beautyberry (*Callicarpa americana*), and Farkleberry (*Vaccinium arboreum*). On 4 September 2011, a high-severity wildfire ignited from multiple initial fire outbreaks across the Lost Pines. The fire could not be controlled initially due to wind gusts in excess of 58 kph resulting from the passage of tropical storm Lee, coupled with extreme drought conditions in central Texas (Lost Pines Recovery Team, 2011). After 18 days, the fire was 95% contained, with the total burn area encompassing 13,406 ha (ca. 39% of the ecoregion). On 4 October 2011, the fire breached a fire break, burning an additional 125 ha. The high-severity wildfires on 4 September 2011 and 4 October 2011 burned 987 ha and 80.5 ha of GLR, respectively. This resulted in a total fire effect on ca. 55% of the property (Fig. 1).

Brown et al. (2013, 2014a, 2014b, 2014c, 2015) described the effects of the wildfires on forest structure, vegetation, and terrestrial arthropods on the GLR. Briefly, mean overstory tree mortality was 87.0% (SD = 28.1%) and mean pole-sized tree mortality was 97.0% (SD = 10.6%; Brown et al., 2015). The fires consumed nearly all of the live and dead ground vegetation, resulting in a 'moonscaped' ground layer, but ground vegetation recovered within a year (Brown et al., 2014c; Fig. 1). The fires changed the arthropod community

Table 1. Summary of lizard monitoring efforts on the Griffith League Ranch (GLR), Bastrop County, Texas, USA.

Initial date	Trap nights	Burn period
03/01/2008	42	Pre-burn
04/17/2008	14	Pre-burn
02/01/2009	89	Pre-burn
07/10/2009	7	Pre-burn
11/20/2009	8	Pre-burn
01/31/2010	90	Pre-burn
07/17/2010	7	Pre-burn
09/05/2010	7	Pre-burn
10/17/2010	7	Pre-burn
11/21/2010	7	Pre-burn
02/13/2011	81	Pre-burn
05/12/2011	11	Pre-burn
07/16/2011	7	Pre-burn
09/25/2011	8	Post-burn (1 st)
11/20/2011	7	Post-burn (2 nd)
02/19/2012	71	Post-burn (2 nd)
03/10/2013	49	Post-burn (2 nd)

composition (e.g., Araneae [spiders] decreased and Gryllacrididae [raspy crickets] increased), but total captures of arthropods was not significantly different before and after the fires (Brown et al., 2014c). At the same time, red-imported fire ants (*Solenopsis invicta*), a potential predator of lizards (Allen et al., 2004; Newman et al., 2014), were more prevalent following the reduction in canopy cover (Brown et al., 2013).

Sample design.—Lizards were monitored from spring 2008 to spring 2013 using drift fence arrays. Traps were open for 17 trapping sessions, each comprised of a variable number of trap nights (Table 1). In spring 2008, 18 Y-shaped drift fence arrays were used for sampling, and prior to spring 2009 an additional seven linear drift fence arrays were built. The linear arrays were located adjacent to, and parallel with, pond borders, whereas Y-shaped arrays were placed in upland habitat that was primarily forested. The original purpose of the trap arrangement was to monitor the population status and assess terrestrial habitat use patterns of the endangered Houston Toad (*Bufo* [*Anaxyrus*] *houstonensis*; Duarte et al., 2011, 2014; Vandeweghe et al., 2013), with arrays constructed in sets of four distributed from the upper banks of the ponds into adjacent upland habitat (see Fig. 1). The aboveground height of the drift fence array flashing was ≥ 18 cm, with the flashing buried ca. 10 cm belowground. Y-shaped arrays consisted of three 15 m arms with a 19 l center bucket and a 19 l bucket at each arm terminus. Linear arrays consisted of a 15 m arm with a 19 l bucket at each end, and a double-throated funnel trap in the center of the array on each side of the flashing (Farallo et al., 2010). Pitfall traps were equipped with flotation devices to mitigate mortality during bucket flooding, and both pitfall and funnel traps had wet sponges to provide a moist environment. Pitfall traps were also equipped with predator exclusion devices (Ferguson and Forstner, 2006). For all trapping sessions, traps were checked each morning to process herpetofaunal captures. In summer 2009, we began cohort marking *S. consobrinus* and *A. sexlineata* via toe clipping. Toe clippings were not carried out on *S. lateralis* to minimize the handling of individuals and avoid tail autotomy.

The fires resulted in a before-after, control-impact (BACI) sample design with four and two years of pre- and post-burn data, respectively (Table 1). The fires destroyed most traps within the burned areas. Destroyed traps were rebuilt in their exact pre-burn locations. Fire breaks installed on the ranch during the September 2011 fire resulted in a nearly balanced sample design for the first post-fire trapping session, with 13 traps (9 Y-shaped arrays and 4 linear arrays) and 12 traps (9 Y-shaped arrays and 3 linear arrays) located in burned and control areas, respectively. The October 2011 fire burned the habitat surrounding two additional arrays, resulting in 15 traps (11 Y-shaped arrays and 4 linear arrays) located in burned areas, and ten traps (7 Y-shaped arrays and 3 linear arrays) located in control areas, for subsequent post-fire trapping sessions.

Precipitation data were collected daily concurrent with checking traps using two rain gauges located on the GLR. We used the mean of the values for this study. Maximum daily temperature data were obtained from the National Oceanic and Atmospheric Administration Climatic Data Center located in Elgin, Texas (the nearest weather station, located ca. 17.7 km northwest of the GLR; <http://www.ncdc.noaa.gov/cdo-web/>).

Statistical analyses.—Data were analyzed using stratified open population N-mixture models (Kéry et al., 2009). N-mixture models leverage spatially and temporally replicated count data to estimate population size and detection probability by partitioning the variation in the data into observation and state processes (Royle, 2004). N-mixture models assume population closure for each sample unit within a trapping session. Since dispersal rates are relatively high at juvenile life stages, juvenile captures for *S. consobrinus* and *A. sexlineata* were discarded. This was not done for captures of *S. lateralis* because of our inability to differentiate juveniles from adults and missing body-size data of individuals. We restricted the analyses to monitoring data collected during the first seven trap nights of each trapping session because some of the trapping sessions were relatively long (see Table 1), which could also result in population closure assumption violations. Data for each lizard species were analyzed separately; however, all analyses used the identical initial model structure described below.

The state process represents the ecological process variation in the number of individuals across time and space (i.e., true fluctuations in abundance). It was assumed that abundance (N) at each sample unit (i) in each trapping session (k) followed a Poisson distribution, and the state process was modeled as follows:

$$N_{i,k} \sim \text{Poisson}(\lambda_{i,k}),$$

$$\log(\lambda_{i,k}) = \alpha_0 + \alpha_1 \times \text{year}_k + \alpha_2 \times \text{hab}_i + \alpha_3 \times \text{burn}_{i,k}.$$

We fit linear trend models across years (*year*) to examine annual trends in lizard abundances and allowed abundance to vary depending on whether the sample unit consisted of pond or upland habitat using a factor variable (*hab*). Importantly, we restricted the evaluation of burn treatment effects on abundance to an intercept adjustment parameterization, also using a factor variable (*burn*). We did not fit models with a $\text{year}_k \times \text{burn}_{i,k}$ interaction because our study is limited to four trapping sessions or three years of post-burn monitoring data and fitting models to estimate slope adjustments (i.e., a change in the direction of abundance

trends following the fires) with three data points seemed unreasonable. Furthermore, the intercept adjustment parameterization should capture any short-term population-level response to the fires, which was the aim of our study.

We were particularly interested in examining the potential influence of burn treatment, temperature, and precipitation on detection probabilities. Yet, herpetofaunal surveys often detect unimodal patterns in captures, with the greatest frequency of captures occurring at the peak of the mating season. Therefore, the observation process was modeled as follows:

$$C_{i,j,k} | N_{i,k} \sim \text{binomial}(N_{i,k}, p_{i,j,k}),$$

$$\begin{aligned} \text{logit}(p_{i,j,k}) = & \beta_0 + \beta_1 \times \text{burn}_{i,k} + \beta_2 \times \text{temp}_{i,j,k} + \beta_3 \times \text{prec}_{i,j,k} \\ & + \beta_4 \times \text{date}_{i,j,k} + \beta_5 \times \text{date}_{i,j,k}^2, \text{ with} \\ & \text{prec}_{i,j,k} \sim \text{normal}(\mu_{\text{prec}}, \sigma_{\text{prec}}^2). \end{aligned}$$

C is the number of lizards captured on trap night j at sample unit i during trapping session k , p is detection probability, burn is a factor variable indicating whether the sample unit was burned, temp is maximum temperature, prec is precipitation, date is Julian day, and date^2 is to permit a quadratic effect of Julian day. Precipitation data were not recorded on four trap nights. Therefore, we estimated these missing data by specifying a prior for all precipitation values and estimating hyper-parameters (i.e., μ_{prec} and σ_{prec}^2) for the prior when fitting the models (Kéry and Royle, 2016).

These models were fitted using a Bayesian framework with JAGS (Plummer, 2003), called from program R (R Core Team, 2016) using the jagsUI package (Kellner, 2014). Explanatory variables were normalized by subtracting the mean value and dividing by the standard deviation to improve convergence (Kéry, 2010). Diffuse prior distributions were used for all of the estimated parameters. Specifically, priors of logit- and log-scale parameters were $\text{normal}(\mu = 0, \tau = 0.37)$ and $\text{normal}(\mu = 0, \tau = 0.001)$, respectively. The respective mean and standard deviation priors for precipitation values were $\text{normal}(\mu = 0, \tau = 0.01)$ and $\text{uniform}(\text{min} = 0, \text{max} = 100)$. Model runs involved four independent chains, each consisting of 600,000 iterations and a burn-in of 500,000 iterations. The Brooks and Gelman diagnostic ($\hat{R}$, Brooks and Gelman, 1998) and visual inspections of the trace and density plots of the posterior distributions were used to assess convergence. Model fit was assessed using a posterior predictive check and calculating a Bayesian P -value when fitting the global model for each species (Kéry, 2010; Link and Barker, 2010). Specifically, the lack of fit of the model when fitted with the realized and predicted (i.e., generated using the parameter estimates from the analysis) data were compared, and the proportion of times the discrepancy measure for the predicted data was greater than the discrepancy measure for the realized data was calculated. Model selection was carried out using indicator variables (Kuo and Mallick, 1998). This model selection process consists of introducing a latent, binary indicator variable (ω) for each explanatory variable and examining the posterior probabilities of indicator variables, where explanatory variables are considered important if the associated indicator variable more frequently receives a “1.” This model selection approach is computationally efficient because it allows for the evaluation of all possible combinations of explanatory variables simultaneously, where each unique sequence of indicator variables is a candidate model (Royle et al., 2014). However, vague priors for model

coefficients can result in convergence problems and indicator variables that fail to turn back on (i.e., switch from 0 to 1, reviewed in O’Hara and Sillanpää, 2009). To avoid this potential issue, we implemented slab and spike priors during the model selection process, where the prior of a coefficient (θ) is conditional on ω as follows:

$$\theta | \omega \sim \omega \times \text{normal}(0, \tau_{\text{prior}}) + (1 - \omega) \times \text{normal}(\mu_{\text{tune}}, \tau_{\text{tune}}).$$

Here, τ_{prior} is the diffuse prior for the precision of the coefficient and μ_{tune} and τ_{tune} are tuning parameters for the coefficient. It is recommended tuning parameters are near the posterior distribution of the coefficients (DellaPorta et al., 2002). Therefore, we fit the global model for each lizard species first and then used the resulting output estimates as the respective tuning parameters during the model selection process. Importantly, the posterior distribution of the coefficients are not heavily influenced by the inclusion of the seemingly informative tuning parameters (Hobbs and Hooten, 2015). We based our inferences on the selected model for each species, and posterior distributions were described by their mean and 95% credible interval (CI).

RESULTS

We based our inferences on 91 (13 trapping sessions), 7 (1 trapping session), and 21 (3 trapping sessions) total nights where traps were open during the pre-burn, post-burn (1st), and post-burn (2nd) periods, respectively. This resulted in 2,877 total trap nights and 106, 230, and 68 total captures of *A. sexlineata*, *S. consobrinus*, and *S. lateralis*, respectively. Since cohort marking began in summer 2009, within-session recaptures accounted for 18.1% and 15.0% of total captures of *S. consobrinus* and *A. sexlineata*, respectively.

Based on the posterior probabilities of the candidate models, data for each species supported the use of different explanatory variables (Table 2). Model diagnostics indicated convergence was achieved with $\hat{R} < 1.02$ for all estimates. The goodness-of-fit tests suggested that the global model fit adequately for *S. lateralis* (Bayesian P -value = 0.42) and *A. sexlineata* (Bayesian P -value = 0.08), but there was evidence of a lack of fit when fitting the global model for *S. consobrinus* (Bayesian P -value = 0.02).

As expected, abundance varied across years for *S. lateralis* and *S. consobrinus*; however, abundance of *A. sexlineata* was stable (Figs. 2, 3). Specifically, the results indicate abundance of *S. consobrinus* increased and abundance of *S. lateralis* decreased across the six years of monitoring. Furthermore, abundance of *S. consobrinus* was higher in upland habitats. An influence of the burn treatment on abundance was not supported for any of the lizard species.

Factors that influenced detection probabilities varied by species (Fig. 3). As expected, detection probabilities of *S. lateralis* and *A. sexlineata* increased with increasing temperatures, detectability of *S. consobrinus* decreased with increasing precipitation, and Julian day was related to detection probabilities for all three lizard species. Interestingly, detection probability of *A. sexlineata* increased in burned areas. Notably, mean detection probabilities were low across species (*A. sexlineata* = 0.03, 95% CI: 0.01–0.07; *S. consobrinus* = 0.08, 95% CI: 0.04–0.12; *S. lateralis* = 0.02, 95% CI: 0.00–0.03).

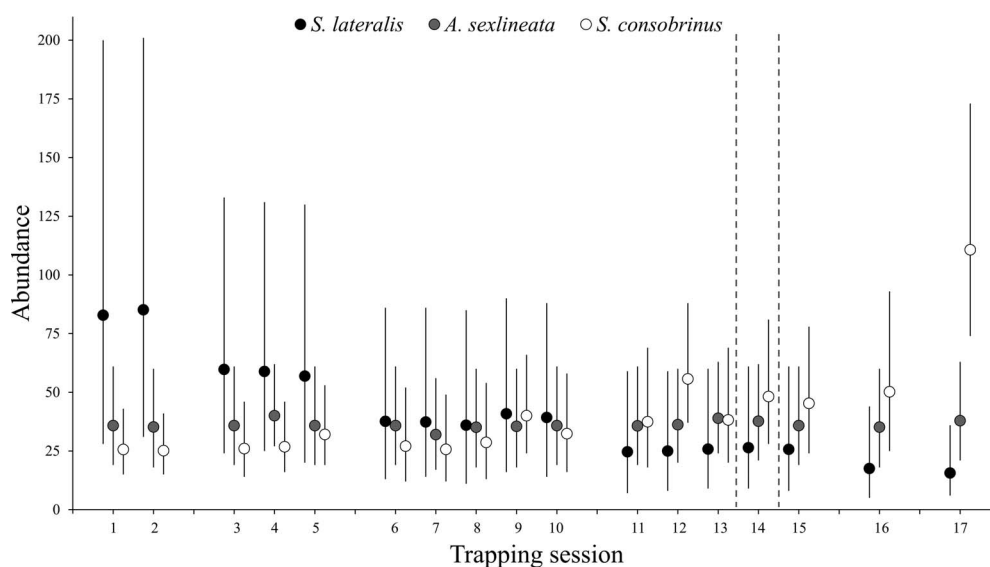
DISCUSSION

We investigated the temporal population dynamics and detection probabilities of three widely distributed lizard

Table 2. Posterior probabilities of the top ten candidate models for *Aspidoscelis sexlineata*, *Sceloporus consobrinus*, and *Scincella lateralis* on the Griffith League Ranch (GLR), Bastrop County, Texas, USA, spring 2008–spring 2013.

Species	Predictor variables		Posterior probability
	Abundance	Detection probability	
<i>S. lateralis</i>	<i>year</i>	<i>date + temp</i>	0.28
	<i>year</i>	<i>date + temp + burn</i>	0.10
	<i>year</i>	<i>temp</i>	0.09
	<i>year</i>	<i>date + date² + temp</i>	0.08
	<i>intercept</i>	<i>date + temp</i>	0.08
	<i>intercept</i>	<i>date + temp + burn</i>	0.06
	<i>year</i>	<i>temp + burn</i>	0.03
	<i>year</i>	<i>date + date² + temp + burn</i>	0.03
	<i>year + hab</i>	<i>date + temp</i>	0.03
	<i>year</i>	<i>date + temp + prec</i>	0.03
<i>S. consobrinus</i>	<i>year + hab</i>	<i>date + date² + prec</i>	0.67
	<i>year + hab</i>	<i>date + date² + prec + burn</i>	0.10
	<i>year + hab</i>	<i>date + date² + temp + prec</i>	0.08
	<i>year</i>	<i>date + date² + prec</i>	0.08
	<i>year + hab</i>	<i>date + temp + prec</i>	0.01
	<i>year + hab</i>	<i>date + date² + prec + temp + burn</i>	0.01
	<i>year</i>	<i>date + date² + prec + burn</i>	0.01
	<i>year</i>	<i>date + date² + temp + prec</i>	0.01
	<i>year + hab</i>	<i>date + prec</i>	0.01
	<i>year + hab + burn</i>	<i>date + date² + prec</i>	0.01
<i>A. sexlineata</i>	<i>intercept</i>	<i>date + date² + temp + burn</i>	0.76
	<i>intercept</i>	<i>date + date² + prec + temp + burn</i>	0.07
	<i>burn</i>	<i>date + date² + temp</i>	0.06
	<i>burn</i>	<i>date + date² + temp + burn</i>	0.04
	<i>intercept</i>	<i>date + date² + temp</i>	0.03
	<i>hab</i>	<i>date + date² + temp + burn</i>	0.01
	<i>intercept</i>	<i>date + date² + burn</i>	0.01
	<i>burn</i>	<i>date + date² + prec + temp</i>	0.01
	<i>burn</i>	<i>date + date² + prec + temp + burn</i>	<0.01
	<i>year</i>	<i>date + date² + temp + burn</i>	<0.01

Note: *intercept* is a null model with no predictor variables, *hab* is a factor variable for sample units located in upland (1) vs. pond habitat (0), *burn* is a factor variable for sample units that were burned (1) vs. not burned (0), *year* is a linear trend across years, *date* is Julian day, *date²* is the quadratic effect of Julian day, *temp* is temperature, and *prec* is precipitation.

**Fig. 2.** Fitted values of abundance and 95% credible intervals for *Aspidoscelis sexlineata*, *Sceloporus consobrinus*, and *Scincella lateralis* on the Griffith League Ranch (GLR), Bastrop County, Texas, USA, spring 2008–spring 2013. Trapping sessions are grouped by year and vertical dashed lines indicate when wildfires occurred.

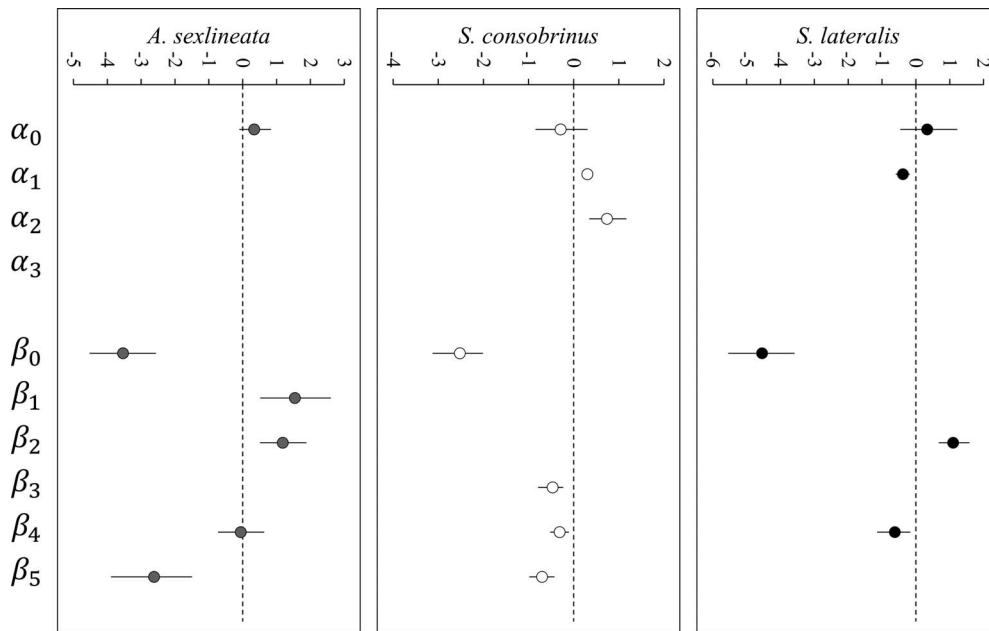


Fig. 3. Mean model intercept and coefficient estimates with 95% credible intervals from the selected model for *Aspidoscelis sexlineata*, *Sceloporus consobrinus*, and *Scincella lateralis* on the Griffith League Ranch (GLR), Bastrop County, Texas, USA, spring 2008–spring 2013. See text for further details on notation, and note the different ranges on the axes.

species within a southern United States mixed pine/hardwood forest before and after high-severity wildfires. A comprehensive understanding of wildlife population-level responses to wildfires is becoming more critical as climatic patterns coupled with broad-scale fire suppression lead to an increase in the frequency of high-severity wildfires (Bisson et al., 2003; Beschta et al., 2004). Nevertheless, relatively few studies have been conducted to assess the impact of high-severity fires on lizard communities, particularly in the United States, because high-severity fires are often unplanned events.

Following high-severity wildfires such as these, the initial concern is typically for the loss of many native flora and fauna through direct mortality. However, our results do not support a relationship between burn treatment and lizard abundance. Previous research found populations of *A. sexlineata* increased following low- to moderate-severity prescribed fires, which restored or maintained early-successional habitat in the sandhill and scrub habitat of the southeastern United States (Mushinsky, 1985; Ruthven et al., 2008; Ashton and Knipps, 2011; Steen et al., 2013a). On the other hand, differences in captures of *S. consobrinus* between control and prescribed burn patches in chaparral habitat of the southern United States were not detected (Ruthven et al., 2008). In unmanaged second-growth mixed pine/hardwood forests of the southeastern United States, captures of *S. consobrinus* and *S. lateralis* increased in woodlands restored through prescribed fires and thinning (Perry et al., 2009). Similarly, an increase in captures of *S. lateralis* was found following a prescribed fire in a southern USA pine savanna (Langford et al., 2007). Nonetheless, there is also evidence that populations of *S. lateralis* decreased after prescribed fires, likely due to reduction of litter (Steen et al., 2013b; Sutton et al., 2014).

The inconsistencies in the above findings may be, in part, due to a lack of analyses that account for imperfect detection. For example, our results indicate detectability of *A. sexlineata* increased following the fires. Thus, if we ignored observation error during analyses, our results would have incorrectly indicated abundance of *A. sexlineata* increased in burned

areas. Moreover, although prescribed fires can generate useful information on community responses to fire, they should not generally be considered proxies for predicting wildlife responses to wildfires since changes in habitat are largely governed by fire severity (Pastor et al., 2011; Brown et al., 2014c). Regardless, the inconsistent results among studies investigating lizard-fire relationships is evidence that lizard responses to fire may be species-specific and also vary by region and habitat type.

The major implication from this study, and our previous research on herpetofaunal responses to high-severity wildfires in the Lost Pines Ecoregion, is that there is no evidence the wildfires resulted in population extirpations, or even detectable decreases in herpetofauna abundance. Thus, post-fire management decisions should be made under the assumption that, despite dramatic changes to understory and overstory forest structure, the habitat remains suitable for the prior herpetofaunal community. When restoration actions require the use of heavy machinery (e.g., tractors, skid steer loaders, etc.), we encourage managers minimize their vehicle footprints off of roads to avoid soil compaction and the potential for direct mortality.

Our results also have implications for future lizard monitoring efforts. Spatial and temporal variation in abundance is often the basis for wildlife management decisions, and managers often rely on population indices, such as a catch-per-unit-effort, as a proxy for variation in abundance of herpetofaunal species (reviewed in Mazerolle et al., 2007). Yet, population indices do not account for imperfect detection and therefore can only provide reliable information concerning population dynamics when the probability of detection does not vary in a systematic way. Variation in herpetofaunal detection probabilities is linked to fire-related disturbance (Hossack and Corn, 2007; Chelgren et al., 2011; Driscoll et al., 2012; Hossack et al., 2013; our results for *A. sexlineata*), albeit there are exceptions (Smith et al., 2012; our results for *S. lateralis* and *S. consobrinus*). We also demonstrate that lizard detection probabilities varied in synchrony with environmental parameters (i.e., temperature, precipitation, and season [Julian day]). Collectively, these findings high-

light the importance of accounting for imperfect detection and considering the possibility of disturbance-related changes in detection probabilities in order to provide reliable information concerning lizard population dynamics.

It seems future lizard monitoring efforts should not solely rely on spatially and temporally replicated count data. Our estimates of mean detection probability were low, which could potentially lead to biased and imprecise estimates of abundance based on simulation studies (Royle, 2004; McIntyre et al., 2012; Couturier et al., 2013; Yamaura, 2013; Veech et al., 2016). Also, the goodness-of-fit test suggested a lack of model fit for *S. consobrinus*. One approach to improve model fit is to accommodate overdispersion (i.e., unexplained heterogeneity in the count data) by including random effects in the model for abundance and/or detection probability (Kéry et al., 2009; Kéry and Schaub, 2012). When random effects were included, however, our data were too sparse to accommodate the same explanatory variable on abundance and detection probability simultaneously, which was needed to examine the influence of burn treatment on both abundance and detectability. Thus, future lizard monitoring efforts should consider combining spatially and temporally replicated count data with more intensive capture-mark-recapture data at a subset of sample units. Integrated models can be fitted to these data, where detectability is modeled across sample units as a random effect drawn from a common logit-normal distribution (e.g., Grabowski et al., 2009). This would allow managers to estimate lizard population parameters with increased accuracy and still take advantage of more cost effective spatially and temporally replicated count data at a majority of sample units, which is important for long-term monitoring programs with uncertain and variable funding.

In summary, we did not detect a population-level response to the high-severity wildfires by the three lizard species we studied, which does not entirely agree with previous studies conducted in other habitats. This reinforces the importance of increasing our knowledge of species-specific responses to disturbances in different regions and habitat types. Population-level responses following fires can change over time (e.g., Hossack et al., 2013). Hence, our study should only be interpreted with respect to short-term responses of these species. In the short-term, a burn effect was only supported for *A. sexlineata*, but the effect was supported for detection probability, not abundance. We suspect this is related to increased movement by the species following the fires, although we cannot directly evaluate this hypothesis with our current monitoring data. Regardless, it is clear lizard detectability varies in synchrony with environmental parameters. Therefore, monitoring efforts seeking to determine lizard population dynamics need to account for variation in detection probabilities to provide meaningful information to managers. We expect the lizard populations in the area will undergo changes as the burned habitat continues to transform through forest succession and post-fire management actions. Therefore, we recommend lizard monitoring efforts that incorporate capture-mark-recapture methods at a subset of sample units continue in the region to better understand the intricacies of lizard-fire relationships.

DATA ACCESSIBILITY

Supplemental material is available at <http://www.copeiajournal.org/ch-16-516>.

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