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RESEARCH ARTICLE

Response of Six-Lined Racerunner (*Aspidoscelis sexlineata*) to Habitat Restoration in Fire-Suppressed Longleaf Pine (*Pinus palustris*) Sandhills

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Abstract

Six-lined racerunner (*Aspidoscelis sexlineata*) is an indicator species of frequently burned Longleaf pine (*Pinus palustris*) forests. To evaluate how the species responded to forest restoration, we conducted a mark-recapture study in formerly fire-suppressed Longleaf pine forests exposed to prescribed fire or fire surrogates (i.e. mechanical or herbicide-facilitated hardwood removal) as well as in fire-suppressed control sites and reference sites, which represented the historic condition. After initial treatment, all sites were exposed to over a decade of prescribed burning with an average return interval of approximately 2 years. We used population-level response of *A. sexlineata* as an indicator of the effectiveness of the different treatments in restoring habitat. Specifically, we compared mean numbers of marked adults and juveniles at treatment sites to that of reference sites. After 4 years, restoration objectives were met at sites treated with burning alone and at sites treated with mechanical removal of hardwoods followed by fire. After over 10 years of prescribed burning, restoration objectives were met at all treatments. We conclude that prescribed burning alone was sufficient to restore fire-suppressed Longleaf pine sandhills for *A. sexlineata* populations.

Key words: before-after-control-impact, Longleaf pine, mark-recapture, *Pinus palustris*, prescribed fire, reptile, squamate.

Introduction

Fire-maintained ecosystems are threatened by changes in landscapes and public attitudes toward fire that result in fire suppression strategies (Frost 1993; Keane et al. 2002). In the absence of fire, fire-adapted species may be unable to reproduce (e.g. Mulligan & Kirkman 2002) and the composition of species assemblages may shift. Thus, an overarching result of fire suppression in fire-adapted systems is the degradation of habitat for highly associated organisms (Means 2006; Nowacki & Abrams 2008).

Restoring fire-suppressed systems may be more complicated than simply reintroducing fire. For example, excessive fuel loads may lead to high-intensity fires that cause mortality of native species (e.g. Varner et al. 2005) and ecological conditions may not be conducive to reintroduction of fire (Martin & Kirkman 2009). Therefore, suggested methods of restoration may include the use of fire surrogates (Agee & Skinner 2005; Schwilk et al. 2009). However, fire surrogates alone are generally insufficient to achieve restoration because of the unique ecological effects of fire (Menges & Gordon 2010). Thus, effective long-term restoration of fire-adapted systems may require the use of fire surrogates followed by reintroduction of fire on regular return intervals. There have been few studies conducted to determine how this management strategy influences species highly associated with a given system.

Longleaf pine (*Pinus palustris*) forests once spanned the coastal plain of the southeastern United States (Ware et al. 1993). These forests historically had a sparse canopy of pines with a diverse herbaceous understory maintained by frequent wildfires that occurred every 1–10 years (Myers 1990). Because of fire suppression, hardwood trees have become established in the midstory of many former Longleaf pine-grassland habitats, which has reduced habitat quality for species associated with the historic condition (Mitchell et al. 2006). Restoration methods for fire-suppressed Longleaf pine forests include direct removal of hardwoods via mechanical means or application of herbicides. However, as noted above in reference to fire-adapted systems, burning is likely an essential component of any successful Longleaf pine forest restoration effort (Brockway et al. 2005).

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Ectothermic organisms allow novel insights into the response of wildlife to habitat change because they are particularly influenced by thermal properties of the landscape, in contrast to homeothermic mammals and birds. In addition, ectothermic species may reach high densities in suitable habitats (e.g. Iverson 1982) because they are freed from the energetic demands of homeothermic metabolisms. Small squamates play important roles in the ecosystems in which they occur (e.g. Means 2006); in addition, they may respond relatively quickly to habitat restoration (e.g. Trainor & Woinarski 1994; Bateman et al. 2008; Lettink et al. 2010). Response of squamates to habitat restoration is generally studied at the assemblage level (e.g. Greenberg et al. 1994; Russell et al. 2002), including within Longleaf pine forests (e.g. Litt et al. 2001; Smith & Rissler 2010; Steen et al. in press *b*). However, without careful attention to what constitutes a target assemblage, general trends may be obscured because reptiles are a diverse group (Barrett & Guyer 2008) and habitat associations of individual species may differ (Steen et al. 2010*a*). Consequently, assemblage-level study may obscure trends among species highly sensitive to forest management (e.g. Maas et al. 2009).

Six-lined racerunners (*Aspidoscelis sexlineata*) prefer open xeric habitats within the southeastern United States (Guyer & Bailey 1993) and are an indicator of frequently burned Longleaf pine forests (Steen et al. in press *b*). Although wildlife populations may exhibit delayed responses to vegetation changes (Brooks et al. 1999), which necessitates long-term study to characterize this response (Block et al. 2001), small squamates have relatively short generation times. Therefore, *A. sexlineata* is likely an appropriate focal species for monitoring the success of restoration efforts in Longleaf pine forests.

Within this study, we used a randomized block design and examined the number of marked adult and juvenile *A. sexlineata* to determine how the species responded to ecological restoration over a 15-year period. Because accurate abundance estimates may be difficult to generate for squamates that have low detection probabilities (Steen 2010; Steen et al. 2012*a*), we compared the mean number of marked adults and the mean number of marked juveniles within each treatment to numbers of these animals on reference sites.

Methods

Study Site

This study took place in fire-suppressed Longleaf pine sandhills on Eglin Air Force Base, Santa Rosa and Okaloosa Counties, Florida, U.S.A. A randomized block design was used to assign hardwood removal treatments to 24 81-ha sites (six blocks; Provencher et al. 2001*a*, 2001*b*). Six sites experienced a single burn between 1977 and 1989, but all other sites had been fire-suppressed since at least 1973 (when records began). Hardwood removal treatments included burning (Burn), herbicide application (Herbicide), or felling-girdling (Mechanical) and a Control, which experienced no hardwood removal. Six 81-ha reference sites were also designated. Provencher et al. (2001*a*) described criteria for selection of reference sites; reference site selection was based on, "an uneven age distribution of *Pinus palustris*; presence of old-growth *P. palustris*; abundance of largely herbaceous understory species interspersed with bare ground; a sparse midstory; presence of *Picoides borealis* (a characteristic bird species); and a history of frequent growing season fires." Reference sites represented the target condition for restoration efforts.

Treatment Application

Initial hardwood reduction treatments occurred in 1995. Burn sites were burned April–June, Herbicide was applied in early May, and Mechanical hardwood removal was conducted between June and November. Herbicide and Mechanical sites were also subjected to a prescribed burn in March–April 1997. After 1999, all sites, including Control sites that were previously fire-suppressed, received prescribed fire, and prescribed fire alone, on an approximately 2- to 3-year rotation.

Vegetation Data Collection

Vegetation data were collected in treatment sites and reference sites in 1998. Data for reference sites were collected again in 2009 and treatment sites were resampled in 2010 (during the same months that reference sites were visited in 2009). Sampling for vegetation occurred in 1-m^2 quadrats along transects in each site (as described in Provencher et al. 2001*a*, 2001*b*). In each quadrat, we estimated percent cover for several groundcover categories including: grasses and sedges, forbs, woody species, bare ground, and woody litter. Groundcover was characterized by cover classes (1–5%, 5–25%, 25–50%, 50–75%, 75–95%, and 95–100%) and converted to midpoints, which were used to generate mean percent cover for all sites. Pine overstory (trees > 10 cm, diameter at breast height, dbh) and pine and oak midstory (pines < 10 cm and oaks < 16 cm, dbh) basal area (m^2/ha) for each site were also collected.

Aspidoscelis sexlineata Trapping

We trapped squamates at a subset of the 24 treatment sites and 6 reference sites that were part of the larger study because of limited access to the remaining sites. Drift fence arrays (Campbell & Christman 1982) were placed in four treatment blocks (one drift fence in each of 16 treatment sites) and four reference sites. However, one reference site was treated with herbicide following the initial sampling, which fell outside of the study design, thus data from this site were excluded from analysis. An array was placed at the center of each site and contained 30 m of 50-cm-tall galvanized aluminum flashing and 16 19-L pitfall traps in 1997 and 1998 (Litt et al. 2001). Animals were trapped from May to August 1997 and April to August 1998. Arrays were placed in the same locations and animals were trapped from May to September 2009 and May to August 2010. In 2009 and 2010, we added box traps (Burgdorf

Figure 1. Six-lined racerunner, *Aspidoscelis sexlineata*. Photo courtesy Aubrey M. Heupel.

et al. 2005; Steen et al. 2010*b*) at the center of arrays but used the same number of pitfall traps per array.

Aspidoscelis sexlineata (Fig. 1) that were ≤500-mm snout-vent length were considered juveniles (slightly smaller than the size of reproductively active females; Trauth 1983). All other individuals were characterized as male or female based on a secondary sexual characteristic, that is, blue coloration on males (Conant & Collins 1998). Animals were individually marked by toe clip and released. Individuals that escaped before receiving a toe clip were not included in the analysis.

Analysis

We used a before-after-control-impact study design and analysis of variance (Stewart-Oaten et al. 1986) to compare the (1) number of marked adults and (2) number of marked juveniles among treatments and over time with SAS 9.2 (SAS Institute, Inc. Cary, NC, U.S.A.). Comparisons of a priori interest were whether mean numbers of marked adults and juveniles within treatment sites were indistinguishable from those of reference sites for both study periods and whether these parameters changed over time. We set our alpha level at 0.05. If the number of marked adults and juveniles within a given treatment did not differ from those on reference sites, we assumed habitat condition was similar to that of references (i.e. provided evidence of a restored condition). To make inferences regarding how conditions changed over time, we assumed that conditions within Controls in 1998–1999 were representative of conditions at all treatment sites prior to hardwood removal. Because previous work has examined the short-term effects of hardwood removal on *A. sexlineata* (Litt et al. 2001), our impact of interest was the reintroduction of prescribed burning on frequent intervals over the long term, which all sites, including Controls, experienced after 1999.

It is important to integrate detection probabilities into analyses (Mazerolle et al. 2007), including when quantifying reptile response to fire (Driscoll et al. 2012). However, mark-recapture analyses may fare poorly at estimating population parameters when capture probabilities are less than 0.30

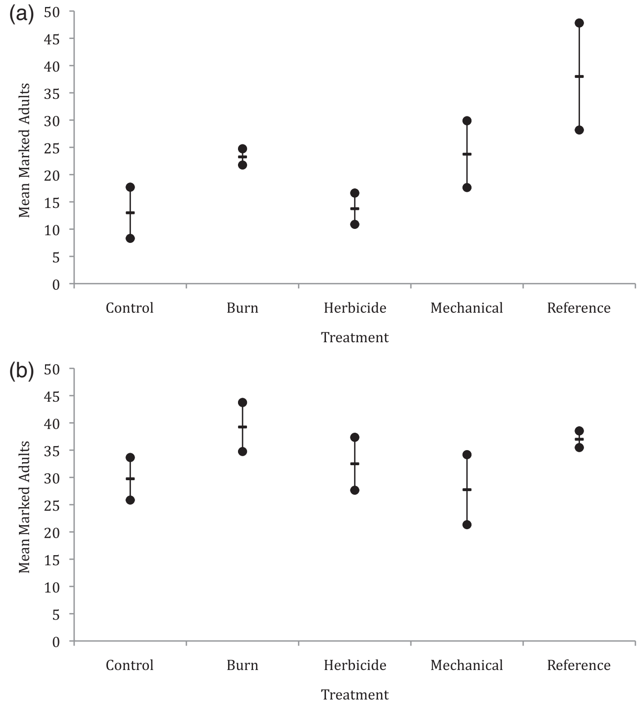

Figure 2. Mean number of marked adults (and standard errors) of *Aspidoscelis sexlineata* in Longleaf pine sandhills subjected to various hardwood removal strategies on Eglin Air Force Base in 1997–1998 (a) and 2009–2010 (b).

(White et al. 1982). Capture probabilities in our study were 0.14 in 1997–1998 and 0.21 in 2009–2010. In addition, we captured a relatively small number of individuals (Figs. 2 & 3), which can increase bias and uncertainty of estimates derived from mark-recapture studies (Menkins & Anderson 1988). Although it is important in principle to incorporate heterogeneity in detection probabilities when quantifying abundances, low detection probabilities confounded our ability to derive reasonable estimates, as has been observed among other terrestrial squamates (i.e. snakes; Steen 2010; Steen et al. 2012*a*). Thus, we chose not to use population or survivorship estimates and instead focus interpretation on mean numbers of marked individuals. Future efforts to derive estimates of squamate population size based on mark-recapture techniques should include multiple trapping arrays within a site to achieve capture probabilities high enough to derive defensible population estimates.

Results

We individually marked 521 and 773 *Aspidoscelis sexlineata* in 1997–1998 and 2009–2010, respectively. There was no significant interaction between treatment and time ($F_{[4,1]} = 1.45$; $p = 0.24$) for the number of marked adults. In 1997–1998, the mean number of marked adults on reference sites (38, SE = 9.8) did not differ significantly from that of Burn (23.25, SE = 1.5; $p = 0.06$) or Mechanical sites (23.8, SE = 6.1; $p = 0.06$), but was greater than on Control (13, SE = 4.7;

$p = 0.002$) and Herbicide sites (13.8, SE = 2.9; $p = 0.003$). In 2009–2010, the mean number of marked adults on reference sites (37, SE = 1.5) did not differ from that of Burn (39.3, SE = 4.5; $p = 0.76$), Control (29.8, SE = 3.9; $p = 0.34$), Herbicide (32.5, SE = 4.9; $p = 0.55$), or Mechanical sites (27.8, SE = 6.4; $p = 0.22$; Fig. 1).

With regard to the number of marked juveniles, there was no significant interaction between treatment and time ($F_{[4,1]} = 0.89$; $p = 0.49$). In 1997–1998, the mean number of marked juveniles on reference sites (10.3, SE = 0.9) was not significantly different from that of Burn (9.5, SE = 2.3; $p = 0.80$) or Mechanical sites (5, SE = 1.2; $p = 0.12$), but was greater than that of Control (2.3, SE = 1.1; $p = 0.02$) and Herbicide sites (3.5, SE = 0.9; $p = 0.046$). In 2009–2010, the mean number of marked juveniles on references (10, SE = 1.7) was not significantly different from that of Burn (7.3, SE = 2.9; $p = 0.41$), Control (5.8, SE = 2.5; $p = 0.21$), Herbicide (5.8, SE = 2.1; $p = 0.21$), or Mechanical sites (10, SE = 3.8; $p = 1.0$; Fig. 2).

In summary, the mean number of marked adults and juveniles on Burn and Mechanical sites was indistinguishable from the mean number of marked adults and juveniles on reference sites in 1997–1998, and the mean number of marked adults and juveniles on all treatments was indistinguishable from the mean number of marked adults and juveniles on references in 2009–2010. Long-term prescribed burning influenced *A. sexlineata* populations similarly on all sites, regardless of initial hardwood removal treatment. The numbers of adults and juveniles at references were relatively stable over time (Figs. 2 & 3); because the numbers of adults and juveniles at Control and Herbicide sites were different than references in 1998–1999 (while the numbers of these animals at Mechanical and Burn were not) and the numbers of these animals were the same in 2009–2010, we expected our before-after-control-impact analysis of variance to return results suggesting significant change. We attribute the lack of significance to relatively small sample sizes and low detection probabilities; relatively high statistical power is required to detect interaction terms.

The long-term effects of hardwood removal on vegetation structure varied by treatment (Table 1). Oak densities decreased in all treatment sites following initial treatment and remained relatively high in Controls. Following 1997–1998, all treatments except Controls experienced gradual increases in midstory oak density, but the trend was most pronounced in Mechanical sites. Change in ground cover over time is presented in Table 2.

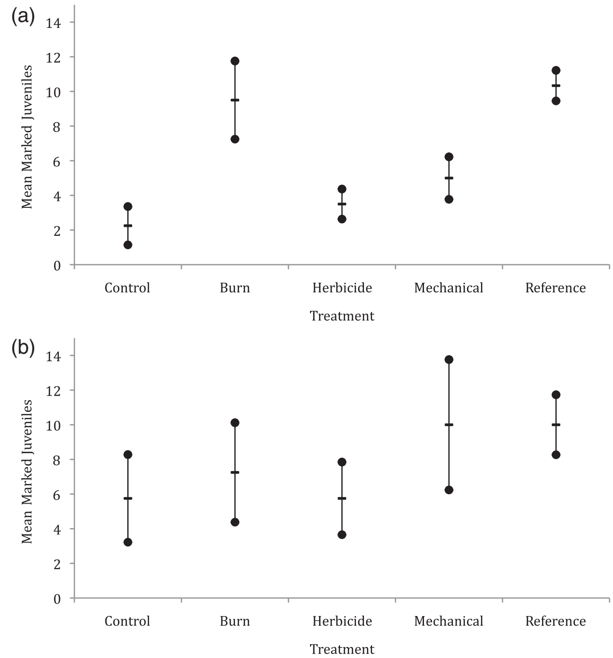

Figure 3. Mean number of marked juveniles (and standard errors) of *Aspidoscelis sexlineata* in Longleaf pine sandhills subjected to various hardwood removal strategies on Eglin Air Force Base in 1997–1998 (a) and 2009–2010 (b).

Discussion

Aspidoscelis sexlineata is an indicator species for Longleaf pine forests in reference condition (Steen et al. in press *b*). In this study, prescribed burning alone resulted in an increase in abundance (i.e. the number of marked adults and juveniles) of this species over relatively short time scales, as did mechanical removal of hardwoods followed by prescribed fire. Over the long term, prescribed burning in all treatments resulted in numbers of animals comparable to the number of animals observed on reference sites. In this sense, our findings corroborate multitaxa, assemblage-level analyses indicating prescribed burning is an effective method of restoring fire-suppressed Longleaf pine sandhills for wildlife (Steen et al. in press *a*, in press *b*) and vegetation (Outcalt & Brockway 2010).

Simply reestablishing normal disturbance regimes may be insufficient to restore a degraded ecosystem (Suding et al. 2004) and the response of ectotherms to habitat management may be unpredictable (Bury 2004; Lindenmayer et al. 2008). However, we found that reintroducing fire on a frequent return interval restored a reptile species that is an indicator of the ecosystem. In this sense, our findings are consistent with other recent work demonstrating that reestablishing natural conditions, including conditions related to canopy cover (Pike et al. 2011), may be sufficient to restore reptiles.

Abundance values alone may not be appropriate as comprehensive indices of how populations respond to habitat change (Todd & Rothermel 2006). For example, in many cases, the number of individuals required to constitute a minimum viable population is unknown and abundance values may not reflect the effective population size; this limits the use of these values when quantifying wildlife response to habitat restoration (Smallwood 2001). Density also cannot be assumed to be positively related to habitat quality; measurement of population dynamics is likely more informative (Van Horne 1983). Nonetheless, although we do not know the number of individuals required to represent a minimum viable population

Table 1. Tree basal area within hardwood removal and reference sites, Santa Rosa and Okaloosa Counties, Eglin Air Force Base, Florida.

	1994	*1998–1999*	*2009–2010*
Pinus palustris midstory			
Burn	0.13	0.05	0.05
Control	0.1	0.07	0.01
Herbicide	0.09	0.04	0.28
Mechanical	0.10	0.03	0.07
Reference	0.03	0.02	0.13
P. palustris overstory			
Burn	12.78	12.01	12.93
Control	7.88	8.71	10.09
Herbicide	11.84	12.01	11.36
Mechanical	12.15	11.14	11.79
Reference	16.15	16.65	18.12
Quercus spp. midstory			
Burn	0.79	0.22	0.56
Control	1.07	1.23	0.72
Herbicide	0.56	0.02	0.14
Mechanical	0.87	0.09	1.59
Reference	0.11	0.17	0.11
Quercus spp. overstory			
Burn	10.08	5.41	5.22
Control	10.10	9.36	3.76
Herbicide	9.08	0.40	0.04
Mechanical	11.74	2.18	7.82
Reference	4.93	2.93	0.93

One reference site was not included in 2009–2010 summaries. All units are m^2/ha.

Table 2. Mean percent ground cover within hardwood removal and reference sites, Santa Rosa and Okaloosa Counties, Eglin Air Force Base, Florida.

	1994	*1998–1999*	*2009–2010*
Grasses and sedges			
Burn	2.86	8.56	9.83
Control	3.31	4.28	11.60
Herbicide	3.26	10.90	13.86
Mechanical	4.20	15.11	20.57
Reference	11.29	11.69	14.86
Forbs			
Burn	2.85	6.06	12.81
Control	3.58	5.30	10.37
Herbicide	1.88	10.60	10.29
Mechanical	2.74	8.50	14.12
Reference	3.91	10.14	22.79
Woody species			
Burn	10.25	24.63	15.58
Control	12.72	18.42	16.53
Herbicide	10.17	19.88	18.48
Mechanical	12.84	16.29	13.33
Reference	10.69	12.79	15.47
Bare ground			
Burn	3.14	6.61	14.39
Control	2.54	3.55	24.06
Herbicide	1.60	14.62	11.58
Mechanical	1.79	15.81	14.92
Reference	5.88	19.94	42.34
Woody litter			
Burn	4.69	9.39	43.01
Control	5.95	5.76	33.57
Herbicide	4.80	9.22	45.50
Mechanical	5.66	10.26	20.33
Reference	5.11	4.95	25.15

One reference site was not included in 2009–2010 summaries.

in *A. sexlineata*, in this study we assumed the number of individuals observed at reference sites were representative of a target condition.

Previous research identifying changes in *A. sexlineata* abundance in relation to prescribed fire frequency suggested that increases in abundance were attributable primarily to immigration (Mushinsky 1985). Our study sites were relatively large (81-ha) and our traps were located in the center of each site, suggesting immigration is unlikely to be the primary mechanism resulting in the trends we observed, at least for 1998–1999. However, we were unable to determine if the populations we sampled were supplemented by immigration following treatment and by extension, whether it is necessary to consider the landscape matrix and neighboring population densities in restoration efforts for this species, although this is an important consideration in determining how populations of small squamates respond to habitat restoration (Mushinsky 1985). Given that we observed as many juveniles in Burn and Mechanical treatment plots as we did in reference sites in 1997–1998, we suggest that relatively high numbers of *A. sexlineata* caught in these areas are due largely to either higher rates of recruitment or increased fecundity. *Aspidoscelis sexlineata* mature relatively quickly (i.e. approximately 1 year of age; Clark 1976); therefore, an increase in reproductive success may quickly increase the number of sexually mature adults.

We suggest *A. sexlineata* benefitted from a change in vegetation structure resulting from fire, rather than a direct response to fire itself (Lindenmayer et al. 2008). This change in vegetation structure could have resulted in more suitable microclimates for *A. sexlineata* and/or a restored or enhanced arthropod prey base (Provencher et al. 2002). Of the ground cover categories we recorded, the change in numbers of *A. sexlineata* most closely mirrors the change observed in grasses and sedges. This ground cover category is relatively high in reference sites initially; grass and sedge cover in treatment plots gradually becomes more similar to reference sites.

Habitat restoration may not be sufficient to recover a population that is already in decline (Schrott et al. 2005). Because we detected *A. sexlineata* in all sites, populations of this species can presumably persist at relatively low levels even in poor-quality habitats, such as those that typify fire-suppressed Longleaf pine sandhills (i.e. our Control sites in 1997–1998). We therefore suggest the species is unlikely to be extirpated in Longleaf pine sandhills following invasion of hardwood trees or easily extirpated from a site that experiences an extended period of inadequate fire frequency. Even wildlife species that are highly associated with the Longleaf pine ecosystem may use or require some hardwood trees (Perkins et al. 2008; Steen et al. 2012*b*); thus, land managers may wish to consider management strategies that do not call for hardwood eradication.

Mushinsky (1985) described increased abundance of *A. sexlineata* in frequently burned habitats, and Greenberg et al. (1994) noted a higher abundance of the species in Sand pine (*Pinus clausa*) stands that were clearcut, which mimicked some effects of fire, when compared with mature Sand pine forests that were infrequently burned. On our study site, the species was previously identified as an important driver of assemblage-level change on multiple time scales in response to prescribed fire (Litt et al. 2001) and an indicator of Longleaf pine forests in reference condition (Steen et al. in press *b*). Our data suggest that *A. sexlineata* abundance in formerly fire-suppressed Longleaf pine sandhills was indistinguishable from that of reference sites following repeated application of prescribed burning. Thus, we conclude that prescribed burning is an effective strategy for restoration of *A. sexlineata* populations in fire-suppressed Longleaf pine sandhills. In this sense, habitat restoration, together with reintroduction of disturbance regimes that mimicked the historic condition, was sufficient to restore an ectotherm that is highly associated with the ecosystem.

Implications for Practice

- Over the long term, numbers of *Aspidoscelis sexlineata* in formerly fire-suppressed Longleaf pine sandhills became indistinguishable from numbers in reference conditions after long-term (15 years) prescribed burning, regardless of fire surrogate use.
- Prescribed burning alone was sufficient to quickly restore *A. sexlineata* populations.
- Restoration of this species, highly associated with the historic condition, was possible by restoring habitat conditions and reintroducing normal disturbance regimes.
- Fire surrogates did not provide an observed benefit to *A. sexlineata* populations over the use of fire alone.

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