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Vegetation structure and the habitat specificity of a declining North American reptile: A remnant of former landscapes

Jayme L. Waldron[a,*,1], *Shane M. Welch*[b], *Stephen H. Bennett*[c]

[a]*Department of Forestry and Natural Resources, Clemson University, Clemson, SC 29634, USA*
[b]*Department of Biological Sciences, University of South Carolina, Coker Life Sciences 706, Columbia, SC 29802, USA*
[c]*South Carolina Department of Natural Resources, Columbia, SC 29201, USA*

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ABSTRACT

Although all species provide some spatial information about past environments, remnant populations of habitat specialists can serve as biological legacies and natural archives of historical landscapes. The endangered longleaf pine ecosystem is home to an array of imperiled fauna that specialize on the habitat. Often referred to as pine savanna, the ecosystem was characterized by longleaf pine (*Pinus palustris*), but included an array of open-canopy habitats within a grassland matrix dominated by a variety of tree species. In this study, we used a coarse scale of description to quantify habitat associations of a declining reptile, the eastern diamondback rattlesnake (*Crotalus adamanteus*), historically associated with pine savannas of the southeastern United States. We made cross-scale habitat comparisons and controlled for land use and geographic variability. Habitat models of within home range and microhabitat selection indicated that the species was associated with an open-canopy savanna community structure. We identified the eastern diamondback rattlesnake as a remnant of the historical southeastern savanna, which is important for species conservation and broader management of the southeastern savanna community. Given their longevity and habitat specificity, remnant eastern diamondback rattlesnake populations are biological legacies of the southeastern savanna community and act as a surrogate for the prioritization of land conservation. Thus, the species' presence provides spatial information that can be used by conservationists to identify habitats that have high restoration potential, and also increases the probability that other species associated with pine savanna occur locally.

1. Introduction

All species are adapted to past environments; thus, all species are encoded with some degree of historical and spatial information. Regional conservation efforts can be enhanced when species-specific habitat studies are placed within an historical context, allowing habitats to be conceptualized at the community-level. Changes in land use patterns often cause species to redistribute through time, which can diminish the historical relevance of the spatial information provided at a site. Habitat specialists tend to provide more spatial information compared to habitat generalists (Morrison, 2001; Welch et al., 2007), and may provide an effective framework for identifying past landscape components (Welch et al., 2007).

* *Corresponding author:* Address: 106 Hayne Street, Walterboro, SC 29488, USA. Tel.: +1 843 782 3206.
E-mail addresses: ditmadden@hotmail.com (J.L. Waldron), shanemwelch@gmail.com (S.M. Welch), bennetts@dnr.sc.gov (S.H. Bennett).
[1] Present address: University of Georgia, Savannah River Ecology Laboratory, Drawer E, Aiken, SC 29802, USA.
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Furthermore, species with low dispersal abilities and slow life histories will have greater spatial fidelity and a longer temporal lag relative to other species. Such species will persist in the landscape as remnant populations containing a degree of historical and spatial information about past environments.

The eastern diamondback rattlesnake (*Crotalus adamanteus*) is a declining species associated with the imperiled longleaf pine (*Pinus palustris*) ecosystem (Martin and Means, 2000; Timmerman and Martin, 2003; Waldron et al., 2006). The species occurs in the southeastern Coastal Plain from southeastern North Carolina through eastern Louisiana, including Florida (Martin and Means, 2000; Timmerman and Martin, 2003); however, populations at the extremes of its range are in severe decline, and the species has likely been extirpated from Louisiana (Martin and Means, 2000). Eastern diamondback rattlesnakes have slow life histories, e.g., long birth intervals (Timmerman and Martin, 2003), long gestation periods (Means, 1985), and >10 year longevity (Means, 1985). Distribution data and habitat studies principally support the hypothesis that habitat loss is a cause of the species decline. At the broadest spatial scale, the historic range of the eastern diamondback rattlesnake is largely congruent with the historic distribution of the longleaf ecosystem (Martin and Means, 2000). At the landscape scale, Waldron et al. (2006) found that eastern diamondback rattlesnake home ranges were largely dependent on savanna structure, and concluded that the species habitat specificity to an imperiled habitat was likely a contributor to its decline. Other habitat descriptions also suggest a dependency on pine savanna (Carr, 1940; Martin and Means, 2000; Hoss, 2007); however, evidence supporting the link between eastern diamondback rattlesnakes and savanna habitat is not conclusive (e.g., Steen et al., 2007). Thus, resolving the issue is an important step in the species recovery and conservation.

Research that defines a species habitat within an historical context can provide conservationists with justification for community-level management. An array of imperiled fauna specialize in longleaf pine savanna (Means, 2006), including the federally protected red-cockaded woodpecker (*Picoides borealis*), flatwoods salamander (*Ambystoma cingulatum*), and gopher tortoise (*Gopherus polyphemus*). With the exception of gopher tortoises and red-cockaded woodpeckers, relatively little is known about the natural history of longleaf pine savanna specialists (Van Lear et al., 2005). This information is essential for the development of restoration protocols that benefit the entire longleaf savanna community (Walker, 1993). A community-level approach to conservation of longleaf pine savannas will ultimately be more successful (Means, 2006) and cost-effective than multiple species-specific approaches. Thus, the recognition of the eastern diamondback rattlesnake as a remnant of the historical southeastern savanna will further aid the conservation of the imperiled longleaf community.

Multi-scale habitat studies more fully elucidate key habitats or habitat patches (Kolasa, 1989; Kotliar and Wiens, 1990) that are not limited to single scales (Wiens, 1989; Orians and Wittenberger, 1991). Scaling inconsistencies among studies may result in conflicting results (Wiens, 1989), which can muddle conservation efforts. In addition to spatial and temporal scales, habitat studies parameterize habitats across a scale of description that is often related to the study's grain and extent (Wiens, 1989; Levins, 1992). The scale of description may be thought of as a unit of measure that stems from perceptions and research conventions, and in habitat studies may be visualized as ranging from fine-scale taxonomic composition (e.g., species-level resolution) through coarser scaled resolutions of functional and structural groups (e.g., ecological guilds and land use categories). At very broad spatial and temporal scales, fine-scales of description (i.e., species composition) may obscure patterns of habitat use by increasing statistical noise and obscuring meaningful signals. Conventionally, the scale of description is usually matched to the study's grain and extent to optimize inferences as a balance between model specificity to the study's data, and model generalization for broader application outside the study area (Wiens, 1989; Levins, 1992). By changing the scale of description, we trade the loss of detail for the gain in predictability; and "extract and abstract fine-scale features that have relevance for the phenomena observed on other scales" (Levins, 1992).

In this study, we used a coarse scale of description to make broad inferences about eastern diamondback rattlesnake habitat. Specifically, we modeled microhabitat selection and within home range habitat selection using structural components that allowed us to make cross-scale comparisons specific to savanna structure. This approach controlled for regional differences in species composition and land use histories, allowing us to make inferences across the range of the species. The goal of this study was to quantify eastern diamondback rattlesnake habitat associations in an historical context, providing conservationists with a description of the historical community to which the species belonged.

2. Methods

2.1. *Study area*

This study was conducted on state-owned property in southeastern South Carolina, USA. Refer to Waldron et al. (2006) for a detailed description of the study area. Management of the 4900-ha study area focused on game species and pine savanna preservation. Prescribed burning was an important management component, consisting of 1–4 year burn intervals.

2.2. *Radiotelemetry*

We used radiotelemetry to monitor rattlesnake movements during 8 field seasons between March 1997 and December 2004. We captured adult eastern diamondback rattlesnakes (females, $n = 15$; males, $n = 6$) during the spring of each year, and surgically implanted transmitters (SI-2, 11–13 g, Holohil Systems, Carp. ON) following techniques modified from Reinert and Cundall (1982). We used an injectable anesthesia (i.e., Ketamine) to anesthetize rattlesnakes prior to and during 2001. From 2002 to 2004, we used isoflurane as an anesthetizing agent that was administered with an anesthesia machine equipped with an isoflurane vaporizer. Following surgery, we monitored rattlesnakes for 3 days before releasing them at their capture locations.

Rattlesnakes were monitored from 1 to 3 years. In cases where study animals were tracked for >1 year, only the first