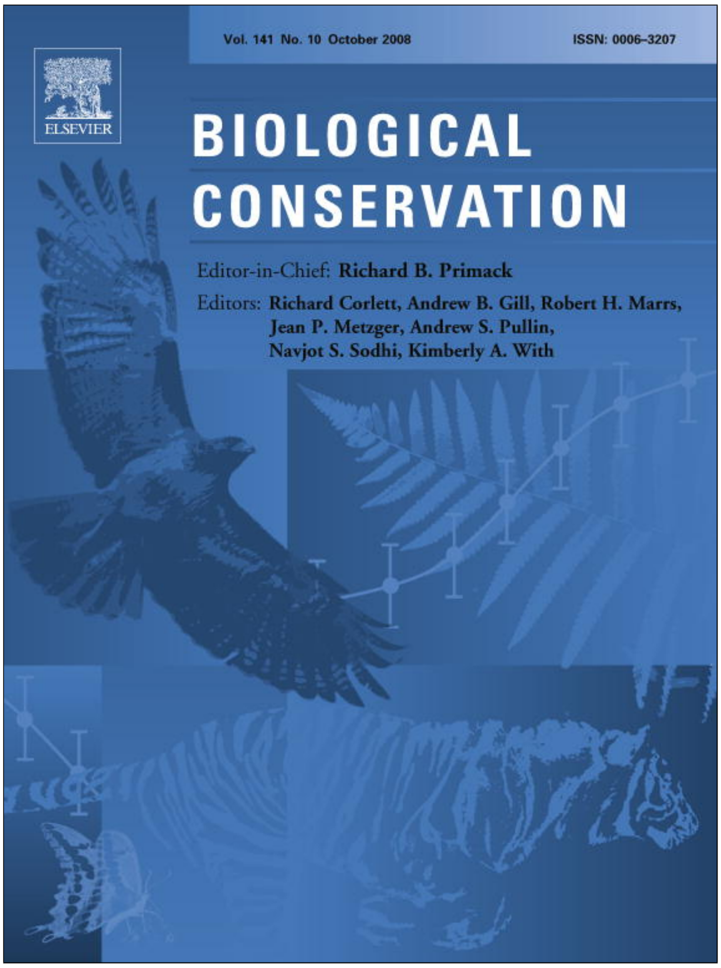
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Vegetation structure and the habitat specificity of a declining North American reptile: A remnant of former landscapes

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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).

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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 year of activity was included in analyses. Prior to 2002, we radio-located study animals approximately 5 days per week during spring, summer, and fall using a radio receiver (Telonics, TR-2, Mesa, AZ) and a directional antenna. During the last 3 years of the study, we located individuals daily until they spent 24 h at one location, at which point they were located every other day until movement was detected. Because rattlesnakes move little during winter months (Timmerman and Martin, 2003), winter radio relocations ranged from biweekly to monthly between December and March. Each snake location was recorded using a Global Positioning System (GPS; Trimble Pro XR, Sunnyvale, CA) with real-time differential correction and an estimated spatial accuracy <5 m. To avoid behavioral anomalies related to capture and surgery, rattlesnakes were allowed a two-week adjustment period following release, during which time no vegetation data were recorded.

2.3. *Within home range habitat selection*

Habitats within the study area were characterized according to Waldron et al. (2006) by combining aerial photographs with National Wetlands Inventory classifications (Cowardin et al., 1979; Table 1) and were verified throughout the study area by field visits to the various habitats. The pine category was divided into 2 classes based on canopy cover. Open-canopy pine, including longleaf, loblolly (*P. taeda*), and slash (*P. elliottii*) pine, was classified as pine savanna. Closed-canopy, planted loblolly, slash, and longleaf pine stands were classified as planted pine. Habitat variables were spatially assigned to snake locations (females, $n = 1688$; males, $n = 974$) recorded within 95% Kernel home range estimates (Waldron et al., 2006) and compared to randomly generated points (females, $n = 3409$; males, $n = 1210$) within the home ranges, allowing habitat selection to be modeled as within home range habitat selection.

We modeled within home range habitat selection separately for male and female rattlesnakes using logistic regression and used maximum likelihood estimates and odds ratios to compare habitat selection across habitat types. To ensure that individual males and females could be pooled by sex for analysis, we investigated the influence of individual snakes in the models. The effect of individual snake was not significant for male ($\chi^2 = 0.57$, df = 5, $P > 0.05$) or female ($\chi^2 = 3.0$, df = 14, $P > 0.05$) rattlesnakes.

2.4. *Microhabitat selection*

While rattlesnakes were radio-located throughout the study period, vegetation analysis was limited to telemetry data collected between 2002 and 2004, and was based on female (gravid, $n = 2$; nongravid, $n = 4$) and random locations. Once a rattlesnake moved from a location where it had been visually observed to spend a minimum of 24 h, we paired measurements of canopy cover and ground cover at the former location with those at the random location, placed 100 m away toward a random compass bearing. We measured percent canopy cover by standing at the snake location and reading a spherical densiometer at the 4 cardinal directions. We quantified percent ground cover within a 6-m radius plot centered on the snake location by visually estimating the percentage of ground that was covered by woody and herbaceous vegetation below 1 m.

Pearson's correlation coefficients indicated that the 2 microhabitat predictor variables were not correlated ($r = -0.1137$; $P > 0.05$). We used conditional (paired) logistic regression to model microhabitat selection. We computed customized odds ratios to represent a 25% unit increase in canopy cover and ground cover. We hypothesized that a significant negative association with canopy cover and a positive association with ground cover would indicate that eastern diamondback rattlesnakes selected savanna structure at the finest scale measured (e.g., intra-patch scale). All statistical analyses were performed using SAS 9.1 (SAS Institute, 2002).

3. Results

3.1. *Within home range habitat selection*

Logistic regression models of within home range habitat selection were significant for males (df = 4; $\chi^2 = 55.85$, $P < 0.0001$) and females (df = 4; $\chi^2 = 46.59$, $P < 0.0001$). Both sexes had significant positive associations with pine savannas (Table 2). Male associations with other habitats were not significant (Table 2). Females also had a positive association

Table 1 – Habitat types used by eastern diamondback rattlesnakes (Crotalus adamanteus) in southeastern South Carolina, USA[a], as classified by Waldron et al., 2006

NWI Classification	Habitat Type	Description
Upland Planted Pine	Pine Savanna	Upland mature pine savanna/wiregrass community with open canopy; dominant tree species include longleaf pine (*Pinus palustris*), slash pine (*P. elliottii*), loblolly pine (*P. taeda*), post oak (*Quercus stellata*), blackjack oak (*Q. marilandica*) and hickory species (*Carya spp.*)
Upland Planted Pine	Planted Pine	Upland planted pine; dominated by closed canopy, unthinned loblolly, slash, or longleaf pine
Palustrine Pine	Pine Hardwood	Forested wetland; holds water seasonally; overstory dominated by loblolly pine and hardwood species, including sweet gum (*Liquidambar styraciflua*), willow oak (*Q. phellos*), and southern red oak (*Q. falcata*)
Palustrine Hardwood	Hardwood Bottom	Forested wetland; holds water seasonally; overstory dominated by hardwoods; dominant species include overcup oak (*Q. lyrata*), Willow oak, red maple (*Acer rubrum*), sweet gum, southern red oak, black gum (*Nyssa sylvatica*), and bald cypress (*Taxodium distichum*)
Crops	Fields	Fields and wildlife openings maintained for game management; seasonally plowed and planted; edges consist mostly of slashpiles resulting from field construction and maintenance

a Habitats within the study area were characterized by combining aerial photos with National Wetlands Inventory classification.

Table 2 – Maximum likelihood estimates from logistic regression models of within home range habitat selection models for male (n = 6) and female (n = 15) eastern diamondback rattlesnakes (Crotalus adamanteus) from a South Carolina study site, USA (1997–2004)

Sex	Variables	Estimate ± SE	χ^2	P
Males	Hardwood Bottom	0.1448 ± 0.1861	0.6047	0.4368
	Pine Hardwood	−0.3198 ± 0.1856	2.9687	0.3931
	Planted Pine	−0.3016 ± 0.0972	9.6352	0.0849
	Pine Savanna	0.3676 ± 0.0844	18.9502	<0.0001
	Field	0.1091 ± 0.1277	0.7293	0.3931
Females	Hardwood Bottom	−0.5829 ± 0.1687	11.9437	0.0005
	Pine Hardwood	0.4377 ± 0.1202	13.2730	0.0003
	Planted Pine	−0.0596 ± 0.0823	0.5246	0.4689
	Pine Savanna	0.3501 ± 0.0628	31.1135	<0.0001
	Field	−0.1454 ± 0.0904	2.1382	0.1437

with pine-hardwood forests, and had a significant negative association with hardwood bottoms (Table 2). Odds ratios indicated that males were two times more likely to use pine savannas than other habitat types, and that females were two times more likely to use pine savannas and pine hardwood forests than the other habitat types.

3.2. *Microhabitat selection*

We measured microhabitat at rattlesnake ($n = 90$) and paired random ($n = 90$) locations. Maximum likelihood estimates revealed a negative association with canopy cover (estimate = −0.0156, SE = 0.0079, $P = 0.05$) and a positive association with ground cover (estimate = 0.0191, SE = 0.0081, $P < 0.05$). Customized odds ratios indicated that for every 25% increase in ground cover, the probability of use increased 1.6 times. Further, probability of use increased 1.5 times for every 25% decrease in canopy cover.

4. Discussion

The results of this study support the hypothesis that eastern diamondback rattlesnakes are associated with a savanna community structure. Our analysis of within home range habitat selection was largely consistent with an analysis of home range selection at the landscape scale (i.e., Waldron et al., 2006), in which both sexes were positively associated with pine savanna. In both studies, pine savanna was classified as upland mature pine savanna/wiregrass community with open-canopy dominated by pines, i.e., longleaf, slash, and loblolly pines, post oak (*Quercus stellata*), blackjack oak (*Q. marilandica*), and hickory (*Carya*) species (Table 1). However, we caution against emphasizing the importance of vegetation composition rather than vegetation structure with respect to these habitat models, which is supported by the results of our microhabitat analysis. Although females were associated with both pine savanna and pine hardwood habitats at the landscape (Waldron et al., 2006) and home range scales, microhabitat selection indicated that individuals selected open-canopy habitat regardless of the habitat patch that was occupied (e.g., pine hardwood, pine savanna, etc.). The multiple scales examined in this study and in Waldron et al. (2006) indicate that eastern diamondback rattlesnakes prefer open-canopy habitats. Other habitats that are structurally similar to longleaf pine savannas (e.g., coastal marshes and barrier islands) are frequented by eastern diamondback rattlesnakes (Martin and Means, 2000; Means, 2006; unpub. data), and the species is sometimes relegated to marginal open-canopy habitats maintained by anthropogenic activities, e.g. hedgerows and along canal berms (Martin and Means, 2000).

The word savanna is derived from an Amerindian term that originally meant a grassy, tree-less plain particular to the New World (Savanna, 1906; Savannah, 1933). The term's contemporary use is more cosmopolitan and denotes a vegetation community emphasizing structure, which is distinguished by an open canopy of trees within a grassland matrix (Vogl, 1973). Open-canopy habitats were common in the southeastern United States during early European settlement (Walker and Peet, 1983; Platt, 1999), and fossil and pollen records provide evidence for these open habitats predating human presence (Watts, 1980a,b). The species composition of historical savannas in the southeastern United States has changed through time (Delcourt and Delcourt, 1987; Watts, 1980a,b; Van Lear et al., 2005). The most extensive savanna community to recently occur in the region was largely maintained by high-frequency, low to moderate intensity fires (Frost, 1998; Van Lear et al., 2005). Collectively referred to as a pine savanna or longleaf ecosystem, it was characterized by longleaf pine, but included an array of open-canopy habitats dominated by a variety of tree species within a grassland matrix and encompassed hydrologic regimes ranging from xeric to seasonally inundated (Peet and Allard, 1993; Van Lear et al., 2005). Fossil records for the eastern diamondback rattlesnake are limited to the southeastern United States and date from 1 to 1.5 million ybp (Martin and Means, 2000). Martin and Means (2000) speculated that eastern diamondback rattlesnakes have always been associated with open-canopy habitats, given that the species presettlement range was congruent with the historical distribution of open-canopy pine communities in the southeastern United States.

Fire exclusion became a dominant silvicultural practice during the early and mid-twentieth century, resulting in a reduction in open-canopy habitat as savannas were converted to forest (Van Lear et al., 2005). The historical extent of longleaf ecosystems was approximately 37 million ha (Frost, 1993), but land use changes reduced its current extent to approximately 1.2 million ha (Outcalt and Sheffield, 1996), a 97% reduction (Ware et al., 1993), making it one of the most imperiled ecological communities in North America (Noss et al., 1995). Similarly, the range of eastern diamondback rattlesnakes has been reduced (Martin and Means, 2000). Many species associated with southeastern savanna habitats are now imperiled (Means, 2006), and many remnant populations are now associated with anthropogenic activities that maintain an open vegetation structure. In much of the southeastern United States, remnant eastern diamondback rattlesnake populations are associated with areas under management practices that include regular prescribed fire, e.g. 1–3 year, (Means, 2006), which maintains an open-canopy savanna structure (Waldrop et al., 1992). As such, it appears that the species is a remnant of the historical savanna habitats of the southeastern United States.

The identification of the eastern diamondback rattlesnake as a remnant of the historical southeastern savanna is important for both the species conservation and broader management of the historical southeastern savanna community. First, the acknowledgement that eastern diamondback rattlesnakes are savanna specialists provides necessary information for the species management and conservation at small, localized scales. Secondly, the occurrence of remnant populations provides spatial information for conservation efforts aimed at pine savanna habitat. Although longleaf pine savannas were common throughout the southeastern Coastal Plain, industrial forestry in the early twentieth century and fire exclusion resulted in habitat loss and fragmentation (Frost, 1993). By the 1960s and 1970s, longleaf savannas were exceedingly rare and patchily distributed (Frost, 1993). Habitat loss continued through the remainder of the twentieth century, and longleaf savannas became virtually absent over much of the historical range. Given their longevity and habitat specificity, remnant eastern diamondback rattlesnake populations can be viewed as biological legacies of the former habitat, indicating the recent existence of the pine savanna community. This is particularly important in areas lacking gopher tortoises and red-cockaded woodpeckers, two longleaf specialists that receive federal protection. The distribution of eastern diamondback rattlesnakes extends far north of the current range of the gopher tortoise, and rattlesnake populations do not always occur in syntopy with red-cockaded woodpeckers. Eastern diamondback rattlesnakes have large home ranges, ranging from 28 to over 80 ha (Timmerman, 1995; Martin and Means, 2000; Waldron et al., 2006; Hoss, 2007), and although quite mobile, their movements outside of the breeding season tend to be infrequent and of short distances (Martin and Means, 2000). The presence of remnant eastern diamondback rattlesnake populations not only serves as an indicator of habitats that have restoration potential, but also increases the probability that other species associated with pine savanna occur locally.

The results of this study support the supposition that conservation efforts should focus on habitat structure rather than taxonomic composition. Single-species sensitivity to landscape change can act as a surrogate for an imperiled ecosystem (Samu et al., 2008), providing valuable spatial information for prioritizing land conservation. Furthermore, this study illustrates how a landscape acts as a palimpsest and maintains a record of the past (Gustavsson et al., 2007; Marrs, 2008). Eastern diamondback rattlesnakes tend to persist in quail plantations (Martin and Means, 2000), reflecting how habitat management for quail, including prescribed burning, the creation and maintenance of forest openings, and forest thinning practices (Kimmel, 1995), benefit the species. Burning is the primary management tool for maintenance of pine savanna structure, but canopy thinning and fuel reduction are necessary for proper habitat restoration (Varner et al., 2005; Varner et al., 2007). Given time and working in concert, these management practices will likely result in a future composition similar to the historical pine savanna as restored sites return to and continue on a fire adapted successional trajectory (Beckage et al., 2005).

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