Habitat specificity and home-range size as attributes of species vulnerability to extinction: a case study using sympatric rattlesnakes

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Abstract

Large home-range size and habitat specificity are two commonly cited ecological attributes that are believed to contribute to species vulnerability. The eastern diamondback rattlesnake *Crotalus adamanteus* is a declining species that occurs sympatrically with the more abundant canebrake rattlesnake *Crotalus horridus* in a portion of the south-eastern Coastal Plain, USA. In this study, we use the ecological similarities of the two species as experimental controls to test the role of home-range size and habitat specificity in the imperilment of the eastern diamondback rattlesnake. We used analysis of variance to investigate differences in home-range size between the two species, and home-range selection was modeled as habitat use versus availability with a case control sampling design using logistic regression. We failed to detect differences in home-range size between the two species; therefore, we could not identify home-range size as an attribute contributing to the imperilment of eastern diamondback rattlesnakes. Eastern diamondback rattlesnakes selected pine savannas to a degree that suggests that the species is a habitat specialist. Of the two factors examined, habitat specificity to the imperiled longleaf pine ecosystem may be a significant contributor to the decline of the eastern diamondback rattlesnake.

Introduction

Many studies have examined the ecological attributes of species vulnerability to extinction (reviewed by McKinney, 1997). Some of the most commonly cited attributes include large home-range size (Woodroffe & Ginsberg, 1998), greater habitat specificity (Primack, 1998), complex social structures (Courchamp, Clutton-Brock & Grenfell, 1999), ‘slow’ life histories (MacArthur & Wilson, 1967; Webb, Brook & Shine, 2002), limited geographic range (Gaston, 1994) and high trophic positions (Crooks & Soule, 1999). The identification of such attributes is important because it helps biologists recognize species at greatest risk of extinction and develop conservation priorities and management strategies for those species. However, few studies have accurately tested these attributes because of problems stemming from multi-taxa comparisons (McKinney, 1997), a lack of basic life-history data (Webb *et al*., 2002) and comparisons of imperilment resulting from different mechanisms (Owens & Bennett, 2000; Purvis *et al*., 2000).

According to Webb *et al*. (2002), ecologically similar, closely related, sympatric species are needed to unambiguously test the role of ecological attributes in species vulnerability. The eastern diamondback rattlesnake *Crotalus adamanteus* is a declining species (Martin & Means, 2000) in need of conservation and management (Dodd, 1987). The species occurs sympatrically with the locally more abundant canebrake rattlesnake *Crotalus horridus* in a portion of the south-eastern Coastal Plain, USA. Although *C. horridus* is imperiled in other parts of its range, for example some montane populations, the species is common and apparently secure in the South Carolina Coastal Plain (Tennant & Bartlett, 2000). Within the area of sympatry, both rattlesnake species are exposed to the same anthropogenic activities, for example habitat loss and fragmentation, wanton killing and collection pressures. Whereas the decline of the eastern diamondback rattlesnake has been attributed to such anthropogenic activities (Martin & Means, 2000; Timmerman & Martin, 2003), canebrake rattlesnake populations have not shown a comparable negative response and remain common in the region (Tennant & Bartlett, 2000).

Furthermore, eastern diamondback rattlesnakes and canebrake rattlesnakes share many of the attributes that are assumed to contribute to vulnerability. Both species have similar social structures, that is they are solitary organisms, and although males become combative during the breeding season (Klauber, 1956; Wagner, 1962), they lack territorial behavior (Gregory, Macartney & Larsen, 1987; Timmerman, 1995). Both are viviparous species that have long gestation periods (Murphy & Shadduck, 1976) and long inter-birth intervals ranging from 2 to 4 years (Gibbons, 1972; Tennant & Bartlett, 2000), indicating that they have 'slow' life histories. Both species are ambush predators that feed primarily on small mammals (Timmerman, 1995; Clark, 2002; Timmerman & Martin, 2003), and they therefore occupy similar trophic levels. Finally, neither species has a limited geographic range. Two attributes of vulnerability to extinction, home-range size and habitat specificity, have not been quantified within the range of sympatry of eastern diamondback and canebrake rattlesnakes.

In this study, we used the ecological similarities of the two species as experimental controls to test the role of home-range size and habitat specificity in the imperilment of the eastern diamondback rattlesnake. Because eastern diamondbacks were the imperiled species within our study area, we hypothesized that the species would have larger home ranges than canebrake rattlesnakes and that eastern diamondback rattlesnakes would show more habitat specificity. We conducted the study in an area where the two species are sympatric to ensure that both species experience the same potential mechanisms that contribute to imperilment. In addition to examining broader ecological patterns of species vulnerability, this study provides important baseline data for conservation management by quantifying habitat requirements of canebrake and eastern diamondback rattlesnakes.

Materials and methods

Study area

This study was conducted on state-owned property in Hampton County, South Carolina. The property consisted of *c.* 4900 ha of a mosaic of upland pine savannas, fields, mixed pine hardwood forests, planted pine forests and hardwood bottoms. The study area (*c.* 2800 ha) was delineated as a minimum convex polygon that encompassed all snake radio relocations recorded during the study. The South Carolina Department of Natural Resources has managed the property since 1971, and their efforts have focused primarily on game species, including bobwhite quail *Colinus virginianus* and white-tailed deer *Odocoileus virginianus*. Fields and wildlife openings within the study area were maintained with yearly plowing and planting and new fields were occasionally created. Debris from field maintenance bordered most field edges as slashpiles that consisted of trees and stumps pulled during field construction. Prescribed fire was an important management tool at the study site; managers used high-frequency burns (every 1–4 years) between January and April to maintain pine savannas.

Radio telemetry

Radio telemetry was used to measure home-range size and to model landscape-scale habitat selection by eastern diamondback rattlesnakes and canebrake rattlesnakes during eight field seasons from March 1997 to December 2004. Adult eastern diamondback rattlesnakes (females, $n = 15$; males, $n = 6$) and canebrake rattlesnakes (females, $n = 10$; males, $n = 8$) were captured and surgically implanted with radio transmitters (SI-2, 11–13 g, Holohil Systems, Carp, ON, Canada). Between 1997 and 2001, eastern diamondback rattlesnakes were anesthetized using an injectable anesthesia (Ketamine) using techniques modified from Reinert & Cundall (1982). Starting in 2002, isoflurane was used as an anesthetizing agent that was administered with an anesthesia machine equipped with an isoflurane vaporizer. Following surgery, snakes were monitored for 3 days before being released at their capture locations.

Eastern diamondback rattlesnakes were radio located throughout the study period and canebrake rattlesnakes were radio located between 2001 and 2004. Some eastern diamondbacks were monitored for as long as 3 years, but most study animals were monitored for only 1 year. In cases where study animals were tracked for more than 1 year, only the first year of activity was included in the analyses. Three canebrake rattlesnakes were monitored between 4 and 6 months due to mortality resulting from either predation or road mortality. Study animals were located *c.* 5 days per week during spring, summer and fall using a radio receiver (Telonics, TR-2, Mesa, AZ, USA) and a directional Yagi antenna. Winter (inactive season) radio relocations ranged from three to five per week for eastern diamondback rattlesnakes before 2002, after which both species were tracked biweekly to monthly between December and March. Each snake location was recorded using a global positioning system (GPS; Trimble Pro XR, Sunnyvale, CA, USA) with real-time differential correction accurate to within 2 m.

Habitat data collection and home-range estimation

Home-range estimates for each study animal were calculated using the GPS positions obtained for each snake location. ArcView GIS version 3.3 (ESRI, Redlands, CA, USA) and Spatial Analyst with the Animal Movement Extension (Hooge & Eichenlaub, 1997) were used to calculate home-range size using fixed kernel analysis (95% activity core), which offers a non-parametric estimation of home-range size (Worton, 1987, 1989). ArcView calculated the smoothing parameter, *h*, used in home-range estimation.

Habitats within the study area were characterized by combining aerial photographs with National Wetlands Inventory (NWI) classifications (Cowardin *et al*., 1979; Table 1). The upland pine category was divided into two classes based on canopy cover. Open-canopy upland pine, including longleaf, loblolly *Pinus taeda* and slash *Pinus elliottii* pine, was classified as pine savanna. Closed canopy, planted loblolly, slash and

Table 1 Habitat types used by eastern diamondback rattlesnakes *Crotalus adamanteus* and canebrake rattlesnakes *Crotalus horridus* in south-eastern South Carolina, USA[a]

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 *Pinus elliottii*, loblolly pine *Pinus taeda*, post oak *Quercus stellata*, blackjack oak *Quercus 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 *Quercus phellos*, and southern red oak *Quercus falcata*
Palustrine hardwood	Hardwood bottom	Forested wetland; holds water seasonally; overstory dominated by hardwoods; dominant species include overcup oak *Quercus 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 (NWI) classification.

longleaf pine stands were classified as planted pine. This classification was systematically verified throughout the study area by field visits to the various habitats. Habitat variables were spatially assigned to randomly generated points within rattlesnake home ranges and compared with randomly generated points across the landscape (use vs. availability), allowing habitat selection to be modeled as home-range selection.

Data analysis

Statistical analysis was performed using SAS 9.1 (SAS Institute, 2002). We used analysis of variance (ANOVA; PROC GLM) to compare home-range size between the two species. Because previous studies indicated that male and female rattlesnakes differ in home-range size (Reinert & Zappalorti, 1988; Timmerman, 1995; A. Savitzky & C. Petersen, pers. comm.), we performed a two-way ANOVA, which allowed us to block by sex and test for a possible species by sex interaction. Gravid females were removed from the analysis because of low sample sizes (eastern diamondback rattlesnake, $n = 2$; canebrake rattlesnake, $n = 1$). Home-range size was log 10 transformed because of problems with normality (Shapiro–Wilk = 0.73, $P = < 0.0001$). Following transformation, assumptions of normality (Shapiro–Wilk = 0.97, $P = 0.42$) and homogeneity of variance (Levene's test, $F = 0.41$, $P = 0.75$) were met.

We modeled landscape-scale home-range selection for males and females (gravid and non-gravid) of both species using logistic regression. We used a case control sampling design, where we randomly removed 25% of the within-home-range observations and 25% of the random observations. Gender significantly affected the model for eastern diamondbacks ($\chi^2 = 88.03$, d.f. = 1, $P < 0.0001$); therefore, males and females were separated for the analysis. To remain consistent, males and females were also separated for canebrake rattlesnakes, although gender did not significantly affect home-range selection ($\chi^2 = 0.56$, d.f. = 1, $P > 0.05$) in this species. Maximum likelihood estimates and odds ratios were used to compare home-range selection across habitat types. To ensure that individual males and females could be pooled within species for analysis, we investigated the influence of individual snakes in the models. The effect of individual snakes was not significant for male ($\chi^2 = 7.03$, d.f. = 6, $P > 0.05$) and female ($\chi^2 = 17.27$, d.f. = 14, $P > 0.05$) eastern diamondback rattlesnakes, or for male ($\chi^2 = 10.89$, d.f. = 8, $P > 0.05$) and female ($\chi^2 = 13.00$, d.f. = 10, $P > 0.05$) canebrake rattlesnakes.

Results

Home-range size

The average 95% kernel home-range estimates are given in Table 2. There was a high degree of inter- and intraspecific home-range overlap at the study area, and both species were commonly observed along the same field edge or in the same habitats simultaneously. Our analysis of eastern diamondback rattlesnake and canebrake rattlesnake home ranges failed to detect interspecific differences in home-range size (d.f. = 1; $F = 0.24$; $P > 0.05$). Male rattlesnakes had significantly larger home ranges than females (d.f. = 1, $F = 5.08$, $P < 0.05$); however, there was no interaction of sex by species (d.f. = 1, $F = 0.07$, $P > 0.05$), supporting our between-species comparison.

Home-range selection

Analysis of home-range selection was based on 21 eastern diamondback rattlesnake and 18 canebrake rattlesnake home ranges. Logistic regression indicated significant home-range selection based on habitat use versus availability for eastern diamondback rattlesnakes (females, d.f. = 4, $\chi^2 = 539.93$, $P < 0.0001$; males, d.f. = 4, $\chi^2 = 159.08$, $P < 0.0001$; Table 3) and canebrake rattlesnakes (females, d.f. = 4, $\chi^2 = 172.66$,

Table 2 Mean 95% kernel home-range estimates (ha) for sympatric adult eastern diamondback rattlesnakes *Crotalus adamanteus* and canebrake rattlesnakes *Crotalus horridus* in south-eastern South Carolina, USA

Species	*n*	x̄ home range (ha)	SE	Range
Eastern diamondbacks				
Male	6	84.82	46.62	16.91–310.48
Non-gravid female	13	28.63	5.23	5.42–61.60
Gravid female	2	18.07	3.14	14.92–21.22
Canebrakes				
Male	8	48.38	12.01	8.6–107.5
Non-gravid female	9	30.82	13.31	10.7–134.1
Gravid female	1	8.00	–	–

Table 3 Maximum likelihood estimates from the logistic regression model of home-range selection by sympatric adult eastern diamondback rattlesnakes *Crotalus adamanteus* and canebrake rattlesnakes *Crotalus horridus* in south-eastern South Carolina, USA

	Variables	Estimate ± SE	χ^2	*P*
Male *C. adamanteus*	Pine savanna	1.3955 ± 0.1611	75.01	< 0.0001
	Planted pine	0.0078 ± 0.1705	0.00	0.9635
	Pine hardwood	−0.8431 ± 0.5008	2.83	0.0923
	Hardwood bottom	−1.4659 ± 0.2591	32.02	< 0.0001
	Field	0.9056 ± 0.2077	19.00	< 0.0001
Female *C. adamanteus*	Pine savanna	1.2293 ± 0.0745	239.09	< 0.0001
	Planted pine	−0.7338 ± 0.0905	65.71	< 0.0001
	Pine hardwood	0.6548 ± 0.1695	14.93	0.0001
	Hardwood bottom	−1.5872 ± 0.1411	126.52	< 0.0001
	Field	0.4368 ± 0.1093	15.99	< 0.0001
Male *C. horridus*	Pine savanna	0.0622 ± 0.0941	0.44	0.5088
	Planted pine	−0.5269 ± 0.0955	30.42	< 0.0001
	Pine hardwood	0.4072 ± 0.2025	4.04	0.0444
	Hardwood bottom	−0.2047 ± 0.1016	4.06	0.0440
	Field	0.3710 ± 0.1302	8.12	0.0044
Female *C. horridus*	Pine savanna	0.5624 ± 0.0908	38.32	< 0.0001
	Planted pine	−0.2086 ± 0.0948	4.83	0.0278
	Pine hardwood	0.0470 ± 0.2187	0.05	0.8297
	Hardwood bottom	−1.3013 ± 0.1392	87.40	< 0.0001
	Field	0.9005 ± 0.1209	55.49	< 0.0001

$P<0.0001$; males, d.f. = 4, $\chi^2 = 37.25$, $P<0.0001$; Table 3). There were differences in the degree to which specific habitats were selected by both species. Odds ratios indicated that pine savannas were the most strongly selected habitat for eastern diamondback rattlesnakes; females were 16.7 and 7.4 times more likely to use pine savannas than hardwood bottoms and planted pine forests, respectively, and males were 17.5 times more likely to use pine savanna than hardwood bottoms. Canebrake rattlesnake home-range selection also varied by sex (Table 3). Male canebrake rattlesnakes did not show a positive association with pine savannas; rather, they most strongly selected fields and pine hardwood forests. Female canebrake rattlesnakes most strongly selected fields and pine savannas. Female canebrake rattlesnakes were 9.0 times more likely to use fields and 7.0 times more likely to use pine savannas than hardwood bottoms. Male canebrake rattlesnakes were both 2.5 times and 2.0 times more likely to use pine hardwood forests than pine savannas and hardwood bottoms, respectively.

Discussion

Home-range size

Contrary to our expectations, we failed to detect differences in home-range size between the two species. Therefore, we could not identify home-range size as an attribute possibly contributing to the imperilment of eastern diamondback rattlesnakes within the study area. The canebrake rattlesnake home-range estimates reported in this study are similar to the estimates of south-eastern Virginia canebrake rattlesnakes and much smaller than the estimates of Coastal Plain timber rattlesnakes *C. horridus* in New Jersey (Table 4). Likewise, there is geographic variation in eastern diamondback rattlesnake home-range size (Table 4). Such regional variation in home-range size likely reflects local habitat quality, prey availability and body size (McNab, 1963; Harestad & Bunnell, 1979; Gregory *et al*., 1987). The relationships between these factors and the home-range sizes observed in

Table 4 Comparisons of home-range sizes of eastern diamondback rattlesnakes *Crotalus adamanteus* and Coastal Plain populations of canebrake rattlesnakes and timber rattlesnakes *Crotalus horridus*

	Home range[a]			
Species/location	Males	Non-gravid females	Gravid females	Source
C. horridus				
SC Coastal Plain	48.32	30.8	8.0	Current study
Chesapeake, VA	74.7	31.3	12.2	A. Savitzky & C. Petersen (pers. comm.)
Pine Barrens, NJ	207.4	41.6	22.2	Reinert & Zappalorti (1988)
C. adamanteus				
SC Coastal Plain	84.82	28.6	18.1	Current study
Putnam Co., FL	158.9[b]	88.8	–	Timmerman (1995)
Desoto N.F., MS[c]	59.5	8.2	–	Kain (2003)

[a]All home ranges were based on 95% isopleths except the Mississippi population, which was based on minimum convex polygon estimates.
[b]Only first year estimates included in average.
[c]Home-range sizes of non-gravid females and gravid females were not distinguished.

this study are not clear, but the similarity in home-range size between the two species precludes the identification of large home-range size as an attribute explaining eastern diamondback rattlesnake imperilment within the study area.

Home-range selection

At the scale of this study, the difference in the degree to which each species selected habitat provides insight into why eastern diamondback rattlesnakes are more imperiled than canebrake rattlesnakes in the South Carolina Coastal Plain. Although female canebrakes were positively associated with pine savannas, odds ratios indicated that eastern diamondbacks were twice as dependent on the habitat. The extent to which eastern diamondback rattlesnakes selected pine savannas implies that the species is more of a habitat specialist, suggesting that the decline of longleaf pine forests in the south-eastern Coastal Plain has likely been a prominent cause of the species decline. Although estimates of the spatial extent of longleaf pine at the time of European settlement vary, most authorities agree that less than 2% of the original habitat coverage remains (Ware, Frost & Doerr, 1993; Platt, 1999). In South Carolina alone, there has been a 55% decline of longleaf pine since 1955 (Smith, Patterson & Trendell, 2000).

Although female canebrake rattlesnakes also had a positive association with pine savannas, males showed no significant association with the habitat. Rather, male canebrake rattlesnakes most strongly selected pine hardwood forests. The open canopy, savanna-like structure of longleaf pine forests results from high-frequency fires, which occur more than once a decade (Greene, 1931; Chapman, 1932; Heyward, 1939; Bruce & Brickford, 1950; Glitzenstein, Platt & Streng, 1995; Platt, 1999) and are effective at suppressing the growth of hardwood trees (Greene, 1931; Chapman, 1932; Williamson & Black, 1981; Rebertus, Williamson & Moser, 1989; Glitzenstein *et al*., 1995). During much of the 20th century, south-eastern pine forests were subjected to fire exclusion that resulted in the succession of open-canopy pine forests to closed-canopy mixed pine hardwood forests (Frost, 1993; Timmerman & Martin, 2003). A large percentage of the existing mixed pine hardwood forests originated as agricultural areas that, through abandonment and fire exclusion, succeeded into mixed pine hardwood stands (Ware *et al*., 1993). Both male canebrake rattlesnakes and female eastern diamondback rattlesnakes had positive associations with pine hardwood forests. The home-range selection patterns observed within the study area may reflect some tolerance on the part of female eastern diamondback and male canebrake rattlesnakes of habitat that has been converted from open-canopy pine to closed-canopy mixed pine hardwood forests.

Both rattlesnake species had strong negative associations with planted pine forests, which have increased from two to 30 million acres in the south-eastern United States between 1952 and 1999 (Conner & Hartsell, 2002). This is not to say, however, that rattlesnakes completely avoided the habitat. Individuals commonly moved through planted pine forests, but did not spend considerable amounts of time there as compared with other habitats. The negative association likely reflects the structure of the habitat, specifically with regard to canopy and ground cover. Pine savannas are an open-canopy habitat that allows a large amount of sunlight to reach the forest floor (Noel, Platt & Moser, 1998) and are noted for high species richness (Peet & Allard, 1993). Conversely, as planted pine forests mature, canopy closure shades out competing vegetation, which leads to reduced structural complexity (Baker & Hunter, 2002) and overall diversity.

The home ranges of both species were positively associated with fields, which likely reflected preference for some structural characteristics of field habitat. Slashpiles, resulting from field maintenance and construction, aligned field edges and provided protective cover and opportunities for thermoregulation for both species. Rattlesnakes in ecdysis frequented slashpiles, where they could bask while remaining partially hidden in debris. Furthermore, some field edges were planted with shrubby lespedeza *Lespedeza bicolor*, which also provided cover for snakes. Field use also potentially reflected foraging opportunities. Prey items common to both rattlesnakes (see Klauber, 1956; Clark, 2002; Timmerman & Martin, 2003), for example cotton rats *Sigmodon hispidus* and gray squirrels *Sciurus carolinensis*, were abundant in fields in the study area (J. L. Waldron, pers. obs.).

Because most fields were planted seasonally with corn and were surrounded by slashpiles, rodents, including major prey species such as gray squirrels and cotton rats, were abundant along field edges. Although gray squirrels rarely move across fields, they forage along field perimeters (Burger, 1969), and cotton rats are old field/edge specialists (Pagels, Erdle & Uthus, 1992).

Of the two attributes common among vulnerable species examined in this paper, specificity to an imperiled habitat appears to be more relevant to the vulnerability of eastern diamondback rattlesnakes. Undoubtedly, the effects of habitat loss, wanton killing and over-collection have all contributed to the decline of the eastern diamondback rattlesnake. However, given that canebrake rattlesnakes are likely subjected to the same killing and collection pressures, it appears that habitat loss and alteration are the most significant contributor to the imperilment of eastern diamondback rattlesnakes. State laws protecting the species from killing and collecting are likely to have limited success without additional habitat protection. Conservation and recovery plans are more effective if focused on preserving ecosystems or communities rather than single species (Dodd, 1987), and the eastern diamondback rattlesnake is one of many imperiled vertebrates associated with longleaf pine savannas.

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