

## Multiscale Influences of Landscape Composition and Configuration on the Spatial Ecology of Eastern Diamond-backed Rattlesnakes (*Crotalus adamanteus*)

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**ABSTRACT.**—Landscape composition and configuration affect ecological processes at the population and community levels, but few studies have demonstrated the effects of landscape pattern on individuals. Because heterogeneity influences abundance and distribution of critical resources, it is hypothesized that it indirectly affects home range size of individuals. To examine the spatial ecology of the declining Eastern Diamond-backed Rattlesnake (*Crotalus adamanteus*; EDB), we conducted a two-year study in southwestern Georgia. We obtained home range estimates via radio-telemetry, employed Euclidean distance analysis to examine habitat associations at two spatial scales, and used the software program FRAGSTATS to analyze landscape heterogeneity and examine its effect on home range size. Although no significant habitat associations were detected, there were trends for a positive association with pine habitat at the landscape scale and a negative association with agriculture within the home range. Home range size was negatively correlated with several landscape metrics representing heterogeneity in patch configuration, such that individuals in heterogeneous landscapes had small home ranges. This relationship was strongest at three spatial scales: the first was similar to mean home range size of EDBs; and the others were three and four times as large as the largest home range recorded. Together, these results suggest that management regimes to enhance population densities of EDBs emphasize the preservation of pine uplands, while maintaining a mosaic of other habitat types, and limit the conversion of forest to agriculture. Also, our results underscore the importance of using robust analytical tools and multiscale approaches in studies of spatial ecology.

The current rate of habitat loss and fragmentation coupled with decreases in biodiversity (Wilcox and Murphy, 1985; Tilman et al., 1994; Fahrig, 2003) gives immediacy to research focused on the spatial ecology of declining species. For example, the Longleaf Pine (*Pinus palustris*) ecosystem of the southeastern United States, which supports an unusually diverse array of reptile and amphibian species (Guyer and Bailey, 1993), has declined at least 97% from its historic extent and is continuing to be converted at an alarming rate (Ware et al., 1993). As a result, many herpetofaunal species that exist primarily or exclusively in this ecosystem have undergone equally severe declines, yet there is a general dearth of knowledge available to direct conservation efforts for the majority of these species (Guyer and Bailey, 1993; Means, 2006).

The Eastern Diamond-backed Rattlesnake (*Crotalus adamanteus*; hereafter referred to as EDB) is an upland snake of the longleaf pine ecosystem that is reported to be undergoing rangewide declines. Significant population declines of EDBs were first recognized in the 1950s (see Timmerman and Martin, 2003) and are thought to be a result of habitat loss and fragmentation (Martin and Means, 2000), road mortality (Timmerman and Martin, 2003), and indiscriminate killing by humans (Dodd, 1987). Despite past and current concerns about the status of this species, it is afforded no specific protection in any of the seven states that comprise their geographic range. Although many researchers have acknowledged that the EDB likely meets criteria for state or federal protection (Enge, 1991; Timmerman, 1995; Martin and Means, 2000; Timmerman and Martin, 2003), there are limited data available to document the most fundamental aspects of its ecology.

The survival and reproductive success of an individual is inextricably linked to how it uses its habitat. Consequently, common conservation practices, such as reintroduction and reserve

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design, have hinged on the knowledge of which resources are critical for the establishment and persistence of particular species (Harig and Fausch, 2002; Cabeza et al., 2004). When determining which habitat characteristics are being selected by an individual or species, it is important to consider whether and how selection differs among varying scales of investigation (Wiens, 1989). Johnson (1980), for example, presented a hierarchical organization of habitat selection and argued that, because availability of habitat types often changes depending on the spatial scale considered (e.g., geographic range, landscape, home range, etc.), selection might also change, and indeed this appears to be the case for a broad range of taxa (e.g., Naugle et al., 1999; Gorrens et al., 2005; Moore and Gillingham, 2006). Thus, caution should be exercised when comparing single-scale studies, because the spatial scale at which the studies were conducted, rather than inherent interpopulation differences, might explain discrepancies in reported patterns of habitat use (e.g., Reynolds, 2006). These discrepancies are particularly troubling for species in need of immediate management for which multiscale studies of a single population do not exist in the literature.

In addition to identifying the habitat composition of the space being used by an individual (i.e., home range), it is also useful to examine factors that might affect the amount of space required for regular activities (e.g., foraging, reproduction). Because landscapes are comprised of a variety of habitat patches that, at some spatial scale, encompass all of the resources an individual requires for maximizing its fitness, variation in the composition and configuration of those patches (i.e., heterogeneity) likely affects space use. Optimal foraging (MacArthur and Pianka, 1966) and ideal free distribution (Fretwell and Lucas, 1970) theories predict that animal space use will be related to the distribution and abundance of resources across a landscape. Because animal movements often come at a cost of increased predation risk and energy expenditure, a logical extension of that prediction is that individuals will occupy the smallest home range that includes adequate amounts of critical resources (e.g., food, refugia, mates) to minimize movement-associated costs. Consequently, if these resources are more easily accessible or more abundant in particularly heterogeneous landscapes, then an individual's home range size may be indirectly affected by heterogeneity.

Our study focused on the influence of landscape composition and configuration on the spatial ecology of EDBs in southwestern Georgia, a region that appears to be a stronghold for the species and, thus, a prime area for

research (Timmerman and Martin, 2003). The objectives of this study were to (1) determine whether individuals exhibited nonrandom habitat associations at two different spatial scales, (2) quantify home range size for comparison among previous studies, and (3) determine whether landscape heterogeneity affected home range size in EDBs.

#### MATERIALS AND METHODS

*Study Site.*—This study was conducted at Ichauway, a 12,000-ha research site of the Joseph W. Jones Ecological Research Center (JWJERC) located in Baker County, Georgia. Management priorities of the JWJERC are restoration of the longleaf pine ecosystem and application of land-use practices that integrate wildlife and timber management. Ichauway consists primarily of Longleaf Pine forest (between 70 and 90 years old, in general, with individual trees >300 years old) with an open midstory and herbaceous understorey, dominated by Wiregrass (*Aristida beyrichiana*). Stands of Loblolly (*Pinus taeda*) and Slash (*Pinus elliottii*) pines, hardwood patches (mostly *Quercus* spp.), and mixed pine-hardwood forests, isolated wetlands, and riparian areas associated with Ichawaynochaway Creek and the Flint River are scattered throughout the property. Numerous food plots for Northern Bobwhite (*Colinus virginianus*) and White-tailed Deer (*Odocoileus virginianus*) are maintained throughout the forest matrix. The site is managed on a 1- or 2-yr prescribed burn rotation, with approximately 4,000–4,900 ha burned each year, which helps maintain features of old-growth longleaf pine forest (e.g., open canopy and intact understorey). An 8,730-ha section of Ichauway was delineated as our study site.

*Study Animals and Radio-Telemetry.*—From 2 September 2003 to 17 July 2004, we captured 14 adult EDBs (seven males and seven nonpregnant females) encountered on roads or in forested habitats. Snakes were brought to the laboratory, anesthetized with isoflourane vapor, and implanted intraperitoneally with 16.1-g temperature-sensitive radio transmitters (Model AI-2, Holohil Systems, Inc., Carp, Ontario, Canada) using the surgical techniques described in Reinert (1992). While anesthetized, mass was obtained to the nearest 0.01 g; snout-vent length (SVL) and tail length were measured to the nearest 0.1 cm; sex was determined; and passive integrated transponders (PIT tags, Biomark®) were injected subcutaneously for unique identification of individuals. Subjects were allowed to recover overnight and were released at their site of capture the following

TABLE 1. Sampling summary for 10 Eastern Diamond-backed Rattlesnakes (*Crotalus adamanteus*) included in radio-telemetry study in southwestern Georgia.

Snake ID	Sex	Composite HR		First-year HR		Dates monitored
		Fixes	MCP (ha)	Fixes	MCP (ha)	
2	M	51	20.35	42	20.33	9/2/03–5/28/05
3	F	42	68.10	38	33.81	9/2/03–6/12/05
6	F	43	27.74	36	22.91	9/15/03–6/12/05
7	M	30	19.34	30	19.34	9/22/03–6/20/04
8	F	33	7.25	33	7.25	9/23/03–5/14/04
9	M	42	76.79	33	59.94	10/3/03–5/28/05
10	F	36	16.48	34	16.02	10/3/03–10/23/04
11	F	13	15.19	13	15.19	4/9/04–9/24/04
12	F	16	40.93	16	28.35	5/14/04–6/12/05
14	M	15	22.34	15	22.34	7/17/04–5/28/05

day. The mass of the transmitters never exceeded 1.7% of the body mass of the subjects.

We radio-tracked EDBs from 2 September 2003 to 20 June 2005. Because of a known mortality, a possible mortality (only transmitter found), a premature transmitter failure, and an individual that moved to an inaccessible area, 10 snakes (four males and six nonpregnant females) were included in the present analyses (Table 1). These snakes were radio-tracked approximately once per week during the active season (late March to early November) and approximately twice per month during the inactive season (late November to early March). Radio-tracking occurred during daylight hours, and over the course of the study, an effort was made to locate each individual across all daylight hours. When a snake was located, the site was flagged and a Global Positioning System (GPS; GeoExplorer 3®, Garmin International, Inc., Olathe, KS) was used to obtain UTM coordinates of the location; GPS locations were accurate to within 3 m. When a subject was found to be greater than 5 m from a previously used site, that location was considered unique.

*Study 1: Habitat Associations.*—To analyze habitat associations, locations of all snakes were added to an existing ArcGIS (vers. 8.2; Earth Systems Research Institute, Redlands, CA, 2002) landcover layer of the study site. This layer was initially created using 1992 color infrared photography (1 : 12,000 scale) and was subsequently updated using 2002 color infrared photography (1 : 12,000 scale) and field surveys. Habitat types considered were pine (all pine species, natural and planted), hardwood, mixed pine-hardwood, and agriculture (including food plots >0.5 ha). These four habitat types were chosen because they were dominant at the site and allowed for comparison with previous studies (Timmerman, 1995; Waldron et al., 2006a, 2008; Steen et al., 2007).

We employed Euclidean distance analysis (Conner and Plowman, 2001; Conner et al., 2003) to determine habitat associations. This analysis allowed a test of nonrandom habitat use by comparing the mean minimum distance from animal locations to each of the designated habitat types to expected distances compiled from random locations. The habitat type within which a location fell received a distance score of zero for that location. To determine whether EDBs exhibited habitat associations at the landscape scale, random points across the study site (generated by Hawth's Tools extension for ArcGIS; Beyer, 2004) were compared to random points within each individual's composite home range (i.e., all locations per snake); this allowed for the availability of habitats within the home range to be compared to the availability of habitats at a larger scale. Home ranges were estimated as 100% minimum convex polygons (MCP; Hayne, 1949) using the Hawth's Tools extension for ArcGIS (Beyer, 2004; potential issues with using MCPs are discussed in Study 2). To assess within-home range habitat associations, random points within each home range were compared to known locations for an individual; this determined whether snakes were selecting specific habitats from among those available within the home range. When a snake was located at the same site on subsequent observations (such as during winter inactivity), those observations were omitted from the data, because they were not considered independent from the initial observation.

The effect of sex on both scales of habitat associations was assessed using a one-factor MANOVA with individual snakes as the experimental unit. Sex did not have a significant effect on habitat associations at either spatial scale (landscape:  $\Lambda = 0.288$ ,  $P = 0.124$ ; within-home range:  $\Lambda = 0.733$ ,  $P = 0.768$ ); therefore, we present only analyses using pooled sexes. All

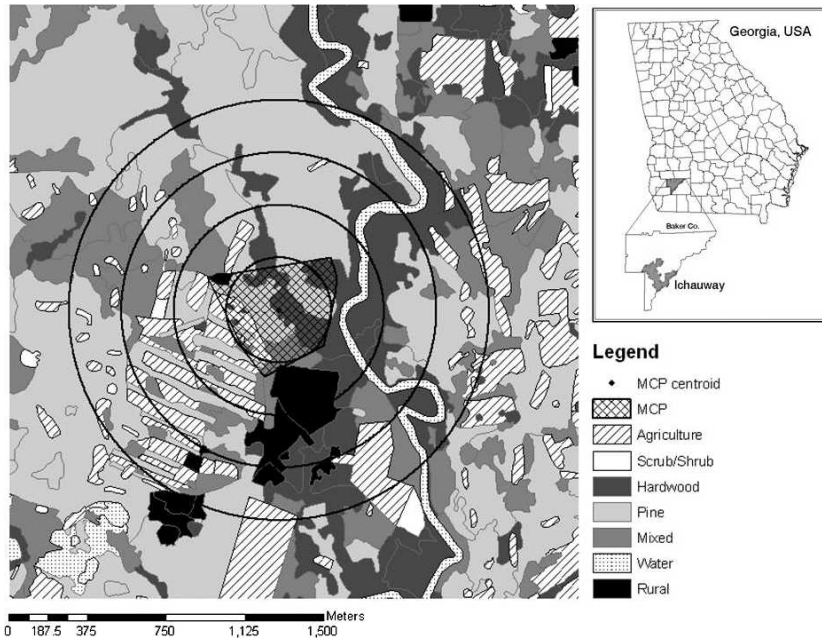


FIG. 1. Location of Ichaaway in Georgia where Eastern Diamond-backed Rattlesnake (*Crotalus adamanteus*) home range data were collected, and buffering step used in the landscape analysis. A home range (MCP) centroid was encircled with four buffers of increasing radii (250, 500, 750, and 1,000 m). The landscape within each of those buffers was analyzed to determine the relationship between heterogeneity and home range size.

statistical analyses were performed in SAS 9.1 (SAS Institute, Inc., Cary, NC), using  $\alpha = 0.05$ .

*Study 2: Home Range Size, Landscape Pattern, and Heterogeneity.*—To compare home range size across studies, we reestimated 100% MCPs using only locations from each animal's first year in the study (i.e., previous studies reported first-year home ranges; Kain, 1995; Timmerman, 1995; Waldron et al., 2006a). Although some researchers suggest that kernel density (KD) estimators are a more accurate measure of home range size than MCP (Kernohan et al., 2001), recent arguments indicate that this is not the case for many reptiles, because of their relatively sedentary nature (Row and Blouin-Demers, 2006). Specifically, when an animal does not move between observations or returns frequently to previous sites, the KD method tends to overestimate home range size, especially when the commonly used, least-squares cross-validation (LSCV) method of calculating the smoothing factor ( $h$ ) is employed (Hemson et al., 2005).

Because of the known benefits of using KD to estimate home range size in certain taxa, we initially calculated KD estimates for EDBs in this study. Not only did home range size appear to be inflated for most of our animals but also the home ranges were broken into multiple polygons, rendering them unusable for subse-

quent habitat analyses. Thus, we chose to use the MCP method, while keeping in mind its limitations. Our greatest concern was that the MCP method might not be appropriate given that some of our animals had a relatively small number of relocations, but because there was no significant relationship between first-year home range size and number of relocations ( $R^2_{adj} = 0.00$ ,  $P = 0.857$ ), we feel confident that our use of this method was, indeed, appropriate.

To examine the effects of landscape pattern and heterogeneity on home range size of Ichaaway EDBs, we used the landcover map described above. Seven landcover types were delineated for this study: pine, mixed pine-hardwood, hardwood, agriculture (wildlife food plots >0.5 ha and cropland), scrub/shrub, rural (buildings and paved roads), and water (ephemeral and permanent wetlands and creeks). All MCPs were overlaid onto the landcover map, and the center of each home range (centroid) was calculated. We delineated four spatial scales around MCP centroids with 250-, 500-, 750-, and 1,000-m buffers that encompassed 20, 77, 178, and 314 ha, respectively (Fig. 1). These spatial scales encompassed the known home range sizes of adult male and nonpregnant female EDBs throughout their range (reviewed in Timmerman and Martin, 2003). Although some individuals in the current

TABLE 2. Matrix of user-defined edge contrast weights for seven landcover types at Ichauway, in Baker County, Georgia. Low values represent low edge contrast between row and column landcover type, whereas high values represent high edge contrast.

Patch type	Agriculture	Scrub/Shrub	Hardwood	Pine	Mixed <sup>a</sup>	Water	Urban/Barren
Agriculture	0						
Scrub/Shrub	0.2	0					
Hardwood	0.8	0.4	0				
Pine	0.8	0.8	0.4	0			
Mixed <sup>a</sup>	0.8	0.6	0.2	0.2	0		
Water	1.0	1.0	1.0	1.0	1.0	0	
Urban/Barren	1.0	1.0	1.0	1.0	1.0	1.0	0

<sup>a</sup>Mixed pine-hardwood

study maintained home ranges smaller than 20 ha, smaller buffers were not used because many landscape metrics could not be calculated at smaller spatial scales.

We used FRAGSTATS (McGarigal and Marks, 1995) to analyze the landscape of individual snake buffers at each of the four spatial scales. McGarigal and Marks (1995) recognized seven categories of landscape metrics that correspond to patch characteristics: area/density, shape, contagion, contrast, proximity, core area, and diversity. From these seven categories, we calculated 25 landscape metrics. One metric from the contrast category (mean edge contrast index) required user-defined weights that approximated edge contrast for each pair of landcover types (Table 2). Although these weights were subjectively chosen, we believe they represented reasonable assumptions concerning structural contrast among these seven distinct landcover types.

Home range estimates were log-transformed to meet normality assumptions of parametric tests. To determine whether males and females differed in home range size, we employed an ANCOVA using body size (SVL) as a covariate. Because males and females did not differ in home range size ( $F_{1,7} = 0.31$ ,  $P = 0.597$ ), sexes were pooled for all subsequent analyses.

Pearson correlation coefficients were calculated for the 25 landscape metrics plotted against log-transformed home range size at each spatial scale. All metrics were assessed for normality and, when necessary, transformed to meet parametric assumptions. Because metrics from the same category (e.g., shape) are often intercorrelated (Hargis et al., 1998), only data for nine metrics (one or two from each category) were selected for further consideration (Table 3). These metrics were chosen because they exhibited the strongest correlation with home range size within their respective category, they provided unique information concerning the relationship between landscape pattern and

home range size, and they were easy to interpret.

Li and Reynolds (1994) suggested that heterogeneity could be described as a function of five landscape components representing the composition (number of patch types and proportion of each patch type) and configuration (patch shape, spatial arrangement of patches, and contrast between neighboring patches) of a landscape. For each spatial scale, we used four metrics representing four of the five components of heterogeneity as independent variables in a multiple regression with log-transformed home range size as the dependent variable. The four metrics were modified Simpson's evenness index (MSEI; represents proportion of patch types), mean fractal index (MFI; represents patch shape), log-transformed area-weighted mean proximity index (logAMPI; represents spatial arrangement of patches), and mean edge contrast index (MECI; represents structural contrast between neighboring patches). Number of patch types was not represented, because there was inadequate variation among individuals with respect to this component.

Li and Reynolds (1994) demonstrated that landscape components representing composition and configuration interact in a nonadditive manner to produce a form of overall heterogeneity; thus, we compared regression models including all four metrics at each spatial scale. However, because we suspected that each of the four metrics alone, as well as in combination with one or more of the other metrics, have the potential to represent equally meaningful forms of landscape heterogeneity, we also developed 15 a priori models for each spatial scale, which included all additive combinations of the four components.

Cunningham and Johnson (2006) discussed potential issues associated with including nested scales in spatial analysis. For example, our 500-m buffer includes the landscape encompassed by the 250-m buffer; thus, landscape

TABLE 3. Landscape metrics used as independent variables associated with adult Eastern Diamond-backed Rattlesnake (*Crotalus adamanteus*) home range size in correlation analysis and multiple regression.

Category	Metric	Description	Heterogeneity <sup>a</sup>
Area/Density	Edge Density (ED)	edge density	+
	Patch Density (PD)	patch density	+
Shape	Mean Fractal Index (MFI)	index of patch shape	+
Core Area	Disjunct Core Area Density (DCAD)	density of disjunct patch core (>5m from edge) area	+
Proximity	Area-Weighted Mean Proximity Index (AMPI)	index of spatial arrangement of patch types	+
Contrast	Mean Edge Contrast Index (MECI)	contrast-weighted (Table 2) edge density	+
Contagion	Interspersion and Juxtaposition Index (IJI)	index of patch type interspersion	-
Diversity	Modified Simpson's Evenness Index (MSEI)	index of patch type diversity and evenness	+
	Modified Simpson's Diversity Index (MSDI)	index of patch type diversity and abundance	+

<sup>a</sup>Sign indicates the direction of the relationship between the metric value and heterogeneity.

metrics measured at these two scales are not independent. We adopted the approach used by Cunningham and Johnson (2006) to mitigate problems of nonindependence and multicollinearity. Specifically, we did not include metrics measured at multiple spatial scales in the same model; rather we built only scale-specific models. To identify the most parsimonious models across spatial scales, we used second-order Akaike's Information Criterion (AIC<sub>c</sub>) for small sample sizes and calculated  $\Delta$ AIC values for each model. We considered all models with  $\Delta$ AIC < 2 to be the best approximating models (Burnham and Anderson, 2002).

Because body size has been shown to influence home range size in snakes (e.g., Whitaker and Shine, 2003; Roth, 2005), we examined the effects of this variable on our analyses. Body size, as measured by SVL, was found to be positively correlated with home range size (Pearson's  $r = 0.77$ ,  $P = 0.009$ ). However, because preliminary analyses revealed weak and inconsistent relationships between body size and the landscape metrics discussed below, we excluded it from subsequent analyses.

To ensure our data met statistical assumptions, we verified normality of all variables and residuals (Shapiro-Wilk  $P > 0.04$ ) and found no evidence of multicollinearity (Collinearity Index < 10) in regression models. The significance level was set at  $\alpha = 0.05$ . All statistical analyses were performed in SAS 9.1 (SAS Institute, Inc., Cary, NC).

## RESULTS

*Study 1: Habitat Associations.*—For the 10 EDBs used in this study, total number of observations was 321 (mean = 32.10, range = 13–51 observations; Table 1), and the mean length of

tracking was 429 days (range = 168–649 days). Mean ( $\pm$  SE) home range size of males was  $34.70 \pm 14.04$  ha, and that for females was  $29.28 \pm 9.12$  ha.

No significant habitat associations at the landscape scale were detected ( $\Lambda = 0.30$ ,  $P = 0.083$ ), although random points within home ranges were closer to all habitat types, especially pine, than were random points across the landscape (Fig. 2). Similarly, within home ranges, snakes appeared to exhibit random habitat associations ( $\Lambda = 0.28$ ,  $P = 0.069$ ). However, in contrast to the landscape scale results, snake locations were further from pine, agriculture, and mixed pine-hardwood, than were random points (Fig. 2).

*Study 2: Home Range Size, Landscape Pattern, and Heterogeneity.*—Ten adult EDBs (6 nonpregnant females, 4 males) that were monitored for an average of 312 days (range = 168–395) and 29 locations (range = 13–42) were included in home range analyses (Table 1). Male and female mean ( $\pm$  SE) home range size was  $30.49 \pm 9.84$  ha and  $20.59 \pm 3.95$  ha, respectively (Table 4).

Only four of nine landscape metrics were significantly correlated with home range size at one or more spatial scales. Core area (DCAD), proximity (logAPMI), and contrast (MECI) were negatively correlated with home range size consistently across spatial scales (Table 5). Contagion (IJI) was positively correlated with home range size at the 500-m scale. Contrast was the only metric significantly correlated with home range size at all spatial scales. Although area/density (ED and PD) and shape (MFI) did not exhibit a significant correlation with home range size, there was a trend for smaller home ranges to be in landscapes with dense edge and dense irregularly shaped patches. The relation-

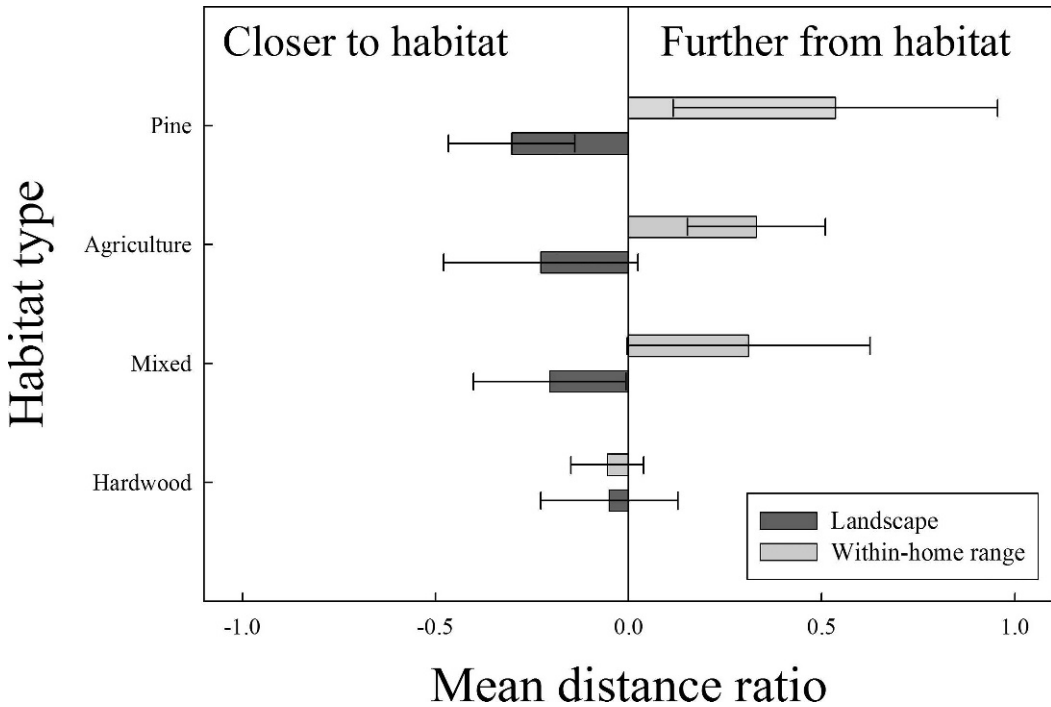


FIG. 2. Mean distance ratios ( $\pm$  1SE) of Eastern Diamond-backed Rattlesnakes (*Crotalus adamanteus*) for habitat types at the landscape and within-home range spatial scales. For each individual, a distance ratio was calculated with the mean distance of snake locations to each habitat type in the numerator and the mean distance of random locations to each habitat type in the denominator. The mean distance ratios are distance ratios averaged across individuals with the constant 1 subtracted from them, such that mean distance ratios  $<0$  indicate that locations were closer to a habitat type than expected (= random locations), and  $>0$  indicate that locations were farther from a habitat type than expected.

ship between home range size and diversity metrics (MSEI and MSDI) did not show a significant or consistent trend across spatial scales.

The global models, which included diversity (MSEI), shape (MFI), proximity (logAMPI), and contrast (MECI), were significant at the 250-m and 750-m spatial scales (Table 6). The 250-m and 750-m scale models were the most likely models as indicated by low  $\Delta$ AIC values. Because the 500-m and 1,000-m scales had  $\Delta$ AIC

values  $>7$ , we considered those models to be unlikely. The model with the most explanatory power (250 m;  $R^2_{adj} = 0.768$ ) corresponded to the mean home range size of EDBs in this study (25 ha); however, the other competing model (750 m) was approximately three times the size of the largest home range in our study (60 ha).

When we allowed for parameter removal, we detected four strongly competitive models ( $\Delta$ AIC  $< 2$ ) and eight moderately competitive models ( $\Delta$ AIC = 2–5; Table 7). The top four

TABLE 4. Published home range sizes for adult male and female Eastern Diamond-backed Rattlesnakes (*Crotalus adamanteus*).

Location (source)	Home range size			Home range method
	Males (N)	Nonpregnant females (N)	Pregnant females (N)	
Baker Co., GA (current study)	30.49 (4)	20.59 (6)	—	100% MCP
Hampton Co., SC (Waldron et al., 2006a)	84.82 (6)	28.63 (13)	18.07 (2)	95% KDE
Forrest Co., MS (Kain, 1995)	74.10 (5)	19.60 (1)	14.30 (3)	100% MCP
Putnam Co., FL (Timmermann, 1995)	50.40 (4) <sup>a</sup>	46.50 (2)	—	100% MCP

Note: MCP = minimum convex polygon; KDE = kernel density estimate

<sup>a</sup>Only 1987 estimate for individual M3 included in average (see Timmerman, 1995).

TABLE 5. Pearson correlation coefficients for associations of landscape metrics and log-transformed home range size of adult Eastern Diamond-backed Rattlesnakes (*Crotalus adamanteus*) at four spatial scales. Buffers at four different spatial scales were placed around centroids of 10 snake home ranges at Ichauway, Baker County, Georgia.

Category	Metric	Spatial Scale			
		250 m	500 m	750 m	1,000 m
Area/Density	ED	-0.28	-0.46	-0.36	-0.37
	PD	-0.49	-0.52	-0.40	-0.51
Shape	MFI	-0.05	-0.48	-0.03	-0.40
Core Area	DCAD	-0.25	-0.31	-0.41	-0.62*
Proximity	logAMPI	-0.45	-0.33	-0.77**	-0.42
Contrast	MECI	-0.77**	-0.72*	-0.78**	-0.79**
Contagion	IJI	-0.17	0.66**	0.32	0.34
Diversity	MSEI	-0.18	0.15	-0.13	0.03
	MSDI	0.07	0.09	-0.10	0.03

\*  $P \leq 0.05$ ; \*\*  $P \leq 0.01$

models were two- and three-parameter models at the 250-m and 750-m spatial scales and a one-parameter model at the 1,000-m scale. Shape, proximity, and contrast were included in the top models, but diversity was not. Contrast was significant in all four top models. Of the eight moderately competitive models, six were at the 750-m scale, and two were at the 250-m scale. None of the 500-m scale or global models was competitive based on  $\Delta AIC$  values.

DISCUSSION

*Habitat Associations.*—Sex (males and non-pregnant females) had no effect on habitat selection of EDBs at either the landscape or within-home range scale in this study, which is consistent with many of the snake species for which similar data exist (e.g., Timber Rattlesnake, *Crotalus horridus*; Reinert and Zappalorti, 1988; Black Rat Snake, *Elaphe obsoleta obsoleta*; Blouin-Demers and Weatherhead, 2001a; Eastern Massasauga Rattlesnake, *Sistrurus catenatus catenatus*; Marshall et al., 2006). Conversely, Waldron et al. (2006a) detected differences in

habitat use in male and female EDBs in South Carolina; however, if only the habitats with which both sexes had a significant relationship are examined (pine savanna, hardwood bottom, and field), there were no obvious differences (i.e., both sexes were either positively or negatively associated with each habitat type). A recent study of *C. horridus*, which is a sympatric congener of EDBs at Ichauway, showed that when within-home range habitat associations were assessed separately for foraging, breeding, and hibernation periods, male and female *C. horridus* exhibited differential habitat use (Waldron et al., 2006b). Data in the current study were combined across seasons because of insufficient seasonal sampling, particularly during winter; therefore, any effects of sex on habitat associations might have been masked, and future studies should investigate the effects of season and sex interactions.

Although Eastern Diamond-backed Rattlesnakes at Ichauway did not exhibit significant habitat associations at the landscape scale, they did trend toward a positive association with pine habitat. This result was not surprising

TABLE 6. Forced global models at four spatial scales. Four metrics representing overall heterogeneity were the predictor variables, and adult Eastern Diamond-backed Rattlesnake (*Crotalus adamanteus*) log-transformed home range size was the dependent variable.

Scale (m)	MSEI	MFI	logAMPI	MECI	$R^2_{adj}$	Overall $P$	AIC <sub>c</sub>	$\Delta AIC$
	$b_1$	$b_2$	$b_3$	$b_4$				
250	0.057	-0.634	-0.435	-0.852***	0.768	0.019	3.266	0.000
500	0.159	-0.115	0.336	-0.894	0.300	0.239	14.319	11.053
750	-0.306	0.247	-0.863*	-0.209	0.745	0.024	4.224	0.958
1,000	-0.144	0.013	-0.318	-0.698*	0.415	0.162	12.513	9.247

Notes: Landscape metric names are as follows: MSEI, modified Simpson's evenness index, MFI, mean fractal index, logAMPI, log-transformed area-weighted mean proximity index, MECI, mean edge contrast index. Regression coefficients ( $b_i$ ) are included for each metric, adjusted  $R^2$  ( $R^2_{adj}$ ), the overall  $P$ -value, second-order Akaike's Information Criterion (AIC<sub>c</sub>), and  $\Delta AIC$  values are provided for the global model at each spatial scale; \*  $P \leq 0.05$ ; \*\*\*  $P \leq 0.001$ .

TABLE 7. Competing models using landscape metrics representing heterogeneity as independent variables and adult Eastern Diamond-backed Rattlesnake (*Crotalus adamanteus*) log-transformed home range size as the dependent variable. Strongly competing models had  $\Delta AIC < 2$ , whereas moderately competing models had  $2 < \Delta AIC < 5$ .

Scale (m)	K	MSEI	MFI	logAMPI	MECI	$R^2_{adj}$	Overall $P$	AIC <sub>c</sub>	$\Delta AIC$
		$b_1$	$b_2$	$b_3$	$b_4$				
Strongly competitive models									
750	3	—	—	-0.507*	-0.520*	0.735	0.004	-7.041	0.000
250	3	—	0.469*	—	-0.976***	0.712	0.005	-6.196	0.845
250	4	—	0.672**	-0.420	-0.844**	0.806	0.005	-5.690	1.351
1000	2	—	—	—	-0.792**	0.580	0.006	-5.396	1.646
Moderately competitive models									
750	2	—	—	—	-0.777**	0.554	0.008	-4.775	2.266
750	3	0.401	—	-0.893**	—	0.663	0.009	-4.652	2.389
250	2	—	—	—	-0.773**	0.547	0.009	-4.632	2.409
750	2	----	----	-0.770**	—	0.542	0.009	-4.519	2.523
750	4	0.398*	0.358	-1.043***	—	0.765	0.008	-3.800	3.241
750	3	—	0.362	-0.923**	—	0.615	0.015	-3.294	3.747
750	4	0.224	—	-0.636*	-0.399	0.743	0.010	-2.877	4.164
250	3	0.358	—	—	-0.970**	0.598	0.017	-2.862	4.179

Notes: Landscape metric names are MSEI, modified Simpson's evenness index, MFI, mean fractal index, logAMPI, log-transformed area-weighted mean proximity index, MECI, mean edge contrast index. Number of parameters, including intercept (K), regression coefficients ( $b_i$ ), adjusted  $R^2$  ( $R^2_{adj}$ ), model  $P$ -value, second-order Akaike's Information Criterion (AIC<sub>c</sub>), and  $\Delta AIC$  values are provided; \*  $P \leq 0.05$ ; \*\*  $P \leq 0.01$ ; \*\*\*  $P \leq 0.001$ .

given that the current range of EDBs is mostly restricted to that of Longleaf Pine (Martin and Means, 2000). Indeed, home ranges of a South Carolina population of EDBs also were closely associated with pine habitat (Waldron et al., 2006a). In a previous study of EDBs at Ichauway, when Longleaf Pine habitat was considered separately from other pine species, such as Loblolly or Slash, it was not a significant predictor of EDB observations (Steen et al., 2007). We suspect that snakes select habitat based on structural characteristics (e.g., canopy density and ground cover), rather than individual species (e.g., Longleaf Pine vs. Slash Pine; Reinert, 1993). Although, pine plantations often differ structurally from old growth pine savannas (e.g., denser canopy, less ground cover), the stands of planted pine used by snakes in the current study were regularly thinned and burned, such that their structural difference was minimal.

Because snakes are ectothermic, habitat selection might be a direct reflection of an individual's ability to maintain body temperatures needed for physiological processes (Huey, 1991; Lillywhite and Navas, 2006). Thus, one possible explanation for finding EDB home ranges associated with pine habitat is that such areas are particularly open across Ichauway; thus, they provide thermoregulatory opportunities and benefits. Both of these attributes might be further enhanced if open-canopy areas are adjacent to other habitat patches with differing degrees of canopy closure (e.g.,

closed-canopy hardwood hammocks). For instance, Canadian populations of Black Rat Snakes preferred edges between open- and closed-canopy habitats (Blouin-Demers and Weatherhead, 2001a,b), and these authors argued that habitat fragmentation allowed snakes close access to areas conducive to thermoregulation. In this study, despite the fact that EDBs did not show significant habitat associations, random points within home ranges were closer to all habitat types than random points across the study site. This suggests that EDBs maintain home ranges that are particularly heterogeneous in their habitat composition, which would be consistent with the ease-of-thermoregulation hypothesis presented by Blouin-Demers and Weatherhead (2001a,b).

When a smaller spatial scale is considered, it appears that habitat associations of EDBs shift. Although they were found to be positively associated with pine habitat at the landscape scale, their tendency was to be farther from pine within the home range. In this study, individuals did not exhibit significant positive association with any habitat type at this spatial scale, but they were found slightly closer to hardwood habitat and farther from agriculture than random points. Similar results were reported for a population from east-central Florida (Timmerman, 1995). In that population, EDBs were negatively associated with pine uplands and positively associated with xeric and mesic hardwoods, but the only significant finding was that snakes were located in agriculture less

than expected. In South Carolina, EDBs were reported to maintain their positive association with pine at smaller spatial scales (Waldron et al., 2008).

Although old fields, wildlife food plots, and croplands (all of which were considered agriculture in this study) likely support high densities of small mammals (Doonan and Slade, 1995), they might not provide adequate cover for large-bodied snakes, and the lack of canopy might result in unfavorably high ambient and substrate temperatures. Indeed, several of the EDBs monitored in the current study whose home ranges included large amounts of agriculture were only rarely observed in fields; rather, they made use of the narrow rows of open-canopied planted Slash Pine that separated these fields, which likely allowed them to exploit the thermal gradients (see Blouin-Demers and Weatherhead, 2001b), and possible high prey densities (Martin et al., 2000; but see Blouin-Demers and Weatherhead, 2001a), available in edge habitat. Apparently, if sufficient "natural" habitat (e.g., open-canopy planted pine with adequate groundcover) is provided near small agricultural areas, EDBs persist; however, the effects of increased exposure to humans and human activities (e.g., roller-chopping of fields) might offset the temporary benefits provided by these areas. In other words, snakes might thrive initially, but ultimately suffer increased mortality above a threshold of reproductive sustainability.

*Home Range Size.*—Nonpregnant females at Ichauway had home range sizes that were similar to those of nonpregnant females in South Carolina (Waldron et al., 2006a). In males, however, home ranges at Ichauway were smaller than those of previous studies (Kain, 1995; Timmerman, 1995; Waldron et al., 2006a) (Table 3). A possible explanation for this finding might be that certain resources (e.g., prey, refugia, and mates) were either more abundant or more evenly distributed at Ichauway than at other EDB study sites. For example, male rattlesnake movements are known to increase significantly during the mating season (e.g., Timmerman, 1995; Reinert and Zappalorti, 1988; Moore and Gillingham, 2006) to locate spatially unpredictable females (prolonged mate-searching polygyny; see Duvall et al., 1993). But under certain conditions, such as when an EDB population is particularly dense or females are uniformly distributed, distances traveled by males to locate receptive females might be reduced (Ims, 1988). Accordingly, a significant increase in male home range size during the mating season would not be expected. In support of this view, one male in this study had a relatively small home range (20.33 ha),

which commonly included three of the females monitored. This suggests that a large home range for this individual was not necessary to locate females. Additionally, common prey of EDBs (e.g., rodents, rabbits, birds; reviewed in Timmerman and Martin, 2003) might be particularly abundant at Ichauway because of intensive management for Northern Bobwhite (see Doonan and Slade, 1995). As such, prey density might tend to reduce home range size in EDBs.

*Landscape Pattern.*—The home range sizes of EDBs at Ichauway were correlated with patch core area and proximity, contrast, and contagion of patch types. These relationships were present across differing and sometimes multiple spatial scales. The contrast between neighboring patch types exhibited the strongest relationship with home range size relative to all other landscape patterns considered, and this relationship was consistent and significant at each spatial scale examined. Specifically, individuals with small home ranges inhabited areas in which adjacent habitat patches were characterized by high structural contrast. This result is not surprising for two key reasons. First, small mammals, which are common prey of EDBs, are often particularly abundant and diverse in edge habitat, especially edge habitat with high structural contrast (Bowers and Dooley, 1999; Manson et al., 1999; Nupp and Swihart, 2000), such as that found between forest and field. Second, given the thermoregulatory requirements of large ectotherms such as EDBs (Lillywhite and Navas, 2006), areas with high contrast likely provide wide thermal gradients within a relatively small space. This may decrease the length of movements associated with behavioral thermoregulation, which could ultimately result in a small home range size, as compared to that of an individual in a landscape with low structural contrast.

The spatial arrangement of patch types also appeared to be important to EDBs at Ichauway. The area-weighted mean proximity index (AMPI) measures the proximity of like patch types and increases as the number of patches or the proximity and contiguity of those patches increases (McGarigal and Marks, 1995). As predicted, EDBs that occupied landscapes with large AMPI values, maintained small home ranges. However, another measure of patch spatial arrangement, IJI, did not show the predicted relationship with EDB home range size. Rather, EDBs with small home ranges were associated with landscapes with relatively low interspersions of patch types. These conflicting results might indicate that increased contiguity of a single patch type (e.g., pine), which would increase proximity values and lower contagion values, outweighs the benefits of a landscape

with maximally interspersed patch types. Because we only calculated these metric values at the landscape level, as opposed to the class level, we cannot determine whether this was the case.

*Habitat Heterogeneity.*—An accumulating body of evidence shows that heterogeneity can significantly affect ecological phenomena, such as species diversity (e.g., Simpson, 1949; MacArthur and Wilson, 1967; Lack, 1969), yet there is no consensus as to the most appropriate definition or means of quantifying heterogeneity (reviewed in Tews et al., 2004), and few models explicitly test the ability of a mathematical definition to adequately capture variations in heterogeneity. Li and Reynolds (1994) conducted simulations to model differing levels of heterogeneity using categorical maps and tested the ability of landscape metrics from five categories of landscape pattern to explain variation in simulated heterogeneity. They concluded that heterogeneity is explained as a function of five components representing both the composition and configuration of patches within the landscape. Herein, we used a combination of four of these five components to examine the relationship between home range size and heterogeneity at four different spatial scales. The model with the best predictive power had a relatively large  $R^2_{adj}$  (0.768), indicating that the combination of these four components, which represented heterogeneity, explained a large portion of the variation in home range size.

When we compared models with different combinations of the four predictor variables, none of the global models (all four variables included) was competitive. However, when we removed parameters with poor predictive power, four different models were highly competitive. The four models included one to three parameters, but none of those models included the diversity parameter (MSEI). This suggests that heterogeneity in composition is not as important to EDB home range size as heterogeneity in configuration. This finding is not unexpected in light of evidence that snakes often use structural cues when selecting habitat (reviewed in Reinert, 1993). For example, Theodoratus and Chiszar (2000) found that Western (= Prairie) Rattlesnakes (*Crotalus viridis*) used structural cues when selecting ambush sites in captive behavioral trials. All of the strongly competitive and single-parameter models included the contrast parameter (MECI), further emphasizing the importance of high contrast edges to EDBs at Ichauway.

*Spatial Scale.*—The spatial heterogeneity of landscapes can vary depending upon the extent of the landscape being measured, and the ecological response to heterogeneity may be

affected by the perception of the focal organism (Turner, 1989; Wiens, 1989; Kotliar and Wiens, 1990). We found that the relationship between landscape pattern and home range size in EDBs varied across spatial scales. When we applied Li and Reynolds (1994) definition of overall heterogeneity, variation in home range size was best explained by heterogeneity at the 250-m and 750-m spatial scales. It is intuitive that snakes would respond to heterogeneity at the scale of their home range; however, if significant variation exists in home range size among individuals, the scale at which heterogeneity should be measured may not be as intuitive.

Kie et al. (2002) determined that home range size of Mule Deer (*Odocoileus hemionus*), which ranged from 39 ha to 2,878 ha, exhibited the strongest relationship with heterogeneity at a scale substantially larger than mean home range size, despite only 6% of the deer having home range sizes greater than the extent of that spatial scale. This further emphasizes the fact that investigations concerned with organism-environment interactions should consider multiple spatial scales (see Johnson, 1980; Tews et al., 2004), because of difficulties in predicting the scale at which animals respond to factors of interest. Variation in home range size of our study animals was relatively small ( $24.55 \pm 4.55$  ha), which explains why the scale of mean home range size (250 m or 20 ha) was competitive. Also, this scale was the only one to include three parameters, which indicates that snakes are responding to a more complex form of landscape heterogeneity at this scale. The competitiveness of larger scale models was likely caused by edge contrast, and to a lesser degree, patch shape, increasing proportionately with increasing spatial scales, although this does not explain the lack of a competitive 500-m scale model.

*Conclusions.*—Despite the limitations of this study, our use of a robust distance-based analysis and multiscale approach allowed us to gain new insights into EDB spatial ecology, which we believe will be valuable for future conservation planning. For example, distance measures revealed that EDBs were positively associated with pine forest but also that they may prefer home ranges that are particularly heterogeneous; thus, management of EDB habitat should focus on the preservation of pine uplands, while maintaining a mosaic of other habitat types within the pine matrix, a practice likely to benefit many sympatric species (Roth, 1976; Law and Dickman, 1998). Additionally, after examining EDB habitat associations at two different spatial scales, we concluded that the nature of these associations, as measured by mean distance ratios, changed depending upon

which spatial scale was considered, although substantial amounts of individual variation prevented these differences from being statistically significant. This finding carries particular importance for future EDB management, because it suggests that habitats that seem unimportant at one scale may be important at another scale, further emphasizing the need for multiscale studies on single populations.

Scale also appeared to be important for examining the influence of heterogeneity on home range size in EDBs. The results of this study, which was the first to determine the relationship between habitat heterogeneity and home range size in a species of reptile, suggest that the degree to which heterogeneity shapes the spatial ecology of snakes is not consistent across spatial scales. Surprisingly, in a recent review of studies related to habitat heterogeneity and species diversity, only one of 85 publications concerned reptiles (Pianka, 1966; reviewed in Tews et al., 2004), emphasizing the need for additional research examining the effects of habitat heterogeneity on this taxonomic group. Furthermore, because habitat heterogeneity positively affects a broad array of taxa, for example, birds (Farley et al., 1994), mammals (Medellin and Equihua, 1998), amphibians (Vallan, 2002), reptiles (Pianka, 1966), and invertebrates (Baz and Garcia-Boyer, 1995), its importance should not be overlooked by land managers and conservation biologists concerned with preservation and restoration of habitat.

*Acknowledgments.*—We thank L. M. Conner, M. Wooten, and B. Zinner for statistical assistance; G. Miller for help with fieldwork; and R. K. Barrett, S. Graham, A. Hein, V. Johnson, C. Romagosa, G. Sorrell, J. Steffen, and A. Subalusky for helpful comments on the manuscript. In particular, we would like to thank D. Goolsby for extensive discussions concerning landscape ecology. Surgical supplies were donated by Zoo Atlanta. Animals were collected and housed under the Georgia Department of Natural Resources scientific collecting permits 29-WMB-04-188 and 29-WTN-05-166 and in accordance with Auburn University Institutional Animal Care and Use Committee guidelines (protocol 2004-0631).

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Accepted: 6 May 2009.