SPATIAL ECOLOGY OF THE EASTERN DIAMOND-BACKED RATTLESNAKE

(CROTALUS ADAMANTEUS)

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(CROTALUS ADAMANTEUS)

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SPATIAL ECOLOGY OF THE EASTERN DIAMOND-BACKED RATTLESNAKE

(*CROTALUS ADAMANTEUS*)

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Shannon Kelleigh Hoss, daughter of Gregg Michael Hoss, Sr., and Tory Lee (Eakin) Hoss, was born January 18, 1977 in Mesa, Arizona. She graduated from Nolan Catholic High School in Fort Worth, Texas in 1995. Upon graduation, she entered Arizona State University in Tempe, Arizona and completed a Bachelor of Science in Zoology and concurrent Bachelor of Science in Psychology in 2001. From 2001 to 2002, she was employed by the Rocky Mountain Research Station branch of the United States Forest Service in Albuquerque, New Mexico. From 2002 to 2004 she worked in the Herpetology Lab of the Joseph W. Jones Ecological Research Center in Newton, Georgia. In August 2004, she began graduate school in the Department of Biological Sciences at Auburn University, Auburn, Alabama.

THESIS ABSTRACT

SPATIAL ECOLOGY OF THE EASTERN DIAMONDBACK RATTLESNAKE

(*CROTALUS ADAMANTEUS*)

Shannon Kelleigh Hoss

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An animal's spatial ecology may be governed by variables operating at more than one spatial scale, which underscores the importance of incorporating multiple spatial scales into habitat selection models. This is particularly relevant if robust evaluations of key habitat characteristics are to be made for understudied species in imperiled ecosystems, such as for the eastern diamond-backed rattlesnake (*Crotalus adamanteus*). We conducted a two-year radio-telemetry study of adult *C. adamanteus* in southwestern

Georgia to determine estimates of home range size, assess multi-scale habitat associations, and investigate the relationship between habitat heterogeneity and home range size. No difference in home range size was detected between male and females and male mean home range size was smaller than that reported from previous studies. We used a multivariate distance-based approach to analyze habitat associations. At the landscape scale, individuals showed a positive association with pine habitat and, within home ranges, there was a negative association with agriculture. Pair-wise comparisons revealed that no one habitat type was selected over another at the landscape scale, but that within home ranges, individuals were located significantly closer to hardwood forests than to agricultural areas. These results are congruent with two previous radio-tracking studies that examined habitat associations of adult *C. adamanteus*, despite the geographical and ecological disparity of the three study sites (Georgia, Florida, and South Carolina). Furthermore, habitat heterogeneity was inversely related to home range size at multiple spatial scales. Variables representing heterogeneity in landscape configuration, rather than composition, most heavily influenced home range size. This relationship was strongest at the scale representing mean home range size, as well as a scale approximately three times the size of mean home range. From these studies, we recommend that management regimes designed to enhance population size of *C. adamanteus* emphasize the preservation of pine uplands, limit the conversion of forest to agriculture, and maintain a mosaic of habitat types within a pine matrix. We also stress the need to conduct spatial ecology research at multiple spatial scales and consider the importance of habitat heterogeneity to variations in space use.

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CHAPTER I

INTRODUCTION

The Coastal Plain of the southeastern United States is characterized by an especially diverse array of reptile and amphibian species, many of which are thought to rely heavily or exclusively on the longleaf-pine (*Pinus palustris*) ecosystem found within the Coastal Plain (Guyer & Bailey 1993, Dodd 1995). Due to agriculture, timber production, and urbanization, this ecosystem has declined approximately 96% from its historic extent (Means & Grow 1985) and is continuing to be converted at an alarming rate (Ware *et al.* 1993). Due in part to habitat fragmentation and alteration, several reptile species, such as the gopher tortoise (*Gopherus polyphemus*) and eastern indigo snake (*Drymarchon couperi*), have become threatened or endangered and many others are thought to be rapidly declining (Dodd 1995). In order to adequately conserve and manage vulnerable, threatened, and endangered species, knowledge of their basic natural history and ecology is essential, yet many such species remain unstudied.

The eastern diamond-backed rattlesnake *(Crotalus adamanteus*; EDB*)* is the largest extant rattlesnake and a resident of the disappearing longleaf pine ecosystem of the southeastern United States. Significant population declines of EDBs were recognized as early as the 1950s (see Timmerman & Martin 2003) and are thought to be a result of habitat loss (Martin & Means 2000), road mortality (Timmerman & Martin 2003), and 'malicious killing' by humans (Dodd 1987). Despite past and current concerns about the status of the EDB, no species-specific protection is afforded it in any of the seven states which comprise its geographic range. And though many researchers have acknowledged that the species may meet criteria for state or federal protection (Enge 1991; Martin & Means 2000, Timmerman 1995; Timmerman & Martin 2003), there is a lack of information regarding the most fundamental aspects of their biology. This thesis examined multiple parameters of the spatial ecology of EDBs, as a first step in understanding the basic ecology of this declining species.

While identifying habitats with which a declining species is associated is of obvious importance to conservation, it may be necessary to determine habitat use at multiple spatial scales in order to fully understand a species' habitat requirements (Cushman & McGarigal 2004; Meyer & Thuiller 2006; Parsons, Thoms, & Norris 1994). For example, an individual which exhibits certain habitat preferences when selecting a home range may show a modification of those preferences once a home range is established. These two levels of habitat selection are termed 2nd and 3rd order selection, respectively (Johnson 1980), and many studies which have integrated this hierarchical concept have been better able to predict habitat patterns of species using multiple spatial scales (see Meyer & Thuiller 2006).

While a handful of studies concerning the spatial ecology of EDBs have been conducted, they have been small in scale, short in duration, and only two have been published in peer-reviewed journals (Steen *et al.* 2007; Waldron *et al.* 2006; but see abstracts in Timmerman & Martin 2003). These studies found EDB home range sizes to be between 59.5-158.9ha for males and 8.2-88.8ha for non-reproductive females. The only study that used known home ranges to quantify habitat use at the landscape-scale (2^{nd} order selection), found that both male and female EDBs in South Carolina selected pine savanna more frequently than planted pine, pine hardwood, hardwood bottom, or field habitat types (Waldron *et al.* 2006). They also found that both males and females had a positive association with fields, which they attributed to the probable high prey density in those areas. Steen *et al.* (2007) used multiple buffer sizes encircling a single point observation of individual EDBs in Georgia to represent potential home range and then compared habitat types within buffers to those of randomly selected points across the study site. They found that EDBs were not significantly associated with any one habitat type and labeled the species a habitat generalist relative to the Timber Rattlesnake (*Crotalus horridus),* which they found was positively associated with certain habitat types (=habitat specialist). Interestingly, these results are opposite those found for these two species in Waldron *et al.* (2006) (i.e., *C. adamanteus* showed greater habitat specificity than *C. horridus*). Furthermore, Timmerman (1995) found EDBs from a Florida population to be negatively associated with pine and agriculture, and positively associated with hardwoods at the within-home range scale (3^{rd} order selection). To determine if these discrepancies among studies were due to geographical differences in habitat preferences of EDBs or simply a result of methodological differences, we assessed multi-scale habitat associations of EDBs in Georgia using radio-telemetry in Chapter 2.

In addition to knowing which habitats an animal utilizes, it is also critical to examine how much of that habitat is used (i.e., home range size) and which factors account for variation in that space use. Home range is a concept that has been discussed since the early 1900s (Seton 1909), but it did not become an area of empirical inquiry until much later. In general, home range is defined as the total area utilized by an organism for regular activities, such as foraging and reproduction (Burt 1943), but various, more specific definitions have been proposed (Powell 2000). The characteristics of an individual's home range are rarely static and often are affected by a multitude of factors such as inter- and intra-specific competition (Bowers & Smith 1979), reproductive condition (Reinert & Zappalorti 1988), season (King & Duvall 1990), and predation (Stamps 1995). Recently, however, evidence has been mounting for the importance of habitat heterogeneity in influencing home range size (e.g., Constible & Chamberlain; Kie *et al.* 2002; Saïd & Servanty 2005). For example, Kie *et al.* (2002) found that variation in landscape composition and configuration (i.e., habitat heterogeneity) accounted for a large proportion of variation in home range size of mule deer. Specifically, smaller home ranges were associated with areas of high heterogeneity. This relationship was found to be strongest at a relatively large spatial scale (larger than mean home range size), which further emphasizes the importance of incorporating multiple spatial scales in studies of ecological processes. To determine whether or not home range sizes of EDBs were influenced by habitat heterogeneity, we examined data from our previous study using a GIS frame-work in Chapter 3. We calculated landscape variables representing heterogeneity in habitat composition and configuration at four different spatial scales, examined how they related to home range size, and determined at which spatial scale the relationship was strongest.

CHAPTER II

USING A DISTANCE-BASED APPROACH TO ASSESS MULTI-SCALE HABITAT ASSOCIATIONS OF EASTERN DIAMOND-BACKED RATTLESNAKES (*CROTALUS ADAMANTEUS)*

Summary

1. Given the current high rate of habitat degradation and species extinction, it is important to assess the spatial ecology of declining species in imperiled ecosystems to guide conservation practices.

2. Despite the increasing need for robust investigations concerning spatial ecology, many studies suffer from theoretical, methodological, and statistical flaws. Among these are the use of simplistic habitat selection metrics and the failure to investigate spatial ecology at multiple spatial scales.

3. 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 and GPS data and employed Euclidean distance analysis to examine habitat associations at two spatial scales (landscape and within-home range).

4. Mean home range size of non-pregnant females was comparable to that reported in previous studies, but was considerably smaller in adult males. This might indicate a particularly dense EDB population at our study site, because males are expected to increase their home range during the mating season if receptive females are sparsely distributed.

5. Individuals showed a non-random positive association with pine habitat at the landscape scale and a non-random negative association with agriculture within the home range. No one habitat type was selected over another at the landscape scale, but within home ranges, individuals were located significantly closer to hardwood forests than to agricultural areas.

6. The use of Euclidean distance analysis revealed a possible association with increased habitat heterogeneity at the landscape scale, which was not detected in previous studies that employed classification-based (as opposed to distance-based) methods. Additionally, our multi-scale approach allowed us to resolve the disparity in results from previous single-scale studies and, thus, conclude that geographically disparate populations of EDBs show similar habitat associations.

7. We recommend that management regimes to enhance population numbers of EDBs emphasize the preservation of pine uplands, while maintaining a mosaic of other habitat types, and limit the conversion of forest to agriculture. Our results also highlight the importance of using robust analytical tools and multiple scales of investigation in spatial ecology studies.

Key Words: Euclidean distance, habitat selection, home range, longleaf pine, spatial scale

Introduction

A primary objective of spatial ecology research is to provide robust evaluations of the space and habitat requirements of species as guidance for current and or future conservation efforts, such as translocation (e.g., Harig & Fausch 2002; Sullivan, Kwiatkowski, & Schuett 2004), reintroduction (e.g., Schadt *et al.* 2002; Carroll *et al.* 2003), and reserve design (e.g., Murphy & Noon 1992; Cabeza *et al.* 2004). The current rate of habitat loss and fragmentation coupled with concomitant decreases in biodiversity (Wilcox & Murphy 1985; Tilman 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 & Bailey 1993), has declined approximately 96% from its historic extent (Means & Grow 1985) and is continuing to be converted at an alarming rate (Ware, Frost & Doerr 1993). As a result, many herpetofaunal species that are thought to rely heavily or exclusively on this ecosystem (i.e., specialists) have undergone equally severe declines (e.g., gopher tortoise, *Gopherus polyphemus*, eastern indigo snake, *Drymarchon corais*, and flatwoods salamander, *Ambystoma cingulatum*) (Guyer & Bailey 1993; Means 2006), yet there is a general dearth of knowledge available to direct conservation efforts for the majority of these species (reviewed by Guyer & Bailey 1993).

The need to distill complex organism-environment interactions so that management recommendations can be made for species of conservation concern has prompted the development of a variety of analytical tools used to investigate resource selection (Manly *et al.* 2002). Although these tools are specifically designed to simplify the inherently intricate relationship between an organism and its environment, they often do so at the expense of statistical and theoretical rigor (see Jones 2001; Keating & Cherry 2004; Thomas & Taylor 2006). Aebischer, Robertson, & Kenward (1993), for example, outlined the properties they considered ideal for resource selection analyses and recommended compositional analysis as the superior tool with which to examine habitat associations. Despite recent concerns about inflated Type I error (i.e., incorrectly rejecting the null hypothesis) rates produced by this method when available habitats are not used by every individual (Pendelton *et al.* 1998; Dasgupta & Alldredge 2002; Bingham & Brennan 2004), compositional analysis continues to be one of the most commonly used habitat selection metrics (Thomas & Taylor 2006).

Euclidean distance analysis is a recently introduced alternative method that satisfies the characteristics deemed ideal for an analysis of habitat association (Conner & Plowman 2001; Conner, Smith, & Burger 2003) and remains robust to the Type I error inflation incurred by compositional analysis (Bingham & Brennan 2004). Additionally, instead of simply classifying the habitat type within which each location falls, as in most other habitat analysis tools (including compositional analysis), distance analysis incorporates the composition of the surrounding habitat into the analysis. Because habitat patches do not exist independently of each other (i.e., landscapes consist of a mosaic of habitat types), it is likely that an individual's use of a particular habitat patch is influenced by the surrounding habitat composition and, thus, distance-based analyses allow for more biologically relevant results than classification-based analyses (Conner and Plowman 2001).

In addition to incorporating information regarding the spatial arrangement of habitat patches, it is also important to consider if 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 change 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; Gorrensen, Willig, & Strauss 2005; Moore & Gillingham 2006). Therefore, caution is needed when comparing single-scale studies in which different scales were investigated, as the spatial scale at which the studies were conducted, rather than inherent inter-population differences, might explain discrepancies in habitat use patterns (e.g., Reynolds 2006). These seemingly contradictory results are particularly troubling for species in need of immediate management for which multi-scale studies of a single population do not exist. For this reason, we chose to employ a multi-scale approach to assess habitat associations of eastern diamond-backed rattlesnakes (*Crotalus adamanteus* (Beauvois); hereafter referred to as EDB), a declining resident of the imperiled longleaf pine ecosystem.

Eastern diamond-backed rattlesnake declines are thought to have resulted from habitat loss and fragmentation (Martin & Means 2000), road mortality (Timmerman & Martin 2003), and indiscriminant killing by humans (Dodd 1987). Despite past and current concerns about the status of this species, no specific protection is afforded them in any of the seven states that comprise their geographic range (Fig. 1). Despite the fact that many researchers have acknowledged that EDBs likely meet criteria for state and or federal protection (Enge 1991; Timmerman 1995; Martin & Means 2000; Timmerman &

Martin 2003), there are few data available to document the most fundamental aspects of their spatial ecology. To date, only two studies that investigated habitat associations of EDBs using radio-telemetry data have been published (Timmerman 1995; Waldron *et al.* 2006), and their results differ substantially. Because these were single-scale studies and the scale used differed between them (landscape vs. within-home range), their contradictory results might be a simple artefact of differing methods. Furthermore, both of the studies used classification-based analyses, which may have hindered their ability to detect more complex habitat associations. For these reasons, we focused on habitat associations of EDBs in southwestern Georgia, a region that appears to be a stronghold for the species and thus a prime area for research (Timmerman & Martin 2003). The objectives of this study were to: (i) quantify home range size of EDBs, (ii) use Euclidean distance analysis to determine whether individuals exhibited nonrandom habitat associations, and (iii) determine if these associations differed between landscape and within-home range scales (i.e., 2^{nd} and 3^{rd} orders, respectively; *sensu* Johnson 1980).

Methods

Study site

This study was conducted at Ichauway, the 12,000 ha research site of the Joseph W. Jones Ecological Research Center (JWJERC) located in Baker County, Georgia. The management priorities of the JWJERC are restoration of the longleaf pine ecosystem and the application of land-use practices that integrate wildlife and timber management. Ichauway consists primarily of longleaf pine forest (between 70 and 90 yrs old, in general, with individual trees > 300 yrs old) with an open midstory and herbaceous understory. Scattered throughout the property are 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. 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-year 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 understory). An 8,730 ha section of Ichauway was delineated as our study site.

Study animals and radio-telemetry

From 02 September 2003 to 17 July 2004, we captured EDBs encountered on roads or in the field. Snakes were brought to the laboratory, anesthetized with isoflourane vapor and implanted intraperitoneally with 16.1g temperature-sensitive radio transmitters (Model AI-2, Holohil Systems Inc., Carp, Ontario) using the surgical techniques described in Reinert & Cundall (1982). While anesthetized, mass was obtained to the nearest 0.01g, snout-to-vent length (SVL) and tail length were measured to the nearest 0.1cm, 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 day. The mass of the transmitter never exceeded 1.7% of the body mass of any individual.

Eastern diamond-backed rattlesnakes 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). Individuals were tracked during daylight hours and effort was made to locate each individual at multiple times of day (i.e., early and late morning and early and late afternoon) over the course of the study. When an individual was located, the site was flagged and a Global Positioning System (GPS) (GeoExplorer 3®, Garmin International, Inc., Olathe, Kansas) was used to obtain UTM coordinates of the location; GPS locations were accurate to within 3 m. When an individual was found to be greater than 5 m from a previously used site, that location was considered unique.

Data analysis

Home Range--EDB locations were entered into ArcGIS (ESRI, Redlands, California) and composite home ranges (i.e., all locations/snake) were estimated using the Hawth's Tools extension (Beyer 2004). The 100% minimum convex polygon method (MCP), which defines home range as the smallest polygon encompassing all known locations (Hayne 1949), was used to estimate home range size for each individual.

Habitat Associations--EDB locations were added to an existing ArcGIS 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 included 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 (Steen *et al.* 2007; Timmerman 1995; Waldron *et al.* 2006).

We employed a distance-based approach (Conner and Plowman, 2001; Conner et al., 2003) to analyze habitat associations. Distance analysis allows a test of nonrandom habitat use by comparing the mean minimum distance from animal locations to each of the designated habitat types (e.g., if there are four habitat types, each location will have four distance measures) to expected distances compiled from random locations. The habitat type within which a location falls receives a distance score of 0 for that location. To determine whether EDBs exhibited habitat associations at the landscape scale, random points across the study site were compared to random points within each individual's home range. To assess within-home range habitat associations, random points within each home range were compared to that individual's known locations. When an individual 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, only analyses using pooled sexes are presented. When a MANOVA detected a significant effect, univariate and pairwise t-tests were used to determine with which habitat types snakes were significantly associated (Conner & Plowman 2001; Conner *et al.* 2003). The significance level was set at $\alpha = 0.1$. All statistical analyses were performed in SAS 9.1 (SAS Institute, Cary, North Carolina).

Results

Home Range Size

From 02 September 2003 to 20 June 2005, we radio-tracked 14 adult EDBs (seven males and seven non-pregnant females). Due to a known mortality, a possible mortality (only transmitter found), a premature transmitter failure, and an individual that moved to an inaccessible area, 10 individuals (four males and six non-pregnant females) were included in the present analyses. The total number of observations for these individuals was 321 (mean = 32.10, range = 13-51) and the mean length of time they were tracked was 429 days (range = 168-649). The mean home range size of males and females was 34.70 ± 14.04 ha (mean ± SE) and 29.28 ± 9.12 ha, respectively (Table 1).

Habitat Associations

Significant habitat associations at the landscape scale were detected ($\Lambda = 0.30$, $P = 0.083$). Random points within home ranges were closer to all habitat types than expected, but pine was the only habitat type to which they were significantly close ($t_9 = -1.85$, $P = 0.097$; Fig. 3). Mean distance ratios did not differ between habitat types (Table 2), indicating that snakes were not closer to any one habitat type than to another.

Also, EDBs exhibited significant habitat associations within their home ranges ($\Lambda = 0.28$, $P = 0.069$), with mean distance from snake locations to agriculture being significantly greater than expected (Fig. 2). Mean distance to mixed pine-hardwood and pine tended to be greater than expected and mean distance to hardwood habitat tended to be less than expected, but none of these observed-expected ratios were significantly different under the null hypothesis of no selection. Although hardwood habitat was not significantly associated with EDB locations, pair-wise tests indicated that individuals were significantly closer to hardwood habitat than to agriculture (Table 2).

Discussion

Home Range

While the mean home range size of non-pregnant female EDBs at Ichauway was similar to that of non-pregnant females in South Carolina (Waldron *et al.* 2006), male home ranges were smaller than those reported in previously published studies (Kain 1995; Timmerman 1995; Waldron *et al.* 2006) (Table 1). In this study, composite home ranges (all locations/individual) were calculated for males tracked over multiple years (other studies reported only single-year estimates) and because home range sizes of some organisms have been shown to increase with the length of time individuals are monitored (e.g., mammals: reviewed in Harris *et al.* 1990), we expected our male mean home range size to be larger than those of previous studies. A possible explanation for this result is that certain resources (e.g., prey, refugia, and mates) were either more abundant and/or more evenly distributed at Ichauway than at other study sites. Previous studies have demonstrated that male rattlesnake movements dramatically increase during the mating season (e.g., *Crotalus horridus*, Reinert & Zappalorti 1988, *Crotalus adamanteus*, Timmerman 1995, *Sistrurus catenatus catenatus*, Moore & Gillingham 2006), as males must make long-distance searches to encounter spatially unpredictable females (prolonged mate-searching polygyny; *sensu* Duvall, Schuett, & Arnold 1993).

Under the condition where an EDB population is particularly dense or females are uniformly distributed, males will not have to travel as far to find receptive females; hence, there will not be a significant increase in male home range size during the mating season. That one male's relatively small home range (20.35 ha) included three of the females monitored in this study, suggests that this scenario might be the case at Ichauway. Additionally, prey (another limiting resource) might be particularly abundant at Ichauway due to intensive management for northern bobwhite (*C. virginianus*) (i.e., supplemental feeding programs for quail may increase small mammal abundance; e.g., Doonan & Slade 1995).

Habitat Selection

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., *Elaphe obsoleta obsoleta*; Blouin-Demers & Weatherhead 2001a; *Crotalus horridus*; Reinert & Zappalorti 1988; *Sistrurus catenatus catenatus*; Marshall, Manning, & Kingsbury 2006). Conversely, Waldron *et al*. (2006) detected differences in habitat use between 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* (canebrake rattlesnake), 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, Lanham, & Bennet 2007). Data in the current study were combined across seasons (due to 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.

Eastern diamond-backed rattlesnakes at Ichauway exhibited a positive association with pine habitat at the landscape scale. This is not surprising given that the historic range of EDBs was mostly restricted to that of longleaf pine (Martin & Means 2000) (Fig. 1). Indeed, home ranges of a South Carolina population of EDBs were also closely associated with pine habitat (Waldron *et al.* 2006). In a previous study of EDBs at Ichauway, when longleaf pine habitat was considered separately from other pine species, such as loblolly or slash pine, 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). This idea is further supported by the claim of Martin & Means (2000) that today, EDBs primarily occupy ruderal open-canopy mixed-pine woodlands not because they prefer such habitat, but because it is the only remaining suitable habitat.

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 & Navas 2006). Thus, one possible explanation for finding EDB home ranges associated with pine habitat is that such areas are particularly open across Ichauway and, thus, they provide thermoregulatory benefits. These benefits 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). Blouin-Demers & Weatherhead (2001a, 2001b) showed that Canadian populations of black rat snakes (*E. o. obsoleta*) preferred edges between open- and closed-canopy habitats and argued that habitat fragmentation allowed snakes close access to areas conducive to thermoregulation. In this study, though pine was the only habitat type with which EDBs associated strongly, 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 of Blouin-Demers & Weatherhead (2001a, 2001b). Indeed, Waldron *et al.* (2006) also found a positive association with three of the four habitat types examined in this study (pine, mixed pine hardwood, and agriculture). Although their results indicated a negative association with hardwoods, we believe that if forested wetlands had been excluded from their hardwood category, as was done in this study, they would have found EDBs to be positively associated with all four habitat types, further suggesting that heterogeneity is important to EDBs.

Another likely benefit of pine habitat for EDBs is access to suitable refugia. Eastern diamond-backed rattlesnakes use stump holes and the burrows of other organisms (e.g., gopher tortoises, *Gopherus polyphemus*, and nine-banded armadillos, *Dasypus novemcinctus*) as retreats from predators, fire, and cold temperatures, and as birthing sites (see Timmerman & Martin 2003). In this study, EDBs primarily used gopher tortoise burrows and stump holes for both active season and winter refuges. Although availability of these microhabitat structures in different habitat types was not quantified in this study, two lines of evidence suggest that they may be more abundant in pine habitats *vs.* other habitat types analyzed. First, gopher tortoises require open-canopy uplands and dry sandy soils for burrow construction, and those conditions are only found in pine-dominated habitats (Auffenberg & Franz 1982). Second, because of the extensive taproot (up to 5m deep) and lateral roots (up to 22m long) of longleaf pine (Heyward 1933), decaying tree stumps offer subterranean refugia for many species of vertebrates, including snakes (see Means 2006). Several researchers have mentioned the intense use of such stump holes by EDBs at various locales throughout their range (Mississippi, Kain 1995; Florida, Timmerman 1995; South Carolina, Waldron *et al.* 2006), and this was also the case for EDBs in this study (Georgia).

When a smaller spatial scale is considered, it appears that habitat associations of EDBs shift markedly. Eastern diamond-backed rattlesnakes were significantly associated with pine habitat at the landscape scale, but they tended to be farther from pine than expected within the home range, although the trend was not statistically significant. Individuals did not exhibit significant positive association with any habitat type at this spatial scale, although they did tend to be closer to hardwood habitat than random points. Rather, they were found significantly farther from agriculture than expected. Strikingly 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.

Although old fields, wildlife food plots, and cropland (all of which were considered ‘agriculture’ in this study) support high densities of small mammals, 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 rarely observed in fields; rather, they made use of the narrow rows of open-canopied planted pine that separated these fields, which likely allowed them to exploit the thermal gradients (Blouin-Demers & Weatherhead 2001b), and possible high prey densities (Martin, Wike, & Paddock 2000; but see Blouin-Demers & 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 can 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 sustainability.

Although we are confident that our results represent real patterns of space and habitat use of EDBs at Ichauway, we recognize that there were several limitations of our analyses. First, we were only able to obtain adequate spatial data for 10 individuals and results might have differed had we monitored a larger sample of the population. Nonetheless, because we detected significant patterns, larger sample sizes would likely reveal similar trends with increasing power. Second, based on the results of Waldron *et* *al.* (2007), with larger data sets within each season, we could have possibly identified effects of both season and sex on habitat associations. Last, our use of the existing broad-scale GIS landcover layer for our study site likely limited our ability to detect habitat associations at a fine scale. For example, although the analysis of within-home range habitat associations failed to detect a significant association with hardwood habitat, field notes collected at each snake location suggest that snakes did show a striking association with small hardwood patches that did not show up on the landcover layer (i.e., the patches were classified as the dominant habitat type in which they were found). This last point is particularly important, because the snakes undoubtedly perceive habitat structure on a much finer scale than can be deduced from aerial photography.

Despite the limitations of our study, our use of a distance-based analysis and multiple scales of investigation allowed us to gain new insights into EDB spatial ecology, as well as clarify the contradictory results of previous studies, both of which we believe will be valuable for future conservation planning. For example, distance measures revealed that EDBs were significantly 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 sympatric species (Roth 1976; Law & Dickman 1998). Additionally, after examining EDB habitat associations at two different spatial scales, we concluded that the differing results of Timmerman (1995) and Waldron *et al.* (2006) were likely not inter-population differences in habitat preferences, but rather resulted from their differing scales of investigation. This finding carries significant importance for future EDB management, because it suggests that, regardless of geographic location, some EDB populations might be able to be managed in a similar fashion, thereby limiting the need for region-specific plans; however, additional studies in more geographically disparate locales need to be conducted before such a conclusion can be made with certainty.

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Table 1: Published home range sizes for male, non-pregnant female, and pregnant female eastern diamondback rattlesnakes (*Crotalus adamanteus*).

	Home Range Size			
Location (source)	**Males (n)**	**Non-pregnant Females (n)**	**Pregnant Females (n)**	**Home Range Method**
Baker Co., GA (current study)	34.70 (4)	29.30 (6)	--------	100% MCP
Hampton Co., SC (Waldron et al., 2006)	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)*	46.50 (2)	--------	100% MCP

* Only 1987 estimate for M3 included in average.

Table 2: Pairwise comparisons of eastern diamondback rattlesnake (*Crotalus adamanteus*) mean distance ratios[a] for habitat types at landscape and within-home range spatial scales[b].

Landscape				
	Pine	**Agriculture**	**Mixed**	**Hardwood**
Pine		0.20 (0.844)	0.29(0.780)	1.10(0.298)
Agriculture			0.12(0.910)	0.59(0.590)
Mixed				0.58(0.578)
Hardwood				

Within-home range				
	Pine	**Agriculture**	**Mixed**	**Hardwood**
Pine		-0.38(0.714)	-0.35(0.733)	-1.24(0.248)
Agriculture			-0.06(0.950)	-3.13(0.012)
Mixed				-1.25(0.244)
Hardwood				

[a]Mean distance of used locations to each habitat type divided by mean distance of random locations to each habitat type averaged across snakes.

[b]Values are t-statistics (p-values) from tests of the null hypothesis that the mean distance ratio of used locations for the column habitat type minus the mean distance ratio of used locations for the row habitat type equals zero.

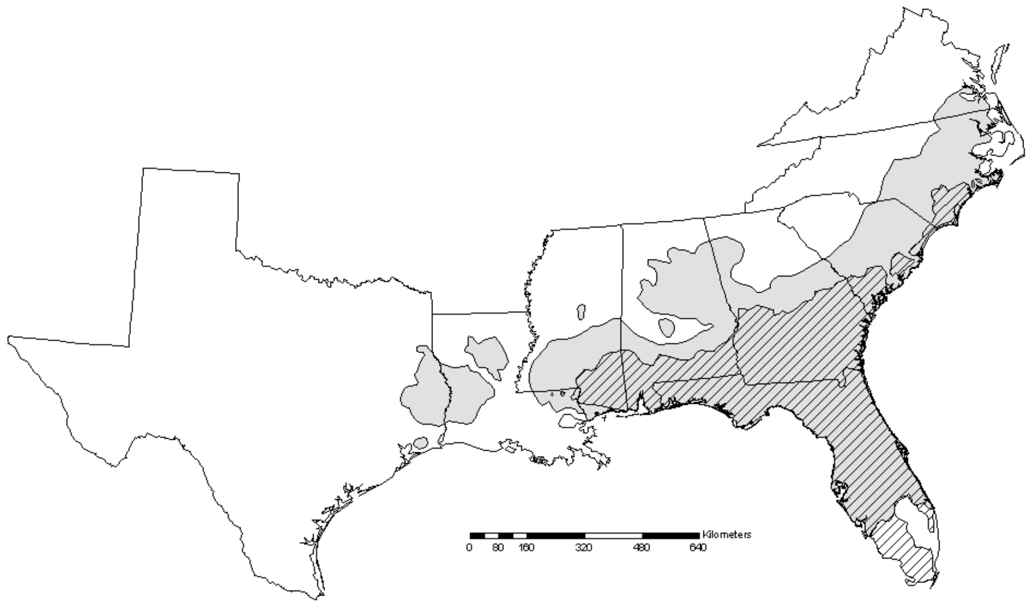

Figure 1. Historic extent of longleaf pine (*Pinus palustris*) forest (grey area) and current distribution of the eastern diamondback rattlesnake (*Crotalus adamanteus*) (hatched area) in North America; range maps modified from Ware et al. (1993) (longleaf pine forest) and Timmerman & Martin (2003) (eastern diamondback rattlesnake).

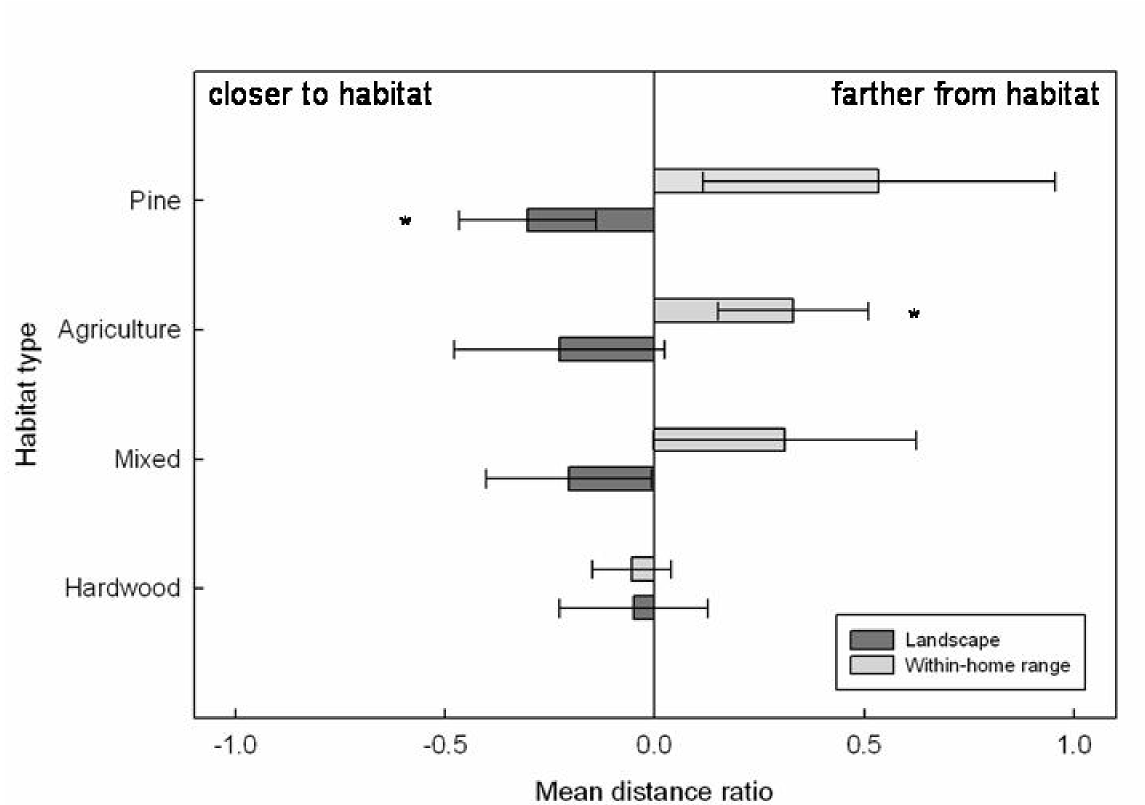

Figure 2. Mean distance ratios (± 1SE) of eastern diamond-backed rattlesnakes (*Crotalus adamanteus*) for habitat types at the landscape and within-home range spatial scales. For each individual, a distance ratio was calculated with the mean distance of snake locations to each habitat type in the numerator 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, so 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. Asterisks indicate mean distance ratios significantly different from 0 ($\alpha = 0.1$).

CHAPTER III

THE ASSOCIATION BETWEEN HABITAT HETEROGENEITY AND HOME RANGE SIZE ACROSS MULTIPLE SPATIAL SCALES IN THE EASTERN DIAMOND-BACKED RATTLESNAKE (CROTALUS ADAMANTEUS)

Summary

1. Landscape heterogeneity affects various 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.

2. Recent research on habitat selection in eastern diamond-backed rattlesnakes (*Crotalus adamanteus*) (EDB) indicated that heterogeneity might influence aspects of their spatial ecology, such as home range size. Data from a home range and habitat use study were examined for effects of landscape pattern and heterogeneity on home range size.

3. The software program FRAGSTATS was used to analyze landscapes within four various-sized buffers around home range centroids of individual snakes. From this analysis, we determined that home range size was negatively correlated with several

landscape metrics representing heterogeneity in patch configuration, such that individuals in particularly heterogeneous landscapes had relatively small home range sizes.

4. Multiple regression revealed that the relationship between heterogeneity and home range size was strongest at two spatial scales: the first was similar to the mean home range size of EDBs at our study site, and the second was approximately three times as large as the largest home range size recorded.

5. Results of the present analysis suggest that heterogeneity is indirectly influencing home range size of EDBs by affecting prey abundance and diversity, as well as the spatial distribution of other critical resources, such as mates. Furthermore, heterogeneity might be directly affecting home range size by providing wide thermal gradients within small areas, such that movements associated with behavioral thermoregulation are minimized.

6. We recommend further examination of how heterogeneity affects the spatial ecology of individuals, especially for species in need of management and or protection. We also advise researchers to consider multiple spatial scales in such analyses.

Key Words: edge contrast, FRAGSTATS, landscape pattern, reptile, spatial heterogeneity

Introduction

A central focus of landscape ecology is to achieve a comprehensive understanding of the influences of landscape pattern on ecological processes (Turner 1989). Variation in landscape pattern can be expressed in terms of heterogeneity, which may be defined as a combination of both spatial (configuration) and non-spatial (composition) landscape components (Li & Reynolds 1994). Heterogeneity has been linked to processes at the community (e.g., Pianka 1966, Roth 1976, Rozenzweig & Winakur 1969) and population levels (e.g., Dempster & Pollard 1986; Deutschewitz *et al.* 2003; Hamer *et al.* 2003); however, the response of individuals to heterogeneity only recently have been investigated (e.g., Constible, Chamberlain, & Leopold 2006; Kie *et al.* 2002; Saïd & Servanty 2005).

Landscapes are comprised of a mosaic of habitat patches that, at some spatial scale, encompass all of the resources an individual requires for survival and maximizing its fitness; thus, variation in the composition and configuration of those patches (i.e., heterogeneity) potentially affects use of space. Optimal foraging (MacArthur & Pianka 1966) and ideal free distribution (Fretwell & Lucas 1970) theories predict that animal space use will be related to the distribution and abundance of resources across the 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 area (i.e., 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 heterogeneous landscapes, then an individual's home range size may be indirectly affected by heterogeneity.

Snakes are appropriate candidates for studies concerning the relationship between heterogeneity and home range size because, like all reptiles, they are ectothermic and require adequate thermal conditions (e.g., gradients) for thermoregulation and structural heterogeneity might be particularly important for providing this resource (Blouin-Demers & Weatherhead 2001a, 2001b; Huey 1991; Peterson, Gibson, & Dorcas 1993; Shine

2005). Additionally, winter refugia are often located in habitats disparate from summer foraging areas (see Reinert 1993) and the spatial arrangement of those habitats likely affect space use patterns. Predators, such as snakes, are expected to be dependent upon landscape patterns that are beneficial to their prey (Hansson 2000), and many studies have documented positive effects (e.g., increased diversity and or abundance) of heterogeneity on common prey species, particularly small mammals (Manson, Ostfeld, & Canham 1999; Martin & McComb 2002; Nupp & Swihart 2000) and birds (Berg 1997; Freemark & Merriam 1986; Roth 1976). Because snakes appear to lack certain types of complex social systems (e.g., territoriality, food-sharing, long-term parental care of progeny) found in most species of birds and mammals (Gillingham 1987, but see Clark 2004; Greene 2002), social behaviour should not confound the effects of heterogeneity on home range size. But despite these characteristics that simplify analysis, no study has directly investigated the effects of heterogeneity on any aspect of snake ecology.

The results of an earlier study on habitat selection in eastern diamond-backed rattlesnakes (*Crotalus adamanteus* Beauvois; EDB) led us to hypothesize that spatial heterogeneity plays an important role in EDB spatial ecology (Chapter 2). In Chapter 2, we found that home ranges were positively associated with the four different habitat types, possibly indicating selection for heterogeneous landscapes. Furthermore, mean home range size was considerably smaller than reported in other studies on EDBs (see Kain 1995; Timmerman 1995; Waldron *et al.* 2006), and this geographic variation might be due to variance in levels of heterogeneity of the different areas. Finally, in contrast to the results of Waldron *et al.* (2006), we found no difference in home range size between males and non-pregnant females (Chapter 2). Because home range size of males should increase in size during the breeding season when females are spatially unpredictable (e.g., prolonged mate-searching polygyny; *sensu* Duvall, Schuett, & Arnold 1993), we postulated that the population studied in Chapter 2 might be at a high density due to an indirect effect of habitat heterogeneity.

To determine whether there was a relationship between landscape heterogeneity and spatial ecology (e.g., home range size) of EDBs, we analyzed data from a previous study (Chapter 2). Because the scale at which individuals respond to landscape pattern is not always intuitive (Weins 1989), we chose to examine this relationship at multiple spatial scales. Our objectives were to: (i) identify landscape patterns associated with EDB home range size, (ii) determine which components of heterogeneity exhibited the strongest relationship with home range size, and (iii) determine at which scale(s) these relationships were strongest.

Methods

Study Site

This study was conducted at Ichauway, the 12,000 ha research site of the Joseph W. Jones Ecological Research Center (JWJERC) located in Baker County, Georgia (Fig. 1). The management priorities of the JWJERC are restoration of the longleaf pine ecosystem and the application of land-use practices that integrate wildlife and timber management. Ichauway consists primarily of longleaf pine (*Pinus palustris*) forest (between 70 and 90 yrs old, in general, with individual trees > 300 yrs old) with an open midstory and herbaceous understory. Scattered throughout the property are stands of loblolly (*P. taeda*) and slash (*P. elliottii*) pines, hardwood patches (mostly *Quercus* spp.), and mixed pine-hardwood forests, isolated wetlands, and riparian habitats associated with the Ichawaynochaway Creek and Flint River. 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-year prescribed burn rotation, with approximately 4,000-4,900 ha burned annually. Prescribed fire at Ichauway contributes to the maintenance of features associated with old-growth longleaf pine forest, e.g., open canopy and herbaceous understory (Glitzenstein, Platt, & Streng 1995; Heyward 1939).

Home Range Analysis

Details concerning study animals and radio-telemetry can be found in Hoss *et al.* (####). Although some individuals were radio-tracked for more than one year, only locations from the first year were used in the present analysis. Locations were entered into ArcGIS (ESRI, Redlands, California) and home ranges were estimated using the Hawth's Tools extension (Beyer 2004). The 100% minimum convex polygon method (MCP), which defines home range as the smallest polygon encompassing all known locations (Hayne 1949), was used to estimate home range size for each individual. Although some researchers suggest that kernel density (KD) estimators are a more accurate measure of home range size than MCP (e.g., Kernohan, Gitzen, & Millspaugh 2001), recent arguments indicate that this is not the case for many reptiles, due to 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). Home range estimates were log-transformed to meet normality assumptions of parametric tests. Because males and females did not differ in home range size (t = -1.08, P = 0.312), sexes were pooled for all subsequent analyses.

Landscape Analysis

We used an ArcGIS landcover map of the study site that was created using color infrared photography (1:12,000) and was validated using field surveys. Seven landcover types were delineated for this study: pine, mixed pine-hardwood, hardwood, agriculture (wildlife food plots > 0.5ha 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 home range centroids were calculated. We delineated four spatial scales around MCP centroids with 250, 500, 750, and 1000m buffers that encompassed 20, 77, 178, and 314ha, respectively (Fig. 1). These spatial scales were chosen because they encompassed the known home range sizes of adult male and non-pregnant female EDBs (Kain 1995; Timmerman 1995; Waldron *et al.* 2006; this study). Although some individuals in the current study maintained home ranges smaller than 20ha, smaller buffers were not used, because many landscape metrics could not be calculated at smaller spatial scales.

We used FRAGSTATS (McGarigal & Marks 1995) to analyze the landscape of individual snakes 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. Several metrics from the contrast and proximity categories required user-defined weights that approximated edge contrast and habitat similarity for each pair of landcover types (Table 1). Although these weights were arbitrarily chosen, we believe they represented reasonable assumptions concerning structural contrast/similarity between these seven distinct landcover types.

Statistical Analysis

Pearson correlation coefficients were calculated for the 25 landscape metrics and 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 inter-correlated (Hargis, Bissonette, & David 1998), only data for 10 metrics (one or two from each category) were selected for further consideration (Table 2). 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, importantly, they were easy to interpret.

Li and Reynolds (1994) suggested that heterogeneity 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 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 non-additive 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. To identify the most parsimonious models across spatial scales, we used second-order Akaike's Information Criterion (AIC_c) for small sample sizes and calculated ΔAIC values for each model. We considered all models with $\Delta AIC < 2$ to be the best approximating models (Burnham & Anderson 2002). To ensure our data met parametric assumptions, we verified normality of all variables and residuals (Shapiro-Wilk $p > 0.04$), excluded variables in regressions that were highly correlated with each other (Pearson's $r > 0.75$), and found no evidence of multicollinearity (Collinearity Index < 10). All statistical analyses were performed using the software SAS 9.1 (SAS Institute 2001, Cary, North Carolina).

Results

Correlation

From 02 September 2003 to 20 June 2005, 10 adult EDBs (6 non-pregnant females, 4 males) were monitored for 7-12 months, including an entire active season (April to October). Home ranges averaged 24.56ha and ranged from 7.25 to 59.94ha. Only five of 10 landscape metrics were significantly correlated with home range size at one or more spatial scales: DCAD (Core Area), APMI and AMSI (Proximity), MECI (Contrast), and IJI (Contagion) (Table 3). DCAD, logAMPI, and MECI were negatively correlated and AMSI and IJI were positively correlated with home range size. The correlation trend for each variable was consistent across spatial scales, except for IJI, which was negatively correlated with home range size at the 250m scale. Although logAMPI was negatively correlated with home range size, which was counter to our prediction, AMSI, which takes into account the structural similarity among habitat types, showed the predicted relationship with home range size. MECI was the only metric significantly correlated with home range size at all spatial scales. Although ED and PD (Area/Density) and MFI (Shape) 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 relationship between home range size and diversity metrics (MSEI and MSDI) did not show a significant or consistent trend across spatial scales.

Multiple Regression

The global models, which included MSEI, MFI, logAMPI, and MECI, were significant at the 250m and 750m spatial scales (Table 4). The 250m scale was the most likely model, but a low ΔAIC value indicated that the 750m scale model was also competitive. Because the 500m and 1000m scales had ΔAIC values < 7, we considered those models to be unlikely. The model with the most explanatory power (250m; $R^2_{adj} = 0.768$) corresponded to the mean home range size of EDBs in this study (25ha); however, the other competing model (750m) was approximately three times the size of the largest home range of our study (60ha).

When we allowed for parameter removal, we detected four strongly competitive models (ΔAIC < 2) and nine moderately competitive models (ΔAIC = 2-5) (Table 5). The top four models were two- and three-parameter models at the 250m and 750m spatial scales. All metrics were included in three of the top four models, except MSEI (Diversity), which was only present in the three-parameter model at the 750m scale. Of the nine moderately competitive models, six were at the 750m scale, two were at the 250m scale, and one was at the 1000m scale. None of the 500m scale or global models was competitive based on ΔAIC values.

Discussion

Landscape Pattern and Home Range

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, the favored prey of EDBs (reviewed in Timmerman & Martin 2003), are often particularly abundant and diverse in edge habitat, especially edge habitat with high structural contrast (Bowers & Dooley 1999; Manson *et al.* 1999; Nupp & Swihart 2000), such as that found between forest and field. Second, given the thermoregulatory requirements of large ectotherms such as EDBs (e.g., Lillywhite & 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 appears to be important to EDBs at Ichauway. Under conditions where patches were distinguished by the dominant vegetation cover (e.g., pine) and not structural similarity, home range size was negatively correlated with proximity measures. Because proximity indices increase as fragmentation increases and because fragmentation is a form of heterogeneity, we would expect home range size to be positively correlated with proximity indices. However, when similarities between different habitat types were incorporated, as in the area-weighted mean similarity index (AMSI), the sign of the relationship changed, such that small home ranges were associated with areas of high fragmentation, as we predicted. Most snakes tend to respond strongly to habitat structure (reviewed in Reinert 1993); therefore, we suggest that metrics incorporating structural information, such as AMSI and MECI, are more informative indices than those that categorize habitats based on the dominant vegetation found within a patch. Given this finding, future studies should consider incorporating these types of analyses.

Heterogeneity and Home Range

An accumulating body of evidence shows that heterogeneity can significantly affect ecological phenomena, such as species diversity (e.g., Lack 1969; MacAruthur & Wilson 1967; Simpson 1949), yet there is no consensus as to the most appropriate definition or means of quantifying heterogeneity (reviewed in Tews *et al.* 2004). Although many suggestions have been offered, few have explicitly tested the ability of their mathematical definition to adequately capture variations in heterogeneity. Li and Reynolds (1994) conducted a simulation experiment 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) were competitive. However, when we removed parameters with poor predictive power, four different models were highly competitive. The four models included two to three parameters, but only one 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). Three single-parameter models were considered moderately competitive and all of them 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 (Kotlier & Weins 1990; Milne 1991; Turner 1989; Weins 1989). We found that, in EDBs, the relationship between landscape pattern and home range size varied across spatial scales. When we used Li and Reynolds (1994) definition of overall heterogeneity, variation in home range size was best explained by heterogeneity at the 250m and 750m spatial scales. It is intuitive that EDBs would respond to heterogeneity at the scale of their mean home range size (i.e., 250m). However, it was unexpected that this relationship would be equally strong at the 750m scale, which was three times greater than the largest home range size recorded at this site. Kie *et al.* (2002) determined that home range size of mule deer (*Odocoileus hemionus*) exhibited the strongest relationship with heterogeneity at a scale significantly larger than mean home range size, as well; however, unlike this study, their model was not considered competitive at the scale size of mean home range. This further emphasizes the fact that investigations concerned with organism-environment interactions should consider multiple spatial scales (see Johnson 1980; Tews *et al.* 2004), due to difficulties in predicting the scale at which animals respond to factors of interest.

In the absence of data on dispersal and home range establishment in juvenile snakes of any species, it is difficult to gauge the likelihood that EDBs sampled the habitat encompassed by the largest spatial scale used in this study. Moreover, because individuals in this study were tracked for a relatively short period of time, we may have underestimated their use of the larger landscape. Regardless, home range size of EDBs showed a strong relationship with heterogeneity at a large spatial scale, which has important implications for how the scale of investigation should be selected in future studies.

Many factors affect home range size in snakes, including reproductive condition (Brown *et al.* 1982; Reinert & Zappalorti 1988), body size (Roth 2005; Whitaker & Shine 2003), and sex (Waldron *et al.* 2006). The results of this study, which is the first to determine the relationship between habitat heterogeneity and home range size in a species of reptile, suggest that heterogeneity has a predominant role in determining the home range size of snakes, and this finding should be considered in future studies of their spatial ecology. 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). Furthermore, because habitat heterogeneity has positive effects on a broad array of taxa (e.g., birds: Farley *et al.* 1994; mammals: Medellin & Equihua 1998; amphibians: Vallan 2002; reptiles: Pianka 1966; invertebrates: Baz & Garcia-Boyero

1995), it should be considered by land managers and conservation biologists concerned with preservation and restoration of habitat.

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Table 1: Matrix of user-defined Edge Contrast and Patch Similarity (in parentheses) weights for seven landcover types at Ichauway, in Baker County, Georgia. Low values represent low edge contrast and high patch similarity between row and column landcover type, whereas high values represent high edge contrast and low patch similarity.

Patch Type	**Agriculture**	**Scrub/ Shrub**	**Hardwood**	**Pine**	**Mixed***	**Water**	**Rural**
Agriculture	0 (1.0)						
Scrub/Shrub	0.2 (0.8)	0 (1.0)					
Hardwood	0.8 (0.2)	0.4 (0.6)	0 (1.0)				
Pine	0.8 (0.2)	0.8 (0.2)	0.4 (0.6)	0 (1.0)			
Mixed*	0.8 (0.2)	0.6 (0.4)	0.2 (0.8)	0.2 (0.8)	0 (1.0)		
Water	1.0 (0)	1.0 (0)	1.0 (0)	1.0 (0)	1.0 (0)	0 (1.0)	
Rural	1.0 (0)	1.0 (0)	1.0 (0)	1.0 (0)	1.0 (0)	1.0 (0)	0 (1.0)

* mixed pine-hardwood

Table 2: Landscape metrics used as independent variables associated with adult eastern diamond-backed rattlesnake home range size in correlation analysis and multiple regression.

Category	Metric	Description	Heterogeneity*
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 core (>5m from edge) area	+
Proximity	Area-weighted Mean Proximity Index (AMPI)	index of spatial arrangement of patch types	-
	Area-weighted Similarity Index (AMSI)	similarity-weighted (Table 1) AMPI	-
Contrast	Mean Edge Contrast Index (MECI)	contrast-weighted (Table 1) edge density	+
Contagion	Interspersion and Juxtaposition Index (IJI)	index of patch type dispersion and interspersion	-
Diversity	Modified Simpson's Evenness Index (MSEI)	index of patch diversity and evenness	+
	Modified Simpson's Diversity Index (MSDI)	index of patch diversity and abundance	+

* sign indicates the direction of the relationship between the metric value and heterogeneity

Table 3: Pearson correlation coefficients for associations of landscape metrics and adult eastern diamond-backed rattlesnake log-transformed home range size at four spatial scales. Buffers at four different spatial scales were placed around centroids of 10 snake home ranges at Ichauway, Baker County, Georgia.

		Spatial Scale			
Category	**Metric**	**250m**	**500m**	**750m**	**1000m**
Area/Density	ED	-0.28^{ns}	-0.46^{ns}	-0.36^{ns}	-0.37^{ns}
	PD	-0.49^{ns}	-0.52^{ns}	-0.40^{ns}	-0.51^{ns}
Shape	MFI	-0.05^{ns}	-0.48^{ns}	-0.03^{ns}	-0.40^{ns}
Core Area	DCAD	-0.25^{ns}	-0.31^{ns}	-0.41^{ns}	-0.62*
Proximity	logAMPI	-0.45^{ns}	-0.33^{ns}	-0.77**	-0.42^{ns}
	AMSI	0.65*	0.54^{ns}	0.30^{ns}	0.20^{ns}
Contrast	MECI	-0.77**	-0.72*	-0.78**	-0.79**
Contagion	IJI	-0.17^{ns}	0.66**	0.32^{ns}	0.34^{ns}
Diversity	MSEI	-0.18^{ns}	0.15^{ns}	-0.13^{ns}	0.03^{ns}
	MSDI	0.07^{ns}	0.09^{ns}	-0.10^{ns}	0.03^{ns}

* $P \leq 0.05$; ** $P \leq 0.01$; "ns" = not significant ($P > 0.05$)

Table 4: Forced global models at four spatial scales. Four metrics representing overall heterogeneity were the predictor variables and adult eastern diamond-backed rattlesnake log-transformed home range size was the dependent variable.

	MSEI	**MFI**	**logAMPI**	**MECI**				
Scale (m)	$\boldsymbol{b_1}$	$\boldsymbol{b_2}$	$\boldsymbol{b_3}$	$\boldsymbol{b_4}$	$\mathbf{R^2_{adj}}$	***Overall P***	$\mathbf{AIC_c}$	**ΔAIC**
250	0.057^{ns}	-0.634^{ns}	-0.435^{ns}	-0.852***	0.768	0.019	-3.734	0.000
500	0.159^{ns}	-0.115^{ns}	0.336^{ns}	-0.894^{ns}	0.300	0.239	7.319	11.053
750	-0.306^{ns}	0.247^{ns}	-0.863*	-0.209^{ns}	0.745	0.024	-2.776	0.958
1000	-0.144^{ns}	0.013^{ns}	-0.318^{ns}	-0.698*	0.415	0.162	5.513	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 ($\boldsymbol{b_i}$) are included for each metric, adjusted R^2 (R^2_{adj}), the overall *P-value*, second-order Akaike's Information Criterion (AIC_c), and ΔAIC values are provided for the global model at each spatial scale.

Table 5: Competing models using landscape metrics representing heterogeneity as independent variables and adult eastern-diamond-backed rattlesnake log-transformed home range size as the dependent variable. Strongly competing models had ΔAIC < 2, whereas moderately competing models had 2 < ΔAIC < 5.

		MSEI	MFI	logAMPI	MECI				
Scale (m)	**K**	b_1	b_2	b_3	b_4	R^2_{adj}	***Overall P***	**AIC$_c$**	**ΔAIC**
250	3	----	0.672**	-0.420^{ns}	-0.844**	0.806	0.005	-38.069	0.000
750	2	----	----	-0.507*	-0.520*	0.735	0.004	-37.706	0.363
250	2	----	0.469*	----	-0.976***	0.712	0.005	-36.861	1.208
750	3	0.398*	0.358^{ns}	-1.043***	----	0.765	0.008	-36.179	1.889
750	2	0.401^{ns}	----	-0.893**	----	0.663	0.009	-35.317	2.751
750	3	0.224^{ns}	----	-0.636*	-0.399^{ns}	0.743	0.010	-35.256	2.813
1000	1	----	----	----	-0.792**	0.580	0.006	-34.989	3.080
750	1	----	----	----	-0.777**	0.554	0.008	-34.369	3.700
250	1	----	----	----	-0.773**	0.547	0.009	-34.225	3.843
750	1	----	----	-0.770**	----	0.542	0.009	-34.112	3.957
750	2	----	0.362^{ns}	-0.923**	----	0.615	0.015	-33.959	4.110
750	3	----	0.123^{ns}	-0.595^{ns}	-0.448^{ns}	0.703	0.016	-33.833	4.235
250	2	0.358^{ns}	----	----	-0.970**	0.598	0.017	-33.527	4.542

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 (K), regression coefficients (b_i), adjusted R^2 (R^2_{adj}), model *P-value*, second-order Akaike's Information Criterion (AIC$_c$), and ΔAIC values are provided.* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$; "ns" = not significant ($P > 0.05$).

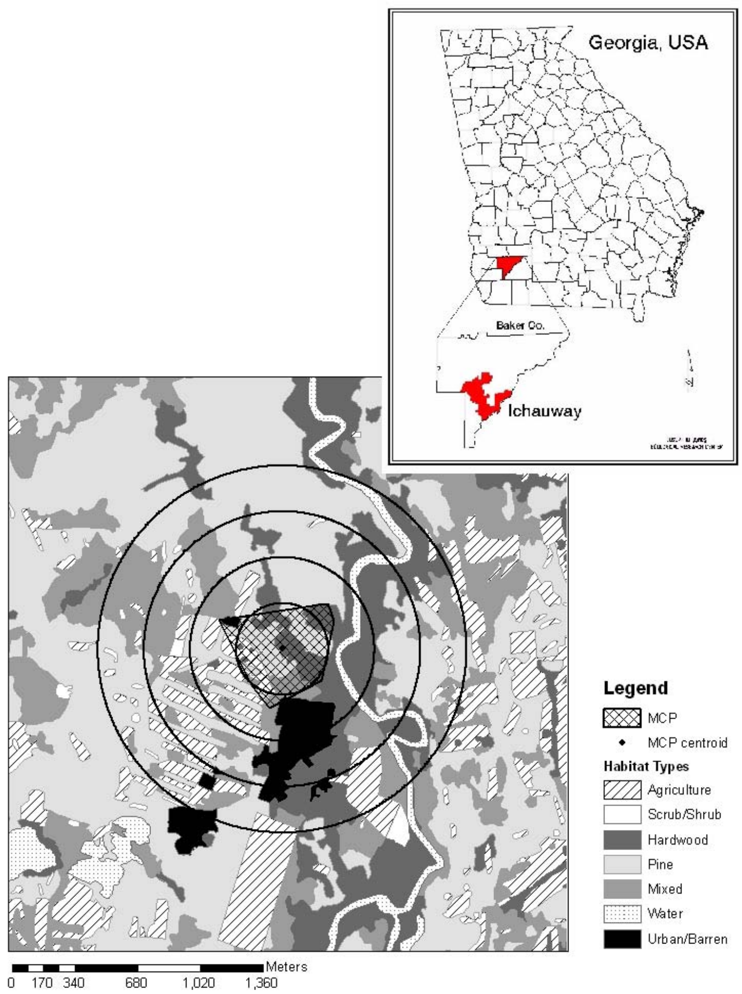

Figure 1: Ichauway study site in Georgia where eastern-diamondback rattlesnake home range data were collected. The larger map represents the buffering step used in the landscape analysis. A home range (MCP) centroid was encircled with four buffers of increasing radii (250, 500, 750, and 1000m). The landscape within each of those buffers was analyzed to determine the relationship between heterogeneity and home range size.

CHAPTER IV

CONCLUSIONS

1. There were no sex differences in EDB home range size and males in this study had a smaller mean home range size than those reported in previous studies. The lack of inter-sexual difference in home range size, as well as the relatively small male home range sizes indicate that males do not have to travel far to find receptive females during the mating season. This may be due to a dense EDB population driven by high prey densities.

2. At the landscape scale, EDBs were positively associated with pine, which was likely due to thermoregulatory benefits and various refugia associated with open-canopy pine savanna. EDBs were also closer to all habitat types than expected, indicating a possible preference for habitat heterogeneity.

3. Within the home range, EDBs were negatively associated with agriculture, but frequented the edges of agricultural fields. While snakes may benefit from high prey densities associated with wildlife food plots, these fields likely confer a cost of increased exposure and mortality associated with management practices (e.g., roller-chopping of the fields).

4. Conducting a multi-scale study on a single population resolved the conflicting results of previous studies.

5. Management for EDBs should include preservation of a mosaic of habitat types within a larger pine matrix and limit the conversion of forest to agriculture.

5. Habitat heterogeneity was inversely related to EDB home range size, which is likely a result of increased prey densities and easier access to resources provided by heterogeneous landscapes.

6. Landscape metrics representing variation in habitat configuration appeared to influence home range size more strongly than metrics representing habitat composition.

7. The relationship between heterogeneity and home range size was strongest at a spatial scale representing mean home range size; this relationship was equally as strong at a spatial scale approximately three times as large as the mean home range size of EDBs at our study site.

8. Future studies should incorporate aspects of habitat heterogeneity at multiple spatial scales when investigating factors that influence spatial ecology.

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