Seasonal Habitat and Shelter Selection by Reintroduced Eastern Indigo Snakes in Conecuh National Forest, Alabama

by

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Abstract

Understanding how reintroduced snakes select habitats is crucial to the success of reintroduction projects. This study examines habitat selection by a federally threatened snake species in the southeastern United States following its reintroduction to Alabama.

In Chapter 1, I introduce my study organism, the Eastern Indigo Snake (*Drymarchon couperi*), illustrating the reasons it was listed as a threatened species. I outline the factors that led to the species' extirpation and a current reintroduction project in Alabama. I describe the habitats documented in studies of wild indigo snakes and explain why it is important to study habitats selected by reintroduced animals.

Chapter 2 describes the study of habitat selection by reintroduced indigo snakes. Habitat selection is examined at multiple spatial and temporal scales. Landscape, home range and shelter scales are investigated for habitat selection, as well as seasonal examinations at the home range and shelter scales. The results of habitat selection by reintroduced snakes in this study are compared to the results from a previous study of habitat selection in a wild population of indigo snakes in Georgia near the source sites of animals in this reintroduction. The results of habitat selection in this study are discussed in the context of hierarchical habitat selection. Strategies for managing habitat for indigo snakes are recommended based on the results of this study.

Chapter 3 summarizes the key results of this study and highlights their importance and application to future indigo snake reintroductions. My results demonstrate that reintroduced snakes selected habitats in a manner mimicking habitat selection in naturally distributed populations. I conclude that management practices that create and maintain open-canopied habitats supporting gopher tortoises will be essential for the successful reestablishment of indigo snakes in the northern portion of their range.

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Chapter 1

Introduction

With reptile populations declining around the globe (Gibbons et al. 2000), reintroduction of extirpated species is gaining popularity as a conservation method (Germano and Bishop 2009). Research that indicates habitat requirements and responses to management regimes is needed to direct science-based recovery plans for declining species (Van Lear et al. 2005) because maintenance of high quality habitat is crucial for conserving these species. This is particularly true for reptile and amphibian reintroduction projects because poor habitat quality at release sites is one of the most frequently reported reasons for failure in amphibian projects and is understudied in reptile projects (Germano and Bishop 2009).

In the southeastern United States, many imperiled reptile species are intimately associated with fire-maintained longleaf pine forests in the Coastal Plain (Guyer and Bailey 1993; Bailey 2004). The longleaf pine ecosystem is now thought to be one of the most imperiled ecosystems in the world (Noss and Peters 1995), with less than 3% remaining in longleaf pine (Frost 1993) and less than 0.002% remaining in old growth (Simberloff 1993). Throughout the current range of longleaf pine, at least 36 vertebrate species adapted to longleaf pine forests are of conservation concern (Means 2006), including the Eastern Indigo Snake (*Drymarchon couperi*).

Historically, Eastern Indigo Snakes ranged across the Coastal Plain from Florida and southeastern Georgia through southern Alabama and into Mississippi (Conant and Collins 1998). This range encompasses much of the 14,000,000 ha historical range of longleaf pine (*Pinus palustris*) in the southeastern United States. As a species closely tied to longleaf pine in the northern portion of its range, the indigo snake has also experienced range-wide declines. In 1978, indigo snakes were listed as Threatened under the federal Endangered Species Act (United States Fish and Wildlife Service 1978). Wild populations of indigo snakes are currently known only from southeastern Georgia and Florida (Diemer and Speake 1983; Moler 1985).

A reintroduction effort to reestablish viable populations of the indigo snake is currently under way within the Conecuh National Forest (CNF) in Alabama, where indigo snakes have been extirpated, with the last confirmed free-ranging snake being observed near the CNF by Neill (1954). The major causes of extirpation are thought to be increased mortality due to gassing of gopher tortoise burrows used by indigo snakes (Speake and Mount 1973) and reduced habitat quality. Return to a natural fire frequency has been recommended for increasing habitat quality for indigo snakes (Gunzberger and Aresco 2007) and fire management on the CNF over the past 20 years has transformed significant portions of this forest to the open aspect of the ancestral landscape required by indigo snakes (Guyer et al. 2007). Additionally, new state regulations outlawing gassing of gopher tortoise burrows and reduced evidence of human predation of tortoises in the CNF indicate increased suitability for indigo snake survival.

Source populations for the reintroduction project are located in areas of southern Georgia that contain the largest viable populations of the species in the northern portion of its range (Diemer and Speake 1983; Moler 1985). Free-ranging individuals in southern Georgia use large home ranges that contain multiple habitats, including xeric uplands and wet lowlands that are used by indigo snakes each year (Hyslop 2007). The presence of gopher tortoises is a particularly important habitat component for indigo snakes (Diemer and Speake 1983; Lawler 1977) because these snakes overwinter in gopher tortoise burrows (Diemer and Speake 1981; 1983), often returning to the same burrows in different years (Stevenson et al. 2003). Gopher tortoise burrows are also used by indigo snakes for nesting, foraging, and as refuges prior to ecdysis (Landers and Speake 1980; Smith 1987).

Snakes are known to demonstrate variation in which habitats they select as well as the scales at which they select habitats. Geographic differences in habitat use between indigo snakes in the northern and southern portions of its current range have been documented (Lawler 1977; Speake et al. 1978; Steiner et al. 1983; Moler 1992; Hyslop 2007). Many studies of habitat selection in snakes have demonstrated the need to examine habitat selection at multiple scales (e.g., Moore and Gillingham 2006; Steen et al. 2010; Hoss et al. 2010). This underscores the importance of documenting which habitats are selected by reintroduced snakes as well as the scale of habitat selection exhibited at release sites.

Studies examining habitats selected by reintroduced animals may provide early indications of the success of reintroduction efforts. If patterns of space use by reintroduced individuals mimic habitat selection by free-ranging animals from source populations then opportunities for achieving growth rates and reproduction levels equivalent to those of the source populations should be maximized on reintroduction sites (Himes et al. 2006). Additionally, gaining an understanding of how reintroduced animals select habitat at release sites, including the scale of selection, may provide valuable insight for adaptive management at current release sites, as well as enhancing the potential for success in future reptile reintroductions. For these reasons, in this study, I examined not only which habitats were selected, but also how habitats were selected by indigo snakes reintroduced to CNF.

Chapter 2

Seasonal Habitat and Shelter Selection by Reintroduced Eastern Indigo Snakes in Conecuh National Forest, Alabama

Abstract

Species reintroduction has become an increasingly popular conservation method for reestablishing extirpated populations of declining species. Because poor habitat quality at release sites has been one of the most frequently reported reasons for failure of reintroductions, evaluating habitats selected by reintroduced animals is of paramount importance. I radio-tracked 38 Eastern Indigo Snakes reintroduced to Conecuh National Forest, Alabama. My study objectives were to: 1) quantify habitat and shelter selection at multiple spatial and temporal scales, 2) compare results from my study to the results of a study of a wild population near the source sites, 3) evaluate whether hierarchical habitat selection occurred in reintroduced snakes, and 4) inform future management of habitat at the release site. My results document that habitat selection in reintroduced snakes occurred at multiple spatial and temporal scales. At a landscape scale, snakes selected fields and roads and mixed pine-hardwood habitats significantly more than wetlands and hardwoods. Habitat selection at a home range scale was not significant overall, although open canopy longleaf pine forest was selected significantly more than mixed pine-hardwood forest. However, when seasons were examined separately, significant differences emerged at the home range scale. During the spring, summer, and fall months, snakes selected open canopy longleaf pine forests significantly more than fields and roads or mixed pine-hardwood habitats. During winter months, snakes selected fields

and roads significantly more than wetlands and hardwood or mixed pine-hardwood habitats. Among sites used as shelters, gopher tortoise burrows ranked highest, followed by stump/root in both non-winter and winter seasons. Snakes in my study used habitats and shelters in a manner similar to that of snakes studied previously in Georgia near the source sites of my snakes. Selection was strongest at shelter and landscape scales when compared to home range scale and, therefore, I conclude that habitat selection by reintroduced snakes in my study was not hierarchical. My observations indicate that maintenance of high quality gopher tortoise habitat, including prescribed burning to maintain open-canopied habitats, will be critical for the successful reestablishment of Eastern Indigo Snake populations in the northern part of its range.

Introduction

Population decline is a growing problem that is affecting reptile species on a global scale (Gibbons et al. 2000). In order to address this burgeoning crisis, species reintroduction has become a practical recourse for reestablishing extirpated populations of declining species. Unfortunately, the success rate for this method has been variable and many attempts have either failed or have lacked conclusive assessments of their success (Fischer and Lindenmayer 2000).

Poor habitat quality at release sites has been one of the most frequently reported reasons for failure in reptile and amphibian reintroductions (Germano and Bishop 2009). Additionally, it has been shown that animals experiencing a new environment may respond with abnormal behaviors including abnormal use of habitat, which may increase mortality (Roe et al. 2010). To minimize these problems, it has been recommended that habitats selected as release sites should be as similar to the habitat at the source site as possible (Osborne and Seddon 2012) and also that chosen habitats be reevaluated after an initial release to inform continuing management at the release sites (Cook et al. 2010).

Habitat selection is the process by which an animal chooses a habitat (Johnson 1980). In habitat selection studies, selection for a particular habitat is inferred when the use of a habitat defined in the study differs from its availability (Manly et al. 2002). Choosing the appropriate scale for habitat selection studies may affect the study's ability to detect how a species responds to its environment because ecological patterns and processes are scale-dependent (Wiens 1989). Jenkins et al. (2009) recommended that a priori scales of investigation not be set, but instead concluded that habitat selection examined at multiple scales would offer a better understanding of how animals relate to their environment.

In snakes, habitat selection has been shown to vary across space (i.e., geographic range of a species; Martino et al. 2012) as well as time (i.e., seasonally; Waldron et al. 2006). This variation underscores the importance of understanding how habitats are selected by reintroduced animals. Habitat selection is thought to be a hierarchical process in which finer scales of selection are dependent on coarser scales. Johnson (1980) defines first, second and third order selection by ranking selection orders from coarser to fine scale. The landscape or coarse scale of selection is thought to be the most revealing for driving selective behaviors that minimize the effects of limiting factors in the environment (Rettie and Messier 2000), but some studies suggest that this may not apply to ectotherms (Harvey and Weatherhead 2006). Understanding the scale of selection is important for gaining insight into the ecology of an animal (Wiens 1989) and is particularly crucial for reintroduced snakes because habitat selection affects animal physiology, especially among ectotherms (Huey 1991). For this reason, I examined habitat selection by reintroduced Eastern Indigo Snakes (*Drymarchon couperi*), referred to hereafter as indigo snakes, at multiple spatial and temporal scales.

Indigo snakes were federally listed as a threatened species in 1978 due to habitat loss and degradation, overcollecting, and mortality caused by gassing of gopher tortoise burrows (Speake 1993). Across most of its historic range, this species is strongly associated with sandhills bordering wetland habitats (Hyslop 2007) within the longleaf pine ecosystem of the southeastern United States, a forest type now recognized as one of the most endangered in the world (Frost et al. 1986; Noss 1989; Stout and Marion 1993). Previous studies of the indigo snake in the northern part of its range have indicated that shelter availability may be a potent environmental constraint (Hyslop et al. 2009; Speake et al. 1978). In particular, indigo snakes in this part of their range are documented to rely chiefly on Gopher Tortoise (*Gopherus polyphemus*) burrows for shelter, especially in winter. These deep burrows provide important protection from temperature extremes and may constitute a critical habitat component limiting the northern distribution of indigo snakes to areas where this commensal species is abundant.

One measure of success for reintroductions is habitat use that mirrors that of individuals from the source populations. Studies that use information gained from wild populations (Himes et al. 2006) may provide early indications of the challenges reintroduced animals face in adapting to a new environment. I compared the results of my study to Hyslop (2007), who examined wild indigo snakes near the source sites of snakes obtained for this multi-partner reintroduction project. My study objectives were to 1) quantify habitat and shelter selection at multiple spatial and temporal scales, 2) compare results from my study to the results of a study of a wild population near the source sites, 3) evaluate whether hierarchical habitat selection was documented in reintroduced snakes, and 4) inform future management of habitat at the release site.

Methods

Study Area

This study was conducted in Conecuh National Forest (CNF), Alabama, a longleaf pine forest encompassing approximately 34,000 hectares and bordering Blackwater River State Forest in neighboring Florida. Combined, these two forests provide ca. 117,000 hectares of connected habitats, representing one of the largest contiguous tracts of longleaf pine forests remaining in the southeastern United States. Additionally, the CNF supports the largest populations of gopher tortoises occurring on public lands in Alabama (Guyer et al. 2011), making it an area vital to indigo snake conservation in the northern portion of the snake's range.

A reintroduction effort for indigo snakes is currently under way in Compartment 28 of CNF within the 9,458 hectare Blue Springs Wildlife Management Area (WMA). Soils in the area include a range of upland and lowland types: Troup loamy sand (0 to 5% slopes), Bonifay loamy fine sand (5 to 10% slopes), and Muckalee, Bibb, and Osier soils (0 to 2% slopes, frequently flooded) (Cotton 1989). These soils support diverse upland and lowland plant communities on CNF including longleaf pine-dominated rolling clay hills and sandhills that support gopher tortoises; pine flatwoods; mesic hammocks and bays; wildlife food plots and old fields; hardwood-dominated ravines; rivers, creeks, permanent, semi-permanent and ephemeral ponds; and herb and shrub bogs. CNF implements management focused on restoring the longleaf pine ecosystem. Active management includes prescribed burning, stand thinning, mechanical and chemical removal of offsite pine species, and replanting of longleaf pines on historical longleaf sites. Wildlife food plots scattered throughout the WMA are planted primarily for white-tailed deer (*Odocoileus virginianus*), wild turkey (*Meleagris gallopavo*), and northern bobwhite (*Colinus virginianus*), but often support high densities of gopher tortoises as well.

Telemetry

Eastern Indigo Snakes in this study were the offspring of gravid wild females captured by hand in Georgia. Eggs laid by captured females were hatched and reared to approximately two years of age in a multi-partner cooperative effort. Surgeries were performed to implant snakes with radiotransmitters. Transmitters used were Holohil SB-2 temperature calibrated with the following specifications: weight of 5.0g, length x diameter (mm) of 19 x 9.5, and lifespan of 10 months (range 6-12 months). Snakes surviving their first year post release were captured and surgically fitted with Holohil SI-2T transmitters with the following specifications: weight of 13.5g, length x diameter (mm) of 50 x 11, and lifespan of 24 months (range of 12-30 months). Following surgery, each snake was placed in a circular fiberglass tub (2.27 meters tall by 4.55 meters across) that was covered by a hardware cloth and shade cloth lid. These tubs were located outdoors at the North Auburn Fisheries Unit and contained a sand bottom, a large water bowl, a variety of artificial surface cover types and access to an underground chamber made of 7.7 cm diameter Polyvinyl chloride (PVC) pipe. Snakes remained in tubs approximately two months before their release on CNF. A total of 38 snakes were fitted with transmitters and released on CNF, 17 snakes on 16 June 2010 (nine males, eight females) and 21 snakes (10 males, 11 females) on 16 May 2011. After release, a Communications Specialist R-1000 Telemetry Receiver coupled with a directional hand-held antenna was used to locate snakes approximately 1-3 times per week. Upon study completion, I recaptured snakes when possible and surgically removed transmitters.

Compositional Habitat Selection Analyses

I radio-tracked Eastern Indigo Snakes (n=38) reintroduced to Conecuh National Forest, Alabama from 17 June 2010 - 1 April 2012 to evaluate post-release habitat and shelter selection. I performed all habitat selection analyses using the Compositional Analysis method (Aebischer et al. 1993) and the program BYCOMP.SAS (Ott and Hovey 1997) in SAS Version 9.2 (SAS Institute, Cary, North Carolina). Habitat types occurring in the study area were characterized from existing AL-GAP categories (Kleiner et al. 2007). Accuracy of data was assessed both visually in GIS and on the ground. Any inaccuracies found were minor and were updated when these fine scale categories were assigned to broader scale habitat categories used in this study. For this method, Aebischer et al. (1993) suggest either removing animals that did not have all habitats available to them, or merging habitats to reduce the number of habitat categories. Rather than excluding a large number of animals from my analysis, I chose to combine some similar habitat categories into a single category. Habitat types that constituted less than three percent of the study area (i.e. open water, low intensity developed, medium intensity developed, evergreen plantations and row cop) were removed because including rare habitats can negatively affect analyses.

If a habitat that was available was not used by an animal, the zero use was replaced by a small non-zero value (0.0001) because this method cannot accept missing use values for available habitats (Moore and Gillingham 2006; Aebischer et al. 1993). For my landscape scale analysis, there were no zero values for use because all animals used every habitat type, therefore no zero values were replaced; all snakes had >15 locations (range 16-115), and no habitat type included was <3% of study area. For my non-seasonal home range analysis, nine zero values were replaced, all snakes had >15 locations (range 16-115), and no habitat type included was <3% of study area. For my non-winter home range scale analysis, eleven zero values were replaced, all snakes had >15 locations (range 16-115), and no habitat type included was <3% of study area. For my winter home range scale analysis, twenty-six zero values were replaced, all snakes had >15 locations (range 16-115), and no habitat type included was <3% of study area.

Four habitat types were delineated for use in landscape and home range scale compositional analyses:

Fields and Roads- This category included dirt and paved roads, anthropogenically disturbed and early successional habitats such as regenerating clearcuts, pasture/ hay fields and wildlife food plots. It is characterized by either a complete lack of canopy or an extremely sparse canopy. This category combines four AL-GAP categories: Developed Open Space, Successional Shrub/ Scrub Clearcut, Successional Shrub/ Scrub Other and Pasture/ Hay.

Wetlands and Hardwood- This category combines upland areas, mesic slope forest, floodplain forest and wetland areas with >75% hardwood overstory. It is characterized by a dense canopy that creates a heavy shade. This category combines three AL-GAP categories: East Gulf Coastal Plain Southern Mesic Slope Forest, Southern Coastal Plain Blackwater River Floodplain Forest, and East Gulf Coastal Plain Interior Upland Longleaf Pine Woodland-Offsite Hardwood Modifier.

Open Canopy Longleaf- This category includes >75% pine with an open canopy maintained by more frequent fire. It is typically composed of longleaf pine with a low herbaceous understory. This category is the AL-GAP category East Gulf Coastal Plain Interior Upland Longleaf Pine Woodland-Open Understory Modifier.

Mixed Pine-Hardwood- This category includes >75% pine with a relatively more dense canopy than open canopy longleaf pine forest resulting from infrequent fire and mature hardwood trees scattered in the canopy. It is characterized by a tall shrub layer and a denser canopy when compared with open canopy longleaf. This category is the AL-GAP category East Gulf Coastal Plain Interior Upland Longleaf Pine-Loblolly Modifier (although on my study site, it is more typically a slash pine and hardwood modifier).

I examined habitat selection at the scale of landscape, home range and shelter. I also examined selection seasonally because habitats used by indigo snakes studied near the source populations differed by season (Hyslop 2007). Therefore, at the home range and shelter scales, I divided data into winter and non-winter seasons. I chose to include two rather than four seasons because: 1) these two categories represent time periods that are relevant for snakes in this area, 2) I expected winter to be particularly challenging for indigo snakes, and 3) this division allowed for robust sample sizes. Individual snakes were used as the sampling unit for all analyses. For snakes tracked in multiple years, data were combined to create a single time sequence (Harvey and Weatherhead 2006).

The study area was defined by creating a 100% minimum convex polygon (MCP) of all known locations for all snakes over the entire study. The 100% minimum convex polygon defines home range as the smallest convex polygon encompassing all known locations (Hayne 1949). I used the Hawth's Tools extension (Beyer 2004) for ArcGIS (ESRI, Redlands, California) to construct MCPs for each snake. For landscape-scale habitat selection, I compared the proportion of habitats within the 100% MCP home range of each snake (n=29; use) to the proportion of habitats available within the total study area (availability).

Home-range-scale habitat selection was examined by comparing the proportion of habitats at telemetry locations for each snake (use) to the proportion of habitats available within the 100% MCP of each snake (available). I first analyzed home range scale using all data (n=29). I then analyzed winter (15 December - 14 March; n= 16) and non-winter (15 March- 14 December; n=29) habitat selection separately.

To examine shelter selection, underground retreats (n=1089) were classified as Gopher Tortoise burrows (tortoise), stumpholes, rootballs or root channels (stump/root), armadillo burrows (armadillo), small mammal burrows (mammal), logs or downed woody debris (log), or other underground shelters (other). If a snake had not moved locations since the last time it was tracked, I included the same location in analyses multiple times (DeGregorio et al. 2011). To examine the importance of Gopher Tortoise burrows in overwintering by reintroduced snakes, I examined shelter use seasonally as winter (15 December -14 March; n=18), and non-winter (15 March-14 December; n=38) periods. In both analyses, individual snakes comprised the sample unit and values were mean proportions of total use. Availability of underground shelters was estimated by raking transects (n=49) at randomly generated points (n=14) in the study area and recording all shelters found in each category. Transects were 100 meters long by 2 meters wide and extended from the center point out to the intercardinal directions. Whenever possible, I surveyed all four of the intercardinal transects at each point, however, occasionally transects landed in areas I could not survey (i.e. private land, open water). Therefore, at each point I surveyed 2-4 of the intercardinal transects. The points were used as the sampling unit and values are mean proportions. Compositional analysis (Aebischer et al. 1993) was used to compare proportional shelter use in both seasons to the proportion of shelters available at my study site. For seasonal analyses, I assumed that shelters were equally available to snakes in winter and non-winter seasons.

Analyses for Comparison with Previous Study

In addition to compositional analyses of habitat selection, I performed additional analyses in order to compare habitat and shelter use by reintroduced snakes to the results documented for wild snakes studied near the source population. Because data were not appropriate for using the Compositional Analysis method on categories characterized in the previous study, I was unable to compare the results of my compositional analysis to results from the previous study using this method. To compare reintroduced snakes to wild snakes studied near the source population of my snakes at landscape and home range scales, I classified habitats into categories matching those identified by Hyslop, (2007). These habitat categories, adapted from GAP classifications, consisted of roads and urban areas (roads); open water, forested and non-forested wetlands (wetland); agricultural and other fields (field); clearcuts and other sparsely vegetated habitats (cc/sparse); forests with at least 75% deciduous trees (deciduous); forests with at least 75% evergreen trees, including pine plantations (evergreen); and pine-hardwood mixed forest, including shrub/scrub habitats (mixed).

For my comparison, I assigned pre-existing AL-GAP categories occurring on my study site in a manner to most accurately fit these categorical descriptions. My categories were as follows: Developed Open Space, Low Intensity Developed and Medium Intensity Developed (roads); Open Water, East Gulf Coastal Plain Southern Mesic Slope Forest and Southern Coastal Plain Blackwater River Floodplain Forest (wetland); Pasture/ Hay and Row Crop (field); Successional Shrub/ Scrub Clearcut and Successional Shrub/ Scrub Other (cc/ sparse); East Gulf Coastal Plain Interior Upland Longleaf Pine Woodland- Offsite Hardwood Modifier (deciduous); Evergreen Plantations and East Gulf Coastal Plain Interior Upland Longleaf Pine Woodland- Open Understory Modifier (evergreen); and East Gulf Coastal Plain Interior Upland Longleaf Pine Woodland- Loblolly Modifier (mixed). I also provide a comparison of mean proportional availability of these habitat types for each site at landscape scale in order to aid the interpretation of the results of my comparison.

To compare shelter use in reintroduced snakes in this study with shelters used by wild indigo snakes in Georgia (Hyslop et al. 2009), categories were classified following the descriptions of the previous study, excepting windrows, which were not available on my study site. The remaining categories included Gopher Tortoise burrows (tortoise), stumpholes, rootballs or root channels (stump/root), armadillo burrows (armadillo), small mammal burrows (mammal), logs or downed woody debris (log), and other underground shelters (other).

Results

Compositional Habitat Selection Analyses

For my landscape-scale compositional analysis, I delineated my 3,334 hectare study area by creating a 100% minimum convex polygon encompassing all telemetry points (n= 1641) collected for all snakes tracked during my study. Results of my Compositional Analysis at a landscape scale (n=29) indicated overall habitat selection (Wilks lambda 0.649; F= 4.73; p= 0.0092). Fields and roads and mixed pine-hardwood were selected significantly more than wetlands and hardwood at this scale (Table 1).

Home-range scale, when examined non-seasonally using all data (n=29), did not indicate selection at p< 0.05 (Wilks Lambda 0.790; F= 2.30; p= 0.1011), indicating that snakes did not demonstrate strong overall habitat selection at this scale of inquiry, although open canopy longleaf was selected significantly more than mixed pine-hardwood (Table 2).

However, when home-range scale was examined seasonally, selection was indicated for both non-winter and winter seasons. Non-Winter home range scale (n=29) analysis indicated overall selection (Wilks Lambda 0.715; F= 3.46; p= 0.0308). Open canopy longleaf was selected significantly more than fields and roads or mixed pine-hardwood (Table 3).

Winter analysis (n=16) at a home-range scale also indicated overall selection (Wilks Lambda 0.521; F= 3.98; p= 0.0325). Fields and roads were selected significantly more than wetlands and hardwood or mixed pine-hardwood (Table 4).

Shelter use in both winter and non-winter seasons differed significantly from availability. Compositional analysis of non-winter shelter use versus availability indicated overall shelter selection (Wilks Lambda 0.213; F= 24.42; p= < 0.0001; Table 5). Tortoise, stump/root, armadillo and other were selected significantly more than mammal or log. Tortoise was also selected significantly more than other. Compositional analysis of winter shelter use versus availability indicated overall shelter selection (Wilks Lambda 0.053; F= 46.16; p= < 0.0001; Table 6). Tortoise, stump/root, armadillo, and other were selected significantly more than mammal or log. Mammal was selected significantly more than log. Tortoise was selected significantly more than all other shelter types.

Comparison with Previous Study

Differences in proportional use and availability of habitats characterized by Hyslop (2007) at a home-range scale indicated that reintroduced snakes in my study used CC/ Sparse more than available and Mixed less than available ($\bar{x}$, 95% CI; n= 30; Figure 1) At a landscape scale, wetlands were used less than available and CC/ sparse and deciduous were used more than available ($\bar{x}$, 95% CI; n= 30; Figure 1).

Hyslop (2007; Figure 2.4) shows the differences in proportional use and availability of habitats for wild indigo snakes ($\bar{x}$, 95% CI; n=27). Roads, wetlands and evergreen areas were used less than available and CC/ Sparse and mixed were used more than available at a home range scale. At a landscape scale, evergreen was used less than available and CC/Sparse and mixed were used more than available.

The mean availability and uses of habitat types characterized after Hyslop (2007) differed from my study site when examined at a landscape scale (Figure 3.1).

Shelter use was similar between my study and that of Hyslop (2009), and snakes used a high proportion of gopher tortoise burrows, roots and stumps as shelters at both study sites. Hyslop (2009) found a high proportion of gopher tortoise burrows were used in all seasons when compared to other shelter types (Figure 3). At my study site, gopher tortoise burrows were also used throughout the year, but use was highest in winter and stump/root use was highest in non-winter (Figure 4).

Discussion

Habitat loss is known to be one of the greatest threats to imperiled species (Wilcove et al. 1998). In recent years, restoration biology has led to an increased effort to restore degraded habitats, but few studies have examined the response of reptiles to habitat restoration (Steen et al. 2013). Reintroductions of extirpated animals to restored habitats as a conservation measure for imperiled species has become an increasingly common procedure (Fischer and Lindenmayer 2000). Despite an increased recognition of the importance of habitat selection in reintroduction success, this aspect of reintroductions remains understudied, especially in reptiles (Germano and Bishop 2009).

Reintroduced indigo snakes in this study selected habitats at multiple spatial and temporal scales. This result was not surprising since a number of snake species have been documented as exhibiting multi-scale selection (e.g., Moore and Gillingham 2006; Steen et al. 2010; Baxley et al. 2011). However, documenting habitat use in imperiled snakes can lead to important recommendations for promoting enhanced conservation of these declining species (e.g., Webb and Shine 2000). Using multi-scale selection studies is less of an attempt to discover the correct scale of investigation for studying habitat in an animal than it is a tool for understanding how selection changes across scales. Determining what information is retained or lost as scales change should aid in our ability to detect patterns (Levin 1992).

In this study, at a landscape scale, reintroduced indigo snakes positioned their home ranges in areas with more fields, roads; and mixed pine-hardwood habitats; these same home ranges contained less wetlands and hardwood habitats than expected by chance. Fields and roads and mixed pine-hardwood habitats may provide resources for reintroduced indigo snakes that are more limited than the resources found within wetlands and hardwoods and open canopy longleaf habitats on my study site.

My non-seasonal compositional analysis at a home-range scale did not indicate significant overall habitat selection for my model, although open canopy longleaf habitat was selected significantly more than mixed pine hardwood habitat. The lack of strong significance in the overall model at this scale suggests that snakes did not demonstrate strong selection for particular habitat types at this scale, suggesting that with the exception of a preference for open canopy longleaf when compared to mixed pine hardwood, other habitats were used in proportion to their availability, indicating no limiting difference in habitat types at this scale.

At the home range scale, I detected a seasonal pattern of habitat selection in Eastern Indigo Snakes. Open canopy longleaf was selected significantly more than fields and roads or mixed pine hardwood habitats in spring, summer and fall. In winter, field and roads habitats were selected significantly more than wetlands and hardwoods or mixed pine-hardwood habitats. I found that habitat selection varied by season, with the most open habitat type (fields and roads) selected most in winter and least in spring, summer and fall. Thermoregulation may be a particularly important aspect of habitat selection in snakes (Webb and Shine 1998). Because the CNF lies at the northern extent of the geographic range of the indigo snake, it may have had a strong influence on habitat selection in this study.

My examination of shelter use in both non-winter and winter seasons indicated that habitat selection by reintroduced indigo snakes was strongest at this finest scale of examination as the snakes selected shelters. My non-winter shelter analysis indicated that the categories tortoise burrow, stump/root, armadillo, and other were selected significantly more than mammal or log, and tortoise was also selected significantly more than other. My compositional analysis of winter shelter selection found selection at this spatial and temporal scale to be the strongest for all scales examined in this study. Stump/ root; armadillo; and other were chosen significantly more than mammal or log. Mammal was chosen significantly more often than log. Gopher tortoise burrows were chosen significantly more frequently than every other shelter type, indicating that this shelter type may be an especially limiting resource for indigo snakes at my study site in the winter season. Although my results suggest that stumps, roots and armadillo burrows may provide adequate shelters for indigo snakes in the non-winter seasons, it appears that gopher tortoise burrows represent a potentially critical habitat component for indigo snakes surviving the winter in this most northern part of their geographic range.

My rigorous examination of habitat selection at multiple spatial and temporal scales demonstrated a complex pattern of habitat selection by reintroduced indigo snakes on my study site. My findings that the strength of habitat selection varied depending on the scale examined underscores the importance of investigating many scales of space and time to better understand how reintroduced snakes are responding to their new environment. Hierarchical habitat selection theory suggests that factors most limiting to animals will be ordered by selection orders, with the coarsest selection orders indicating the most relevant limitations to animals (Rettie and Messier 2000; Mayor et al. 2009). Selection at multiple scales does not necessarily imply a "top down" hierarchy however, and if finer scale resources such as shelter are not constrained by broader scales such as habitat type, then it is possible that fine scale decisions are influencing broad scale patterns detected in a "bottom up" manner (Mayor et al. 2009).

For snakes selecting habitat at my study site, the order of selection by strength was winter shelter, non-winter shelter, landscape, non-winter home range, winter home range and lastly non-seasonal home range. Although my results initially appeared to support a pattern of hierarchical habitat selection grading from coarse scale to fine scale by reintroduced indigo snakes, I conclude that hierarchical habitat selection was not documented in my study. Selection was strongest at the finest spatial and temporal scales. It is possible that ectothermy impedes free distribution between habitats at coarser scales and thermoregulation may affect the process of habitat selection in reptiles (Rubio and Carrascal 1994). Although I was unable to quantify the availability of shelter types by habitat type during this study, I believe as suggested by Harvey and Weatherhead (2006) that the strength of selection found in my landscape scale compositional analysis is likely to be a result of the shelter types available within these broad scale habitats rather than the occurrence of the habitat types themselves in my study area. Future studies should attempt to resolve this in order to better understand how selection in snakes and reintroduced snakes might differ from the hierarchical pattern documented for other vertebrate species.

My comparison of the results of habitat and shelter use by reintroduced snakes in my study on categories characterized by Hyslop (2007) with the results from the previous study (Hyslop 2007, 2009) indicate that indigo snakes in my study used habitats and shelters in a manner similar to snakes studied previously near the source sites of my snakes. Apparent differences can be attributed to differing availabilities of habitat types at each study site (See Figure 3.1.).

At the landscape scale, snakes in my study used CC/ Sparse and Deciduous more than available and Wetland less than available, whereas, Hyslop's snakes used CC/Sparse and Mixed more than available and Evergreen less than available. CC/Sparse was used more than available at both study sites, indicating that this habitat type may be a limiting resource for indigo snakes in the northern part of their range.

At the home range scale, snakes in my study used CC/ Sparse more and Mixed less than available, whereas, Hyslop's snakes used CC/ Sparse and Mixed more than available and Roads, Wetlands and Evergreen less than available at this scale. The finding that the CC/Sparse category was used more than available at this scale as well as the landscape scale in both studies, again emphasizes the potential for this habitat type to contain a limited resource for snakes in this part of their geographic range.

Hyslop (2007) described the CC/ Sparse habitat category as clearcuts and other habitats with sparse canopy cover, and added in her discussion that the specific areas used by snakes were not clearcuts, but predominantly young longleaf pine plantations with gopher tortoise populations used especially in winter. On my study site, this category contained the AL-GAP categories Successional Shrub/ Scrub-Clearcut and Successional Shrub/ Scrub-Other. For my compositional analyses, these two categories were combined with Developed Open Space and Pasture/ Hay to create a single category, Fields and Roads. It is likely no coincidence that this habitat category, which has the most open canopy of all habitat types in my analyses and has a large number of gopher tortoise burrows within it, ranked highest in my compositional analyses at both landscape and winter home range scales. Both the CC/Sparse categories in my comparison and the Fields and Roads category used for compositional analyses are likely to represent a limiting habitat component tied to thermoregulation constraints. This relationship between open-canopied habitats, gopher tortoise burrow abundance and thermoregulation should be explored further in future studies of indigo snakes in the northern part of their range.

A comparison of shelter use by reintroduced snakes at my study site and snakes studied near the source site also indicated that habitat use by reintroduced snakes at my site was similar to shelters used by snakes in a previous study. Indigo snakes used a high proportion of gopher tortoise burrows, roots and stumps as shelters at both study sites. Hyslop et al. (2009) found a high proportion of gopher tortoise burrows were used in all seasons when compared to other shelter types. At my study site, gopher tortoise burrows were also used throughout the year, but use was highest in winter and stump/root use was highest in non-winter. Stumpholes and rootballs are known to be an important habitat component for many snake species (Means 2006). On CNF snakes were using primarily stumpholes left from fallen longleaf pine trees that had rotted away to heartwood. These holes were likely to be deep because the tap root of the longleaf pine tree can penetrate up to 5 meters deep and its lateral roots can be 22 meters long (Heyward 1933). The practice of pulling stumps for turpentine production and to clear agricultural fields still persists in this area on surrounding private lands and has made these components of the landscape increasingly rare.

Because poor habitat quality at release sites is frequently reported as a reason for failure in reptile and amphibian reintroductions (Germano and Bishop 2009), habitat use that mirrors that of individuals from the source populations can be viewed as a measure of success for reintroductions. Reintroduced indigo snakes in my study used shelters in a manner similar to snakes studied previously near the source sites of my snakes. Conecuh National Forest lies in the northern extent of the geographic range of *Drymarchon couperi*. Previous studies in the northern part of its range have indicated that shelter availability may be a potent environmental constraint for indigo snakes (Hyslop et al. 2009; Speake et al. 1978). My results documented that habitat selection by reintroduced indigo snakes occurred at multiple spatial and temporal scales, but was driven strongest by shelter, especially winter shelter. These results reinforce conclusions from other studies that the distribution of gopher tortoise burrows might be the most limiting factor for survival in this part of the range.

Understanding how spatial and temporal scales affect the strength of habitat selection for a species may allow us to better predict how animals may respond to environmental changes. It is also vital for informing decisions in adaptive management and aiding land managers in future decisions for appropriate reintroduction sites. Based on the results of my study, I recommend that areas chosen for reintroduction sites for indigo snakes in the northern part of their range contain habitats that include open canopies and abundant gopher tortoise burrows. Managers should retain stumpholes across the landscape, especially the deep holes left by longleaf pine. Release sites lacking these habitat characteristics may force reintroduced snakes into roads and open areas like food plots which may increase their vulnerability to traffic fatalities and human persecution. My observations indicate that maintenance of high quality gopher tortoise habitat, including prescribed burning to maintain habitats with open canopies will be critical for reestablishing indigo snake populations in this part of their range.

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Habitat Type	Fields and Roads	Wetlands and Hardwood	Open Canopy Longleaf	Mixed Pine Hardwood	Rank
Fields and Roads	.	+++	+	+	3
Wetlands and Hardwood	---	.	-	---	0
Open Canopy Longleaf	-	+	.	-	1
Mixed Pine Hardwood	-	+++	+	.	2

Table 1. Ranking Matrix from Compositional Analysis Comparing Proportional Landscape Scale Habitat Use Versus Proportion Available to Eastern Indigo Snakes (n=29). Higher rank indicates higher disproportionate use. A single sign indicates the row category was used more (+) or less (-) than the column category, but was not significantly different. A triple sign indicates the row category was used significantly more (+++) or less (---) than the column category with a significant deviation from random at $p < 0.05$.

Habitat Type	Fields and Roads	Wetlands and Hardwood	Open Canopy Longleaf	Mixed Pine Hardwood	Rank
Fields and Roads	.	-	-	-	0
Wetlands and Hardwood	+	.	-	+	2
Open Canopy Longleaf	+	+	.	+++	3
Mixed Pine Hardwood	+	-	---	.	1

Table 2. Ranking Matrix from Compositional Analysis Comparing Proportional Non-Seasonal Home Range Scale Habitat Use Versus Proportion Available to Eastern Indigo Snakes (n=29). Higher rank indicates higher disproportionate use. A single sign indicates the row category was used more (+) or less (-) than the column category, but was not significantly different. A triple sign indicates the row category was used significantly more (+++) or less (---) than the column category with a significant deviation from random at $p < 0.05$.

Habitat Type	Fields and Roads	Wetlands and Hardwood	Open Canopy Longleaf	Mixed Pine Hardwood	Rank
Fields and Roads	.	-	---	-	0
Wetlands and Hardwood	+	.	-	-	1
Open Canopy Longleaf	+++	+	.	+++	3
Mixed Pine Hardwood	+	+	---	.	2

Table 3. Ranking Matrix from Compositional Analysis Comparing Proportional Non-Winter Home Range Scale Habitat Use Versus Proportion Available to Eastern Indigo Snakes (n=29). Higher rank indicates higher disproportionate use. A single sign indicates the row category was used more (+) or less (-) than the column category, but was not significantly different. A triple sign indicates the row category was used significantly more (+++) or less (---) than the column category with a significant deviation from random at $p < 0.05$.

Habitat Type	Fields and Roads	Wetlands and Hardwood	Open Canopy Longleaf	Mixed Pine Hardwood	Rank
Fields and Roads	.	+++	+	+++	3
Wetlands and Hardwood	---	.	-	-	0
Open Canopy Longleaf	-	+	.	+	2
Mixed Pine Hardwood	---	+	-	.	1

Table 4. Ranking Matrix from Compositional Analysis Comparing Proportional Winter Home Range Scale Habitat Use Versus Proportion Available to Eastern Indigo Snakes (n=16). Higher rank indicates higher disproportionate use. A single sign indicates the row category was used more (+) or less (-) than the column category, but was not significantly different. A triple sign indicates the row category was used significantly more (+++) or less (---) than the column category with a significant deviation from random at $p < 0.05$.

Shelter Type	Tortoise	Stump/Root	Armadillo	Mammal	Log	Other	Rank
Tortoise	.	+	+	+++	+++	+++	5
Stump/Root	-	.	+	+++	+++	+	4
Armadillo	-	-	.	+++	+++	+	3
Mammal	---	---	---	.	-	---	0
Log	---	---	---	+	.	---	1
Other	---	-	-	+++	+++	.	2

Table 5. Ranking Matrix Comparing Proportional Non-Winter Shelter Use Versus Proportion Available to Eastern Indigo Snakes (n=38) at Home Range Scale. Higher rank indicates higher disproportionate use. A single sign indicates the row category was used more (+) or less (-) than the column category, but was not significantly different. A triple sign indicates the row category was used significantly more (+++) or less (---) than the column category with a significant deviation from random at $p < 0.05$.

Shelter Type	Tortoise	Stump/Root	Armadillo	Mammal	Log	Other	Rank
Tortoise	.	+++	+++	+++	+++	+++	5
Stump/Root	---	.	+	+++	+++	+	4
Armadillo	---	-	.	+++	+++	-	2
Mammal	---	---	---	.	+++	---	1
Log	---	---	---	---	.	---	0
Other	---	-	+	+++	+++	.	3

Table 6. Ranking Matrix Comparing Proportional Winter Shelter Use Versus Proportion Available to Eastern Indigo Snakes (n=18) at Home Range Scale. Higher rank indicates higher disproportionate use. A single sign indicates the row category was used more (+) or less (-) than the column category, but was not significantly different. A triple sign indicates the row category was used significantly more (+++) or less (---) than the column category with a significant deviation from random at $p < 0.05$.

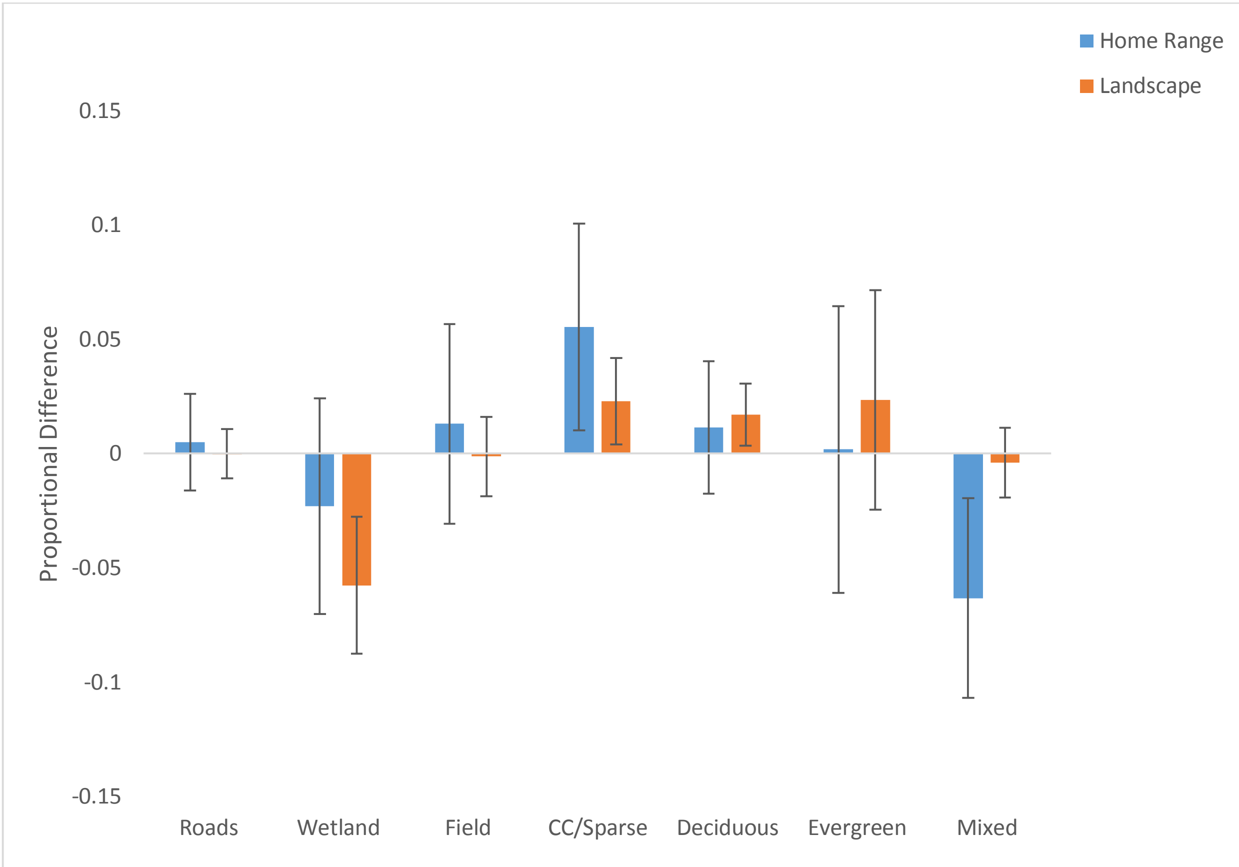

Figure 1. Differences in proportional use and availability of habitats characterized after Hyslop 2007 at home range and landscape scales for reintroduced indigo snakes in Conecuh National Forest, 2010-2012 ($\bar{x}$, 95%CI; n=30).

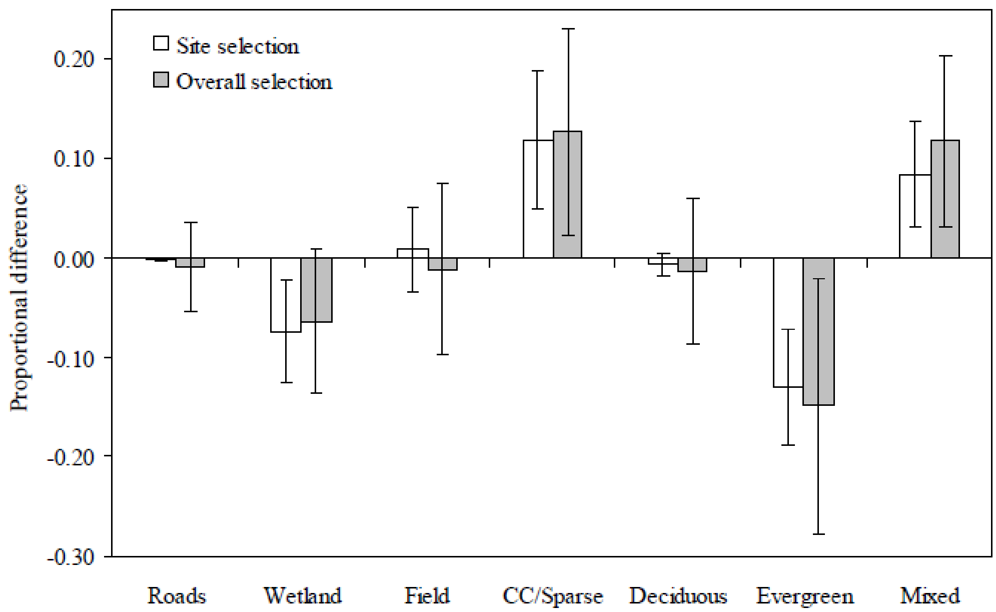

Figure 2.4. Differences in proportional use and availability of habitats ($\bar{x}$, 95% CI; n = 27) for relocated eastern indigo snakes, 2003–2004, Georgia. Site selection compares habitat at radiolocations to MCP home ranges. Overall selection compared habitat at radiolocations to the proportion of habitats available at the study site. Habitat types from GAP classifications included roads and urban areas (roads); open water, forested, and non-forested wetlands (wetlands); agricultural and other fields (field); clearcuts and other sparsely vegetated habitats (cut/sparse); forests with at least 75% deciduous trees (deciduous); forests with at least 75% evergreen trees, including managed pine plantations (evergreen); and pine-hardwood mixed forest, including shrub/scrub habitats (mixed).

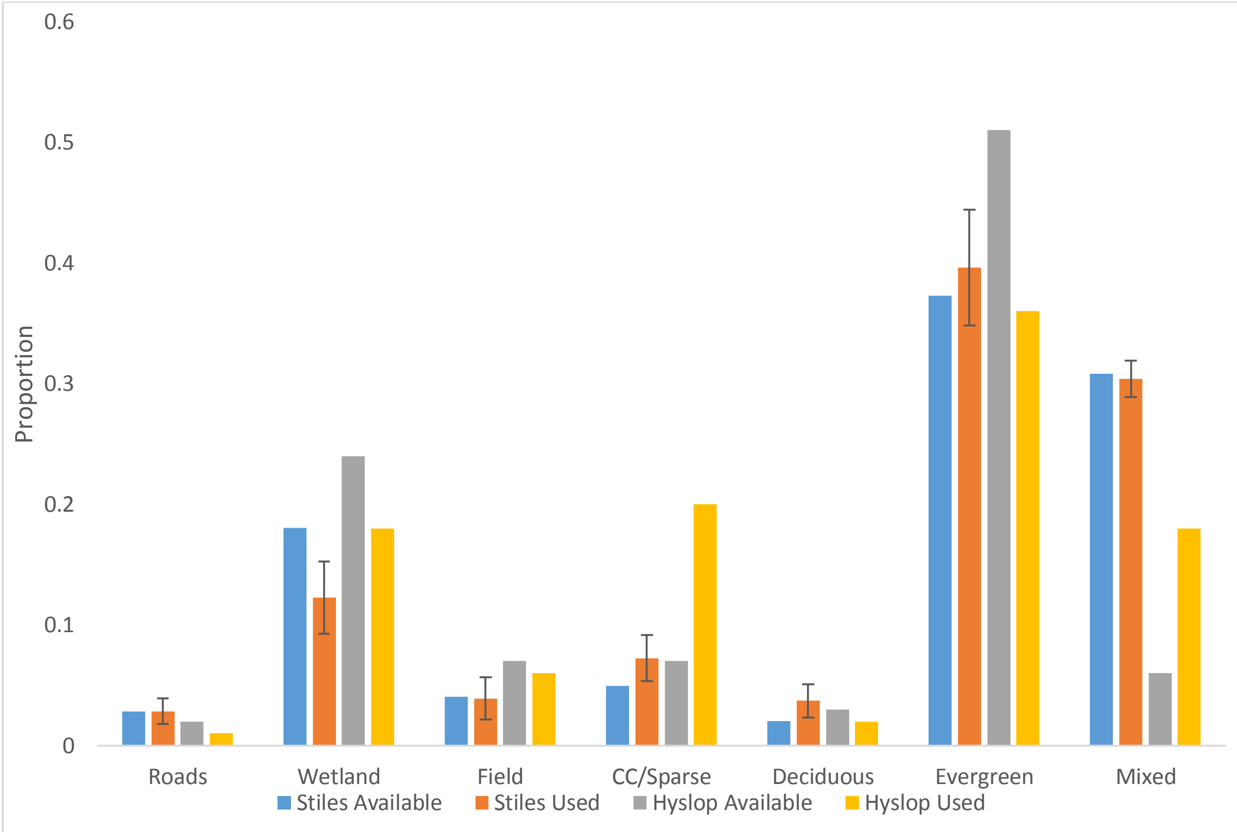

Figure 3.1. Comparison of landscape scale mean availability and use of habitat types for Hyslop 2003-2004 and Stiles 2010-2012.

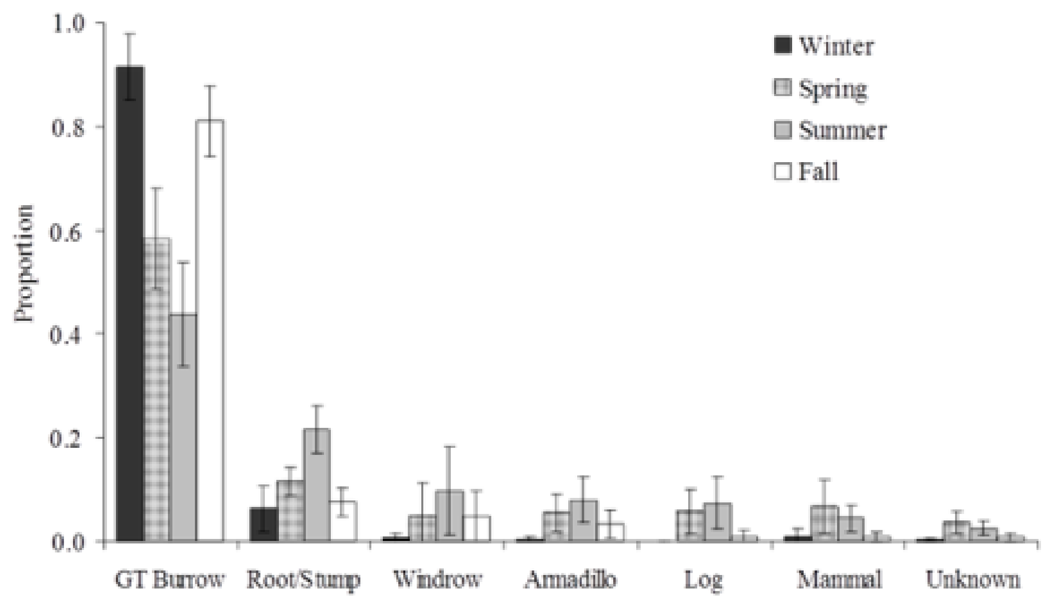

Figure 3. Underground shelter ($\bar{x}$, 95% CI) use by *Drymarchon couperi* radiotracked 2002-2004, Georgia. (Hyslop et al. 2009).

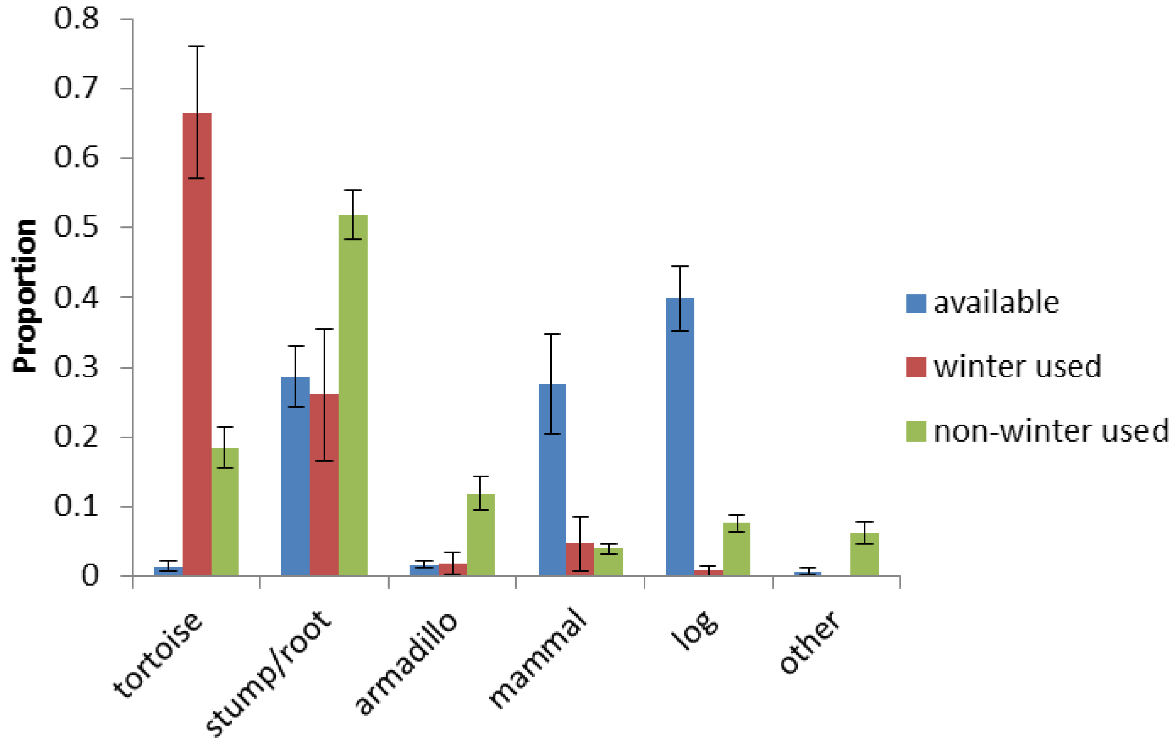

Figure 4. Mean proportion of shelter use and availablity ($\bar{x}$, 95% CI) by *Drymarchon couperi* in winter (n=18) and non-winter seasons (n=38), Conecuh National Forest, AL with individual snakes as the sampling unit.

Chapter 3

Conclusions

1. Habitat selection by reintroduced Eastern Indigo Snakes occurred at multiple spatial and temporal scales and selection varied in strength according to the scale examined. This result underscores the importance of examining habitat selection at many scales.

2. At a landscape scale, indigo snakes selected fields and roads and mixed pine-hardwood habitats significantly more than wetlands and hardwoods. At my study site, fields and roads; and mixed pine-hardwoods are likely to provide resources for indigo snakes that are more limited than resources found in wetland and hardwood habitats.

3. At home range scale, open canopy longleaf habitats were selected more than mixed pine-hardwood habitats; however selection at this scale was strongest when examined seasonally. During winter months, snakes selected fields and roads significantly more than wetlands and hardwood or mixed pine-hardwood habitats.

During the spring, summer, and fall months, snakes selected open canopy longleaf significantly more than fields and roads or mixed pine-hardwood habitats.

4. Among sites used as shelters, gopher tortoise burrows ranked highest, followed by stump/root in all seasons.

5. Reintroduced snakes in this study used habitats and shelters in a manner similar to that of snakes studied previously near the source sites of my snakes.

6. Hierarchical habitat selection was not documented in reintroduced snakes at my study site. Selection was instead strongest at shelter and landscape scales when compared to home range scale.
7. Based on my results, I recommend maintaining high quality gopher tortoise habitat on current and future release sites for snakes. Management for reintroductions that includes prescribed burning to create and maintain open-canopied habitats will be critical for the successful reestablishment of Eastern Indigo Snake populations in the northern part of its range.

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