SNAKE ECOLOGY IN THE RED HILLS OF GEORGIA AND FLORIDA

by

Seth Patrick Stapleton

(Under the Direction of John P. Carroll)

ABSTRACT

Land management practices are implemented in the Southeast to maintain upland habitats but potential implications are not wholly understood. Snakes represent an ecosystem component in need of greater research. I used radio telemetry and systematic trapping on 3 sites to address objectives of community ecology and to describe resource partitioning and survival of sympatric rat snakes. I documented 1956 captures representing 16 species during 2002 – 2003 trapping. Commonly captured species demonstrated variability in activities by season and habitat. Using radio telemetry, seasonal partitioning of movements was not evident among rat snakes, but species did exhibit habitat partitioning: corn snakes focused activities around upland ground structures, and arboreal eastern rat snakes frequented hardwood trees and bottomlands. Survival estimates were comparable to figures reported elsewhere and suggest an acclimation period. Current management strategies such as prescribed fire are essential in maintenance of upland forests and are thus important for upland snake communities.

INDEX WORDS: Eastern rat snake, Corn snake, *Pantherophis*, Snake communities, Resource partitioning, Habitat use, Movements, Radio telemetry, Trapping, Upland pine forests

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Introduction

Upland forests dominated by longleaf pine (*Pinus palustris*) have dwindled across the southeastern United States. (Frost 1993, Ware et al. 1993). Concurrently, wildlife species dependent on these landscapes, such as the Northern bobwhite (*Colinus virginianus*; hereafter bobwhite) and red-cockaded woodpecker (*Picoides borealis*), have diminished. The bobwhite in particular has contributed to a rich cultural tradition and makes a significant economic impact in the southeastern United States (Burger et al. 1999). In some areas of the Southeast (e.g., the Red Hills of southern Georgia and northern Florida), intensive land management focused on the maintenance of open upland habitats has thus become widespread under the premise that targeted species will benefit. However, a full understanding of the faunal communities within these habitats and of the potential implications of such management is absent.

Snakes are integral members of southeastern ecosystems and are undoubtedly impacted by intensive management. Although it is generally accepted that snake and herpetofaunal populations are declining on a global scale (Dodd 1987, Gibbons et al. 2000), little data exists that assesses the current status of snake communities and population trends (Parker and Plummer 1987, Vitt 1987). Basic ecological information is sparse for some common and ecologically important snakes (Parker and Plummer 1987, Dodd 1987, Dodd 1993, Dodd 1995).

In addition to their own conservation status, snakes are of particular because of their role in the trophic hierarchy. They serve as prey to raptors and meso-mammalian predators, and some species are in turn substantial predators of bobwhite and songbird nests as well as a host of small mammals and other species (Hamilton and Pollack 1956, Fitch 1963, Jackson 1970, Brown 1979, Fendley 1980, Mirarchi and Hitchcock 1982, Hensley and Smith 1986, Phillips and Gault 1997, Staller 2001, Ernst and Ernst 2003, Thompson and Burhans 2003, Thornton 2003, Staller et al. 2005). Given the potential effects of management for bobwhites, both habitat management and manipulation of the mammalian predator community, and the declining population trends of several species within the trophic hierarchy, further assessment of regional snake community ecology is necessary. This research will direct future studies and help to establish better management practices.

Literature Review

Decline of Upland Habitats

Historically, much of the southeastern U.S. was dominated by upland pine savannahs and forests including longleaf pine. Longleaf forests once covered more than 35 million ha (Frost 1993), extending from Texas to Florida and northward to Virginia (Landers et al. 1995). Frequent fires in these stands maintain a predominantly open, early successional groundcover structure (Noss 1989). However, the ecosystem declined dramatically as a result of fire suppression, unsustainable timber harvest, and conversion of land for development, agriculture, and other uses (Frost 1993, Ware et al. 1993). Loblolly (*P. taeda*) pine forests are superficially similar in structure and have replaced longleaf savannas in portions of the Southeast (Ware et al. 1993), but continued shifts in land use threaten these upland forests as well. Furthermore, intensive agriculture and clean farming practices have replaced traditional farming techniques, thereby causing deterioration of comparable early successional farmland habitats.

This trend has predictably resulted in population declines for a host of floral and faunal species and thus propelled upland ecosystems and associated vegetation to the forefront of conservation issues in the Southeast. Songbirds that require grassland habitats have experienced population declines over the past 3 decades across North America (Sauer et al. 1997). Numerous additional species associated with upland pine forests, including herpetofauna such as the eastern indigo snake (*Drymarchon corais couperi*), flatwoods salamander (*Ambystoma cingulatum*), and gopher tortoise (*Polyphemus gopherus*), are declining and have been granted conservation protection (Guyer and Bailey 1993, Dodd 1995, USFWS 2004).

Recent trends illustrate that the bobwhite, another species associated with these habitats, has declined dramatically over the past several decades as well (Brennan 1991, Church et al. 1993). The bobwhite is an economically and culturally important species, generating an estimated $193 million economic impact for the Southeast in 1991 (Burger et al. 1999). Management practices targeting bobwhite, grassland songbirds, and other species as beneficiaries have thus become widespread across the Southeast to combat declining population trends. These practices primarily address the maintenance of open upland habitats, utilizing annual prescribed burns, hardwood logging, and extensive mechanical practices to inhibit hardwood encroachment in upland pine forests. Additional strategies including supplemental feeding and meso-mammalian [e.g., raccoon (*Procyon lotor*), bobcat (*Lynx rufus*), red fox (*Vulpes vulpes*), gray fox *(Urocyon cinereoargenteus*), armadillo (*Dasypus novemcinctus*) and opossum (*Didelphis virginianus*)] predator removal programs attempt to further enhance the recovery of the targeted species. However, the broader ecological implications of these practices remain largely unknown.

Southeastern U.S. Snake Communities

Snakes are one taxon impacted by the decline of upland pine forests and the subsequent management actions. Snakes and other herpetofauna fulfill integral ecological roles in the trophic hierarchy, functioning as both predator and prey to a host of species. However, snake populations around the world appear to be diminishing as a result of numerous factors, including habitat loss, malicious killing, over-harvest, disease, pollution, and invasive species (Dodd 1987, Gibbons et al. 2000). Dodd (1987) notes 186 snake species from across the globe that may be declining.

Despite the ecological significance of snakes and the perceived decreasing population trends, there are significant gaps in our knowledge of general snake ecology. In fact, some of the conservation concern surrounding snakes is presumptuous, as the limited and unreliable literature base makes accurate assessments of population status difficult (Dodd 1987, Dodd 1993, Dodd 1995). Numerous species remain completely unstudied and much of the current literature is tainted by anecdotal evidence or research based on biased techniques and interpretations (Parker and Plummer 1987, Dodd 1987, Dodd 1993). Long-term and even baseline studies assessing demographics and dynamics are largely non-existent due to obstacles encountered when studying snakes (Parker and Plummer 1987, Vitt 1987, Gibbons et al. 2000). The cryptic nature, low detectability rates and perceived low densities, and irregular foraging and activity patterns contribute to such difficulties and the resulting scarcity of data (Parker and Plummer 1987, Vitt 1987, Gibbons et al. 2000).

The South is home to the highest concentration of at-risk snake species in the U.S., with 18 species identified for conservation concern by Dodd (1987). Numerous species associated with longleaf pine forests are granted protection or in need of conservation attention (Guyer and

Bailey 1993, Dodd 1995, Tuberville et al. 2000). Federal, state, and natural heritage programs list over 30% of the snakes of 5 southern Appalachian states as being of conservation concern (Mitchell et al. 1999). In the region, studies have addressed ecological issues such as spatial ecology and activity patterns for some populations of species, including black racers (*Coluber constrictor*) (Plummer and Congdon 1994), eastern hognose (*Heterodon platirhinos*) (Plummer and Mills 2000), gray rat snakes (*Elaphe obsoleta spiloides*) (Mullin et al. 2000, Burger et al. unpubl. data), corn snakes (*E. g. guttata*) (Franz 1995), eastern diamondback rattlesnakes (*Crotalus adamanteus*) (Martin and Means 2000), cottonmouths (*Agkistrodon piscivorus*) (Cross and Petersen 2001), and copperheads (*A. contortrix*) (Cross and Petersen 2001). However, these studies are not comprehensive in either their geographic or ecological scope. Population dynamics remain almost completely unexamined, and spatial ecology requires greater attention to address conservation objectives. There remains a deficit of basic ecological data on most populations in the region.

Not surprisingly, comprehensive snake community research has been sparse relative to taxa such as birds and mammals (Vitt 1987). Despite recent research addressing snake community assemblages (e.g., Akani et al. 1999, Sullivan 2000, Kjoss and Litvaitis 2001, Luiselli and Akani 2002), literature detailing the snake communities in the southeastern U.S. remains limited (e.g., Dodd and Franz 1995, Enge and Wood 2002). Furthermore, much of the existing regional literature focuses upon the broader herpetofaunal community and does not extensively document snake communities (e.g., Greenberg et al. 1994, McLeod and Gates 1998, Moseley et al. 2003). Additionally, further recognition and quantification of potential variations in detectability are necessary to obtain more accurate community assessments. Studies of sympatric species are reported elsewhere (e.g., Reinert 1984*a*, Reinert 1984*b*, Diller and Wallace 1996, Keller and Heske 2000, Cross and Petersen 2001, Laurent and Kingsbury 2003), but the Southeast is in need of continued research at this level as well.

The lack of data demonstrates that baseline studies are needed at multiple organizational levels. Objective, comprehensive studies must focus on research deficits such as basic ecology (Dodd 1987, Dodd 1993) and population monitoring (Dodd 1987, Parker and Plummer 1987, Dodd 1993, Dodd 1995, Gibbons et al 2000). Research addressing these shortcomings for both individual species and overall community structure is critical to build a foundation from which we may assess trends and revise management and conservation efforts.

Snakes in Managed Forests

As previously noted, intensive land management in portions of the Southeast emphasizes the use of prescribed fire, hardwood removal, and mechanical treatments to prevent hardwood establishment in open upland pine forests. Prescribed fire is necessary to maintain fire-adapted herpetofaunal communities in the Southeast (Means and Campbell 1981, Guyer and Bailey 1993). Frequent (1 to 3 year) fire intervals are necessary to maintain diverse amphibian assemblages (Means et al. 2004). Research suggests that reptile diversity increases with prescribed fire in pine sandhills (Mushinsky 1985) and bottomland hardwoods (Moseley et al. 2003). An adverse response to recently burned lands may appear in some snake species (Cavitt 2000, Setser and Cavitt 2003), but recolonization of the burned tract can occur quickly (Setser and Cavitt 2003). Furthermore, direct mortality of snakes from fire is minimal and is largely outweighed by the beneficial effects on herpetofauna (Means and Campbell 1981).

Forest management techniques, such as clearcuts, may result in initial negative effects on snakes but with subsequent rebounds (Russell et al. 2002). The effects of clearcuts on reptile communities may also mimic intense wildfire and subsequent salvage logging in scrub habitats

(Greenberg et al. 1994). Responses to fire and timber management will, of course, vary depending on species requirements (Greenberg et al. 1994, McLeod and Gates 1998).

A mosaic of burned and unburned parcels is optimal for providing refuge for fire-adapted snakes (Setser and Cavitt 2003). Such disturbance-maintained patchwork habitats may result in increased herpetofaunal diversity (McLeod and Gates 1998). The land management regime in the Red Hills region may thus be conducive to a diverse and abundant snake community, although not necessarily a benefit to all species. Research must continue to establish components of general ecology such as distribution, habitat requirements, and demography in fire-dependent systems (Russell et al. 1999).

Rat Snakes as Avian Predators

Central to classical ecology are questions surrounding faunal communities and the associated natural population controls. Predation is recognized as one of these natural population controls (Colinvaux 1986). Interactions between predator and prey are thus instrumental to understanding community ecology and population controls. Stoddard (1931) suggested that a limiting factor of the bobwhite and other birds might be nest predation. Hence, investigations of species predating these and other at-risk species are of particular interest to managers and conservationists in the region.

Rat snakes are non-venomous secondary predators in southeastern U.S. communities. They function as prey to apex carnivores such as raptors and meso-mammalian predators and compete with these same carnivores for trophically lower prey items. Rat snakes are efficient predators of birds, bird nestlings, and eggs, as well as various small mammals (Hamilton and Pollack 1956, Fitch 1963, Jackson 1970, Brown 1979, Fendley 1980, Mirarchi and Hitchcock 1982, Hensley and Smith 1986, Phillips and Gault 1997, Staller 2001, Thompson and Burnhans

2003, Thornton 2003, Staller et al. 2005,). The exceptional climbing ability of the genus, particularly the gray rat snake (Jackson 1976), makes arboreal nesters very susceptible to rat snake predation. Rat snakes also are a major component of the predator community of the ground-nesting bobwhite (Staller 2001, Thornton 2003, Staller et al. 2005) and songbirds (Thompson and Burhans 2003). Data examining the regional species of rat snakes is thus of particular interest to southeastern conservationists to assess management alternatives to minimize nest depredations.

Rat Snake Ecology

Habitat use, population demographics, and activity patterns of the black rat snake (*E. o. obsoleta*) are fairly well documented throughout the northern and western extent of its range. Density and population estimates vary across the range of the snake (Fitch 1963, Stickel et al. 1980, Weatherhead et al. 2002). Populations in both Maryland and Ontario consistently use the forest-field edge interface and thrive in small-scale mosaic habitats (Weatherhead and Charland 1985, Durner and Gates 1993, Blouin-Demers and Weatherhead 2001). Habitat interfaces may provide productive hunting grounds and abundant refuge sites (Weatherhead and Charland 1985, Durner and Gates 1993, Blouin-Demers and Weatherhead 2001), but in Ontario, such edge habitats are primarily used for thermoregulatory purposes (Blouin-Demers and Weatherhead 2001). Activity of black rat snakes in Maryland (Stickel et al. 1980) and Kansas (Fitch 1963) peaks during the late spring breeding season and again heightens in autumn as snakes return to denning sites. Canadian populations exhibit a shorter overall active season (Blouin-Demers et al. 2002) and a movement peak later in the summer (Weatherhead and Hoysak 1989). Additionally, at central latitudes of the range, males tend to move more frequently and farther in the early season than females (Durner and Gates 1993), whereas sexual differences are most pronounced in mid-season in the northern range (Weatherhead and Hoysak 1989).

Despite the large amount of habitat use and activity data provided for the black rat snake, there is a deficiency of parallel knowledge about other members of the genus found in the Southeast, such as the gray rat snake. The foraging ecology of the gray rat snake has been examined only in a controlled environment in relation to habitat structural complexity and varying prey types (Mullin et al. 1998, Mullin and Gutzke 1999, Mullin and Cooper 2000). Gray rat snake home range size is reported as 5.5 ha in the western portion of its distribution (Mullin et al. 2000). However, this study had a small sample size of only 8 individuals. Gray rat snakes in east-central Mississippi maintain smaller home ranges (approximately 0.9 ha) and primarily used drains and mixed pine-hardwood stands (Burger et al. unpubl. data). This research, however, examined snakes exclusively in habitat managed for the red-cockaded woodpecker and focused capture efforts on those individuals climbing RCW cavity trees or potential cavity trees.

The closely related corn snake also has garnered much less attention than the black rat snake. Corn snakes in the sandhills of northern Florida exhibited highly terrestrial activity patterns, using various forested and open habitats and maintaining large, highly variable home ranges (Franz 1995). However, only 4 snakes were radio-tagged by Franz (1995), lending some doubt to the reliability of the data. Subspecies and their respective distributions have been described in the south-central United States (Smith et al. 1994, Vaughan et al. 1996). An extensive study examining the spatial ecology and habitat use of the corn snake is markedly absent.

Rat Snake Taxonomy

Several recent changes have affected the taxonomy of the rat snake complex (Crother et al. 2003). Color variation has traditionally been used to distinguish between the 7 to 8 recognized subspecies of the North American rat snake. Mitochondrial DNA does not support this classification, however, and instead points to 3 evolutionarily and genetically distinct clades for the rat snakes (Burbrink et al. 2000). Morphological characteristics further support the recognition of 3 species and, with the inclusion of *E. bairdi* in central Texas, an additional species (Burbrink 2001). The changes classify the rat snake in the area of interest as part of the eastern clade (*E. alleghaniensis*), although the division between the eastern and central (*E. spiloides*) clades, the Appalachicola River, lies in close proximity to the study region.

Corn snake taxonomy also has been modified recently (Crother et al. 2003) to reflect recommendations presented in Burbrink (2002). Molecular evidence suggests the recognition of 3 distinct species of corn snake [red (*E. guttata*), Slowinski's (*E. slowinskii*), and Great Plains (*E. emoryii*)] rather than the traditional 5 to 6 recognized subspecies (Burbrink 2002). These modifications classify the corn snake in the study area as the red corn snake.

Finally, using molecular evidence, Utiger et al. (2002) identified enough phylogenetic differences between Old World and New World rat snakes to propose recognition of different genera. This shift identifies the New World rat snakes as *Pantherophis* while the Old World rat snakes remain *Elaphe*. Despite the confusion and recent alterations surrounding their taxonomic classification, regional studies of the rat snake clearly remain lacking. The remaining chapters of this volume recognize the new taxonomy of rat snakes.

Objectives

The paucity of information addressing snake spatial and community ecology in the Southeast, coupled with the widespread implementation of habitat and predator management practices and the relative unknowns surrounding potential implications of such management demonstrate significant gaps in our knowledge. Furthermore, realized and perceived population trends demonstrate that numerous upland species including snakes and the species upon which they prey may be at risk. My objectives with this study are:

1. To document habitat use, movements, home range size, and resource partitioning of eastern rat and corn snakes in intensively managed upland pine forests in the Southeast.
2. To assess components of snake community ecology, including community structure and interspecific variation in activity patterns by season and macrohabitat type, in intensively managed upland pine forests in the Southeast.
3. To estimate survival of eastern rat and corn snakes in managed upland pine forests in the Southeast.
4. Based on information from objectives 1-3, develop management and research recommendations to address the upland pine forest ecosystem concerns, including the conservation of snake communities and the reduction of nest depredations of bobwhite and grassland songbird species.

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CHAPTER 2

SPATIAL ECOLOGY AND HABITAT USE OF EASTERN RAT SNAKES AND CORN SNAKES IN MANAGED UPLAND PINE FORESTS OF THE SOUTHEASTERN U.S.A.[1]

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[1] Stapleton, S.P., J.P. Carroll, and W.E. Palmer. To be submitted to *Journal of Herpetology*.

Abstract

Habitat management in pine (*Pinus* spp.) forest ecosystems has been implemented across portions of the Southeast to combat declining populations of several upland species, but there remains a dearth of information addressing general snake ecology. During 2002 to 2004, I used radio-telemetry to assess home range size, movements, and habitat use of 2 sympatric rat snake species at 2 sites in southern Georgia and northern Florida. A total of 45 individuals (14 corn snakes, 31 eastern rat snakes) were considered in the analyses. Minimum convex polygon home range estimates (eastern rat: 7.3 ha, 0.9 SE; corn: 10.7 ha, 2.8 ha) were similar to estimates from other areas. Female home ranges were smaller than male home ranges for both MCP and kernel home range estimates. Movements by both species were infrequent and sporadic. I did not find strong evidence of seasonal partitioning of movements between species or sexes. However, corn snakes tended to move more frequently than eastern rat snakes, whereas eastern rat snakes traveled greater distances during movements. Although these differences may be an artifact of tracking constraints, results suggest interspecific differences in movement strategies. Interspecific habitat partitioning was evident at multiple spatial scales. Corn snakes focused activities around fields, uplands, and ground structure features, whereas eastern rat snake sites were more commonly associated with bottomland drains, edges, and hardwood trees. Results of habitat use analyses suggest that removal of hardwoods may be a management option to limit interactions between eastern rat snakes and economically important Northern bobwhite. Manipulative approaches and food studies are necessary to examine the efficacy of this strategy. My results are consistent with predictions of competitive exclusion, but factors other than competition likely influence observed habitat partitioning.

Introduction

Numerous species associated with pine savannahs and open grassland habitats in the eastern U.S., including songbirds (Sauer et al. 1997) and Northern bobwhite (*Colinus virginianus*; hereafter bobwhite; Brennan 1991, Church et al. 1993), have exhibited population declines in recent decades. Additionally, populations of various upland herpetofauna are diminishing and accordingly granted protection or warrant further conservation attention [e.g., eastern indigo snake (*Drymarchon corais couperi*), eastern diamondback rattlesnake (*Crotalus adamanteus*), Florida pine snake (*Pituophis melanoleucus mugitus*), flatwoods salamander (*Ambystoma cingulatum*), and gopher tortoise (*Polyphemus gopherus*)] (Guyer and Bailey 1993, Dodd 1995). Loss and modification of upland habitats including longleaf pine (*Pinus palustris*) forests (Frost 1993, Ware et al. 1993) is viewed as a major contributor to herpetofaunal declines (Guyer and Bailey 1993, Dodd 1995). In an effort to curb these trends, in particular bobwhite declines, land managers have instituted intensive land management regimes across portions of the Southeast. Techniques aim to reclaim and maintain open savannah-like habitats and minimize hardwood encroachment into upland pine forests through extensive mechanical treatment and restoration of historical burn regimes with prescribed fire. Despite widespread implementation of such strategies, however, various components of the ecology of upland wildlife communities remain unknown and potential ecological implications of intensive management remain unidentified.

Regional species of rat snakes [the corn snake (*Pantherophis guttatus*) and the eastern rat snake (*P. alleghaniensis*)] are common throughout much of the Southeast and are undoubtedly impacted by land management practices. Despite their abundance, however, these species are a component of the Southeast's upland ecosystems that remains largely unstudied. Regional studies of habitat use and activity patterns are restricted to Maryland (Stickel et al. 1980, Durner and Gates 1993) and minor studies in central Florida (Franz 1995) and Tennessee (Mullin et al. 2000). However, the closely related gray rat snake (i.e., central clade) (*P. obsoletus*) is well-documented throughout the northern extent of the range (Weatherhead and Charland 1985, Weatherhead and Hoysak 1989, McAllister 1995, Blouin-Demers and Weatherhead 2001). Previous works provide a framework for development of hypotheses pertaining to southeastern rat snakes. Research details the affinity of eastern and gray rat snakes for edge habitats, describing optimal landscapes as small-scale mosaics of structurally variable habitats (Weatherhead and Charland 1985, Durner and Gates 1993, Blouin-Demers and Weatherhead 2001). Additionally, active seasons and movement peaks of the eastern and gray rat snakes vary somewhat with latitude (Stickel et al. 1980, Weatherhead and Hoysak 1989, Durner and Gates 1993, Blouin-Demers et al. 2002) and by sex (Weatherhead and Hoysak 1989, Durner and Gates 1993).

Rat snakes present a particularly compelling case study on multiple levels. First, rat snakes afford the opportunity to document the ecology of sympatric species of snakes, a topic which Vitt (1987) notes as deficient in the snake literature (exceptions include Reinert 1984, Diller and Wallace 1996, Keller and Heske 2000, Laurent and Kingsbury 2003). The principle of competitive exclusion proposes that for multiple species to coexist in a stable environment, species must maintain some degree of resource separation or niche differentiation (Gause 1934, Hardin 1960). This partitioning can occur via several dimensions including macro- and microhabitat utilization, food sources, time of daily or seasonal activity, and temperature (Schoener 1974).

Habitat separation is considered the most frequent mechanism enabling coexistence of faunal species (Schoener 1974). Conversely, Vitt (1987) and Toft (1985) suggests that food is the primary dimension of partitioning in snakes, thereby structuring snake communities. A review of documented food items of these *Pantherophis* species, however, reveals that the species are largely generalists and appear to exhibit substantial overlap along the food partitioning axis (e.g., Hamilton and Pollack 1956, Fitch 1963, Jackson 1970, Brown 1979, Fendley 1980, Mirarchi and Hitchcock 1982, Hensley and Smith 1986, Phillips and Gault 1997, Staller 2001, Ernst and Ernst 2003, Thompson and Burnhans 2003, Thornton 2003, Staller et al. 2005). According to competitive exclusion, rat snakes may partition other resource dimensions to obtain adequate niche differentiation to permit coexistence. Rat snakes therefore provide the opportunity to test predictions of competitive exclusion by examining partitioning along habitat and activity axes.

Furthermore, rat snakes have attracted particular attention from wildlife managers and conservationists in recent years because of their role in the trophic hierarchy. These species may function as prey to raptors and mammals (Fitch 1963, Ernst and Ernst 2003) and, in turn, have been documented as significant nest predators of economically and culturally significant bobwhite (Staller 2001, Thornton 2003, Staller et al. 2005) as well as songbirds (Thompson and Burhans 2003). Nest predation may be a limiting factor for bobwhite and other birds (Stoddard 1931). Declining population trends of bobwhite (Brennan 1991, Church et al. 1993), grassland songbirds (Sauer et al. 1997), and other prey species as well as the implementation of meso-mammalian predator removal in some areas further underscore the need to understand the ecology of these rat snake species.

My objectives are:

1. To document habitat use, resource partitioning, and home range size of eastern rat snakes and corn snakes in intensively managed upland pine forests.

2. To document seasonal movements of eastern rat snakes and corn snakes in intensively managed upland pine forests.

Study Areas

Research was conducted in the Red Hills region of northern Florida and southern Georgia between Tallahassee, Florida, and Thomasville, Georgia. Plantations in the region are intensively managed for bobwhite, using annual prescribed burning and extensive mechanical techniques to maintain open savannah-like habitat in upland pine forests and to inhibit upland encroachment of hardwood trees. Practices such as supplemental feeding and meso-mammalian predator control often are implemented as well. Two individual areas functioned as the study sites: Tall Timbers Research Station (TTRS) and Pebble Hill Plantation (PH).

TTRS is located in Leon County, Florida and covers approximately 1,500 ha. TTRS is dominated by upland longleaf, shortleaf (*P. echinata*), and loblolly pine (*P. taeda*) forests. Bottomland hardwood drains and annually harrowed fields are interspersed across the landscape. Common drain species include oaks (*Quercus* spp.), hickories (*Carya* spp.), sweet gum (*Liquidambar styraciflua*), and black gum (*Nyssa sylvatica*). Mature hardwoods also dot portions of the upland landscape. Old-field vegetation is the predominant groundcover vegetation type (eg., *Andropogon*, *Lespedeza*, and *Quercus* spp.). Soils at TTRS are primarily clay.

PH includes approximately 1,250 ha in Thomas and Grady counties, Georgia. The landscape primarily consists of upland longleaf, loblolly, and shortleaf pine forests. PH also contains numerous bottomland hardwood forest drains and annually harrowed fields as well as large stands of planted loblolly pines. Drain hardwood species composition and presence of upland hardwoods are similar to TTRS. Vegetation at PH includes a continuum spanning old-field vegetation to intact native groundcover. Soils range from clay to sand.

Methods

Trapping

Snakes were captured with drift fence arrays constructed of silt erosion control fencing. Four 7.5-m fence arms radiated from a central point in each array. A single-ended, hardware cloth funnel trap (Fitch 1987) was set at the end of each fence arm, and a large box trap constructed of plywood and hardware cloth (D. Richardson, pers. comm.) was placed in the center of each array. In 2002, I randomly placed 4 arrays in each of 3 habitat types (bottomland hardwood drains, upland pine forests, and an intermediate "buffer" zone) at TTRS and PH using ArcView version 3.2 (ESRI, Redlands, CA) to obtain a random and representative sample. In 2003, fences were again randomly set in these habitats and moved at least 400 m from 2002 fence locations to maximize sample independence. I additionally set fences in regularly harrowed fields and in a 2x3 grid as part of a pilot study in 2003. Traps were set for approximately 2 to 3 weeks per month from March through October. I collected additional individuals via opportunistic encounters in the field.

All captured rat snakes were measured [snout-vent length (SVL) to cm, mass to gram] and sexed by probing for inverted hemipenes. Individuals were marked via subcutaneous implantation of a passive integrated transponder (PIT) tag (InfoPET Identification Systems, Inc., Burnsville, MN) using procedures modified from Reading and Davies (1996). Tags were injected ventrally approximately 5 to 10 cm anterior to the vent.

Telemetry

Snakes were selected for radio-tagging on the basis of location, sex, and size (typically >300 g) in an effort to obtain equal representation of the study sites and sexes while using only those individuals large enough to permit tagging. During 2002, radio transmitters were implanted subcutaneously following procedures outlined in Weatherhead and Anderka (1984) after anaesthetization with meoxyflurane (Aird 1986). Transmitters (American Wildlife Enterprises, Monticello, FL) were equipped with whip antennas and weighed 5 to 10 g (less than 3.5% of body mass). Necrosis, general non-healing, and subsequent radio expulsion were frequently noted in individuals implanted with this technique. Because of these initial complications, methodologies were altered in July 2002 to follow procedures modified from Hardy and Greene (1999) and Reinert and Cundall (1982). Isoflurane and clear plastic tubing were used to anaesthetize subjects such that individuals were restrained with and isoflurane administered via the tubing (Hardy and Greene 1999). Coiled antenna radios (Model R1170, Advanced Telemetry Systems, Inc., Isanti, MN) were implanted into the intraperitoneal cavity. Radios weighed 4 g (<1.5% of individual body mass) with an anticipated life of at least 195 days. Individuals were provided with heat sources following surgery and held for 48 to 72 hours prior to release to facilitate healing.

Radio-tagging began in March and continued through August 2002 - 2003. In 2002, individuals were located 4 to 5 times per week in the summer (May through August), 2 to 3 times weekly during the spring (March to April) and fall (September to October), and less frequently during the winter months. Summer telemetry locations were conducted within 1 of 4 time blocks to ensure that individuals were not located at the same time every day. Preliminary results demonstrated that movements were sporadic and infrequent. Thus, in 2003, tracking was reduced in tracking to approximately 3 times per week during the summer months and followed tracking patterns similar to 2002 during the remainder of the season. Tracking continued through April, 2004.

Snakes were located using homing techniques and close range triangulation (<2m) to minimize disturbance. The subject's activity, height, visibility, movement from a previous location, and use of structural features and macrohabitat type were recorded. Locations were flagged and mapped using handheld GPS units (Pro XR series and GeoExplorer series, Trimble Navigation Limited, Sunnyvale, CA) and differentially corrected. Although most GPS positions were recorded with sub-meter accuracy units, some (<25%) were recorded with less accurate units (2-5 m) due to logistical constraints (i.e., limited units). For locations less than 15 m from a previous position, an azimuth and measurement were taken to obtain the relevant coordinates. Locations were plotted onto existing landcover maps in ArcView. Collection, marking, and radio-tagging procedures were covered under: University of Georgia IACUC permit no. A2001-10100-c1,c2; Georgia collection permit nos. 29-WMB-01-80 (2002) and 29-WMB-04-128 (2003), and Florida collection permit nos. WX01277 (2001-2002) and WX02136 (2002-2003).

Analyses

For analyses, I used an information theoretic approach, Akaike's Information Criteria (AIC), as a means of model selection. AIC permits testing of multiple candidate models and ranks models based on maximum likelihood and model parsimony (Anderson et al. 2000). Results are provided with values of AICc (correction for small sample sizes), AICc weights (ω), and model likelihoods. I additionally calculated model-averaged estimates ($\hat{\bar{\beta}}$) of model parameters when appropriate using the respective AICc weights. Model-averaged estimates were only calculated for those parameters included in the 90% confidence set of models (i.e., those models within 10% of the weight of the top models); other parameters were likely not important in explanation of the response variable. For the most highly weighted model in each analysis, I additionally calculated r-square as suggested by Nagelkerke (1991). This r-square value is a maximum likelihood approach and is not adjusted for number of parameters in the model. All modeling was conducted using SAS version 8 (SAS Institute Inc., Cary, NC).

Home Ranges

Minimum convex polygons (MCPs) are 1 of the most commonly applied methods of home range estimation in snakes (Gregory et al. 1987). Home ranges constructed with this method, however, may include large areas which are not used by an individual and do not indicate how the area is actually used (i.e., MCPs are not based on a utilization distribution). The kernel method (Worton 1989) is a nonparametric estimation of an individual's utilization distribution and offers an alternative to traditional MCP approaches. Although the kernel method is frequently utilized in other taxa, application has been very limited in snakes (Rodriguez-Robles 2003). I thus constructed minimum convex polygons (MCP) for comparative purposes with other studies, 95% kernel home ranges to incorporate an individual's utilization distribution, and 50% kernel home ranges to identify core areas of activity.

Preliminary bootstrap resampling of data by telemetry locations was used to create MCPs and assess minimum standards for inclusion in home range analyses. Bootstrapping indicated that approximately 25 locations would be sufficient to explain home range size. Although snake movements were irregular, I concluded that individuals with at least 8 weeks of tracking data, approximately equal to 25 telemetry locations, would be sufficient for inclusion in analyses. Additional individuals were excluded, however, because of uncertainties of an individual's status. Individuals identified for inclusion in home range analyses were those subjects used in all other analyses.

Snakes frequently remained at a particular site for multiple telemetry locations. Although statistically independent data should be used for analyses (White and Garrott 1990), I believed that inclusion of all locations would provide valuable information about the utilization distribution of an individual. Seasonal and annual variations in tracking intensity, however, may have impacted kernel estimates because of irregular movement patterns. Therefore, I initially used 2 sets of data to calculate home ranges: 1) all telemetry locations from a defined season (April 1 to November 30), during which the majority of the telemetry locations and movements were concentrated, and 2) only locations in which an individual moved from its previous location to remove potential biases of tracking intensity and spatial non-independence of successive telemetry locations. An individual was considered to have moved if it was >2 m from its previous location (Weatherhead and Charland 1985; see also Weatherhead and Hoysak 1989, Durner and Gates 1993) on a horizontal plane. Movements >3 m above ground were frequently difficult to detect and therefore were excluded when accuracy was inadequate. Because snakes did not use denning sites exclusive of active season home ranges, I included all movements in home range estimation. I additionally included movements regardless of whether or not an individual returned to a site at which it was located previously. A few individuals were tracked for portions of 2 active seasons. Data from both years were pooled to construct a single home range, as an individual's second year of tracking provided few observations and the second season locations did not differ from the previous season's home range.

Home ranges were calculated with the Animal Movements extension (Hooge and Eichenlaub 2000) in ArcView 3.2. Data were ln transformed to meet normality assumptions.

Home ranges calculated with the "movements only" data set and the 'all locations data' set were highly correlated (n=45, MCPs: $P<0.001$, $r=0.99$; 95% kernels: $P<0.001$, $r=0.85$; 50% kernels: $P<0.001$, $r=0.76$). To remove impacts of spatial non-independence of successive locations and potential biases of variable tracking intensity, I used the "movements only" data set for all analyses.

I analyzed home range size variation using linear regression. Using *a priori* hypotheses, I constructed several models to explain home range size (Tables 2.1-2.3). The following parameters were incorporated into my models: species (SPP), sex (SEX), snout-vent length (SVL), number of weeks tracked beyond the minimum 8 week cut-off (WEEKS), site (SITE), and implantation technique (TECH). Although the species are closely related, I anticipated some difference in home range size because of inherent biological differences. Additionally, given that some previous studies report sexual differences in home range size (Weatherhead and Hoysak 1989, Mullin et al. 2000), I hypothesized that males would have larger home ranges than females. No evidence of size relationship with home range size exists (e.g., Mullin et al. 2000). However, I predicted that biological requirements (e.g., energetics and mating opportunities) may differ by size and thus anticipated a positive relationship between body size and home range size. Finally, home range estimates, particularly MCPs, are sensitive to the sample sizes used for the calculations (Kernohan et al. 2001). Thus, although minimum standards were established for inclusion in analyses, I believed that increasing the duration of tracking may result in increased home range size.

Although I was not concerned with the specific effects of SITE and TECH on home range size, I believed it was necessary to control for them and thus included these parameters in all models. Parameters were coded such that the estimate of SEX refers to females, SPP to corn snakes, TECH to subcutaneous methods, and SITE to TTRS. SVL was standardized about a mean of 122 cm (2.3 SE) for eastern rat snakes and 92 cm (1.7 SE) for corn snakes. Additionally, year and habitat type were largely confounded with TECH and SPP, respectively, therefore these parameters were excluded from models. A lack of individuals spanning an entire active season precluded analysis of seasonal variations in home range.

Movements

To assess movements, I considered 2 components: 1) movement frequency (number of movements per total telemetry locations) and 2) movement distance (minimum horizontal distance traveled per movement) (Weatherhead and Hoysak 1989, Durner and Gates 1993). As with home range calculations, I only considered a snake to have moved if it was more than 2 m from its previous location (Weatherhead and Charland, 1985; see also Weatherhead and Hoysak 1989, Durner and Gates 1993). Vertical movements were not considered in these analyses as it was impossible to accurately incorporate vertical distance. As previously noted, determining an exact position frequently proved difficult if a snake was >3 m above ground, and thus such movements were included only when accuracy permitted. Distance per movement was calculated using the Animal Movements extension in ArcView 3.2.

To simplify seasonal comparisons of activity patterns, I considered movement frequency and distance traveled over monthly intervals. Only individuals tracked for at least 2 weeks in a given month were included in analyses. I believed that seasonally and annually variable tracking intensity might impact the intensity-dependent movement response variables. Thus, to minimize any potential impact of seasonally variable tracking intensity, I further restricted inclusion in these analyses to individuals averaging 2 to 4 locations per week. To remove the effects of annually variation in tracking intensity, I randomly subsampled 2002 data such that intensity would be approximately equivalent between years (i.e., no more than 4 locations in a given week in 2002).

As a result of the staggered entry design of project and frequent premature radio failure, few animals were tracked for a complete active season. I therefore conducted 2 sets of analyses: 1) a repeated measures set of analyses spanning June to September in which only individuals tracked for all months were included and 2) an additional set of repeated measures analyses spanning June to September in which all individuals were included. I additionally compiled more complete season (May to October) graphics in which I included all individuals. Although movements were documented occasionally during April to November, inadequate samples did not permit inclusion of these data in graphics. Repeated measures models are multilevel modeling approaches; for my purposes, measurements (level 1) are nested within individuals (level 2). Covariance parameters represent the variation in measurements attributable to observations on the same individual. I used logistic regression to analyze movement frequency. I assumed that data followed a binomial distribution (i.e., number of moves, “events”, versus total locations, “trials”) and used a logit link function to restrict predicted values between 0 and 1. I used linear regression to examine movement distance data. These data were natural log transformed to meet assumptions of normality. I employed AICc to objectively select the appropriate covariance structure for the repeated measures analyses.

Previous studies of rat snake movement patterns have generally pooled data across all individuals or considered the experimental unit to be the individual sample point (telemetry location) rather than the animal itself (e.g., Weatherhead and Hoysak 1989, Durner and Gates 1993). Such approaches constitute a form of pseudoreplication and restrict inferences to the individuals studied. Although I dealt with some aspects of non-random sampling (i.e., treatment of the individual as the experimental unit), the repeated measures analyses with the full data set present some difficulties. SAS mixed model analyses are capable of handling missing or unbalanced data but maintain the assumption that values are missing at random. Whether data are randomly missing is debatable, but individual parameters (e.g., species or sex) were similar in relative seasonal representation. While I concede that this approach is potentially not as valid as the shortened season repeated measures analyses, it was necessary to consider the bulk of the summer tracking data.

The following parameters were integrated into my models: species (SPP), sex (SEX), month (MONTH), site (SITE), implantation technique (TECH), and standardized snout-vent length (SVL). For the restricted data set, SVL standardization was about a mean of 121 cm (3.9 SE) for eastern rat snakes and 90 cm (3.6 SE) for corn snakes. SVL standardization for the complete data set was identical to the home range analyses. Proportions of eastern rat snakes and corn snakes in each sex were not similar for the restricted data set repeated measures analysis, and an initial review of these data revealed an interaction between SPP and SEX for both movement parameters. Consideration of either SPP or SEX individually or in an additive format was thus inappropriate. Therefore, all models I constructed included a SPP*SEX interaction (Tables 2.7, 2.9). Because of sample size and SPP*SEX constraints, I was unable to consider models specifically addressing inter- or intraspecific partitioning of seasonal movements with the restricted repeated measures analyses. However, the proportion of eastern rat snakes and corn snakes in each sex was similar for the complete data set. Thus, both the complete repeated measures analyses and graphics afforded the opportunity to test hypotheses of seasonal partitioning of movements by sex (MONTH*SEX), species (MONTH*SPP), and species by sex (MONTH*SPP*SEX). Additional *a priori* model hypotheses were developed using concepts and findings suggested in literature (Tables 2.8, 2.10). For the best-fitting restricted data set models, I obtained estimates of differences between least-squares means (analogous to a treatment effect) for parameters of interest. Model goodness-of-fit for repeated measures analyses was assessed using methods outlined in the home range section.

Similar to the home range analyses, I held specific hypotheses with regard to the predictor variables and interactions. I believed that the species may employ different strategies with regard to movements, which would be demonstrated by differences in movement frequency and distances. Previous research further suggests that movements may differ by sex (Weatherhead and Hoysak 1989, Franz 1995), indicating that males in this population might move greater distances and more frequently than females. Additionally, rat snakes in other regions vary somewhat in seasonal movements, typically peaking in late spring and early summer (Fitch 1963, Stickel et al. 1980); I therefore hypothesized that movements in the Southeast would peak during this period. I further predicted that males would have increased movements early in the year and female movements would increase later (Weatherhead and Hoysak 1989, Durner and Gates 1993). Although I did believe that the movement axis would be partitioned seasonally by species, I did not develop specific hypotheses as to how this separation would be manifested. Previous research provides little evidence of size relationships with movement, but I predicted that individuals of different size (SVL) would employ different strategies of frequency and distance per movement. Year was not considered in analyses because it was largely confounded with implantation technique.

Parameters were coded as in the home range analyses. Model-averaged estimating is unnecessary with repeated measures models (J. Peterson, pers. comm.). Therefore, I provided parameter estimates from my 90% confidence set of models. I also supplied covariance parameter estimates from these models.

Habitat Use

As with movement analyses, telemetry locations are frequently pooled across individuals or locations rather than the individual subject are treated as the experimental unit for assessment of habitat use of rat snakes (e.g., Weatherhead and Charland 1985, Durner and Gates 1993, Franz 1995, Blouin-Demers and Weatherhead 2001). Although this approach may be necessitated by small samples, studies with apparently adequate samples still improperly handle data sets with respect to the experimental unit (e.g., Durner and Gates 1993, Blouin-Demers and Weatherhead 2001). As detailed above, such treatment restricts inferences to the individuals sampled rather than the population (Erickson et al. 2001). To properly analyze data and permit broader population level inferences, I considered the individual animal to be the replicate.

I considered 2 scales of habitat use: 1) 2nd order, or how home ranges are established within the region, and 2) 3rd order, or how individuals use home ranges (Johnson 1980). At the 2nd order scale, I defined use by the MCP home range. Initially, I did not consider availability at the 2nd order scale; I was primarily interested in modeling habitat partitioning and I believed individuals had the same habitats available (i.e., study areas) from which to establish home ranges. For the 3rd order scale, I defined use by the specific site at which an individual was located and availability by the MCP home range. I used MCPs to permit inclusion of all telemetry sites in the 3rd order availability estimate and to maintain consistency between 2nd and 3rd order analyses. As with previous analyses, new sample points were collected only when an individual moved >2 m from its previous location (Weatherhead and Charland, 1985; see also Weatherhead and Hoysak 1989, Durner and Gates 1993). Again, this strategy removed impacts of variable tracking intensity and spatial non-independence of successive locations. Sites in which an individual returned to a point at which it was previously located were included in analyses, however, as I believed such sites represented an independent selection event. As an index of habitat selection for 3rd order scale, I subtracted habitat availability from use (i.e., percent of sites in a habitat type minus percent of that habitat type in the home range) for each individual (White and Garrott 1990, Keller and Heske 2000). Therefore, a positive value indicated use exceeded availability and a negative value indicated availability exceeded use.

I initially employed logistic regression to model habitat partitioning between the species such that the species served as binary response variables. However, preliminary results indicated complete separation of data points for most 3rd order models (i.e., candidate models explained the data perfectly); hence, logistic regression was not possible and unnecessary to explain interspecific partitioning (J. Peterson, pers. comm.). I thus simplified analyses at both scales by constructing graphics and performing appropriate statistical tests (i.e., *t*-tests and Wilcoxon Rank Sums tests). I additionally incorporated availability at the 2nd order scale as study area characteristics and indexed habitat selection as described above.

I considered several habitat parameters with analyses. Hardwood canopy coverage was defined with satellite imagery obtained during spring “green-up.” A supervised classification was conducted in ERDAS Imagine (Leica Geosystems GIS and Mapping, LLC, Atlanta, GA) and ArcGIS 9 (ESRI, Redlands, CA) to delineate total hardwood coverage.

I also pooled habitats on the basis of structural similarities to establish 4 more general macrohabitat types: drains (bottomland drains, large drainage gullies, and a large structurally similar upland hardwood forest at TTRS), uplands (burned and unburned upland pine forests and planted pine stands), fields (fallow and harrowed fields, young longleaf pine plantings) and other (roads, open water, developed areas). Additionally, portions of wetlands used by snakes were most similar to fields in terms of vegetative structure and classified accordingly. I hypothesized that partitioning would be manifested through greater use by eastern rat snakes use of hardwood forests (i.e., drains) (Durner and Gates 1993, Franz 1995, Keller and Heske 2000).

I additionally examined use of edge habitats. Drain edge was defined by establishing a 15-m buffer around drain borders for comparability with previous studies (e.g., Weatherhead and Charland 1985, Keller and Heske 2000). I defined non-drain edges as boundaries between pooled macrohabitat types excluding drains (e.g., major roads and upland boundaries) and including boundaries between burned and unburned uplands. Although use of edges has not been documented in some populations (Keller and Heske 2000), I hypothesized that both species would exhibit greater use of edge habitats (Weatherhead and Charland 1985, Durner and Gates 1993, Franz 1995, Blouin-Demers and Weatherhead 2001).

Results

Radio transmitters were implanted in 44 individuals via subcutaneous methods in 2002. However, only 8 eastern rat snakes implanted subcutaneously were included in analyses. Intraperitoneal techniques were used to implant 4 individuals in 2002 and 45 individuals in 2003. A total of 45 individuals [14 corn snakes (11 males, 3 females), 31 eastern rat snakes (22 males, 9 females)] were included in analyses. Individuals were located an average of 61 times (3.0 SE, range 27 to 96) over an average of 168 days (14.1 SE) (24 weeks, range 8 to 49 weeks]. Individuals averaged 30 movements (1.7 SE, range 12 to 57) during tracking. During the April thru November period, individuals were located an average of 57 times (2.8 SE) over an average of 133 days (7.8 SE), or 19 weeks. Seventeen snakes were included in the restricted repeated measures analyses, and all 45 individuals were included in the less restrictive repeated measures analyses.

Home Ranges

MCP home range size was 10.7 ha (2.8 SE) for corn snakes (males: 12.2 ha, 3.4 SE; females: 5.3 ha, 2.5 SE), and 7.3 ha (0.9 SE) for eastern rat snakes (males: 8.2 ha, 1.1 SE; females: 5.16 ha, 1.1 SE). Corn snakes maintained 95% kernel home ranges of 12.9 ha (2.6 SE) (males: 14.8 ha, SE 3.0; females: 6.1 ha, 2.4 SE), and eastern rat snake 95% kernels were 10.36 ha (1.3 SE) (males: 11.0, 1.6 SE; females: 8.86 ha, 2.2 SE). Core areas, identified by 50% kernel home ranges, were 1.8 ha (0.45 SE) for corn snakes (males: 2.11 ha, 0.5 SE; females: 0.73 ha, 0.41 SE) and 1.7 ha (0.28 SE) for eastern rat snakes (males: 1.85, 0.36 SE; females: 1.28, 0.39 SE).

Both the 95% and 50% kernel home range global models confirmed adequate goodness of fit. Although the MCP global model demonstrated some uneven scatter in the residuals versus predicted means plot (i.e., some heterogeneity of variances), I believed this was largely due to a lack of data in specific areas of the plot. Additionally, I wanted to maintain consistency in model structure and data transformation between the home range analyses. I therefore considered MCP model fit adequate.

The models {SEX} (ω=0.304, r^2=0.15) and {SEX+SVL} (ω=0.222) best explained MCP home range size (Table 2.1). The 90% model confidence set for MCP analyses included 7 of the 12 candidate models. For the 95% kernel home range analyses, {SEX} (ω=0.392, r^2=0.11) was the best fitting model (Table 2.2). Although the disparity between the top model weights was larger than with MCP analyses, 8 of 12 candidate models were included in the 90% confidence set. Similar to the other analyses, {SEX} (ω=0.449, r^2=0.14) was the best fitting model for the core 50% kernel home range analyses (Table 2.3). The 90% confidence set included 6 of 12 candidate models.

In the MCP and 50% kernel analyses, SEX (i.e., being female) had a negative relationship with home range size (Tables 2.4 and 2.6). Confidence intervals of predictor variables in all other analyses spanned 0, lending some uncertainty to their individual influence (Tables 2.4 – 2.6). Upon closer examination, however, the confidence intervals of several predictor variables were heavily skewed (i.e., only the tail of the confidence interval included zero), suggesting some impact of the respective variables on home range size. If such skewed distributions are considered, SEX demonstrated a negative relationship with all home range estimates and WEEKS a positive relationship with MCP estimates. Additionally, SVL was positively related to MCP home range size. SPP did not demonstrate a relationship with home range size.

Activity and Movements

Movement frequency was sporadic and movement distance irregular for both species (Figure 2.1). Restricted and complete data set analyses included 17 and 45 individuals, respectively. I used data from the April to November period meeting the previously outlined criteria for inclusion in analyses to obtain summary statistics of movement frequency and distance traveled per movement. Number of movements per telemetry location during this period was 0.60 (0.03 SE) for corn snakes (n=14) [males (n=11): 0.63, 0.03 SE; females (n=3): 0.56, 0.04 SE] and 0.46 (0.02 SE) for eastern rat snakes (n=31) [males (n=22): 0.48, 0.03 SE; females (n=9): 0.44, 0.03 SE]. Mean distance traveled per movement was 85.1 m (7.3 SE) for corn snakes (males: 91.0 m, 8.2 SE; females: 56.4 m, 8.1 SE) and 122.9 m (6.8 SE) for eastern rat snakes (males: 126.7 m, 8.1 SE; females: 113.7 m, 12.3 SE).

As suggested by the summary statistics, corn snakes appeared to move with more frequency than eastern rat snakes (Figure 2.2). Conversely, distance traveled per movement was greater for eastern rat snakes (Figure 2.3). There was relatively great variability among individuals. Movement frequency was highest for males of both species during May, although male corn snake movements suggested a secondary peak during autumn. Female corn snakes moved with greatest frequency during the summer months, whereas female eastern rat snakes were more irregular with movement frequency with a notable decline in June. Distance traveled per movement for males of both species peaked in late spring and early summer, declining thereafter. Distance traveled remained relatively constant for female eastern rat snakes from the June through October period, whereas female corn snakes movements were greatest in June and August.

Dispersion estimates initially suggested some underdispersion for repeated measures models assessing distance traveled per movement (i.e., lower variance than expected), but I did not consider this a problematic issue (M. Conroy, pers. comm.). Residual versus predicted means plots of global models in both the repeated measures and mixed model analyses verified adequate model goodness-of-fit.

For movement frequency with the restricted data set, {MONTH} (ω=0.531, r^2=0.39) and {SPP*SEX} (ω=0.251) were the highest weighted models, with 4 of 5 candidate models included in the 90% confidence set (Table 2.7). Inclusion of the complete data set identified {MONTH+SPP} (ω=0.214, r^2=0.30) and {MONTH+SPP+SEX} (ω=0.184) as the best fitting models; 9 of 17 models were contained in the confidence set (Table 2.8).

For distance traveled per movement, the restricted data set identified {SPP*SEX+SVL} (ω= 0.516, r^2=0.63) and {SPP*SEX} (ω=0.422) as the best-fitting models, with only these models contained in the 90% confidence set (Table 2.9). Alternatively, {MONTH+SPP} (ω=0.350, r^2=0.42) and {SPP} (ω=0.192) were the best-fitting models with the full data set, and 7 models were included in the confidence set (Table 2.10).

With the restricted data set analysis, movement frequency peaked in July and August; considering skewed distributions as described in the home ranges section, movements were more frequent in June, July, and August than in September (Table 2.10). The effect of SPP (i.e., being a corn snake) was not evident within the SPP*SEX models, although SEX (i.e., being female) was negative and the interaction term positive (i.e., being a female corn snake). The skewed confidence interval of SVL suggested a positive relationship with movement frequency. Parameter estimates of the differences in least-squares means of the SPP*SEX model indicated an overall difference between species (least squares means difference, logit scale: 0.772, 0.240 SE), with female corn snakes (1.316, 0.407 SE) and male corn snakes (1.005, 0.363 SE) moving more frequently than female eastern rat snakes. Female eastern rat snakes also moved less frequently than male conspecifics (-0.777, 0.337 SE).

The complete data set analysis of movement frequency also revealed greater activity from June through August (Table 2.11). SPP had a positive effect and SEX was skewed negatively in additive models. When a SPP*SEX interaction was included, the effects of SPP and SEX shifted somewhat, as SPP was only positively skewed and the effect of SEX became negative. Additionally, the SPP*SEX interaction term was skewed positively. The effect of MONTH*SPP interaction terms was evident only in June. Although I treated SITE as a nuisance variable, its effect (i.e., being at TTRS) was negative in both movement frequency analyses.

For the restricted data set analysis of distance traveled per movement, estimates of SPP were inconclusive, but models did estimate SPP*SEX as negative (Table 2.13). Both SEX and

SVL were skewed positively. Parameter estimates of differences in least-squares means as calculated from the {SPP*SEX+SVL} model indicated an overall effect of SPP (least squares means difference, logit scale: -0.511, 0.149 SE), as female corn snakes moved less distance than female eastern rat snakes (-0.868, 0.254 SE) and male eastern rat snakes (-0.512, 0.205 SE). Male corn snakes also moved less distance than female eastern rat snakes (-0.510, 0.224 SE).

The complete data set identified a clear peak of distance traveled peaked in June (Table 2.14). Both additive and interactive models estimated a negative effect of SPP. The effects of SEX and SPP*SEX, however, did not demonstrate a clear relationship with distance.

Habitat Use

Both species demonstrated familiarity with the landscape, as individuals frequently returned to sites at which they had been previously located. Sites were commonly habitat structural features including trees, snags, brush piles, burrows (e.g., gopher tortoise and small mammal), deadfalls, and stumps (Figure 2.4). Corn snakes were most commonly associated with underground or ground level structures such as burrows, whereas eastern rat snakes used trees more frequently. When individuals were located in trees, eastern rat snakes were found in hardwoods nearly exclusively, whereas corn snakes used both pines and hardwoods (mean percent of arboreal sites in hardwood trees: eastern rat: 97.3±1.5 SE; corn: 43.6±15.2 SE; Wilcoxon Rank Sums test, Z=-3.6082, P=0.0003). Not surprisingly, hardwood trees were sites of eastern rat snakes more frequently than corn snakes (mean percent of sites in hardwood trees: eastern rat: 35.9±3.0 SE; corn: 2.6±1.1 SE; Wilcoxon Rank Sums test, Z=-5.3053, P<0.0001). Snakes were documented in at least 22 species of trees, including 19 species of hardwoods and 3 species of pines. Oaks (*Quercus* spp.), sweet gum (*Liquidambar styraciflua*), and black gum (*Nyssa sylvatica*) were the species eastern rat snakes most commonly used.

A review of the heights at which sites were located provides further evidence of partitioning: eastern rat snake sites were frequently elevated, whereas corn snakes made less use of above ground structure (mean percent of sites above ground: eastern rat: 40.2±3.2 SE; corn: 6.0±1.5 SE; Satterthwaite *t*-test, $t = 9.72$, 40.1 df, $P < 0.0001$). Elevated sites were typically >3 m from ground level for both species (mean proportion of locations: eastern rats: 0.81±0.03 SE; corn: 0.88±0.09 SE).

Based on the supervised classification, eastern rat snake home ranges also contained more total hardwood coverage than corn snake home ranges (mean percentage of hardwoods: eastern rat: 23.9±2.36 SE; corn: 10.3±1.97 SE; Satterthwaite *t*-test, $t = 4.42$, 40.7 df, $P<0.0001$). Eastern rat snakes generally established home ranges in proportion to site-wide macrohabitat availability (Figure 2.5). Conversely, corn snake home ranges contained less drain and more field than predicted (Figure 2.5). Home ranges of both species contained less "other" habitat than was available. At the 3rd order scale, inclusion of all individuals and only those individuals which had the habitat of interest available to them revealed similar trends. Eastern rat snakes used drains, drain edges, and total edges more than expected by availability and uplands less than expected by availability (Figures 2.6 and 2.7). Corn snake use of upland was greater than predicted by availability (Figure 2.6 and 2.7). Additionally, the highly skewed confidence of drains suggests than corn snakes used this habitat less than available. Corn snakes exhibited no selection of edge habitats.

Discussion

Home Ranges

MCP home ranges of eastern rat snakes reported here are comparable with MCPs documented by most other research (Weatherhead and Hoysak 1989, Durner and Gates 1993, Mullin et al. 2000). However, Burger et al. (unpublished data) report smaller MCP home ranges of approximately 0.9 ha in Mississippi. Study sites appear comparable in macrohabitat composition, and explanations for this discrepancy are unknown. Furthermore, estimates from radio-tagged individuals in the northern Florida sandhills report larger and highly variable annual home ranges for both corn and eastern rat snakes (15.4 to 1,560 ha) (Franz 1995). Although research was based on few individuals, it documented distinct winter and summer home ranges connected by extensive migratory routes. Despite the geographic proximity of this study to mine, I found that snakes in the Red Hills did not exhibit separate winter and summer ranges. Obviously, the presence and inclusion of migratory routes and seasonal ranges explains the observed differences in home range size between the 2 regions. Franz (1995) hypothesizes that some individuals make long migratory movements and maintain different seasonal home ranges to escape competitive interactions. The absence of such long distance migrations and shifts in home ranges in the Red Hills region suggests either that Red Hills' populations are able to partition resources more efficiently or that resources may not be limiting enough to promote such seasonal movements (i.e., the Red Hills are better able to support these species than the Sandhills).

The MCP analysis did not clearly identify a model to best explain home range size, as witnessed by bunched model weights and the inclusion of numerous candidate models in the 90% confidence set. Although kernel estimates more heavily weight the best-fitting model, kernel analyses include numerous models in the confidence set as well. These results demonstrate some uncertainty as to which model and associated hypothesis best explain home ranges. Increased data, either in the form of lengthened tracking sessions per individual or an overall larger sample, may be beneficial. Alternatively, additional candidate models, perhaps with predictor variables not considered in this study, may aid in identification of plausible candidate models. For example, home range size may decrease with the inclusion of more optimal habitat in the home range. Using results from the habitat use analyses, proportion of suitable habitat by species could be incorporated into hypotheses and models as a predictor variable.

Despite model uncertainty, some conclusions can be drawn as to hypotheses explaining home range size. Across all analyses, {SEX} was the most highly weighted model, demonstrating that this model best explain home range size regardless of the estimator. The inclusion of an individual's sex in the majority of the highest weighted models further suggests the importance of this parameter in explanation of home range size. Although models containing a species-by-sex interaction were included in the confidence sets, the most highly weighted models do not include this interaction term. This finding suggests the insignificance of the inclusion of the species-by-sex interaction in home range modeling.

Trends in parameter estimates were comparable across all home range analyses. I did not find evidence of differences between species. Although limited by a small sample and great variability, *Pantherophis* species did not appear to differ in the Sandhills either (Franz 1995). I did find differences between the sexes, as male home ranges were larger than female home ranges. These results agree with findings from some regions (Ontario: Weatherhead and Hoysak 1989; Tennessee: Mullin et al. 2000), but contradict those from other regions (Maryland: Durner and Gates 1993). Reproductive behaviors, which influence movements and home range size (Gregory et al. 1987), may be responsible for the differences between sexes seen in rat snakes (Weatherhead and Hoysak 1989). Durner and Gates (1993) postulate that decreased activity of gravid snakes (e.g., Gibbons and Semlitsch 1987, Blouin-Demers and Weatherhead 2001), coupled with a reduced active season in the northern range (e.g., Blouin-Demers et al. 2002), may result in the discrepancy between studies: in the North, females are gravid for a greater proportion of the activity season and thus may have less ability to move, thereby decreasing home range size. According to this hypothesis, rat snakes in the South, with an even longer activity season, would not exhibit sexual differences in home range size. However, given that sexual differences are present in the extreme Southeast, this hypothesis should be rejected.

I attempted to remove the effects of tracking duration on home range estimates by setting minimum boundaries for inclusion in the analyses. However, the parameter estimates indicated a positive association with MCP estimates. Conversely, tracking duration did not demonstrate a clear relationship with either kernel estimate technique. Additionally, although WEEKS was not included in the most highly weighted models in any analysis, the parameter was included in the model confidence sets, most notably with MCP analyses. WEEKS reaffirms the sensitivity of some home range estimators, particularly MCPs, to small sample sizes (Kernohan et al. 2001). The absence of an impact of sample size on kernel estimates and the exclusion of unused areas by kernel methods provide benefits unavailable with traditional MCP techniques. To my knowledge, this study represents the first application of kernel home range methods to *Pantherophis* species and only the second usage of kernel methods with snakes in general (Rodriguez-Robles 2003). I believe that application of kernel methods would be advantageous to future snake research.

Movements

Comparison with general estimates of movement frequency and distance traveled documented by other researchers is complicated by differences in sampling intensity between studies. Although movement estimates appear to be relatively similar to results presented for rat snake species elsewhere, estimates of movement distance in central Florida exceed my estimates due to migratory movements as discussed above (Franz 1995). Moreover, general distance traveled per movement in the Red Hills appears somewhat greater than that documented in more northern latitudes (Weatherhead and Hoysak 1989, Durner and Gates 1993). Movements also appear to be more frequent in the Red Hills than in Canada (Weatherhead and Hoysak 1989).

As with the home range analyses, clumped model weights and variability in model selection by analysis prove problematic, and the identification of which models best explain rat snake movements remains difficult. Trends in the model ranking do provide some insight for future model development and hypothesis testing. The inclusion of SPP in the majority of the most highly weighted models establishes the importance of including this parameter in rat snake movement hypotheses. Furthermore, incorporation of MONTH appears relatively important when assessing movement frequency.

Finally, I hypothesized that species may partition resources by seasonal variation in activity levels. I additionally considered seasonal partitioning of movements by sex and by both species and sex. The respective models corresponding to these hypotheses, MONTH*SPP, MONTH*SEX, and MONTH*SPP*SEX, had low relative weights in both of the full data set analyses. Therefore, hypotheses of seasonal partitioning of the movement axis by sex or species do not appear to be likely explanations for *Pantherophis* movements. My data provide only limited support for seasonal partitioning of movements by species and sex. Some potential differences are suggested, however, particularly with respect to interspecific differences between females, early season activity differences between the sexes, and the late season surge in activity of male corn snakes and female eastern rat snakes. Future treatment of month as a linear or quadratic term as opposed to categorical terms would result in a less parameterized model and may thus increase the likelihood of models addressing partitioning of movements by season and/or sex. Moreover, extension of the analyses to encompass more of the year and collection of additional data may result in greater support for partitioning hypotheses. Others (Weatherhead and Hoysak 1989, Durner and Gates 1993) report some seasonal separation of movements by sex, but misleading analyses (i.e., consideration of each telemetry location as the experimental unit) render their results and conclusions largely questionable.

Because limited evidence exists for seasonal partitioning of activities, consideration of general seasonal movement patterns is warranted. The apparent increased activity of males versus females in May strongly suggested by the data should be noted, however, as this increase corresponds with the spring breeding seasons (Fitch 1963, Durner and Gates 1993, Ernst and Ernst 2003). Movement frequency, as estimated by models, was greatest from June through August but dropped in September. Distance traveled per movement peaked in June, suggesting that snakes do not consistently travel furthest when they are the most active. Although the Southeast's climate permits a longer active season, patterns appear generally similar to northern latitudes in that activity is greatest during the summer months (Weatherhead and Hoysak 1989, Durner and Gates 1993). In the nearby Sandhills, movement distances are greater and peaks are slightly earlier due to long distance migrations (Franz 1995). Elsewhere, rat snake activity reportedly also peaks during the late spring breeding season but again heightens in autumn as snakes return to denning sites (Fitch 1963, Stickel et al. 1980). This disparity may be a product of the different techniques employed by the studies (Weatherhead and Hoysak 1989).

Estimates from all analyses as well as summary statistics suggest that corn and eastern rat snakes exhibit different movement strategies. Corn snakes tended to move more frequently than eastern rat snakes; however, when eastern rat snakes did move, they traveled greater distances.

Parameter estimates of many models including a species-by-sex interaction provide more information this relationship. By calculating the predicted movements for all species and sex combinations, it becomes apparent that females of each species may be driving the observed interspecific differences. The estimated differences in least-squares means support this concept as well.

This trend, however, may be partially an artifact of data collection limitations. I excluded vertical movements from analyses and I was frequently unable to assess an individual's horizontal movements when it was >3 m high in a tree. Because eastern rat snakes spent more time in arboreal settings than corn snakes, I may have missed shorter movements of eastern rat snakes, thereby potentially underestimating movement frequency and overestimating distance traveled per movement. However, because I included only movements >2 m, the impact of potentially missing such short distance movements likely was minimal.

Parameter estimates obtained from the restricted data set analyses demonstrated differences between sexes, as females tended to move less frequently and traveled shorter distances than males. Similar to the species parameter, predicted values and differences in least-squares means suggest that species differences are driving the sexual differences: female corn snakes are largely responsible for the negative relationship between sex and distance traveled and female rat snakes are largely responsible for the negative relationship between sex and movement frequency. A similar effect of sex and a species-by-sex interaction also is obvious with the full data set analysis of movement frequency, but the full data set analysis of distance traveled does not suggest such patterns. Although the results of movement distance are not conclusive, some interspecific differences in activity between females seem probable. Some previous research, though limited because of analytical methods, also reports that females move less frequently than males and travel less distance for portions of the active season (Weatherhead and Hoysak 1989, Durner and Gates 1993). Franz (1995) also suggests such patterns, but his results are not statistically verified.

Combined, species and sex parameters have potentially important implications. Because reproduction can affect movements (Gibbons and Semlitsch 1987, Gregory et al. 1987), female corn snakes and eastern rat snakes may use different reproductive strategies (e.g., a gravid state, nest site searching, or mate searching). Additional data collection and assessment of interspecific seasonal variation between females may provide further insight into differences in reproductive behaviors. Hypotheses of reproductive differences remain to be tested with future research.

SVL estimates from the restricted data set analyses suggest that individuals may be more active and travel farther with increasing size. I did not find research which has previously documented this relationship in rat snakes. I believe that different energetic requirements or reproductive patterns may be responsible for the trend. Although radio implant technique did not impact either home range size or movement patterns, I believe that this is largely attributable to the fact that I was conservative when establishing minimum boundaries for inclusion of individuals in these analyses. Additionally, it was impossible to completely separate the effects of implantation technique from either species or potential annual variation, as only eastern rat snakes tagged via subcutaneous methods were included in analyses, and this technique was used only in 2002. The subcutaneous methods outlined in Weatherhead and Anderka (1984) are not appropriate for eastern rat snakes and corn snakes, evidenced by the widespread non-healing and subsequent radio expulsion, generally occurring within weeks of the procedure. I further advocate a cautious approach when implanting whip antennas subcutaneously in these species. It was my observation that the procedure disarticulates a great deal of vascularized connective tissue, occasionally resulting in erosion of the antenna through the skin at the anterior end of the implant.

Some caution should be exercised when interpreting the results of the movement and home range analyses because of sample size constraints. The data set included relatively few female snakes, particularly female corn snakes. The restricted data set analyses included observations from only 17 individuals as well. Anecdotally, however, female corn snakes demonstrated similar movement patterns. Therefore, there is some validity in extrapolating to the population. Of course, larger data sets will help to examine the results and conclusions reported here. Regardless, these analyses provide much needed information of eastern rat snakes and corn snakes in the Southeast.

Habitat Use

Contrary to activities, habitat partitioning was evident at multiple spatial scales for eastern rat and corn snakes in the Red Hills. Partitioning of vertical space and structural features was among the most striking components of this separation. I did anticipate some partitioning of vertical strata and structure. I was somewhat surprised, however, by the magnitude of this separation. Both species are excellent climbers (Jackson 1976, S. Stapleton, personal observation), and use of trees by gray and eastern rat snakes is particularly well established (Stickel et al. 1980, Durner and Gates 1993, Franz 1995, Keller and Heske 2000, Blouin-Demers and Weatherhead 2001). Although Franz (1995) and Keller and Heske (2000) report separation of vertical strata between sympatric rat snake species in peninsular Florida and Illinois, respectively, I attributed some of this disparity to small samples. However, even with a much larger sample, I found that such differences remained striking. I did document use of trees by 10 of 14 radio-tagged corn snakes, whereas Franz (1995) reported no use of trees by corn snakes. It remains unclear whether the disparity between regional corn snake populations is an artifact of sample size or accurately reflects behavioral differences between populations in peninsular Florida scrublands and the managed pine forests of the Red Hills.

Equally conspicuous was interspecific partitioning of specific tree types. While eastern rat snakes focused nearly exclusively on hardwoods, corn snakes demonstrated much more variable use of pines and hardwoods. Although the patterning of these species is highly similar, coloration is contrasting: the gray and black of regional eastern rat snakes (formerly known as gray rat snakes) bear a remarkable resemblance to the bark of common hardwood species. Such differences suggest a relationship between specific evolutionary processes and the observed behaviors.

Indices of habitat use versus availability suggested some interspecific differences in the habitat selection process and provided further conclusive evidence of habitat partitioning. Eastern rat snakes appear to be more generalist in the establishment of home ranges and included more hardwood canopy coverage, whereas corn snakes exhibit clear differences in habitat use versus availability, particularly in exclusion of drain habitats and inclusion of fields and non drain edges.

My 3rd order analyses are comparable to other studies of rat snake habitat use (Weatherhead and Charland 1985, Durner and Gates 1993, Keller and Heske 2000). Both corn and eastern rat snakes exhibited obvious patterns in habitat use versus availability at the 3rd order scale. Eastern rat snake habitat use in the Red Hills is generally similar to habitat use of closely related rat snakes reported elsewhere with respect to hardwood forests (Durner and Gates 1993, Franz 1995, Keller and Heske 2000) and forest edges (Weatherhead and Charland 1985, Durner and Gates 1993, Blouin-Demers and Weatherhead 2001). Some conflicting evidence does exist, however [e.g., for forests (Weatherhead and Charland 1985, Blouin-Demers and Weatherhead 2001) and for edges (Keller and Heske 2000)]. Although I documented greater use of drain edges and total edges by eastern rat snakes, I did not detect increased use of non-drain edges. Eastern rat snakes may require greater structural contrast than these "soft" edges offer. These habitat interfaces are primarily used for thermoregulatory purposes in Ontario (Blouin-Demers and Weatherhead 2001), but may also provide productive hunting grounds and abundant refuge sites (Weatherhead and Charland 1985, Durner and Gates 1993, Blouin-Demers and Weatherhead 2001).

It should be noted that drains at my sites are fingerlike and have a high edge-to-interior ratio. I did not want to further partition habitats into additional categories (e.g., bottomland edge, bottomland interior, upland edge., upland interior) because I believed that doing so would minimize the possibility of detecting habitat use patterns. The reported use of edges may be somewhat attributable to the high use of drains and, conversely, the high use of drains may be a partial product of high edge use. Qualitative evidence, however, indicated that high use of both drains and drain edges both represent real patterns in eastern rat snake habitat use.

Corn snakes in the Red Hills demonstrated greater than anticipated use of uplands and lower use of drains and "other" habitats. In contrast, Franz (1995) reports corn snakes in the sandhills of northern Florida used a variety of pine and hardwood forests, but noted lower than expected use of upland pine forests. These observations reveal yet another potential disparity between these regional corn snake populations, but I again emphasize that his results and conclusions were drawn from only 4 individuals.

My data provide conclusive evidence of partitioning of habitat between sympatric eastern rat and corn snakes. Although Schoener (1974) states that habitat is the most common dimension facilitating coexistence of faunal species, Vitt (1987) and Toft (1985) contest that snakes primarily separate resources along the food axis. Existing literature provides inconclusive evidence as to the importance of interspecific habitat partitioning in snakes (Reinert 1993). However, other studies between sympatric rat snake populations also suggest some separation of habitats (Franz 1995, Keller and Heske 2000). The issue is somewhat confounded when it is considered that the food and habitat dimensions are generally not independent (Reinert 1993). Given the apparent overlap in food resources as previously described and the magnitude of the habitat separation observed in this study, it seems unlikely that interspecific differences in food resources are solely driving observed resource separation. Future work should aim to clarify the role of and relationship between the habitat and food axes.

Learning and site fidelity are generally not well understood in the context of habitat use in snakes (Reinert 1993), but may have large ecological implications. For example, such behaviors may facilitate exploitation of new structural features or a return to productive foraging grounds and refuges for periods of inactivity (e.g., ecdysis). Anecdotally, some taxa have demonstrated an ability to exploit new structural features in the environment (Reinert 1993). Manipulative approaches will be required to quantify and test hypotheses of plasticity in habitat use. However, qualitative evidence provides preliminary clues. Rat snakes are well-known for use of man-made structures, residential habitats, and general coexistence with humans (Durner and Gates 1993, Blouin-Demers and Weatherhead 2001, Ernst and Ernst 2003). At TTRS and PH, both species regularly used recently constructed brush piles, and individual eastern rat snakes made use of man-made structures when such features were present. Additionally, familiarity with the landscape, as evidenced by fidelity to specific areas and repeated usage of particular structural features, is reported here and elsewhere for some rat snake species (e.g., Stickel et al. 1980, Weatherhead and Charland 1985). Such observations point to some amount of plasticity in habitat use and provide a framework for future hypothesis testing.

Finally, I was primarily interested in gross patterns of habitat use and partitioning between the species. Therefore, I did not examine seasonal or intraspecific (e.g., intersexual) variation. These factors, as well as others (e.g., thermoregulatory requirements), may be important determinants of habitat use in snakes (Reinert 1993; e.g., Blouin-Demers and Weatherhead 2001). Conflicting evidence exists regarding seasonal variation in rat snake habitat use elsewhere (Weatherhead and Charland 1985, Durner and Gates 1993, Blouin-Demers and Weatherhead 2001), but some differences in habitat use are apparent between males, nongravid females, and gravid females (Blouin-Demers and Weatherhead 2001). These topics may be addressed thoroughly in the future with larger samples of female snakes and more comprehensive tracking seasons.

Together, these habitat use and partitioning data have important implications for wildlife managers in the Red Hills (see also Chapter 5, this volume). Regionally, rat snakes are important nest predators of bobwhite (Staller 2001, Thornton 2003, Staller et al. 2005). Staller (2001) suggests that removal of hardwoods may reduce nest predations by eastern rat snakes. If eastern rat snakes are the primary snake species predating bobwhite nests in the region, removal of upland hardwood trees may limit accessibility to upland habitats, thereby reducing negative interactions between these snakes and bobwhite. Although this notion may be an oversimplification of the system (e.g., unaccounted plasticity in habitat use, unknown interspecific food partitioning), the concept merits further attention. Manipulative approaches will be necessary to examine the effects of hardwood removal on bobwhite nest predations by snakes and provide quantitative data on rat snake plasticity in habitat use. Moreover, this notion highlights the need for research addressing food partitioning between these rat snake populations. Rat snake ecology, particularly with respect to food habits and responses to habitat manipulation, should remain of great interest to both herpetofaunal and avian conservationists and managers.

Conclusions

Competitive exclusion predicts that species must maintain some degree of resource separation or niche differentiation to permit coexistence in a stable environment (Gause 1934, Hardin 1960). My data are consistent with such predictions. Limited evidence exists for seasonal variation in activities between eastern rat and corn snakes, but evidence for habitat partitioning is conclusive and exists at multiple spatial scales for these sympatric populations. As such, competition may have played a role in either shaping or maintaining differences between these populations. However, other factors [e.g., predation (Holt 1977, Schoener 1982, Toft 1985), physiological differences (Reinert 1984, Toft 1985), disease (Grosholz 1992)] may be driving or contributing to the observed ecological differences as well. In fact, Toft (1985) stated that neither competition nor other factors are likely to act alone in shaping observed differences.

Although the ultimate cause of apparent interspecific resource partitioning remains uncertain, the data demonstrate clear ecological differences between sympatric eastern rat and corn snakes. Examination of other potential partitioning axes (e.g., food) would provide a more complete picture of interspecific variability. Analytical approaches integrating movements and habitat use, as well as intraspecific and seasonal variation in habitat use, may promote a better understanding of the complexities of eastern rat and corn snake ecology.

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Table 2.1. Candidate models, delta AICc values, and associated AICc weights and likelihoods for analysis of minimum convex polygon (MCP) home ranges calculated for rat snakes radio-tracked during 2002 - 2004 at TTRS and PH in South Georgia and North Florida. All models additionally included SITE and TECH which are not listed in the model structure.

Model	**AICc**	**ΔAICc**	**Model Likelihood**	**Weight (ω)**	**Parameters**
SEX	102.272	0.000	1.000	0.304	5
SEX + SVL	102.902	0.629	0.730	0.222	6
SPP + SEX	104.415	2.142	0.343	0.104	6
SPP + SEX + WEEKS	104.550	2.277	0.320	0.097	7
SPP + SEX + SVL	104.886	2.613	0.271	0.082	7
WEEKS	106.116	3.844	0.146	0.044	5
SPP + SVL	106.282	4.010	0.135	0.041	6
SPP * SEX + WEEKS	107.241	4.969	0.083	0.025	8
SPP * SEX	107.208	4.936	0.085	0.026	7
SPP * SEX + SVL	107.827	5.554	0.062	0.019	8
SPP	107.796	5.523	0.063	0.019	5
SPP * SEX + WEEKS + SVL	108.167	5.895	0.052	0.016	9

[*] SPP: Species (corn or eastern rat); SEX: Sex (male or female); WEEKS: Weeks radio-tracked beyond 8 week minimum; SVL: Standardized snout-vent length; SITE: Study site; TECH: Implantation technique

Table 2.2. Candidate models, delta AICc values, and associated AICc weights and likelihoods for analysis of 95% kernel home ranges calculated rat snakes radio-tracked during 2002 - 2004 at TTRS and PH in South Georgia and North Florida. All models additionally included SITE and TECH which are not listed in the model structure.

Model	**AICc**	**ΔAICc**	**Model Likelihood**	**Weight (ω)**	**Parameters**
SEX	96.776	0.000	1.000	0.392	5
SPP + SEX	98.860	2.084	0.353	0.138	6
SEX + SVL	98.883	2.107	0.349	0.137	6
SPP	100.118	3.342	0.188	0.074	5
WEEKS	100.880	4.104	0.129	0.050	5
SPP * SEX	100.894	4.118	0.128	0.050	7
SPP + SEX + SVL	100.957	4.181	0.124	0.048	7
SPP + SVL	101.071	4.295	0.117	0.046	6
SPP + SEX + WEEKS	101.653	4.877	0.087	0.034	7
SPP * SEX + SVL	103.386	6.611	0.037	0.014	8
SPP * SEX + WEEKS	103.730	6.955	0.031	0.012	8
SPP * SEX + WEEKS + SVL	106.419	9.643	0.008	0.003	9

[*] SPP: Species (corn or eastern rat); SEX: Sex (male or female); WEEKS: Weeks radio-tracked beyond 8 week minimum; SVL: Standardized snout-vent length; SITE: Study site; TECH: Implantation technique

Table 2.3. Candidate models, delta AICc values, and associated AICc weights and likelihoods for analysis of 50% kernel home ranges calculated for rat snakes radio-tracked during 2002 - 2004 at TTRS and PH in South Georgia and North Florida. All models additionally included SITE and TECH which are not listed in the model structure.

Model	AICc	ΔAICc	Model Likelihood	Weight (ω)	Parameters
SEX	118.482	0.000	1.000	0.449	5
SPP + SEX	120.892	2.410	0.300	0.135	6
SEX + SVL	120.994	2.512	0.285	0.128	6
SPP * SEX	122.560	4.078	0.130	0.058	7
SPP	122.681	4.199	0.123	0.055	5
WEEKS	122.976	4.494	0.106	0.047	5
SPP + SEX + SVL	123.496	5.014	0.081	0.037	7
SPP + SEX + WEEKS	123.592	5.110	0.078	0.035	7
SPP + SVL	124.394	5.912	0.052	0.023	6
SPP * SEX + WEEKS	125.155	6.673	0.036	0.016	8
SPP * SEX + SVL	125.465	6.983	0.030	0.014	8
SPP * SEX + WEEKS + SVL	128.247	9.765	0.008	0.003	9

[*] SPP: Species (corn or eastern rat); SEX: Sex (male or female); WEEKS: Weeks radio-tracked beyond 8 week minimum; SVL: Standardized snout-vent length; SITE: Study site; TECH: Implantation technique

Table 2.4. Model-averaged ln transformed parameter estimates obtained from analysis of minimum convex polygon home ranges calculated for rat snakes radio-tracked during 2002 - 2004 at TTRS and PH in South Georgia and North Florida. The parameter SPP*SEX was not included in the 90% model confidence set.

Parameter	**Estimate ($\hat{\hat{\beta}}$)**	**SE**	**Lower 95% CI**	**Upper 95% CI**
Intercept	1.9977	0.1972	1.6112	2.3842
SPP	0.1849	0.2243	-0.2547	0.6245
SEX	-0.5475	0.2296	-0.9975	-0.0975
WEEKS	0.0218	0.0133	-0.0043	0.0479
SVL	0.1648	0.1087	-0.0482	0.3778
SITE	-0.1689	0.2139	-0.5881	0.2502
TECH	-0.0439	0.2757	-0.5842	0.4965

[*] SPP: Corn snake; SEX: Female; WEEKS: Number of weeks radio-tracked beyond 8 week minimum; SVL: Standardized snout-vent length; SPP*SEX: Female corn snakes; SITE: TTRS; TECH: Subcutaneous radio implantation technique

Table 2.5. Model-averaged ln transformed parameter estimates obtained from analysis of 95% kernel home ranges calculated for rat snakes radio-tracked during 2002 - 2004 at TTRS and PH in South Georgia and North Florida.

Parameter	**Estimate ($\hat{\beta}$)**	**SE**	**Lower 95% CI**	**Upper 95% CI**
Intercept	2.2934	0.1728	1.9547	2.6322
SPP	0.1940	0.2203	-0.2378	0.6258
SEX	-0.4191	0.2193	-0.8489	0.0108
WEEKS	0.0024	0.0132	-0.0235	0.0283
SVL	0.0901	0.1040	-0.1137	0.2939
SPP*SEX	-0.4300	0.4840	-1.3786	0.5186
SITE	-0.1854	0.2000	-0.5774	0.2066
TECH	0.1463	0.2563	-0.3561	0.6486

[*] SPP: Corn snake; SEX: Female; WEEKS: Number of weeks radio-tracked beyond 8 week minimum; SVL: Standardized snout-vent length; SPP*SEX: Female corn snakes; SITE: TTRS; TECH: Subcutaneous radio implantation technique

Table 2.6. Model-averaged ln transformed parameter estimates obtained from analysis of 50% kernel home ranges calculated for rat snakes radio-tracked during 2002 - 2004 at TTRS and PH in South Georgia and North Florida.

Parameter	**Estimate ($\hat{\beta}$)**	**SE**	**Lower 95% CI**	**Upper 95% CI**
Intercept	0.2810	0.2091	-0.1288	0.6907
SPP	0.1850	0.2876	-0.3786	0.7487
SEX	-0.5745	0.2806	-1.1245	-0.0244
WEEKS	0.0062	0.0169	-0.0269	0.0393
SVL	0.0521	0.1301	-0.2029	0.3071
SPP*SEX	-0.6643	0.6158	-1.8713	0.5427
SITE	-0.1379	0.2548	-0.6374	0.3616
TECH	0.4035	0.3203	-0.2243	1.0312

[*] SPP: Corn snake; SEX: Female; WEEKS: Number of weeks radio-tracked beyond 8 week minimum; SVL: Standardized snout-vent length; SPP*SEX: Female corn snakes; SITE: TTRS; TECH: Subcutaneous radio implantation technique

Table 2.7. Candidate models, delta AICc values, and associated AICc weights and likelihoods for repeated measures analysis (restricted data set) of movement frequency for rat snakes radio-tracked during June - September, 2002 and 2003 at TTRS and PH in South Georgia and North Florida. Site and Technique were included in all models and are not listed in the model structure. 'Parameters' includes the covariance parameter.

Model	**AICc**	**ΔAICc**	**Model Likelihood**	**Weight (ω)**	**Parameters**
MONTH[*]	155.8	0	1.000	0.531	7
SPP * SEX	157.3	1.5	0.472	0.251	7
SPP * SEX + SVL	158.8	3	0.223	0.119	8
MONTH + SPP * SEX	159.3	3.5	0.174	0.092	10
MONTH + SPP * SEX + SVL	164.6	8.8	0.012	0.007	11

[*] SPP: Species (corn or eastern rat); SEX: Sex (male or female); MONTH: Months of radio-tracking (June – September); SVL: Standardized snout-vent length; SITE: Study site; TECH: Implantation technique

Table 2.8. Candidate models, delta AICc values, and associated AICc weights and likelihoods for repeated measures analysis (complete data set) of movement frequency during June – September, 2002 and 2003 at TTRS and PH in South Georgia and North Florida. Site and Technique were included in all models and are not listed in the model structure. 'Parameters' includes the covariance parameter.

Model	**AICc**	**ΔAICc**	**Model Likelihood**	**Weight (ω)**	**Parameters**
MONTH + SPP[*]	273.2	0	1.000	0.214	8
MONTH + SPP + SEX	273.5	0.3	0.861	0.184	9
MONTH	273.9	0.7	0.705	0.151	7
MONTH + SEX	274	0.8	0.670	0.144	8
MONTH + SPP * SEX	275.2	2	0.368	0.079	10
MONTH * SPP	275.9	2.7	0.259	0.056	11
SPP	276.3	3.1	0.212	0.045	5
SPP + SEX	277.1	3.9	0.142	0.030	6
MONTH + SEX * SEX + SVL	277.5	4.3	0.116	0.025	11
SPP + SVL	278.4	5.2	0.074	0.016	6
SEX * SEX	278.7	5.5	0.064	0.014	7
SEX	278.7	5.5	0.064	0.014	5
SPP + SEX + SVL	279.3	6.1	0.047	0.010	7
MONTH * SEX	279.6	6.4	0.041	0.009	11
SEX + SVL	280.9	7.7	0.021	0.005	6
SPP * SEX + SVL	281	7.8	0.020	0.004	8
MONTH * SPP * SEX	289.8	16.6	0.000	0.000	19

[*] SPP: Species (corn or eastern rat); SEX: Sex (male or female); MONTH: Months of radio-tracking (June – September); SVL: Standardized snout-vent length; SITE: Study site; TECH: Implantation technique

Table 2.9. Candidate models, delta AICc values, and associated AICc weights and likelihoods for repeated measures analysis (restricted data set) of distance traveled per movement during June – September, 2002 and 2003 at TTRS and PH in South Georgia and North Florida. Site and Technique were included in all models and are not listed in the model structure. 'Parameters' includes the covariance parameter.

Model	**AICc**	**ΔAICc**	**Model Likelihood**	**Weight (ω)**	**Parameters**
SPP * SEX + SVL[*]	83.3	0	1.000	0.516	9
SPP * SEX	83.7	0.4	0.819	0.422	8
MONTH + SPP * SEX + SVL	88.9	5.6	0.061	0.031	12
MONTH + SPP * SEX	89.2	5.9	0.052	0.027	11
MONTH	93.4	10.1	0.006	0.003	8

[*] SPP: Species (corn or eastern rat); SEX: Sex (male or female); MONTH: Months of radio-tracking (June – September); SVL: Standardized snout-vent length; SITE: Study site; TECH: Implantation technique

Table 2.10. Candidate models, delta AICc values, and associated AICc weights and likelihoods for repeated measures analysis (complete data set) of distance traveled per movement during June – September, 2002 and 2003 at TTRS and PH in South Georgia and North Florida. Site and Technique were included in all models and are not listed in the model structure. 'Parameters' includes the covariance parameter.

Model	**AICc**	**ΔAICc**	**Model Likelihood**	**Weight (ω)**	**Parameters**
MONTH + SPP*	160.5	0	1.000	0.350	9
SPP	161.7	1.2	0.549	0.192	6
MONTH + SPP + SEX	162.5	2	0.368	0.129	10
SPP + SEX	163.7	3.2	0.202	0.071	7
MONTH + SPP * SEX	163.8	3.3	0.192	0.067	11
SPP + SVL	163.8	3.3	0.192	0.067	7
SPP * SEX	164.8	4.3	0.116	0.041	8
MONTH * SPP	165.2	4.7	0.095	0.033	12
SPP + SEX + SVL	165.9	5.4	0.067	0.024	8
SPP * SEX + SVL	167.1	6.6	0.037	0.013	9
MONTH + SPP * SEX + SVL	167.2	6.7	0.035	0.012	12
MONTH	172.5	12	0.002	0.001	8
MONTH + SEX	174.5	14	0.001	0.000	9
SEX	175.1	14.6	0.001	0.000	6
MONTH * SEX	175.9	15.4	0.000	0.000	12
SEX + SVL	176.9	16.4	0.000	0.000	7
MONTH * SPP * SEX	181.3	20.8	0.000	0.000	20

*SPP: Species (corn or eastern rat); SEX: Sex (male or female); MONTH: Months of radio-tracking (June – September); SVL: Standardized snout-vent length; SITE: Study site; TECH: Implantation technique

Table 2.11. Parameter estimates (logit scale) obtained from restricted data set repeated measures analysis of movement frequency for rat snakes radio-tracked during June - September, 2002 and 2003 at TTRS and PH in South Georgia and North Florida.

Model	**Parameter**	**Estimate**	**SE**	**Lower 95% CI**	**Upper 95% CI**
MONTH	Intercept	-0.344	0.211	-0.756	0.069
	June	0.468	0.249	-0.021	0.956
	July	0.545	0.232	0.091	0.999
	Aug	0.565	0.190	0.192	0.938
	SITE	-0.333	0.236	-0.795	0.130
	TECH	-0.034	0.290	-0.603	0.535
Covariance	Autoregressive Correlation Coeff.	0.433			
	Residual	1.735			
SPP*SEX	Intercept	0.087	0.182	-0.270	0.444
	SPP*	0.228	0.265	-0.292	0.747
	SEX	-0.777	0.333	-1.429	-0.125
	SPP*SEX	1.088	0.488	0.132	2.044
	SITE	-0.505	0.199	-0.895	-0.114
	TECH	0.073	0.254	-0.424	0.571
Covariance	Autoregressive Correlation Coeff.	0.189			
	Residual	1.540			
SPP*SEX+SVL	Intercept	0.038	0.182	-0.318	0.393
	SPP	0.216	0.260	-0.294	0.726
	SEX	-0.725	0.327	-1.367	-0.083
	SPP*SEX	1.234	0.489	0.276	2.192
	SVL	0.169	0.113	-0.054	0.391
	SITE	-0.545	0.197	-0.931	-0.159
	TECH	0.242	0.273	-0.293	0.777
Covariance	Autoregressive Correlation Coeff.	0.173			
	Residual	1.501			
MONTH+SPP*SEX	Intercept	-0.290	0.225	-0.732	0.151
	June	0.477	0.235	0.017	0.937
	July	0.553	0.227	0.108	0.999
	August	0.575	0.199	0.185	0.966
	SPP	0.220	0.265	-0.300	0.739
	SEX	-0.811	0.333	-1.463	-0.159
	SPP*SEX	1.096	0.487	0.141	2.051
	SITE	-0.518	0.199	-0.909	-0.128
	TECH	0.004	0.255	-0.496	0.503

Table 2.11 (cont.). Parameter estimates (logit scale) obtained from restricted data set repeated measures analysis of movement frequency for rat snakes radio-tracked during June - September, 2002 and 2003 at TTRS and PH in South Georgia and North Florida.

Model	**Parameter**	**Estimate**	**SE**	**Lower 95% CI**	**Upper 95% CI**
Covariance	Autoregressive Correlation Coeff.	0.243			
	Residual	1.411			

*SPP: Corn snake; SEX: Female; SVL: Standardized snout-vent length; SPP*SEX: Female corn snakes; SITE: TTRS; TECH: Subcutaneous radio implantation technique.

Table 2.12. Parameter estimates (logit scale) obtained from complete data set repeated measures analysis of movement frequency for rat snakes radio-tracked during June - September, 2002 and 2003 at TTRS and PH in South Georgia and North Florida.

Model		**Parameter**	**Estimate**	**SE**	**Lower 95% CI**	**Upper 95% CI**
MONTH+SPP		Intercept	-0.386	0.158	-0.695	-0.076
		June	0.492	0.182	0.134	0.849
		July	0.574	0.173	0.235	0.912
		Aug	0.494	0.149	0.202	0.786
		SPP*	0.354	0.162	0.036	0.671
		SITE	-0.299	0.147	-0.587	-0.010
		TECH	-0.111	0.202	-0.507	0.284
	Covariance	Autoregressive Correlation Coeff.	0.326			
		Residual	1.516			
MONTH+SPP+SEX		Intercept	-0.319	0.160	-0.632	-0.006
		June	0.510	0.181	0.155	0.864
		July	0.589	0.172	0.252	0.926
		Aug	0.506	0.150	0.212	0.799
		SPP	0.351	0.158	0.042	0.660
		SEX	-0.285	0.162	-0.603	0.032
		SITE	-0.308	0.143	-0.589	-0.027
		TECH	-0.131	0.197	-0.516	0.255
	Covariance	Autoregressive Correlation Coeff.	0.301			
		Residual	1.470			
MONTH		Intercept	-0.271	0.153	-0.570	0.028
		June	0.532	0.184	0.171	0.893
		July	0.606	0.173	0.266	0.945
		Aug	0.507	0.148	0.218	0.796
		SITE	-0.273	0.154	-0.575	0.029
		TECH	-0.267	0.201	-0.660	0.126
	Covariance	Autoregressive Correlation Coeff.	0.234			
		Residual	1.600			
MONTH+SEX		Intercept	-0.203	0.155	-0.507	0.101
		June	0.551	0.183	0.192	0.909
		July	0.622	0.172	0.284	0.960
		Aug	0.519	0.148	0.229	0.808
		SEX	-0.293	0.171	-0.628	0.041
		SITE	-0.282	0.151	-0.577	0.013
		TECH	-0.285	0.196	-0.669	0.100

Table 2.12 (cont). Parameter estimates (logit scale) obtained from complete data set repeated measures analysis of movement frequency for rat snakes radio-tracked during June - September, 2002 and 2003 at TTRS and PH in South Georgia and North Florida.

Model	**Parameter**	**Estimate**	**SE**	**Lower 95% CI**	**Upper 95% CI**
Covariance	Autoregressive Correlation Coeff.	0.354			
	Residual	1.551			
MONTH+SPP*SEX	Intercept	-0.278	0.163	-0.597	0.042
	June	0.514	0.181	0.160	0.868
	July	0.594	0.172	0.257	0.931
	August	0.506	0.150	0.212	0.800
	SPP	0.257	0.178	-0.092	0.607
	SEX	-0.414	0.201	-0.807	-0.021
	SPP*SEX	0.371	0.343	-0.301	1.044
	SITE	-0.337	0.144	-0.619	-0.054
	TECH	-0.139	0.195	-0.521	0.243
Covariance	Autoregressive Correlation Coeff.	0.289			
	Residual	1.454			
MONTH*SPP	Intercept	-0.298	0.174	-0.638	0.042
	June	0.242	0.221	-0.191	0.675
	July	0.524	0.207	0.118	0.930
	August	0.447	0.176	0.103	0.791
	SPP	0.079	0.290	-0.490	0.647
	June*SPP	0.718	0.382	-0.030	1.465
	July*SPP	0.152	0.360	-0.552	0.857
	Aug*SPP	0.147	0.314	-0.467	0.762
	SITE	-0.310	0.146	-0.596	-0.023
	TECH	-0.087	0.201	-0.479	0.306
Covariance	Autoregressive Correlation Coeff.	0.333			
	Residual	1.464			
SPP	Intercept	-0.007	0.113	-0.229	0.215
	SPP	0.393	0.158	0.083	0.703
	SITE	-0.296	0.144	-0.579	-0.014
	TECH	-0.003	0.195	-0.386	0.380
Covariance	Autoregressive Correlation Coeff.	0.248			
	Residual	1.605			

Table 2.12 (cont). Parameter estimates (logit scale) obtained from complete data set repeated measures analysis of movement frequency for rat snakes radio-tracked during June - September, 2002 and 2003 at TTRS and PH in South Georgia and North Florida.

Model		**Parameter**	**Estimate**	**SE**	**Lower 95% CI**	**Upper 95% CI**
SPP+SEX		Intercept	0.060	0.119	-0.174	0.293
		SPP	0.393	0.155	0.090	0.696
		SEX	-0.244	0.160	-0.557	0.069
		SITE	-0.304	0.141	-0.580	-0.028
		TECH	-0.019	0.191	-0.394	0.356
	Covariance	Autoregressive Correlation Coeff.	0.225			
		Residual	1.572			
MONTH+SPP*SEX+SVL		Intercept	-0.282	0.163	-0.602	0.038
		June	0.517	0.181	0.163	0.871
		July	0.597	0.172	0.259	0.934
		August	0.507	0.150	0.213	0.801
		SPP	0.256	0.178	-0.094	0.606
		SEX	-0.405	0.202	-0.800	-0.009
		SPP*SEX	0.399	0.352	-0.292	1.089
		SVL	0.028	0.079	-0.127	0.182
		SITE	-0.349	0.148	-0.640	-0.058
		TECH	-0.120	0.203	-0.517	0.278
	Covariance	Autoregressive Correlation Coeff.	0.289			
		Residual	1.453			

[*]SPP: Corn snake; SEX: Female; SVL: Standardized snout-vent length; SPP*SEX: Female corn snakes; SITE: TTRS; TECH: Subcutaneous radio implantation technique.

Table 2.13. Parameter estimates (ln transformed) obtained from restricted data set repeated measures analysis of distance traveled per movement for rat snakes radio-tracked at TTRS and PH during June - September, 2002 and 2003 in South Georgia and North Florida.

Model	**Parameter**	**Estimate**	**SE**	**Lower 95% CI**	**Upper 95% CI**
SPP*SEX+SVL[*]	Intercept	4.646	0.113	4.424	4.867
	SPP	-0.154	0.164	-0.475	0.167
	SEX	0.356	0.206	-0.047	0.758
	SPP*SEX	-0.714	0.306	-1.313	-0.115
	SVL	0.128	0.071	-0.011	0.267
	SITE	0.115	0.121	-0.123	0.352
	TECH	0.245	0.164	-0.076	0.565
Covariance	Autoregressive Correlation Coeff.	0.234			
	Residual	0.154			
SPP*SEX	Intercept	4.686	0.117	4.456	4.916
	SPP	-0.139	0.173	-0.478	0.199
	SEX	0.323	0.216	-0.101	0.746
	SPP*SEX	-0.842	0.314	-1.457	-0.226
	SITE	0.143	0.127	-0.105	0.391
	TECH	0.117	0.156	-0.190	0.423
Covariance	Autoregressive Correlation Coeff.	0.268			
	Residual	0.168			

[*] SPP: Corn snake; SEX: Female; SVL: Standardized snout-vent length; SPP*SEX: Female corn snakes; SITE: TTRS; TECH: Subcutaneous radio implantation technique.

Table 2.14. Parameter estimates (ln transformed) obtained from complete data set repeated measures analysis of distance traveled per movement for rat snakes radio-tracked during June - September, 2002 and 2003 at TTRS and PH in South Georgia and North Florida.

Model		Parameter	Estimate	SE	Lower 95% CI	Upper 95% CI
MONTH+SPP		Intercept	4.692	0.101	4.495	4.889
		June	0.265	0.116	0.038	0.492
		July	0.021	0.112	-0.199	0.241
		August	0.093	0.101	-0.104	0.290
		SPP	-0.407	0.098	-0.600	-0.214
		SITE	-0.053	0.089	-0.226	0.121
		TECH	-0.025	0.119	-0.258	0.207
	Covariance	Autoregressive Correlation Coeff.	0.219			
		Residual	0.183			
SPP		Intercept	4.789	0.071	4.650	4.928
		SPP	-0.399	0.099	-0.593	-0.205
		SITE	-0.058	0.089	-0.233	0.118
		TECH	-0.009	0.119	-0.242	0.224
	Covariance	Autoregressive Correlation Coeff.	0.036			
		Residual	0.186			
MONTH+SPP+SEX		Intercept	4.705	0.103	4.504	4.906
		June	0.270	0.116	0.043	0.497
		July	0.027	0.112	-0.194	0.247
		August	0.097	0.101	-0.101	0.294
		SPP	-0.408	0.098	-0.600	-0.215
		SEX	-0.061	0.102	-0.261	0.139
		SITE	-0.055	0.089	-0.228	0.119
		TECH	-0.030	0.119	-0.264	0.203
	Covariance	Autoregressive Correlation Coeff.	0.219			
		Residual	0.183			
SPP		Intercept	4.802	0.076	4.652	4.951
		SPP	-0.398	0.099	-0.592	-0.204
		SEX	-0.047	0.103	-0.248	0.155
		SITE	-0.059	0.090	-0.235	0.116
		TECH	-0.012	0.119	-0.246	0.221
	Covariance	Autoregressive Correlation Coeff.	0.037			
		Residual	0.191			

Table 2.14 (cont.). Parameter estimates (ln transformed) obtained from complete data set repeated measures analysis of distance traveled per movement for rat snakes radio-tracked during June - September, 2002 and 2003 at TTRS and PH in South Georgia and North Florida.

Model		**Parameter**	**Estimate**	**SE**	**Lower 95% CI**	**Upper 95% CI**
MONTH+SPP*SEX		Intercept	4.681	0.104	4.477	4.884
		June	0.265	0.115	0.039	0.492
		July	0.020	0.112	-0.200	0.240
		August	0.093	0.101	-0.105	0.291
		SPP	-0.349	0.111	-0.566	-0.132
		SEX	0.022	0.125	-0.223	0.268
		SPP*SEX	-0.234	0.214	-0.654	0.186
		SITE	-0.036	0.089	-0.210	0.138
		TECH	-0.024	0.117	-0.253	0.206
	Covariance	Autoregressive Correlation Coeff.	0.206			
		Residual	0.180			
SPP+SVL		Intercept	4.788	0.041	4.708	4.869
		SPP	-0.395	0.099	-0.589	-0.200
		SVL	0.020	0.047	-0.072	0.111
		SITE	-0.065	0.091	-0.243	0.113
		TECH	0.005	0.123	-0.236	0.247
	Covariance	Autoregressive Correlation Coeff.	0.187			
		Residual	0.193			
SPP*SEX		Intercept	4.772	0.079	4.617	4.927
		SPP	-0.338	0.111	-0.556	-0.121
		SEX	0.040	0.126	-0.207	0.287
		SPP*SEX	-0.244	0.216	-0.667	0.179
		SITE	-0.040	0.090	-0.215	0.136
		TECH	-0.006	0.117	-0.236	0.223
	Covariance	Autoregressive Correlation Coeff.	0.173			
		Residual	0.191			

[*] SPP: Corn snake; SEX: Female; SVL: Standardized snout-vent length; SPP*SEX: Female corn snakes; SITE: TTRS; TECH: Subcutaneous radio implantation technique.

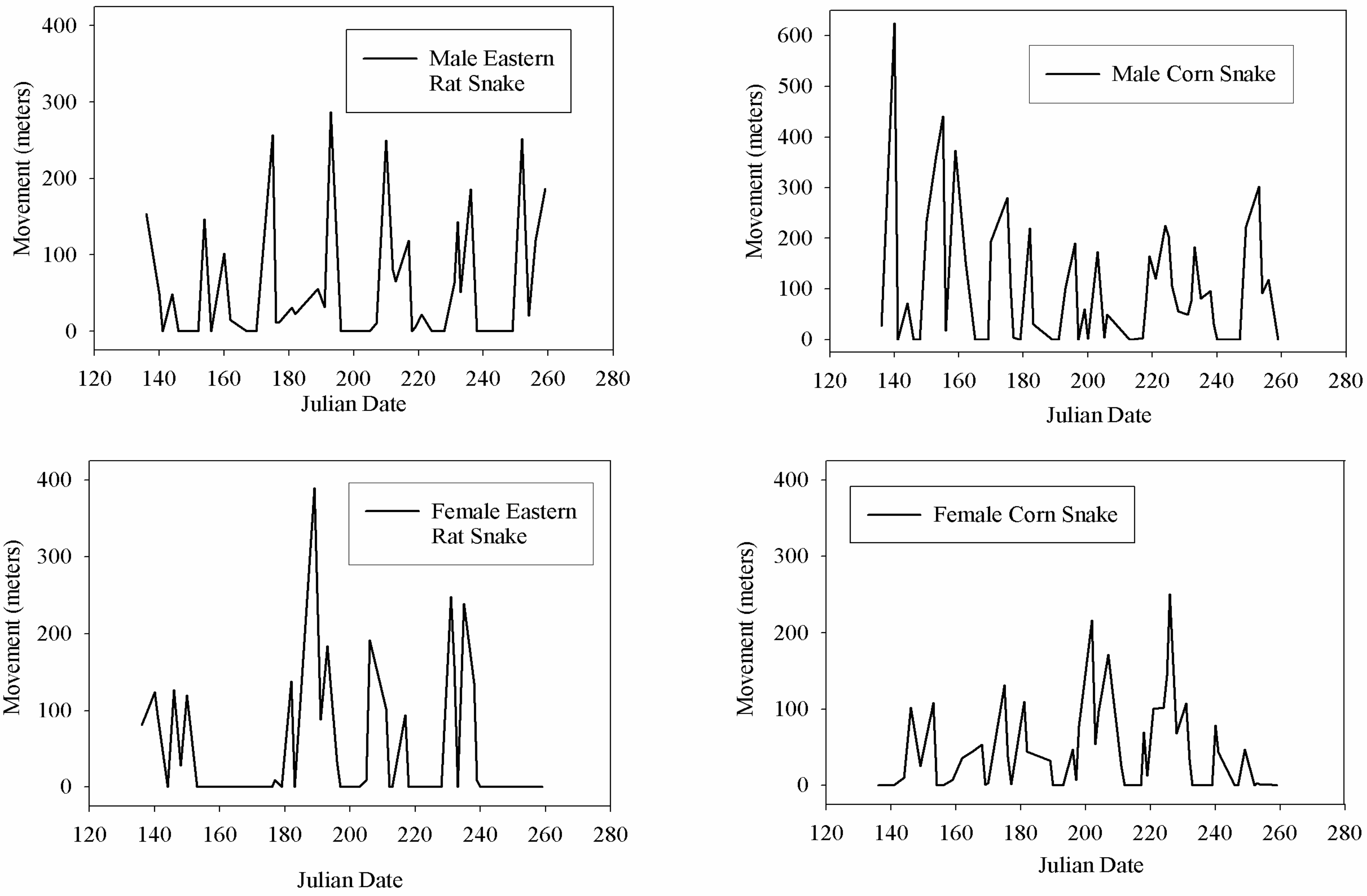

Figure 2.1 Movement trajectories of 4 snakes radio-tracked at Pebble Hill Plantation in South Georgia during May 15 – September 15, 2003. Note the different movement scale of the male corn snake.

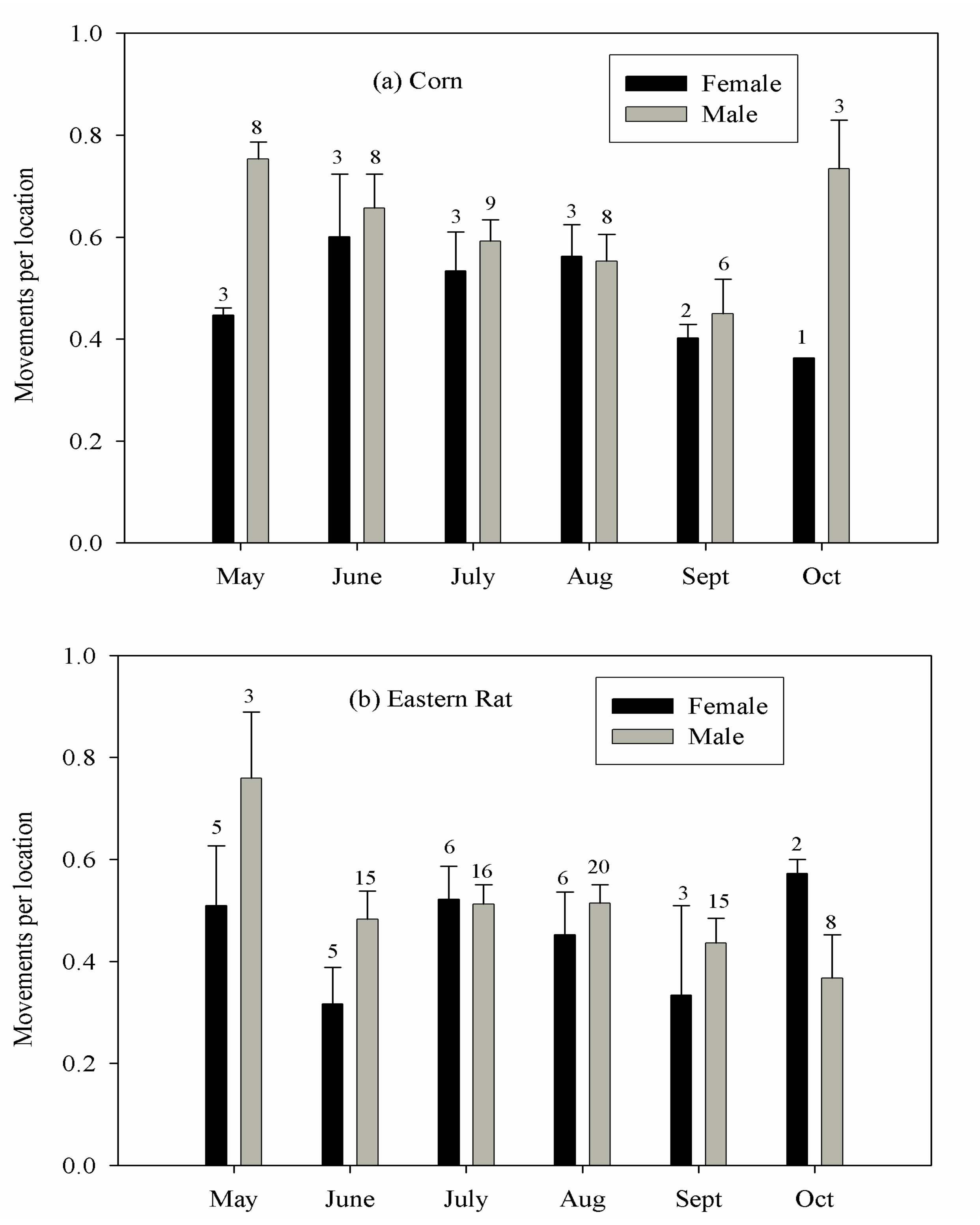

Figure 2.2. Proportion of movements per telemetry location (±SE) for (a) corn snakes and (b) eastern rat snakes radio-tracked at Tall Timbers Research Station and Pebble Hill Plantation in South Georgia and North Florida during 2002 – 2003. Sample sizes are noted above error bars.

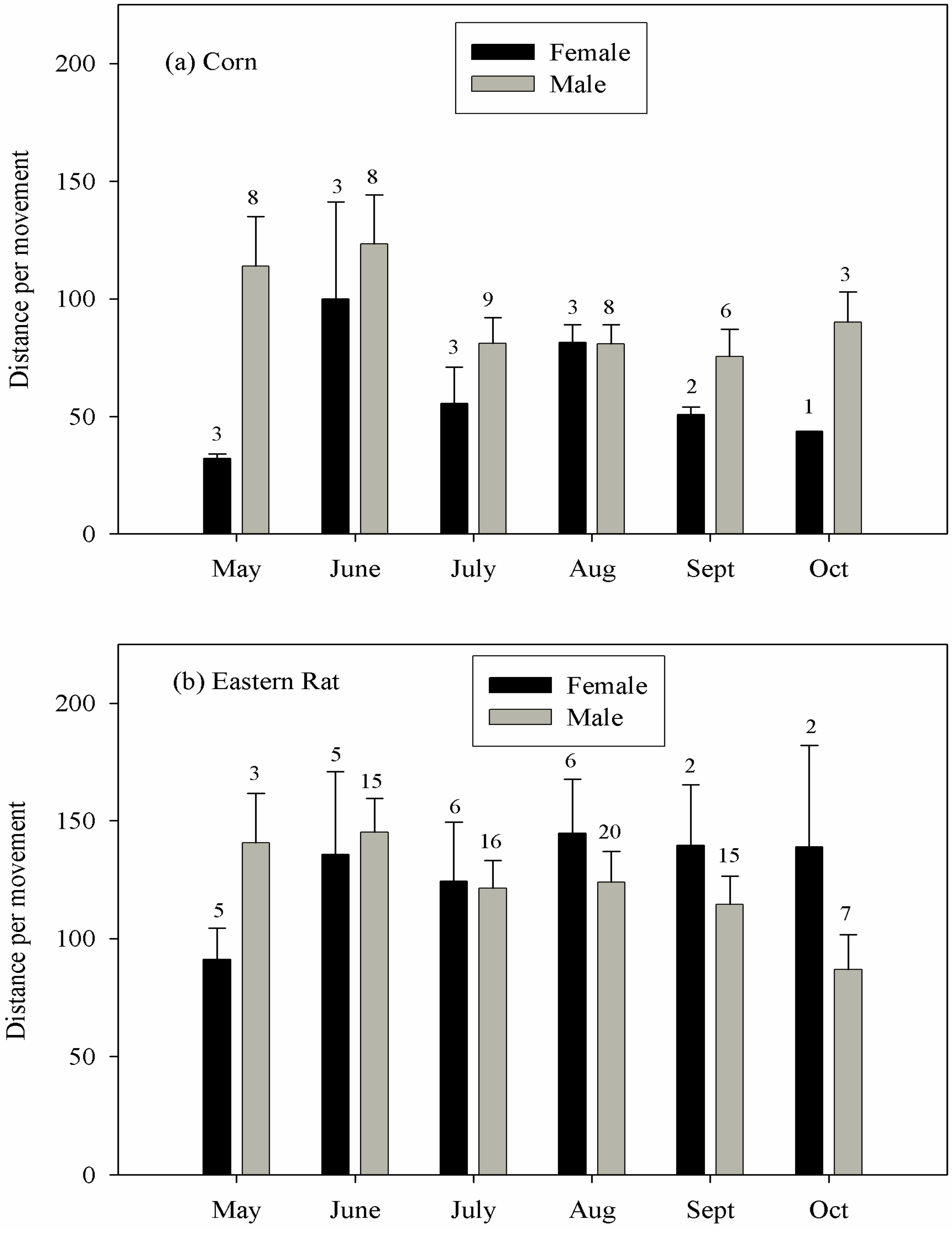

Figure 2.3. Proportion of movements per telemetry location (±SE) for (a) corn snakes and (b) eastern rat snakes radio-tracked at Tall Timbers Research Station and Pebble Hill Plantation in South Georgia and North Florida during 2002 – 2003. Sample sizes are noted above error bars.

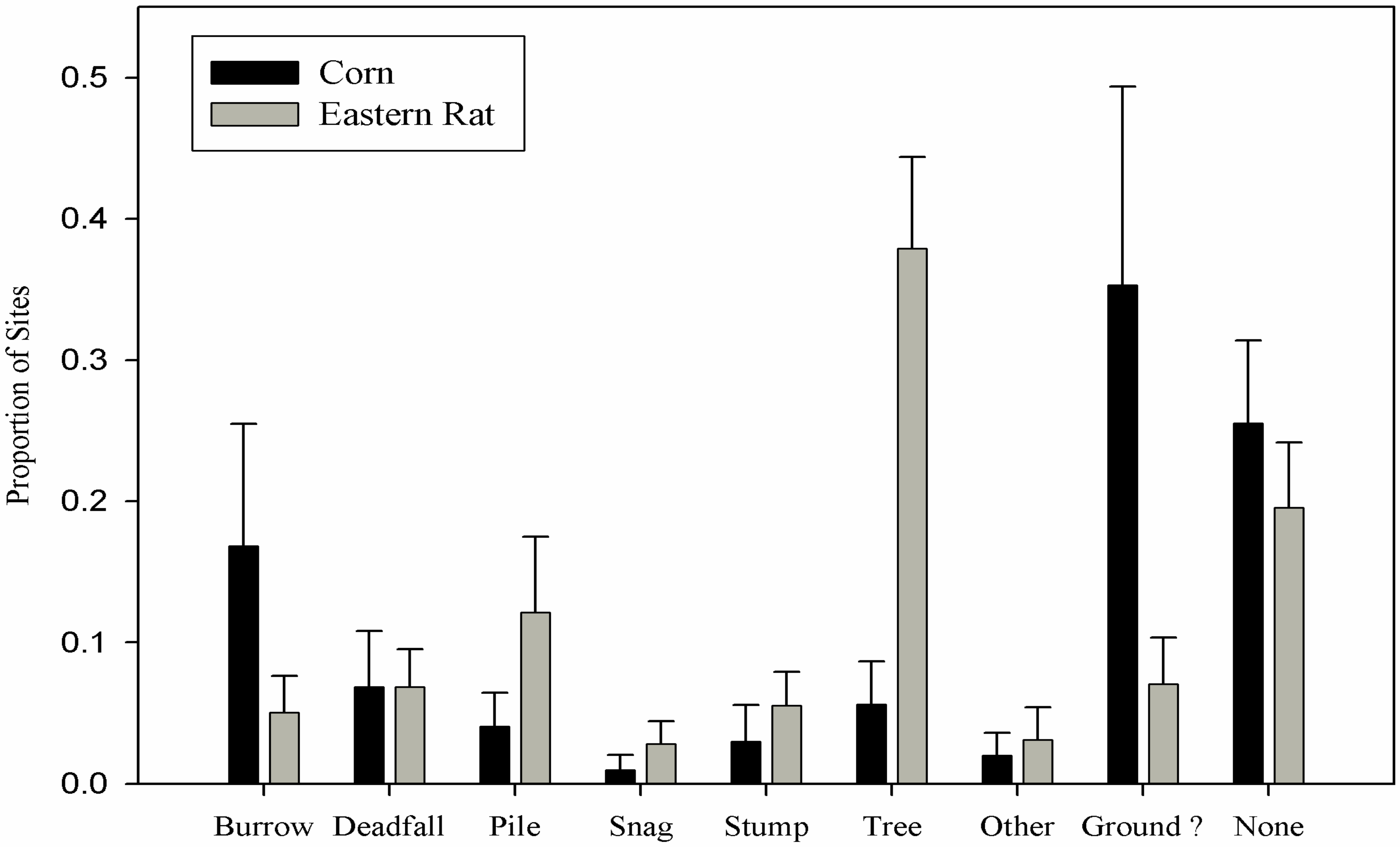

Figure 2.4. Proportion of telemetry sites (±95% CI) in which corn snakes (n=14) and eastern rat snakes (n=31) used various structural habitat features. Data are from radio-tracking during 2002-2004 at TTRS and PH in South Georgia and North Florida. "Ground ?" refer to locations in which an individual was either on ground or underground and use of structure was unknown (e.g., using either small mammal burrow or no structure).

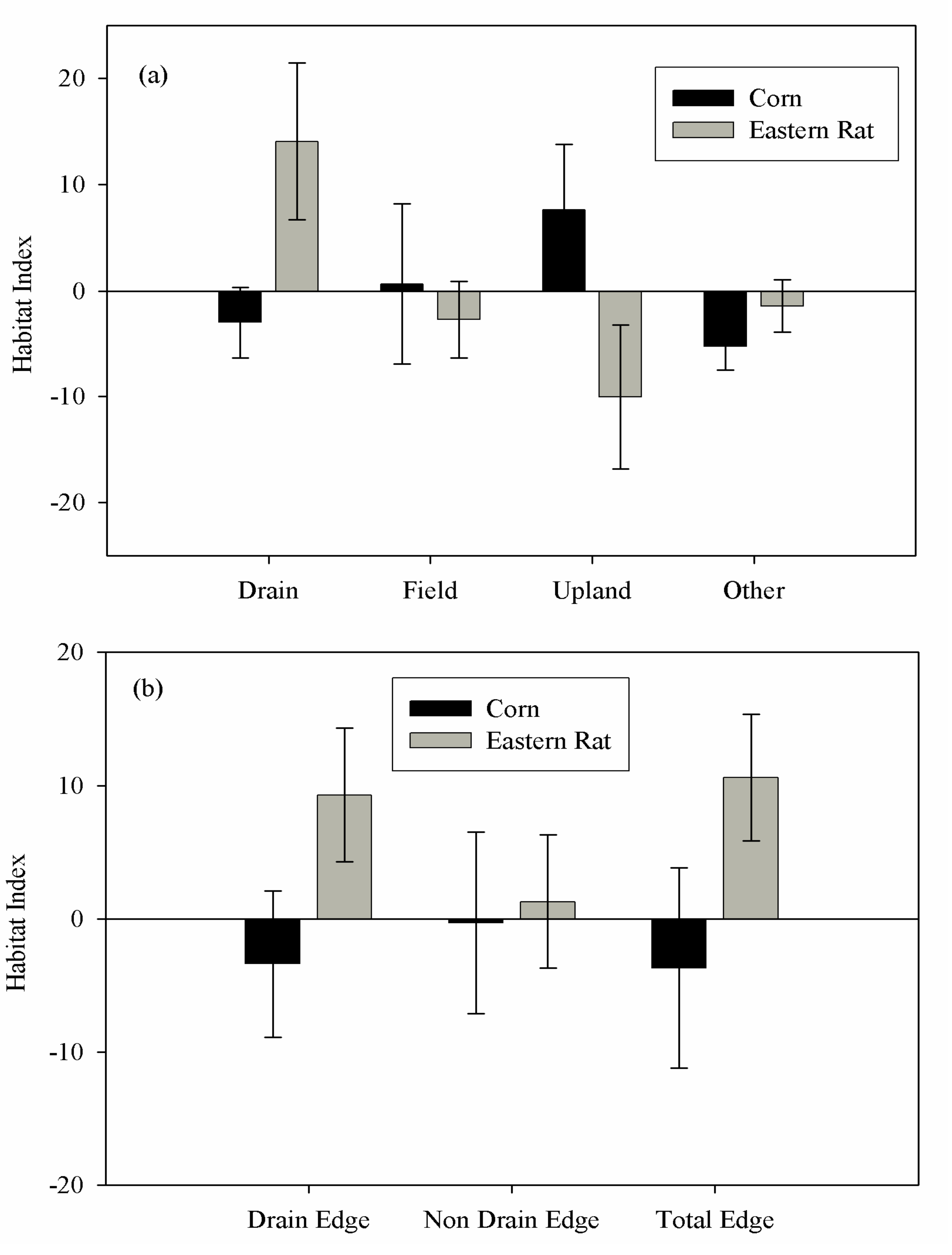

Figure 2.5. Second order habitat selection values (± 95% CI) of (a) macrohabitat type and (b) edges for corn (n=14) and eastern rat snakes (n=31) radio-tracked at Tall Timbers Research Station and Pebble Hill Plantation in South Georgia and North Florida during 2002 – 2004. The habitat index was computed as percentage of habitat used minus percentage of habitat available for each individual.

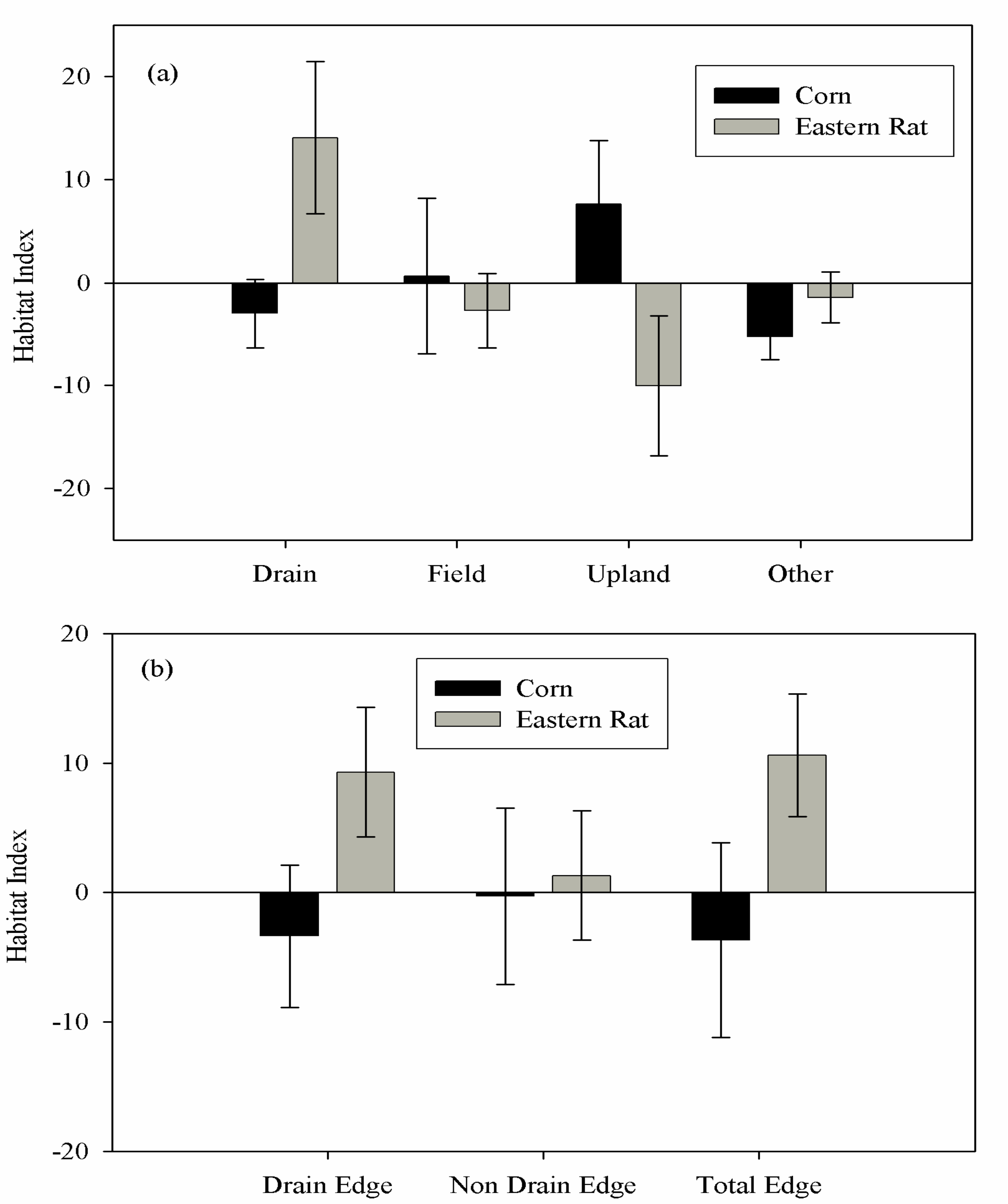

Figure 2.6. Third order habitat selection values (± 95% CI) of (a) macrohabitat type and (b) edges for corn (n=14) and eastern rat snakes (n=31) radio-tracked at Tall Timbers Research Station and Pebble Hill Plantation in South Georgia and North Florida during 2002 – 2004. All individuals are included. The habitat index was computed as percentage of habitat used minus percentage of habitat available for each individual.

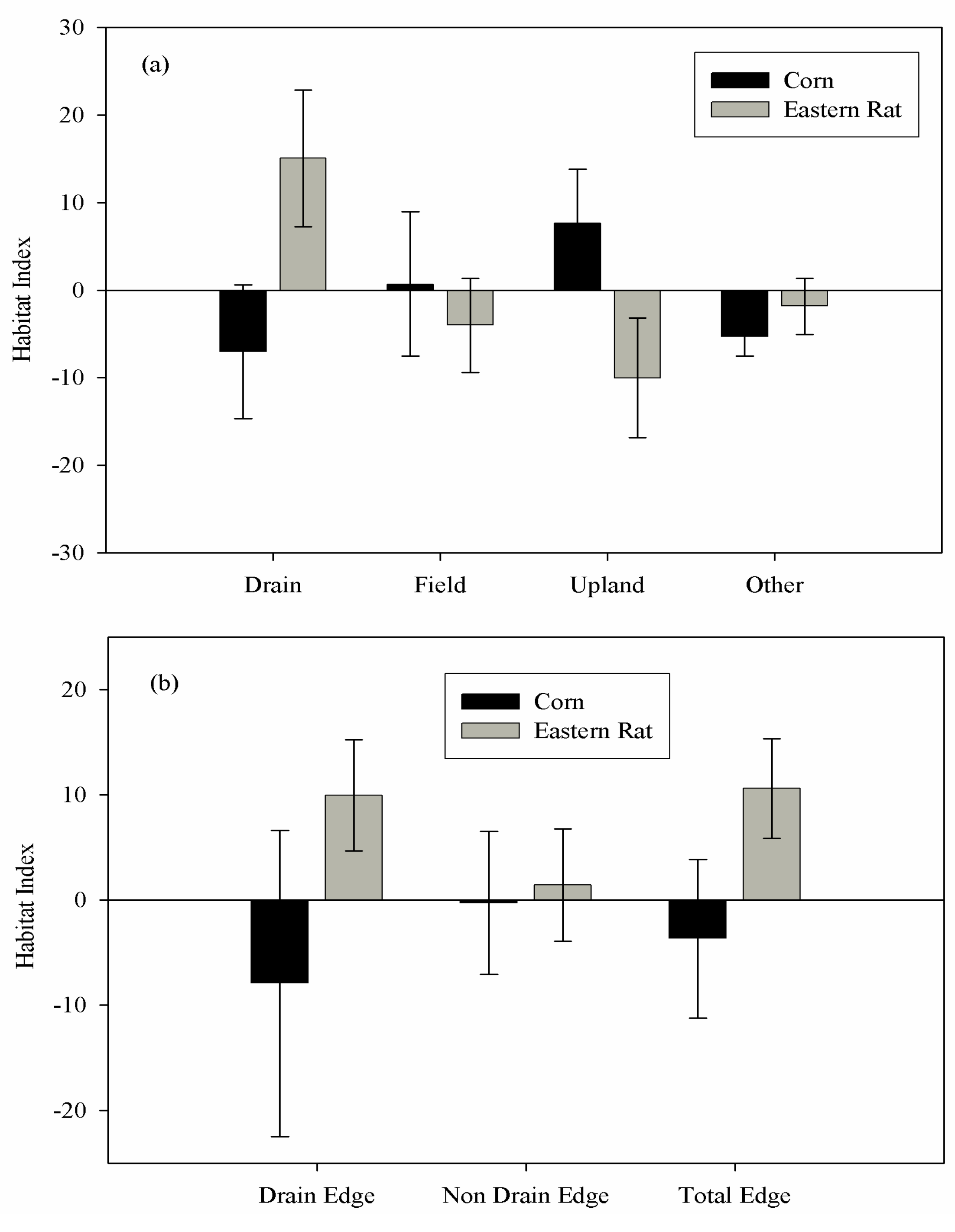

Figure 2.7. Third order habitat selection values (±95% CI) of (a) macrohabitat type and (b) edges for corn (n=14) and eastern rat snakes (n=31) radio-tracked at Tall Timbers Research Station and Pebble Hill Plantation in South Georgia and North Florida during 2002 – 2004. Only individuals having a particular habitat type available are included in that category. The habitat index was computed as percentage of habitat used minus percentage of habitat available for each individual.

CHAPTER 3

ECOLOGY OF SNAKE COMMUNITIES IN MANAGED UPLAND PINE FORESTS IN THE RED HILLS OF GEORGIA AND FLORIDA[1]

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[1] Stapleton, S.P., J.P. Carroll, and W.E. Palmer. To be submitted to *Southeastern Naturalist*.

Abstract

Intensive land management regimes implemented in portions of the Southeast and perceived declining populations have established a need for collection of baseline data addressing both community and species level ecology of snakes. I studied snake community assemblages and activity patterns by season and macrohabitat type during 2002 - 2003 at 3 sites in the Red Hills region of southern Georgia and northern Florida. I recorded 1956 captures representing 16 species during 9012 drift fence array nights. Black racers (*Coluber constrictor*), corn snakes (*Pantherophis guttatus*), eastern rat snakes (*Pantherophis alleghaniensis*), cottonmouths (*Agkistrodon piscivorus*), eastern garter snakes (*Thamnophis sirtalis*), and eastern coachwhips (*Masticophis flagellum*) constituted the majority of captures. Species exhibited differences in seasonal movements, with activity of most common species peaked in early spring to early summer. Adult male movements generally were driving the peaks of observed patterns. Captures also varied by habitat among species, and common species demonstrated seasonal partitioning of activity by habitat. Such differences may be driven by differences in foraging ability and shifts in prey availability or thermoregulatory requirements. Recaptures of black racers suggest the development of an aversion to box traps, although potential causes such as visual or olfactory cues remain speculative at this point. My data suggest that the managed upland pine forests support an abundant upland snake community. As development and habitat loss progress in the region, these managed lands will prove increasingly important to conservation efforts.

Introduction

Although community research of taxa such as fish, birds, and mammals has advanced in the past several decades, there remains a relative dearth of research examining snake community ecology (Vitt 1987). Long-term and baseline studies assessing demographics and dynamics are largely absent (Parker and Plummer 1987, Vitt 1987, Dodd 1995, Gibbons et al. 2000). Furthermore, anecdotal evidence and research biases compromise much of the available literature, (Parker and Plummer 1987, Dodd 1987, Dodd 1993), rendering results and conclusions potentially invalid. Researchers frequently attribute such deficiencies to difficulties snakes present, such as cryptic behaviors, low detectability rates and perceived low densities, and irregular foraging and activity patterns (Parker and Plummer 1987, Vitt 1987, Gibbons et al. 2000). However, solutions such as development of innovative approaches and proper pairing of question and technique allow researchers to overcome some of these perceived difficulties (Seigel 1993).

Wide-scale loss of upland habitats including longleaf pine (*Pinus palustris*) forests has occurred in the Southeast (Frost 1993, Ware et al. 1993). Subsequent declines of a host of faunal species, particularly the Northern bobwhite (*Colinus virginianus*; hereafter bobwhite) (Brennan 1991, Church et al. 1993), have resulted in application of intensive management regimes. Such management focuses on the maintenance of open, savannah-like upland habitats via prescribed burning and mechanical methods to inhibit upland hardwood encroachment. Although these ecosystems are granted much conservation attention, associated snake communities remain largely unstudied. Regional studies have addressed some individual species [e.g., black racers (*Coluber constrictor*) (Plummer and Congdon 1994); eastern hognose (*Heterodon platirhinos*) (Plummer and Mills 2000); rat snakes (*Pantherophis* spp.) (Franz 1995, Mullin et al. 2000, Burger et al. unpubl. data); eastern diamondback rattlesnakes (*Crotalus adamanteus*) (Martin and Means 2000); cottonmouths (*Agkistrodon piscivorus*) (Cross and Petersen 2001)]. However, consideration of community-level ecology is more limited in scope [e.g., peninsular Florida

(Campbell and Cristman 1982, Dodd and Franz 1995, Enge and Wood 2002) and Savannah River Ecology Laboratory in South Carolina (e.g., Gibbons and Semlitsch 1991)].

Although literature is sparse, some fundamental patterns of snake community ecology are recognized. Species richness tends to increase with lower latitudes and greater habitat complexity (Vitt 1987). Species diversity follows a similar relationship with latitude (Dalrymple et al. 1991*a*), although estimates of relative abundance should be viewed cautiously because of potential biases associated with capture techniques (Vitt 1987). Richness and abundance of prey types may underlie the apparent relationships between community structure, latitude, and other factors (Vitt 1987).

The Southeast has the highest reptile richness in the United States (Kiester 1971). Dodd (1995) identifies nearly 50 snake species overlapping the historical range of longleaf pine, and Guyer and Bailey (1993) and Means (2004) list 25 and 29 species resident in longleaf pine savannahs, respectively. Numerous snake species associated with historical longleaf pine forests are presumably in decline (Guyer and Bailey 1993, Dodd 1995, Tuberville et al. 2000, Means 2004, USFWS 2004), underscoring assessment of snake communities in managed uplands as a research priority.

General works addressing the effects of management on herpetofaunal communities provide further insight. Prescribed fire is necessary to maintain fire-adapted herpetofaunal communities in the Southeast (Means and Campbell 1981). Frequent (1 to 3 year) fire intervals are necessary to maintain diverse amphibian assemblages (Means et al. 2004). Further research suggests that reptile diversity increases with prescribed fire in pine sandhills (Mushinsky 1985). An adverse response to recently burned lands may appear in some snakes (Cavitt 2000, Setser and Cavitt 2003), but recolonization of the burned tracts can occur quickly (Setser and Cavitt 2003).

Furthermore, direct mortality from fire is minimal and is largely outweighed by the beneficial effects to herpetofauna (Means and Campbell 1981).

Forest management techniques such as clearcuts may result in initial negative effects, but with subsequent rebounds (Russell et al. 2002). The effects of clearcuts on reptile communities may also mimic intense wildfire and subsequent salvage logging in scrub habitats (Greenberg et al. 1994*a*). Responses to fire and timber management, of course, vary depending on species requirements (Greenberg et al. 1994*a*, McLeod and Gates 1998).

A mosaic of burned and unburned parcels is optimal for providing refuges for fire-adapted snakes (Setser and Cavitt 2003). Such disturbance-maintained patchwork habitats may result in increased herpetofaunal diversity (McLeod and Gates 1998). Similarly, Vitt (1987) suggests that snake species richness tends to increase with greater habitat diversity. These studies suggest that the Southeast's upland pine forests may thus be conducive to a diverse and abundant upland snake community. However, Russell et al. (1999) note that research must continue to establish components of general ecology in fire-dependent systems.

My objectives for this study are:

1. To assess snake community structure in intensively managed upland pine forests.
2. To document seasonal activity patterns and macro-habitat associations of the snake community in intensively managed upland pine forests.

Study Areas

Research was conducted in the Red Hills region of northern Florida and southern Georgia between Tallahassee, Florida, and Thomasville, Georgia. The region, dominated by upland pine forests, is intensively managed for bobwhite. Annual prescribed burning and extensive mechanical techniques are employed to inhibit upland encroachment of hardwood trees;

additional practices such as supplemental feeding and meso-mammalian predator control are implemented as well. Three individual areas functioned as the study sites: Tall Timbers Research Station (TTRS), Pebble Hill Plantation (PH), and the Wade Tract (WT).

TTRS, located in Leon County, Florida, covers approximately 1,500-ha. The site primarily consists of upland loblolly (*Pinus taeda*), longleaf (*P. palustris*) and shortleaf (*Pinus echinata*) pine forests interspersed with bottomland hardwood drains and annually harrowed fields. Common drain species include oaks (*Quercus* spp.), hickories (*Carya* spp.), sweet gum (*Liquidambar styraciflua*), and black gum (*Nyssa sylvatica*). Mature hardwoods also dot portions of the upland landscape. Old-field vegetation is the dominant groundcover type (including *Andropogon*, *Lespedeza*, and *Quercus* spp.) with limited native groundcover [e.g., wiregrass (*Aristida stricta*)]. Soils are primarily clay, and a large lake establishes the southern border.

PH covers approximately 1,250 ha in Thomas and Grady Counties, Georgia. The area also is dominated by an upland longleaf, loblolly, and shortleaf pine forest. PH also contains numerous bottomland hardwood drains and annually harrowed fields as well as stands of planted loblolly pines. Drain hardwood species composition and presence of upland hardwoods are similar to TTRS. Vegetation at PH spans a continuum from old-field vegetation to intact native groundcover. Soils range from clay to sand.

WT is a 100-ha plot located on Arcadia Plantation in Thomas County, Georgia. The site is an entirely intact longleaf pine – wiregrass ecosystem with few mature upland hardwoods. An ephemeral wetlands area is located in the northeast region of the plot. Soils are sandy.

Methods

Trapping Arrays

Snakes were captured with 1-m high drift fences used in conjunction with hardware cloth funnel traps (Fitch 1987) and large box traps constructed of plywood and hardware cloth (D. Richardson, pers. comm.). Arrays were arranged such that 4 7.5-m arms radiated from the central box trap. One funnel trap was set at the distal end of each arm. A hardware cloth partition in the funnel prevented snakes from avoiding a trap after following the fence length. Leaves, grass, soil, and debris were scattered in the funnel opening to simulate a natural entrance. Pine boughs and other natural covers were placed over funnel traps to provide cover from predators and reduce the risk of hyperthermia.

In 2002, 24 arrays were randomly distributed at TTRS and PH in 3 habitats: bottomland hardwood drains, managed upland pine forests, and an intermediate ‘buffer’ zone. Four arrays were placed in each of the habitat types per site using ArcView GIS (Arcview version 3.2, ESRI systems), with minimum spacing between arrays typically at least 300 m. The intermediate zone was delineated by establishing a buffer zone around hardwood drains of approximately 100 m. Hence, the habitats represent differing degrees of association with bottomland hardwood drains. Upland and intermediate zone fences were evenly distributed between burned and unburned parcels to obtain a representative sample of the habitats.

In 2003, 42 total trap arrays were distributed among TTRS, PH, and WT. Arrays from 2002 were relocated to new sites. As in 2002, 24 arrays were randomly distributed among the 3 aforementioned habitats at TTRS and PH. Additionally, fields were included as a habitat type at TTRS and PH, and 3 arrays were set in fields at each site. Spacing from 2002 arrays and between 2003 arrays was increased to at least 400 m to achieve greater independence between traps. Six fences were placed in upland pine forest at WT, with arrays evenly distributed between burned and unburned parcels. Because of logistical constraints, WT arrays were spaced at approximately 250-m intervals. The remaining 6 fences were configured into a 2x3 grid at TTRS with arrays spaced at 150-m intervals. The grid served as a pilot study to assess the efficacy of estimation of demographic parameters and movements for various species.

In 2002, traps were opened sporadically from March through October, with fences set for at least 11 trap nights per month. In 2003, to maintain a more consistent trap effort and permit seasonal comparisons, arrays were set for 18 trap nights per month from March through October with 1 exception. In early May at WT, the 3 fences located in a parcel to be burned were removed. Weather conditions, however, did not permit burning of this parcel until the end of May. These traps were set for longer periods in June and July to standardize annual trapping effort, but May data does not exist for these 3 fences.

Fences were checked as early as possible after sunrise. Non-target captures (e.g., small mammals, birds, other herpetofauna, insects) were immediately released from traps. Venomous snakes [i.e., eastern diamondback rattlesnakes, cottonmouths, pygmy rattlesnakes (*Sistrurus miliarius*)] were recorded and generally released immediately. All non-venomous captures returned to TTRS for processing.

Marking and Processing

Snakes were measured [snout-vent length (SVL) to cm, mass to gram] and sexed by probing for inverted hemipenes. Black racers, eastern rat snakes, corn snakes, and eastern coachwhips (*Masticophis flagellum*) were individually marked via subcutaneous implantation of a passive integrated transponder (PIT) tag ventrally approximately 5 to 10 cm anterior to the vent. Procedures were modified from Reading and Davies (1996). Individuals of other nonvenomous species were marked via a unique ventral scute clip (Brown and Parker 1976). Some coachwhips were marked via scute clipping rather than PIT tagging in 2002. During April - October 2003, individuals which were marked with a PIT tag also were marked with a non-unique scute clip posterior to the vent to assess PIT tag loss or failure. Snakes typically were released within 24 hours at the capture location. Some eastern rat snakes and corn snakes were collected as part of a radio-telemetry study, handled according to those protocols, and subsequently released (see Chapters 2 and 4). Collection and marking procedures were covered under: University of Georgia IACUC permit number A2001-10100-c1, c2; Georgia collection permit numbers 29-WMB-01-80 (2002) and 29-WMB-04-128 (2003), and Florida collection permit numbers WX01277 (2001-02) and WX02136 (2002-03).

Analyses

I calculated detected site-wide and pooled diversity using the Shannon-Weiner diversity (H') and equitability (E') statistics. Although I did not estimate detectability to calibrate the diversity indices, these statistics are useful for comparative purposes between sites and with other studies. Individuals of nonvenomous species and all captures of venomous species were included in diversity and equitability estimates because venomous species were not marked.

Captures may be used as an index of snake activity (Gibbons and Semlitsch 1987). Therefore, to assess general seasonal activity patterns, I initially computed total individuals captured per month and total captures (i.e., individuals and recaptures) by month for commonly detected species. When adequate samples permitted, data were separated by site to assess local variation in activity and then pooled to assess regional activity patterns. To facilitate comparisons with WT, I standardized total captures to attain captures per unit effort (100 trap array nights). Individuals captured and total captures revealed nearly identical trends of activity.

To avoid individuals counted multiple times within a month, results are presented in terms of individuals captured by month. For 4 common species with adequate samples [black racers, coachwhips, corn snakes, and eastern rat snakes], I used pooled data from PH and TTRS to examine sexual and size differences in activity patterns. I categorized individuals as adult male, adult female, or juvenile using estimates of size at maturity obtained from literature (Wright and Wright 1957, Fitch 1963*a*, Stickel et al. 1980, Rosen 1991, Ford and Seigel 1994, Mitchell 1994, Blouin-Demers et al. 2002, Ernst and Ernst 2003). No substantial data existed for categorization of maturity in coachwhips; therefore I adopted an approximation of 80 cm for both sexes (Ernst and Ernst 2003). I calculated total detected species richness by month as well.

To examine differences in activity by habitat, I computed detected species richness, individuals captured, and total captures per trapping array by habitat type. As with general seasonal activity patterns, individuals captured per array and total captures per array revealed similar patterns. Results are presented graphically in terms of individuals captured. Although individuals were occasionally captured at different trapping arrays, I considered the arrays independent (i.e., the experimental unit) for calculation of these summary statistics. Because I believed captures within an array may not be independent, I additionally calculated the proportion of arrays detecting the species within a habitat type. To examine seasonal variability of activity by habitat, I calculated individuals captured per array and proportion of arrays detecting a species within habitat by season for these 4 species.

I assessed trap efficiency for box and funnel traps by species using 2003 data and χ^2 statistics. I only considered species with more than 50 individual captures which permitted inclusion of 6 species in the analyses. Funnel traps outnumbered box traps by a 4-to-1 ratio. However I assumed that, if no differences were present, traps should capture equal numbers of individuals given the layout of the arrays and the 4 funnels present on each box trap. Only initial captures were considered to ensure that individual biases would not impact results. I documented enough individual black racer recaptures to examine the development of trap aversion. I again utilized only the first recapture of each individual for these analyses to remove potential individual biases.

I excluded the pilot grid on TTRS from all statistics except trap efficiency due to potentially variable trap biases associated with different array spacing. Because trapping effort varied seasonally in 2002 and between 2002 and 2003, I summarized data from the 2 years separately. Furthermore, due to sporadic trapping effort in 2002, I did not examine components of seasonal variation with 2002 data.

Results

Drift fence arrays were set for 2964 trap nights in 2002 (TTRS: 1488; PH: 1476) and 6048 trap nights in 2003 (TTRS: 2160; PH: 2160; Grid: 864; WT: 864). During 2002, a total of 519 individuals representing 9 nonvenomous species were captured a total of 624 times (Table 3.1). Additionally, 3 venomous species were captured a total of 46 times. Drift fence trapping detected 9 species at TTRS and 12 species at PH in 2002.

During 2003, 920 individuals representing 13 nonvenomous species were captured a total of 1147 times in drift fence arrays (Table 3.2). Three venomous species were captured a total of 139 times. All species which were documented in 2002 also were recorded in 2003. Twelve species were detected at TTRS, 14 species at PH, and 10 species at WT in 2003. The 3 sites shared 9 species in common. Black racers were the dominant species and constituted the majority of captures at TTRS and PH in both 2002 and 2003, and at WT in 2003 (Figure 3.1). Corn snakes and eastern garter snakes (*Thamnophis sirtalis*) constituted a much larger proportion of total captures at WT than at PH and TTRS. Conversely, only 1 eastern rat snake was detected at WT, whereas the species was a relatively common component of the other sites. During 2003, corn snakes comprised a greater proportion of captures than in 2002 at both TTRS and PH. I documented PIT tag loss or malfunction in 4 of 101 individuals recaptured which were double marked; all were black racers.

Estimated diversity and equitability were comparable at TTRS and PH in 2002 (Table 3.3). In 2003, diversity and equitability was higher at both sites but maintained the same relationship (i.e., PH slightly greater than TTRS). WT diversity and equitability were similar to measures computed at other sites. When I considered pooled data, total diversity and equitability increased slightly.

Activity patterns differed by species over the course of the season (Figure 3.2). Generally, capture patterns were highly similar between sites. Most species exhibited unimodal patterns. Black racer captures peaked in April, coachwhip captures during May and June, eastern rat snakes in May, and southern water snake captures in March. Conversely, eastern diamondback captures suggested a bimodal pattern of activity. Other species [e.g., corn snakes, eastern garter snakes, and cottonmouths] exhibited more irregular patterns, with apparent multiple activity peaks varying in amplitude. For the 4 species examined for sexual partitioning of seasonal activity, males were most active early in the spring and generally driving the overall spring peak in activity witnessed with pooled data (Figure 3.3). Female corn snake captures suggested a peak in activity later in early summer, female coachwhips exhibited a peak coinciding with male movements, and female black racers captures declined over the season. Captures of juvenile snakes and female rat snakes were relatively uniform throughout the season, though juvenile corn snake captures suggested a bimodal activity pattern. Captures for common species at WT were similar to the other sites (Figure 3.4). Captures of other species were too limited to assess movement patterns. Total species richness detected was variable during the season, with the greatest number of species observed in March and during the May – June period (Figure 3.5).

Nearly all commonly captured species were detected in each habitat type in both 2002 and 2003 (Figures 3.6 and 3.7). Individuals captured per array and the proportion of arrays which detected a species suggested activities differed by habitat. Black racers, eastern rat snakes, and eastern garter snakes were largely ubiquitous, and detection of cottonmouths and scarlet kingsnakes was relatively uniform among habitats. Conversely, corn snakes, coachwhips, and eastern diamondbacks were detected more frequently in non-drain habitats, and pine snakes (*Pituophis melanoleucus*) and eastern hognose were detected exclusively in non-drain habitats. Southern water snakes (*Nerodia fasciata*) were most commonly captured in drain arrays, but were recorded in other habitats, particularly in 2003. Other species were too infrequently captured to permit examination of habitat trends. Species richness detected by arrays did not differ by habitat in 2002, but non-overlapping confidence intervals demonstrate that drain arrays detected fewer species than did upland and field fences (Figure 3.8).

Further analyses provided evidence of seasonal shifts in activity by habitat for some species. Captures were highly variable among arrays, as evidenced by large standard errors. Corn snake captures were relatively equal among non-drain habitats in spring and fall but were greater in fields during June and July (Figure 3.9). Conversely, eastern rat snakes were most commonly captured in drains in the spring, with activity shifting to uplands in June and July to fields in August and September (Figure 3.10). In October, rat snakes were detected only in drains. Black racer detection was fairly uniform throughout the season, though captures were disproportionately high in fields in April and low in drains from May to June (Figure 3.11). Coachwhip detection was relatively common in fields from May to June but diminished in both April and July as activities shifted to uplands (Figure 3.12).

I found some evidence of differences in trap effectiveness by species ($\chi^2 = 9.60$, 5 df, $P = 0.09$), as eastern rat snakes were captured more frequently than expected in box traps (n = 85, $\chi^2 = 7.35$, 1 df, $P = 0.007$) (Figure 3.13). Other species demonstrated no differences in captures by trap type. Although initial black racer captures did not exhibit differences in trap efficacy, racers were recaptured more frequently in funnel traps (n = 99, $\chi^2 = 11.0$, 1 df, $P < 0.001$). Initial captures of this subsample did not differ by trap ($\chi^2 = 0.49$, 1 df, $P = 0.48$). Racers initially captured in box traps were subsequently recaptured more frequently than expected in funnel traps (n = 46, $\chi^2 = 5.57$, 1 df, $P = 0.02$), and individuals initially captured in funnel traps were recaptured more frequently recaptured than expected in funnel traps as well (n = 53, $\chi^2 =5.46$, 1 df, $P = 0.02$).

Discussion

General Site Trends

Detected species richness, diversity, and equitability were comparable among my study sites. Diversity and equitability indices increased with greater proportions of the longleaf – wiregrass ecosystem on the site, suggesting the importance of this ecosystem in conservation of snake fauna (Guyer and Bailey 1993, Franz 1995, Means 2004). Richness, diversity, and equitability computed from pooled data appear to be in general agreement with latitudinal predictions presented in Vitt (1987) and Dalrymple et al. (1991*a*). Some of the observed changes in diversity and equitability from 2002 to 2003 were probably artifacts of different sampling periods and sampling intensity. Proportionately, more trapping was conducted in the

March to April period in 2002 versus 2003. This sampling shift may have skewed annual results due to the early season peak in black racer activity.

Detected community composition varied somewhat among the 3 sites, however. Site-wide habitat differences including soil composition and proximity to water bodies are probably responsible for some of this disparity. Eastern hognose snakes were captured exclusively at PH in 2003 in uplands, fields, and "buffered" zones. This species preys primarily upon toads and is commonly found in open woodlands and near fields with porous soils (Gibbons and Semlitsch 1991, Palmer and Braswell 1995, Ernst and Ernst 2003). Anecdotally, all captures occurred in arrays located in sandy soils with simultaneous captures of numerous amphibians, particularly eastern spadefoot toads (*Scaphiopus holbrookii*). The eastern hognose also may be present on other sites, particularly at WT given the sandier soils and highly abundant herpetofauna (S. Stapleton, personal observation). Captures of the pine snake, a fossorial upland species presumed to be in decline (Franz 1992, Guyer and Bailey 1993, Dodd 1995, Means 2004), were restricted to the uplands and fields of PH and WT. Eastern diamondbacks, another upland species apparently declining (Dodd 1995, Means 2004), were more commonly captured at PH and WT. Gopher tortoise (*Gopherus polyphemus*) burrows serve as a common refuge for both species (Jackson and Milstrey 1989) and were present at all sites, but were greater in density at PH and WT (S. Stapleton, personal observation). Additionally, the sandier soils of these sites may be more conducive to fossorial behaviors of the pine snake. The scarlet snake is another fossorial upland species generally associated with sandy or well-drained soils (Gibbons and Semlitsch 1991, Palmer and Braswell 1995, Means 2004). Such behavior may thus explain why the species was captured more frequently at PH and WT, with detection rates highest at WT.

Site-wide patterns of more commonly detected species differed among study areas. Because WT traps were only in uplands, comparison is most meaningful between upland areas of all sites. Eastern garter snakes were captured more frequently at WT than either PH or TTRS, whereas captures of black racers and eastern rat snakes at TTRS and PH far exceeded rates at WT. Rat snakes were commonly captured in drains on TTRS and PH. Upland hardwoods and drains are frequently used by rat snakes (Chapter 2, this volume). The absence of these habitat components on WT suggests that hardwoods and/or drain habitat may be important for the presence of eastern rat snakes. A seemingly more abundant herpetofaunal prey base at WT (S. Stapleton, personal observation) may have resulted in higher detection of garter snakes at WT. Estimates of wide-ranging, active species such as the racer may be impacted by trap spacing greater than less mobile species. Apparent site differences in capture rates as well as diversity and equitability indices (WT versus PH and TTRS) should therefore be interpreted cautiously.

Conversely, examination of total site-wide captures reveals that TTRS captures of southern water snakes and cottonmouths far exceeded capture rates at PH and WT. The southern portion of TTRS borders a large wetland, and a sizeable pond is located in the south central portion of the site. Proximity to wetlands at TTRS far exceeds these measures at PH and WT, thus explaining site-wide differences in captures of these species. High spring water levels during 2003 (S. Stapleton, personal observation) probably were responsible for the spike in detected cottonmouth and southern water snake activity at TTRS. Additional site-wide trends such as greater coachwhip detection at PH may likewise be attributable to the wetlands at TTRS. The coachwhip is a wide-ranging upland species (Palmer and Braswell 1995, Ernst and Ernst 2003), and the southern wetland border may create large areas of unsuitable habitat. A possible explanation for low captures of coachwhips at WT versus PH remains unclear.

During 2003, captures of eastern rat snakes were markedly higher at PH than TTRS. Another notable change was the decline of black racer captures from 2002 to 2003 at TTRS, whereas racer captures on PH remained consistent. As previously discussed, some of this difference in racers may be a product of inter-annual variation in sampling. However, management strategies also may have played a role in these observed variations. During 2001 - 2003, meso-mammalian predators [e.g., raccoon (*Procyon lotor*), bobcat (*Lynx rufus*), red fox (*Vulpes vulpes*), gray fox *(Urocyon cinereoargenteus*), armadillo (*Dasypus novemcinctus*), opossum (*Didelphis virginianus*), coyote (*Canis latrans*)] were removed from PH as part of a study examining the effects of predator control programs on bobwhite populations. Research suggests that top-level carnivores may suppress lower predatory species (Palomares et al. 1995, Courchamp et al. 1999, Henke and Bryant 1999). Regionally, meso-mammals are now top-level predators in the ecosystem and may prey on nearly all snake species commonly captured in the region (e.g., Fitch 1963*b*, Ernst and Ernst 2003) and compete with them for trophically lower prey items. Thus, a reduction in meso-mammals may "release" snake populations or alter activity patterns via diminished predation pressure or an increased prey base. Higher detection of these species at PH may thus result from predator management. The crossover design of the predator removal study whereby predator removal will begin on TTRS and will cease on PH should help clarify the impacts of predator removal.

Undetected species

For a 6-year period beginning in 1976, B. Means (unpublished data) documented snakes opportunistically encountered on TTRS. The sampling protocol was not as intensive or systematic as my study, thus precluding absolute comparison of data sets to assess long-term community changes. However, large changes in the snake community and relative rates of detection are noteworthy. Specifically, he recorded 24 eastern kingsnakes (*Lampropeltis getula*) which constituted 20% of all nonvenomous captures during this period. Despite the more intensive sampling effort of my study, eastern kingsnakes were not documented on any of the 3 sites. No individuals were otherwise encountered in the field from 2001 to 2003. Furthermore, cameras identifying nest predators did not document this species on TTRS or PH despite extensive monitoring (Staller et al. 2005). However, kingsnakes were commonly documented by nest-monitoring cameras in the Albany, Georgia area, approximately 100 km north (Staller et al. 2005). Local populations thus appear to have diminished over the past several decades, although causes underlying this apparent local decline remain speculative at this point. Kingsnakes are common in low-lying wetland areas (Gibbons and Semlitsch 1991, Palmer and Braswell 1995), but also may occur in pine forests (Ernst and Ernst 2003). Superficially, landscapes in the Albany area and my sites appear similar, as both are intensively managed as upland pine forests. Additionally, current habitat at TTRS is generally similar to habitat 3 decades ago, although hardwoods had increased by the 1990's and a hardwood thinning did occur during 1997-1998 (W. Palmer, personal communication). The species is considered rare in Florida, with specimen collection, vehicle mortality, and habitat loss as potential causes of population declines (Ernst and Ernst 2003). The apparent decline of the eastern kingsnake certainly warrants further investigation.

Although eastern hognose snakes were captured, the closely related southern hognose (*Heterodon simus*) was not detected during the study. The sandy soils and longleaf forests at PH and WT appear to provide suitable habitat for the species (Gibbons and Semlitsch 1991, Palmer and Braswell 1995, Ernst and Ernst 2003), but proximity to paved roads may be problematic given its susceptibility to road mortality (Tuberville et al. 2000, Enge and Wood 2002). Roads may create a population gradient in which areas closer to roads are less densely populated than those areas farther from roads. The species is apparently declining across its historical range (Tuberville et al. 2000), but it is notoriously difficult to detect with drift fence studies (Enge and Wood 2002), creating uncertainty as to the occurrence of the species on my sites. In addition, the ring-necked snake (*Diadophis punctatus*) and rough green snake (*Opheodrys aestivus*) were captured on my sites, but not detected during trapping sessions, and other upland species such as the coral snake (*Micrurus fulvius*) may occur on these sites as well (Guyer and Bailey 1993, Ernst and Ernst 2003, Means 2004).

General Activity Patterns

For most commonly captured species, general seasonal activity patterns were similar among sites. Seasonal activities thus appear to be primarily governed by regional cues such as climatic patterns, though local variables (e.g., greater local densities, locally explosive prey populations) may influence activity at a site-wide scale. Fewer species were detected in mid-summer (July and August), suggesting that the upland community as a whole is less active in the hottest months. Moreover, none of the commonly captured species demonstrated a primary peak of activity during these months.

Species exhibited variable patterns of activity, indicating some partitioning of the movement axis. General activity patterns varied in similarity to regional patterns documented elsewhere via collection and telemetry methods. Black racer activity, for instance, peaked slightly later in southern Florida (Dalrymple et al. 1991*b*) and South Carolina (Gibbons and Semlitsch 1987), but similarly in peninsular Florida (Dodd and Franz 1995). Separation of seasonal captures into components of sex and stage of maturity provides for more valuable ecological comparisons (Dalrymple et al. 1991*b*). Male captures of these species peaked during spring breeding seasons (Fitch 1963*a*, Fitch 1963*b*, Dalrymple et al. 1991*b*, Ernst and Ernst 2003). In southern Florida, adult male activities of *Coluber* (racers) and *Pantherophis* (rat snakes) also coincided with the overall peak in activity (Dalrymple et al. 1991*b*). However, female activities differed somewhat between the 2 regions, perhaps due to slightly different reproductive schedules or resource availability. Other regional studies in which individuals were separated by sex have reported generally similar primary peaks of activity to those I observed [corn snakes (Dalrymple et al. 1991*b*, Franz 1995, see Chapter 2 this volume); eastern rat snakes (Stickel et al. 1980, Dalrymple et al. 1991*b*, Durner and Gates 1993, Franz 1995, see Chapter 2 this volume)]. To my knowledge, this study represents the first attempt to document activity differences between sex and stage of maturation in coachwhips. Reports of general activity patterns of coachwhips are likewise sparse; Palmer and Braswell (1995) similarly report a spring peak in collection, whereas peninsular Florida studies found no discernible pattern (Franz and Dodd 1995).

My capture records did not document a clear secondary autumn peak in activity reported elsewhere for eastern rat snakes (Stickel et al. 1980, Dalrymple et al. 1991*b*, Franz 1995) and corn snakes (Dalrymple et al. 1991*b*). In some parts of the region, such secondary peaks can be attributed to migratory movements to winter ranges (Franz 1995) or hibernacula (Gibbons and Semlitsch 1987). Telemetry evidence has demonstrated that snakes do not migrate to separate winter ranges at my sites (see Chapter 2 this volume) and I did not expect an autumn peak in adult captures. Conversely, secondary autumn peaks of *Pantherophis* in southern Florida were attributable to large numbers of young-of-the-year (YOY) and juvenile snakes (Dalrymple et al. 1991*b*). I therefore anticipated greater captures of juveniles and YOY in the late summer and fall months. However, this pattern was not observed. Upon closer examination, it appears that I captured fewer juvenile vs. adult snakes than Dalrymple et al. (1991*b*) throughout the season. This disparity may reflect variation in growth rates or age structure between the sites, but probably is at least partially due to biases associated with different sampling techniques. Specifically, funnel traps may be less efficient at catching smaller snakes versus other techniques (Greenberg et al. 1994*b*, Dodd and Franz 1995, Kjoss and Litvaitis 2001; see also *Trapping*).

Although eastern garter snakes were not separated into categories of sex and maturation stage, activity patterns were similar to those reported elsewhere in the region (e.g., Dalrymple et al. 1991*b*), but differed from others (e.g., Gibbons and Semlitsch 1987). The bimodal captures of the eastern diamondback agree with predictions of activity of sit-and-wait predators (Gibbons and Semlitsch 1987). Moreover, my findings generally support the hypothesis that spring breeding seasons are more common in oviparous species whereas viviparous species emphasize fall or spring and fall mating (Dalrymple et al. 1991*b*). This hypothesis is supported given that the large increase in captures during March of 2003 of 2 viviparous species, southern water snakes and cottonmouths, probably reflect the heavy rains and associated high water table that month as described above.

Habitat Trends

A review of gross patterns of captures by habitat is informative, revealing general trends such as the ubiquitous nature of black racers, eastern rat snakes, and garter snakes, the low detection of coachwhips, eastern diamondbacks, and corn snakes in drains, and other patterns as discussed above. However, as with seasonal activities, partitioning captures by both habitat and other factors such as season provides for more informative comparisons which would otherwise go unrecognized. For example, the shift in activity of eastern rat snakes from drains to uplands to fields and back to drains would be overlooked if seasonal variation was not considered.

Although captures were highly variable among arrays, all examined species appeared to shift activities by habitat over the course of the season to some extent.

As noted above, reproduction is a major determinant of movement patterns (Gibbons and Semlitsch 1987, Gregory et al. 1987) and may result in some shifts in activity centers via mate searching and searches for oviposition sites. However, other factors such as foraging strategies and resource availability impact activities as well (Gibbons and Semlitsch 1987, Gregory et al. 1987). Conflicting evidence exists regarding the magnitude and direction of seasonal shifts in habitat use of rat snakes, but an affinity for edge habitats is apparent (Weatherhead and Charland 1985, Durner and Gates 1993, Blouin-Demers and Weatherhead 2001). Food availability (Weatherhead and Charland 1985) and thermoregulatory requirements (Blouin-Demers and Weatherhead 2001) have been proposed to explain such shifts. Food studies demonstrated that, in Canada, rat snakes do not specialize on avian prey during peak early season availability but rather feed opportunistically on birds and mammals throughout the season (Weatherhead et al. 2003). However, given the vastly different latitudes, the prey availability hypothesis should not be discounted for southern populations of rat snakes. Hypotheses of prey availability, thermoregulation, and predation pressure can obviously be extended to other species. Increased samples will allow data to be further partitioned to assess seasonal movements of species by sex and size class within different macrohabitat types to gain a better understanding of the complexities of the system. Additionally, future emphasis on seasonal variation in prey items and thermoregulatory preferences would be beneficial.

Trapping

I did find differences in efficiency with the 2 trap types used. Although initial captures of black racers were equivalent, subsequent recaptures demonstrated that racers may develop an aversion to box traps. I did not have enough recaptures to test if similar trends existed within other species. Anecdotally, however, 17 of 23 initial corn snake recaptures and 14 of 25 initial coachwhip recaptures were in funnel traps, suggesting a shift in trap efficiency from initial captures as well. The racer is an active, highly visual species. Box traps may appear more obtrusive in the environment, as they are larger than funnel traps and, in my study, were not covered with pine boughs or other debris. Moreover, because box traps were constructed of plywood, they may have better absorbed scents from various species and thus deterred recaptures. Such visual or olfactory cues may underlie the differences in trap efficiency of eastern rat snakes as well. Causes of this potential aversion remain speculative. Future research should address efficiency of traps constructed of different materials and of varying degrees of trap "camouflage." At this point, if objectives include demographic estimates where recaptures are critical, research should explore the use of appropriately covered funnel traps.

Biases exist with all survey methods of snakes (e.g., Gibbons and Semlitsch 1982, Gibbons and Semlitsch 1987, Greenberg et al. 1994b, Dodd and Franz 1995, Enge 2001, Kjoss and Litvaitis 2001, Prior et al. 2001). With drift fence funnel trapping, active foragers such as black racers and coachwhips may be over-represented in the sample (Dodd and Franz 1995), whereas smaller taxa, heavy-bodied species, and species with arboreal or fossorial tendencies may be under-represented (Greenberg et al. 1994b, Dodd and Franz 1995, Enge 2001). Not surprisingly, several species including the arboreal rough green snake and small ring-necked snake are present on the study areas but went undetected during my trap sessions; additional species such as those outlined above (e.g., southern hognose) may also be present on my sites. Because of such trap biases, others have recommended employing numerous survey methods for more thorough community assessment (e.g., Greenberg et al. 1994*b*, Dodd and Franz 1995, Enge 2001, Kjoss and Litvaitis 2001).

My findings were not always consistent with the biases of funnel traps and drift fences reported elsewhere. I captured numerous adults of heavier-bodied snakes such as eastern diamondbacks, cottonmouths, and pine snakes, frequently with maximum body girth appearing to exceed funnel diameter. The highly arboreal eastern rat snake (see Chapter 2, this volume) was commonly captured. My methodologies did differ slightly from many other community sampling studies. I employed only 1 large single-ended funnel trap at the end of each array arm such that the arm bisected the funnel entrance with a partition to prevent an individual from passing around the fence without entering the trap. Funnel traps also were covered with natural debris, which may have simulated a more natural environment. Additionally, in the center of arrays I used large box traps infrequently used elsewhere (exceptions include Kjoss and Litvaitis 2001). Whether the observed in trap efficiency differences reflect differences in snake community composition between study sites or my techniques were better able to overcome some of the traditional drift fence biases remains to be addressed.

Although use of various survey methods would most likely increase species detection and perhaps more accurately reflect relative abundances, employing several methodologies does not adequately address biases. Utilizing multiple strategies does not ensure 100% detection. Results presented in this chapter do not account for potentially variable detection probabilities, and results and conclusions should be interpreted as such. For example, my data do not necessarily signify that coachwhips do not use bottomland drains, but rather that coachwhip activities are greater (i.e., detection is more frequent) in non-drain habitats. Similarly, while the presence of a species from a site or habitat can be unequivocally confirmed, non-detection does not indicate that the species is truly absent from the location (Mackenzie et al. 2002, Mackenzie 2005). Future approaches should attempt to assess species detectability to calibrate indices. Standardized indices facilitate more accurate assessments of both communities and species via presence-absence models, other habitat models, and measures of community and population dynamics.

Conclusions

The Red Hills region appears to support a rich and abundant upland snake community. Underscoring this notion is the realization that species richness and diversity most likely exceed my estimates given the potential trap biases outlined above. Current management in the region plays an essential role in the maintenance of upland habitats and is thus necessary for the upland snake community. For instance, prescribed fire, a critical tool in maintenance of the open savannah-like structure, is important for fire-evolved herpetofaunal species (Means and Campbell 1981, Mushinsky 1985, Means et al. 2004). As habitat loss and shifts in land use continue across the Southeast, these managed lands will prove increasingly critical to conservation efforts. Accordingly, research addressing both community and general ecology of snakes will become increasingly important. Thus, continuation of community research in the Red Hills and elsewhere is necessary to establish long-term population and community dynamics and to meet conservation objectives and maintain the ecological integrity of the snake community. Manipulative approaches to quantify community and species-level responses to management regimes are of particular importance.

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Table 3.1. Drift fence captures of snakes at Tall Timbers Research Station and Pebble Hill Plantation in southern Georgia and northern Florida during March - October, 2002. See Appendix A for species lists.

	TTRS		**PH**		**Total**	
Nonvenomous Species	**Individuals**	**Recaptures**	**Individuals**	**Recaptures**	**Individuals**	**Recaptures**
Scarlet snake	0	0	2	0	2	0
Black racer	184	55	140	37	324	92
Scarlet kingsnake	3	0	4	0	7	0
Eastern coachwhip	19	5	35	4	54	9
Southern water snake	8	0	1	0	9	0
Eastern rat snake	28	0	29	2	57	2
Corn snake	17	2	22	0	39	2
Pine snake	0	0	2	0	2	0
Eastern garter snake	10	0	15	0	25	0
Total	269	62	250	43	519	105

Venomous Species	**Captures**	**Captures**	**Total Captures**
Cottonmouth	14	2	16
Eastern diamondback rattlesnake	5	20	25
Pygmy rattlesnake	0	5	5
Total	19	27	46

Table 3.2. Drift fence captures of snakes at Tall Timbers Research Station, Pebble Hill Plantation, and the Wade Tract in southern Georgia and northern Florida during March - October, 2003. See Appendix A for species lists.

	TTRS		**PH**		**WT**		**Grid**		**Total***	
Nonvenomous Species	**Indiv.**	**Recaps**	**Indiv.**	**Recaps**	**Indiv.**	**Recaps**	**Indiv.**	**Recaps**	**Indiv.**	**Recaps**
Scarlet snake	1	0	2	0	6	0	0	0	9	0
Black racer	154	41	181	53	34	23	31	20	399	138
Eastern hognose	0	0	7	0	0	0	0	0	7	0
Scarlet kingsnake	2	0	6	0	5	0	0	0	13	0
Eastern coachwhip	16	4	50	24	10	0	14	15	88	45
Southern water snake	34	3	2	0	0	0	2	0	38	3
Red-bellied water snake	0	0	1	0	0	0	0	0	1	0
Florida green water snake	1	0	0	0	0	0	0	0	1	0
Eastern rat snake	21	1	56	0	1	0	7	2	85	3
Corn snake	51	3	67	12	33	4	17	10	168	29
Pine snake	0	0	7	1	8	2	0	0	15	3
Ribbon snake	1	0	0	0	0	0	0	0	1	0
Eastern garter snake	25	1	34	1	29	3	7	1	95	6
Total	306	53	413	91	126	32	78	48	920	227

Venomous Species	**Captures**	**Captures**	**Captures**	**Captures**	**Captures**
Cottonmouth	69	5	6	10	90
Eastern diamondback rattlesnake	6	22	9	7	44
Pygmy rattlesnake	0	5	0	0	5
Total	75	32	15	17	139

* 1 black racer and 2 coachwhips were captured at both the TTRS habitat and grid trapping arrays. The total reflects these occurrences in individuals captured and recapture events.

Table 3.3. Shannon-Weiner diversity (H') and equitability (E') indices calculated from individual snakes captured with drift fence trapping at TTRS, PH, and WT in southern Georgia and northern Florida during March – October, 2002 – 2003.

	2002			**2003**				
	TTRS	**PH**	**Pooled**	**TTRS**	**TTRS Grid**	**PH**	**WT**	**Pooled**
Diversity (H')	1.34	1.65	1.68	1.77	1.85	1.85	1.96	1.98
Equitability (E')	0.61	0.66	0.67	0.71	0.89	0.70	0.85	0.71

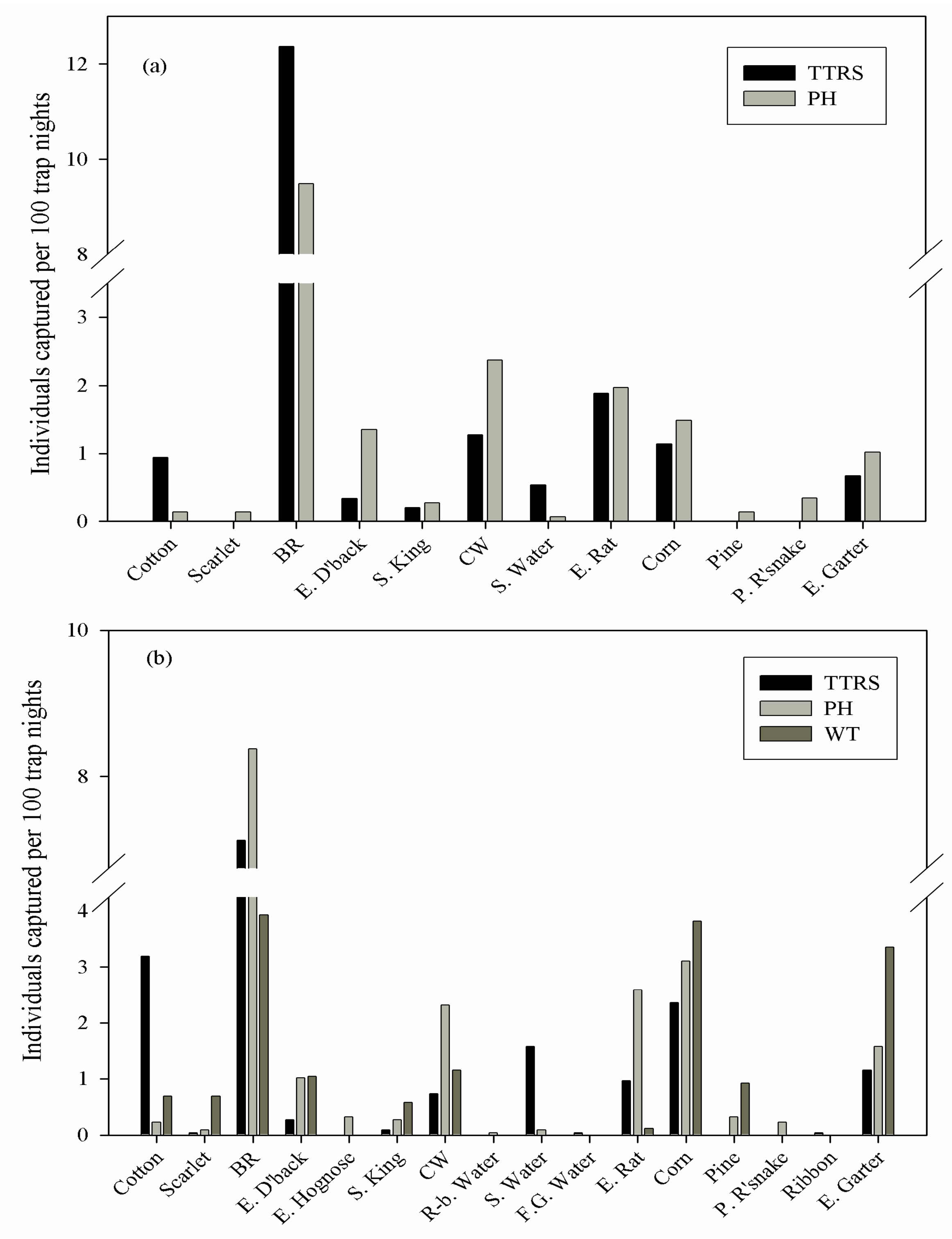

Figure 3.1. Individual snakes captured per 100 trap array nights with drift fence trapping at Tall Timbers Research Station, Pebble Hill Plantation, and the Wade Tract in South Georgia and North Florida during March – October, (a) 2002 and (b) 2003. Data from the grid at TTRS are excluded. Arrays are pooled by site. See Appendix A for species lists.

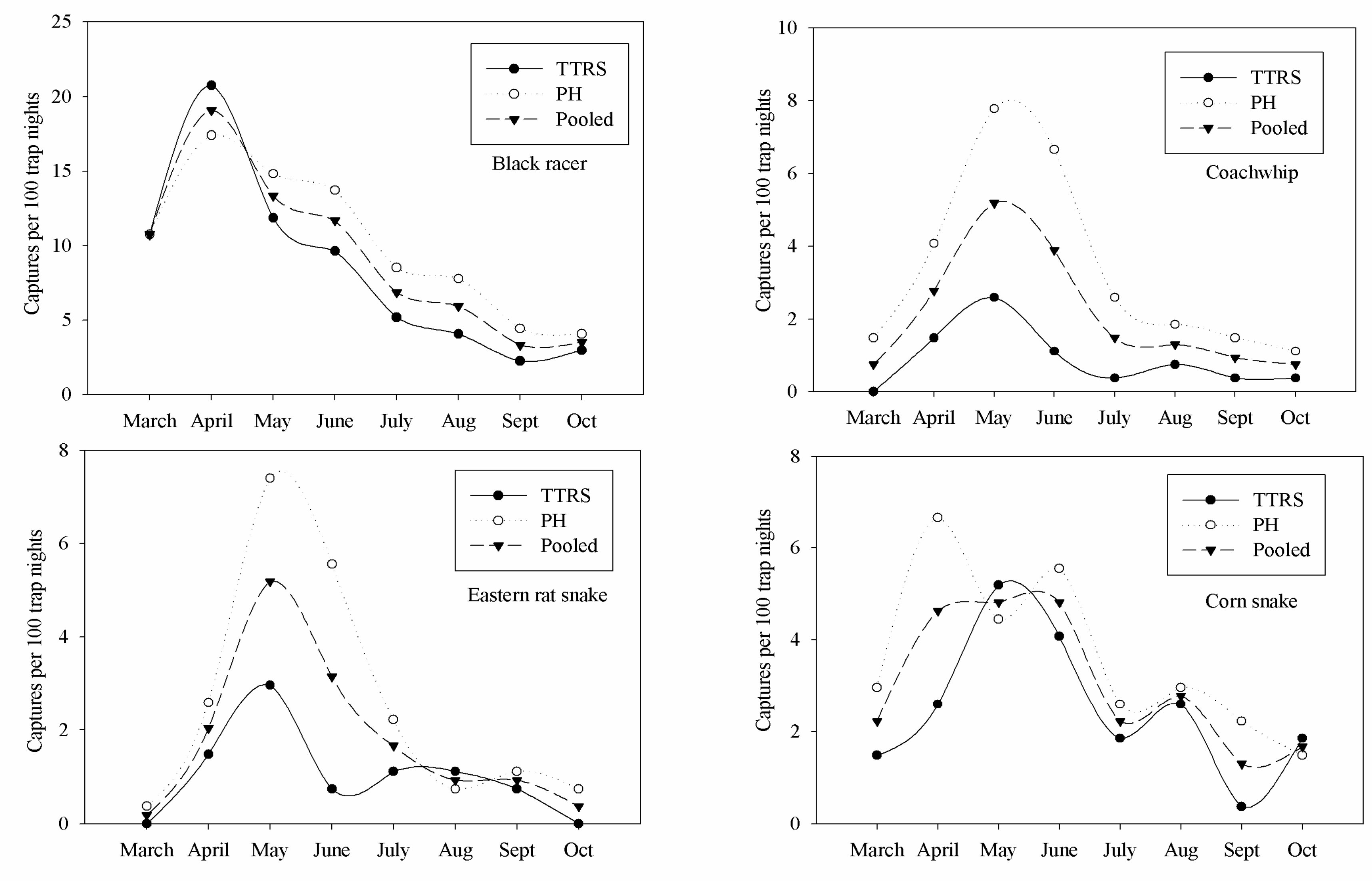

Figure 3.2. Individual snakes captured by month with drift fence trapping Tall Timbers Research Station, Pebble Hill Plantation, and the Wade Tract in South Georgia and North Florida during March – October, 2003. Captures from the grid at TTRS are excluded.

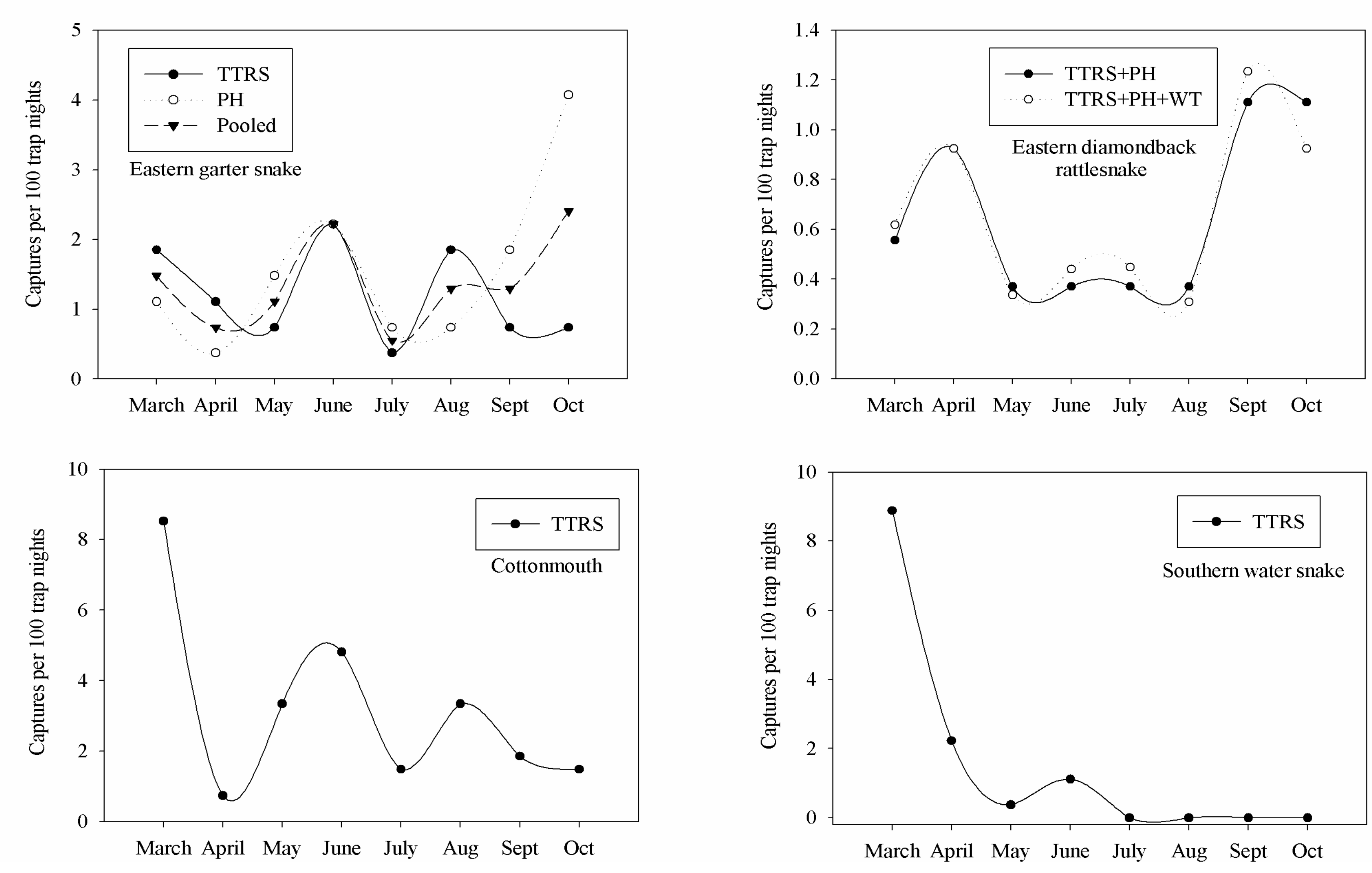

Figure 3.2 (cont). Individual snakes captured by month with drift fence trapping Tall Timbers Research Station, Pebble Hill Plantation, and the Wade Tract in South Georgia and North Florida during March – October, 2003. Captures from the grid at TTRS are excluded.

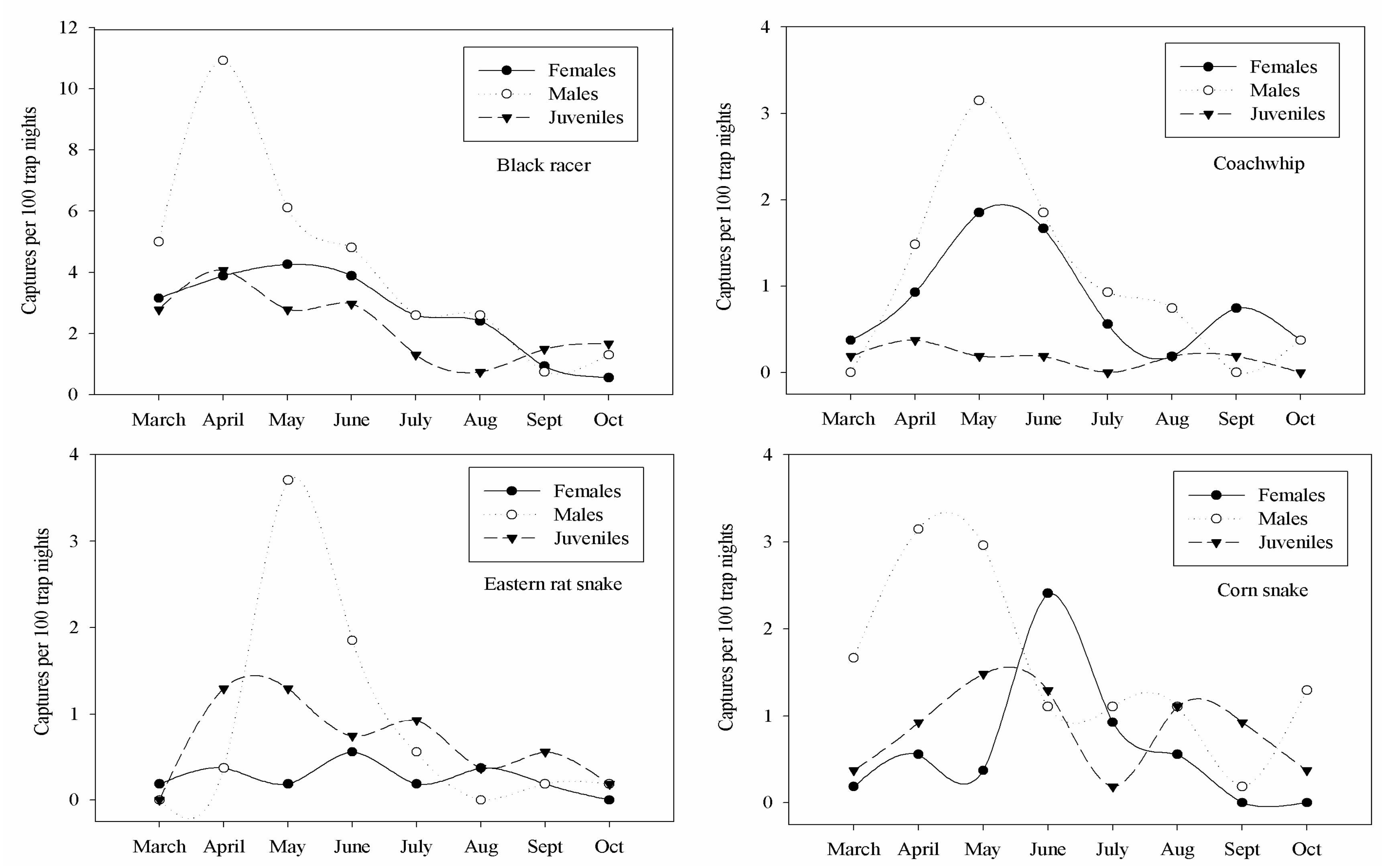

Figure 3.3. Individual snakes captured per 100 trap array nights by sex with drift fence trapping at Tall Timbers Research Station and Pebble Hill Plantation in southern Georgia and northern Florida during March – October, 2003. Captures from grid at TTRS are excluded.

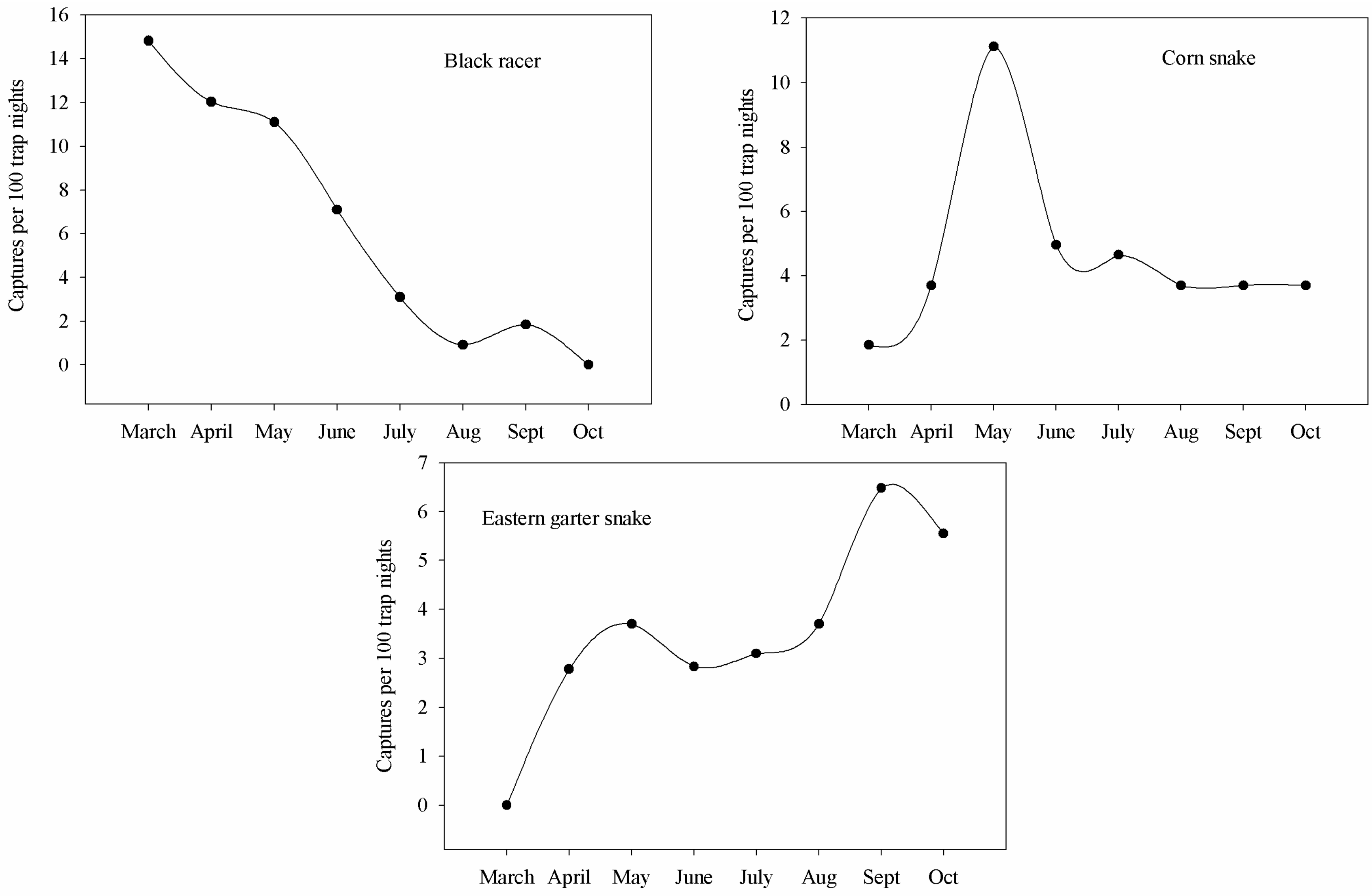

Figure 3.4. Individual snakes captured by month with drift fence trapping at the Wade Tract in southern Georgia during March – October, 2003.

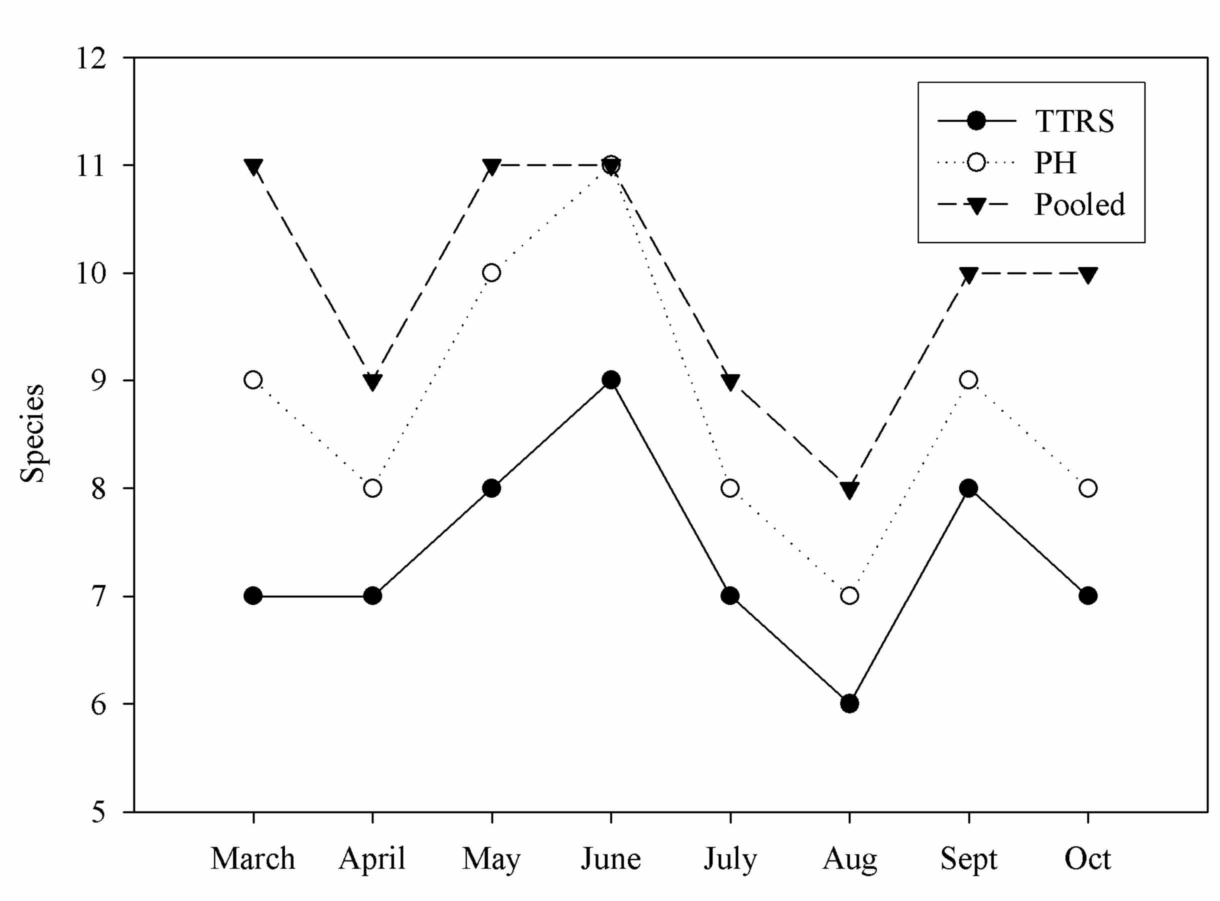

Figure 3.5. Seasonal snake species richness detected with drift fence trapping at Tall Timbers Research Station and Pebble Hill Planatation in southern Georgia and northern Florida during March – October, 2003. Data from all arrays are pooled.

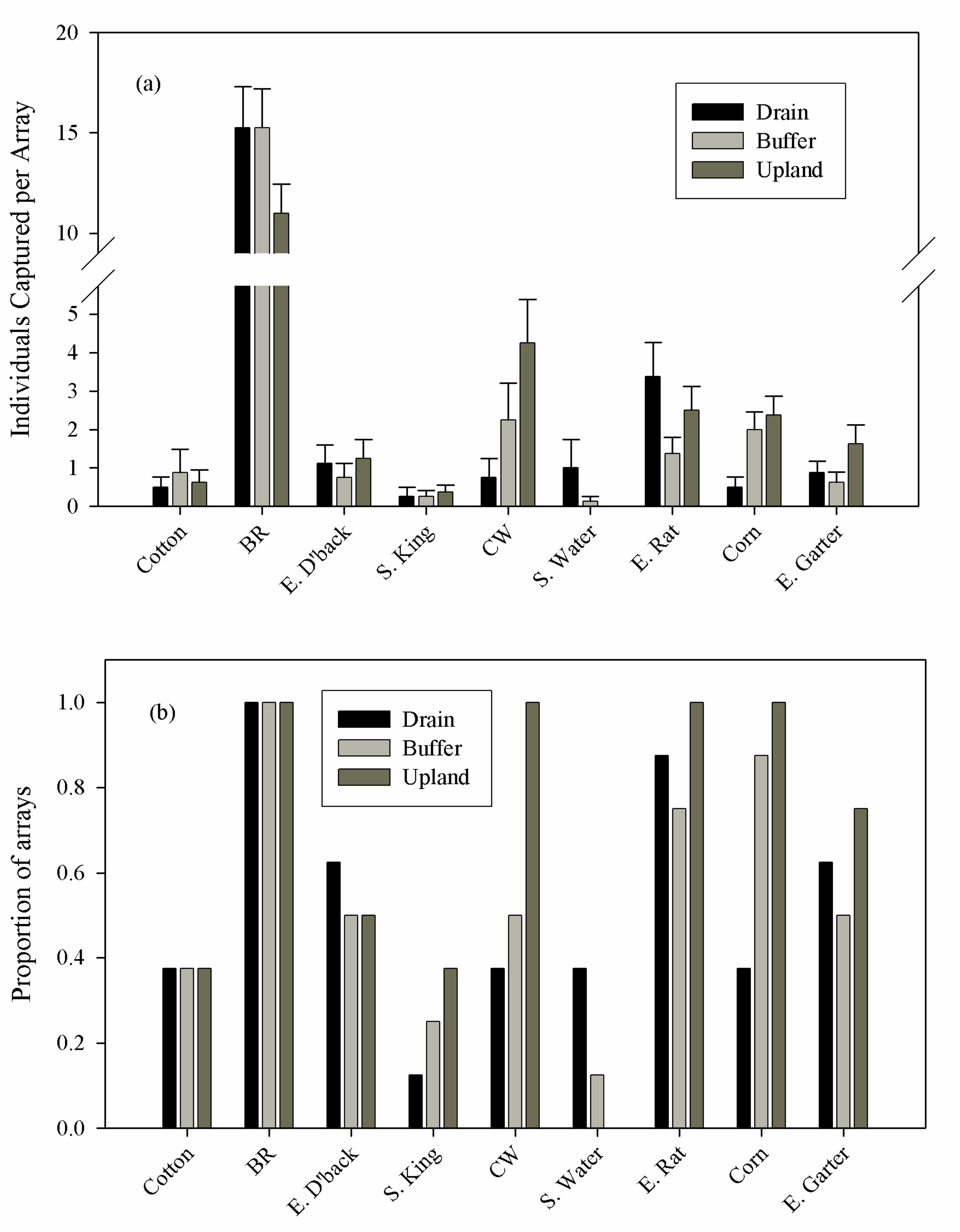

Figure 3.6. (a) Individual snakes captured per array (SE) and (b) proportion of arrays by habitat type at which species were detected with drift fence trapping in southern Georgia and northern Florida during March – October, 2002. Data from Tall Timbers Research Station and Pebble Hills Plantation are pooled. See Appendix A for species lists.

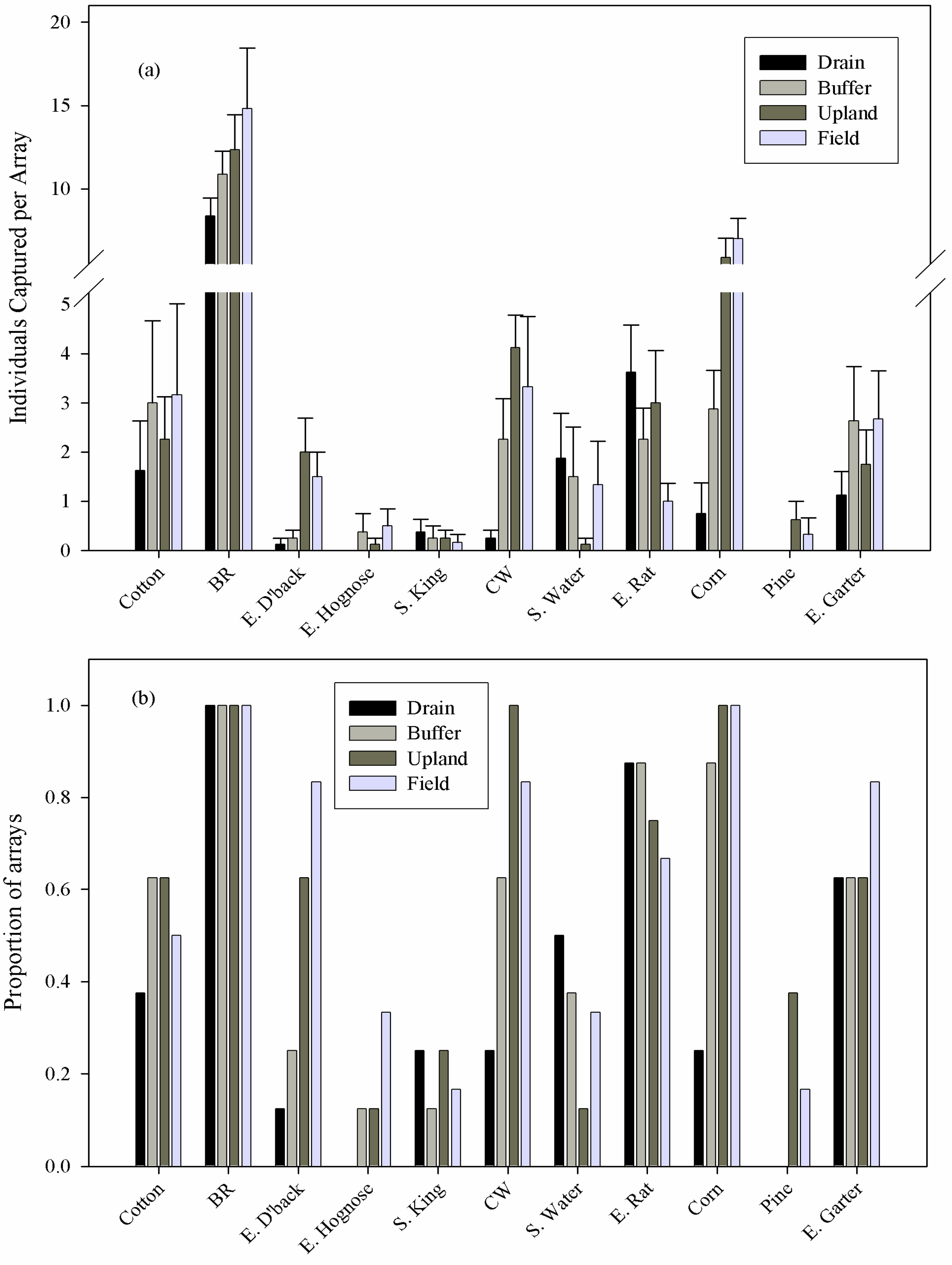

Figure 3.7. (a) Individual snakes captured per array (SE) and (b) proportion of arrays by habitat type at which species were detected with drift fence trapping in southern Georgia and northern Florida during March – October, 2003. Data from Tall Timbers Research Station and Pebble Hill Plantation are pooled. See Appendix A for species lists.

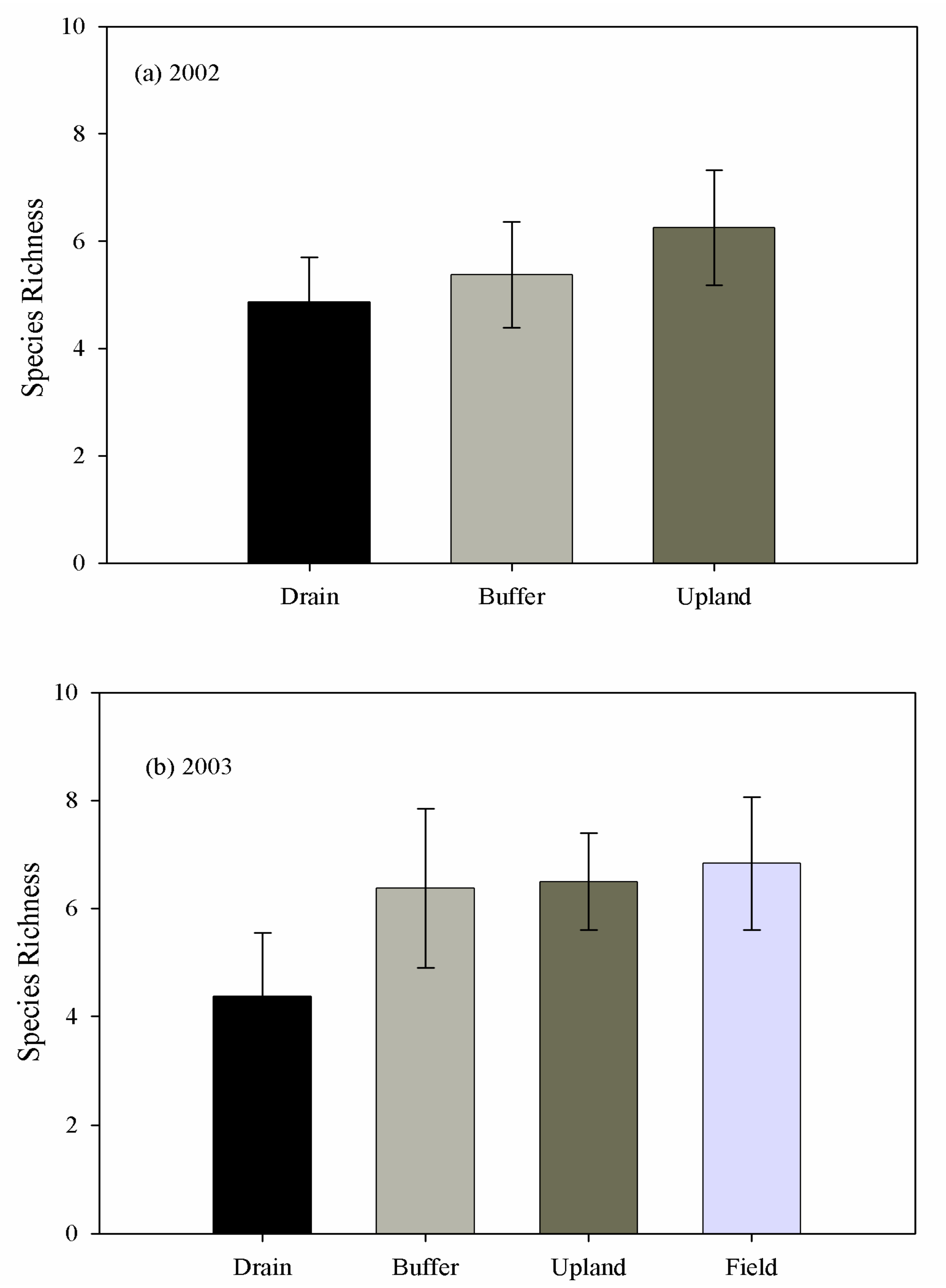

Figure 3.8. Mean snake species richness by habitat type (±95% CI) detected with drift fence trapping in southern Georgia and northern Florida during March – October, (a) 2002 and (b) 2003. Data from Tall Timbers Research Station and Pebble Hill Plantation are pooled.

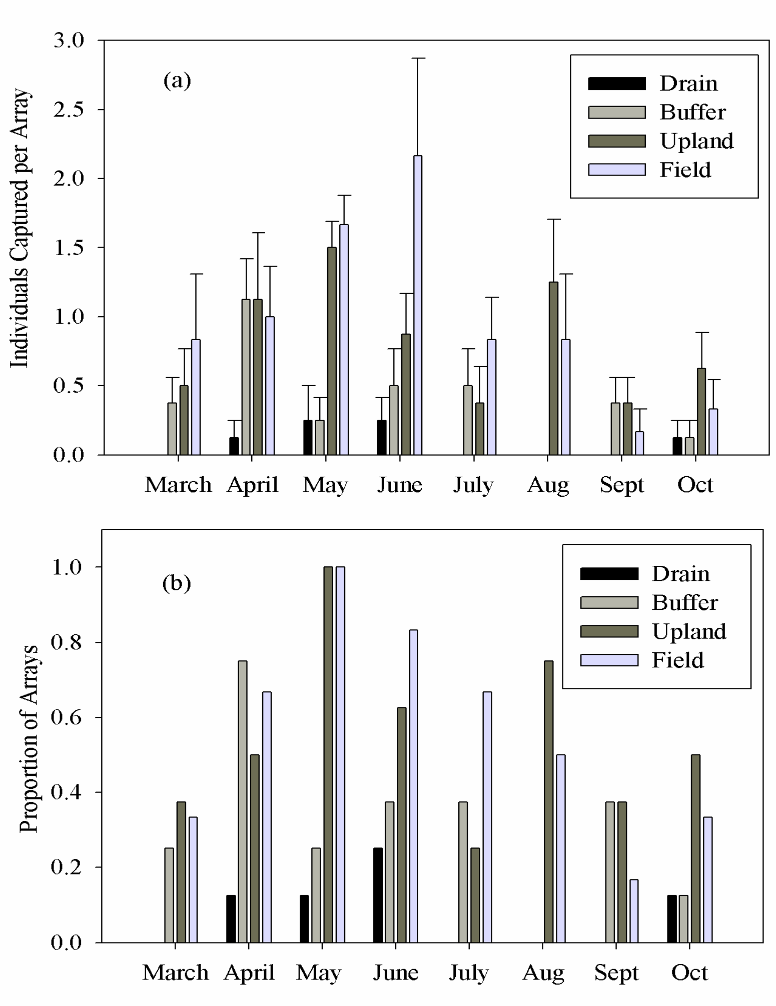

Figure 3.9. (a) Individuals captured per trapping array (±SE) and (b) proportion of arrays detecting corn snakes by habitat and season during drift fence trapping at Tall Timbers Research Station and Pebble Hill Plantation in southern Georgia and northern Florida during March – October, 2003.

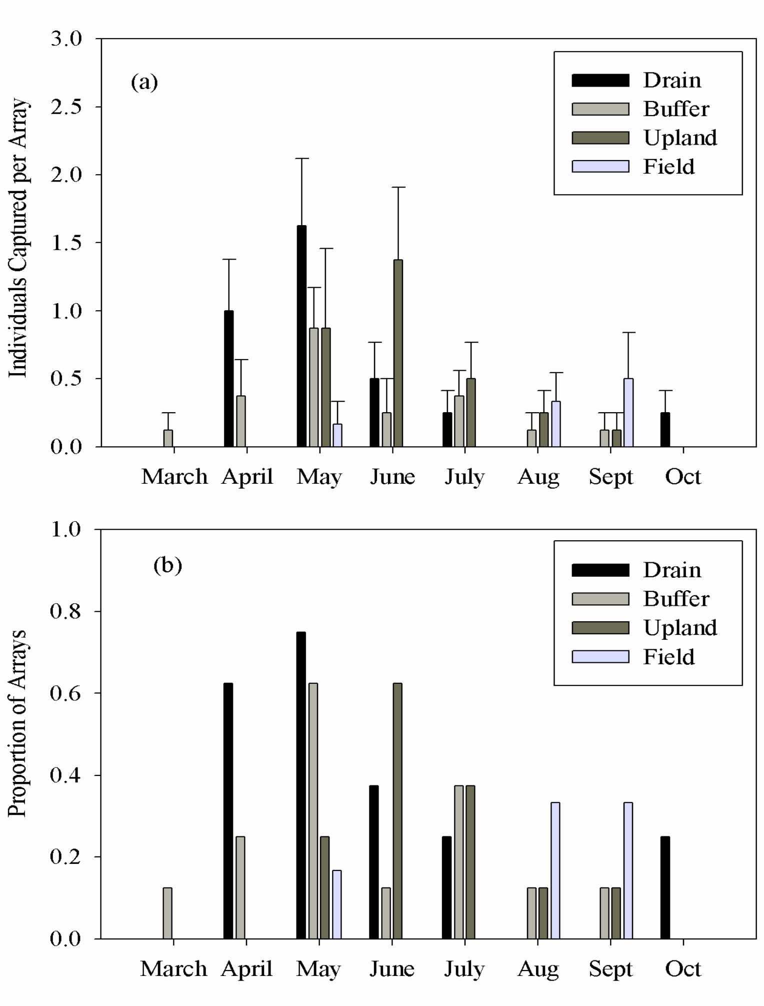

Figure 3.10. (a) Individuals captured per trapping array (±SE) and (b) proportion of arrays detecting eastern rat snakes by habitat and season during drift fence trapping at Tall Timbers Research Station and Pebble Hill Plantation in southern Georgia and northern Florida during March – October, 2003.

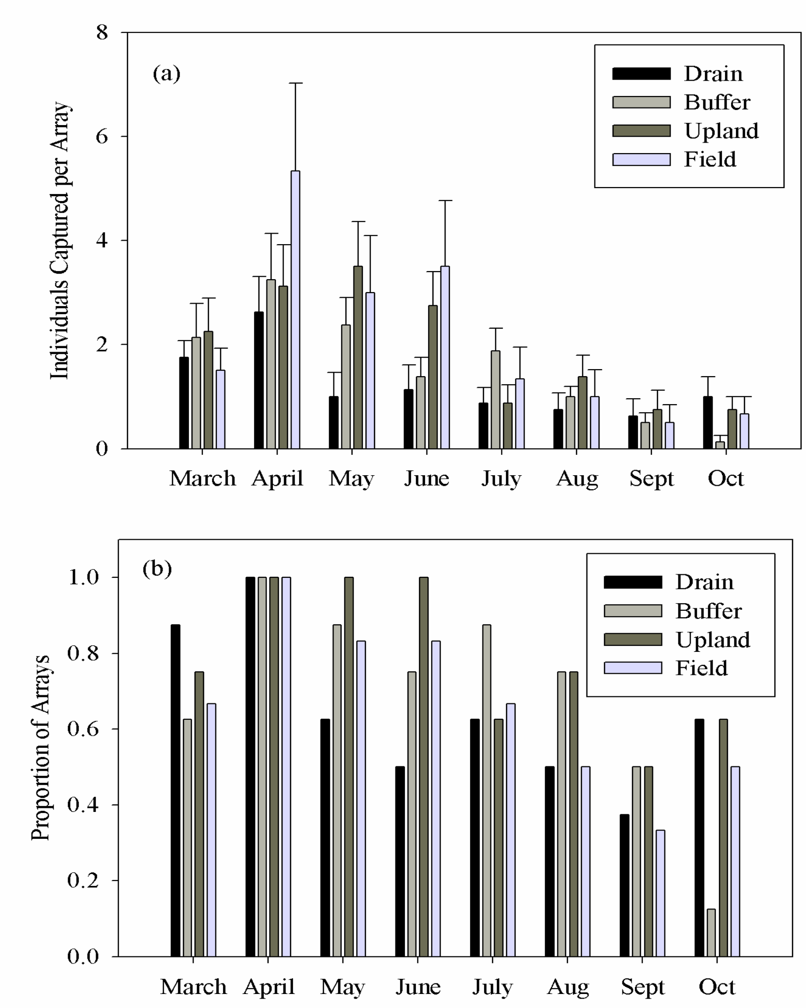

Figure 3.11. (a) Individuals captured per trapping array (±SE) and (b) proportion of arrays detecting black racers by habitat and season during drift fence trapping at Tall Timbers Research Station and Pebble Hill Plantation in southern Georgia and northern Florida during March – October, 2003.

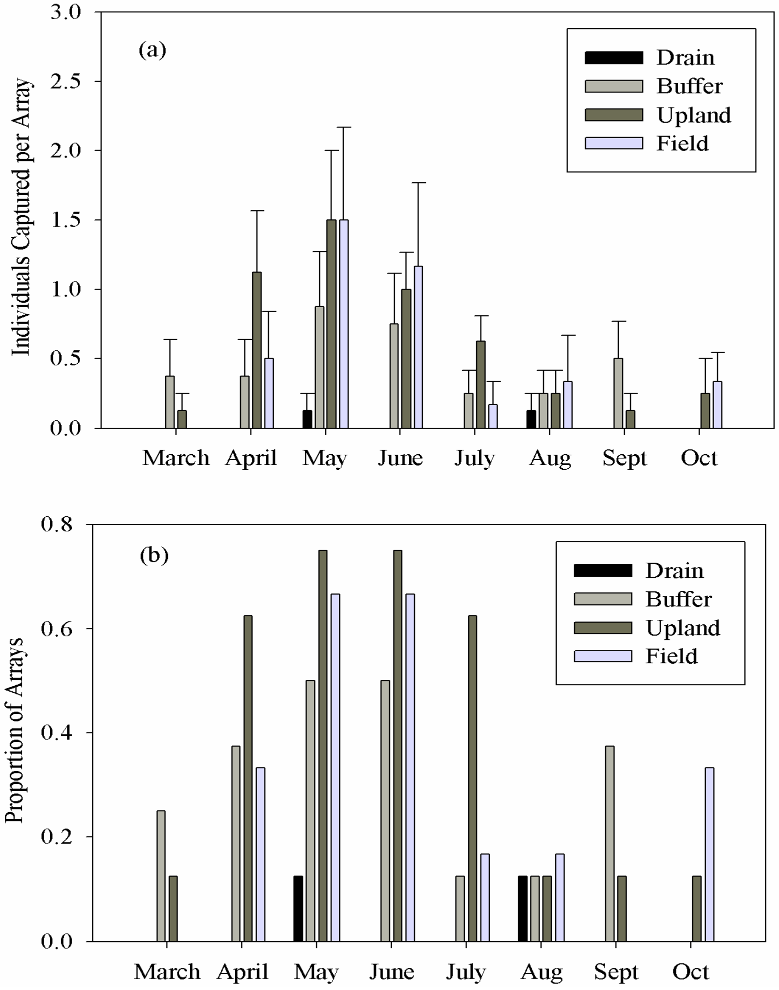

Figure 3.12. (a) Individuals captured per trapping array (±SE) and (b) proportion of arrays detecting coachwhips by habitat and season during drift fence trapping at Tall Timbers Research Station and Pebble Hill Plantation in southern Georgia and northern Florida during March – October, 2003.

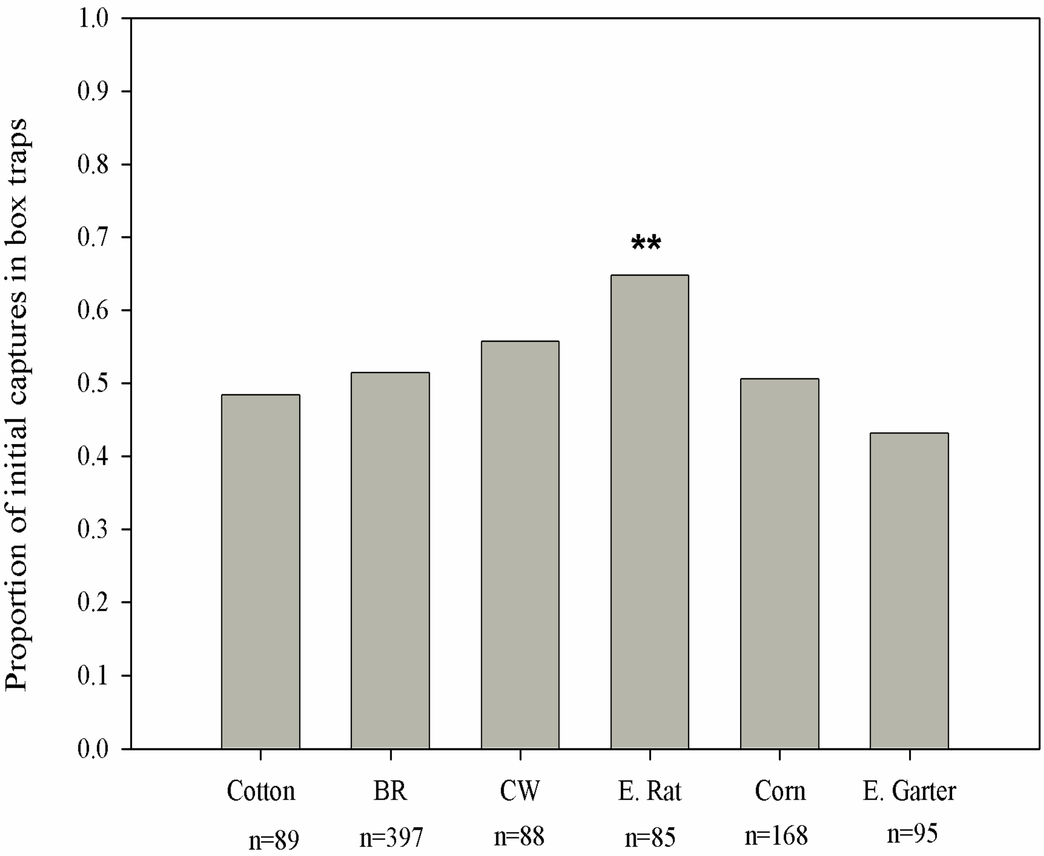

Figure 3.13. Proportion of snakes initially captured in box traps versus funnel traps with drift fence trapping at Tall Timbers Research Station, Pebble Hill Plantation, and the Wade Tract in southern Georgia and northern Florida during March – October, 2003. ** Indicates $P<0.05$. See Appendix A for species lists.

CHAPTER 4

SURVIVAL OF EASTERN RAT SNAKES AND CORN SNAKES IN THE RED HILLS OF GEORGIA AND FLORIDA[1]

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[1] Stapleton, S.P., J.P. Carroll, and W.E. Palmer. To be submitted to *Copeia*.

Abstract

Although radio telemetry affords researchers the opportunity to examine survival rates in a diversity of species, application of these techniques in snakes remains sparse. I used radio-telemetry to estimate survival, test candidate models, and estimate relevant covariates of eastern rat snakes and corn snakes using a Kaplan-Meier staggered entry analysis. I radio-tagged 29 eastern rat snakes and 18 corn snakes on 2 study areas in southern Georgia and northern Florida in 2003. Although censoring can be treated by survival models, assumptions of random censoring must still be met. Based on inconclusive fates of some individuals, 2 sets of data were considered in which these individuals were either right-censored or treated as mortalities. I found survival rates during primary active season (April to October) to be 0.84 (0.37 – 0.97, 95%CI) and 0.67 (0.25 – 0.92, 95%CI) with the right-censored and mortality analyses, respectively. These estimates were not different from estimates reported in northern populations. Model ranking varied according to analysis, although generally the least parameterized models ranked higher. No covariates (species, sex, site, size, time since radio-tagging) affected survival in either analysis. Biased distributions of the parameters time since tagging and species, however, suggested possible relationships with survival. An acclimation period, during which an individual has heightened risk of mortality or transmitter rejection, may be present in snakes. Variable results demonstrate that future research must attempt to ascertain the fate of individuals to accurately explain survival.

Introduction

Population parameters are critical components from which biologists develop an understanding of population dynamics. More importantly, researchers must examine the factors that impact those parameters and assess the magnitude of the effects to attain management and conservation objectives. Much emphasis has been placed on the estimation of parameters and the associated quantification of covariates in taxa such as birds and mammals. Within snakes, although widespread perceived declining population trends (Dodd 1987, Gibbons et al. 2000) and uncertain statuses (Dodd 1987, Dodd 1993) provide justification for research, population dynamics and parameters remain relatively unknown (Parker and Plummer 1987, Seigel 1993). Therefore, there is a need for comprehensive assessment of snake demographic parameters such as survival.

This paucity of data may be attributed to the difficulties snakes present to researchers, ranging from cryptic behavior and an inability to obtain adequate sample sizes to irregular foraging and active periods (Parker and Plummer 1987, Vitt 1987, Gibbons et al. 2000). Although recapture rates generally are low for mark-recapture studies (Parker and Plummer 1987), technologies such as radio telemetry offer opportunities to overcome some of these obstacles (Seigel 1993). Additionally, technological advances in telemetry, specifically the miniaturization of transmitters, have made telemetry suitable for many herpetofaunal species (Rodgers 2001). Current telemetry studies, however, rarely consider survival estimation. Those telemetry studies addressing survival are hampered by small sample sizes and typically fail to quantify potentially important covariates (e.g., Reinert and Rupert 1999, Plummer and Mills 2000).

A critical assumption of radio telemetry studies states that tags do not influence the behavior and physiology of the study animal (Pollock et al. 1989, White and Garrott 1990). Studies should attempt to quantify the magnitude of the effect of the transmitter itself and the attachment method (Millspaugh and Marzluff 2001). However, few studies report the effects of radio tagging study animals (Withey et al. 2001). In snakes, where morphological constraints dictate that radios be implanted into the body cavity, the effect of the radios and the surgical procedure itself may be heightened due to the invasive nature of the technique. Despite this potentially significant problem, virtually no studies report or attempt to quantify the effects of radio transmitters (Petersen et al. 1993). The limited existing research reports that radio tagging may result in lower growth rates, decreased reproductive output, and decreased survival (Weatherhead and Blouin-Demers 2004) and that an acclimation period may be present (Rudolph et al. 1998).

Rat snakes (*Pantherophis* spp.) in the Southeast present a particularly interesting case study for biologists and conservationists. Rat snakes are substantial predators of the economically and culturally significant Northern bobwhite (*Colinus virginianus*; hereafter bobwhite) (Staller 2001, Thornton 2003, Staller et al. 2005) as well as numerous other birds, small mammals, and other species (e.g., herpetofauna) (Hamilton and Pollack 1956, Fitch 1963, Jackson 1970, Brown 1979, Fendley 1980, Mirarchi and Hitchcock 1982, Hensley and Smith 1986, Phillips and Gault 1997, Thompson and Burnhans 2003). Given the declining population trends of bobwhite (Brennan 1991, Church et al. 1993) and other prey species including grassland songbirds (Sauer et al. 1997), information addressing the predator community is critical to devise efficient management strategies.

Although rat snakes fulfill a key role in the trophic hierarchy and are common throughout much of the Southeast, regional survival of these species [the eastern rat snake (*P. alleghaniensis*), the gray rat snake (*P. spiloides*), and the corn snake (*P. guttatus*)] remains wholly unexamined. Research does describe longevity and survival in other portions of their ranges, however. In Ontario, individuals survive at increased rates with greater size and are estimated to have a maximum longevity 1.5 times that of rat snakes in Maryland (Blouin-Demers et al. 2002). Weatherhead et al. (2002) further report on synchronous variation of parameters including survival for 2 Canadian populations. Fitch (1963) indirectly infers longevity using growth rates of the closely related western rat snake (*P. obsoletus*) in Kansas. However, studies of population parameters of corn snakes are completely lacking (Ernst and Ernst 2003). Data from southern portions of their range (e.g., Georgia and Florida) thus proves valuable for establishing concrete baseline data for corn snakes and regional information of rat snakes.

My objectives for this study are:

1. To estimate the active season survival of 2 common species in the southeastern U.S., the eastern rat snake and the corn snake.
2. To test *a priori* hypotheses and models explaining survival of these species.
3. To estimate the potential impact of environmental and biological parameters on survival.

Study Areas

Research was conducted on Tall Timbers Research Station (TTRS) and Pebble Hill Plantation (PH) in the Red Hills region of southern Georgia and northern Florida. Both sites are intensively managed for bobwhite with prescribed burning, hardwood control and removal, annual disking and mowing, and supplemental feeding.

PH is situated in Thomas and Grady Counties, Georgia. Total area is approximately 1,250 ha, primarily consisting of upland pine forests interspersed with bottomland drains, planted pine stands, and fields. Groundcover ranges from intact native vegetation to old-field vegetation. TTRS is an approximately 1,500-ha research station located in Leon County, Florida. Upland pine forests dominate the landscape. Bottomland drains, wetlands, and fields are scattered across the landscape; groundcover primarily consists of old-field vegetation. During this research, meso-mammalian predators were actively removed from PH during March through October as part of a larger 7-year study examining the effects of predator management on the ecosystem. TTRS functioned as a control site with no meso-mammalian predators removed during this project.

Methods

Trapping

Snakes were captured with drift fences used in conjunction with hardware cloth funnel traps and large box traps constructed of plywood and hardware cloth (D. Richardson, pers. comm.). I randomly distributed fences in major macrohabitat types at TTRS and PH (bottomland hardwood drains, upland pine forests, an intermediate “transition zone,” and regularly harrowed fields) using ArcView Version 3.2 (ESRI, Redlands, CA) to obtain a random and representative sample of the populations. Additional individuals were collected via opportunistic encounters. Subjects were returned to TTRS for processing. Snakes were measured (snout-vent length (SVL) to cm, mass to gram) and sexed by probing for inverted hemipenes. Each individual was marked via subcutaneous implantation of a passive integrated transponder (PIT) tag (InfoPET Identification Systems, Inc., Burnsville, MN) ventrally approximately 5 to 10 cm anterior to the vent. Procedures were modified from Reading and Davies (1996).

Telemetry

Isoflurane and clear plastic tubing were used to anaesthetize subjects such that individuals were restrained with and isoflurane administered in the tubing (Hardy and Greene 1999). Snakes were implanted with coiled antenna radios (Model R1170, Advanced Telemetry Systems, Inc., Isanti, MN) into the intraperitoneal cavity following procedures modified from

Hardy and Greene (1999) and Reinert and Cundall (1982). Radios weighed 4 g (less than 1.5% of individual body mass) with an anticipated life of at least 195 days. Individuals were provided with heat sources following surgery and held for 48 to 72 hours prior to release to facilitate healing.

Radio tagging began in July and August of 2002, and additional tagging resumed in March and continued through early August of 2003. A small sample size dictated that the study period run from April through October of 2003. Individuals were tracked using homing techniques and close range triangulation (White and Garrott 1990) at least 2 to 3 times a week during this period. Collection, marking, and radio-tagging procedures are permitted under: University of Georgia IACUC permit no. A2001-10100-c1,c2; Georgia collection permit nos. 29-WMB-01-80 (2002) and 29-WMB-04-128 (2003), and Florida collection permit nos. WX01277 (2001-02) and WX02136 (2002-03).

Analyses

To simplify the analyses, survival periods were broken into 1-week blocks such that an individual was deemed to have either survived or not survived a given week. I used Program MARK (version 4.2, Gary White) Known Fates analysis with a logit-link function to conduct analyses. MARK Known Fates is a Kaplan-Meier (Kaplan and Meier 1958) analysis facilitating staggered-entry (Pollock et al. 1989) and the incorporation of both continuous and categorical covariates. MARK employs Akaike's Information Criteria (AIC) as a means of model selection. AIC, an information theoretic approach, allows for testing of multiple candidate models and ranks them based on model parsimony (Anderson et al. 2000). Results are provided with values of AICc (correction for small sample sizes), AICc weights (ω), and model likelihoods.

On a few occasions, radios were found with no sign of either the snake or a predation event. For 1 such instance, the individual in question was recaptured more than a month after its radio was found. Although all radios were sutured into the peritoneal cavity, this individual somehow expelled the transmitter. Therefore, it was impossible to conclude whether similar situations reflected mortality or radio expulsion. Analyses were thus conducted twice: once in which the inconclusive events were considered mortalities, and once in which inconclusive events were right-censored.

Covariates

I considered the following covariates in this analysis: site (SITE), sex (SEX), species (SPP), snout-vent length (SVL), and time since radio implantation (RADIO). Rudolph et al. (1998) report heightened mortality of individuals implanted in the late season (i.e., autumn) versus those individuals implanted earlier, suggesting that snakes may have an extended post-surgery acclimation period (i.e., several months of altered behavior). I therefore defined the transmitter implantation acclimation period as a 12-week post-release period to test for radio and implantation effects on survival. I believed that this definition would be conservative enough to allow sufficient time for healing and acclimation. As such, time since radio implantation was expressed in binary terms, with 0 denoting that a tagged individual had not reached the 12-week threshold and 1 denoting that an individual had exceeded this period. Although simply assessing the impact of a radio on an individual's survival does not demonstrate a null effect of the transmitter (Millspaugh and Marzluff 2001), it represents a first step in understanding impacts of tagging on snakes.

SITE (TTRS as 1), SEX (male as 1), and SPP (rat snakes as 1) were additionally coded in binary format. SVL was standardized by species prior to analyses. I calculated model-averaged estimates for covariates using the respective AICc weights. Because a model's impact in parameter estimation diminishes as ΔAICc increases, I considered only those models with a relative ΔAICc of less than 3 for model-averaged estimates.

I maintained the following hypotheses to explain covariate effects. Covariates are listed in descending order of importance in explaining survival as based on *a priori* expectations.

Species: Different habitat use between the species will result in species differences in survival. Eastern rat snakes more frequently utilize bottomland hardwoods (see Chapter 2) which are important habitats for predators in the region (W. Palmer, personal communication). This disparity will result increased predation pressure on eastern rat snakes, thereby lowering survival.

Time since tagging: The transmitter implantation will result in an extended acclimation period (Rudolph et al. 1998) and will reduce survival following tagging. Survival will increase as an individual heals and becomes acclimated to the radio.

Site: Top-level carnivores may suppress lower predatory species, such that their removal may release secondary predators (Palomares et al. 1995, Courchamp et al. 1999, Henke and Bryant 1999). Meso-mammalian predator management at PH will release snakes and correspondingly increase survival.

Sex: Movement patterns will dictate varying seasonal survival between the sexes. Male eastern rat snakes tend to move more frequently in the early season (Durner and Gates 1993) and therefore will experience reduced survival in the early season. Similar late season movements between the sexes (Durner and Gates 1993) will result in similar late season survival.

Size: Survival rates increase with size in rat snakes in Canada (Blouin-Demers et al. 2002). A similar relationship will unfold at my sites because of increased landscape familiarity and decreased susceptibility to predation.

Candidate Models

I constructed models based upon *a priori* hypotheses of relative parameter importance and hypothesized interactions between parameters (Tables 4.1 and 4.2). For some models, I allowed for parameter variation by season. Early season and late season were partitioned at the mid-point of the study period. I had no *a priori* reason to believe that survival would differ from week to week; this model is therefore not included in the set of candidate models.

Survival

In order to estimate weekly survival, I used model-averaged estimates of model parameters β (i.e., intercept and covariates) such that:

$$\mathbf{S(w_j) = (1+e\wedge\text{-}(\beta_0+\beta_i x_{ij}\ldots\ ))^{-1}}$$

where x_{ij} is the value x of covariate i for an individual in week j. I calculated the probability of surviving the entire study period as the product of all weekly survival rates.

Results

Radio telemetry

Four eastern rat snakes were radio-tagged in July and early August, 2002. Three of these individuals (2 males, 1 female) survived with functional radios through spring 2003. During March through July 2003, an additional 44 individuals were radio-tagged and released (18 corn snakes: 14 males, 4 females; 26 eastern rat snakes: 17 males, 7 females). Animals were tracked for an average of 14.2 weeks (range: 1 to 31 weeks) during the study period. I documented 6 mortalities and collected 6 radios for which there was neither sign of mortality nor a subsequent recapture. Radios were expected to remain functional for more than 6 months. However, faulty radios led to widespread early radio failure and thus resulted in numerous individuals which were prematurely right-censored for analyses.

Models

When snakes of unknown fate were right-censored, {SPP} (ω=0.206) and {Constant survival} (ω =0.205) were the best fitting models (Table 4.1). One model, {SITE*SPP}, did not converge and was thus eliminated from further analyses. Seven of the 15 remaining candidate models produced a ΔAICc of less than 3. When snakes of unknown fate were considered mortalities, {SPP + SEX varying by season} (ω=0.121), {SPP varying by season} (ω =0.117), and {Constant survival} (ω =0.113) were the best fitting models (Table 4.2). Similarly, a model, {RADIO*SPP}, did not converge and was removed from additional analyses. Twelve of the 15 remaining candidate models resulted in a ΔAICc score of less than 3.

Covariates

The confidence intervals for all covariates spanned 0 when individuals of unknown fate were right-censored (Table 4.3) and when individuals of unknown fate were considered mortalities (Table 4.4). This result suggests that the covariates did not impact survival. Although confidence intervals did overlap regardless of analysis, parameter estimates did vary somewhat based on the analysis. Not surprisingly, RADIO serves as the clearest example, as the censored analysis estimated RADIO as β=-0.11 (0.90 SE), while the mortality analysis estimated β =0.86 (0.80 SE). Standardization of SIZE resulted in a mean of 123.3 cm (2.25 SE) for rat snakes and a mean of 92.7 (1.8 SE) for corn snakes. The SIZE β estimate refers to a change in snout-vent length of the respective SE value.

Survival

I assumed constant survival and no covariate effects because all covariate confidence intervals spanned zero. The model averaged estimate of weekly survival was 0.994 (0.967 – 0.999, 95%CI) in the right-censored analysis and 0.987 (0.955 – 0.996, 95%CI) in the mortality analysis. Probability of surviving the entire April to October study period was 0.838 (0.367 – 0.970, 95%CI) for the right-censored analysis and 0.670 (0.250 – 0.892, 95%CI) for the mortality analysis.

Discussion and Recommendations

Relatively clumped AICc weights and model likelihoods in the mortality analysis demonstrated that none of the hypothesized models was clearly established to best explain survival. Conversely, the censored analysis more clearly identified 2 models ({SPP} and {Constant survival}) as best-fitting, although weights and likelihoods of subsequent models in this set are relatively close as well. Furthermore, although the least parameterized models tended to score the lowest AICc values for both analyses, specific model ranking varied by analysis. Such variable model ranking makes it difficult to draw conclusions regarding the best explanation of survival.

The inclusion of 0 in all confidence intervals suggested that covariates did not impact survival. For some covariates, however, only the “tail” of the confidence interval crossed 0. Such distributions suggest a potential effect of the covariate on survival. Subsequent review of covariate hypotheses illustrates that some predictions were potentially supported. For instance, in both sets of analyses, species was negatively skewed. Although the mechanism behind this apparent difference requires further investigation, it implies that rat snakes may have lower survival rates than corn snakes. Additionally, in the mortality analysis, the effect of the transmitter was positively skewed, thus suggesting increased survival once an individual surpasses the 12-week post-release threshold. Conversely, the transmitter did not affect survival under the censored analysis. These results leave the impact of radio implantation on survival in question. However, deaths in the mortality analysis can be considered to represent a failed tagging attempt, regardless of whether the snake actually died or simply rejected the radio. It therefore appears that snakes require an acclimation period, during which they are more susceptible to rejection or mortality. These findings are in agreement with the extended periods of altered behavior reported by Rudolph et al. (1998). Additionally, although their survival estimation methods were crude, Weatherhead and Blouin-Demers (2004) report negative impacts of radio transmitters on snake survival as well as growth rates and reproductive output.

Conversely, several covariate hypotheses were not supported by the data. Site did not affect survival, perhaps as a result of compensatory mortality (e.g., greater raptor predation upon snakes in the absence of mammalian predators). Quantification of sources of mortality, scarce in the snake literature (Parker and Plummer 1987), may provide further explanation for the mechanisms of such conclusions. Similarly, size had no impact on survival. Previous research, which reports increased survival with greater size, was based on mark-recapture data collected from a diversity of size classes (Blouin-Demers et al. 2002). The radio-tagged snakes in my research, however, were by necessity relatively large to support a radio transmitter. Relative size uniformity of radio-tagged snakes thus may have resulted in an absence of size impact on survival. Although results were not significant, both analyses showed a more positively skewed impact of sex in late season. This trend warrants further attention, as others have come to different conclusions that as to the effects of sex on rat snake survival (e.g., Stickel et al. 1980, Blouin-Demers et al. 2002).

Actual survival of this population probably lies somewhere between the right-censored and mortality analyses. As outlined above, the disparity between the analyses creates some uncertainty with interpretation and points to the need to accurately determine the fate of individuals.

Blouin-Demers et al. (2002) hypothesize that a relationship exists between growth rates, latitude, and survival in rat snakes. Growth rates for rat snakes in Maryland are more rapid than rates in Ontario, allowing the southern population to mature more than twice as quickly the northern population (Blouin-Demers et al. 2002). This phenomenon may be attributed to the longer active season in Maryland (Blouin-Demers et al. 2002). However, longevity decreases with these higher growth rates, as the maximum longevity in Ontario is 1.5 times greater than Maryland (Blouin-Demers et al. 2002). Given this information, rat snakes in the southern extent of their range (e.g., Georgia and Florida) with a longer active season may be expected to have increased growth rates at the expense of survival rates. Comparison of survival estimates reported here and from Canadian populations in Weatherhead et al. (2002) does not support this concept, perhaps due to large error estimates. More precise estimates across the range are necessary to assess potential differences.

Although 47 radio-tagged individuals represents a relatively large sample in the snake literature, greater sample sizes may be required to better assess model ranking and determine covariate effects on survival. Pollock et al. (1989) recommend a minimum 40 to 50 individuals tagged at all times for high precision estimates. The staggered entry design, however, did not permit such a sample. Widespread radio failure compounded the issue. Nineteen individuals were right-censored during the study period because of premature radio failure, and 5 of these individuals were right-censored by the 12-week mark. The number of at-risk individuals thus diminished, thereby reducing precision by increasing the size of confidence intervals (Pollock et al. 1989).

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Table 4.1. Candidate survival models, delta AICc values, and associated AICc weights and likelihoods obtained from known fates analysis of rat snakes radio-tracked during April – October, 2003 at Tall Timbers Research Station and Pebble Hill Plantation. Individuals of unknown fate were right-censored.

Model	**ΔAICc**	**Weight (ω)**	**Model Likelihood**	**Parameters**	**Deviance**
SPP	0.00	0.206	1.000	2	66.492
CONSTANT	0.01	0.205	0.995	1	68.514
SITE	1.89	0.080	0.389	2	68.382
RADIO	2.00	0.076	0.369	2	68.487
SPP+SVL	2.01	0.075	0.366	3	66.485
SVL	2.01	0.075	0.366	2	68.504
SPP varying by season	2.01	0.075	0.366	3	66.487
SPP + SEX varying by season	3.04	0.045	0.219	4	65.490
SEX varying by season	3.30	0.040	0.192	3	67.775
RADIO + SITE	3.88	0.030	0.144	3	68.350
RADIO + SPP + SITE	3.89	0.029	0.143	4	66.342
RADIO * SPP	3.91	0.029	0.142	4	66.359
RADIO + SEX varying by season	5.04	0.017	0.080	4	67.491
RADIO * SVL	5.41	0.014	0.067	4	67.859
RADIO + SPP + SITE + SVL + SEX varying by season	8.40	0.003	0.015	7	64.744

Table 4.2. Candidate survival models, delta AICc values, and associated AICc weights and likelihoods obtained from known fates analysis of rat snakes radio-tracked during April – October, 2003 at Tall Timbers Research Station and Pebble Hill Plantation. Individuals of unknown fate were considered mortalities.

Model	ΔAICc	Weight (ω)	Model Likelihood	Parameters	Deviance
SPP + SEX varying by season	0.00	0.121	1.000	4	114.319
SPP varying by season	0.06	0.117	0.971	3	116.402
CONSTANT	0.13	0.113	0.938	1	120.501
SPP	0.30	0.104	0.862	2	118.658
RADIO	0.37	0.100	0.832	2	118.729
SEX varying by season	0.50	0.094	0.780	3	116.840
SVL	1.32	0.062	0.517	2	119.682
SITE	1.71	0.051	0.425	2	120.074
SPP + SVL	1.78	0.050	0.411	3	118.120
RADIO + SITE	1.89	0.047	0.390	3	118.229
RADIO + SITE + SPP	2.05	0.043	0.358	4	116.372
RADIO + SEX varying by season	2.10	0.042	0.349	4	116.423
SITE * SPP	3.26	0.024	0.196	4	117.583
RADIO * SVL	3.51	0.021	0.173	4	117.831
RADIO + SPP + SITE + SVL + SEX varying by season	4.91	0.010	0.086	7	113.124

Table 4.3. Model-averaged parameter estimates on the logit scale obtained from known fates analysis of rat snakes radio-tracked during April – October, 2003 at Tall Timbers Research Station and Pebble Hill Plantation. Individuals of unknown fate were right-censored.

Parameter	**Estimate**	**Unconditional SE**	**Lower 95% CI**	**Upper 95% CI**
Intercept	5.135	0.894	3.381	6.889
RADIO	-0.111	0.903	-1.882	1.660
SPP (Early season)	-1.364	1.128	-3.576	0.847
SPP (Late season)	-1.377	1.112	-3.557	0.803
SEX (Early season)	-0.960	1.172	-3.257	1.336
SEX (Late season)	-0.298	1.231	-2.710	2.115
SITE	0.308	0.871	-1.398	2.014
SVL	-0.004	0.420	-0.827	0.818
RADIO * SVL	-0.697	0.906	-2.473	1.078
RADIO * SPP	-0.523	1.658	-3.773	2.728

Table 4.4. Model-averaged parameter estimates on the logit scale obtained from known fates analysis of rat snakes radio-tracked during April – October, 2003 at Tall Timbers Research Station and Pebble Hill Plantation. Individuals of unknown fate were considered mortalities.

Parameter	**Estimate**	**Unconditional SE**	**Lower 95% CI**	**Upper 95% CI**
Intercept	4.314	0.643	3.054	5.574
RADIO	0.861	0.801	-0.708	2.430
SPP (Early season)	-1.022	0.714	-2.421	0.378
SPP (Late season)	-0.742	0.769	-2.250	0.765
SEX (Early season)	-0.645	0.707	-2.031	0.740
SEX (Late season)	0.776	0.920	-1.028	2.580
SITE	-0.299	0.767	-1.802	1.205
SVL	-0.241	0.310	-0.849	0.366
RADIO * SVL	-0.357	0.858	-2.038	1.324
SPP * SITE	-1.056	1.405	-3.811	1.698

CHAPTER 5

CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

The scarcity of data addressing snake communities in managed landscapes in the Southeast, coupled with population declines of various predator and prey species, demonstrates the necessity for continued research. To address this need and fulfill objectives of community- and species-level ecology, I employed radio telemetry, systematic trapping, and mark-recapture methods. I assessed snake communities in the Red Hills, recording 1956 captures representing 16 species over 3 sites during the 2 years of the study. The managed pine forest ecosystems that dominate portions of the region appear to support a rich and abundant snake community. Commonly captured species demonstrated some differences in seasonal activity patterns and varied in detection by habitat type. I described habitat use, activities, home ranges, and survival of two snake species [eastern rat (*Pantherophis allegheniensis*) and corn (*P. guttata*)] in the region. Movements and home ranges were similar to estimates from other portions of the range, with male home ranges larger than female home ranges. Although movements suggested different strategies in terms of movement frequency and distance traveled, seasonal partitioning of activities was not evident. Conversely, eastern rat snakes and corn snakes demonstrated clear differences in habitat use. Specifically, corn snakes focused activities around ground structural features in upland pine forests and fields, whereas eastern rat snakes were more arboreal and frequented more hardwoods and bottomland drains. Survival estimates were comparable to rat snakes from northern portions of the range, and analyses provided some evidence for interspecific variation in survival. Moreover, analyses suggested an acclimation period may be required for radio-tagged individuals.

Wildlife management practices will always be beneficial to some species and detrimental to others. Specific objectives will obviously dictate how managers interpret and utilize this research. As part of a larger 7 year project, an objective of this study was the development of management recommendations to maximize the diversity and richness of the regional upland snake communities while minimizing the impact of snake predations on species such as the northern bobwhite (*Colinus virginianus*) and early successional songbirds. Here I utilize results and conclusions from my research to discuss possible management strategies and present hypotheses and opportunities for future research.

Land management regimes now in place across portions of the Southeast target bobwhite as beneficiaries and focus on the maintenance of upland pine forest habitats and restoration of more natural burn regimes. Accordingly, such management should be expected to be favorable for those species which require open upland habitats. For example, prescribed fire regimes are critical to maintain the open savannah-like structure upon which fire-evolved herpetofaunal populations depend (Means and Campbell 1981, Mushinsky 1985, Means et al. 2004). Based on my results snake communities appear to be healthy in pine tracts managed for bobwhites: these systems support a host of snake species and overall community abundance is apparently high. Diversity and equitability estimates meet levels predicted by latitudinal gradients of richness and diversity in the Southeast (Vitt 1987, Dalrymple et al. 1991). This notion is strengthened considering that actual levels of diversity and richness probably exceed these estimates due to trap biases. Additionally, many snakes of conservation concern are associated with upland habitats [e.g., eastern indigo snake (*Drymarchon courais couperi)*, eastern diamondback rattlesnakes (*Crotalus adamanteus*), Florida pine snake (*Pituophis melanoleucus mugitus*), southern hognose (*Heterodon simus*)] (Guyer and Bailey 1993, Dodd 1995, Tuberville et al. 2000, Means 2004), further demonstrating potential benefits of pine forest management to the upland snake community. Moreover, as regional habitat losses increase and land uses shift due to encroaching urbanization, such managed lands will become increasingly important to maintain the integrity of upland snake communities. There is little doubt that this management regime is overall beneficial to upland snake communities, as well as bobwhite and early successional songbirds.

Hence, one option is simply to maintain current land management regimes. The bobwhite would continue to act as an umbrella species to protect other fauna of upland ecosystems including snakes. This strategy would operate under the premise that the most effective management for both bobwhite and snakes is via maintenance and restoration of the habitats upon which these species depend (i.e., the open savannah structure of the upland pine forests). Although snakes do comprise an important component of the bobwhite nest predator community, it appears that the regional rat snake species, eastern rat snakes and corn snakes, are responsible for the bulk of nest predations of bobwhite in the Red Hills (Staller 2001, Thornton 2003, Staller et al. 2005). Other species, including Florida pine snakes, eastern diamondbacks, and additional species of conservation concern are insignificant predators of bobwhite nests. Potential benefits accrued by the upland snake community as a whole thus may be viewed as auxiliary benefits of upland management regimes.

Within this context, additional habitat manipulation presents another management option to reduce nest predations by rat snakes. Staller (2001) suggested that removal of hardwood patches may limit accessibility of eastern rat snakes to bobwhite nesting habitats, thereby reducing negative interactions between predator and prey. Although this option might prove to have merit, I believe that this view may underestimate the complexities of the system. Specifically, the observed patterns of interspecific habitat partitioning between rat snakes, uncertainties with plasticity in rat snake macrohabitat and structural use, and questions surrounding the relative importance of each rat snake species as a nest predator establish that potential impacts of such manipulations are largely unknown. For example, in the absence of hardwood trees, eastern rat snakes may shift activity centers to ground level features such as deadfalls and burrows or may increase use of snags and pines. Such shifts may place eastern rat snakes in more direct competition with corn snakes, thereby potentially putting more predation pressure on ground-dwelling prey species.

Of course, the only way to determine the actual impacts of additional habitat manipulation on snake nest predations is through continued research. Solid baseline data now exist for snake community structure, rat snake habitat use and movements, and bobwhite demographics. Continued monitoring of the dynamics and ecology of various trophic components, in combination with habitat manipulation, will provide answers to questions of the efficacy of removal of hardwood patches on minimizing negative interactions between snakes and bobwhite.

Although potential implications of hardwood removal on snake predations of avian nests remain uncertain, numerous benefits of such management are apparent in the broader ecosystem context. Removal of hardwoods [e.g., sweet gums (*Liquidambar styraciflua*)] has become an important component of management in the region and is necessary to restore and maintain the open, savannah-like structure of the Southeast's upland pine forests. As such, hardwood removal helps to establish more suitable habitat for bobwhite, upland snakes, and other upland fauna.

Thus, hardwood removal should remain a component of upland forest management despite the uncertainties surrounding specific effects on bobwhite–rat snake interactions.

Durner and Gates (1993) recommended limiting edge to interior ratio as a mechanism to minimize the impact of rat snakes on avian species. Although my results also suggest high use of drain edge habitats by eastern rat snakes and high inclusion of non-drain edges in corn snake home ranges, such habitat interfaces are beneficial to bobwhite as well. This option has the same associated uncertainties as previously described, but its merits also may be examined with manipulative approaches. In addition, removal of structural features from the landscape to limit refugia should not be viewed as a management option to minimize rat snake nest predations. Coarse woody debris (e.g., snags and deadfalls) are of great utility to a host of avian, mammalian, and herpetofaunal species (Harmon et al. 1986).

Finally, some people may view killing snakes opportunistically as a solution to reduce nest predations. This concept is not a viable alternative for numerous reasons. The option obviously violates the initial management objective to develop a set of management options beneficial to bobwhite and herpetofauna. Killing nongame species is largely illegal, and malicious killing of snakes poses a major threat to some populations and conservation objectives (e.g., rattlesnake roundups) (Dodd 1987). Such actions also attract negative attention from herpetologists and other conservationists and may stress what some perceive as an already tenuous relationship between game and nongame managers. Moreover, the broader trophic implications are unknown. Although bobwhite may be targeted as the beneficiary of such actions, removal of snakes may also release small mammal populations. Greater small mammal populations may increase stress on food resources and/or increase densities of other predatory species (e.g., raptors, mammals). Therefore, compensatory mortality, increased competition, and other forces may act to negate any potential benefits to bobwhite.

Education and open-mindedness will be critical to successfully integrate avian and herpetofaunal conservation objectives. Outreach programming will enhance the public's awareness of these taxa's conservation statuses, their specific roles in the trophic hierarchy, and their respective ecological, economic, and intrinsic values. Education thus should form a foundation for future conservation efforts.

In conclusion, objectives of snake conservationists and avian managers may not be as conflicting as they superficially appear. Lands in the Southeast managed to benefit bobwhite populations appear to also benefit upland snake community. I believe that, given the conservation status of numerous upland snakes and the fact that two rat snake species are responsible for the majority of bobwhite nest predations, an ecosystem approach to management focused on maintenance of the region's pine savannahs may appease both parties. However, manipulative approaches to further modify habitats may have additional value to managers and therefore warrant further investigation. Education and outreach will be an important component of future efforts.

Numerous additional opportunities exist for future research. As outlined above, a foundation has also been laid for long-term monitoring of rat snake habitat use and general population and community dynamics via continuation of telemetry and mark-recapture studies. Although sample sizes for this study were large relative to other snake studies, my analyses were conducted with and conclusions drawn from limited numbers of individuals, particularly with respect to radio telemetry. Continued assessment of rat snakes via telemetry will provide valuable data by which models can be further developed and validated. The apparent acclimation period of radio-tagged individuals warrants further attention as well. Dietary research would also be of particular interest to obtain a more complete picture of resource partitioning and assess relative importance of rat snake species as avian predators. Finally, genetic work to assess population structure and reproductive investment (e.g., multiple paternity) would address important questions in general snake ecology. For all future snake research, standardized and systematic methods as well as proper statistical treatment remain essential to provide more meaningful information and conclusions.

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Appendix A. Scientific names, common names, and abbreviations of species captured during drift fence trapping at Tall Timbers Research Station, Pebble Hill Plantation, and the Wade Tract in southern Georgia and northern Florida during March – October, 2002 – 2003.

Scientific Name	**Common Name**	**Abbreviation**
Agkistrodon piscivorus	Cottonmouth	Cotton
Cemophora coccinea	Scarlet snake	Scarlet
Coluber constrictor	Black racer	BR
Crotalus adamanteus	Eastern diamondback rattlesnake	E. D'back
Heterodon platyrhinos	Eastern hognose	E. Hognose
Lampropeltis triangulum	Scarlet kingsnake	S. King
Masticophis flagellum	Eastern coachwhip	CW
Nerodia erythrogaster	Red-bellied water snake	R-b. Water
Nerodia fasciata	Southern water snake	S. Water
Nerodia floridana	Florida green water snake	F.G. Water
Pantherophis alleghaniensis	Eastern rat snake	E. Rat
Pantherophis guttatus	Corn snake	Corn
Pituophis melanoleucus	Pine snake	Pine
Sistrurus miliarus	Pygmy rattlesnake	P. R'snake
Thamnophis sauritus	Ribbon snake	Ribbon
Thamnophis sirtalis	Eastern garter snake	E. Garter