MOVEMENTS, HABITAT USE, AND SURVIVAL OF THE THREATENED EASTERN INDIGO SNAKE (*DRYMARCHON COUPERI*) IN GEORGIA

by

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(Under the Direction of Robert J. Cooper and J. Michael Meyers)

ABSTRACT

Drymarchon couperi (Eastern Indigo Snake), a threatened species of the southeastern Coastal Plain of the United States, has experienced population declines because of extensive habitat loss, fragmentation, and degradation across its range caused primarily by development, fire exclusion, some forestry practices, and agriculture. I conducted a radiotelemetry study on *D. couperi* from December 2002 to December 2004 on Fort Stewart Military Reservation and adjacent private lands to determine movements, habitat use, survival, and shelter use of the species in Georgia. Annual home ranges were large (35-1538 ha, n = 27) and positively related to increases in body size and sex (male), and negatively associated with use of habitats managed for wildlife compared to areas used primarily for commercial timber production. Habitat use analyses suggested positive selection for wetland, evergreen forest, pine-hardwood forest, and field habitats, with avoidance of urban areas and deciduous forests. Annual survival in 2003 was 0.890 (CI = 0.736-0.972, n = 25) and 0.723 (CI = 0.523-0.862; n = 27) in 2004. Survival analysis suggested that body size, standardized by sex, was the best predictor of adult *D. couperi* survival, with lower survival probability for larger individuals within each sex. Microhabitat use was most influenced seasonally compared to sex, site, or body size. Underground shelter type and duration of use were influenced by season and habitat type. During winter, >90% of underground locations were at tortoise burrows; however, reliance on these burrows was less pronounced in spring for males and in summer for males and females, when snakes used a wider diversity of shelters. Because of the large amount of land and wide variety of habitats used by the species, alteration of management and conservation goals to include *D. couperi*, as an umbrella species, would benefit more species and assist in larger-scale biodiversity conservation. In Georgia, conservation of large tracts of relatively undisturbed land is potentially the most important factor for maintaining *D. couperi*; however, quality of the habitats, including a matrix of uplands and adjacent wetlands, in addition to availability of appropriate shelters are also necessary for *D. couperi* populations.

INDEX WORDS: Burrow, *Drymarchon couperi*, Eastern indigo snake, Gopher tortoise, *Gopherus polyphemus*, Habitat use, Home range, Information-theoretic approach, Microhabitat, Movement, Refuge, Shelter, Georgia, Spatial, Telemetry, Tortoise, Umbrella species

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

INTRODUCTION

Habitat loss, degradation, and fragmentation are the primary threats to most herpetofaunal species globally (Alford and Richards 1999, Gibbons et al. 2000), and have been implicated as the primary causes of decline in >85% of all imperiled species and >97% of imperiled herpetofauna in the United States (Wilcove et al. 1998). Many herpetofauna species require specific management techniques, in part because of their life history characteristics, including late age of maturation and longer lives (e.g., Trani-Griep 2002). These factors emphasize the importance of understanding spatial requirements, such as land area, type, and other necessary components for maintaining populations of species across their geographic range.

Many terrestrial ecosystems also are imperiled because of severe loss in area and degradation of remaining habitats. For example, longleaf pine (*Pinus palustris*) and wiregrass (*Aristida stricta*) communities in the southeastern Coastal Plain of the United States, recognized for their high herbaceous vegetation and fauna diversity (Ricketts et al. 1999, Chaplin et al. 2000), are classified as one of the most endangered natural ecosystems in the United States (Noss and Peters 1995, Ricketts et al. 1999). As of 1995, <1.2 million hectares remain, as isolated fragments, of an estimated 30 million original hectares of longleaf pine forests (Landers et al. 1995). These biologically diverse forests, with moisture gradients from xeric sandhills to mesic flatwoods, exist as a natural mosaic of upland and lowland habitats that require frequent, low to moderate intensity fire to maintain their diversity (Engstrom et al. 1984, Mushinsky and McCoy 1985, Van Lear et al. 2005). Fire exclusion leads to an increase in ground litter and tree density resulting in lower herbaceous vegetation growth (Lawler 1977), conditions non-conducive for many native vertebrate species. For successful science-based conservation, restoration, and management of longleaf pine-wiregrass communities, detailed information is required on the spatial and habitat requirements, population dynamics, and distribution of plant and animal species dependent on these habitats.

The southeastern Coastal Plain is a center of herpetofaunal diversity in the United States (e.g., Trani-Griep 2002), supporting the highest diversity of amphibian and reptile species in the country (Gibbons et al. 1997); however, approximately 70% of southern herpetofaunal species are imperiled (Trani-Griep 2002). *Drymarchon couperi* (Eastern Indigo Snake), the longest snake in North America (up to 2.6 m; Conant and Collins 1998), is an imperiled herpetofaunal species and an important predator of the southeastern longleaf pine forests. *Drymarchon couperi* is threatened throughout its range in the southeastern Coastal Plain (United States Fish and Wildlife Service 1978); however, despite federal and state protection of the species, important habitats, such as longleaf pine forests, continue to decline in quality and quantity. *Drymarchon couperi* occupies a variety of habitats, including longleaf pine-turkey oak sandhills, pine and scrub flatwoods, dry prairie, tropical hardwoods, freshwater wetlands, and coastal dunes; however, winter survival, especially in northern portions of its range, depends on the availability of appropriate sheltered retreats. These shelters, primarily *Gopherus polyphemus* (Gopher Tortoise) burrows, are used as protection from temperature extremes, predators, and as over-wintering shelters (Holbrook 1842, Lawler 1977, Landers and Speake 1980, Speake and

McGlincy 1981, Speake et al. 1987). *Gopherus polyphemus* (Gopher Tortoise), a keystone species of these southeastern forests (Eisenberg 1983, Jackson and Milstrey 1989), is also declining throughout its range primarily due to the drastic reductions, fragmentation, and degradation of habitats (Auffenberg and Franz 1982, McCoy et al. 2006).

The recovery plan for *D. couperi* detailed steps necessary for the protection, recovery, and removal of the species from federal protection (Speake et al. 1982, Speake 1993). These steps include delineating, maintaining, and protecting existing populations, while emphasizing the need to determine habitat requirements and conduct studies on population ecology, movements, and food habitats. Other steps in the plan included reestablishing populations where viable and improving the public's attitude towards the species (Speake et al. 1982).

Drymarchon couperi faces a variety of threats, which led to its federal listing in 1978. Protective status at federal and state levels was enacted because of population declines caused primarily by commercial pet trade collection and extensive habitat loss across the southeastern geographic range of the species (United States Fish and Wildlife Service 1978). Other threats include wanton killings, highway fatalities, and residual pesticide exposure (Lawler 1977). In a recent Florida telemetry study, vehicles caused 40% of in-field mortality (R. Bolt, unpublished data). An additional threat to the species is attributable to its association with *Crotalus adamanteus* (Eastern Diamondback Rattlesnake). Gassing, the practice of introducing gasoline into animal burrows, such as tortoise burrows, to expel rattlesnakes, is usually fatal to *D. couperi* (Speake and Mount 1973, Speake et al. 1978, Speake and McGlincy 1981) and may be a limiting factor in portions of the range where "rattlesnake roundups" are held (Lawler 1977). Federal and state protection prevents commerce in the pet trade and has curtailed commercial collecting, presumably reduced its impact on natural populations (Lawler 1977).

Current understanding of natural history and ecology of *D. couperi* is limited, despite federal protective status. For example, insufficient information exists to determine spatial and habitat requirements for *D. couperi* populations (e.g., Hallam et al. 1998). These data are vital for the development of conservation and management strategies. Previous research on movement, home range, and habitat associations conducted on *D. couperi* in the northern portions of the range primarily used translocated and captive-reared individuals, with limited tracking durations due to technology limitations (Speake et al. 1978, Diemer and Speake 1983, Smith 1987). In addition, since Georgia presently constitutes the northern extent of the genus, results from studies in peninsular Florida may not apply to Georgia populations because of habitat and climatic differences. In Georgia, *D. couperi* is commensal with *G. polyphemus* burrows primarily during winter; however, use of *G. polyphemus* burrows and other shelters are unknown during the rest of the year.

Information on *D. couperi* is needed for Georgia, especially its spatial, shelter, and habitat use. To address these informational needs, my objectives were to: (1) quantify habitat use and its seasonal variation, (2) estimate home ranges and movements, including seasonal movement patterns and home ranges, (3) assess biological and ecological factors influencing intraspecific variation of home range size, (4) quantify and describe the microhabitat characteristics associated with these shelters (5) determine degree of seasonal use of underground shelters, and (6) estimate annual survival and correlates of variation in survival probabilities. Following this chapter, a literature review of *D. couperi*, I divided my results into four independent manuscripts, focusing on related, but separate aspects of *D. couperi*'s natural history in Georgia. In Chapter 2, I present home range, movement, and habitat use results from radiotelemetry data collected from January 2003 through January 2005. In Chapter 3, I detail underground shelter use and associated microhabitat characteristics. Chapter 4 is a comparison of two capture methods for *D. couperi* in the northern portions of its range in south Georgia and northern Florida. In Chapter 5, I used known-fate modeling to estimate survival and elucidate the influence of individual covariates on probability of survival. Chapter 6 then summarizes my conclusions and conservation implications. In addition to conservation and management implications of this work, results will help direct future *D. couperi* ecology and management studies and contribute to our overall understanding of southeastern biotic communities.

LITERATURE REVIEW

> The Eastern Indigo Snake… "is perfectly harmless, frequenting the neighborhood of settlements, where it is usually unmolested, from its inoffensive character, and the prevalent belief that it destroys the Rattlesnake, which it attacks with courage… Although a harmless snake, it is a bold one, and when provoked, it faces its enemy with courage, vibrating its tail rapidly" (J. Hamilton Couper as quoted in Holbrook 1842).

Description

Drymarchon couperi (Family Colubridae, Eastern Indigo Snake), named for its bright bluish-black coloration, is uniformly colored dorsally with reddish or cream-colored areas around the gular region (Holbrook 1842, Conant and Collins 1998). This large, stout-bodied, nonvenomous snake is the longest North American snake species, obtaining maximum lengths up to 2.6 m (Wright and Wright 1957, Conant and Collins 1998). Throat and head coloration is highly variable in both extent and hue and potentially correlated with geographic location (Moler 1992). Ventrally, and posterior of the head, *D. couperi* has light bluish-slate or a whitish-black iridescent coloration (Holbrook 1842, Conant and Collins 1998). Scales are large and smooth in 17 scale rows at midbody and the anal plate is undivided. Adult males usually exhibit light keels on 1 to 5 middorsal scale rows (Layne and Steiner 1984, Stevenson et al. 2003). The antepenultimate supralabial scale does not contact the temporal or postocular scales, as found in the Texas indigo *(D. corais erebennus,* Wright and Wright 1957*)*. Young *D. couperi* are similar in appearance to the adults, although some individuals may have blotched dorsal pattern and more reddish color on the head and anterior portion of the ventral side (White and Garrott 1990).

Taxonomy

Holbrook, in 1842, originally described the Eastern Indigo Snake as *Coluber couperi*, with the type locality as a dry pine hill lying south of the Altamaha River, Georgia (Holbrook 1842). In 1853, Baird and Girard reassigned the species to genus *Georgia*. Cope transferred it to genus *Spilotes* in 1860 and relegated it as a subspecies of *Spilotes corais* in 1892. In 1917, Stejneger and Barbour assigned it to *Drymarchon*, designating the species as *Drymarchon corais couperi* which remained stable until 2000 (McCraine 1980).

Throughout most of the twentieth century, genus *Drymarchon* was considered monotypic, *Drymarchon corais*, with multiple subspecies ranging from the Coastal Plain of the southeastern United States, extreme southern Texas, and southward to Northern Argentina. Recently, Collins (1991) proposed that the Eastern Indigo Snake be raised to full species status (*Drymarchon couperi*) because of consistent differences in head scalation compared to the Texas Indigo Snake (*Drymarchon corais erebennus*) and geographic separation. This designation has been accepted provisionally by the Society for the Study of Amphibians and Reptiles (Crother 2001). Currently, the United States Fish and Wildlife Service (FWS) has not adopted the Eastern Indigo Snake's designation to full species status and uses *Drymarchon corais couperi.*

In 2002, a new species of *Drymarchon* was described in northwestern Venezuela, *D. caudomelanurus* (Wuster et al. 2001). Motivated by the discovery, the authors reevaluated the systematics of the genus. They suggested that *Drymarchon* be split into five full species, with five subspecies of *D. melanurus*, including assigning the Eastern Indigo Snake (or Florida Indigo

Snake) to *D. couperi* as previously suggested (Collins 1991). They also raised the Texas Indigo Snake to full species status as *Drymarchon corais*; however, the authors concluded by stating that further studies are necessary to clarify the status of the genus (Wuster et al. 2001).

Distribution

Drymarchon are primarily tropical, ranging from the southeastern United States to northern Argentina. Two forms are found in the United States: *D. couperi* and *D. corais erebennus* (Texas Indigo Snake). Historic accounts report that *D. couperi* maintained a relatively continuous geographic distribution along the Coastal Plain from South Carolina to southern Louisiana (Smith 1941). By 1957, reports indicated that distribution information from Alabama, Mississippi, and Louisiana was inconclusive, with extirpation of populations in these areas likely (Wright and Wright 1957). The last known record from South Carolina was in Jasper County, 1954 (Diemer and Speake 1981); however, this specimen may have been incorrectly identified. South Carolina Department of Natural Resources (DNR) has proposed removal of the species from the state's official species list (S. Bennett, SC DNR, 2005, personal communication).

The current distribution of *D. couperi* is reported as extending from the Coastal Plain of southern Georgia to peninsular Florida and the lower Florida Keys west to southeastern Mississippi (Conant and Collins 1998). Inclusion of Mississippi in the distribution of the species, however, may have been attributed to the release of captive individuals to the area (Conant and Collins 1998), and the species is believed to have been extirpated from the state in the 1930s and 1940s (Lawler 1977). Status of the species in Alabama is currently unknown, despite documentation of the species in western parts of the Florida panhandle (Moler 1992). From 1976 until ca. 1994, the Alabama Cooperative Fish and Wildlife Research Unit released

537 individual adult and juvenile *D. couperi* at 19 sites in Georgia (5 sites), Alabama (9 sites), Florida (2 sites), South Carolina (1 site), and Mississippi (2 sites; Speake 1990). A recent survey of 8 of the 9 Alabama release sites found no *D. couperi*; however, since 1986 in Alabama, there has been an increase in reported, although unconfirmed, *D. couperi* sightings (n = 9), 3 of which were at release sites from the Alabama Cooperative Fish and Wildlife Research Unit (Hart 2003). Although evidence suggests that most releases failed to establish breeding populations of *D. couperi,* potentially, some of the sites may have individuals remaining (D.W. Speake, personal communication).

An investigation into *D. couperi* distribution in Georgia, using mailed questionnaires, museum records, and recent sightings, found evidence of *D. couperi* in 52 of the 94 counties in the Coastal Plain (Diemer and Speake 1983). The highest number of *D. couperi* records was in the Tifton Upland providence, a large physiographical region of the state bordering South Carolina south of Savannah and continuing south to the Florida border (Diemer and Speake 1983). The authors reported only a few records from the coast or the Okefenokee Swamp and no reliable records from Georgia's barrier islands. A similar study investigating the distribution of the species in Florida, examining historical, museum, and current records, found the species in all but three Florida counties (Gulf, Lafayette, and Union; Moler 1985a). Remaining viable natural populations of *D. couperi* likely occur only in southern Georgia and Florida (Lawler 1977) and are considered uncommon to rare where populations remain.

Habitat associations

In Georgia, *D. couperi* is primarily associated with Miocene and Plio-Pleistocene marine terrace sand deposits in middle and lower Coastal Plain often located on north or northeastern sides of major Coastal Plain streams (Lawler 1977, Wharton 1977). These sand deposits, referred to as sandhills or longleaf pine-turkey oak forests (Wharton 1977), are composed of well-drained, deep sandy soils (e.g., Kershaw and Lakeland) and often support populations of *G. polyphemus* (Speake et al. 1978, Speake et al. 1982, Diemer and Speake 1983). Longleaf pine (*Pinus palustris*), scrub oak (*Quercus* spp.) and turkey oak (*Q. laevis*), with occasional live oaks (*Q. virginiana*) dominate these upland habitats in Georgia (Diemer and Speake 1983).

Habitat used by *D. couperi* during summer in Georgia is not well documented; however, evidence suggests that snakes move seasonally into more mesic and hydric habitats and may prefer sandhill uplands adjacent to or near tupelo or bald cypress wetlands, river bottoms, or large pine flatwood tracts (Lawler 1977, Speake and McGlincy 1981, Diemer and Speake 1983). In Georgia and northern Florida, snakes use upland sandhill habitats with *G. polyphemus* populations during the winter breeding season (Speake et al. 1978).

Evidence suggests that habitat preferences are more general in the southern portion of *D. couperi's* range. Throughout peninsular Florida, the species associates with a wide range of xeric to hydric habitats, including mangrove swamps, wet prairies, xeric pinelands, hydric hammocks, citrus groves, scrub (Lawler 1977, Moler 1992), and other habitats without high-density urban development (Moler 1985a). They are relativity common in the hydric hammocks of the gulf hammock region of north Florida and in similar habitats throughout peninsular Florida. In extreme south Florida (Everglades and Florida Keys), *D. couperi* uses tropical hardwood hammocks, pine rock lands, freshwater marshes, fallow fields, coastal prairie, mangrove swamps, and various human-altered areas (Steiner et al. 1983). Of these habitats, hammocks and pine forest appear to be used proportionally more than their level of availability would suggest. North of Lake Okeechobee, *D. couperi* s are primarily associated with xeric sandhill (Moler 1992). Apparent geographic differences in habitat use between northern and southern portions of the snake's range may be attributable to the warmer temperatures further south and available habitats (Speake et al. 1982, Moler 1992).

Drymarchon couperi requires shelters from temperature extremes, desiccating conditions, predator avoidance, and potentially for nest sites (Holbrook 1842, Speake et al. 1978, Landers and Speake 1980, Speake and McGlincy 1981, Speake et al. 1982). These shelters may include active or abandoned *G. polyphemus* burrows, other animal burrows, stumps, logs, and debris piles (Lawler 1977, Speake et al.1978). When occupying areas with *G. polyphemus*, *Drymarchon couperi* regularly associates with their burrows. In mesic habitats lacking *G. polyphemus*, *D. couperi* may take shelter in hollowed root channels, rodent burrows, armadillo burrows, hollow logs or crab burrows (Lawler 1977, Moler 1985b). Speake et al. (1978) found 108 shelter sites used by *D. couperi*. Of these, 77% were located in active or inactive *G. polyphemus* burrows, 18% under decaying logs and stumps, and 5% under plant debris.

Life history

Diet

Drymarchon couperi actively forages diurnally on a wide variety of prey and will consume most vertebrates small enough to overpower. The species is not a constrictor, but instead uses its strength and size to subdue and consume prey. While a rare occurrence, *D. couperi* may also climb trees or shrubs to flee or to capture prey (Taylor and Kershner 1991, Stevenson et al. 2003). Foraging observations in the wild have been observed at wetland edges (Moler 1992). Reported food items include fish, frogs, toads, lizards, turtles, turtle eggs, small alligators, birds, small mammals, and snakes including both venomous and nonvenomous species (Keegan 1944, Groves 1960, Landers and Speake 1980, Steiner et al.

1983, Moler 1985b; 1992, Belson 2000, Alexy et al. 2003, Stevenson et al. 2003). Juveniles may consume invertebrates (Rossi and Lewis 1994); however, this may only occur as secondarily ingested prey items.

Home range and movement

Evidence suggests that the species is likely exclusively diurnal (Moulis 1976, Steiner et al. 1983, Moler 1985b; 1992) and can be active year round on days $\geq 11^{\circ}$C (Speake et al. 1978). Reported *D. couperi* home ranges vary between 4.8 to >300 ha (Speake et al. 1978, Moler 1985b, Dodd and Barichivich 2007). In Georgia, home ranges were smallest from December through April (ca. 4.8 ha), intermediate in May through June (ca. 42.9 ha), and largest from August through November (ca. 97.4 ha) as snakes returned to their over-wintering habitats (Speake et al. 1978). Radiotelemetry data for these home range estimates were collected from individuals tracked over varying periods, generally less than a season, and were primarily translocated (24 of 28) from other areas in south Georgia (Speake et al. 1978).

Drymarchon couperi radiotelemetry studies in peninsular Florida indicated cumulative home ranges (100% minimum convex polygon, MCP) between 65-300 ha for males ($\bar{x}$ = 118, n = 31) and 30–115 ha for females ($\bar{x}$ = 41, n = 18; R. Bolt, unpublished data). Other studies in northern Florida reported male home ranges in the summer from 23 to 281 ha (Moler 1985b) and of a single male with a 185 ha home range (Dodd and Barichivich 2007).

Reproduction and growth

Information on reproductive behavior of *D. couperi* populations is sparse, with most available information originating from captive observation (Hallam et al. 1998). Breeding occurs from October to March (Groves 1960, Speake et al. 1978, Steiner et al. 1983, Moler

1992), and possibly though April in Georgia (Moulis 1976). Gestitation period can last 130-140 days (Speake et al. 1987, O'Connor 1991). *Drymarchon couperi* is oviparous. A single clutch of 4 to 12 relatively large eggs (37–89g; Speake et al.1987, Steiner et al. 1983) is laid in May and June (Moler 1985b, Moulis 1976, Steiner et al. 1983). There is little information available on nesting locations, but there are at least two reports of egg deposition sites located in *G. polyphemus* burrows (Moulis 1976, Speake et al. 1978). A study on captive reared and translocated gravid females found nest sites in abandoned *G. polyphemus* burrows (4 nests) and stumps in more mesic habitats (3 nests; Smith 1987). Eggs hatch after approximately 3 months, with peak hatching activity from August through September (Groves 1960, Wright and Wright 1957, Smith 1987). Hatchlings can be between 45–61 cm in length (Speake et al. 1987, Moler 1992). Sexual maturity may be reached in 3–4 years and females may be capable of reproduction annually (Speake et al. 1987). Delayed fertilization (female sperm storage) may be possible (Carson 1945). Adult male *D. couperi* may be territorial in the breeding season, resulting in combat and possibly cannibalism (Waide and Thomas 1984, Moler 1992, Stevenson 2003); however, only cannibalism between yearlings (one occurrence observed) has been reported (Smith 1987).

Ecdysis in *D. couperi* occurs every 30-60 days (Moler 1985b, Dodd and Barichivich 2007). Prior to shedding, snakes may be inactive for 10-20 days (Moler 1985b, Dodd and Barichivich 2007). Estimates of *D. couperi* inactivity related to ecdysis span up to one third of an individual’s life (Moler 1985b, 1992). The sex ratio of wild populations has not been shown to differ significantly from 1 male:1 female (Moulis 1976, Steiner et al. 1983); however, a recent study conducted in Georgia, using searches concentrated on *G. polyphemus* burrows, reported a 2:1 sex ratio in wild populations (Stevenson et al. 2003). No information is available on individual longevity in the wild. Maximum reported captive longevity is 25 years and 11 months (Shaw 1959, Bowler 1977).

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CHAPTER 2

SEASONAL HOME RANGE AND HABITAT USE OF THE THREATENED EASTERN INDIGO SNAKE IN GEORGIA[1]

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[1] Hyslop, N. L., J. M Meyers, and R. J. Cooper. To be submitted to *The Journal of Wildlife Management.*

ABSTRACT

The threatened eastern indigo snake (*Drymarchon couperi*), native to the southeastern Coastal Plain of the United States, has experienced population declines because of habitat loss, degradation, and fragmentation caused primarily by development, fire exclusion, some forestry practices, and agriculture. We radiotracked eastern indigo snakes from January 2003 to December 2004 on Fort Stewart Military Reservation and adjacent private lands in Georgia to examine habitat use, movements, and home ranges. We estimated annual and seasonal home ranges and evaluated candidate models for home range size using an information-theoretic approach. We analyzed habitat use hierarchically, examining use within home ranges and across study sites. Annual home ranges were large (minimum convex polygon: $\bar{x}_{\text{male}} = 510$ ha; $\bar{x}_{\text{female}} = 101$ ha), possibly representing the largest values yet reported for a North American snake species. Home range size was associated negatively with use of habitats managed primarily for wildlife compared to areas used mostly for commercial timber production. Habitat use analyses on Gap Analysis Program habitat categories suggested positive selection for wetland, evergreen forest, pine-hardwood forest, and field habitats, with an avoidance of roads, urban areas, and deciduous forests. Snakes used the highest diversity of habitats as they transitioned from uplands used in winter and early spring to wetlands, clearcuts, and uplands (other than sandhills) used in summer; however, snakes continued to use sandhill habitats throughout warmer months. Because of the large amount of land and variety of habitats used by indigo snakes, we recommend that a shift in management and conservation goals to include eastern indigo snakes, as an umbrella species, may benefit more species and assist in larger-scale biodiversity conservation. In Georgia, we suggest that conservation of large tracts of undeveloped land is potentially the most important factor for conservation of indigo snakes; however, the quality of habitats, including a matrix of xeric uplands and adjacent wetlands, is likely also necessary.

Index words: *Drymarchon couperi*, eastern indigo snake, Georgia, habitat use, home range, information-theoretic approach, movement, telemetry, seasonal, spatial

INTRODUCTION

Habitat loss, degradation, and fragmentation are the primary threats to most herpetofaunal species globally (Alford and Richards 1999, Gibbons et al. 2000), and have been implicated as the primary causes of decline in >97% of imperiled herpetofauna in the United States (Wilcove et al. 1998), including the federally threatened eastern indigo snake (*Drymarchon couperi;* United States Fish and Wildlife Service 1978). The decline of indigo snake populations attributed to habitat loss and alteration has occurred primarily because of development, fire exclusion, certain forestry practices, and agriculture (USFWS 1978). The species is largely associated with longleaf pine communities that support gopher tortoise (*Gopherus polyphemus*) populations, where tortoise burrows are used by the snakes as protection from environmental extremes and predators (Holbrook 1842, Lawler 1977, Landers and Speake 1980, Speake and McGlincy 1981, Stevenson et al. 2003). This association is especially pronounced in northern portions of the range in the Coastal Plain of Georgia and northern Florida, where habitat use in late fall through early spring is primarily restricted to these upland areas (Diemer and Speake 1983). Eastern indigo snakes may occupy a wide variety of habitats in other seasons, including pine and scrub flatwoods, dry prairie, tropical hardwoods, bottomland forests, and other freshwater wetlands (Speake et al. 1978, Landers and Speake 1980). Mean land area requirements estimated for indigo snakes using radiotelemetry range from 41–141 ha (R. Bolt, Dynamac Corporation, Kennedy Space Center, FL, personal communication; P. E. Moler, Florida Game and Fresh Water Commission, personal communication). Because of these potential habitat shifts during their annual cycle, large body size (up to 2.6 m; Conant and Collins 1998), and large area requirements (Speake et al. 1978), eastern indigo snakes could function potentially as an umbrella species for other herpetofauna and wildlife using similar habitats (Lambeck 1997, Fleishman et al. 2000). That is, meeting the habitat management needs for indigo snakes could potentially meet the requirements of many other sympatric wildlife, including other herpetofaunal, species (Roberge and Angelstam 2004).

Accurate natural history information for a species is necessary for developing appropriate management and conservation strategies, especially for declining populations. Many herpetofaunal species require specific management techniques. This is in part because of their life history characteristics, including late age of maturation, long lives (e.g., Trani-Griep 2002), and energetic and behavioral consequences associated with ectothermy, such as the ability to behaviorally regulate body temperature (Shine 2005). These characteristics emphasize the importance of understanding spatial requirements, such as land area, type, and other necessary components central for maintaining herpetofaunal populations across their geographic range. Despite the protective status of the eastern indigo snake, only a limited understanding of its natural history exists, with insufficient information to determine spatial and habitat requirements (Hallam et al. 1998). We initiated this research to address information needs associated with the eastern indigo snake, including spatial and habitat requirements in Georgia. Our objectives were (1) to quantify habitat use and seasonal variation in use; (2) to estimate annual and seasonal home range sizes and movements; and (3) to investigate biological and ecological factors influencing intraspecific home range size variation.

STUDY AREA

We conducted telemetry research of indigo snakes on Fort Stewart Military Reservation and tracts of adjacent private land located in southeastern Georgia. We delineated our study sites using a rectangle created from all radiolocations, which we buffered by 200 m, using the Animal Movements Extension (Hooge and Eichenlaub 1997) to ArcView GIS, with Spatial Analyst

(Environmental Systems Research Institute, Inc., 1999). Fort Stewart study sites covered approximately 8,000 ha of its total 111,600 ha (Stevenson et al. 2003). Private lands adjacent to Fort Stewart covered approximately 6,000 ha in a single, uninterrupted tract.

Upland habitats at Fort Stewart included extensive sandhills, mixed pine-hardwood forests, and pine flatwoods. Interspersed with upland habitats were wetlands, including blackwater swamps, bottomland hardwood forests, and impoundments. Further habitat details specific to the Fort Stewart sites are provided in Stevenson et al. (2003). Neither site contained paved roads, but did have maintained and un-maintained unpaved roads. Paved roads bounded two sides of the private lands site. Both sites supported gopher tortoise populations with hatchling tortoises observed.

Management activities on Fort Stewart centered on restoration and conservation of native habitats, specifically longleaf pine forests. Activities included prescribed burning on 1–10 year intervals, seeding wiregrass, planting longleaf pine, controlling and removing turkey oak (*Quercus laevis*), and thinning pine plantations. Land use also included commercial timber harvesting. Habitat management included food plots primarily targeting white-tailed deer (*Odocoileus virginianus*), wild turkey (*Meleagris gallopavo*), and northern bobwhite (*Colinus virginianus*). Management activities on private land varied by landowner, but most tracts were managed for pine timber production (primarily loblolly pine, *Pinus taeda*) and game similar to Fort Stewart. Private lands had long histories of fire exclusion (>15 yr), resulting in hardwood encroachment (turkey oak), increased midstory and canopy cover, and reduced native ground cover in upland areas.

To identify areas with gopher tortoise burrows, we used aerial photographs to locate upland areas, which we then systematically surveyed for the presence of burrows. We delineated, in

ArcView GIS, land compartments within the study area containing >5 identifiable gopher tortoise burrows. We chose this value because compartments with fewer burrows were primarily areas where burrows were restricted to edges. On Fort Stewart sites, we identified 24 distinct areas with tortoise burrows ($\bar{x}$ = 35 ha, 0.14 – 176.4 range), totaling 838 ha, or approximately 17% of Fort Stewart study sites. We identified 18 distinct areas with tortoise burrows ($\bar{x}$ = 29.4 ha, 0.28 – 120.0 range), covering 440 ha, or approximately 14% of the private land sites. Of the 440 ha with tortoise burrows on private lands, approximately 50% were sandhills, 11% were planted sand pine (*Pinus clausa*), 21% in loblolly and longleaf pine plantations <10 years old, <1 % in loblolly pine plantations >10 years old, and 18% in actively managed hay fields. All sites supporting tortoises on Fort Stewart were managed for wildlife protection with no timber extraction or agricultural activities in >10 years, with the exception of small-scale timber harvests for restoration in areas where the canopy was dominated by a species other than longleaf pine.

METHODS

Telemetry

We captured snakes by hand on upland sandhill habitats with gopher tortoise populations (Stevenson et al. 2003) on Fort Stewart and private land sites during late fall to early spring, 2002-2004. We selected adult snakes for radio implantation based on sex and site of capture to represent the study areas and sexes as evenly as possible. We implanted 20 snakes (7 F, 13 M) with transmitters from 12 December 2002 to 11 April 2003, and 12 additional snakes (6 F, 6 M) from 10 October 2003 to 1 March 2004. In the first year, we used radiotransmitters weighing approximately 16 g with whip antennas (AI-2T, 36 mo., 15x37 mm; Holohil Systems, Ltd., Ontario, Canada), and in the second year we used a smaller 18-month transmitter (SI-2T, 9g, 11x33 mm). Surgical implantation procedures followed Reinert and Cundall (1982) with modifications by T. Norton, DVM, Wildlife Conservation Society. Transmitters were implanted approximately two-thirds from the anterior in the coelomic cavity with the antenna threaded subcutaneously anterior of the transmitter. Isoflurane was administered via tracheal tube throughout the procedure.

Following surgery, while anesthetized, individuals were weighed, measured, and sexed by cloacal probing. Snakes were held in captivity for 10–16 days post-operatively at elevated temperatures for recovery (21–27°C thermogradient within the enclosure). We released snakes at their point of capture during late morning, on days with forecasted maximum temperatures >15.5°C and overnight lows >4°C. In spring 2004, we used ultrasound or radiographs on 9 of 10 females to assess reproductive condition. Upon study completion, we recaptured snakes and surgically removed transmitters for all but six snakes. Removal procedures and snake care were identical to those used for implantation. The University of Georgia IACUC (A2002-10111-0) and USGS Patuxent Wildlife Research Center Animal Care and Use Committees approved study procedures.

Radiotelemetry began approximately 24-hours after release. We relocated snakes 2–3 times per week by foot and vehicle using homing techniques (Mech 1983), randomly staggering periods of the day that we tracked each individual. We determined coordinates using global positioning system (GPS) in Universal Transverse Mercator (NAD83). If the snake had not relocated since its previous position, we used coordinates previously recorded to ensure identical GPS positions.

Home range

To estimate area used by the snakes, we used minimum convex polygons (MCP) to estimate home ranges (Mohr 1947; Southwood 1966) and kernel density analysis (KD) to estimate utilization distributions (Worton 1987, 1989). To address possible sample size biases associated with MCPs (e.g., Arthur and Schwartz 1999), we used bootstrap analysis to examine sample size to home range area relationships with 500 iterations. If incremental area curves visually reached an asymptote, we included the home range in analyses. We calculated KD at 95% isopleths, representing home ranges, and at 50% isopleths, representing core areas of activity (AC; Samuel et al. 1985) using the fixed kernel method, with a least squares cross-validation smoothing parameter (Silverman 1986, Worton 1989, Seaman and Powell 1996, Gitzen and Millspaugh 2003). The probability of observation is higher for an animal that has not moved since its last location. We maintained a relatively consistent tracking effort throughout the study; however, seasonal variations in snake activity and movement lead to differences in days between successive telemetry locations. For calculation of KD home ranges, we retained only novel radiolocations and removed consecutive repeated locations to alleviate potential bias in tracking frequency caused by seasonal variations in snake activity and movement (Hemson et al. 2005).

We calculated annual home ranges from December 15- December 14, using breeding season and associated return to breeding and over-wintering areas to delineate years. We estimated seasonal MCP home ranges for winter (December 15- March 14), spring (March 15- June 14), summer (June 15- September 14), and fall (September 15- December 14). Only individuals with complete seasons of data were included in analyses. We conducted analyses with Animal Movements Extension (Hooge and Eichenlaub 1997) to ArcView GIS with Spatial

Analyst. We used ANOVA for seasonal home range analysis on natural log-transformed data, and used a Tukey-Kramer multiple comparison procedure (PROC GLM; SAS Institute Inc 2005). We considered individuals as the experimental unit in all analyses.

We used repeated measures linear regression on candidate models created from a priori hypotheses to examine biological and ecological correlates of intraspecific home range size variation. Home range data were natural log-transformed to approach normality. Because of repeated measures within our data set (home ranges lack independence for the same individual between years) and fixed and random effects, we used mixed, or hierarchical, modeling for linear regression (PROC MIXED, SAS Institute Inc. 2005). Model selection was performed using an information theoretic approach (Burnham and Anderson 2002), in which Akaike's Information Criterion (AIC; Akaike 1973), corrected for small sample sizes (AICc; Hurvich and Tsai 1989), was the metric used for model comparison. We also used AICc to objectively select the appropriate covariance structure for the data. Model averaging may be inappropriate with repeated measures designs (Reiman et al. 2006); instead, we report Akaike weights and parameter estimates for model parameters in 90% confidence sets.

We used comparable hypotheses and modeling for examining MCP and 95% KD annual home ranges, and 50% KD centers of activity. Variation in modeling occurred because of different data structures and home range estimation techniques. Parameters included sex (dummy variable coded for female), snout-vent length (size), interaction of sex and size, over-wintering location (site, dummy variable coded for over-wintering on private lands), and number of radio locations (locations). The locations variable was not used in KD and AC models because repeated locations were removed. We standardized size by sex using residuals of size versus sex regression as a covariate in our survival models (size standardized). Individual covariates were standardized and logit link functions were used for all models.

We hypothesized that sex influenced home range size, with males maintaining larger ranges than females because of differences in reproductive condition (Blouin-Demers and Weatherhead 2001). Alternatively, we hypothesized that home range size was not directly affected by sex, but that an apparent sexually dimorphic pattern emerges because males, on average, are larger and therefore have potentially higher resource needs (e.g., Harstad and Bunnell 1979, Tufto et al 1996). We also predicted that quality of over-wintering habitat would affect annual home range size. The habitat at the private land sites, although sufficient to support indigo snakes, differed from habitats on Fort Stewart because of variation in spatial distribution of resources, management, and land use objectives between sites. We therefore predicted larger home ranges with individuals over-wintering on private lands, potentially influenced by these habitat differences (Tufto et al. 1996). By setting a minimum tracking duration for inclusion of individuals into annual and seasonal home range analyses, in addition to bootstrap analyses, we assumed that home and seasonal ranges included in these models are relatively stable with sufficient locations; however, as an additional measure, we also incorporated into our modeling the number of locations collected per individual.

Patterns of movement

We calculated frequency of movement as the proportion of tracking days that an individual changed locations. We divided 24 months of radiotelemetry data into 14–day periods and calculated proportion of days moved compared with number of days located within that 14-day period. We used this method to standardize tracking effort across seasons and individuals. We deleted records for snakes with only 1 location in a 14-day period, (31 deleted locations among 18 individuals).

To determine average distance moved per day, or daily movement index, we calculated straight-line distances between successive locations as an index of minimum distance traveled (Animal Movements Extension, Hooge and Eichenlaub 1997). Calculations were based on number of days in each season that individual snakes were located. For calculations, we again used 14-day periods to standardize data. For both movement analyses, we retained the individual as the sampling unit and used repeated measures analyses of variance (ANOVA; SAS Institute Inc 2005).

Habitat association analyses

We delineated available habitat as the collective extent of observed telemetry locations. Habitat types, as delineated by Gap Analysis Program land cover data (GAP; Kramer at al. 2003), included roads and urban areas (roads); open water, forested, and non-forested wetlands (wetlands); agricultural and other fields (field); clearcuts and other habitats with sparse canopy cover (cut/sparse); forests with >75% deciduous trees (deciduous); forests with >75% evergreen trees, including managed pine plantations (evergreen); and pine-hardwood mixed forest, including shrub-scrub habitats (mixed).

Habitat selection may vary with scale; therefore, we examined habitat use hierarchically (Johnson 1980). We examined the snake's position within the habitat (within home range) by comparing habitat at telemetry locations to 100% MCP home ranges. We also compared habitats within home ranges to proportion of habitats available at the site (range selection; Johnson 1980). We used compositional analysis (Aitchison 1986, Aebischer et al. 1993) for habitat use comparisons (Bycomp Version 1.0 in Ott and Hovey 1997, SAS Institute Inc 2005).

In addition to habitat use analyses performed on standardized GAP habitat categories, at each location we also noted habitat type based on hydrology, land use, management, vegetation, and gopher tortoise presence. We included this additional habitat use summary in part to distinguish between sandhill and plantation areas, which are combined within the Evergreen GAP category. Sandhill habitats are also included within mixed and cut/sparse categories. Habitat categories included sandhill (xeric uplands with longleaf pine overstory and gopher tortoise burrows), clearcut (primarily harvested mesic pine flatwoods with windrows, bedding for loblolly pine planting, and occasional isolated wetlands), field (included old-field, hay fields, and food plots), plantation (areas planted by rows in pine trees, may or may not support gopher tortoise burrows), slope forest (transitional habitat between xeric uplands and wetlands), miscellaneous uplands (xeric uplands with pine-hardwood mixed overstory composition), and wetlands (isolated upland wetlands and bottomlands, no gopher tortoise populations). We used ANOVA on arcsine transformed data, with a Tukey-Kramer multiple comparison procedure, for examining seasonal differences in habitat use between males and females (PROC GLM, SAS Institute Inc 2005). We expected intersexual separation in spring habitat use because of differences in reproductive condition, when females may use more open areas for thermoregulation while gravid (Blouin-Demers and Weatherhead 2001). We predicted comparable habitat use patterns between males and females in other seasons because of similarity in types of resources needed, such as prey and thermal requirements, outside of female gestation.

RESULTS

Telemetry

We collected 4,993 telemetry locations for 32 snakes relocated between January 2003 and December 2004. Individuals were relocated from 89 to 711 days ($\bar{x}$ = 420, 39-254 locations per individual). We relocated 30 snakes for >6 months and 18 of these for >12 months. Male average snout-vent length (SVL) was 158 cm (range 120-191), with a mean mass at capture of 2.2 kg (range 0.72-4.3). Females averaged 138 cm SVL (range 110-156) and 1.5 kg (range 0.55-2.3).

We observed foraging behavior or consumption of prey on 65 occasions; about 0.84 of these observations occurred in spring and summer, with 0.17 in fall. Approximately 0.65 of observations were in wetlands and 0.20 in sandhills. We observed 11 feeding events in the field, 9 of these involved other snakes as prey, 3 of which were rattlesnakes (*Crotalus horridus).* We also recorded, either in the field or indirectly though expelled prey items in captivity, individuals consuming: black racers (*Coluber constrictor*), yellow rat snakes (*Elaphe obsoleta),* eastern hognose snakes (*Heterodon platirhinos*), unidentified water snake (*Nerodia* spp.), anurans (*Rana* spp), and gopher tortoise hatchlings.

Home range

Bootstrap analysis of MCP annual home ranges and seasonal home ranges yielded area curves that approximated asymptotes. Eighteen snakes in 2003 (11 M, 7 F) and 20 snakes in 2004 (13 M, 7 F) were included in annual home range calculations (Fig. 2.1). Males, on average, occupied annual home ranges about 5 times larger (2003 MCP $\bar{x}$ = 538 ha; 2003 95% KD $\bar{x}$ = 762 ha; 2004 MCP $\bar{x}$ = 481 ha; 2004 95% KD $\bar{x}$ = 552 ha) than females (2003 MCP $\bar{x}$ = 126 ha; 2003 95% KD $\bar{x}$ = 173 ha; 2004 MCP $\bar{x}$ = 77 ha; 2004 95% KD $\bar{x}$ = 79 ha). KD analysis at 50% isopleths for annual ranges yielded 1–3 distinct regions of core habitat use for each snake. Males, on average, had larger AC areas ($\bar{x}_{2003}$ = 120.2 ha ± 50.7 SE; $\bar{x}_{2004}$ = 75.5 ha ± 18.9 SE) than females ($\bar{x}_{2003}$ = 24.7 ha ± 9.50 SE; $\bar{x}_{2004}$ = 9.50 ha ± 1.60 SE). Core areas averaged approximately 12% of the area calculated for 95% KD ranges for both males and females.

Home ranges varied seasonally ($F_{7, 109}$ = 49.8, $P < 0.001$) and by sex ($F_{1, 30}$ = 34.8, $P < 0.001$) with no interaction ($F_{7, 109}$ = 0.24, P = 0.973; repeated measures ANOVA). Males had larger seasonal home ranges overall; however, this differences was not significant in Tukey-adjusted multiple comparisons of individual seasons. Lack of confidence interval overlap may suggest that results from this conservative comparison test masked actual differences in home ranges in spring, summer, and fall. Home ranges were at minimums and similar for males and females in the winter (Fig. 2.2).

Global models for MCP, 95% KD, and 50% KD home ranges confirmed adequate goodness of fit ($P < 0.05$). Residual normality plots of natural log-transformed data supported normality of transformed data in annual home range estimates. AICc analyses on global models suggested autoregressive covariance structure as the most appropriate. The 90% confidence set of models for estimating annual MCP home ranges contained 2 of 12 candidate models (Table 2.1). The model with the most support included sex, size, and over-wintering site (ω = 0.824) and was 6.2 times more likely than the next best approximating model, which contained sex and size (ω = 0.132; Table 2.1). Parameter estimates were similar between the two models, including smaller home ranges for females, for smaller individuals, and for individuals on Fort Stewart (Table 2.2). Results were similar for 95% KD annual home ranges and for 50% KD activity centers.

Sex ranked as the most important variable, according to Akaike importance weights, for all annual home range estimates. Size ranked second and site ranked third (Table 2.3). The confidence set of models suggested a negative influence on home range size for both sex (being female) and association with Fort Stewart; however, 95% CI spanned 0 in all models, lending doubt to conclusions about its influence. Home range size correlated positively with body size in all models. Within the most plausible models for each range estimate, the 95% CI of sex and size predictor variables did not span 0, further suggesting that these variables influenced home range size variation (Table 2.2).

Patterns of movement

All snakes tracked ≥9 months returned to the same discrete sandhill used the previous winter. Individual degrees of fidelity to specific shelters varied; however, all snakes returned to at least four gopher tortoise burrows they used the previous year. Several large-ranging males (n = 3) traveled 5–8 km linear distance from winter to summer locations. One male used the same travel corridor (ca. 2 km) for 2 consecutive years, despite clearcutting of the corridor (ca. 75%) in the intervening winter. Although we recorded 6 individuals within 100 m of paved roads, all snake locations collected were within boundaries created by paved roads. Radio-tagged snakes crossed non-paved roads and trails regularly within Fort Stewart and private lands.

The proportion of snake locations that were novel varied by season (repeated measures ANOVA, $F_{3,\,70} = 61.1$, $P < 0.001$) but not by sex ($F_{1,\,30} = 2.8$, $P = 0.10$), and with a sex x season interaction ($F_{3,\,70} = 5.73$, $P = 0.002$). Differences in least square means indicated males had higher use of novel locations than females in spring ($\bar{x}_M = 0.542$, CI = 0.494-0.890; $\bar{x}_F = 0.453$, CI = 0.391-0.515; $t_{70} = 2.27$, $P = 0.026$) and fall ($\bar{x}_M = 0.626$, CI = 0.576-.676; $\bar{x}_F = 0.476$, CI = 0.410-0.542; $t_{70} = 3.61$, $P < 0.001$), but no difference of novel locations between males and females in winter ($\bar{x}_M = 0.277$, CI = 0.223-0.331; $\bar{x}_F = 0.302$, CI = 0.240-0.364; $t_{70} = 0.60$, P = 0.550) or summer ($\bar{x}_M = 0.626$, CI = 0.576-0.676; $\bar{x}_F = 0.691$, CI = 0.625-0.757; $t_{70} = 1.57$, P = 0.121).

Mean daily linear movement distances (Fig. 2.3), averaged across 14–day periods, varied by sex (repeated measures ANOVA, $F_{1,30} = 14.7$, $P < 0.001$) and season ($F_{3,84} = 79.3$, $P < 0.001$), with no interaction ($F_{3,84} = 1.8$, $P = 0.16$). Females had smaller daily movement distances than males, regardless of season (Fig 2.3). Least squared estimates of differences in average daily movement distance within sexes suggested similar movements in spring and fall for males ($t_{84} = 1.5$, $P = 0.15$) and females ($t_{84} = 0.9$, $P = 0.38$). Winter movements were smaller than other seasons, with no difference between sexes ($t_{84} = 0.1$, $P = 0.91$).

Mean biweekly movement frequency varied by sex (repeated measures ANOVA, $F_{1,\,30} = 4.6$, $P = 0.04$) and season ($F_{3,\,81} = 65.8$, $P < 0.001$), with an interaction effect ($F_{3,\,81} = 5.9$, $P \leq 0.001$). Males had larger movement frequency across all seasons when compared to females (Fig. 2.3). Least squares estimates of differences in movement frequency indicated similar movement patterns between fall and spring for females ($t_{1,\,81} = 0.8$, $P = 0.44$), but difference in movement for males between spring and fall ($t_{1,\,81} = 3.3$, $P = 0.003$). We recorded more frequent movements in summer compared to all other seasons. Winter movement frequency was smaller than other seasons, with no difference between sexes ($t_{1,\,81} = 0.5$, $P = 0.60$; Fig. 2.3).

Habitat use

Mean use of GAP category habitats (% availability) consisted of 1% (2%) road and urban areas, 18% (24%) wetlands, 6% (7%) agricultural and other fields, 20% (7%) clearcuts and areas with sparse canopy cover, 2% (3%) deciduous forest, 36% (51%) evergreen forest including evergreen plantations, and 18% (6%) pine-hardwood forest and shrubland (Fig. 2.4). Compositional habitat use analyses suggested nonrandom habitat use at both levels of selection examined (home range selection: $\lambda = 0.212$, $P < 0.001$; site selection: $\lambda = 0.324$, $P = 0.01$). Rankings for habitat use for home range selection, comparing habitats within individual home ranges to available habitat, in descending order, included wetland, evergreen, mixed, cut/sparse, fields, roads/urban, and deciduous. There was no difference among the 5 most selected habitats or between the least 2 selected habitats (Table 2.4). Habitat use rankings for within home range selection, from most to least selected included: evergreen, wetland, mixed, cut/sparse, field, deciduous, and roads. There was no difference between the 4 most selected habitats or between the last 3 habitats (Table 2.4).

Habitat use, as described by habitat types collected in the field, varied seasonally. Winter habitat use was primarily restricted to xeric uplands with gopher tortoise burrows; 67% of all locations from this period were in sandhills and 22% were located in young, upland pine plantations with gopher tortoise burrows. Habitat use in spring, summer, and fall was concentrated less on xeric upland habitats than observed in winter; however, snakes continued to use sandhill habitats throughout the warmer months, with mean use >35% for all seasons (Fig. 2.5). Wetland use in summer ($\bar{x}$ = 30%, 95% CI = 0.23-0.36) was higher than recorded in any other season.

Use of habitats varied within different seasons (winter $F_{6,\,189} = 30.0$, $P < 0.001$; spring $F_{6,\,196} = 45.22$, $P < 0.001$; summer $F_{6,\,182} = 20.6$, $P < 0.001$; fall $F_{6,\,168} = 28.1$, $P < 0.001$) with no differences between males and females and a sex x season interaction only in spring ($F_6 = 3.09$, $P = 0.006$). Tukey-Kramer post hoc tests of habitat use indicated that females used sandhills more than males only in spring ($P = 0.041$), with no other seasonal differences in habitat use between sexes.

DISCUSSION

Home range

Annual home ranges for indigo snakes in this study ranged from 35–354 ha for females ($\bar{x}$ = 126) and from 140–1,530 ha for males ($\bar{x}$ = 538, MCP). These data may represent the largest home ranges reported in the literature for a North American snake species (Macartney et al. 1988). Results of bootstrapping analyses suggest our radiotelemetry efforts were sufficient to describe home ranges and that individuals maintained definable annual home ranges. Previous studies in northern portions of the indigo snake's range reported home ranges between 5–100 ha (Smith 1987, Speake et al. 1987); however, these results were primarily from translocated and captive-reared individuals. In southeastern peninsular Florida, annual home ranges (MCP) were 65–300 ha for males ($\bar{x}$ = 118, n =31) and 30–115 ha for females ($\bar{x}$ = 41, n =18; R. Bolt, Dynamac Corporation, Kennedy Space Center, FL, personal communication). In northeastern peninsular Florida, mean annual home ranges for males (n = 4) was 141 ha (32–281 ha; P.E. Moler, 1985, Florida Game and Fresh Water Commission, personal communication).

We identified models explaining potential sources of variation for home range area, suggesting a strong negative relationship with being female and a slight positive effect of increasing body size. Although indigo snakes are male-biased in size, our sample had considerable overlap between large females and smaller males. Reproductive condition and associated behaviors may account for some differences in home range size between males and females, especially in the spring when females remained on over-wintering habitats while males began using more lowland areas. Size standardized by sex had no predictive power, suggesting potentially that intersexual differences, rather than differential resource needs for larger individuals, influenced home range. Home ranges in other snake species that have been shown to vary by sex (Gibbons and Dorcas 2004) were attributed to differential energetic needs and reproductive condition (Gregory at al. 1987, Whitaker and Shine 2003).

Home range model analyses indicated an increase in home range size with over-wintering on private lands or with an increasing proportion of locations on private lands, suggesting a possible effect of habitat type on home range size. Because of large areas of agricultural and commercial timber production and lack of prescribed burning, the private lands site may represent lower quality habitat for indigo snakes than habitat found on Fort Stewart. Evidence suggests that a higher rate of tortoise burrow abandonment occurs with changes in overstory structure consistent with canopy closure in maturing pine plantations (Aresco and Guyer 1999), which was evident on the private lands.

Indigo snakes occupied their smallest seasonal home ranges in winter, intermediate-sized in spring and fall, and largest in summer. Previously, radiotelemetry of indigo snakes in Georgia with translocated individuals, reported the smallest home ranges from December through April ($\bar{x}$ = 4.8 ha), intermediate-sized from May through July ($\bar{x}$ = 42.9 ha), and largest from August through November ($\bar{x}$ = 97.4 ha, Speake et al. 1978). The annual trend presented in these data appears similar to our data, although direct comparisons are not possible because of the presence of translocated snakes in the sample and differences in partitioning the annual cycle.

The large eastern indigo snake annual home range sizes observed in this study may be attributed to multiple factors. The large home ranges may represent the needs of a larger terrestrial species, which, on average requires more food and area to forage. Consistent patterns, however, of influence of body size on home range size in snakes have not been established inter- or intra-specifically (Gregory et al. 1987, Macartney et al. 1988). If these large home ranges were an artifact of snakes seeking new overwintering and breeding areas (i.e., emigration), we would expect a proportion of snakes to not return to the preceding year's over-wintering area. All snakes relocated in this study returned to the same area used the previous winter, a pattern observed during 3 winters of telemetry. If intraspecific competition was influencing large home ranges, we would expect to see some avoidance of individuals, at least outside of the breeding period; however, all snake paths crossed those of other snakes and the two largest home ranges were from males found in close proximity to each other in summer and winter. Therefore, in addition to sex and body size, indigo snake home ranges, at least in warmer months, may be influenced by foraging needs. We recorded approximately 0.84 of foraging observations in spring and summer, when snakes exhibited larger and more frequent movements than in cooler months.

Previous studies of indigo snakes have suggested that adult males may be territorial, at least during the breeding season, resulting in combat and possibly cannibalism (Waide and Thomas 1984, Moler 1992, Stevenson 2003). Evidence of territoriality or even avoidance of conspecifics in snakes is rare (Gregory et al. 1987, Macartney et al. 1988, Whitaker and Shine 2003), with few instances of this behavior reported (Webb and Shine 1997, Whitaker and Shine 2003). All home ranges in our sample overlapped with ≥6 other home ranges, regardless of sex. We did not find data that indicated potential cannibalism or avoidance behavior of adults in the non-breeding season.

Patterns of movement

Many snake species exhibit larger and more frequent movements during the breeding season (e.g., Gibbons and Dorcas 2004); however, snakes in this study showed the opposite activity pattern. Indigo snake breeding occurs during or just prior to the coldest months of the year when movements are greatly reduced compared to other seasons (Fig. 2.3). There was less difference between male and female movement frequency outside of spring than seen with movement distance, suggesting similar activity patterns throughout much of the year but at a reduced spatial scale for females.

Indigo snakes followed two general movement patterns during the year. All females and approximately half of males maintained associations with their over-wintering sandhill throughout the year. Most larger-ranging males made directional movements in late spring and did not return to their respective over-wintering sandhills until mid-fall. We defined both of these movement patterns as home ranges because of returns to over-wintering sandhills and results from bootstrapping analyses (Burt 1943).

Habitat use

Habitat use analyses conducted on GAP categories indicated that wetlands, cut/sparse, mixed, and evergreen forests were used in higher proportions relative to their availability at both levels of selection tested. Closer inspection of clearcut and sparse areas suggests that the snakes were not preferentially using clearcuts, but instead were using predominantly young longleaf pine plantations with gopher tortoise populations, especially in winter.

Habitat use by eastern indigo snakes varied seasonally. Sandhills were used more than any other habitat for both males and females in all seasons, except for summer when wetland use was similar to sandhill use. Winter included breeding activities on upland habitats and extended periods of inactivity during cold temperatures. During spring males began dispersing from sandhills to surrounding habitats, including wetlands, clearcuts, and other uplands. Females remained on sandhill habitats until late spring and early summer when oviposition is completed (Speake et al. 1987). Similar patterns have been reported of earlier male dispersal from over-wintering locations compared to females (Parker and Brown 1980, Shine 2003); however, few studies have been conducted on temperate species that are active in cold seasons, such as indigo snakes. During summer, males and females depended less on sandhill habitats, but continued to use upland habitats and tortoise burrows for shelter prior to ecdysis and often following foraging. Both Fort Stewart and private land sites had extensive bottomland hardwoods that were used by snakes. Other wetlands used included cypress domes imbedded in large clearcuts, which were previously mesic pine flatwoods before timber harvesting and bedding for new plantings. In fall, habitat use was transitional, while snakes returned to over-wintering sandhills.

MANAGEMENT IMPLICATIONS

Ecosystem approaches to management often focus necessarily on a few key species that may serve as indicators of ecosystem integrity, as keystone species, or as umbrella species (e.g., Lambeck 1997, Simberloff 1998). Wildlife management in longleaf pine forests has primarily focused on red-cockaded woodpecker (*Picoices borealis*) or gopher tortoise populations. Management activities targeting these species, which include maintaining a low basal area, sparse canopy cover, low midstory cover, native groundcover vegetation, and prescribed fire, will also benefit eastern indigo snakes. These management activities, however, often exclude the extensive tracts of wetlands that historically exist between uplands in the region (Wharton 1978). We propose that a shift in management and conservation goals to include eastern indigo snakes would benefit more species and assist in larger-scale conservation of biodiversity. We suggest that the eastern indigo snake, because of the large amount of land and wide variety of habitats used, is an appropriate model to serve as an umbrella species in an ecosystem-based management approach (Grumbine 1994, 1997, Noss 2000). This strategy will likely be even more effective when combined with management needs of red-cockaded woodpeckers and gopher tortoises, by adding components to current management and conservation practices that may have been excluded previously (Fleishman et al. 2000, Roberge and Angelstam 2004).

As of 1995, <1.2 million hectares of longleaf pine forests remain as isolated fragments, of an estimated 30 million original hectares (Landers et al. 1995). Of longleaf pine forests remaining in Georgia, 0.002 of remaining sandhills and 0.13 of remaining longleaf pine forests are protected with some management activities directed at maintaining the landscape in its natural state. These activities include allowing natural disturbances, such as wild and prescribed fire (Kramer et al. 2003), which is required to maintain the forest's diversity (Engstrom et al. 1984, Mushinsky and McCoy 1985, Van Lear et al. 2005). Historically, sandhill habitats occurred as physiographically disjunct segments, interspersed with other habitats, such as streams and wetlands (Lawler 1977, Wharton 1978). As development and agriculture eliminated natural areas between remaining sandhills, islands of habitat within a matrix of unsuitable, altered habitat were created, with little to no connectivity between remaining areas (McCoy and Mushinsky 1999). Habitat fragmentation and land development, even at low densities, exacerbates impacts of habitat loss because of the snake's large home ranges and movements. The area used for this study, Fort Stewart and adjacent private lands, is one of the largest areas of longleaf pine forest remaining in Georgia, representing one of the last remaining large-scale areas of habitat for the species in the northern half of its range.

Habitat loss, fragmentation, and degradation remain primary threats to indigo snake populations. Our results suggest that longleaf pine ecosystem conservation and restoration is important to indigo snake populations when it includes an appropriate matrix of wetland and upland habitats. Currently, these habitats exist in a few large undeveloped tracts of land, such as Fort Stewart and adjacent private lands, which can potentially serve as core areas for large-scale conservation plans. Focusing on conservation and restoration of natural structure, flora, and fauna, connectivity of habitats, and natural ecosystem processes, especially fire, may effectively and efficiently benefit not only eastern indigo snakes but many other species that use these systems.

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Table 2.1. Candidate models for annual minimum convex polygon (MCP) home ranges for relocated eastern indigo snakes, 2003–2004, Georgia. Models are listed in AICc order by predictor variables, with number of parameters (K), AICc, ΔAICc, model likelihood, and Akaike weights (*ω*) for the set of candidate models (*i*).

Model[1]	K	AICc	ΔAICc	Model likelihood	ω_i
Sex, Size, Site	6	114.60	0.00	1.00	0.824
Sex, Size	5	118.26	3.66	0.16	0.132
Sex, Size, Sex x Size	6	121.40	6.80	0.03	0.027
Sex, Size, Site, Locations, Sex x Size	8	122.40	7.80	0.02	0.017
Sex, Site	5	136.46	21.86	0.00	0.000
Sex	4	143.82	29.22	0.00	0.000
Size, Site	5	144.06	29.46	0.00	0.000
Size	4	148.62	34.02	0.00	0.000
Site	4	175.02	60.42	0.00	0.000
Size (standardized), Site	5	173.66	59.06	0.00	0.000
Locations	4	184.22	69.62	0.00	0.000
Size (standardized)	4	181.82	67.22	0.00	0.000

[1] Model parameters: sex (being female), size (snout-vent length), site (over-wintering location on Fort Stewart versus private lands), locations (number of telemetry locations), and size (standardized; snout-vent length standardized by sex).

Table 2.2. Estimates of fixed and random effects for the 90% confidence set of models for minimum convex polygon (MCP) home ranges for relocated eastern indigo snakes, 2003–2004, Georgia. Data suggests negative effect of being female and positive effect of body size on home range size.

Model[1]	Effect	Parameter	Estimate	Lower 95% CL	Upper 95% CL
Sex, Size, Site	Fixed	Sex	-0.985	-1.423	-0.547
		Size	0.021	0.009	0.033
		Site	-0.382	-0.794	0.029
	Random	Intercept	2.786	0.948	4.624
		Residual	0.245	0.159	0.938
		Year (repeated)	0.610	0.282	0.427
Sex, Size	Fixed	Sex	-1.050	-1.510	-0.591
		Size	0.024	0.011	0.036
	Random	Intercept	2.220	0.393	4.048
		Residual	0.276	0.179	0.482
		Year (repeated)	0.657	0.371	0.944

[1] Model parameters: sex (being female), size (snout-vent length), and site (over-wintering location on Fort Stewart versus private lands).

Table 2.3. Importance of sex and size in intraspecific home range size variation. Data shown are Akaike importance weights for model parameters from annual minimum convex polygon (MCP) home ranges, 95% kernel density (KD) home ranges, and 50% KD core areas for relocated eastern indigo snakes, 2003–2004, Georgia. The location variable was excluded in KD analysis because only novel locations were used in generation of these home ranges.

		Importance weights		
Parameters[1]	Candidate models	Annual MCP	Annual 95% KD	Annual 50% KD
Sex	6	1.00	1.00	1.00
Size	6	0.99	0.99	0.98
Site	5	0.84	0.71	0.39
Size x Sex	2	0.04	0.19	0.12
Locations	2	0.02	-	-
Size (standardized)	2	0.00	0.00	0.00

[1] Model parameters: sex (being female), size (snout-vent length), site (over-wintering location on Fort Stewart versus private lands), locations (number of telemetry locations), and size (standardized; snout-vent length standardized by sex).

Table 2.4. Differential use of habitats compared to availability within the study site and within individual home ranges for relocated eastern indigo snakes (*n* = 27), 2003–2004, Georgia. Data present the log-ratio matrix of differences in preference between GAP habitat types calculated as the log of the ratio between the relative preferences for. Positive values indicate the column habitat was used relatively more than the row habitat; negative values indicate less use. * = deviation from random at $P < 0.05$. Rank 6 represents the most important habitat to the study animals when comparing relative use to availability, rank 0 represents the least important habitat.

	Road/Urban		Wetland		Field		Clearcut/Sparse		Deciduous		Evergreen		
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Rank
Home range selection													
Road/Urban													1
Wetland	-1.13*	0.30											6
Field	-0.01	0.46	0.71	0.45									3
Clear-Cut/Sparse	-0.64	0.43	0.72	0.40	-0.66	0.51							3
Deciduous	0.14	0.61	1.10	0.38	0.74	0.51	0.38	0.47					0
Evergreen	-1.17*	0.26	0.05	0.14	-0.92	0.47	-0.67	0.34	-1.05	0.44			5
Mixed	-0.49	0.56	0.51	0.32	0.16	0.43	-0.22	0.48	-0.59	0.26	0.46	0.38	3
Within home range													
Road/Urban													0
Wetland	-1.51*	0.38											5
Field	-0.45	0.69	1.22*	0.51									2
CC/Sparse	-1.03	0.60	0.31*	0.51	-1.06	0.78							3
Deciduous	-0.31	0.72	-1.25	0.49	0.05	0.78	0.94	0.71					1
Evergreen	-1.47*	0.41	0.04	0.17	-1.05*	0.52	-0.35	0.51	-1.29*	0.48			6
Mixed	-1.12	0.59	0.02	0.43	-0.48	0.75	-0.29	0.56	-1.23	0.67	0.06	0.40	4

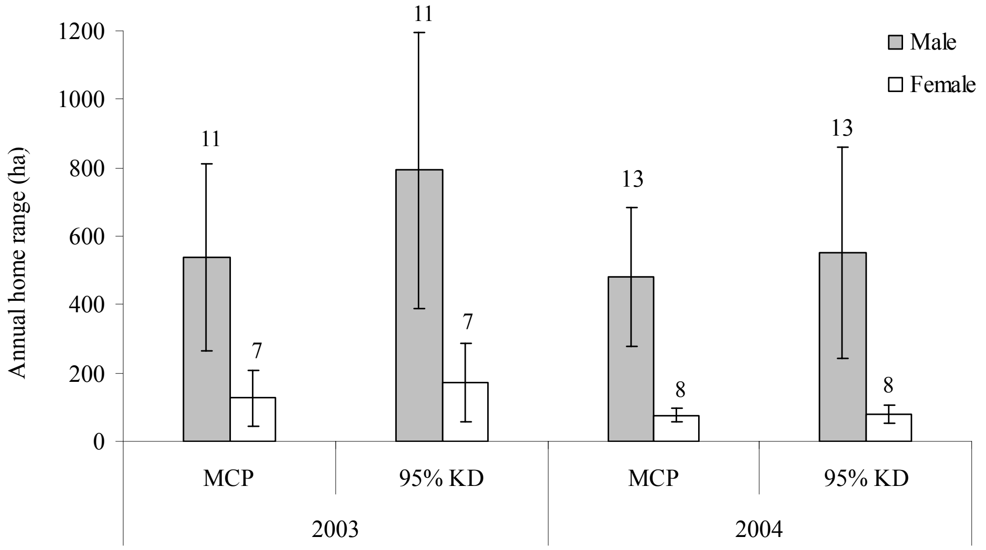

Figure 2.1. Minimum convex polygons (100% MCP) and 95% kernel density (KD) annual home ranges ($\bar{x}$ ha, 95% CI) for male and female eastern indigo snakes relocated $\geq$9 months, 2003–2004, Georgia. Sample sizes indicated above bars.

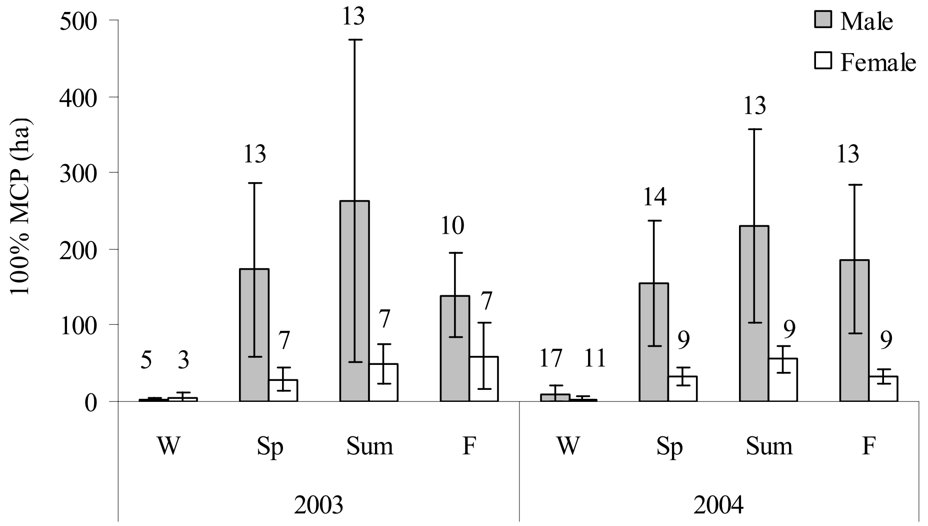

Figure 2.2. Seasonal minimum convex polygon (100% MCP) home ranges ($\bar{x}$, 95% CI) for male and female eastern indigo snakes relocated for complete seasons, 2003–2004, Georgia.

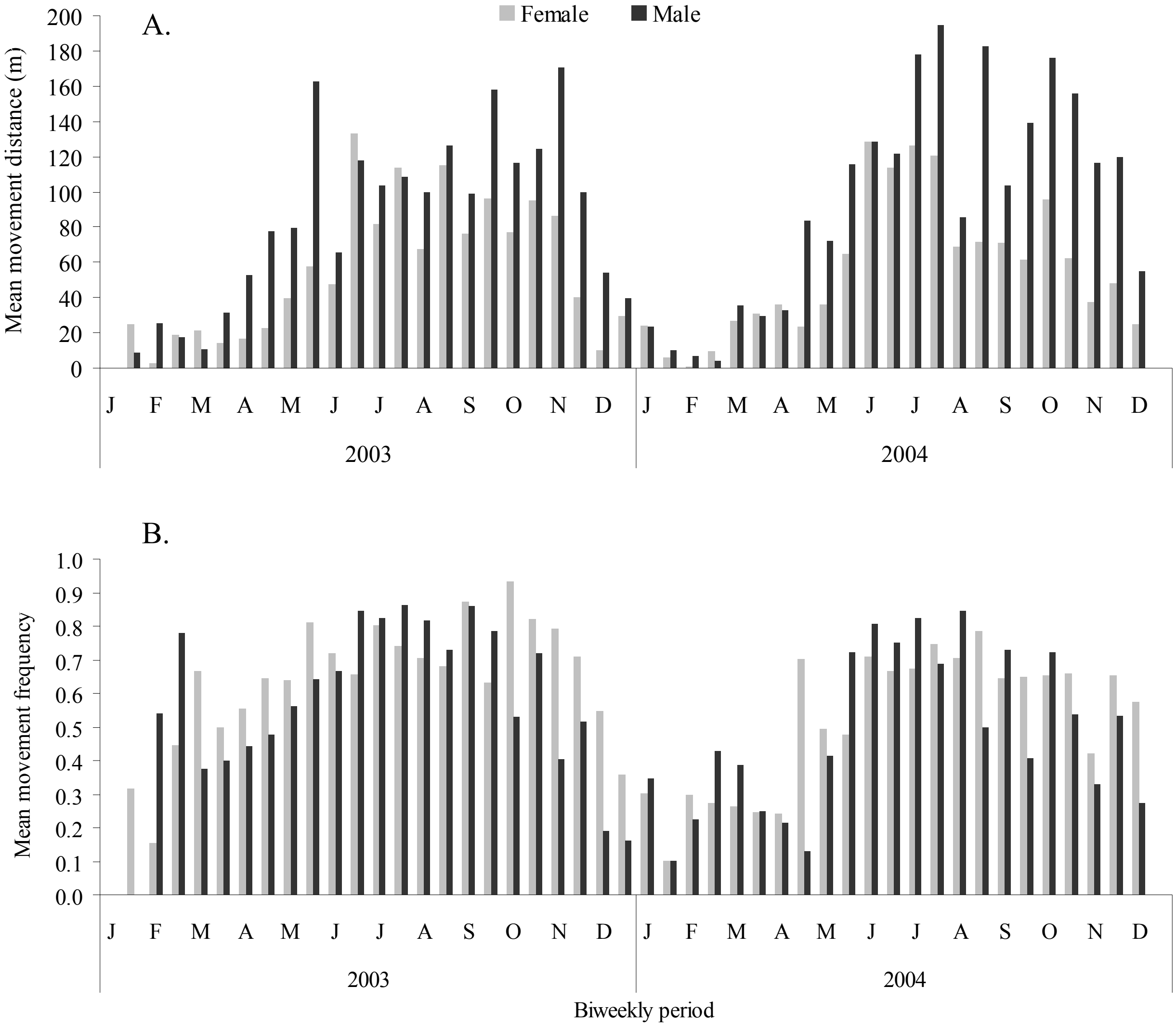

Figure 2.3. Mean daily movement distance (A) and movement frequency (B) for 2-week periods for relocated male and female eastern indigo snakes (*n* = 32), 2003–2004, Georgia. Individual animals were retained as the sampling unit for calculations.

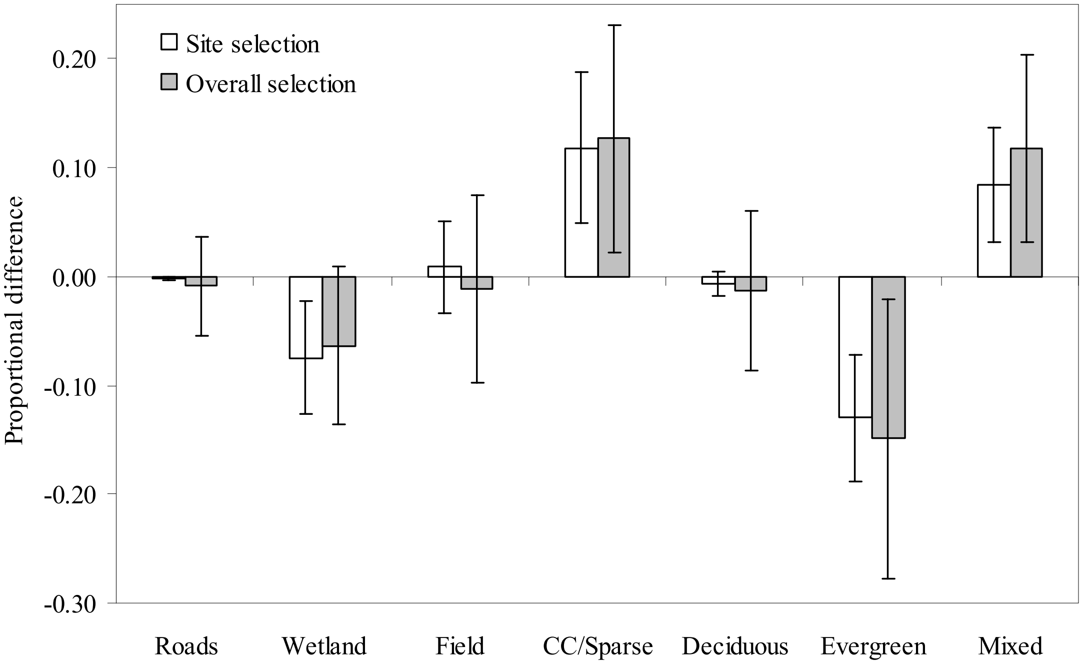

Figure 2.4. Differences in proportional use and availability of habitats ($\bar{x}$, 95% CI; *n* = 27) for relocated eastern indigo snakes, 2003–2004, Georgia. Site selection compares habitat at radiolocations to MCP home ranges. Overall selection compared habitat at radiolocations to the proportion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

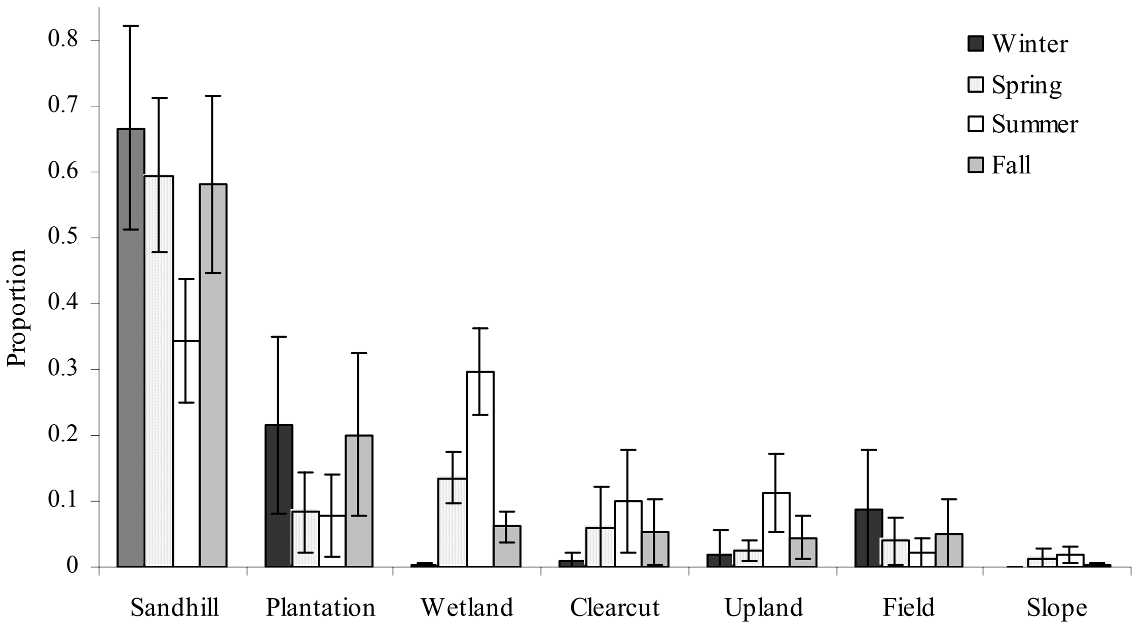

Figure 2.5. Proportional ($\bar{x}$ relocations of individual snakes, 95% CI) seasonal habitat use for eastern indigo snakes relocated in 2003–2004, Georgia ($n_{\text{winter}} = 31$, $n_{\text{spring}} = 32$, $n_{\text{summer}} = 28$, $n_{\text{fall}} = 28$). Habitat categories recorded at locations included: sandhill (oak-pine xeric uplands with longleaf pine overstory and gopher tortoise burrows), clearcut, field (includes old-fields, low maintenance hay fields, and food plots), pine plantation, slope forest (transitional habitat between xeric uplands and wetlands), miscellaneous uplands (xeric uplands with mixed overstory composition), and wetlands.

CHAPTER 3

SEASONAL SHIFTS IN SHELTER AND MICROHABITAT USE OF THE THREATENED EASTERN INDIGO SNAKE (*DRYMARCHON COUPERI*) IN GEORGIA[1]

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[1] Hyslop, N. L., R. J. Cooper, J. M. Meyers. To be submitted to *Copeia*.

ABSTRACT

Drymarchon couperi (Eastern Indigo Snake), a threatened species of the southeastern Coastal Plain of United States, has experienced population declines because of extensive habitat loss, fragmentation, and degradation across its range. In Georgia, the species is associated primarily with longleaf pine forests that support *Gopherus polyphemus* (Gopher Tortoise) populations. From January 2003 to December 2004, we conducted radiotelemetry of *D. couperi* to examine its use of shelters and microhabitat at Fort Stewart Military Reservation and adjacent private lands in Georgia. To examine microhabitat use at underground shelters, we used principal component scores, derived from analysis of microhabitat variables, on a candidate set of models using repeated measures linear regressions. Proportion of locations recorded underground ($\bar{x}$ = 0.76, 95% CI = 0.74–0.78) did not differ seasonally ($F_{3, 70} = 1.29$, $P = 0.28$) or between sexes ($F_{1, 37} = 0.36$, $P = 0.55$). Microhabitat use was most influenced by season compared to sex, site, or body size. Modeling results indicated that females, in spring and summer, used more open microhabitat compared to males, which may suggest different thermoregulatory needs during gestation. Shelter type and duration of use was influenced by seasons and habitat type. In winter, we recorded >90% of underground locations at tortoise burrows; however, use of these burrows was less pronounced in spring for males (47%) and in summer for males and females, 37% and 50%, respectively. Females used abandoned tortoise burrows more frequently than males year-round and used them on approximately 60% of their underground locations during spring. The availability of suitable underground shelters, especially *G. polyphemus* burrows, may be a limiting factor in the northern range of *D. couperi* and could have important implications for its survival.

KEY WORDS: burrow, ecdysis, Gopher Tortoise, information-theoretic approach, radiotelemetry, refuge

INTRODUCTION

Drymarchon couperi (Eastern Indigo Snake), a threatened species of the southeastern Coastal Plain of the United States (United States Fish and Wildlife Service, 1978), has experienced population declines because of extensive habitat loss and fragmentation across its range (USFWS, 1998). In Georgia and northern Florida, the species is associated primarily with longleaf pine (*Pinus palustris*) and wiregrass (*Aristida stricta*) upland communities and is found in association with *Gopherus polyphemus* (Gopher Tortoise) populations that inhabit these xeric habitats. *Drymarchon couperi* requires shelters for protection from environmental extremes including fire, predation, and possibly for nest sites (Holbrook, 1842; Landers and Speake, 1980; Speake and McGlincy, 1981; Smith, 1987; Speake et al., 1987). Availability of shelters varies locally and geographically as habitats and climatic conditions change. Shelters may include *G. polyphemus* burrows, woody debris, windrows, stump and root channels, small mammal and armadillo burrows, and hollow logs (Lawler, 1977; Speake et al., 1978; Smith, 1987; Moler, 1992; Stevenson et al., 2003).

Upland longleaf pine forests, also referred to as longleaf pine-turkey oak uplands or sandhills, have declined in extent and area with <1.2 million of the original estimated 30 million hectares remaining (Landers et al., 1995). *Gopherus polyphemus,* a keystone species of these xeric habitats (Eisenberg, 1983; Jackson and Milstrey, 1989), is a primary excavator, creating burrows averaging 3–6 m long and 2 m deep (Smith et al., 2005). Longleaf pine forests require frequent, low to moderate intensity fire to maintain their diversity (Engstrom et al., 1984; Mushinsky and McCoy, 1985; Van Lear et al., 2005). Fire exclusion leads to an increase in ground litter cover and tree density, which inhibits growth of shade intolerant forbs and wiregrass (Lawler, 1977), conditions non-conducive for native vertebrates including *G.*

polyphemus, which is declining throughout its range (Auffenberg and Franz, 1982; McCoy et al., 2006).

In arid regions, humid, thermally stable shelters are critical habitat components, often required for hibernation, reproduction, and protection from environmental extremes (Kinlaw, 1999). Accessibility, size, and structure of shelters affects their suitability for different species (Beck and Jennings, 2003) and availability of appropriate shelters may be a limiting resource for some wildlife populations (Huey, 1991). This may be especially true for non-excavator ectotherms, including most snake species, which rely on naturally existing shelters and animal burrows (Pringle et al., 2003; Webb et al., 2004). For example, decline of *Hoplocephalus bungaroides* (Elaphe) in Australia has been linked to loss of appropriate shelters (Shine et al., 1998) and an increase in vegetation density which negatively influenced thermal conditions (Pringle et al., 2003). Although many snake species require shelters for survival, the identification and detailed measurement of these resources is often lacking.

Drymarchon couperi is a commensal with *G. polyphemus* primarily during the winter breeding period (Diemer and Speake, 1983); however, the species use of *G. polyphemus* burrows and other shelters is not well understood. Details of seasonal shelter requirements of *D. couperi* are needed for effective management of uplands, wetlands, and other habitats used. We initiated this research to address deficiencies in knowledge of seasonal shelter use and associated aboveground microhabitat characteristics of these shelters for *D. couperi* in the northern portion of its range. We conducted a two-year radiotelemetry study of *D. couperi* to examine these questions, both temporally and spatially, in southeastern Georgia. Our objectives were to quantify, by season and habitat type, use of underground shelters, types of shelters used, physical characteristics of shelter openings, and associated microhabitat characteristics of aboveground areas immediately surrounding shelters.

METHODS

Study sites

We conducted a radiotelemetry study on *D. couperi* on Fort Stewart Military Reservation and tracts of adjacent private land located in the Coastal Plain of southeastern Georgia. We delineated our study sites using a minimum convex polygon created around all radiolocations, which we buffered by 200 m, using the Animal Movements Extension (Hooge and Eichenlaub, 1997) to ArcView GIS, with Spatial Analyst (Environmental Systems Research Institute, Inc., 1999). The Fort Stewart site covered approximately 4,870 ha of its total 111,600 ha (Stevenson et al. 2003). Private lands adjacent to Fort Stewart covered approximately 3,200 ha in a contiguous tract.

Upland habitats at the study sites included extensive sandhills along the north and northeastern banks of streams and mixed pine-hardwood forests (Stevenson et al., 2003). Interspersed with upland habitats were wetlands, including blackwater swamps, bottomland hardwood forests, bay swamps, cypress and gum ponds, and impoundments (Stevenson et al., 2003). Neither site contained paved roads, but did have maintained and un-maintained unpaved roads. Paved roads bounded two sides of the private lands site. Both sites supported *G. polyphemus* populations, i.e., hatchling tortoises were observed.

Habitat management at Fort Stewart centered on restoration and conservation of native habitats, including longleaf pine forests. Activities included prescribed burning on 1–10 year intervals, seeding wiregrass, planting longleaf pine, controlling and removing turkey oak, harvesting commercial timber, and thinning pine plantations (Stevenson et al. 2003). Management also included maintaining food plots targeting *Odocoileus virginianus* (white-tailed deer), *Meleagris gallopavo* (wild turkey), and *Colinus virginianus* (northern bobwhite). Management activities on private land varied by landowner, but most compartments were managed for pine timber (primarily loblolly pine, *Pinus taeda)* and game similar to Fort Stewart. Private lands had histories of fire exclusion (>15 years), which caused hardwood encroachment (primarily turkey oak, *Quercus laevis*), increased cover, and reduced native ground cover in upland areas.

Approximately 17% of the Fort Stewart site and 14% of the private land site contained *G. polyphemus* burrows (Chapter 2). Private lands with *G. polyphemus* included approximately 50% sandhills, 11% planted sand pine (*Pinus clausa*), 21% pine plantations <10 years old, <1% ha in pine plantations >10 years old, and 18% actively managed hay fields. All sites supporting *G. polyphemus* on Fort Stewart were managed for wildlife with no timber extraction or agricultural activities in >10 years, with the exception of timber harvests for restoration of areas where the canopy was dominated by species other than longleaf pine.

Radiotelemetry

We captured snakes by hand on sandhill habitats occupied by *G. polyphemus* on Fort Stewart and private land sites. We implanted 32 snakes (13 F, 19 M) with transmitters between 12 December 2002 and 1 March 2004 (see Chapter 2 for further details). We relocated snakes 2-3 times per week on foot using homing techniques (Mech, 1983).

Shelter use

To examine shelter use by relocated D. couperi, we classified underground locations as burrows; root/stump channels; under logs or woody debris; or within windrows. Snake locations recorded on the surface, under litter, under vegetation, or those in trees, were classified as surface locations. Windrows, constructed during site preparation for planting, were composed primarily of a mixture of woody debris and soil with vegetation growing on and around them. We recorded windrow locations as underground when snakes were under woody debris or under the soil in an animal burrow or other opening. If the snake was exposed, under vegetation or leaf litter, we recorded it as a surface location. We used repeated measures ANOVA on arcsine-transformed data to examine influence of sex and season on proportion of locations recorded underground versus surface.

At each underground location, we recorded shelter type, maximum horizontal width at opening (m), and surface linear distance (m) from snake location to shelter opening (nearest 0.5 m). Underground shelter categories included *G. polyphemus* burrows, root and stump channels (root/stump), debris piles created during timber harvest and site preparation (windrows), shelters associated with fallen woody debris (log), armadillo burrows (*Dasypus novemcinctus*), and burrows created by mammals other than armadillos (mammal). We examined armadillos separately because of interest in this species (Dodd, 1993) and because its burrows may provide shelters for *D. couperi* (Lawler, 1977; Moler, 1985; Layne and Steiner, 1996). Due to limited sample sizes for many shelter types, we were only able to conduct analysis of shelter structure on tortoise burrows.

Gopherus polyphemus burrows were classified based on external characteristics, including signs of recent tortoise activity, structural characteristics of the burrow, and amount of litter and vegetation around the burrow opening (Auffenberg and Franz, 1982; McCoy and Mushinsky, 1992). We defined active burrows as those with structurally intact burrow openings, with signs of tracks or shell scraping marks. We classified a burrow as inactive if there was no evidence of recent use of the burrow (no tracks or slightly obstructed burrow entrance). Abandoned burrows were classified as those with compromised structural integrity of the opening, no sign of tortoise tracks or shell scrapings, and litter and vegetation obscuring the opening. Because of documented difficulties in accurately classifying inactive burrows, we combined active and inactive burrows for analyses (active/inactive; Smith et al. 2005).

We also recorded general habitat type at shelter locations based on hydrology, land use, management, vegetation, and presence of *G. polyphemus* burrows. Habitat categories included sandhill (uplands with longleaf pine overstory and *G. polyphemus* burrows), clearcut (primarily harvested mesic pine flatwoods with windrows, bedding for loblolly pine planting, and occasional cypress dome wetlands), field (included old-field, hay fields, and food plots), plantation (planted pine trees in rows, may or may not support *G. polyphemus* burrows), slope forest (transitional habitat between uplands and wetlands), miscellaneous uplands (uplands with pine-hardwood mixed overstory composition), and wetlands (isolated upland wetlands and bottomlands, no *G. polyphemus* burrows).

Microhabitat use

Microhabitat analysis focused on identification of vegetation and structural conditions immediately surrounding areas of use (North and Reynolds, 1996; Morrison et al., 1998). We collected these data on 3-m diameter circular plots centered on openings to underground shelters associated with individual radiolocations. *Drymarchon couperi* are active predators, rarely found basking or in a coiled resting position outside of winter; therefore, we recorded microhabitat characteristics only when snakes were associated with underground shelters. Microhabitat data included percent vegetated understory cover (<150 cm in height), percent vegetated canopy cover (>150 cm in height), substrate composition, and tree basal area. We used a modified version of the James and Shugart (1970) method for measuring microhabitat vegetation and substrate in forest and shrub habitats (Martin et al., 1997). We used visual estimation (ocular tube) at 20 points within 3-m diameter plots to measure percent vegetation cover to the nearest 0.05. Understory cover categories included total vegetation cover; forbs, grass, sedge, and rush cover (grass and forbs); and woody shrub, vine, and palmetto cover (woody vegetation/palm). Substrate composition was measured as percent cover of bare ground, litter, and course woody debris including litter cover. We recorded basal area of the surrounding habitat from the center of each 3-m sampling plot using an angle gauge. We collected microhabitat variables at all underground radiolocations from January 2003 to January 2004 (n = 427 locations). From February 2004 to December 2004, we randomly selected a subset of underground locations to collect microhabitat data, averaging one location per individual per week (n = 192 locations). For analyses, we only included locations at specific shelters (novel locations) once.

Although logistic regression analysis is common for microhabitat use data, the method relies on potentially problematic assumptions regarding quality of habitats designated as available (North and Reynolds, 1996). At our sites, there was no reliable means to determine available underground shelters. This was primarily because of uncertainties in determining the subsurface structure of potential shelters or their suitability for *D. couperi*. Therefore, we analyzed patterns of use within our sample as a function of selected ecological factors.

We used principal components analysis (PCA; PROC FACTOR, SAS Institute Inc, 2005) to summarize the major dimensions of variation present in microhabitat used by *D. couperi* at underground shelters. Data were arcsine transformed (except basal area, which approached normality) and standardized before analysis. We retained all components with eigenvalues ≥ 1

(Kaiser, 1960) and used orthogonal rotation (Varimax). Correlations between variables within factors, or factor loadings, were interpreted as strong if >0.50.

We used principal component scores as dependent variables in repeated measures linear regressions, with individual animals retained as the sampling unit, to examine ecological correlates of microhabitat use (PROC MIXED, SAS Institute Inc, 2005). Linear regression was performed on a candidate set of models created from a priori hypotheses and selected using Akaike's Information Criterion (Akaike, 1973; Burnham and Anderson, 2002) corrected for small sample sizes (AICc; Hurvich 1989). We also used AICc to objectively select the appropriate covariance structure for data. Model averaging may be inappropriate with repeated measures designs (Reiman et al., 2006); therefore, we reported Akaike weights for model parameters. Our global model included the parameters sex (dummy variable coded for female), snout-vent length (size), over-wintering location (site, dummy variable coded for over-wintering on private land), and season. Candidate models were created as subsets from this global model. Models with interactions also included the associated main effects. We selected the confidence set of models for weights within 0.10 of the highest weighted model (90% confidence set; Burnham and Anderson, 2002).

We expected variation in microhabitat use to be influenced primarily by season. Snakes used a higher proportion of mesic areas in warmer months and higher proportion of upland areas in cooler months (Chapter 2), thus likely influencing the type and quantity of shelters available. We also expected sex to influence microhabitat use, with females using more open canopy patches, especially during gestation in spring, to meet thermoregulatory requirements associated with reproduction (Blouin-Demers and Weatherhead, 2001). Alternatively, we expected that size, not sex, may instead influence microhabitat use i.e., availability of suitable underground shelters decreased with increasing body size because large shelters may be limited. We did not include the interaction between sex and size in our modeling because these variables were correlated (male-biased size for species). We also predicted that land use differences between Fort Stewart and private land sites would influence microhabitat use because of differences in proportions of land with tortoise burrows in timber production and in field habitats. We hypothesized that there may be an interaction effect of sex and season, with microhabitat requirements for males and females differing unevenly among seasons. Lastly, we predicted that microhabitat use may also be a function of site and season, i.e., habitats used in different seasons may not be available on each site in each season.

RESULTS

Radiotelemetry

Males averaged 158 cm SVL (range 120-191 cm) and 2.2 kg (range 0.72-4.3 kg) at capture; females averaged 138 cm SVL (range 110-156 cm) and 1.5 kg (range 0.55-2.3 kg; Chapter 2). Further radiotelemetry details are available elsewhere (Chapter 2). The proportion of radiolocations at novel locations varied by season (repeated measures ANOVA; $F_{3,70} = 61.1$, $P < 0.001$) but not by sex ($F_{1,30} = 2.8$, $P = 0.10$), with a sex x season interaction ($F_{3,70} = 5.73$, $P = 0.002$). Differences in least square means (95% CI) indicated males had higher use of novel locations than females in spring ($\bar{x}_M = 0.542$, 0.495-0.589; $\bar{x}_F = 0.453$, 0.391-0.515; $t_{70} = 2.27$, $P = 0.026$) and fall ($\bar{x}_M = 0.626$, 0.576-0.676; $\bar{x}_F = 0.476$, 0.409-0.542; $t_{70} = 3.61$, $P < 0.001$), but no difference in proportion of novel locations between males and females in winter ($\bar{x}_M = 0.277$, 0.224-0.331; $\bar{x}_F = 0.302$, 0.240-0.364; $t_{70} = 0.60$, $P = 0.550$) or summer ($\bar{x}_M = 0.626$, 0.576-0.676; $\bar{x}_F = 0.691$, 0.625-0.758; $t_{70} = 1.57$, $P = 0.121$).

Shelter use

We recorded snakes in underground shelters on 3,825 of 4,993 total locations collected for the 32 relocated snakes. Proportion of locations recorded underground ($\bar{x}$ = 0.76, 95% CI = 0.74–0.78) did not differ between seasons ($F_{3,70}$ = 1.29, P = 0.284) or sexes ($F_{1,37}$ = 0.36, P = 0.551), but did indicate a potential interaction ($F_{3,70}$ = 2.96, P = 0.053). Shelter use, in all seasons, was closely associated with *G. polyphemus* burrows (>0.40), even during warmer months when tortoise burrow use was lowest (Fig. 3.1). In spring, snakes used *G. polyphemus* burrows less ($\bar{x}$ = 0.58 of underground locations) and used more root and stump openings ($\bar{x}$ = 0.12). In summer, use of *G. polyphemus* burrows was lowest ($\bar{x}$ = 0.44), but root and stump use was higher than in any other season ($\bar{x}$ = 0.22). In fall, underground shelter use was similar to the snakes' use in winter, i.e., high tortoise burrow use and lower use of all other categories (Fig. 3.1).

We found 27 shed skins from 17 relocated snakes (12 males, 5 females; 1–3 sheds/snake); 25 sheds were found behind *G. polyphemus* burrows, 1 outside a mammal burrow, and 1 near a railroad track. Snakes were inactive (i.e., we did not observe movement from an underground shelter) for 1–3 weeks prior to ecdysis in 16 of 27 occasions (14 individuals). Four shedding events were documented in winter during long periods (>1 mo) of inactivity (4 individuals). We recorded no inactivity prior to ecdysis for 3 occasions (2 individuals). Snakes inactive for 1–3 weeks prior to ecdysis rested 1–2 days post-ecdysis, followed by a period of increased activity during which foraging behavior was often observed. We also observed that all snakes shed within 2 weeks following transmitter implantation surgery.

Types of *G. polyphemus* burrows used by *D. couperi* differed by season and sex (Fig. 3.2). In winter, males used a higher proportion of active burrows and females used an equal proportion of active/inactive and abandoned ones. In spring, females associated more with abandoned burrows, but males began using burrows less and increased their use of other shelters. During spring, approximately 60% of female underground locations were in abandoned burrows compared to approximately 24% of male underground locations. In summer, *G. polyphemus* burrow use was lowest for males and females, although females continued to use abandoned burrows (40% of underground locations). In fall, males and females used similar proportions of both burrow categories.

Drymarchon couperi use of underground shelters changed with habitats used (Table 3.1). In sandhill habitats, snakes used *G. polyphemus* burrows predominantly. *Drymarchon couperi* also used tortoise burrows in plantation ($\bar{x}$ = 0.92), and field habitats ($\bar{x}$ = 0.72). Wetlands did not have *G. polyphemus* burrows; however, in these habitats, snakes predominantly used hummocks of soil and roots and woody debris for shelter. Underground shelter use in clearcuts was largely restricted to windrows ($\bar{x}$ = 0.81). In other upland forests, snakes most often sought shelter in root/stump channels and mammal burrows.

Diameter of *G. polyphemus* burrows used by snakes ($\bar{x}$ = 29.0 cm, 95% CI = 27.8-30.2) differed only by burrow category ($F_{1,143} =$ 82.5 cm, $P > 0.001$) and not by season ($F_{3,143} =$ 1.5, $P = 0.22$) or sex ($F_{1,25} =$ 0.26 cm, $P = 0.61$). Throughout the year, snakes used larger active/inactive ($\bar{x}$ = 33.5 cm, 95% CI = 32.4-34.6; 6-39 cm range) than abandoned burrows ($\bar{x}$ = 24.4, 95% CI = 22.8-26.0; 9-40 cm range). Linear, horizontal distances of *D. couperi* locations in tortoise burrows to burrow openings ($\bar{x}$ = 2.7 m, 95% CI = 2.6-2.9; 9 m maximum) varied seasonally ($F_{3,153} = 21.2$, $P > 0.001$), by tortoise burrow category ($F_{1,150} = 26.7$, $P > 0.001$), and between sexes ($F_{1,26} = 4.26$, $P = 0.490$), with no interactions. Snakes remained farther back in burrows in fall and winter and closer to entrances in spring and summer. On average, snakes were closer to active/inactive burrow entrances and farther back in abandoned ones.

Microhabitat use

Patterns of microhabitat use at underground shelters differed seasonally for most variables (Table 3.1). Microhabitat use in winter corresponded with the lowest cover values for canopy, understory vegetation, woody vegetation, and palm. Basal area ranged from 0.0-40.2 m^2/ha and was lowest, along with canopy cover, in fall and winter. In spring and summer, snakes, on average, used areas with higher canopy cover, basal area, woody understory, and palm cover. Use of microhabitat with higher proportions of grass/forbs and woody debris/logs was lowest in summer.

Principal component analysis extracted 3 orthogonal components with eigenvalues >1 accounting for 0.87 of the common variance among 6 microhabitat variables (Table 3.3). Principal component 1 (PC1) had positive loadings for percent understory cover, woody vegetation, and palm cover, and a negative loading for course woody debris and litter cover (Table 3.3). We interpreted locations with high PC1 scores as plots dominated by woody vegetation and palm cover and mostly void of other vegetation. Principal component 2 (PC2) had positive loading for basal area and canopy cover. We interpreted locations with high PC2 scores as representing areas of denser, more closed canopy forest (Table 3.2). Principal component 3 (PC3) had negative association with woody understory vegetation cover and positive association with grass/forbs. We interpreted locations with high PC3 scores as patches dominated by grass and forb understory cover (Table 3.4).

Global models for all 3 components confirmed adequate goodness of fit ($P < 0.001$). AIC_c analyses on global models suggested the autoregressive covariance structure as most appropriate for modeling. The 90% confidence set of models for PC1 included 1 of 12 candidate models, which contained season as the only model parameter (ω = 0.914; Table 3.3). Coefficient estimates for effect of season on use of PC1 suggested higher use of PC1 patches in summer and fall (Table 3.4). The 90% confidence set of models for PC2 included 1 of 12 candidate models, suggesting an effect of season and sex on use of PC2 areas (ω = 0.98; Table 3.4). Coefficient estimates for effect of season on use of PC2 suggested higher use of PC2 patches in spring and summer and a relatively strong influence of sex (being female) on use of PC2 throughout the year (Table 3.5). The 90% confidence set of models for PC3 included 2 of 12 candidate models. The model with most support included season, sex, and site (ω = 0.60) and was 1.58 times more likely than the next approximating model, given the data and candidate models. Coefficient estimates for the top-ranked model suggest an effect of season on use of PC3, with higher use of these patches in all seasons except winter, a negative associated with Fort Stewart sites, and an indefinite effect of size (Table 3.5). The second-ranked model included season and site (ω = 0.38). Coefficient estimates for the effect of season also suggested higher use of PC2 patches in all seasons except winter and a negative association with Fort Stewart sites (Table 3.5).

In all microhabitat modeling, season ranked highest or second highest in importance (Table 3.6). This was the only common variable among 3 analyses. Site had the highest importance for PC3 (1.00), but lowest for PC1 (0.02) and PC2 (0.02).

DISCUSSION

Shelter use

In winter, male and female indigo snakes primarily used *G. polyphemus* burrows*;* males used a higher proportion of active burrows and females used abandoned burrows almost twice as frequently as males. In the spring, females found shelter mainly in abandoned tortoise burrows, but males began using other shelters to a larger extent. Approximately 0.60 of all female underground locations during the spring were in abandoned tortoise burrows, compared to 0.28 of male locations during the same season. In summer, snakes used *G. polyphemus* burrows the least, but females continued to use abandoned burrows an average of 0.40 of their underground locations. Snakes used tortoise burrows in the fall and winter in similar proportions; males and females use was comparable for both burrow categories.

Warm season shelter use by *D. couperi* in Georgia has been previously reported; however, the study was conducted primarily on translocated and captive-reared individuals (Speake et al. 1978). Of 108 shelters they described, 77% were located in tortoise burrows, 18% under decaying logs and stumps, and 5% in windrows. These snakes used tortoise burrows an average of 88% (December-April), 61% (May-July), and 82% (August-November); these data were pooled across individuals and sexes (Speake et al. 1978). Our results agree with these data for winter and fall; however, our study showed lower tortoise burrow use in summer as snakes used a higher proportion of other shelters.

Drymarchon couperi habitat and underground shelter use may vary geographically. In southern Florida, *D. couperi* appears to rely less on tortoise burrows than populations found in more northern latitudes (Moler, 1985; Layne and Steiner, 1996). These southern areas are generally warmer in the winter months, possibly allowing a more diverse selection of suitable underground shelters, with depth of shelters unimportant; however, the snakes in these areas would still require protection from environmental extremes, including fire and high temperatures, in addition to protected nesting sites.

Drymarchon couperi burrow use was influenced by structural differences between abandoned and active/inactive tortoise burrows. On average, we relocated snakes farther into the interior of abandoned than into active/inactive burrows during spring and summer. *Drymarchon couperi* relocated in this study, especially females in spring, used abandoned burrows extensively throughout the year. Smith (1987) reported that relocated *D. couperi* females (translocated) released in Florida used abandoned burrows for 70% of recorded locations during gestation and following oviposition. Females may use abandoned burrows during this period because of the disadvantages associated with ovipositing in active burrows, such as potential damage to eggs from tortoise activity. Abandoned burrows are subject to structural degradation from weathering and vegetation growth; however, burrows may remain structurally intact for decades (Guyer and Hermann, 1997). *Drymarchon couperi's* activity within a shelter also has the ability to modify or reinforce internal structure of shelters, including abandoned *G. polyphemus* burrows, potentially increasing their longevity (Kinlaw, 1999).

Microhabitat use

Microhabitat use at underground shelters was most influenced by season compared to sex, size, or site. In summer and fall, snakes selected areas with higher than average understory vegetation cover, dominated by woody vegetation and palmettos, and higher than average bare ground (PC1) compared to other seasons. PC1 showed no relationship with canopy cover; however, dense shrubs, vines, and palmettos provided shading from direct sun, which would be important for snake thermoregulation during summer. Snake use of areas with higher than average basal area and canopy cover (PC2) was influenced most by season and sex (Table 3.5). These patches were used more in spring and summer and less by females than males, supporting our prediction that females used more open patches in the spring during gestation. In Georgia, female *D. couperi* usually complete oviposition by late spring to early summer (Speake et al., 1987); therefore, it is unlikely that the inclusion of summer in this model is caused solely by reproductive differences between males and females.

Model results suggested that *D. couperi*'s use of microhabitat patches (grass and herbaceous understory vegetation cover, PC3) was influenced by season, site and potentially by size. Snakes used these patches less in winter compared to other seasons and exhibited a strong negative relationship to use of these patches on private land sites, regardless of season (Table 3.5). These results do not necessarily suggest lower use of shelters at these patches in winter, but could be related to different microhabitat characteristics caused by seasonal vegetation composition. The strong negative effect of association with private land sites provides support for our prediction that land use on tracts with tortoise burrows influences the indigo's microhabitat use. The effect, if any, of body size was inconclusive and provided no support for our prediction that larger individuals have a limited choice of underground shelters because of their need for larger structures, given our sites and data.

Conservation implications

For ectothermic vertebrate species, physiological and survival costs are higher when using thermally unsuitable shelters (Huey, 1991). The availability of certain habitat features, rather than food supply or other factors, may be critical in determining endangerment for some snake species (Shine and Fitzgerald, 1996). *Drymarchon couperi* is considered a diet generalist and will consume most vertebrates small enough to overpower, such as mammals, birds, amphibians, and reptiles, including venomous and non-venomous snakes (Landers and Speake, 1980; Stevenson et al., 2003; Chapter 2). Therefore, it is possible that prey availability may not be a significant limiting resource for this species, even in disturbed areas (e.g., Mushinsky, 1987). Alternatively, we sugest that appropriate underground shelters, especially *G. polyphemus* burrows, may be a limiting factor in the northern portion of *D. couperi's* range.

Reduction in suitable underground shelters caused by habitat degradation and loss, which reduces or eliminates *G. polyphemus* populations, is likely an important factor in extirpation of the species from areas otherwise perceived as suitable habitat. We recommend continuance or adoption of management practices beneficial to *G. polyphemus* in upland habitats, including prescribed burning, which will also benefit *Drymarchon couperi* populations. Declines of *G. polyphemus* have been detected even on protected lands, emphasizing the importance of habitat quality, in addition to land conservation, for this keystone species (McCoy et al., 2006). Additional upland practices that may benefit *D. couperi* are conserving or creating other shelter types, including retaining stumps, creation of windrows in site preparations, and retention of downed woody debris.

Previous investigations of *D. couperi,* especially in the northern portions of the range, have suggested strong ties to *G. polyphemus* burrows in winter (Speake et al., 1978; Speake, 1993); however, this use has been thought of as opportunistic throughout other times of the year. We suggest that use of *G. polyphemus* burrows is not a casual relationship, but an important requirement for the snake's survival in its northern range. We believe that in addition to conservation of large tracts of land, it is as important to restore and mange lands for *D. couperi* so that adequate shelters are present in all seasons.

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Table 3.1. Mean proportion of underground shelter use by shelter and habitat type for *Drymarchon couperi* relocated in 2003-2004, Georgia. Habitat categories included sandhill (longleaf pine dominated xeric uplands with *G. polyphemus* burrows; *n* = 29), clearcut (primarily harvested mesic pine flatwoods bedded for loblolly pine planting, with windrows; *n* = 8), field (includes old-field, hay fields, and food plots; *n* = 9), plantation (managed pine plantations, may or may not support *G. polyphemus* populations; *n* = 16), slope forest (transitional habitat between uplands and wetlands; *n* = 8), miscellaneous uplands (xeric uplands with pine-hardwood mixed overstory composition; *n* = 18), and wetlands (isolated upland wetlands and bottomlands, no *G. polyphemus*; *n* = 26).

Shelter	Sandhill	Plantation	Field	Upland	Slope	Clearcut	Wetland
Active/Inactive *G. polyphemus*	0.48	0.55	0.50	0.10	0.00	0.00	0.00
Abandoned *G. polyphemus*	0.36	0.37	0.21	0.06	0.10	0.06	0.00
Root/Stump	0.06	0.03	0.12	0.59	0.40	0.01	0.65
Windrow	0.00	0.01	0.00	0.01	0.00	0.81	0.00
Mammal	0.03	0.01	0.11	0.06	0.45	0.00	0.03
Wood Debris	0.01	0.01	0.01	0.12	0.00	0.12	0.28
Armadillo	0.06	0.01	0.04	0.06	0.05	0.00	0.04

Table 3.2. Seasonal microhabitat characteristics associated with underground shelters used by *Drymarchon couperi* relocated 2003–2004, Georgia. Values are non-transformed proportions of cover in 3-m diameter circular plot centered at entrances of shelters used by *D. couperi*. Basal area (m^2/ha) was collected from a single point at the center of each 3-m diameter plot.

	Winter			Spring			Summer			Fall		
Variable	Mean	SE	*n*	Mean	SE	*n*	Mean	SE	*n*	Mean	SE	*n*
Understory	0.34	0.02	102	0.48	0.02	164	0.54	0.03	117	0.44	0.02	236
Canopy	0.09	0.02	102	0.18	0.02	164	0.22	0.03	117	0.12	0.01	236
Woody debris and litter	0.45	0.02	102	0.42	0.02	164	0.33	0.03	117	0.41	0.02	236
Woody understory/palm	0.15	0.02	102	0.32	0.02	164	0.38	0.03	117	0.22	0.02	236
Grass and forbs	0.18	0.02	102	0.16	0.01	164	0.15	0.02	117	0.20	0.01	236
Basal area (m^2/ha)	4.28	0.35	91	6.66	0.50	144	6.12	0.55	97	19.41	1.23	211

Table 3.3. Summary of principal components analysis of microhabitat variables for underground shelter use for relocated *Drymarchon couperi*, 2003-2004, Georgia. Boldface type indicates loadings >0.50.

	Component		
Variable	PC1	PC2	PC3
Understory cover	**0.962**	-0.040	0.076
Canopy cover	-0.074	**0.822**	-0.215
Woody debris and litter cover	**-0.874**	0.184	-0.256
Woody vegetation/palm cover	**0.789**	0.028	**-0.589**
Grass and forbs cover	0.152	-0.089	**0.962**
Basal area	-0.063	**0.874**	0.082
Eigenvalue	2.347	1.485	1.380
Percent total variance	39.1	24.8	23.3

Table 3.4. Effects of season and individual covariates on use of microhabitat features as summarized in a principal components analysis. Component 1 (PC1) represents microhabitat patches dominated by woody vegetation and palm cover, mostly void of other vegetation or ground cover. Component 2 (PC2) represents patches with higher basal area and canopy cover; and component 3 (PC3) indicates patches dominated by grass and forb understory cover. Models are listed by Akaike weights in descending order for PC1 only (*n* = 31 snakes).

		Component								
		PC1			PC2			PC3		
Model	K[1]	AICc	ΔAICc	w_i	AICc	ΔAICc	w_i	AICc	ΔAICc	w_i
Season	4	4526.34	0.00	0.91	3946.14	42.07	0.00	3609.34	98.79	0.00
Sex, Season	7	4532.27	5.93	0.05	3904.07	0.00	0.98	3613.27	102.72	0.00
Size, Season	7	4534.07	7.73	0.02	3929.87	25.80	0.00	3618.67	108.12	0.00
Site, Season	7	4534.67	8.33	0.01	3954.47	50.40	0.00	3511.47	0.92	0.38
Site, Season, Size	8	4536.35	10.01	0.01	3933.55	29.48	0.00	3510.55	0.00	0.60
Season, Site, Season x Site	14	4577.65	51.31	0.00	3912.05	7.98	0.02	3551.05	40.50	0.00
Site, Size	5	4554.40	28.06	0.00	4006.40	102.33	0.00	3517.60	7.05	0.02
Site	4	4553.74	27.40	0.00	4025.74	121.67	0.00	3518.54	7.99	0.01
Sex	4	4553.14	26.80	0.00	3970.74	66.67	0.00	3613.14	102.59	0.00
Size	4	4553.94	27.60	0.00	4003.74	99.67	0.00	3619.54	108.99	0.00
Sex, Season, Sex x Season	14	4567.45	41.11	0.00	3931.85	27.78	0.00	3634.05	123.50	0.00
Global	23	4713.11	186.78	0.00	4073.51	169.44	0.00	3672.71	162.17	0.00

[1] Number of parameters includes intercept, residual, and random term.

Table 3.5. Estimates of fixed and random effects for 90% confidence set of models for estimation of microhabitat use by relocated *D. couperi*, 2003–2004, Georgia. Parameters include sex (sex, dummy variable coded for female), snout-vent length (size), over-wintering location (site, dummy variable coded for over-wintering on private land), and season. Factor PC1 represented patches dominated by woody vegetation and palm cover, mostly void of other vegetation or ground cover; factor PC2 represented patches with higher basal area and canopy cover; and factor PC3 indicated patches dominated by grass and forb understory cover.

Factor	Model	Effect	Parameter	Estimate	Lower 95% CI	Upper 95% CI
PC1	Season	Fixed	Winter	0		
			Spring	0.392	-0.024	0.807
			Summer	0.880	0.423	1.338
			Fall	0.451	0.050	0.852
		Random	Intercept	-0.440	-0.787	-0.092
			Residual	2.359	2.105	2.661
			Repeated	0.227	0.149	0.306
PC2	Season, Sex	Fixed	Winter	0		
			Spring	0.697	0.376	1.017
			Summer	0.925	0.572	1.277
			Fall	0.219	-0.089	0.528
			Sex	-0.639	-0.888	-0.390
		Random	Intercept	-0.038	-0.351	0.276
			Residual	1.411	1.261	1.591
			Repeated	0.213	0.134	0.293
PC3	Season, Site, Size	Fixed	Winter	0		
			Spring	0.335	0.068	0.603
			Summer	0.348	0.055	0.641
			Fall	0.358	0.099	0.618
			Site	-0.748	-0.949	-0.547
			Size	-0.004	-0.010	0.001
		Random	Intercept	0.679	-0.238	1.596
			Residual	1.005	0.899	1.131
			Repeated	0.162	0.080	0.245
PC3	Season, Site	Fixed	Winter	0		
			Spring	0.330	0.061	0.598
			Summer	0.342	0.048	0.635
			Fall	0.344	0.084	0.604

	Site	-0.720	-0.918	-0.522
Random	Intercept	0.010	-0.219	0.239
	Residual	1.010	0.904	1.137
	Repeated	0.166	0.083	0.249

Table 3.6. Importance of season on microhabitat use for *Drymarchon couperi* relocated 2003–2004, Georgia. Akaike importance weights for model parameters included in microhabitat analysis. Parameters include sex (dummy variable coded for female), snout-vent length (size), over-wintering location (dummy variable coded for over-wintering on private land, site), and season. Factor PC1 represented patches dominated by woody vegetation and palm cover, mostly void of other vegetation or ground cover; factor PC2 represented patches with higher basal area and canopy cover; and factor PC3 suggested patches dominated by grass and forb understory cover.

		Importance weights		
Model parameter	Candidate Models	PC1	PC2	PC3
Season	8	1.00	1.00	0.97
Size	5	0.20	0.00	0.00
Sex	4	0.05	0.98	0.00
Site	5	0.02	0.02	1.00
Site*Season	2	0.00	0.02	0.00
Sex*Season	2	0.00	0.00	0.00

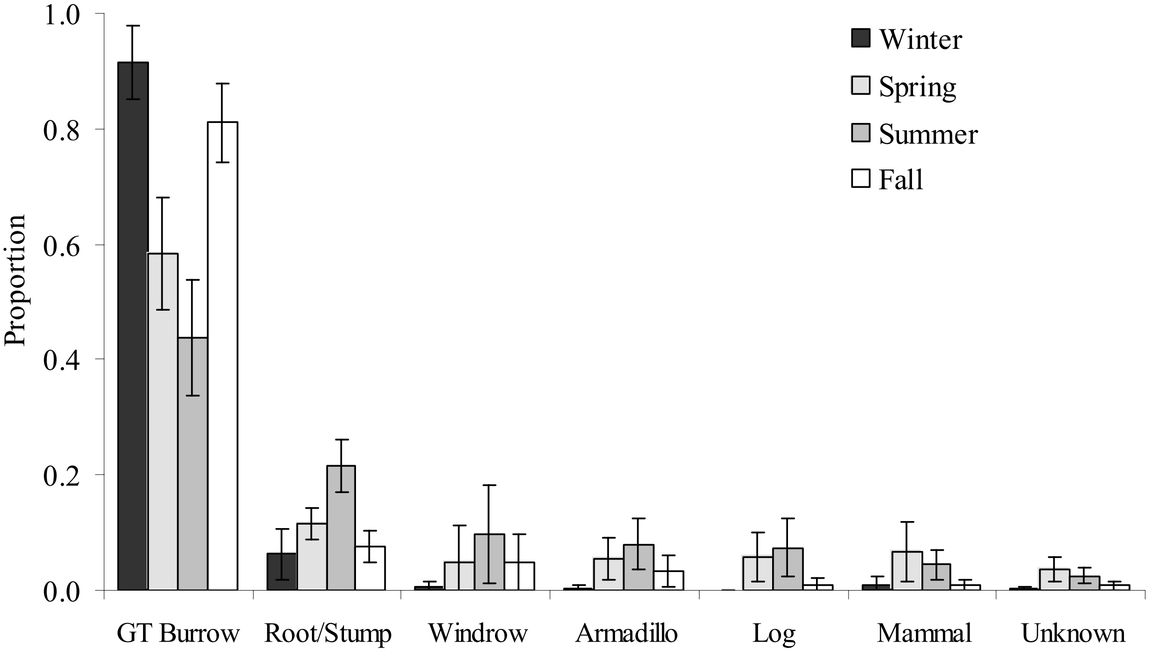

Figure 3.1. Underground shelters ($\bar{x}$, 95% CI) used by *Drymarchon couperi* relocated in winter (*n* = 30), spring (*n* = 32), summer (*n* = 28), and fall (*n* = 26), 2002–2004, Georgia. Shelter types: *G. polyphemus* burrows (GT burrow), root and stump channels (root/stump), debris piles created during timber harvest and site preparation (windrow), armadillo burrows, shelters associated with fallen woody debris (log), burrows created by mammals other than armadillos (mammal), and unknown underground shelters. Values are mean proportion of underground locations, with individuals retained as the sampling unit.

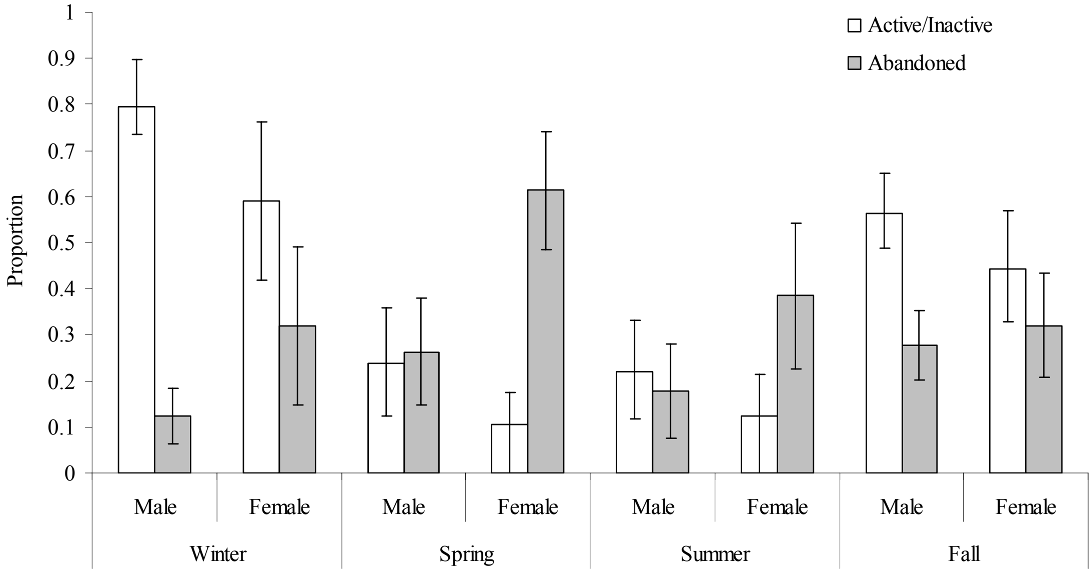

Figure 3.2. Seasonal *Gopherus polyphemus* burrow use for male and female relocated *Drymarchon couperi* at active/inactive and abandoned burrows ($\bar{x}$, 95% CI, $n = 32$) in 2003–2004, Georgia. Values are the mean proportion of underground locations, with the individual retained as the sampling unit.

CHAPTER 4

INDIGO SNAKE CAPTURE METHODS: RELATIVE EFFECTIVENESS OF TWO SURVEY TECHNIQUES FOR *DRYMARCHON COUPERI* IN GEORGIA[1]

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[1] Hyslop, N. L., J. M. Meyers, R.J. Cooper, and D. J. Stevenson. To be submitted to *Herpetological Review*.

INTRODUCTION

The ability to accurately detect and monitor wildlife species across their geographic range is vital to management and conservation, especially for species of concern. Detection of rare and cryptic taxa often requires survey techniques specific to those species (McDonald, 2004); however, for many species there is inadequate natural history data for development of appropriate techniques. In the Southeastern Coastal Plain of the United States, *Drymarchon couperi* (Eastern Indigo Snake) is an example of a threatened and cryptic species for which limited survey and capture methods have been developed (Diemer and Speake, 1981; Stevenson et al., 2003). To help address this deficiency and to capture snakes for a radiotelemetry study, we examined the relative effectiveness of capture techniques for *D. couperi*. Specifically, our objectives were to compare and evaluate effectiveness of trapping and systematic searching for capturing *D. couperi.*

METHODS

Habitat used by adult *D. couperi* is primarily restricted to xeric upland sandhills in the northern part of its range (northern Florida and the Coastal Plain of southern Georgia) and during late fall through early spring. *Drymarchon couperi* associate with *Gopherus polyphemus* (Gopher Tortoise) burrows, which are used as shelters from environmental extremes and predation (Lawler, 1977; Diemer and Speake, 1983). We systematically searched for *D. couperi* in sandhills near active/inactive and abandoned *G. polyphemus* burrows (Cox et al., 1987; Smith et al., 2005); nine-banded armadillo (*Dasypus novemcinctus*) burrows; stump and root channels; and other potential shelters (hereafter referred to as burrow surveys). Our study areas were located on approximately 4,870 ha of Fort Stewart Military Reservation (FSMR, ca. 111,600 ha total) and tracts of adjacent private lands (ca. 3,150 ha), in Southeastern Georgia. We conducted burrow surveys for *D. couperi* from 1 December 2002 through 12 March 2003 on days with air temperatures >10.6°C. We also searched for shed skins and snake tracks near underground shelters to identify areas with recent snake activity. We recorded field search effort (person hours per day and survey results) for 18 *D. couperi* captured (12 males, 6 females).

In fall 2002, we constructed and installed 18 drift fences at FSMR (12) and adjacent private lands (6) on sandhills known to support overwintering *D. couperi*. Each trap array had a 1.2 m x 1.2 m x 0.3 m plywood and hardware cloth (6.4 mm mesh) box trap with one funnel entrance, also constructed of hardware cloth, on each side of the box,. Fifteen meters of 1-m high silt fence, installed approximately 0.15 m below the surface, radiated perpendicular from each funnel midpoint. This design was adapted from traps used to survey *Pituophis ruthveni* in Louisiana and Texas (Rudolph et al., 1999; Burgdorf et al., 2005) and *Pituophis melanoleucus* in Tennessee and southern Alabama (Gerald et al. 2006; M.A. Bailey, personal communication). Details of this design, including diagrams, are available in Burgdorf et al. (2005). Our modifications of this design included a wider funnel apex (ca. 7.5 cm min. diameter) to accommodate the larger *D. couperi* and a reduced trap height of 0.30 m from 0.45 m used by Burgdorf et al. (2005). We also added a side door (0.3 x 0.3 m) in addition to the top door that allowed animals to exit traps when not in use. In March 2003, we modified the design with the addition of horizontal panels (0.75 m x 0.75 m) placed on top of traps and extending, parallel to the ground, approximately 0.60 m out from each funnel entrance (Fig. 1). These additions were intended to make funnel trap entrances less exposed and to limit opportunities for snakes to crawl over the box traps. We checked traps daily and activated them only when overnight temperatures were >5°C and maximum daily temperatures were <33°C. We conducted both trapping and burrow searches concurrently on seven sandhills located on the study sites.

RESULTS

Between 1 December 2002 and 12 March 2003, we searched for snakes on 43 days totaling 249 person-hours. We found 13 *D. couperi* sheds (19.2 person-hours/shed) and 18 *D. couperi* adults (13.8 person-hours/snake). Captures occurred between 1050-1500 h and within 15 m of a *G. polyphemus* burrow ($\bar{x}$ = 3.7 m). Four captures occurred at abandoned *G. polyphemus* burrows and 14 at active/inactive burrows.

Construction, installation, and maintenance of traps required approximately 367 person-hours from fall 2002 until we ceased trapping. Maintenance was the most time-consuming activity (172 person-hours) and included clearing vegetation from around fences prior to prescribed burning. Construction was the least time-consuming activity (68 person-hours), followed by installation (120 person-hours). On each trapping day, we spent about one person-hour activating and checking traps, totaling approximately 166 person-hours from December 2002 through April 2004.

From December 2002 to April 2004, we opened traps in groups of six, for 847 trap-days. Traps captured several small mammal species, one bird (Bachman's Sparrow, *Aimophila aestivalis*), seven amphibian species, and nine reptile species, including six snake species (number of captures): *Coluber constrictor* (5), *Crotalus adamanteus* (1), *D. couperi* (6), *Heterodon platirhinos* (5), *Masticophis flagellum* (4), and *Micrurus fulvius* (1). Overall trapping efficiency, including time spent constructing, installing, maintaining, and checking traps was approximately 87 person-hours per *D. couperi* capture or 26.6 person-hours per capture excluding these activities (Table 1).

During December 2002 through March 2003 we opened traps (first design, December–February; second design, March) for 306 trap-days (61 person-hours activating and checking traps) with no *D. couperi* captures. We activated traps only sporadically through most of spring and summer 2003 because of lack of assistance and high temperatures. From September 2003 through November 2003 we opened traps (second design) for 363 trap-days (70 person-hours activating and checking traps), and captured six *D. couperi* (5 males, 1 female). Two captures were adult males (SVL = 145, 150 cm), four were sub- or small adults (107 - 120 cm SVL), and one was a recent hatchling (SVL = 59 cm). Trapping efficiency in this period was approximately 72 person-hours per *D. couperi* captured including trap construction, installation, and maintenance, and 11.6 person-hours per capture excluding these activities (Table 1).

DISCUSSION

Our capture efficiency for burrow surveys was similar to another study of *D. couperi* on some of the same sites, which recorded 88 captures during eight consecutive years and averaged approximately one snake per 10 person-hours (Stevenson et al 2003; D. Stevenson, unpublished data). Efficiency of burrow surveys for capturing *D. couperi* often relies on experience of the individual, their knowledge of the area, ability to discern snake sign, familiarity with tortoise burrow locations, and life history knowledge of the species (Stevenson et al., 2003). It may take weeks or months of searching in appropriate conditions to capture *D. couperi* (N. Hyslop, personal observation; D. Stevenson, unpublished data), which is indicative of the learning period even for experienced herpetologists.

Trapping was most successful during fall, a period when burrow searching is less effective compared to late fall through early spring surveying (Diemer and Speake, 1981; Stevenson et al., 2003). Trapping may have been more effective in the fall because of behavioral changes in the snakes (Gibbons and Semlitsch, 1981) when we recorded large, frequent movements coupled with repeated visits to sandhill habitats (Chapter 2). Comparatively, in winter, we recorded the smallest movement distances and frequencies of the year (Chapter 2). These behavioral factors may have contributed to the increased trapping efficiency we observed in fall 2003 compared with winter 2002-2003.

Although the large snake traps we installed captured *D. couperi*, trapping captured *D. couperi* at fewer sandhills than burrow surveys at our study sites. Using burrow surveys we captured *D. couperi* on six of seven sandhills where we installed traps and where *D. couperi* were known to occur. Traps detected *D. couperi* on four of these seven sandhills, although not on the sandhill without captures by surveying. Thirteen of 18 trap locations did not catch *D. couperi*. The high costs of building and maintaining traps, especially in areas with prescribed burning, may make trapping practical only in conjunction with sampling for other upland fauna, including other snake species (Gibbons and Semlitsch, 1981).

Trapping *D. couperi* has been challenging and most biologists have experienced low capture success throughout the Southeast. On military land in central Florida, 15 box traps arranged in 3 arrays, similar to those used in Rudolph et al. (1999) and Burgdorf et al. (2005), captured seven *D. couperi* in 2001 (M. Legare, personal communication). Twelve *D. couperi* were captured in a recent study in southern Florida using box traps described in Rudolph et al. (1999) modified with only two funnel trap entrances into the box trap and two funnel entrances at the end of the two fences Trapping efficiency was 86 trap-days per capture during 12 months using 24 traps (Dyer 2004). Another study in Florida captured five *D. couperi* during 1,638 trap-days using linear drift fences with two funnel traps at the end of fences (378 trap-days per capture; Layne and Steiner 1996). A second trap design used by Layne and Steiner (1996) in Florida consisted of 7.6 m of drift fence radiating perpendicular from a center with funnel traps placed midway on each side of the fences, captured one *D. couperi* in 2,672 trap-days (1984-1996). At Archbold

Biological Station in south-central Florida, wire funnel traps placed at the entrance of 80 *G. polyphemus* burrows captured 2 *D. couperi* during 240 trap-days (120 days per capture; Lips 1991). Herpetofaunal surveys on a Wildlife Management Area on the west coast of Florida captured four *D. couperi* during 6,000 trap-days (1,500 trap days per capture; Enge and Wood 2000). Their trap design used 30 standard drift arrays comprised of three, 10-m silt fence arms radiating from a center point at 120 degree angles and with 12 funnel traps (86 x 25 cm) per array (Enge and Wood, 2000). Our trapping efficiency at FSMR and adjacent private lands was 141 trap-days per *D. couperi* capture, but cannot be objectively compared to other studies because of likely differences in population densities.

The trap design we adopted from Rudolph et al. (1999) and Burgdorf et al. (2005) has been used successfully in other surveying for large snakes in the Southeast (Rudolph et al., 2006). Our traps, however, were only 0.30 m tall with 0.85 m high drift fencing and this reduction in trap height may have influenced the capture efficiency. Trapping is likely an effective supplement to burrow surveys, especially during the fall and in studies where surveyors change frequently or experienced biologists familiar with locating *D. couperi* via burrow surveys are not available. Advantages include a potential method of capturing yearlings and sub-adults, ability to use less experienced biologists, and similar capture rates to surveying in the fall when snakes exhibit large movements centered around sandhill habitats (especially with the modified trap design). In the northern portion of *D. couperi*'s range, where the species is associated with xeric pine-oak sandhills and *G. polyphemus* populations (Chapter 2), we recommend a combination of burrow surveys and trapping to most effectively detect and monitor *D. couperi* populations. We also recommend that further experimentation be conducted with different trap designs and methods for detecting and surveying *D. couperi*.

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Table 4.1. Trapping and searching efforts for *D. couperi* in 2002–2004, Georgia

					Hours/capture		
	Trap or search days	Field person-hours[1]	Total person-hours	*D. couperi* captures	Total activity[2]	Field activity[3]	Trap days/ capture
Burrow surveys							
12/2002 - 03/2003	43	249	249	18	14	14	-
Trapping							
12/2002 - 03/2003	306	61	367	0	-	-	-
04/2003 - 08/2003	108	23	131	0	-	-	-
09/2003 - 11/2003	363	70	433	6	72	12	60
12/2003 - 04/2004	70	12	82	0	-	-	-
Trapping total	847	166	1013	6	87	27	141

[1] - Hours in the field conducting burrow surveys or activating and checking traps.

[2] - Includes trap construction, installation, and maintenance hours.

[3] - Excludes trap construction, installation, and maintenance hours.

Figure 4.1. Trap used for *Drymarchon couperi*, 2002–2003, Georgia. Photo highlights the horizontal panels (0.75 m x 0.75 m) extending over each funnel entrance into the box trap.

CHAPTER 5

SURVIVAL OF RADIO-IMPLANTED EASTERN INDIGO SNAKES (*DRYMARCHON COUPERI)* IN RELATION TO BODY SIZE AND SEX[1]

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[1] Hyslop, N. L., R. J. Cooper, J. M. Meyers, and T. M. Norton. To be submitted to *Journal of Herpetology* (Shorter communications).

ABSTRACT

Drymarchon couperi (Eastern Indigo Snake), a threatened species of the Coastal Plain of the southeastern United States, has experienced population declines across its range because of habitat loss, fragmentation, and degradation. We conducted a radiotelemetry study on 32 individuals of *D. couperi* on Fort Stewart Military Reservation and adjacent private lands located in southeastern Georgia. We used known-fate modeling to estimate survival and its relationship to individual covariates including sex, size, size standardized by sex, and overwintering location. Annual survival in 2003 was 0.890 (95% CI = 0.736-0.972, *n* = 25) and 0.723 (95% CI = 0.523-0.862; *n* = 27) in 2004. Body size, standardized by sex, was the most important covariate determining survival of adult *D. couperi*, suggesting lower survival probability for larger individuals within each sex. It is unclear what influenced this result, but possibilities may include effect of higher resource needs for larger individuals or more conspicuous nature of larger snakes. These results may also suggest a population in which some individuals survive long enough to senesce.

INTRODUCTION

Drymarchon couperi (Eastern Indigo Snake), the longest North American snake species (Holbrook, 1842; Conant and Collins, 1998), is threatened throughout its range in the southeastern Coastal Plain of the United States (United States Fish and Wildlife Service, 1978). The species has experienced population declines leading to and since its federal listing because of habitat loss, fragmentation, and degradation, which remain primary threats to indigo snake populations (USFWS, 1978, 1998); however, highway fatalities, wanton killings, pesticide and other chemical exposure, and illegal collection also remain sources of concern for recovery (Lawler, 1977; USFWS, 1978). *Drymarchon couperi* occupies a wide variety of habitats including longleaf pine-turkey oak sandhills, pine and scrub flatwoods, dry prairie, tropical hardwoods, and freshwater wetlands. Breeding occurs from October through February in the northern portions of the range in south Georgia and northern Florida (Speake et al., 1987). Oviposition occurs during late spring and eggs hatch after approximately 3 months (Groves, 1960; Speake et al., 1987).

Factors influencing survival are often not well understood in wildlife populations, especially for snake species. This is primarily because of inherent difficulties in locating and recapturing snakes, their secretive nature, long periods of inactivity, and low densities of many populations (Parker and Plummer, 1987). Mark-recapture studies of snakes often suffer from low recapture rates because of these difficulties (Turner, 1977; Parker and Plummer, 1987), potentially influencing survival estimations. Errors in survival estimation can result in incorrect assessments of population trends and uninformed management decisions. Radiotelemetry allows for consistent monitoring of individuals, which can improve survival estimates and ability to estimate influence of individual covariates on survival. Complications from radio implantation procedures and implanted transmitters, however, may confound survival estimates from telemetry efforts (White and Garrott, 1990). Our objectives were to estimate monthly and annual survival in addition to estimating effects of individual covariates (sex, body size, and overwintering location) on survival probabilities for relocated *D. couperi* in Georgia.

MATERIALS AND METHODS

Study Area

We conducted a radiotelemetry study on *D. couperi* on Fort Stewart Military Reservation and adjacent private lands located in the Coastal Plain of southeastern Georgia. Fort Stewart study sites covered approximately 8,000 ha of its total 111,600 ha (Stevenson et al. 2003). Private lands adjacent to Fort Stewart covered approximately 6,000 ha in a contiguous tract. Details of study site habitats and land use are available elsewhere for Fort Stewart (Stevenson et al., 2003; Chapter 2) and private lands (Chapter 2).

Telemetry

We captured snakes by hand on xeric upland sandhill habitats with *G. polyphemus* populations (Stevenson et al., 2003) on Fort Stewart and private land sites during late fall to early spring, 2002-2004. We initially selected adult snakes for radio implantation as they were encountered, then more selectively based on sex and site of capture to ensure the study areas and sexes were represented as evenly as possible. We began fieldwork in March 2002. Transmitter implantation surgery for the first snake was successful; however, the snake (female) died the day following surgery. From 12 December 2002 to 11 April 2003, we captured and implanted 20 snakes (7 F, 13 M) with transmitters, and 12 additional snakes (6 F, 6 M) from 10 October 2003 to 1 March 2004. We used temperature sensitive radiotransmitters, weighing approximately 16 g, with whip antennas in the first year (AI-2T, 36 mo., 15x37 mm; Holohil Systems, Ltd., Ontario, Canada), and a smaller 18-month transmitter in the second year (SI-2T, 9g, 11x33 mm).

Radio implantations in snakes during winter may increase mortality (Rudolph et al., 1998); however, the only developed method of locating indigo snakes in Georgia was late fall and winter surveys near *G. polyphemus* burrows (Stevenson et al., 2003). Therefore, we worked to develop surgical and care protocols that reduced risks to the animals from implantation procedures. Prior to surgery, we acclimated snakes to higher temperatures for 1 to 2 days (21-27°C thermogradient). We prepared snakes for surgery using standard sterile techniques. Transmitters were surgically implanted by TMN approximately two-thirds from the anterior in the coelomic cavity. The antenna was threaded subcutaneously anterior of the transmitter using sterilized copper tubing. To remove the tubing, a small incision was necessary at the anterior end of the tube. Implantation procedures followed Reinert and Cundall (1982), with minor modifications. Isoflurane was administered throughout the procedure via intubation with an un-cuffed endotracheal tube and snakes were manually ventilated throughout the procedure.

Following surgery, while anesthetized, individuals were weighed, measured (snout-vent and tail length), and sexed by cloacal probing. We implanted passive integrated transponders subcutaneously approximately 20 scale rows anterior of the vent to provide an additional means of individual identification. Snakes were held individually, in enclosures, for 10-16 days post-operatively at elevated temperatures (21-27°C thermogradient) for recovery. For 1 to 2 days prior to release, snakes were provided an acclimation period of cooler temperatures to reflect daytime conditions when released (15-21°C thermogradient). We released snakes at their point of capture during late morning, on days with forecasted maximum temperatures >15.5°C and overnight lows >4°C. In spring 2004, we used ultrasound or radiographs on 9 of 10 females in the study at that time to assess reproductive condition. Upon study completion, we recaptured all but six snakes and surgically removed transmitters. Removal procedures and snake care were identical to those used for implantation. Radiotelemetry began approximately 24-hours after release. We relocated snakes 2-3 times per week by foot and vehicle using homing techniques (Mech, 1983).

Survival analyses

We used known-fate modeling in program MARK (White and Burnham, 1999) to estimate survival and its relationship to individual covariates for radio-implanted *D. couperi* (Kaplan and Meier, 1958; Pollock et al., 1989). Radiotelemetry ended in December 2004; however, we continued to relocate snakes monthly through June 2005 to capture snakes for transmitter removal, which provided survival data from January 2003–June 2005. We divided the data into 30, 1-month periods for survival analysis, retaining the individual as the experimental unit.

We included four individual covariates in analysis: sex, overwintering site (site, dummy variable coded for overwintering on private lands versus Fort Stewart), size at capture (size, snout-vent length), and size scaled by sex (size, standardized). Because *D. couperi* is sexually dimorphic with, on average, larger males, we standardized size by sex using residuals of size versus sex regression and used these residuals as a covariate in our survival models. Individual covariates were standardized and logit link functions were used for all models.

We generated hypotheses based on previous research of snake survival (Parker and Plummer, 1987; Bronikowski and Arnold, 1999) and natural history information. Candidate models tested for effect of time, sex, size, and over-wintering site on survival. We hypothesized that survival would be time dependent, with lower probability of survival in late winter and early spring. Large movement distances may increase probability of mortality by increasing encounters with predators, humans, and other hazards, especially roads. Therefore, we hypothesized that the larger movements generally seen in males compared to females (Chapter 2), would negatively influence survival probability. Habitat and land use differences (site) may also influence survival because of differences in the spatial arrangement of resources needed for long-term survival. *Drymarchon couperi* home range size was correlated with size and sex (Chapter 2); therefore, we did not include home range as an individual covariate in survival modeling. We used an information-theoretic approach, Akaike's Information Criterion (Akaike, 1973) corrected for small sample sizes (AICc; Hurvich and Tsai, 1989), to assess candidate models and select the best approximating confidence set of models for inference (90% confidence set; Burnham and Anderson, 2002).

RESULTS

Radiotelemetry

Male snout-vent length (SVL) averaged 158 cm (range 120-191); average weight at capture was 2.2 kg (range 0.72-4.3; Chapter 2). Females averaged 138 cm SVL (range 110-156) and 1.5 kg (range 0.55-2.3, Chapter 2). All females examined for reproductive condition in spring 2004 (*n* = 9) showed signs of egg formation. Complications from transmitters were found in two implanted snakes. Both cases included the transmitter antenna protruding from the skin, leading to localized infections of the area around the protrusion and transmitter. Transmitters were surgically removed prematurely in both snakes.

A necropsy of a snake implanted in March 2002 and died a day after surgery, revealed high internal parasite loads and significant skin lesions over the body. Histopathology studies indicated that the snake's death was related to a septic infection likely caused by skin and/or internal lesions (N.L. Stedman, University of Georgia, College of Veterinary Medicine, Athens Diagnostics Laboratory, unpublished report A2-046010). Several species of bacteria were involved in the skin lesions, indicating that infection was opportunistic secondary to another compromising factor such as high environmental humidity. Internal lesions were attributed to gastric nematode and migrating immature pentastome activity. Opportunistic bacteria, possibly introduced by pentastomes, also infected the sites.

Of the 20 snakes captured and implanted December 2002–April 2003, we censored 11 snakes (6 F, 4 M) because of mortality (*n* = 8), transmitter complication (*n* = 2), and depleted transmitter battery (*n* = 1). We also removed 3 (1 F, 2 M) of 12 snakes radio-marked between October 2003 and March 2004 because of mortality (*n* = 2) and unknown fate (*n* = 1). Cause of death was determined conclusively in only one case, which was a large-ranging male that was hit by a vehicle on an unpaved road. Three individuals died within a 12-day period in February 2004. Two of the three were found dead in *G. polyphemus* burrows and the other was found dead coiled on the surface with no observable external trauma. The other mortalities occurred in fall 2003 (*n* = 1), spring 2004 (*n* = 3), summer 2004 (*n* = 1), fall 2004 (*n* = 1), and spring 2005 (*n* = 1), Table 5.1). Necropsies were performed by TMN on snakes found with significant body tissue remaining (*n* = 5); however, all were inconclusive for cause of death.

Survival analysis

The model-averaged estimate of monthly survival for snakes relocated from January 2003–June 2005 was 0.984 (95% CI = 0.972-0.996). Annual survival in 2003 was 0.890 (95% CI = 0.736-0.972, *n* = 25) and 0.723 (95% CI = 0.523-0.862; *n* = 27) in 2004. The model-averaged estimate of probability of survival for relocated snakes was 0.609 (95% CI = 0.395-

0.823) from January 2003–June 2005. Only one model was included in the 90% model confidence set evaluating survival probabilities, given the data and candidate models (Table 5.2). This model ($\omega_i = 0.44$) included size as standardized by sex. Survival model-averaged parameter estimates indicated a strong negative relationship of size standardized by sex, suggesting lower survival probability with increasing size within each sex. No other variables had predictive power (Table 5.3). We failed to detect a predictive relationship of time on survival; all models that included time or changes with time had little or no support (Table 5.2).

DISCUSSION

Mean annual survival rates in this study were similar to those previously reported for other late-maturing, temperate snakes. In a review of snake survival, Parker and Plummer (1987) reported annual survival of 0.70 for late-maturing temperate colubrids (5 species) and 0.77 for late-maturing temperate viperids (5 species). Modeling suggested a negative effect of size, standardized by sex, as the strongest predictor of adult *D. couperi* survival, indicating that larger snakes within each sex are more susceptible to mortality than smaller ones. Similar patterns were found in marine iguanas (*Amblyrhynchus cristatus*), where survival was highest in intermediate-sized individuals and lower for sub-adults and for the largest-sized age class (Laurie and Brown, 1990). Our results may be attributable to numerous factors including resource needs or age of larger individuals; however, we cannot exclude influence of sample size on modeling or the possibility that other factors, such as individual variation, environmental conditions, and effects of surgery may also influence adult *D. couperi* survival at our study sites.

Modeling of individual covariates affecting home range size (Chapter 2) and survival in the population we studied produced contrasting results. Home ranges size was affected most by sex. Males maintained larger home ranges, regardless of their body size, indicating a biological difference in home range size between males and females (Chapter 2). We expected that survival probability would decrease with increasing movements because of the potential for increased interactions with predators and humans; however, home range modeling indicated that larger individuals within each sex did not show larger movements (Chapter 2). We do not clearly understand what was driving this result, but possibilities may include effect of age or more conspicuous nature of larger snakes.

Although there is no evidence relating larger home ranges with larger individuals within each sex (Chapter 2), greater movements may have important survival implications for *D. couperi* populations in more fragmented habitat. For example, although our study sites lacked paved roads within areas used by snakes, road mortality in areas with higher densities of paved roads can negatively influence survival rates (Rudolph and Burgdorf, 1997; Bonnet et al., 1999; Andrews and Gibbons, 2005). We incidentally observed four *D. couperi*, not in our radiotelemetry study, killed by vehicle on paved roads surrounding our study sites. Therefore, our survival results may not represent typical relationships observed between movement and survival because of high overall habitat quality and lack of paved roads.

We found disproportionately higher mortality in female snakes, given the sex ratio of relocated snakes in this study (13 F: 19 M); however, modeling did not show an effect of sex on survival. All females examined in spring 2004 ($n = 9$) were gravid. During a 10-year study, Speake et al. (1987) captured 21 female *D. couperi* during spring and found that all but one snake was gravid; indicating that annual reproduction in *D. couperi* may be possible. Physiological stresses related to gestation and migration to reach appropriate egg-laying habitats have been implicated with higher female mortality (Parker and Plummer, 1987); although, we did not observe higher mortality of females during gestation or following oviposition.

To avoid negatively biased survival estimates, an assumption of survival analysis is that capture and radio-implantation procedures do not influence survival of the individual (Winterstein et al., 2001). To address this concern, we only implanted adult snakes, monitored snake health throughout the study, and used the smallest transmitters possible, given battery-life requirements. With the exception of the first implanted snake, no other individual perished within 95 days of implantation surgery; suggesting that capture, surgery, and transmitters did not have immediate negative effects on survival. Eight of 10 mortalities in this study were from snakes implanted in the first season (December 2002 – April 2003) with the larger transmitters. Smaller individuals within each sex, however, had higher survival probabilities, so it unlikely that transmitter size was a factor in these deaths. In a review of radiotelemetry papers published from 1972-2000 in five journals, including Journal of Wildlife Management and Copeia, Withey et al. (2001) identified 96 papers that addressed the effects of transmitters on relocated animals, none of which included amphibian or reptile species. This review illustrates the need for critically examining effects of transmitters on herpetofauna.

Survival of snakes in natural environments may fluctuate annually, as may the relationship between body size and survival (Forsman, 1993). Our annual survival rates did not differ between years; however, there is insufficient temporal data to conclude that survival rates are relatively stable in the population we studied. Our results, suggesting lower survival with larger individuals within each sex, may be indicative of a population in which some individuals survive long enough to senesce or succumb to deleterious factors encountered at larger sizes.

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Table 5.1. Sex, size, weight, and radiotelemetry details for mortalities of relocated *Drymarchon couperi*, 2003–2004, Georgia.

ID	Sex	SVL (cm)	Total length (cm)	Weight (kg)	Captured	Site[1]	Days monitored	Removed from study
5	F	151.0	177.0	1.94	01/09/03	FS	609	09/28/04
8	F	142.5	168.5	1.54	01/21/03	FS	390	02/27/04
9	F	146.0	173.0	1.64	02/02/03	FS	490	06/24/04
14	F	124.5	150.0	1.20	02/25/03	FS	335	02/15/04
20	F	152.0	181.0	1.90	04/11/03	PL	363	04/20/04
26	F	145.0	175.0	1.70	11/28/03	PL	92	03/15/04
12	M	191.0	225.5	4.26	02/24/03	FS	189	09/14/03
15	M	152.0	182.0	1.60	02/26/03	PL	626	05/01/05
16	M	178.0	210.0	2.78	03/09/03	PL	205	10/17/03
24	M	182.0	217.0	3.58	11/16/03	FS	89	02/29/04

[1.] Site: Fort Stewart (FS) or private lands (PL).

Table 5.2. Candidate models used to evaluate annual survival of relocated *Drymarchon couperi*, January 2003–June 2005, Georgia. All models include an intercept term.

Model[1]	K	AICc	ΔAICc	ω_i	Model likelihood
Size (standardized)	2	98.790	0.000	0.436	1.000
Size (standardized), Site	3	100.61	1.817	0.175	0.402
Sex	2	101.31	2.516	0.124	0.284
Intercept	1	101.56	2.765	0.109	0.250
Size	2	102.53	3.739	0.067	0.154
Sex, Site	3	103.27	4.477	0.046	0.106
Site	2	103.56	4.764	0.040	0.092
Sex (time)	29	135.39	36.60	0.000	0.000
Time	30	137.69	38.90	0.000	0.000
Site (time)	28	138.38	39.59	0.000	0.000
Size (standardized; time)	30	140.15	41.35	0.000	0.000

[1] Model parameters: Sex (being female), Size (snout-vent length), Site (on private lands), Size (standardized; snout-vent length standardized by sex).

Table 5.3. Importance of size as standardized by sex on probability of survival for relocated *Drymarchon couperi*, January 2003–June 2005, Georgia. Values are model-averaged parameter estimates, unconditional standard errors, and confidence intervals for individual covariate effects on annual survival.

		95% Confidence Interval	
Parameter	Beta	Lower	Upper
Intercept	3.835	1.860	5.811
Size (standardized)	-0.880	-1.721	-0.038
Site	0.148	-0.372	0.667
Sex	-0.070	-0.448	0.317
Size	-0.030	-0.292	0.238

[1] Model parameters: Sex (being female), Size (snout-vent length), Site (on private lands), Size (standardized; snout-vent length standardized by sex)

CHAPTER 6

CONCLUSIONS AND CONSERVATION IMPLICATIONS

CONCLUSIONS

Despite federal and state protection since 1978, previous understanding of *Drymarchon couperi* natural history and ecology is limited, especially for its northern range in southern Georgia and northern Florida. My objectives for this research were to determine the species spatial and temporal use of the landscape, including movements, home range, habitat, shelter use, and survival. I used radiotelemetry to collect this information for 32 indigo snakes (13 F: 19 M) from December 2002 to December 2004 at Fort Stewart Military Reservation and adjacent private lands in southeastern Georgia. Herein, I conclude with a summary of the research and its conservation implications.

Annual home ranges from this study, of 35–354 ha for females ($\bar{x}$ = 126) and 140–1,530 ha for males ($\bar{x}$ = 538, MCP), represent the largest yet reported for a North American snake species (Macartney et al. 1988). Although I did not specifically test hypotheses regarding why *D. couperi* home ranges were large, they may reflect the needs of larger terrestrial species, which on average, require more food and area to forage. How body size influences home range size in snakes, however, has not been established inter- or intra-specifically (Gregory et al. 1987, Macartney et al. 1988). If home range size were an artifact of seeking new overwintering and breeding areas (i.e., emigration), I would expect a proportion of snakes to not return to previous over-wintering areas. All relocated snakes, however, returned to the same sandhills used in previous winters. If intraspecific competition affects home ranges, I would expect avoidance between individuals, at least outside of the breeding period; however, all home ranges overlapped with at least four others. Therefore, I suggest that in addition to sex and body size, indigo snake home ranges, at least in warmer months, may be influenced by foraging and thermoregulatory needs. These results may indicate a need for additional research on mechanisms influencing home range size in *D. couperi*.

Home range size was correlated negatively with being female and affected positively by increasing body size, although to a lesser extent than sex alone. Reproductive condition and associated behaviors may account for some differences in home range size between males and females, especially in the spring when females remained on over-wintering habitats while males began using lowland habitats. Size, standardized by sex, had no predictive power for home range size, thus, suggesting that sexual differences, rather than different resource needs of larger individuals, influenced home range size.

Intersexual differences by habitat use were most pronounced in the spring when males began dispersing from sandhills to surrounding habitats, including wetlands, clearcuts, and other uplands. Females remained on sandhill habitats until late spring and early summer when oviposition was completed (Speake et al. 1987). During the summer, males and females depended less on sandhill habitats, but continued to use upland habitats and tortoise burrows for shelter prior to ecdysis and often following observation of foraging behavior (Hyslop, unpublished data). Fort Stewart and private land sites had extensive bottomland hardwood wetlands along a river bisecting the study area. Other wetlands used by indigo snakes included cypress domes embedded in large clearcuts. In fall, habitat use was transitional, i.e., snakes returned to over-wintering sandhills for short periods before moving back to habitats used primarily during the summer.

Microhabitat use at underground shelters was influenced by season more than by sex, size, or overwintering on Fort Stewart or private lands. In summer and fall, snakes used areas with higher than average understory vegetation cover, dominated by woody vegetation and palms when compared to other seasons. The dense understory likely provided shading from direct sun, which is important for snake thermoregulation. Microhabitat use in spring differed by sex, with females using more open areas than males, possibly for thermoregulation during gestation. Modeling results suggested a strong negative effect of association with private land sites on use of microhabitat sites with higher than average grass and herbaceous cover. This provides support for my prediction that management of land with tortoise burrows influences microhabitat use. It is possible that greater proportions of land in managed timber production, lack of thinning, and fire exclusion caused site differences. These activities created forests with sparse grass and herbaceous vegetative cover (personal observation), thus influencing microhabitat use by *D. couperi*.

In winter, male and female indigo snakes used shelters restricted primarily to *G. polyphemus* burrows, with males using a higher proportion of active burrows and females using abandoned burrows almost twice as frequently as males. In the spring, females again had a higher association with abandoned tortoise burrows while males began using other shelters to a larger extent. Approximately 60% of all female underground locations during the spring were in abandoned tortoise burrows, compared to 28% of male locations during the same season. In the summer, snake use of *G. polyphemus* burrows was lowest, although females continued to use abandoned burrows an average of 40% of their underground locations.

Survival modeling results suggested a negative effect of size, standardized by sex, as the strongest predictor of adult indigo snake survival. Because of the observational nature of this study, I cannot exclude influence of sample size on modeling or the possibility that other factors, such as individual variation, environmental factors, and effects of surgery also influenced adult survival. Although there was no evidence associating larger home ranges with larger individuals within each sex, longer movements may have important survival implications for *D. couperi* populations in more fragmented and smaller habitat patches. For example, my study sites did not have paved roads within areas used by snakes, but did have paved roads along two boundaries of the private property sites, with no snake relocations on the opposite side of either road. In areas with higher densities of paved roads, road mortality could have much more of a negative impact (Bonnet et al. 1999). My survival results may not represent the typical relationship between movement and survival because of high overall habitat quality and lack of paved roads.

CONSERVATION IMPLICATIONS

Ecosystem approaches to management often necessarily focus on a few key species that may serve as indicators of ecosystem integrity, as keystone or umbrella species (Lambeck 1997, Simberloff 1998). Wildlife management in longleaf pine forests has focused primarily on red-cockaded woodpecker (*Picoices borealis*) or gopher tortoise populations. Management activities targeting these species, which include maintaining a low basal area, sparse canopy cover, little to no midstory cover, native groundcover vegetation, and prescribed fire, will also benefit *D. couperi*. These management activities, however, often disregard extensive tracts of wetlands that exist between uplands in this region (Wharton 1978); therefore, managing to include *D. couperi* as a conservation goal may benefit more species. I suggest that *D. couperi*, because of the large amount of land and variety of habitats used, is an appropriate model to serve as an umbrella species in an ecosystem-based management approach (Grumbine 1994; 1997, Noss 2000). This strategy will likely be more effective when combined with management needs of red-cockaded woodpeckers and Gopher Tortoises, involving integration of management and conservation practices that may have been excluded previously (Fleishman et al. 2000, Roberge and Angelstam 2004). Focusing on conservation and restoration of natural structure, flora, and fauna, connectivity of habitats, and natural ecosystem processes, especially fire, will most effectively and efficiently benefit not only *D. couperi* but most other herpetofauna that use these systems.

Habitat loss, fragmentation, and degradation remain primary threats to *D. couperi* populations; however, highway fatalities, wanton killings, and pesticide and other chemical exposure remain sources of concern for indigo snake recovery (Lawler 1977). Results of this study reaffirm that longleaf pine ecosystem conservation and restoration is important to *D. couperi* populations when it includes an appropriate matrix of wetland and upland habitats. Currently, such areas exist in a few large undeveloped tracts of land, such as Fort Stewart and adjacent private lands, which can serve as core areas for large-scale conservation plans. Such strategies will benefit *D. couperi* and many other wildlife populations in these habitats.

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