



Research Article

# Effects of Body Size and Sex of *Drymarchon couperi* (Eastern Indigo Snake) on Habitat Use, Movements, and Home Range Size in Georgia

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**ABSTRACT** The federally threatened eastern indigo snake (*Drymarchon couperi*), native to the southeastern Coastal Plain of the United States, has experienced population declines caused primarily by habitat loss, degradation, and fragmentation. To examine spatial and habitat use requirements of the species, we radiotracked 32 eastern indigo snakes from 2002 to 2004 on Fort Stewart Military Installation and adjacent private lands in Georgia. We estimated annual and seasonal home ranges and evaluated a priori hypotheses examining morphometric and ecological factors (sex, body size, location) associated with intraspecific differences in home range size. We analyzed habitat use hierarchically by examining use across the study area and within home ranges. Annual home range size varied from 33 ha to 1,528 ha (average minimum convex polygon:  $\bar{x}_{2003} = 378$  ha;  $\bar{x}_{2004} = 340$  ha). Individual home range size was most influenced by sex (males with larger home ranges) followed by body size. Compositional analysis of habitat use suggested positive selection for wetland, evergreen forest, and pine-hardwood (mixed) forest, with an avoidance of roads and deciduous forests. Seasonally, indigo snakes used the highest diversity of habitats as they moved from xeric uplands (sandhills) in winter and early spring to wetlands and uplands other than sandhills in summer; however, snakes continued to use sandhill habitats (35–58% of locations seasonally) with gopher tortoise (*Gopherus polyphemus*) burrows throughout the warmest months. In Georgia, management and conservation of the eastern indigo snake should include conservation of large tracts of undeveloped land, containing a matrix of xeric uplands with suitable underground shelters and adjacent wetland habitats. © 2013 The Wildlife Society.

**KEY WORDS** conservation, *Drymarchon couperi*, eastern indigo snake, Georgia, gopher tortoise, habitat use, home range, movement, telemetry.

Accurate natural history information, including the spatial and habitat requirements of a species, is necessary for development of adaptive conservation and management plans. These needs emphasize the importance of understanding habitat components and spatial requirements for maintaining populations across their geographic range. Spatial patterns of population structure can often be understood by examining the distribution of individuals in relation to required resources (Pope et al. 2000). Possible influential factors include the spatial arrangement, connec-

tivity, and availability of necessary resources such as prey, suitable shelters, thermoregulatory opportunities, and mates (Gibbons and Semlitsch 1987, Gregory et al. 1987, Macartney et al. 1988). Understanding the scale at which populations are structured and determining factors associated with home range size and habitat use are important for management strategies and the design of adequately sized reserves (Dodd 1987).

In the southeastern Coastal Plain, a center of reptile and amphibian diversity in the United States, habitat loss is the primary cause of most herpetofaunal declines (Gibbons et al. 1997). Contributing to these declines has been the loss of the once dominant longleaf pine (*Pinus palustris*)–wiregrass (*Aristida stricta*) habitats, which historically covered approximately 30 million ha of the southeastern Coastal Plain prior to European settlement. Currently, only about 2% of this habitat remains, primarily in isolated fragments (Frost 2006). The eastern indigo snake (*Drymarchon couperi*) is a wide-ranging

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predator closely associated with xeric upland longleaf pine-wiregrass habitats, often referred to as sandhills, and the burrows of gopher tortoises (*Gopherus polyphemus*), which may inhabit these upland areas. This association is especially pronounced in the northern portions of the species' range in south Georgia and northern Florida. Indigo snake populations have continued to decline since federal listing in 1978 (U.S. Fish and Wildlife Service [USFWS] 2008). These declines are primarily attributed to habitat loss and degradation caused by development, fire exclusion, agriculture, and conversion of native longleaf pine habitats to commercial plantations of off-site pine species (USFWS 1978, 2008).

Gopher tortoise burrows, along with other underground shelters, are used by indigo snakes as protection from temperature extremes, fire, and predators, and may also be used for foraging, shelter prior to ecdysis, and nesting (Landers and Speake 1980, Moler 1992, Stevenson et al. 2003, Hyslop 2007, Hyslop et al. 2009a). The association with tortoise burrows is especially pronounced from late fall through early spring, which includes the indigo snake's breeding season from October–February (Speake et al. 1978, Diemer and Speake 1983, Hyslop et al. 2009a). Evidence suggests that indigo snakes may spend on average approximately 76% of their time underground, regardless of season or sex (Hyslop et al. 2009a) and that underground shelters, especially tortoise burrows, may be a limiting factor for indigo snakes in the northern portion of their range (Diemer and Speake 1983, Hyslop et al. 2009a). Outside of the breeding season, and during their period of greatest activity with respect to movements and foraging, indigo snakes may use a variety of other habitats, including pine flatwoods, mixed pine-oak forests, bottomland forests, and other freshwater wetlands (Speake et al. 1978, Landers and Speake 1980).

We addressed information needs associated with the eastern indigo snake in Georgia, including spatial and habitat requirements. Our objectives were to determine if eastern indigo snakes maintained definable home ranges, to estimate annual and seasonal home range sizes and describe movements within home ranges, to examine ecological factors associated with intraspecific home range size variation, and to quantify habitat use and seasonal variation in use.

Home range size in eastern indigo snakes may vary intersexually. In Georgia, female indigo snakes have been shown to use more open microhabitats than males, especially on sandhill habitats with tortoise burrows during spring (Hyslop et al. 2009a), thus resulting in intersexual differences in home range size arising from smaller, less frequent movements from females in the spring. This pattern has also been shown for other snake species, and is likely attributable to differences in reproductive condition and related thermoregulation needs (such as increased temperatures) when gravid (Reinert 1993, Blouin-Demers and Weatherhead 2001). In addition, males may also move greater distances when searching for mates, a behavior found in several other snake species (Gregory et al. 1987). Therefore, we would predict that sex influences home range

size in indigo snakes, with males occupying larger ranges than females because of behavioral differences. Alternatively, home range size may not be directly affected by sex, but a sexually dimorphic pattern may emerge because males, on average, are larger (male-biased sexual size dimorphism; Layne and Steiner 1984; Stevenson et al. 2003, 2009), and therefore have potentially greater resource needs that influence home range size (Harsted and Bunnell 1979, Tufto et al. 1996). Patterns and scale of movement and habitat use within a landscape may be correlated with arrangement of necessary resources (Gibbons and Semlitsch 1987, Gregory et al. 1987, Macartney et al. 1988). Therefore, we also predicted that variation in spatial distribution of resources, influenced in part by different management and land use objectives across the landscape, may additionally affect home range size (Tufto et al. 1996, Moyer et al. 2007).

Habitat use in snakes may also be driven by multiple factors similar to those influencing home range sizes, such as prey and thermal requirements (Reinert 1984). We did not expect intraspecific separation of habitat use throughout most of the year because of assumed similarities in resource needs between sexes; however, female indigo snakes may be limited to using more open microhabitats for thermoregulation while gravid in the spring (Hyslop et al. 2009a). Thus, we predicted intersexual separation in spring habitat use because of differences in reproductive condition.

## STUDY AREA

We conducted a radiotelemetry study of indigo snakes on Fort Stewart Military Installation (hereafter Fort Stewart) and adjacent tracts of private land in southeastern Georgia. The Fort Stewart study site spanned approximately 8,000 ha of its total 111,600 ha (Stevenson et al. 2003); private lands were contiguous with our Fort Stewart site and covered approximately 6,000 ha. Paved roads bordered 2 sides of the private lands, but no paved roads were present within the study area. Both sites contained maintained and non-maintained unpaved roads. The study sites also supported populations of gopher tortoises, although potential tortoise habitats on private lands were generally fire-suppressed, in planted pine plantations, clear-cuts, and actively managed hay fields, with clusters of active burrows more localized. In comparison, gopher tortoise burrows on Fort Stewart were more densely and uniformly distributed primarily throughout uneven-aged pine forests.

Fort Stewart and private land study sites contained intact, longleaf pine–turkey oak (*Quercus laevis*)–wiregrass habitat, young (5–15 yr) to medium (16–40 yr) age slash (*Pinus elliotii*) and loblolly (*Pinus taeda*) pine plantations, and recently restored (i.e., formerly in slash or loblolly pine plantations that were clearcut) longleaf pine–wiregrass habitats. Recent (1990–present) habitat management and restoration practices at the Fort Stewart sites have promoted or enhanced open-canopied longleaf pine habitats (i.e., prescribed burning from Aug to Oct, selective thinning, longleaf pine planting, wiregrass seeding, and control of xerophytic oaks via herbicide application). Other actions included discontinuing the removal of remnant pine stumps,

which are known shelters for indigo snakes (Hyslop et al. 2009a); limiting winter timber harvests on xeric uplands supporting tortoise burrow to avoid possible burrow collapse at a time when snakes are more likely to be resident; and retaining debris piles (windrows) following timber harvest and site preparation, which indigo snakes have also been shown to use (Hyslop et al. 2009a).

Management activities on non-cultivated areas of the private lands included some of the same methods as Fort Stewart; however, some sandhills on private lands had long histories of fire exclusion (>25 yr), resulting in hardwood encroachment (e.g., turkey oak), increased midstory and canopy cover, and reduced native ground cover. Xeric sandhills at both sites were intergraded with mesic pine flatwoods, mixed pine-oak forests, bottomland hardwood habitats, and other wetlands (including isolated depressional wetlands, blackwater creek swamps, seepage-influenced bay swamps, and impoundments; Wharton 1978).

## METHODS

### Field Methods

We captured 32 snakes, 31 by hand and 1 individual in a large snake trap (Hyslop et al. 2009c) on upland sandhill habitats with gopher tortoise burrows (Stevenson et al. 2003) during late fall to early spring of 2002–2004. We implanted 20 snakes (7 F, 13 M) with radiotransmitters between December 2002 and April 2003 and 12 additional snakes (6 F, 6 M) from October 2003 to March 2004. For details of surgical and care procedures see Hyslop et al. (2009b). We located snakes 2–3 times per week by foot and vehicle using homing techniques (Mech 1983), with accuracy <1 m if the animal was underground or immobile (e.g., basking; behavior noted if individual was observed). We staggered periods randomly during the day that we tracked each individual. Animal Care and Use Committees of The University of Georgia IACUC (A2002-10111-0) and USGS Patuxent Wildlife Research Center approved study procedures.

### Home Range

To examine area used by the snakes, we used 100% minimum convex polygons (MCP) to estimate home ranges (Mohr 1947, Southwood 1966) and kernel density (KD) analysis to estimate utilization distributions (Worton 1989). To address possible sample size bias associated with MCPs (e.g., Arthur and Schwartz 1999), we used bootstrap analysis (500 iterations) to examine sample size to home range area relationships and included home ranges in analysis only if incremental area curves visually reached an asymptote. We calculated KD at 95% isopleths (home range) and at 50% isopleths (core activity areas; Samuel et al. 1985) using the fixed kernel method with a least squares cross-validation smoothing parameter (Worton 1989, Seaman and Powell 1996, Gitzen and Millspaugh 2003). For calculation of KD home ranges, we retained only novel radiolocations and removed consecutive repeated locations (individual in same underground shelter or within approx. 2 m of previous location if on the surface) 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 15 December to 14 December 2002 to 2003 and 2003 to 2004. We estimated seasonal MCP home ranges for winter (15 Dec–14 Mar), spring (15 Mar–14 Jun), summer (15 Jun–14 Sep), and fall (15 Sep–14 Dec). We excluded individuals without complete seasons of data from that season's analysis. We conducted analyses with the Animal Movements Extension (Hooge and Eichenlaub 1997) to ArcView GIS (Environmental Systems Research Institute, Inc., Redlands, CA) and used repeated measures analysis of variance (ANOVA) for seasonal home range analysis (PROC GLM; SAS Institute, Inc. 2005). We retained the individual as the sampling unit in all analyses.

We used repeated measures linear regression on 12 candidate models created from a priori hypotheses to examine biological and ecological correlates of intraspecific variation of home range size (PROC MIXED; SAS Institute, Inc. 2005). We compared models using Akaike's Information Criterion (AIC; Akaike 1973, Burnham and Anderson 2002) corrected for small sample sizes (AIC<sub>c</sub>; Hurvich and Tsai 1989). We also used AIC<sub>c</sub> to select the covariance structure for the data from an a priori selection of potential structures. Model averaging may be problematic with repeated measures designs (Reiman et al. 2006); therefore, we report Akaike weights and parameter estimates for model parameters included in 90% model confidence sets.

Model parameters included sex, snout-vent length (size), interaction of sex and size, overwintering location (Fort Stewart or private lands), and number of radio locations. We standardized size by sex using residuals of size versus sex regression as an additional covariate in our models (size standardized). In addition to setting a minimum tracking duration for inclusion of individuals into annual and seasonal home range and bootstrap analyses, we also incorporated the number of locations collected per individual to evaluate if home ranges were maintained.

### Patterns of Movement

To calculate frequency of movement, we divided the 24 months of radiotelemetry data into 14-day periods and calculated proportion of days moved compared with number of days radiotracked within that 14-day period. This method standardized tracking effort across seasons and individuals. We deleted records for snakes with only 1 novel location during a 14-day period (31 deleted locations, 18 individuals). To generate a minimum daily movement index, we calculated straight-line distances between successive locations (Animal Movements Extension; Hooge and Eichenlaub 1997). We based the calculations on the number of days in each season that individual snakes were located; we again averaged movement for each individual during 14-day periods to standardize data. For movement analyses, we used repeated measures ANOVA and retained the individual as the sampling unit (SAS Institute, Inc. 2005).

### Habitat Association Analyses

Conclusions regarding habitat use may vary with spatial scale examined; therefore, we analyzed habitat use hierarchically

(Johnson 1980). We examined the snake's position within its home range by comparing habitat at telemetry locations to habitat within MCP home ranges (site selection) and compared proportional habitat composition within home ranges to proportion of habitats available at the site (home range selection; Johnson 1980). We used compositional analysis (Aitchison 1986, Aebischer et al. 1993) for habitat use comparisons (Bycomp Version 1.0; Ott and Hovey 1997; SAS Institute, Inc. 2005). We categorized Gap Analysis Program land cover data (GAP; Kramer et al. 2003) into 7 major land cover types: 1) roads and urban areas (road-urban); 2) open water, forested bottomland wetlands, depressional wetlands, bay swamps, and non-forested wetlands (wetlands); 3) agricultural and other fields (field); 4) clearcuts and other habitats with sparse canopy cover, including regenerating forests generally <10 years in age with low canopy cover (sparse); 5) forests with >75% deciduous trees generally >10 years in age (deciduous); 6) forests with >75% evergreen trees, including managed pine plantations generally >10 years in age (evergreen); and 7) pine-hardwood mixed forest, including shrub-scrub habitats (mixed).

At each snake radiolocation, we also measured habitat characteristics in the field and defined in-field habitat categories based on hydrology, vegetation, management, and presence of gopher tortoise burrows. We included this additional habitat use analysis primarily to distinguish sandhill habitats from evergreen, mixed, and sparse GAP categories, each of which contained some sandhill habitat. In-field habitat categories included 1) xeric uplands with longleaf pine and/or xerophytic oak canopy and gopher tortoise burrows (sandhill); 2) harvested pine flatwoods with windrows, low to no canopy cover, bedding for loblolly pine planting, embedded isolated wetlands, without tortoise burrows (clearcut); 3) old-field, hay fields, and food plots, some areas with tortoise burrows (field); 4) pine plantations of various ages, may or may not contain tortoise burrows (pine plantation); 5) areas of mixed pine-hardwood canopy composition, occasional tortoise burrows (miscellaneous uplands); and 6) low-lying seasonally flooded areas with no tortoise burrows (wetlands).

The in-field habitat categories field and wetland were similar to the GAP land cover categories of the same name. No in-field category corresponded with the road-urban GAP category because we did not record any snake locations in this habitat type. We separated the evergreen, mixed, deciduous, and sparse GAP categories into the in-field categories

clearcut, sandhill, pine plantation, and miscellaneous uplands as described in the in-field habitat category explanations. We used repeated measures ANOVA with arcsine transformed data and a Tukey-Kramer multiple comparison procedure for examining seasonal differences in habitat use between males and females (PROC GLM; SAS Institute, Inc. 2005).

## RESULTS

We collected 4,993 telemetry locations for 32 snakes from January 2003 to December 2004 (24 months). Individuals were tracked 89–711 days ( $\bar{x}$  = 420 days, 39–254 locations per individual). Male snout-vent length averaged 158 cm (range = 120–191) and mass at capture averaged 2.2 kg (range = 0.7–4.3). Female snout-vent length averaged 138 cm (range = 110–156) with an average mass of 1.5 kg (range = 0.6–2.3).

### Home Range

Bootstrap analysis of MCP annual and seasonal home ranges yielded area curves that reached asymptote, suggesting sufficient locations were collected for the home range area to stabilize. We included 18 snakes in 2003 (11 M, 7 F) and 20 snakes in 2004 (13 M, 7 F) in annual home range calculations (13 snakes from 2003 also included in 2004). Annual home ranges (MCP) averaged 378 ha (95% CI = 185–571) in 2003 and 340 ha (95% CI = 184–496) in 2004, with individual home ranges from 33–354 ha for females and from 140–1,528 ha for males. Males, on average, occupied annual home ranges approximately 4.5 times larger than females in 2003 and approximately 6.6 times larger than females in 2004 for MCP and KD (Table 1). Kernel density analysis at 50% isopleths yielded 1–5 distinct regions of core habitat use for each snake ( $\bar{x}$  = 1.7), with no differences between sexes or years. Males, on average, also occupied larger individual core activity areas than females; although core areas averaged 12% of 95% KD home ranges regardless of sex. All annual home ranges in our sample overlapped with  $\geq 6$  other home ranges, with no evidence of inter- or intraspecific avoidance.

Global models for MCP, 95% KD, and 50% KD annual home ranges confirmed adequate fit (likelihood ratio test:  $P < 0.05$ ). Residual normality plots of natural log-transformed data supported normality of transformed data in annual home range estimates. Analyses of global models suggested autoregressive covariance structure was the most appropriate. The 90% confidence set of models for estimating annual MCP home ranges contained 2 of 12 candidate models (Table 2). The model with the most

**Table 1.** Home range and activity center areas for male (M) and female (F) eastern indigo snakes radiotracked 2003–2004, Georgia. Values (ha) are averages with 95% confidence intervals (CI) for 100% minimum convex polygon (MCP) home ranges, 95% kernel density (KD) utilization distributions, 50% KD activity centers, and average number of distinct 50% KD core areas. Of the snakes tracked in 2003 with complete years of data ( $n = 18$ ), 13 of those were also tracked in 2004 (11 M, 2 F).

Year	Sex	<i>n</i>	100% MCP		95% KD		50% KD		
			$\bar{x}$	95% CI	$\bar{x}$	95% CI	$\bar{x}$	95% CI	Average number of core areas
2003	M	11	538	264–812	792	390–1,194	120	21–219	1.7
	F	7	126	45–207	173	59–587	25	6–44	1.6
2004	M	13	482	279–685	552	242–862	76	42–110	1.6
	F	7	77	57–97	79	54–104	10	7–13	1.8

**Table 2.** Candidate models for annual 100% minimum convex polygon (MCP) home ranges for radiotracked eastern indigo snakes ( $n=32$ ), 2003–2004, Georgia. Models are listed in order of corrected Akaike's Information Criterion ( $AIC_c$ ), with number of parameters ( $K$ ), difference in  $AIC_c$  ( $\Delta AIC_c$ ), model likelihood, and Akaike weights ( $\omega_i$ ) for the set of candidate models ( $i$ ).

Model <sup>a</sup>	$K$	$AIC_c$	$\Delta AIC_c$	Model likelihood	$\omega_i$
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 $\times$ size	6	121.40	6.80	0.03	0.027
Sex, size, site, locations, sex $\times$ 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

<sup>a</sup> Model parameters: sex (being female), size (snout-vent length), site (overwintering location on Fort Stewart vs. private lands), locations (number of telemetry locations), and size (standardized; snout-vent length standardized by sex).

support included sex, size, and overwintering site ( $\omega = 0.824$ ) and was 6.2 times more likely than the next best approximating model, which contained sex and size ( $\omega = 0.132$ ). Parameter estimates were similar between the 2 models, suggesting smaller home ranges for females, for smaller individuals, and for individuals overwintering on Fort Stewart (Table 3). Results were similar for 95% KD annual home ranges and 50% KD activity centers. Sex ranked as the most influential factor modeled, according to Akaike importance weights, for all annual home range estimates; size ranked second and site ranked third (Table 4).

Seasonal home range size varied annually ( $F_{7,109} = 49.8$ ,  $P < 0.001$ ) and by sex ( $F_{1,30} = 34.8$ ,  $P < 0.001$ ), with no interaction ( $F_{7,109} = 0.24$ ,  $P = 0.97$ ; repeated measures ANOVA). In the winter, home ranges were smallest and most similar in size for males and females (Fig. 1).

### Patterns of Movement

All snakes tracked  $\geq 9$  months returned to sandhills used the previous fall and winter. Individual degrees of fidelity to specific shelters used by each snake varied; however, all snakes tracked in fall and winter 2003–2004 and 2004–2005 returned to a minimum of 4 different underground shelters that they had specifically used the preceding fall and winter.

Several large-ranging males ( $n = 3$ ) traveled 5–8 km linear distance from winter to summer locations. One of these males used the same travel corridor (approx. 2 km) for 2 consecutive years, despite about 75% of the corridor having been clearcut in the intervening winter. Although we recorded 6 individuals  $< 100$  m from paved roads, no snake locations were outside boundaries created by paved roads. During the study, however, 2 indigo snakes not included in the telemetry study were found dead on these roads. Radiotracked snakes, however, crossed unpaved roads and trails regularly on Fort Stewart and private lands.

Average daily distance moved (Fig. 2), averaged biweekly, varied by sex ( $F_{1,30} = 14.7$ ,  $P < 0.001$ ) 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). Winter movements were smaller than other seasons, with no difference between sexes ( $t_{84} = 0.1$ ,  $P = 0.91$ ). Average frequency of biweekly movement also varied by sex ( $F_{1,30} = 4.6$ ,  $P = 0.04$ ) and season ( $F_{3,81} = 65.8$ ,  $P < 0.001$ ) with an interaction effect ( $F_{3,81} = 5.9$ ,  $P \leq 0.001$ ). Males moved more often than females in all seasons (Fig. 2). Least squares estimates of differences in movement frequency indicated similar movement patterns in fall and spring for females

**Table 3.** Estimates of fixed and random effects for the 90% confidence set of models examining minimum convex polygon (MCP) home ranges of radiotracked eastern indigo snakes ( $n = 32$ ), 2003–2004, Georgia. Data suggest a negative effect of being female and a positive effect of body size on home range size.

Model <sup>a</sup>	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
Sex, size	Fixed	Sex	-1.050	-1.510	-0.591
		Size	0.024	0.011	0.036
		Intercept	2.220	0.393	4.048
	Random	Residual	0.276	0.179	0.482
		Year (repeated)	0.657	0.371	0.944

<sup>a</sup> Model parameters: sex (being female), size (snout-vent length), and site (overwintering location on Fort Stewart vs. private lands).

**Table 4.** Influence of sex and size on variation of intraspecific home range size in eastern indigo snakes radiotracked ( $n = 32$ ) in Georgia, 2003–2004. Data 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 activity areas.

Parameters <sup>a</sup>	Candidate models	Importance weights		
		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 × sex	2	0.04	0.19	0.12
Locations	2	0.02	—	—
Size (standardized)	2	0.00	0.00	0.00

<sup>a</sup> Model parameters: sex (being female), size (snout-vent length), site (overwintering location on Fort Stewart vs. private lands), locations (number of telemetry locations), and size (standardized; snout-vent length standardized by sex).

( $t_{1,81} = 0.8$ ,  $P = 0.44$ ), but not for males ( $t_{1,81} = 3.3$ ,  $P = 0.003$ ). We recorded more frequent movements in summer compared to other seasons. Snakes moved least often in winter with no difference between sexes ( $t_{1,81} = 0.5$ ,  $P = 0.60$ ; Fig. 2).

### Habitat Use

Average use of GAP land cover types across the study site (average proportion within home ranges [proportion available across study sites]) were 0.01 (0.02) road-urban, 0.26 (0.24) wetlands, 0.05 (0.07) fields, 0.08 (0.07) sparse, 0.02 (0.03) deciduous forest, 0.49 (0.51) evergreen, and 0.09 (0.06) mixed. Compositional analysis indicated nonrandom use of habitat at both levels of selection examined (home range selection:  $\lambda = 0.212$ ,  $P < 0.001$ ; site selection:  $\lambda = 0.324$ ,  $P = 0.01$ ). Use of habitats in home range selection ranked in descending order was wetland, evergreen, mixed, field, sparse, road-urban, and deciduous. Selection differed between the 5 most selected habitats and the 2 least selected habitats. Habitat use rankings for site selection analysis, from

most to least selected included evergreen, wetland, mixed, sparse, field, deciduous, and roads. Selection of the top 4 land cover types was significantly different from the last 3 habitats (Table 5).

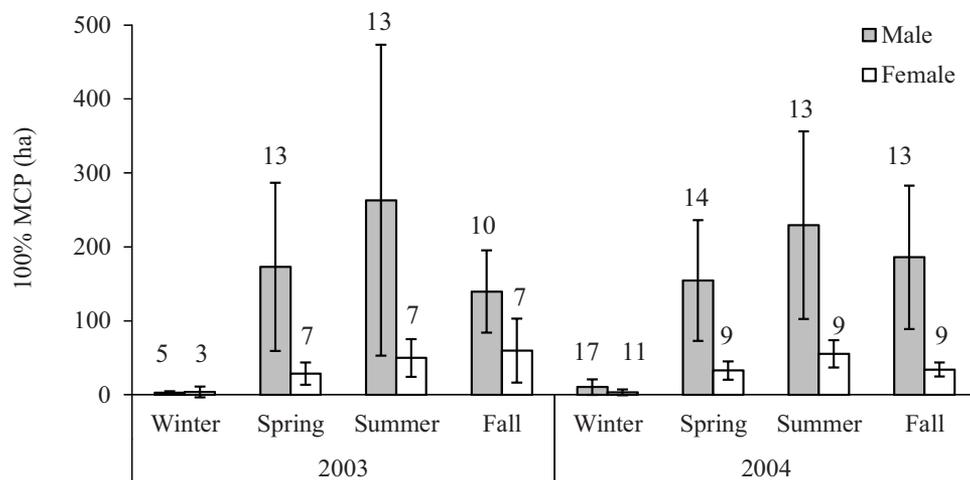
Habitat use varied seasonally for in-field habitat types (Fig. 3). In winter, snakes restricted their habitat use primarily to sandhills with gopher tortoise burrows (sandhill). About 67% of all locations in winter were in sandhills and 22% occurred in young, upland pine plantations with gopher tortoise burrows (pine plantation). Snakes exhibited less concentration in use of sandhill habitats in spring, summer, and fall than during winter; however, snakes continued to use sandhill habitats throughout the warm months ranging from 35% to 58% of locations depending on the season (Fig. 3). Use of wetlands in summer ( $\bar{x} = 30\%$ , 95% CI = 0.23–0.36) was greater than recorded in any other season and was concentrated primarily in bottomland hardwood areas between sandhills and other upland habitat types.

Use of in-field habitat categories also varied within each season (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 male and female habitat use detected, but with a sex × season interaction effect in spring ( $F_6 = 3.09$ ,  $P = 0.006$ ). Tukey–Kramer post hoc tests of habitat use in spring indicated that females used sandhills more than males ( $P = 0.04$ ), with no other seasonal differences in habitat use between sexes.

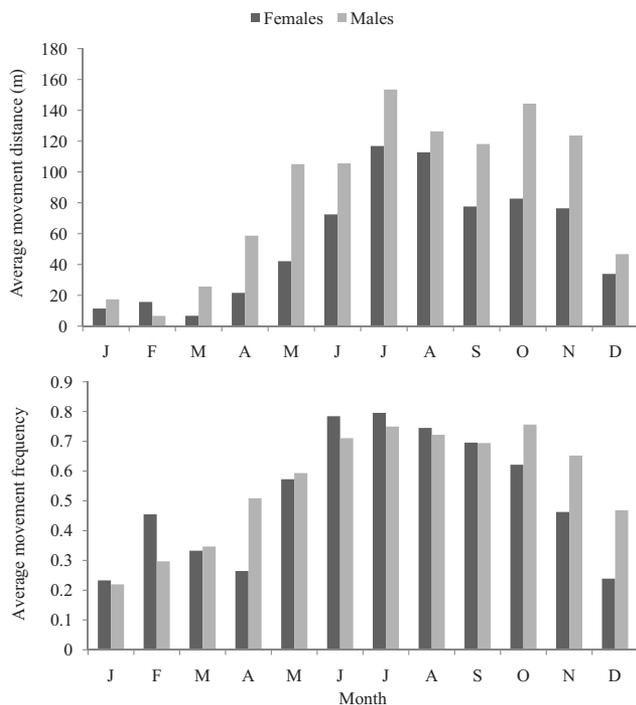
## DISCUSSION

### Home Range

Results of bootstrap analyses and modeling suggest our telemetry efforts were sufficient to describe home ranges and indicated that individuals maintained definable annual home ranges. The male indigo snake home ranges (140–1,528 ha) reported herein may represent the largest reported for an indigenous terrestrial North American snake species



**Figure 1.** Seasonal and sex differences in 100% minimum convex polygon (MCP) home ranges ( $\bar{x}$ , 95% CI) for male (gray bars) and female (white bars) eastern indigo snakes radiotracked for complete seasons, 2003–2004, Georgia. Values represent sample size for each estimate. Males, outside of winter, had seasonal home ranges approximately 4.5 times larger than females.



**Figure 2.** Seasonal and sex differences in daily movement distance (top) and average movement frequency (bottom) consistent with seasonal home range patterns. We calculated values biweekly for radiotracked male (black) and female (gray) eastern indigo snakes ( $n = 32$  total), 2003–2004, Georgia. Individual animals were retained as the sampling unit for calculations.

(Macartney et al. 1988, Reinert and Zappalorti 1988, Dodd and Barichivich 2007, Kapfer et al. 2008, Waldron et al. 2008). In a review of the genus *Pituophis* (pine and bullsnakes), Kapfer et al. (2008) reported male home range sizes averaged 79 ha (MCP). Eastern coachwhips (*Masticophis flagellum flagellum*), another large North American snake

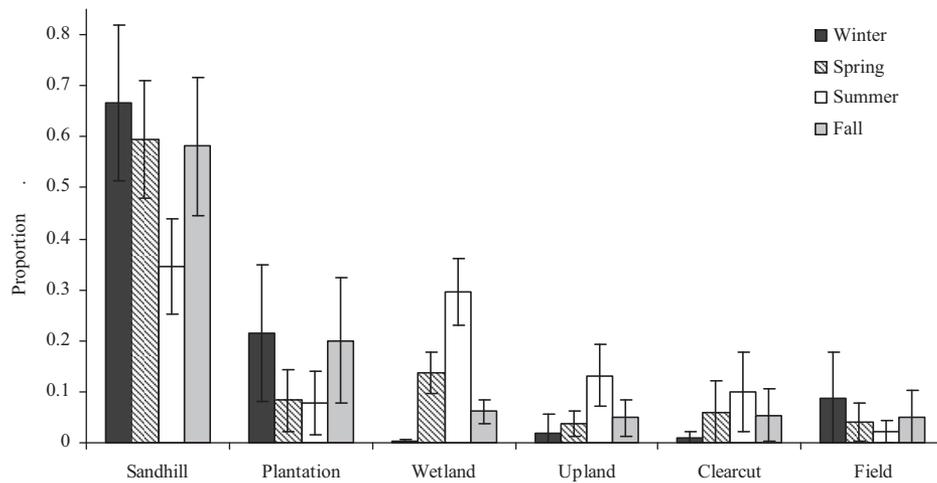
species, have reported MCP home ranges of <1 ha to 183 ha ( $n = 4$ ; Dodd and Barichivich 2007). The eastern diamondback rattlesnake (*Crotalus adamanteus*), another large species, has home ranges reported between 28 ha and >80 ha (see Waldron et al. 2008 for review). Home ranges (MCP) of male timber rattlesnakes (*Crotalus horridus*) are reported averaging around 112 ha (Macartney et al. 1988, Reinert and Zappalorti 1988).

Previous studies of eastern indigo snakes in northern portions of the range reported individual home range sizes of 5–230 ha (Speake et al. 1978, Smith 1987, Speake 1993); however, these results included data from translocated and captive-reared individuals, making comparisons to our results problematic. In central and coastal peninsular Florida, cumulative home ranges (100% MCP), for periods between 10 months and over 2 years, were 39–583 ha for radiotracked male indigo snakes ( $\bar{x} = 202$ ,  $n = 23$ ) and 13–313 ha for females ( $\bar{x} = 76$ ,  $n = 21$ ; Breininger et al. 2011). In northern peninsular Florida, annual home ranges for males ( $n = 4$ ) averaged 141 ha (32–281 ha; Moler 1985) and 185 ha for 1 male tracked for 322 days (Dodd and Barichivich 2007).

Models evaluating potential sources of variation for home range area suggested a strong relationship with sex (females have smaller home ranges on average) and a slight positive effect of increasing body size (larger snakes have larger home ranges on average). Although indigo snakes are male-biased sexually size dimorphic, the snakes in our sample exhibited considerable overlap in body size between larger adult females and smaller adult males. Reproductive condition and associated behaviors may account for some differences in home range size between sexes, especially in the spring when females remained on sandhill habitats where they overwintered, whereas males dispersed into a variety of habitats, including wetlands. Size standardized by sex had no predictive power in our models, further suggesting that

**Table 5.** Differential use of habitats compared to availability within the study site and within individual home ranges for radiotracked eastern indigo snakes ( $n = 27$ ), 2003–2004, Georgia. Data present the log-ratio matrix of differences in use between GAP land cover types calculated as the log of the ratio between the relative use of habitat types for home range selection (comparison of habitat within individual home ranges to habitat available at the study site) and site selection (comparison of habitat at radiolocations to habitat available within individual home ranges). Positive values indicate the habitat in the column was used relatively more than habitat in the row; negative values indicate less use. An asterisk denotes deviation from random at  $P < 0.05$ . Rank 1 represents the most used relative to available habitat to the study animals when comparing relative use to availability; rank 7 represents the least.

Rank	Road-urban		Wetland		Field		Sparse		Deciduous		Evergreen	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Home range selection												
Road-urban	6											
Wetland	1	-1.13*	0.30									
Field	3	-0.01	0.46	0.71	0.45							
Sparse	3	-0.64	0.43	0.72	0.40	-0.66	0.51					
Deciduous	7	0.14	0.61	1.10*	0.38	0.74	0.51	0.38	0.47			
Evergreen	2	-1.17*	0.26	0.05	0.14	-0.92	0.47	-0.67	0.34	-1.05	0.44	
Mixed	3	-0.49	0.56	0.51	0.32	0.16	0.43	-0.22	0.48	-0.59*	0.26	0.46 0.38
Site selection												
Road-urban	7											
Wetland	2	-1.51*	0.38									
Field	5	-0.45	0.69	1.22*	0.51							
Sparse	4	-1.03	0.60	0.31*	0.51	-1.06	0.78					
Deciduous	6	-0.31	0.72	1.25	0.49	0.05	0.78	0.94	0.71			
Evergreen	1	-1.47*	0.41	-0.04	0.17	-1.05*	0.52	-0.35	0.51	-1.29*	0.48	
Mixed	3	-1.12	0.59	0.02	0.43	-0.48	0.75	-0.29	0.56	-1.23	0.67	0.06 0.40



**Figure 3.** Proportionally high use of sandhill habitats annually and wetland habitats in summer ( $\bar{x}$ , 95% CI) for eastern indigo snakes radiotracked in 2003–2004, Georgia ( $n_{\text{winter}} = 31$ ,  $n_{\text{spring}} = 32$ ,  $n_{\text{summer}} = 28$ ,  $n_{\text{fall}} = 28$ ). Habitat types recorded at radiolocations: sandhill (pine-oak xeric uplands with longleaf pine canopy and gopher tortoise burrows), pine plantation (included windrows), wetlands, miscellaneous uplands (xeric uplands with mixed canopy composition), clearcut, and field (old-fields, maintained hay fields, food plots). Individual animals were the sampling unit for calculations.

intersexual differences, rather than differential resource needs for larger individuals, affected home range size variation between sexes.

Analyses also indicated an increase in home range size with indigo snakes overwintering on private lands (MCP models) or with an increasing proportion of locations on private lands (KD models). Our results suggest a possible effect of habitat type and land use on home range size indicating that although necessary resources were likely available on private lands, they may have existed in lower densities than those at Fort Stewart. Confidence intervals for the site variable, however, spanned 0 in all models, lending uncertainty regarding its influence (Table 3). The site variable was not ranked as high in models for 50% KD cores of activity as with 95% KD and MCP models (Table 4). Cores of activity (50% KD) were primarily located around individual overwintering areas, which indicated little influence of site on the size of cores of activity and overwintering areas.

Consistent effects for body size on home range size have not been established inter- or intra-specifically in snakes (Gregory et al. 1987, Macartney et al. 1988). Large home range sizes such as those observed in this study, however, may represent the needs of a large terrestrial predator, which on average, requires more food and area to forage than a smaller species (McNab 1963) or potentially better quality habitat with greater density of prey available. If these large home ranges were an artifact of snakes seeking new overwintering and breeding areas (i.e., emigration), we would expect that a proportion of snakes would not return to the overwintering area used the previous year. All snakes tracked in our study returned to the same area used the previous winter, a pattern observed during 3 winters of telemetry. A mark–recapture study at Fort Stewart, however, documented occasional use of multiple overwintering sites between years by at least 4 of 63 marked male snakes (Stevenson et al. 2009).

If intraspecific competition influenced home range sizes in this study, we would expect to see some avoidance between

individuals, at least during the non-breeding period. All snake home ranges, however, overlapped those of multiple other snakes ( $n \geq 6$ ) both temporally and spatially, and the 2 largest home ranges (both males) occurred in close proximity to and overlapped each other in both summer and winter. Home ranges in other snake species that have been shown to vary by sex have been attributed to differential energetic needs and reproductive condition (Gregory et al. 1987, Whitaker and Shine 2003). Eastern indigo snakes are active foragers; we recorded approximately 84% of foraging observations ( $n = 65$  observations) in spring and summer (also see Stevenson et al. 2010 for review), when snakes exhibited much larger and more frequent movements than in cooler months. Approximately 65% of observations of foraging or prey consumption behavior were in wetlands and 20% in sandhills. Therefore, in addition to effects of sex and body size, availability of prey resources likely influences indigo snake home ranges at least in warmer months.

Indigo snakes maintained their smallest home ranges in winter, intermediate-sized in spring and fall, and largest in summer. Previous radiotelemetry of indigo snakes in Georgia reported the smallest home ranges from December to April ( $\bar{x} = 4.8$  ha,  $n = 8$ ), intermediate-sized from May to July ( $\bar{x} = 42.9$  ha,  $n = 9$ ), and largest from August to November ( $\bar{x} = 97.4$  ha,  $n = 4$ ; Speake et al. 1978). The annual trend is similar in both studies, although direct comparisons are not possible because some translocated snakes were used and seasons were designated differently in the previous study.

### Patterns of Movement

Patterns of movement were consistent with home range data, reflecting seasonality in movements and differences between sexes. Many snake species exhibit larger and more frequent movements during the breeding season (e.g., Gibbons and Dorcas 2004); however, snakes in this study exhibited the opposite pattern. In our study population, breeding occurs when adult snakes congregate on xeric sandhills during or

just prior to the coldest months of the year when movements are greatly reduced compared to other seasons (Fig. 3). Seasonally, we found fewer differences in movement frequency between males and females outside of spring than for movement distances, suggesting similar vagility throughout much of the year, but at a reduced spatial scale for females.

Indigo snakes radiotracked in this study followed 2 general movement patterns. All females and approximately half the males maintained associations with their overwintering sandhill sites throughout the year, despite greater use of non-sandhill habitats in warmer seasons. Males with the largest home ranges in this study made directional movements of between 1,500 m and 7,500 m in late spring and did not return to their respective overwintering sandhills until mid-fall ( $n = 6$ ). We considered both of these movement patterns home ranges because of return to overwintering sandhills and asymptotic results from bootstrapping analyses (Burt 1943).

### Habitat Use

Our data from southeastern Georgia indicate that eastern indigo snakes exhibit specific affinities for open-canopied sandhill habitats supporting gopher tortoise populations in the winter and for lowlands including expansive wetlands in the warmer months. Habitat use analyses conducted on GAP land cover categories indicated that wetlands, sparse, mixed, and evergreen forests were used at greater rates than expected relative to their availability at both spatial scales examined. Assessment of sparse areas used by snakes revealed some use of clearcut sites (e.g., former mesic pine flatwoods) for males in warmer months, but most areas were predominantly comprised of young longleaf pine plantations supporting gopher tortoise populations, especially in winter.

Of the habitat types recorded in the field, sandhills were used more than any other habitat for both males and females in all seasons, except for summer when wetland and sandhill use was comparable. Winter included breeding activities on upland habitats, extended periods of inactivity, and use of tortoise burrows during cold temperatures (Hyslop et al. 2009a). During spring, males began dispersing from sandhills to surrounding habitats, including wetlands, clearcuts, and other upland habitats. Females remained on sandhill habitats until late spring and early summer when oviposition is completed (Speake et al. 1987). In spring 2004, ultrasound and/or radiographs on 9 of 10 females in the study at that time showed signs of initial egg formation (Hyslop et al. 2009b), supporting our prediction that greater use of open habitats by females was associated with thermoregulatory requirements during gestation. Similar patterns of movement have been reported of earlier male dispersal from overwintering locations compared to females (Parker and Brown 1980, Shine 2003); however, few studies have been conducted on temperate species, such as the eastern indigo snake, that are frequently surface-active throughout cooler seasons.

Both Fort Stewart and private land sites had extensive bottomland hardwood habitats that were used extensively by snakes. Other wetlands used, although to a lesser extent, included cypress domes embedded in large clearcuts, which

were mesic pine flatwoods prior to timber harvesting and contained bedding for new plantings. Approximately 65% of observations of foraging behavior or prey consumption were in wetland habitats. During summer, males and females depended less on sandhill habitats, but continued to use these habitats and tortoise burrows for shelter during ecdysis and often following foraging (Hyslop et al. 2009a). In fall, habitat use was transitional between summer and winter use, as snakes began to return to overwintering sandhills.

Ecosystem approaches to management often focus on a few key species that may serve as indicators of ecosystem integrity (Lambeck 1997, Roberge and Angelstam 2004). Wildlife management for nongame species on many public lands in the southeastern United States with longleaf pine habitats has often focused on red-cockaded woodpecker (*Picoides borealis*) and gopher tortoise populations (Fort Stewart 2001, USFWS 2008). These activities often include maintaining a low basal area of trees, sparse canopy cover, low midstory cover, native groundcover vegetation, and prescribed fire (Brockway et al. 2005, FFWCC 2007). Although these management strategies are likely to benefit indigo snakes, if the habitat complementation needs (Dunning et al. 1992, Pope et al. 2000) of indigo snakes are not considered (such as adjacent wetlands), then current management strategies and land acquisition plans may be inadequate for indigos and other snake species (Steen et al. 2012).

## MANAGEMENT IMPLICATIONS

Habitat loss, fragmentation, and degradation remain primary threats to indigo snake populations (USFWS 2008). This study adds to our understanding of the space use and potential habitat requirements of the species. First, indigo snakes may require more land than previously recommended. Although land area requirements were not directly addressed, a recent review of the status of the species (USFWS 2008) noted a reserve size of 4,046 ha as likely beneficial for indigo snakes, whereas others have recommended multiple 1,000-ha tracts of land for conservation of the species in Florida (Moler 1992). The collective extent of the radiolocations for the 32 snakes in this study spanned an area of 8,000 ha (MCP of all locations) to 14,000 ha (rectangular area). Second, longleaf pine-wiregrass habitats exist as a natural mosaic of upland and lowland areas that require frequent, low to moderate intensity fire to maintain biological diversity (Mushinsky and McCoy 1985, Van Lear et al. 2005). Because development and agriculture has eliminated natural habitats between sandhills, islands of remnant habitat within an unsuitable matrix may have little to no connectivity (McCoy and Mushinsky 1999). Movement patterns and habitat use in this study support variable permeability of these matrix types to indigo snake movement, implicating that patch connectivity may be as important as habitat patch size for population persistence. Thus, habitat fragmentation, roads, and land development, even at low densities, may exacerbate impacts of habitat loss on indigo snakes because of their use of multiple habitats, large home ranges, and seasonal movements within those ranges (Breininger et al. 2012). Given our results, we propose

that the inclusion of eastern indigo snakes into biodiversity management and conservation in the southeastern Coastal Plain would benefit a broad range of species (Grumbine 1994, Noss 2000).

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