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EASTERN INDIGO SNAKE (*DRYMARCHON COUPERI*) SHELTER SITE USE IN PENINSULAR FLORIDA, USA, AND IMPLICATIONS FOR HABITAT CONSERVATION

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Abstract.—**Shelters are critical for many species as protection from predators and extreme temperatures. Successful conservation of reptiles requires understanding both shelter site requirements and availability. The Eastern Indigo Snake (EIS; *Drymarchon couperi*) is endemic to the southeastern U.S. and is federally listed. Recovery has focused on maximizing unfragmented landscapes, with less attention on fine-scale features such as shelter sites. In the northern EIS range, Gopher Tortoise (*Gopherus polyphemus*) burrows are used extensively for shelter. Although EIS in peninsular Florida often shelter in tortoise burrows, they also use other shelters where tortoise burrows are scarce or absent. Solely focusing EIS survey and management efforts where Gopher Tortoises are present may overlook occupied habitats and misallocate resources. We investigated the importance of different shelter sites in central Florida using data from radio-tracked EIS. We modeled the use of shelter categories as a function of sex, season, and habitat using Bayesian multinomial Generalized Linear Models. Results showed that EIS in peninsular Florida used Gopher Tortoise burrows across all seasons and habitats. Tortoise burrow use was highest in xeric habitats and lowest in mesic habitats where burrows are most and least abundant, respectively. There was less variability in shelter site use in disturbed habitats and flatwoods. Tortoise burrow use by EIS in the cool season across sexes and habitats in our study was much lower than in southern Georgia. Our results indicate that EIS are less dependent on Gopher Tortoise burrows in peninsular Florida and that suitable habitats with few or no tortoise burrows could still provide conservation value for EIS.**

Key Words.—Bayesian hierarchical modeling; burrows; Gopher Tortoise; *Gopherus polyphemus*; habitat; multinomial Logistic Regression; season

INTRODUCTION

Shelter sites are critical habitat features for many herpetofauna, providing protection from predators and extreme temperatures (Webb and Shine 1998; Beck and Jennings 2003; Pike and Mitchell 2013). As ectotherms, reptile body temperatures are strongly influenced by the external environment and shelter sites play an important role in reptile thermoregulation (Huey et al. 1989; Peterson et al. 1993). Subterranean hibernacula provide shelter from cold in temperate climates (Gregory 1982) and may reduce overheating and desiccation risk in hot, dry climates (Beck and Jennings 2003). The availability of sufficiently large and thermally suitable shelter sites may be particularly important for some reptiles. For example, many rattlesnake species need sizeable, thermally stable rocks under which gravid females can hide and maintain a constant body temperature to facilitate gestation (Graves and Duvall 1993; Peterson et al. 1993). The physical characteristics of a shelter are important in determining the thermal suitability of a site (Huey et al. 1989; Croak et al. 2013) and physically suitable sites may be limited in some environments. Successful conservation efforts for reptiles require an understanding both of shelter site requirements and the spatiotemporal availability of those sites.

The Eastern Indigo Snake (EIS; *Drymarchon couperi*) is the longest native snake in North America (> 2 m long and > 3 kg) and is endemic to the southeastern Coastal Plain of the USA (Enge et al. 2013; U.S. Fish and

Wildlife Service [USFWS] 2019). This terrestrial and diurnal species has a diverse diet and actively forages (Stevenson et al. 2010). EIS are capable of moving >1 km per day and have some of the largest home ranges reported for terrestrial snakes (Breininger et al. 2011; Hyslop et al. 2014; Bauder et al. 2016). The EIS is listed as Threatened under the U.S. Endangered Species Act due in large part to habitat loss, degradation, and fragmentation (Breininger et al. 2004, 2012; USFWS 2019). Identifying areas capable of supporting viable EIS populations both within and beyond the bounds of existing conservation lands is widely recognized as critical to EIS persistence and recovery (USFWS 2019). Although most previous effort identifying important EIS habitat has focused on maximizing the area of relatively undisturbed natural landscapes (USFWS 2019; Bauder et al. 2022), less attention has focused on identifying important fine-scale habitat features such as shelter sites.

Previous research has identified marked latitudinal variation in EIS habitat and behavioral ecology despite its relatively restricted geographical range of approximately 875 km from north to south (Enge et al. 2013). Within the northern part of its distribution (southern Georgia and northern Florida), EIS are closely associated with the Longleaf Pine (*Pinus palustris*) ecosystem (Speake et al. 1978; Enge et al. 2013; Hyslop et al. 2014; Bauder et al. 2017). Within that ecosystem, patches of relatively open sandhills with well-drained xeric soils supporting Gopher Tortoise (*Gopherus polyphemus*) burrows are used by EIS as overwintering sites (Speake et al. 1987; Stevenson et al. 2003; Hyslop et al. 2014; Bauder et al. 2017). Additionally, female EIS often use tortoise burrows for nesting (Stevenson et al. 2021), potentially increasing female EIS use of tortoise burrows during the nesting season. Gopher Tortoise burrows vary greatly in length (1.5–16.7 m) and depth (0.6–4.4 m), depending on soil characteristics and depth to the water table (Ashton and Ashton 2008; Castellón and Rothermel 2012; Kinlaw and Grasmueck 2012). EIS in the northern regions almost exclusively use tortoise burrows for shelter sites during the winter (Hyslop et al. 2009a) and these burrows provide the warmest available thermal environment during cold winter nights (DeGregorio et al. 2012; unpubl. data). The close association of EIS with the longleaf pine ecosystem and Gopher Tortoises often results in conservation and management efforts being primarily focused on tortoises and their burrows because of the direct benefits to EIS. In addition, sandhill is a relatively discrete and identifiable community type upon which to focus management efforts. During the spring and fall, EIS in the northern regions will use varied habitats and shelter sites, migrating up to 7.5 km away from sandhills (Hyslop et al. 2014; unpubl. data).

In contrast, EIS in peninsular Florida use a much greater diversity of habitats throughout the year, including virtually every natural vegetation community, as well as many anthropogenic habitats such as cattle pastures, canal banks, and rural and urban development (Steiner et al. 1983; Moler 1985; Breininger et al. 2011; Bauder et al. 2018; Metcalf et al. 2021). Although EIS in peninsular Florida will often use tortoise burrows (Layne and Steiner 1996; Bauder et al. 2016), they also occur in habitats where tortoise burrows are scarce or absent and can use mammal burrows, stump holes and root channels, and even crab holes as shelter sites (Moler 1985; Jackson 2013). Therefore, focusing EIS survey and management efforts within peninsular Florida on areas where Gopher Tortoises are present may result in overlooking other habitats potentially occupied by EIS. To avoid misallocating scarce conservation resources, it is important to understand the association more fully between EIS and Gopher Tortoises within peninsular Florida.

Our objective was to investigate the use and relative importance of different shelter sites for EIS in central Florida across seasons and habitats. We hypothesized that, given the more generalist habitat use patterns of EIS in peninsular Florida, EIS use of tortoise burrows will differ between Florida and Georgia. We predicted that EIS in our study would use tortoise burrows less frequently than EIS in southern Georgia (Hyslop et al. 2009a). We also predicted that tortoise burrows would not be used preferentially and that there would be little difference in types of shelter sites used across seasons and habitats. Finally, we hypothesized that tortoise burrows offer a more thermally stable and protected microhabitat for gestation and egg laying, and we predicted that female use of tortoise burrows would be highest during the winter and spring reproductive season.

MATERIALS AND METHODS

***Study site*.**—We included data in this analysis from two studies in central Florida, USA (Fig. 1): 1998–2002 in Brevard County (hereafter Brevard Study), located on the east coast (28.26N, 80.72W); and 2011–2013 in Highlands County (hereafter Highlands Study), located on the Lake Wales Ridge in the interior of the peninsula (27.34N, 81.34W). Within each area there are diverse natural and anthropogenic habitat types, including sandhill, scrub, flatwoods, hammock, wetlands, coastal scrub, cattle pasture, citrus, and a range of rural and urban land uses (Breininger et al. 2011; Bauder et al. 2016). Additional detailed descriptions of the natural communities found within our study areas are provided in Abrahamson et al. (1984) and Myers and Ewel (1990).

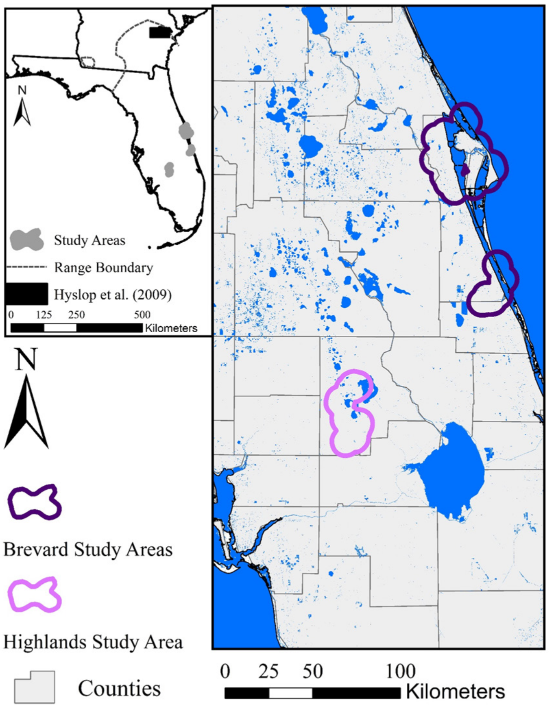

Figure 1. Study sites included in the analysis of Eastern Indigo Snake (*Drymarchon couperi*) shelter site use in central Florida, USA. The smaller map also shows the approximate contemporary distribution of the Eastern Indigo Snake and the study area from Hyslop et al. (2009a,b) in southern Georgia, USA.

Data collection.—We captured adult EIS opportunistically by hand and they were surgically implanted with very high frequency (VHF) radio transmitters (models SB-2 and SI-2T; Holohil Systems, Ltd., Carp, Ontario, Canada) by a veterinarian (Reinert and Cundall 1982; Hyslop et al. 2009b). We replaced transmitters on select individuals to extend tracking duration. We typically tracked Brevard snakes at least once per week and Highlands snakes approximately every 2 d. Although our tracking frequency was less than daily, the relatively long duration of our studies and balanced sex ratio of transmittered snakes permitted a comprehensive sample of shelter site use. More detailed descriptions of the radio telemetry procedures are in Breininger et al. (2011) and Bauder and Barnhart (2014).

We considered a snake as using a shelter site when it was radio tracked to a specific location underground or if it was under a pile of brush or debris (but potentially above ground). We recorded data in one of three categories: (1) tortoise burrow (including active, inactive, abandoned, and undetermined status burrows; Auffenberg and Franz 1982); (2) debris (including woody debris, man-made debris, and brush pile); and (3) other hole (including mammal holes and root holes). For analysis, we combined all tortoise burrow types because of possible inconsistencies among observers in classifying burrow activity status. We described the vegetation community in the immediate vicinity of the shelter site as disturbed (including Citrus Grove, Residential, Disturbed, Ruderal, and Urban), marsh (Freshwater Marsh and Saltwater Marsh), Hammock, Pine Flatwoods, or scrub (Scrub and Scrubby Flatwoods). The habitat types were aggregated to account for the variation in classification between observers and differences in habitat descriptions between studies. Because we lacked ground-based habitat records for 734 of the 3,046 shelter sites from the Highlands Study observations (24%), we also used land cover data from a Geographic Information System (GIS) to characterize the habitat surrounding every shelter site in both study areas. We used the Cooperative Land Cover (CLC) Map v. 3.0 from Bauder et al. (2018) for all protected areas and within the Highlands Study area, and land cover data from regional Florida Water Management Districts (WMD) for all remaining areas (https://data-floridaswater.opendata.arcgis.com/search?groupIds=5abc29185336421990c247662271845f.; https://www.floridagio.gov/datasets/sfwmd::sfwmd-land-cover-land-use-2004-2005/about; https://data-swfwmd.opendata.arcgis.com/datasets/2004-land-use-land-cover-1/explore?location=28.155650%2C-82.062250%2C8.51). We reclassified WMD land cover classes into the CLC classification system following Knight (2010) and resampled all rasters to 15-m pixel rasters. We assigned each telemetry observation the majority land cover classification within a 60-m radius around each point using the raster package (Hijmans 2021) in R (v. 4.1.0; R Development Core Team 2021). We then reclassified the GIS-based habitats into eight broader classes: (1) disturbed (e.g., Citrus, Agriculture, Rural, Urban, Spoil); (2) flatwoods (e.g., Flatwoods, Upland Forest, Coastal Vegetation); (3) Scrubby Flatwoods; (4) scrub (e.g., Scrub, Sandhill); (5) Improved Pasture; (6) Unimproved Pasture; (7) Forested Wetland; and (8) Non-forested Wetland.

***Data analysis*.**—We modeled the proportional use of our different shelter site categories using multinomial Generalized Linear Models (GLM), which allow for multiple discrete response categories. We set Gopher Tortoise burrow as the reference category in all analyses so that covariate effects could be interpreted as change in shelter site use relative to tortoise burrows. We then used a multinomial logit link to model probability of using debris or other holes as a function of covariates while ensuring that all probabilities for a given observation summed to one (i.e., $p_3 = 1 - p_1 - p_2$; Kéry and Royle 2021). Covariates included sex, season, and shelter habitat. Seasons were defined as spring (March-May), summer (June-August), fall (September-November), and winter (December-February).

We fit Bayesian multinomial GLMs using JAGS (v. 4.3.0; http://mcmc-jags.sourceforge.net/) called from R (v. 4.1.0, R Development Core Team 2021) through the package jagsUI (v. 1.5.2, Kellner 2021). We then modeled our response using a categorical distribution (i.e., data catalog vocabulary or dcat). We specified independent random intercepts by snake for each response variable. We used Uniform (0, 10) priors for random effects variances. We fit models containing additive effects of each covariate (sex, season, and habitat) and excluded observations with missing ground or GIS-based habitat covariates.

We used indicator variable model selection to calculate posterior inclusion probabilities and evaluate covariate importance (Kuo and Mallick 1998; Royle and Dorazio 2008). Specifically, during each posterior draw, each coefficient from each linear predictor (*b*) was multiplied by a binary indicator variable (*w*) that was drawn from a Bernoulli prior with 0.50 probability:

$$\beta_i = b_i \times w_b,\ w \sim \text{Bernoulli}\ (0.50)$$

The mean of each indicator variable (w_b) is the posterior inclusion probability. We excluded intercepts and coefficients in the linear predictor for the reference category from variable selection. We report the means and 95% highest posterior density intervals (HPDI) from the posteriors of model-averaged coefficients (β). We maintained constant prior uncertainty, as recommended by Link and Barker (2006), by giving the prior for each *b* a constant variance (τ_{Model}) scaled to *V*/*K* where *K* is the number of fixed effects in the model and *V* was drawn from a gamma distribution with shape = 3.29 and scale = 7.80. Each coefficient (*b*) was given the prior Gaussian$(0, (1/\tau_{\text{Model}})^{1/2})$. Finally, we calculated the predicted probability of use for each response level and covariate combination.

We fitted a post-hoc model to test the hypothesis that females would show greater use of tortoise burrows than males during the winter and spring reproduction season. We reclassified our categorical covariates to estimate interactive effects between sex, season, and habitat for xeric (e.g., Scrub, Scrubby Flatwoods, Unimproved Pasture) and mesic (e.g., Hammock, Wetland) habitats. We fitted models using 50,000 adaptive iterations and 50,000 burn-in iterations followed by 125,000 iterations where every 25th posterior draw across three parallel chains was retained. We examined trace plots and we confirmed appropriate levels of mixing. Gelman-Rubin statistics ($\hat{R}$) were ≤ 1.02 for parameters except one posterior inclusion probability ($\hat{R}$) = 1.189 for the full sex, season, and habitat model (Brooks and Gelman 1998; Gelman and Hill 2006).

RESULTS

We tracked 102 snakes a median of 268 d (range, 1–1,149), resulting in a median of 18 shelter site observations per snake (range, 1–169). The median percentage of shelter types used by all EIS was 38%, 25%, and 25% for tortoise burrows, other holes, and debris, respectively (range, 0–100%). The median percentage of shelter types used by EIS having at least 30 locations (n = 35 snakes tracked for 114–982 d) was 50% for tortoise burrows (range, 0–86%), 26.5% for other holes (range 7.4–80.0%), and 17.5% for debris (range 0–83.9%). Considering only the Highlands Study EIS (median of 53 locations per snake; range, 19–169), the median tortoise burrow use was 54% (range, 9.5–86.4%). We never observed 12 males and 12 females, all from the Brevard Study, using a tortoise burrow. These 24 snakes had a median of seven tracking locations (range, 1–30 locations) over a median of 185 d (range, 1–959 d) collectively spanning every month of the year. Three of these 24 snakes had locations in at least 10 mo of the year. Within the 248 telemetry observations of these 24 snakes, 44% were in other holes, 21% in brush pile, 21% in human-made debris, and 15% in woody debris. Across sexes and habitats at both sites, mean tortoise burrow use was 0.43 (95% HPDI = 0.36–0.50) in spring, 0.23 (95% HPDI = 0.18–0.29) in summer, 0.34 (95% HPDI = 0.27–0.42) in fall, and 0.52 (95% HPDI = 0.44–0.59) in winter.

Model with ground-based habitat types.—For the ground-based habitat data model, we used 2,206 observations from 53 male and 41 female EIS. The most observations were in tortoise burrows (39%), followed by debris (32%), and other hole (28%; Table 1). We found little evidence of differences in debris and other holes use between males and females as posterior inclusion probabilities for the effect of sex were less than their prior inclusion probabilities (w_b = 0.23–0.43; Table 2). In contrast, season and on-the-ground habitat strongly influenced EIS shelter site use (Fig. 2). Seasonal covariates had moderate to high posterior inclusion probabilities (w_b = 0.69–1.00) with the exception of the effect of fall on other hole (w_b = 0.20, Table 2). All ground-based habitat covariates had high inclusion probabilities (w_b = 0.87–1.00; Table 2, Fig 2). Use of different shelter types was generally similar across seasons in disturbed habitats and, to a lesser extent, Pine Flatwoods (Fig. 3). For example, in disturbed habitats, the mean of the mean posterior predicted use across sexes and seasons was 0.24 for tortoise burrow, 0.31 for other hole, and 0.44 for debris, while these same values in Pine Flatwoods were 0.41, 0.26, and 0.33, respectively (Fig. 3). In contrast, within the mesic habitats (hammock and marsh), tortoise burrow use was low (mean posterior = 0.02–0.18) relative to other hole and debris (Fig. 3). Conversely, within the most xeric habitat (scrub), tortoise burrow use was high (mean posterior = 0.48–0.75) relative to other hole and debris (Fig. 3). In all habitats, tortoise burrow use was highest in the coolest seasons (spring and winter) and

Table 1. Summary of proportional use of different shelter types and associated habitats by Eastern Indigo Snakes (*Drymarchon couperi*) in central Florida, USA, across all shelter site observations (n = 2,939). The number of data points for each response variable category (shelter type) or covariate category (habitat type) is given by n.

Covariate	Category	n	Proportion
Shelter type	Tortoise burrow	1,319	0.45
	Other hole	813	0.28
	Debris	808	0.27
Season	Spring	957	0.32
	Summer	718	0.24
	Fall	492	0.16
	Winter	773	0.25
Ground-based habitat	Disturbed	871	0.30
	Scrub/Scrubby Flatwoods	774	0.26
	Hammock	305	0.10
	Pine Flatwoods	134	0.05
	Marsh	122	0.04
	Missing	734	0.25
GIS-based habitat	Pine Flatwoods	804	0.28
	Disturbed	401	0.14
	Scrub	397	0.14
	Scrubby Flatwoods	387	0.13
	Forested Wetland	257	0.09
	Unimproved Pasture	237	0.08
	Improved Pasture	237	0.08
	Non-Forested Wetland	201	0.07

lowest during summer (Fig. 3). In contrast, use of debris peaked during summer and fall, whereas use of other holes generally peaked in the spring (Fig. 3).

Use of tortoise burrows in xeric habitats was generally higher by females than males (Fig. 4); females used tortoise burrows more frequently during the winter (males: 0.73, 95% HPDI = 0.60–0.87; females: 0.88, 95% HPDI = 0.77–0.97) and the spring (males: 0.51, 95% HPDI = 0.32–0.70; females: 0.69, 95% HPDI = 0.51–0.85). In mesic habitats, males used tortoise burrows more frequently than females during the winter (males: 0.24, 95% HPDI = 0.02–0.52; females: 0.17, 95% HPDI = 0.02–0.35), but the difference was less extreme during the spring (males: 0.08, 95% HPDI = 0.01–0.17; females: 0.12, 95% HPDI = 0.02–0.24).

Table 2. Posterior inclusion probabilities (w) for covariates from a Bayesian multinomial Generalized Linear Model used to model Eastern Indigo Snake (*Drymarchon couperi*) shelter site use in central Florida, USA. Gopher Tortoise (*Gopherus polyphemus*) Burrow was the reference category. Results are presented for models with ground-based and GIS-based habitat categories and prior inclusion probabilities were 0.5 for each covariate in the table.

Covariate	Other Hole	Debris	Habitat Source
Sex (Male)	0.224	0.395	Ground-based
Summer	0.674	1.000	Ground-based
Fall	0.184	0.939	Ground-based
Winter	0.999	0.727	Ground-based
Scrub	1.000	1.000	Ground-based
Pine Flatwoods	0.924	0.961	Ground-based
Hammock	0.827	1.000	Ground-based
Marsh	0.997	1.000	Ground-based
Sex (Male)	0.559	0.934	GIS-based
Summer	0.985	1.000	GIS-based
Fall	0.683	0.994	GIS-based
Winter	0.988	0.661	GIS-based
Scrub	1.000	1.000	GIS-based
Scrubby Flatwoods	1.000	1.000	GIS-based
Pine Flatwoods	1.000	0.799	GIS-based
Unimproved Pasture	1.000	1.000	GIS-based
Improved Pasture	0.164	0.317	GIS-based
Forested Wetland	1.000	1.000	GIS-based
Non-forested Wetland	0.313	0.892	GIS-based

Model with GIS-based habitat types.—For the model with eight GIS-based habitat classifications (Disturbed, Flatwoods, Scrubby Flatwoods, Scrub, Improved Pasture, Unimproved Pasture, Forested Wetland, and Non-forested Wetland), we used 2,921 observations from 58 male and 43 female EIS. Most of these observations were in tortoise burrows (45%), followed by debris (27%), and other holes (28%). Posterior inclusion probabilities for the effect of sex (i.e., males) were typically low ($w_b \leq 0.56$, Table 2) with the exception of debris in the GIS-based habitat model ($w_b = 0.93$) whose coefficient indicated that males used debris less frequently than females (Fig. 2). Seasonal covariates had moderate to high posterior inclusion probabilities (w_b = 0.66–1.00), and also indicated

Table 3. Mean Gopher Tortoise (*Gopherus polyphemus*) burrow use by Eastern Indigo Snakes (*Drymarchon couperi*) during all seasons in central Florida, USA, for males, females, and across sexes (this study; 95% highest posterior density intervals in parentheses) versus southern Georgia, USA (Hyslop et al. 2009a).

Season	Central Florida Males	Central Florida Females	Central Florida Both Sexes	Southern Georgia
Spring	0.48 (0.39–0.57)	0.36 (0.27–0.46)	0.43 (0.36–0.50)	0.58
Summer	0.28 (0.20–0.36)	0.18 (0.12–0.25)	0.23 (0.18–0.29)	0.44
Fall	0.39 (0.29–0.49)	0.28 (0.19–0.37)	0.34 (0.27–0.42)	0.80
Winter	0.57 (0.47–0.65)	0.44 (0.34–0.55)	0.52 (0.44–0.59)	0.90

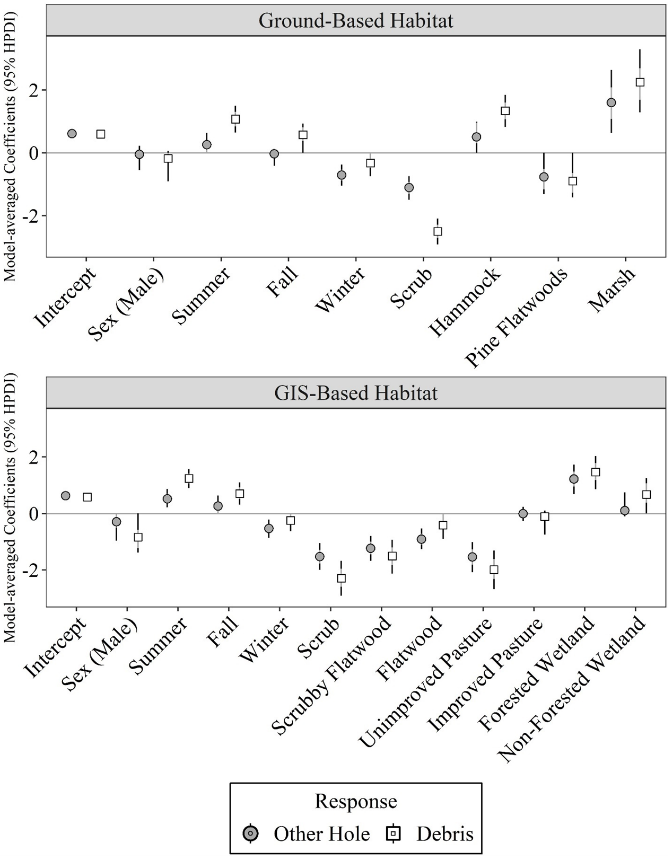

Figure 2. Means and 68% and 95% highest posterior density intervals (HPDI; thick gray and thin black vertical lines, respectively) for coefficient posteriors from a Bayesian multinomial Generalized Linear Model predicting shelter site use by Eastern Indigo Snakes (*Drymarchon couperi*) in central Florida, USA. Results are for ground-based and GIS-based habitat categories (see text for details). Gopher Tortoise (*Gopherus polyphemus*) Burrow was the reference category and Debris includes woody debris, brush piles, and man-made debris.

increasing importance of tortoise burrows during winter and spring, while debris was most frequently used in summer (Fig. 5). Shelter site use differed strongly among GIS-based habitats (w_b = 0.80–1.00) with the exception of Improved Pasture (w_b = 0.16–0.32) and other hole in Non-forested Wetland (w_b = 0.31; Table 2, Fig. 5). Overall trends were similar to those of the ground-based habitat model with tortoise burrow use being highest in xeric habitats (Scrub and Scrubby Flatwoods), lowest in mesic habitat (Wetland), and intermediate in Disturbed, Flatwoods, and Improved Pasture (Fig. 5). EIS in Unimproved Pasture used tortoise burrows most frequently while EIS in Open Wetland used debris most frequently (Fig. 2 and 5). In GIS-based xeric habitats, use of tortoise burrows was similarly high for both sexes during the winter (males: 0.80, 95% HPDI = 0.70–0.88; females: 0.89, 95% HPDI = 0.80–0.97) and spring (males: 0.80, 95% HPDI = 0.70–0.89; females: 0.82, 95% HPDI = 0.74–0.91) (Fig. 4). In mesic habitats, males used tortoise burrows more frequently than females during the winter (males: 0.29, 95% HPDI = 0.09–0.50; females: 0.11, 95% HPDI = 0.02–0.22) and spring (males: 0.26, 95% HPDI = 0.11–0.41; females: 0.08, 95% HPDI = 0.02–0.15).

Discussion

Our prediction that EIS in central Florida would show less extensive use of Gopher Tortoise burrows relative to EIS in southern Georgia was strongly supported and held true across sexes and habitats. Moreover, we never observed several EIS in our study using tortoise burrows despite having access to them. This contrasts with studies of EIS in southern Georgia where tortoise burrows were often the most frequently used shelter site (Hyslop et al. 2009a). Similarly, Speake et al. (1978) reported that active/inactive tortoise burrows were the most frequently used shelter site by EIS in south-central Georgia, particularly in winter when they constituted 88% of the total shelter site use. Shelter site use by captive-born, reintroduced EIS in Alabama, USA, resembled patterns in Georgia where an assortment of shelter types was used in the warmer seasons, but Gopher Tortoise burrows were used almost

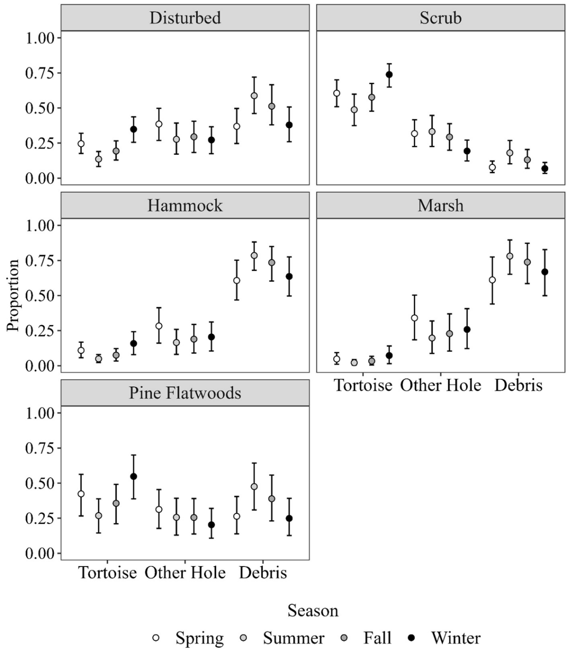

Figure 3. Predicted probabilities (posterior mean and 95% highest posterior density intervals) for shelter site use by male Eastern Indigo Snakes (*Drymarchon couperi*) in central Florida, USA, by on-the-ground habitat type and season.

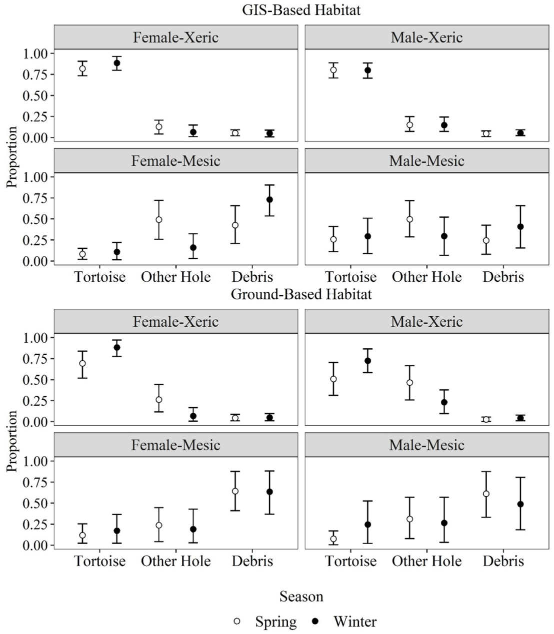

Figure 4. Predicted probabilities (posterior mean and 95% highest posterior density intervals) for shelter site use by Eastern Indigo Snakes (*Drymarchon couperi*) in central Florida, USA, from a post-hoc analysis testing for seasonal differences in shelter site use between males and females, winter and spring seasons, and xeric and mesic habitats. Xeric habitats include Scrub, Scrubby Flatwoods, and Unimproved Pasture, and mesic habitats include Hammock and Wetlands.

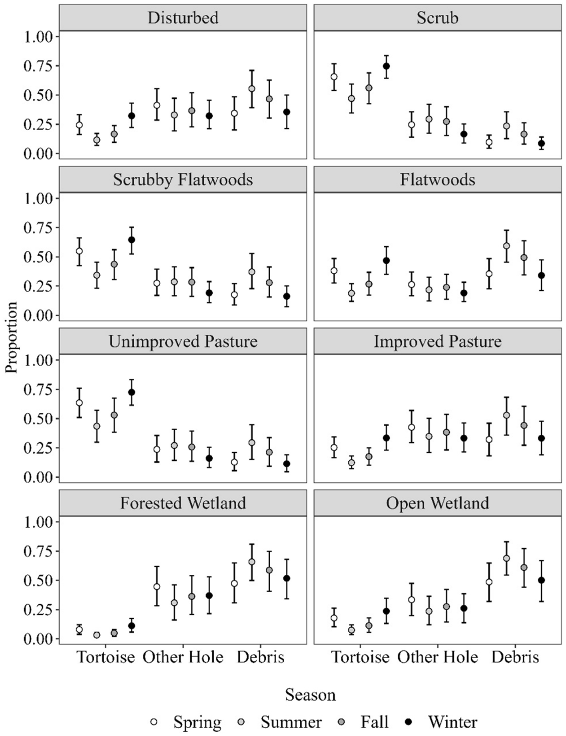

Figure 5. Predicted probabilities (posterior mean and 95% highest posterior density intervals) for shelter site use by Eastern Indigo Snakes (*Drymarchon couperi*) in central Florida, USA, from a post-hoc analysis testing for seasonal differences between sexes, seasons, and GIS-based habitats. Xeric habitats include scrub, scrubby flatwoods, and unimproved pasture. Mesic habitats include wetland. Disturbed includes urban, rural, spoil, citrus, and improved pasture. Sexes and seasons were combined for disturbed and flatwoods habitats.

exclusively in winter (Stiles 2013). Tortoise burrows were frequently used by EIS in our study, particularly in xeric habitats during the winter, when tortoise burrow use was higher than in other seasons and approached levels seen in southern Georgia (Speake et al. 1978; Hyslop et al 2009a). Similarly, four EIS radio tracked at a coastal site in southern Florida used tortoise burrows (50%), followed by mammal burrows (e.g., Nine-banded Armadillo burrows, *Dasypus novemcinctus*; 36%), bunch grass clumps (9%), root systems (3%), and human-made debris (2%; Metcalf et al. 2021).

Although our results illustrate the value of tortoise burrows for EIS in Florida, we argue that our results reflect opportunistic use of a locally abundant resource rather than dependence upon tortoise burrows. First, EIS in Disturbed and Flatwoods habitats used other holes and debris with similar frequency to tortoise burrows across all seasons. Second, in peninsular Florida, Gopher Tortoises are generally most abundant in xeric upland habitats (e.g., Sandhill, Scrub, Scrubby Flatwoods; Landers and Speake 1980; Auffenberg and Franz 1982), but they are also present at varying densities in other types of habitat, including Mesic Flatwoods and Disturbed (Diemer 1986; Smith et al. 1997; Castellón et al. 2012). Our observations of tortoise burrow use were highest in habitats where we expect the highest abundances of Gopher Tortoises. Similarly, the relatively high use of tortoise burrows by EIS reported in Metcalf et al. (2021) may reflect EIS selection for xeric upland pine habitats relative to Mangrove Swamps (made up of Red Mangrove, *Rhizophera mangle*, Black Mangrove, *Avicennia germinans*, and White Mangrove, *Laguncularia racemose*) and marshes. Although we did not measure tortoise burrow availability in our study areas, the frequency of tortoise burrow use increased along a gradient of mesic to xeric habitats as would be expected if EIS were using tortoise burrows opportunistically. Measuring tortoise burrow availability would allow for greater insights into shelter site selection. Third, EIS in our study areas used a variety of xeric and mesic habitats throughout the year (Bauder et al. 2018) in contrast to EIS in southern Georgia (Speake et al. 1978; Hyslop et al. 2014). Finally, other studies in peninsular Florida have documented EIS persistence in habitats largely devoid of tortoise burrows (Steiner et al. 1983; Moler 1985; Jackson 2013). At an abandoned citrus grove in southern Florida that lacked tortoise burrows, two males and one female EIS used artificial (42%) or natural burrows (e.g., mammal burrows, 58%) as shelter sites (Jackson 2013). Similarly, Moler (1985) radio tracked four males and one female EIS in Hardwood Hammock habitat in northern peninsular Florida. He reported winter (1 January to 16 March) shelter site use consisting of holes at the bases of oak trees (*Quercus* spp.; 59%), limestone solution holes (17%), hollow logs (14%), and armadillo burrows (10%). Collectively, this evidence indicates that EIS in peninsular Florida are not completely dependent on tortoise burrows, even for overwintering.

The seasonal variation in shelter site use was not as substantial as the variation in shelter site use among habitats. Use of tortoise burrows was highest in the spring and winter, and use of debris peaked during the summer. Debris piles may be the least thermally stable of our three shelter site classes and EIS may selectively use them less during the winter and spring, although additional data are needed to test this hypothesis. Another potential explanation for the increased use of debris in the summer is the likelihood of deeper refugia (i.e., tortoise burrows) being flooded during the summer rainy season (Castellón et al. 2015). Other holes (e.g., small mammal holes, armadillo holes, root and stump holes) are not typically as deep as tortoise burrows yet were used with similar consistency across seasons. In contrast to snakes in peninsular Florida, EIS in southern Georgia used tortoise burrows much more frequently in fall compared to summer (Hyslop et al. 2009a). This is likely due to the earlier onset of cold weather in southern Georgia, which prompts EIS to migrate from their summer foraging habitats to the sandhills for overwintering (Hyslop et al. 2014). Stiles (2013) reported that approximately 65% of EIS observations in tortoise burrows were during the winter (mid-December through mid-March) and 18% in non-winter seasons.

Inter-habitat variation in shelter site use was consistent between ground-based and GIS-based habitat classifications. Although EIS in xeric upland habitats predominately used tortoise burrows, EIS in other habitats routinely used a variety of shelter sites. Shelter site use appeared most plastic in disturbed habitats where snakes were frequently found using human-made debris such as piles of lumber, asphalt, and discarded tires.

We did not find strong evidence to support our third prediction that female EIS use tortoise burrows more than males during the reproduction season (winter and spring). Tortoise burrows may be more important as gestation and nesting resources in the northern part of the range. Hyslop et al. (2009a) found that 0.60 of female shelter locations were in burrows in the spring, compared to 0.24 for males. Female EIS in southern Georgia also generally remained on sandhills later in the year (i.e., early summer) when oviposition was likely complete compared to males, which tended to emigrate from sandhills earlier in the year (Speake et al. 1978; Hyslop et al. 2014). Furthermore, every reported nest of wild EIS, all from southern Georgia, was associated with a tortoise burrow (Stevenson et al. 2021). In our study, males and females in xeric habitats used tortoise burrows with similarly high frequencies during winter and spring, and males in mesic habitats actually tended to use tortoise burrows more frequently than females during the reproduction season. Given the generalist habitat use patterns of EIS in peninsular Florida, female EIS may have a wider variety of nesting sites available to them. The potential for significant geographic variation in nest site selection and timing of oviposition are clearly fundamental knowledge gaps for this imperiled species.

In conclusion, EIS in peninsular Florida used Gopher Tortoise burrows across all seasons and habitats, illustrating the value of burrows as an important resource. Our results indicate, however, that EIS are not dependent on tortoise burrows, not even as overwintering sites. Granted, the presence of Gopher Tortoises can play an important role in identifying potential EIS habitat (Hyslop et al. 2014; Bauder et al. 2017; USFWS 2019), but within peninsular Florida, a failure to consider undeveloped landscapes with few or no Gopher Tortoises may result in missed opportunity to protect available EIS habitats. Peninsular Florida represents an important conservation region for EIS

(Enge et al. 2013; USFWS 2019). Unfortunately, rural lands and native habitats within peninsular Florida are critically threatened due to an increasing human population that is expected to reach 26.5 million people by 2040 (https://www.fdot.gov/planning/demographic/default.shtm). Losses of both coastal and inland habitats will be exacerbated by the direct and indirect effects of sea level rise; levels along the U.S. coastline are expected to rise on average as much over the next 30 y (0.25–0.30 m over 2020–2050) as they have over the last 100 y (1920–2020; Sweet et al. 2022). These trends will negatively influence the persistence of EIS populations already imperiled by habitat loss and fragmentation (Breininger et al. 2004, 2012). This highlights the importance of identifying, protecting, and connecting potentially suitable EIS habitat. Because EIS in peninsular Florida are generalists in habitat use (Bauder et al. 2018), diet (Stevenson et al. 2010), and shelter site use (our study), the presence or absence of Gopher Tortoises or tortoise-suitable habitat on specific pieces of property should not be a determining factor for purchase or management. EIS conservation will likely benefit from protecting and connecting large, unfragmented lands containing a range of habitats (Breininger et al. 2004), particularly land not likely to be impacted by sea level rise.

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