Movement of the Eastern Indigo Snake (*Drymarchon couperi*) in Southern Florida, USA

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Abstract.—The Eastern Indigo Snake (*Drymarchon couperi*) is a large, non-venomous snake endemic to the southeastern coastal plains of the U.S. that is federally listed as threatened because of habitat loss and fragmentation. To implement effective management strategies, we must better understand the life history and movement patterns of this species. Our understanding of *D. couperi* remains limited, however, as previous studies focused on central and northern populations. To address this knowledge gap, we used radio telemetry to study *D. couperi* detectability, home range size, seasonal variation, habitat preferences, and shelter use in southwest Florida. We conducted this study in Collier County, Florida, USA, an environment with comparatively stable year-round temperatures, higher hydrological variations, and expansive saline environments relative to other areas in the range of the species. These *D. couperi* were most active during midday hours (1000–1400) and breeding seasons (October-March). These snakes prioritized upland features dominated by Gopher Tortoise (*Gopherus polyphemus*) burrows but would occasionally use wetland habitats including mangrove swamps. These snakes also maintained large annual home ranges (female mean = 110 ha; male range, 207–233 ha) similar to the most northern populations. Understanding the diverse behaviors of *D. couperi* is essential to the overall conservation of the species throughout its range. Current survey protocols, which encourage surveying snakes at sunrise and sunset during summer months, may not be appropriate for animals in southern Florida and could result in mismanagement of *D. couperi* if these patterns were replicated in similar locations.

Key Words.—conservation; Eastern Indigo Snake; management; movement; South Florida

Introduction

Understanding ecological requirements of a species, particularly an imperiled species at the limit of its ecological range, is imperative for local conservation decisions and management practices. Populations at the historical range limit (peripheral populations) of a species frequently inhabit unique ecological niches that can affect their survival and reproduction differently from elsewhere within the range of the species. These peripheral populations can exist in disjunct populations that experience decreased connectivity to source populations, which can reduce gene flow (Thomas et al. 2001; Squires et al. 2012). Peripheral populations may also reside in suboptimal landscapes for that species (Brown 1984), which can introduce physiological stressors such as higher susceptibility to parasitic infections (Briers 2003). Additionally, populations at range limits may be more affected by global disturbances such as climate change and sea level rise (Sexton et al. 2009). Despite the many factors affecting individuals in peripheral habitats, these populations are often under-sampled compared to those nearest the range center (Sagarin and Gaines 2002). Natural history may be divergent at the opposite ends of the geographical range of a species, particularly if they have strong climatic differences (Wiens and Graham 2005). Ultimately, increased attention to geographic distribution is needed to accurately forecast the implications of anthropogenic alterations to the climate and habitats (Sexton et al. 2009).

Eastern Indigo Snakes (*Drymarchon couperi*; Fig. 1) are a large Colubrid species endemic to the southeastern U.S. (Enge et al. 2013). This species is listed as threatened under the U.S. Endangered Species Act because of urbanization, fragmentation, and collection

Figure 1. Eastern Indigo Snake (*Drymarchon couperi*) preying on a Black Racer (*Coluber constrictor*) in Florida, USA. (Photographed by Matthew Metcalf).

for the pet trade, with current populations restricted to southern Georgia and peninsular Florida (U.S. Fish and Wildlife Service [USFWS] 1978, 2008, 2018). This latitudinal distribution reflects a variety of landscapes and climates that *D. couperi* inhabit. Populations in the northern half of the distribution of the species inhabit more temperate regions with longer periods of cooler weather and occasional freeze events and southern populations exist in sub-tropical areas, rarely experience freezing events, and are exposed to more hydric soils and mangrove ecosystems than in the north. Despite these variations, previous research only sampled northern populations in Georgia (Hyslop et al. 2014) and central Florida (Breininger et al. 2011; Bauder et al. 2016; Rebecca Bolt, pers. comm.) to create the species management plan. Basing management plans on animals from differing parts of their geographic range may have limited effectiveness for *D. couperi* in South Florida, which experience hydrologic and climatic features that differ from other populations (Steiner et al. 1983).

Landscapes in South Florida are dominated by Freshwater Marshes and Brackish Mangrove Forests, including the largest distribution of mangroves in the U.S. (Odum et al. 1982). South Florida also experiences land development in the form of both urban and agriculture expansion with Lee and Collier counties ranking in the top ten of the fastest growing metropolitan areas in the USA (U.S. Census Bureau. 2015. New census bureau population estimates reveal metro areas and counties that propelled growth in Florida and the nation. Release number: CB15-56. U.S. Census Bureau. Available from https://www.census.gov/newsroom/press-releases/2015/cb15-56.html# [Accessed 15 December 2017]). This has led to fragmented landscapes and reduced viable wildlife habitats and corridors (Kautz 1998; Smith and Nogle 2001). In addition, South Florida has seen the establishment of many exotic flora and fauna, which compete with native species for resources (Hart et al. 2015; McCleery et al. 2015) and expose *D. couperi* to novel pathogens (Reed 2005; Miller et al. 2018).

This research explores how multiple landscape features affect *D. couperi* movement and spatial ecology in the southernmost population of the species in the Rookery Bay National Estuarine Research Reserve (Rookery Bay NERR), providing the opportunity for comparisons with other studied populations. Overall, we expect this population of *D. couperi* to show many similarities with the most northern populations as both locations represent peripheral populations at extreme ends of the range of the species. For example, we predict large home ranges similar to northern populations (e.g., Hyslop et al. 2012) so snakes can acquire necessary but sparsely distributed resources. We also predict that *D. couperi* will select upland features during the breeding season (October-March; Groves 1960; Hyslop et al. 2012), in association with Gopher Tortoise (*Gopherus polyphemus*) burrow locations (USFWS 2018), if this population is consistent with other locations (Hyslop et al. 2012; James Layne and Todd Steiner, unpubl. report). We expect some differences in how *D. couperi* in the Rookery Bay NERR use the landscape, however, resulting from unique environmental features found in this most southerly population. We expect *D. couperi* to be active year-round, as there is less of a need to escape cooler temperatures (Dalrymple et al. 1991) than in the north, and *D. couperi* may move from upland areas during the non-breeding season, which corresponds with the wet season in South Florida.

MATERIALS AND METHODS

Study site.—We conducted this study in the Rookery Bay NERR in southwest Collier County, Florida, USA (Fig. 2). This reserve is situated along the Gulf Coast of Florida and comprises a diversity of habitats, including Mangrove Swamps, Upland Pine Hammocks, and Coastal Scrub. We focused on *D. couperi* that occupied approximately 900 ha of the total 44,500 ha within the reserve. Portions of what is now the Rookery Bay NERR were once marked for development. Today, open, sandy pathways and a low-trafficked paved road remain, as well as a public access boardwalk. Additionally, a heavily trafficked state road and the large urban centers of Naples (22,088 people as of 2021) and Marco Island (17,947 people as of 2021) border the reserve.

Field and telemetry methods.—We began visual encounter surveys for *D. couperi* at the Rookery Bay NERR in June 2014 with the first sighting in July 2015. We focused efforts on previous *D. couperi* sightings within the reserve and habitats used frequently by
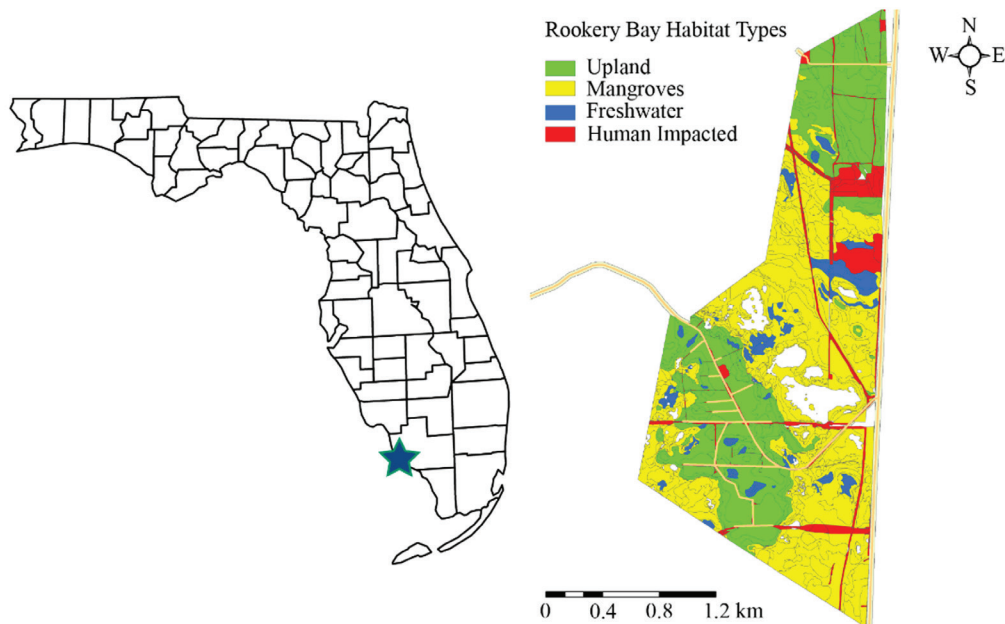
Figure 2. Geographic location of the study site in Collier County, Florida, USA, and habitat types used by the Eastern Indigo Snakes (*Drymarchon couperi*) in the Rookery Bay National Estuarine Research Reserve (NERR). Staff at the Rookery Bay NERR configured and assessed the habitat mapping that we used in analyses (Barry et al. 2013).

the species as described in previous studies, such as upland scrub and areas around tortoise burrows, but we expanded our searches to all habitats within the Rookery Bay NERR. In total, our search effort was 656 person-hours spread across 223 sampling days (Breeding Season, n = 138 d; Non-breeding Season, n = 85 d).

During these Visual Encounter Surveys, we captured snakes by hand (n = 9), and held snakes for telemetry (n = 5) in approved containment at Florida Gulf Coast University, Fort Myers, for an average of one week. We measured all snakes for snout-vent length (SVL), total length, mass, and we determined their sex by cloacal probing that was supplemented by examination for male-specific keels along the mid-dorsal scales (Layne and Steiner 1984; Stevenson et al. 2003). Our permit allowed up to five adult *D. couperi* to be collected and implanted surgically with radio transmitters. We used SI-2T internal transmitters (Holohil Systems Ltd., Carp, Ontario, Canada) that weighed 13 g each and had an average battery life of 2 y. We surgically implanted transmitters into the coelomic cavity following procedures described in Reinert and Cundall (1982). We held radio-tagged snakes at Florida Gulf Coast University for approximately 3–5 d post-surgery for recovery (Waldron et al. 2006; Breininger et al. 2011). We released radio-tagged snakes near tortoise burrows within 10 m of their original capture site, then located individuals 1 h later to confirm the status of the snake. Unfortunately, one snake (RB3) died 2 mo into the study for unknown reasons and was therefore excluded from analyses.

We tracked radio-tagged snakes to collect location data once a day for 3 d per week from 20 July 2015 to 29 April 2017 using a Communication Specialists (Communications Specialists, Inc., Orange, California, USA) handheld Yagi antenna and a car-mounted roof antenna in conjunction with a Communications Specialists R-1000 handheld receiver. Search time averaged approximately 3 h/d to detect the four radio-tagged snakes. To detect a signal, we started at the last known location and spread out to various habitats of the reserve by foot. We also drove down the main road and access roads surrounding the reserve. We identified snakes as detected if a confirmed radio signal could be traced to a specific location. After locating a snake, we used a Garmin (Garmin International, Inc., Olathe, Kansas, USA) eTrex 10 GPS unit (accuracy within 3 m) to record coordinates, time, temperature, if the snake was actively moving or stationary, and shelter type (if applicable). We attempted visual confirmation during each tracking event. For snakes not seen visually but confirmed with a radio signal, we recorded the landscape features where the snake may have been hidden, such as a burrow. If we did not detect a signal within 2 h of searching, we recorded that snake as not found for that day. In five instances, two snakes remained undetected for one week. We then employed the Conservancy of Southwest Florida to search for the missing animals during their aerial telemetry surveys for Burmese Pythons (*Python bivittatus*). When the Conservancy detected a missing snake, we walked to the detected

location and searched until the snake was found.

Statistical analyses.—For snakes we tracked but did not find visually, we recorded the landscape feature that may have been used as a shelter. We categorized these landscape features into distinct categories (i.e., active and inactive tortoise burrows as well as mammal burrows). We also recorded when snakes appeared to be in bunch grass (such as Fakahatchee Grass, *Tripsacum floridanum*, and Muhly Grass, *Muhlenbergia capillaris*), roots, or anthropogenic features, which may have provided the animal with cover. We then combined data from each snake to describe the frequency of potential shelter types. We did not statistically determine preference and/or avoidance of particular shelter types because the number of available shelter types within the home range of each snake could not be assessed and, therefore, we could not determine the number of times that a shelter type was used relative to its availability.

We also aggregated location data from the four radio-tagged snakes (n = 435) to determine a best-fit model for predicting snake detectability in this location. To determine which abiotic factors (season, time of day, and air temperature) best predicted the likelihood of visually detecting these snakes when there was a confirmed radio signal, we used a Generalized Linear Mixed Model with individuals treated as a random effect to control for differences in the intercepts. We used a backward stepwise approach starting with a full model of the main effects and then removed poor-fitting abiotic factors until resolving on a best-fit model with the lowest Akaike Information Criterion (AIC) score. We reported AIC scores instead of AICc scores, which control for small sample size (Anderson and Burnham 2002). Although the number of snakes in this study was small (n = 4), the data used to evaluate the probability of detecting snakes visually was based on the cumulative number of tracking events for all snakes together (n = 435), making AIC the appropriate measure based on the number of evaluated parameters (Anderson and Burnham 2002). In addition, we evaluated the Bayesian Information Criterion (BIC) score, which accounts for both the number of parameters in the chosen model and the sample size, to confirm that this information criterion also was minimized for the described model.

We computed the visual detection probabilities ($\hat{p}_v$) by inverting the fitted model for logit (log-odds) response regressed on the significant factors. The fitted model is

$$logit(\hat{p}_v) = Y_j = \hat{\beta}_0 + \sum_{i=1}^{3} \hat{\beta}_i X_i + \varepsilon_j$$

where, X_1 = Season (breeding and non-breeding), X_2 = Time of Day (morning, midday, afternoon), $\hat{\beta}_0$

= estimated model intercept with variability of the jth group (Hidden = 0, Seen = 1) is distributed as $\varepsilon_j \sim$ *Gaussian* $(0, \sigma^2)$, $\hat{\beta}_1$ = estimated model coefficient for Season, $\hat{\beta}_2$ = estimated model coefficient for Time of Day (midday), $\hat{\beta}_3$ = estimated model coefficient for Time of Day (morning), $\hat{p}_v$ = estimated probability for visual detection probability (p_v), and the estimated probabilities were given by,

$$\text{Pr}(\text{Visible}|\hat{\beta}_0, \hat{\beta}_1, \hat{\beta}_2) = \hat{p}_v = \frac{1}{1+e^{\hat{\beta}_0 + \Sigma_{i=1}^2 \hat{\beta}_i x_i}}$$

We computed the relative odds ratio using the glmer package in R (Bolker et al. 2009). The response had two levels: Hidden and Seen. We set the Hidden level as the reference. We used dummy coding (Daly et al. 2016) to code the predictors (Season and Time of Day) and the response (Visibility). Response variables for the dummy codes included Hidden = 0 and Seen = 1. Similarly, we coded the Season predictor as Breeding = 0 and Non-Breeding = 1. Because the Time of Day predictor had three levels, it was coded with Afternoon = (0, 0) as the reference level, and we coded Morning and Midday levels as (1, 0) and (0, 1) respectively. Therefore, the matrix for estimating visibility probabilities consisted of six rows that were 3-tuple (triplet) binary codes.

All subsequent analyses examined each individual snake separately producing four specific results for each examined question. We limited data that defined home range and habitat use of each animal to movements > 5 m from the previous known location (RB1: n = 108; RB2: n = 38; RB4: n = 80; RB5: n = 89). We pursued this approach to determine how animals actively moved through their habitat rather than simply occupying the habitat (Benhamou and Cornélis 2010).

We calculated 100% minimum convex polygons (MCP) to quantify the maximum home range and for making comparisons with previous *D. couperi* studies. We also calculated 95% MCP to correct for cases where some snake locations could have been outliers. We calculated Kernel Density Estimates (KDE; 95% activity area and 50% core area) for each snake, using an *h*-ref method for a bivariate kernel that assumes the utilization distribution is bivariate normal (Worton 1995). One snake (RB2) made a long-distance move to a completely different area within the reserve at one point in the study. Over the course of the study, this individual traveled from the southern half of the study site to the northern edge of the reserve. During this time, the snake went undetected for approximately 2 mo, leaving a large gap in the overall home range. Calculating Kernel Density Estimates based on the entire annual home range produced unrealistic estimations, suggesting the density estimate of this snake was well beyond the scope of the study area. For example, the 50% core area was

dramatically larger than the maximum home range as defined by its 100% MCP for this animal. To calculate a more biologically realistic estimate, we split the home range of RB2 into two distinct ranges, the southern and northern areas. We then calculated and reported kernel density estimates for the two areas separately and added these values to generate more biologically realistic activity and core areas for RB2. The three other snakes stayed in the same area throughout the course of the study and did not require any modifications to the Kernel Density Estimates.

To determine habitat selection of individual *D. couperi*, we used 100% MCP configurations and overlaid habitat data provided by staff at the Rookery Bay NERR (Barry et al. 2013) that fit within the home range of the snake. We aggregated habitats into four categories based on hydrological and floral components: Upland Pine Forests (xeric environments that included Slash Pines, *Pinus elliottii*, and Saw Palmetto, *Serenoa repens*), human-impacted areas (xeric environments that included paved roads and parking areas), Freshwater Marshes (hydric environments that included Sawgrass, *Cladium jamaicensis*, and Carolina Willows, *Salix caroliniana*), and Mangrove Swamps (brackish environments with White Mangrove, *Laguncularia racemosa*, Black Mangrove, *Avicennia germinans*, and Red Mangrove, *Rhizophora mangle*). Because the dry and wet seasons in South Florida coincide with *D. couperi* breeding and non-breeding seasons, respectively (Stevenson et al. 2009; Bauder et al. 2016), we analyzed and described the data in terms of reproductive seasonality to keep the focus on the behavior of snakes. We performed Chi-square tests to determine how each snake associated with specific habitats. The null expectations for these tests were based on the relative amount of the home range of a snake that included each of the four habitat types. For example, the dispersion pattern of a snake that occupied a home range with 40% upland, 30% wetland, 20% mangrove, and 10% human-altered habitats would be compared to these relative values: 0.4, 0.3, 0.2, and 0.1, respectively. We described strong significant habitat selection and avoidance from Pearson residuals that were more than expected (> 2) or less than expected (< -2). We described weak selection and avoidance based on residuals > 1 or < -1. We used a Contingency Table test to determine whether snakes changed how they used the habitat between seasons.

We analyzed all data in the base package of R unless stated otherwise (R Core Team 2018). We used package rms (Harrell 2019) to determine which abiotic factors were associated with the likelihood of visually detecting a tracked snake. We calculated MCP home ranges and Kernel Density Estimates for each of the four snakes in the package adehabitatHR (Calenge 2006). We calculated Contingency Table tests in the package vcd

(Meyer et al. 2017). We based strong significance on an alpha-value of 0.05 and weak significance was described for alpha-values 0.051–0.100.

RESULTS

We radio tracked snakes from 20 July 2015 to 11 May 2017. One female and three male snakes kept their radio tags for approximately one calendar year ($\bar{x}$ = 435 d, range, 334–546 d). For radio-tagged snakes, we relocated snakes 73% of the time (n = 435); a signal was not detected 27% of the time (n = 162). When a signal was confirmed, we visually observed snakes 25% of the time (n = 107). We failed to visually observe snakes 75% of the time (n = 328) despite receiving a strong radio signal indicating the snake was within a few meters. Snakes that we located but did not find visually were associated with some form of shelter 85% of the time (n = 279). The four snakes in this study made consistent use of active (n = 43, 15%) and inactive (n = 97, 35%) *G. polyphemus* burrows for shelter. These snakes also used mammal burrows (n = 100, 36%). In addition, snakes associated with alternative structures that may have been used for shelter, included bunch grasses (n = 26, 9%), root systems (n = 7, 3%), and human-impacted structures (n = 6, 2%).

The model that included season and time of day did the best job describing the likelihood of visually detecting a tracked snake. The ability to visually locate a radio-tagged snake was not associated with air temperature (AIC = 503.8, BIC = 528.5). Once we removed temperature from the model, both season and time of day associated significantly with the detectability of snakes (AIC = 501.9, BIC = 522.4). The likelihood of visually detecting *D. couperi* during the breeding season was 70% higher compared to the non-breeding season (βnon-breeding= -0.58, 95% confidence interval [CI] = -1.05, -0.14). In addition, the likelihood of visually detecting these snakes was 125% and 60% higher in the midday than the morning ($\beta_{morning}$ = -0.45, 95% CI = -1.01–0.10) and afternoon ($\beta_{afternoon}$ = -0.63, 95% CI = -1.13, -0.12]), respectively. Throughout the study, the visual detection probabilities ($\hat{p}_v$) were highest during the midday hours of the breeding season and lowest during the afternoon hours of the non-breeding season (Table 1).

The home range sizes of the radio-tagged snakes varied considerably (Table 2). The female (RB1) had the smallest annual home range (113 ha). In comparison, the three males (RB2, RB4, and RB5) maintained annual home ranges that were approximately twice as large (233 ha; 223 ha; and 207 ha, respectively) as that of the female. Seasonally, however, the home ranges of these snakes showed individual trends. RB1 and RB2 had reduced home ranges from the breeding season (RB1:

TABLE 1. Probability of visually confirming the location of a radio-tagged Eastern Indigo Snake (*Drymarchon couperi*) that was tracked successfully at the Rookery Bay National Estuarine Research Reserve in Collier County, Florida, USA. Seasonal differences (breeding: October-March; non-breeding: April-September) show varying probabilities of detecting a snake visually across various times of day, which are aggregated into three categories: Morning (before 1000), Midday (1000–1400), and Afternoon (after 1400). The abbreviations VDP = visual detection probability and CI = confidence interval.

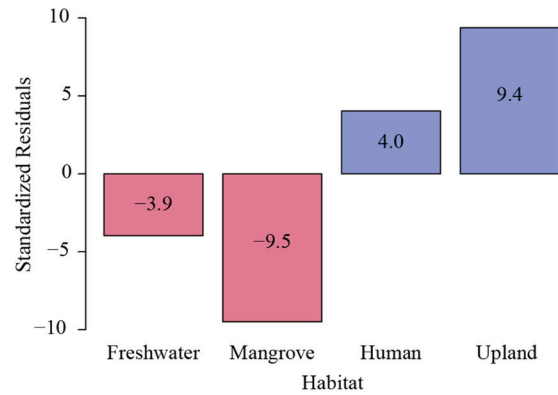| Season	Time of day	VDP ($\hat{p}_v$)	95% CI for $\hat{p}_v$
Breeding	Morning (< 1000)	0.2716	(0.1160, 0.5058)
	Midday (1000–1400)	0.3679	(0.1842, 0.5963)
	Afternoon (> 1400)	0.2375	(0.1662, 0.3218)
Non-breeding	Morning (< 1000)	0.1715	(0.0440, 0.4702)
	Midday (1000–1400)	0.2441	(0.0735, 0.5615)
	Afternoon (> 1400)	0.1474	(0.0654, 0.2914)

FIGURE 3. Habitat associations for the four Eastern Indigo Snakes (*Drymarchon couperi*), collectively, in the Rookery Bay National Estuarine Research Reserve in Collier County, Florida, USA. Pearson residuals of ≥ 2 show a significant affinity for a habitat type (blue), while ≤ -2 show a significant avoidance of a particular habitat (red).

107 ha, n = 82 fixed locations; RB2: 224 ha, n = 37 fixed locations) to the non-breeding season (RB1: 75 ha, n = 69 fixed locations; RB2: 33 ha, n = 24 fixed locations). RB4 maintained a relatively consistent home range between the breeding (158 ha, n = 54 fixed locations) and non-breeding (151 ha, n = 48 fixed locations) seasons. In contrast, RB5 increased his home range from the breeding (75 ha, n = 65 fixed locations) to the non-breeding (166 ha, n = 63 fixed locations) season. Activity areas (KDE 95%) and core areas (KDE 50%) displayed similar patterns as the MCP configurations, with male snakes having approximately double to triple the home range area compared to the female (Table 3). Activity areas ranged from 131 ha (RB1) to 349 ha (RB5) and core areas ranged from 25 ha (RB1) to 77 ha (RB5).

The four snakes spent disproportionately more time in the Upland Pine Forests and human-disturbed areas than the freshwater and mangrove habitats (Fig. 3; RB1, RB2, RB4, and RB5: *P* < 0.001). Although snakes showed a strong association for upland and human-disturbed habitats throughout the year, collectively the four snakes spent more time in wetlands during the breeding season and the uplands during the non-breeding season (Fig. 4). RB1 and RB2 showed this significant change across seasons (*P* < 0.001 and *P* = 0.014, respectively).

DISCUSSION

Drymarchon couperi show considerable variation in home range size across their geographic distribution. Snakes in peripheral populations at the northern limit of the *D. couperi* range occupy some of the largest home ranges of any studied snake (Hyslop 2007); however, snakes in the center (e.g., James Layne and Todd Steiner, unpubl. report) and southern areas (e.g., Jackson 2013) make use of much smaller home ranges. Home range sizes for individual snakes in the Rookery Bay NERR were large, similar to those in the most northern study on the species (Hyslop 2007). As the southernmost studied population to date, *D. couperi*

TABLE 2. Annual and seasonal home range estimations for the four Eastern Indigo Snakes (*Drymarchon couperi*) radio-tracked at the Rookery Bay National Estuarine Research Reserve in Collier County, Florida, USA, from 2015–2017. Estimations include 100% and 95% minimum convex polygons (MCP) for annual and seasonal home ranges as well as 95% activity area kernel density estimates (KDE) and 50% core area KDE. Sex abbreviations are F = female and M = male.

Snake ID	Sex	Annual 100% MCP home range	Annual 95% MCP home range	Annual 95% KDE activity area	Annual 50% KDE core area	Breeding season 100% MCP range	Non-breeding season 100% MCP range
RB1	F	113	80	131	25	107	75
RB2	M	233	221	211	40	224	33
RB4	M	223	113	264	46	158	151
RB5	M	207	175	349	77	75	166

TABLE 3. Mean annual home ranges (100% minimum convex polygon estimations), sample sizes (n), and tracking duration for this study and previous Eastern Indigo Snake (*Drymarchon couperi*) studies arranged in geographic order from north in Georgia, USA, to south in Florida, USA.

Location	Source	Tracking duration (d)	Females		Males	
			Home Range (ha)	n	Home Range (ha)	n
Southeast Georgia	Hyslop 2007	89–711	101	10	510	22
North-central Florida	Paul Moler, unpubl. report	Unknown	—	—	141	5
North-central Florida	Dodd and Barichivich 2007	322	—	—	185	1
South-central Florida	James Layne and Todd Steiner, unpubl. report	8–197	19	7	74	12
South-central Florida	Rebecca Bolt pers. comm.	Unknown	41	18	118	31
South-central Florida	Breininger et al. 2011	224–1113	76	21	202	23
South-central Florida	Jackson 2013	83–365	10	1	43	4
Southwest Florida	This study	334–546	113	1	221	3

at Rookery Bay experience a subtropical climate with relatively stable year-round temperatures but varying hydrological changes including exposure to more saline environments (e.g., Mangrove Swamplands). Peripheral populations may encounter different limiting factors and ecological challenges than core populations (Vanek and Wasko 2017) as a result of occupying suboptimal landscapes and climates (Brown 1984) and decreased population connectivity (Thomas et al. 2001; Squires et al. 2012). Whereas *D. couperi* in the northern part of range are subjected to freezing and a shortened activity season, the snakes at the Rookery Bay NERR experience dramatic changes in hydrology, which may help to explain why snakes in both locations occupy such large home ranges. Changes in home range size,
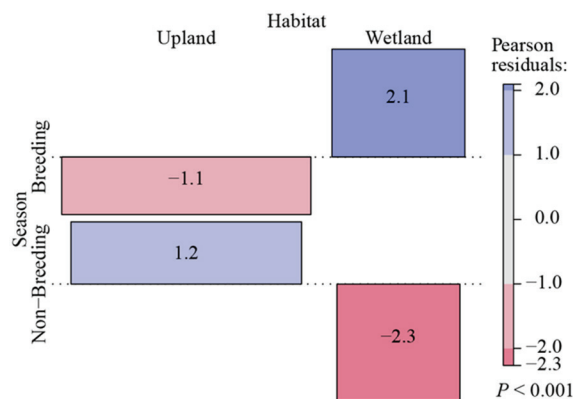

FIGURE 4. Association plots represent the locations of the four sampled Eastern Indigo Snakes (*Drymarchon couperi*), collectively, during the breeding and non-breeding seasons relative to available habitat in the Rookery Bay National Estuarine Research Reserve in Collier County, Florida, USA. Pearson residuals of ≥ 2 show a significant affinity for a habitat type (blue), while ≤ -2 show a significant avoidance of a particular habitat (red). Weak statistical affinity (i.e., light blue or light red) are described for residuals > 1 or < -1.

however, may not directly correlate to the location of a population along an environmental gradient. Although the snakes in this study maintained large home ranges, *D. couperi* from the nearest study to the Rookery Bay NERR occupied the smallest home ranges recorded (Table 3.1 in Jackson 2013). The Jackson (2013) study was conducted in a heavily altered landscape: a fallow citrus grove with a network of canals. The small home ranges described by Jackson (2013) may have reflected the high habitat quality at this site, where necessary resources were found in more condensed areas.

Drymarchon couperi at the Rookery Bay NERR selected drier areas consistent with observations for this species elsewhere (Lawler 1977; Steiner et al. 1983; Hyslop 2007). The presence of *D. couperi* in these upland areas, however, may have reflected the ability to find the snakes more easily in these environments relative to other areas (i.e., wetlands and mangrove swamps) in the study site, although we have no evidence that the sampling was biased to one habitat type over the other. Each habitat was similarly accessible, and trails and roads used to locate the radio signal of a snake crossed all available habitat types. When we detected a signal, we entered the habitat to locate the snake regardless of whether it was a Mangrove Swamp, wetland, Upland Pine Forest, or human-impacted area.

Upland Pine Forests and human-impacted areas included *G. polyphemus* and mammal burrows that snakes made extensive use of in this study. This pattern is all the more pronounced as a recent survey determined that tortoise burrows were confined to a relatively small area of the study site (about 40 ha; Hengstebeck 2018). Although not traditional refugia, landscape features such as bunch grasses, roots, and anthropogenic structures may have provided these snakes with additional forms of cover. For example, bunch grasses in Florida can form dense clumps of stems that bend to the sides by the

flowers. In addition, bunch grasses can grow in thick clusters. In these cases, grasses, such as *Tripsacum floridanum* and *Muhlenbergia capillaris*, can limit predatory access to snakes from the ground and obscure sightings from above. These structures may also help regulate temperature and humidity extremes by shading and holding in moisture. Although we found *D. couperi* using bunch grasses, roots, and anthropogenic structures, their potential value to these snakes, if any, remains unclear.

Despite some similarities, our study highlighted distinct differences between the snakes of the Rookery Bay NERR compared to other locations. For example, the ability to find *D. couperi* in the reserve was not affected by ambient air temperature. Snakes in this southernmost location were equally likely to be found at all temperatures during the course of the study (air temperature range, 13°–33° C). By comparison, Speake et al. (1987) reintroduced *D. couperi* in Georgia and found these snakes to be more often seen in the warmer summer months and unseen during the winter. Snake movements also decreased during cooler months in northern regions, often restricting the snakes to prolonged stays in shelter (Hyslop 2007). In contrast, snake movement did not appear to be limited by temperature extremes or seasonality alone at the Rookery Bay NERR. Although ectotherms are dependent on the balance between costs and benefits of thermoregulation during various times of year (Brown and Weatherhead 2000; Blouin-Demers and Weatherhead 2001), organisms in more stable and warmer year-round temperatures, such as Southwest Florida, may not need to prioritize this requirement.

At the Rookery Bay NERR, we encountered *D. couperi* visually most often during the midday hours (1000–1400), despite higher ambient air temperatures. Current survey protocols for north and central Florida suggest Visual Encounter Surveys for active *D. couperi* should take place from October to April and from 0900–1600 (USFWS 2011). Current protocol also suggests ideal survey day air temperatures are 15°–21° C preceding cool or cold days. North and central Florida, however, are exposed to much cooler temperatures for longer periods of time than South Florida. Additional research is needed to better understand *D. couperi* activity patterns in South Florida, but the snakes from this study suggest that more concentrated surveys can be conducted during midday hours throughout the year in this region.

Research based on small sample sizes is inevitable for threatened species, especially large snakes, that exist in disjunct locations, including peripheral populations. A case-study approach based on the examination of individual animals, particularly cryptic and threatened species such as *D. couperi*, in such small populations can provide valuable information, similar to case-studies in medical and social sciences (Mittra et al. 2015; Zainal 2007). For example, this case-study approach was used to understand and develop management strategies for the Florida Panther (*Puma concolor coryi*) when the species was critically endangered towards the end of the 20th Century (Shrader-Frechette and McCoy 1993). Understanding nuances within smaller, peripheral populations can also lead to location-specific management plans that are beneficial to the animals at that location. Understanding these population-specific differences in *D. couperi* may also encourage more inclusive dialogue on how best to conserve the entire species, including peripheral populations that may consist of a smaller number of individuals living in novel habitats. Despite these benefits, however, broad ecological inferences are not possible when studying populations with few individuals. Findings in such cases may represent biological anomalies that differ dramatically from the species as a whole. To fully understand threatened species, such as *D. couperi*, a balanced approach that integrates findings from large, generalizable populations with studies of smaller, location-specific populations may provide the most useful insights.

We identified important factors that should be considered for future research and proper management of *D. couperi* in South Florida. Our data suggest that *D. couperi* in the Rookery Bay NERR are restricted to more elevated, less saline environments, although snakes will use freshwater and mangrove habitats. As expected throughout their range, snakes in this location made extensive use of tortoise burrows; however, both our study and that of Jackson (2013) found that *D. couperi* can make use of alternative shelter types, such as Nine-banded Armadillo (*Dasypus novemcinctus*) burrows or man-made structures. Additional studies throughout the range of the species are needed to assist management strategies that best reflect *D. couperi* activity in each location, including South Florida. This could increase the likelihood that all populations of *D. couperi*, including peripheral populations, can be sustained into the future.

Ceilley, Ian Bartoszek, Ian Easterling, Kate Davis, Kodiak Hengstebeck, Sam Troast, Forrest Wallace, Logan Stone, Dakoeta Pinto, Damian and Shandez Baker, Santiago Luaces, the FGCU Animal Behavior Group, and an army of volunteers. We would like to dedicate this work to our dear friend, colleague, and co-author John Herman, who passed away 3 July 2018. His guidance, friendship, and passion for all things scaly is deeply missed!

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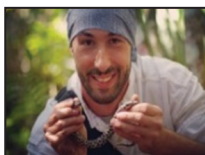
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