Seasonal Variation in Eastern Indigo Snake (*Drymarchon couperi*) Movement Patterns and Space Use in Peninsular Florida at Multiple Temporal Scales

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ABSTRACT: Many snake populations display seasonal variation in movement patterns in response to spatiotemporal variation in prey, mates, and other resources. Eastern Indigo Snakes (*Drymarchon couperi*) are federally threatened and endemic to the southeastern coastal plain of the United States. Although previous studies have described seasonal variation in *D. couperi* movement patterns at the northern limit of their range (southern Georgia), such information is currently lacking from peninsular Florida. We describe sex-specific seasonal variation in *D. couperi* movement patterns and space use in peninsular Florida across multiple temporal scales. We found that males made longer, more frequent movements, and had larger home ranges than females during the winter breeding season. Although movement frequency and distance were similar between sexes during the nonbreeding season, males still had larger home ranges. The degree of within-individual home-range overlap was consistent over time and not indicative of seasonal migrations between winter and summer habitats. Our observations of increased male movements during the winter are consistent with observations of breeding activity by snakes at our study sites, and across the species' range. The levels of winter activity that we observed for *D. couperi* contrast with the spring/autumn breeding seasons and low winter activity reported for other North American snake species. In contrast to our results, previous studies of *D. couperi* in southern Georgia found that both sexes exhibited the lowest rates of movement and smallest home-range sizes during winter, despite the occurrence of breeding activity. We hypothesize that differences in winter climate between these two areas allow for greater surface activity among snakes in peninsular Florida.

Key words: Colubridae; Home range; Mate-searching; Spatial ecology; Spatial overlap; Utilization distribution

ANIMAL movements can vary across multiple spatiotemporal scales in response to variation in resource availability or the relative importance of a given resource (e.g., Lister and Aguayo 1992; Trierweiler et al. 2013). Seasonal variation in movement patterns is widespread throughout many snake taxa and can occur in response to spatiotemporal variation in hibernacula (Gregory 1982), prey (Madsen and Shine 1996a; Sperry and Weatherhead 2009a), mates (King and Duvall 1990; Glaudas and Rodriguez-Robles 2011), gestation or oviposition sites (Blouin-Demers and Weatherhead 2002; Brown et al. 2005), and thermally suitable shelters (Croak et al. 2013). Because snakes are ectotherms, their activity is also strongly influenced by environmental temperature (Peterson et al. 1993; George et al. 2015), and seasonal variation in temperature may constrain their activity to periods of thermally conducive weather (Sperry et al. 2010). Some of the most pronounced seasonal movements in snakes occur in populations in north-temperate regions in the form of seasonal migrations between communal hibernacula and summer foraging/breeding habitats (Larsen 1987; Jorgensen et al. 2008; Gardiner et al. 2013). Many snake species with broad geographical ranges appear to exhibit more pronounced migratory behavior at higher latitudes (Reed and Douglas 2002; Rodriguez-Robles 2003; Carfagno and Weatherhead 2008; Klug et al. 2011; Gardiner et al. 2013). Nevertheless, species in mild climates might still undertake lengthy migrations in response to seasonal variation in other resources, such as prey (Madsen and Shine 1996a).

Eastern Indigo Snakes (*Drymarchon couperi*) are large (>2 m) colubrids endemic to the southeastern coastal plain of the United States (Smith 1941; Conant and Collins 1998; Enge et al. 2013) and listed as Threatened under the U.S. Endangered Species Act (U.S. Fish and Wildlife Service 1978). This species shows male-biased sexual dimorphism, with males being longer and heavier than females (Stevenson et al. 2009). In the northern part of their range (southern Georgia), *D. couperi* exhibit strong seasonal variation in movement patterns (Speake et al. 1978; Hyslop et al. 2014). In this region, *D. couperi* maintained small (<10 ha) winter home ranges on xeric sandhills that support Gopher Tortoises (*Gopherus polyphemus*), but used much larger (≤1500 ha) home ranges and a greater diversity of habitat types during spring through autumn (Speake et al. 1978; Stevenson et al. 2003, 2009; Hyslop et al. 2009, 2014). In one study, several individuals undertook lengthy (1.5–7.5 km) linear migrations between winter and summer home ranges in a manner analogous to many north-temperate snake species (Hyslop et al. 2014). However, less is understood about seasonal variation in *D. couperi* movements in peninsular Florida. Breininger et al. (2011) reported smaller home-range sizes (≤538 ha) than those reported for southern Georgia and noted that *D. couperi* did not make seasonal migrations. More detailed descriptions are needed, however, to quantify seasonal variation in *D. couperi* spatial ecology in peninsular Florida.

Reproductive behavior is also known to have a strong influence on seasonal variation in snake movements both within and between sexes. Males in many species search for females during the breeding season and therefore move

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more extensively during those times (Waldron et al. 2006; Glaudas and Rodriguez-Robles 2011; Lelievre et al. 2012; Putman et al. 2013). Females might also move more extensively during the breeding season (Blouin-Demers and Weatherhead 2002; Brown et al. 2005) or exhibit reduced movement while gestating or prior to oviposition (Reinert and Zappalorti 1988; Graves and Duvall 1993; Carfagno and Weatherhead 2008). *Drymarchon couperi* appear to maintain a late fall through early spring breeding season throughout their range, during which males engage in mate searching, male–male ritualized combat, and, possibly, guarding of females (Moler 1992; Stevenson et al. 2003; Hyslop 2007; Stevenson et al. 2009; D.S. Stevenson, personal observation). In southern Georgia, however, breeding activity is largely confined to overwintering sites, presumably because *D. couperi* has a cool-season reliance on Gopher Tortoise burrows (Stevenson et al. 2003; Hyslop et al. 2009, 2014). In contrast, *D. couperi* breeding activity in peninsular Florida could potentially occur over a broader spatial extent because individuals can move throughout their home ranges during both the breeding and nonbreeding seasons (Breininger et al. 2011). Although Breininger et al. (2011) found that male *D. couperi* had larger home ranges than females, they did not examine the extent to which this might have been related to male breeding season movements, nor did they quantify the degree of within-individual seasonal home-range overlap.

Our goals were to describe seasonal variation in the spatial ecology of *D. couperi* in central Florida at multiple temporal scales, and to ascertain the degree to which seasonal variation in spatial parameters differs between sexes. Given that male *D. couperi* appear to search for females during the breeding season in southern Georgia (Stevenson et al. 2009), we hypothesized that male *D. couperi* in central Florida would also exhibit mate-searching behavior. However, given the greater potential for year-round surface activity in peninsular Florida (Breininger et al. 2011), we predicted that male mate-searching behavior in our study would result in longer, more frequent movements and larger home ranges during the breeding season compared to the nonbreeding season. We also expected that females would show either seasonally invariant movement patterns or increased movements during spring oviposition (e.g., Blouin-Demers and Weatherhead 2002). Finally, we predicted that within-individual home-range overlap would be moderate to high (Breininger et al. 2011), but that such overlap would be lowest for males when comparing breeding and nonbreeding seasons, indicating that males expanded and/or shifted their breeding season home ranges in their search for females.

Materials and Methods
Study Site and Data Collection

We used radio telemetry data collected from two separate studies. The first study occurred on the southern 40 km of the Lake Wales Ridge in Highlands County, Florida (27°17′N, 81°21′W; datum = WGS84 in all cases) from 2011–2013. This study area included both state and private lands and was a mix of natural habitats (scrub, scrubby flatwoods, mesic flatwoods, forested and nonforested wetlands), cattle ranches, citrus groves, and rural and urban development. Abrahamson et al. (1984) and Layne and

Steiner (1996) provide additional details about this study area. Sampling methodologies, including *D. couperi* capture, surgical implantation of radio transmitters, and radio telemetry procedures were described in Bauder and Barnhart (2014). Although the majority of our telemetry fixes were obtained via homing, a small number (113 of 3219 = 3.5%) were obtained via triangulation (White and Garrott 1990) with Lenth's maximum likelihood estimator (Lenth 1981) with LOAS (v4.0, Ecological Software Solutions LLC, Hegymagas, Hungary). We predicted the linear error of these locations as described in Bauder and Barnhart (2014).

The second study occurred primarily at three locations in central peninsular Florida, including Brevard (28°38′N, 80°42′W), Indian River (27°50′N, 80°35′W), and Polk counties (27°37′N, 81°19′W). These study areas included federal, state, and private lands and a diversity of natural habitats (scrub, scrubby flatwoods, mesic flatwoods, hammocks, forested and nonforested wetlands, coastal scrub) and rural and urban development. Data were collected from 1998 to 2003 as described in Breininger et al. (2011). We hereafter refer to these two data sets as Highlands and Brevard, respectively.

Movement Patterns

We used the Highlands data to analyze fine-scale movement patterns because the data were collected more frequently (approximately every 2 d) than the Brevard data (approximately weekly). We further restricted our movement analyses to telemetry fixes obtained via homing and separated by ≤7 d ($n = 2735$). All analyses were conducted in R (v3.0.2, R Foundation for Statistical Computing, Vienna, Austria) and values are reported as mean ± 1 SE unless otherwise noted.

We estimated daily probability of moving (DPM) as the per-day probability of a snake leaving its current location. Because we did not obtain daily locations on our telemetered snakes, we considered the probability of a snake leaving its current location as a binomial probability with trial size equal to the number of days until the next consecutive telemetry fix (Days) and per-trial (i.e., per day) probability (P) of moving from that location as the DPM. We estimated DPM by first calculating the sum-of-squares error (SSE) between our observed data (0 or 1 denoting whether or not the snake moved from that location) and the predicted probability of the snake moving from that location with trial size equal to Days and per-trial probability equal to P. Then, we used the function optimize to find the value of P that minimized the SSE, which we retained as our estimate of DPM. To determine how DPM varied seasonally, we used a 40-d moving window to calculate DPM and a bootstrapped 95% confidence interval for each day of the year (DOY). We selected a 40-d window because it was the smallest window size that allowed model convergence in subsequent analysis, although we found that window size had little effect on the overall pattern of our results. To create a smoothed fit to our time series of DPM, we fit a generalized additive model (GAM) to DPM for males and females separately with the use of the mgcv package (Wood 2015). We used a cyclic P-spline smooth term to ensure that the predicted DPM for DOY = 1 and DOY = 365 were equal, and a generalized approximate cross-validation to select the degree of smoothing. We calculated bootstrapped prediction intervals by

randomly sampling our data with replacement, calculating the DPM for each DOY with the use of a 40-d moving window, fitting a GAM to the new estimates of DPM, and then calculating the predicted DPM for each DOY. We repeated this process 1000 times and took the 2.5 and 97.5 percentiles of each DOY's predicted values.

We calculated daily movement rate as meters moved per day. Although most researchers obtain this value by dividing the distance between consecutive telemetry observations by the number days between those observations, this approach assumes the distance was covered equally over each day, an assumption that is unrealistic in nature. Therefore, we used our predicted DPM from the GAM to adjust our uncorrected estimates of daily movement rate, as follows:

(1) We measured the distance between consecutive telemetry locations with the package adehabitatLT in R (Calenge 2006).

(2) For each telemetry location, we calculated the probability that the telemetered snake moved from that location (P_{moved}) as a binomial probability with trial size equal to Days and P equal to the GAM-predicted DPM for that snake's sex and DOY.

(3) For $1,\ldots,n$ where n = Days, we multiplied the uncorrected movement rate (distance/n) by the binomial probability of moving from that location with trial size n = Days and per-trial probability P normalized by P_{moved}. For example, if Days = 3, P = 0.50, and distance between locations = 100 m, then P_{moved} = 0.875. We would then calculate the probability of moving 100 m over 1 d (0.375), normalize that value by P_{moved} (i.e., 0.375/0.875 = 0.429), and then multiply the resulting value by 100/1. We would then calculate the probability of moving 100 m over 2 d (0.375), normalize that value by P_{moved}, and multiply the resulting value by 100/2. Lastly, we would calculate the probability of moving 100 m over 3 d (0.125), normalize that value by P_{moved}, and multiply the resulting value by 100/3. Finally, we would sum these values to obtain the adjusted daily movement rate (i.e., [0.429 × 100 m/d] + [0.429 × 50 m/d] + [0.143 × 33 m/d] = 69.07 m/d; compared with 100 m/3 d = 33.33 m/day).

Because the frequency distribution of daily movement rate was highly right-skewed, we modeled our data using a generalized Pareto distribution (GPD) with the package texmex (Southworth and Heffernan 2013). Texmex uses a GPD with two parameters, scale and shape. The scale controls the spread of the distribution while the shape controls the shape of the distribution and can be positive or negative. In our application, both an increasing scale and shape indicate a greater frequency of longer daily movement rates, although shape had a trivial effect on the overall form of our distributions so we only report the estimates of scale. To determine how daily movement rate varied seasonally, we used a 40-d moving window to calculate scale and its bootstrapped 95% confidence interval for each DOY.

Home-Range Estimation

We estimated annual and seasonal home ranges for both Highlands and Brevard data. We used triangulated locations from Highlands County with predicted linear error ≤150 m (Bauder and Barnhart 2014) because fixed-kernel home-range estimates are robust to triangulation error at the scale observed in our study (Moser and Garton 2007). We estimated annual (i.e., 9–12 mo) home ranges with fixes from individuals tracked ≥255 consecutive days (∼9 mo), because home-range estimates are unbiased at these sampling durations (i.e., home-range size estimated with 9 mo of data is ≥0.90 of home-range size estimated with 12 mo of data; Bauder et al. 2015). We defined the breeding season as October–March and the nonbreeding season as April–September based on observations of *D. couperi* breeding activity throughout its range (Layne and Steiner 1996; Stevenson et al. 2009; Hyslop et al. 2014). We estimated seasonal home ranges for each 6-mo season with the use of individuals tracked for ≥105 consecutive days (∼3.5 mo) because estimates are unbiased at these sampling durations (i.e., home-range size estimated with 3.5 mo of data is ≥0.90 of home-range size estimated with 6 mo of data; Bauder et al. 2015), and our results were similar for individuals tracked for 6 mo. The greater sampling intensity for Highlands snakes also allowed us to calculate 3-mo home ranges for winter (January–March), spring (April–June), summer (July–September), and autumn (October–December). We used individuals tracked for ≥73 consecutive days (∼2.5 mo), and our results were similar to those using individuals tracked for 3 mo. We did not estimate 3-mo home ranges for Brevard because of insufficient telemetry fixes.

We estimated home ranges with the use of 95% fixed-kernel utilization distributions (UD) and 100% minimum convex polygons (MCP). We used the plug-in and reference bandwidths with unconstrained bandwidth matrices (Duong and Hazelton 2003) because they were robust to variation in sampling intensity and allowed for a more flexible degree of smoothing compared to single-parameter bandwidth matrices (Bauder et al. 2015). We estimated the bandwidth matrix with the use of the ks package (v1.9.2; Duong 2007, 2014). Home-range sizes estimated using the reference bandwidth were highly correlated with home-range sizes estimated using the plug-in bandwidth ($r_s \geq 0.97$) and MCP ($r_s \geq 0.97$), so we report the results of the home-range size analyses using the reference bandwidth. Because some seasonal home ranges in the Brevard data had as few as 10 fixes, we calculated area-observation plots for all seasonal home ranges by subsampling the data for each home range at $5,\ldots,n-1$ fixes, where n is the total number of fixes for that home range (Harris et al. 1990; Laver and Kelly 2008). We ran 500 iterations at each number of subsampled fixes and considered our home-range estimates to have reached an asymptote if the mean home-range size for $\geq (n \times 0.50)$ subsampled fixes was within 0.10 of the full home-range size. The number of fixes for seasonal home ranges reaching an asymptote ranged from 11 to 84. We found that the results of our subsequent analyses were similar to those obtained using all seasonal home ranges with ≥10 fixes.

We tested for effects of sex, study site (Highlands and Brevard), and their interaction on annual home-range size with the use of linear mixed-effects models with individual treated as a random effect (package nlme v3.1–111; Pinheiro et al. 2013) and ranked models with the use of AIC adjusted for small sample sizes (AIC$_c$; Burnham and Anderson 2002). We report model-averaged parameter estimates and 95% confidence interval (CI). We also tested for an effect of sex,

season, and their interaction on seasonal home-range size with the use of linear mixed-effects models. Preliminary analyses indicated a three-way interaction between sex, season, and study site for 6-mo home-range size, so we analyzed those data separately for Highlands and Brevard. The number of fixes was not correlated with home-range size for any of our analyses ($|r_s| \leq 0.12$, $P \geq 0.19$), but we nevertheless included it in our models to control for unequal sampling intensities within individuals. We also tested for an effect of body size (snout–vent length [SVL]) in all analyses because Hyslop et al. (2014) found SVL was positively associated with annual home-range size for *D. couperi* in southern Georgia. We used mean SVL values for individuals for which we had >1 measure of body size (31 of 71 subjects = 46%).

Within-Individual Spatial Overlap

We used individuals with multiple seasonal home ranges meeting the aforementioned criteria to measure the degree of spatial overlap within individuals over time. We calculated the percentage of home-range overlap at the 95% volume contour between pairs of home ranges (dyads) following Chaverri et al. (2007). However, the percentage of home-range overlap does not incorporate information provided by the UD about variation in the intensity of space use within the home range. Therefore, we calculated the volume of intersection (VI) and utilization overlap index (UDOI) at the 95% volume contour to quantify the degree of UD overlap (Fieberg and Kochanny 2005). As an additional measure of spatial overlap, we measured the Euclidean distance between home-range centroids defined as the mean *x/y* coordinates for a given home range.

We used linear mixed-effects models to test for effects of sex, seasonal combinations (e.g., breeding–breeding, nonbreeding–breeding), and their interaction on the degree of spatial overlap with individual as a random effect. The effect of body size had virtually no model support and was not included in the analyses. For 6-mo home ranges, seasonal combination was a four-level categorical variable consisting of nonbreeding vs. breeding, breeding vs. breeding, nonbreeding vs. nonbreeding, and nonbreeding vs. nonbreeding with two intervening seasons (i.e., nonbreeding 2011 to breeding 2012). We excluded home-range dyads that were separated by >2 intervening seasons. We had insufficient data within the Highlands 6-mo seasonal home ranges to fit our models, so we combined the Highlands and Brevard data (results were similar regardless). We represented seasonal combinations for the 3-mo home ranges as a four-level categorical variable with the following combinations: B–B = within the same breeding season (e.g., Fall 2011 to Winter 2011), NB–NB = within the same nonbreeding season, B–NB = adjacent 3-mo seasons within adjacent breeding and nonbreeding seasons, and B–NB1 = nonadjacent 3-mo seasons within adjacent breeding and nonbreeding seasons separated by one 3-mo season (e.g., Autumn 2011 to Spring 2012). We compared models with the use of AIC_c and report model-averaged parameter estimates and 95% CI. We examined our model residuals for homogeneity of variances and specified alternate variance structures available in the lme function as necessary to meet the assumption of homogeneity of variances. We also transformed our depen-

dent variables as necessary to meet the assumption of normality.

RESULTS
Movement Patterns

We collected data from a total of 30 *D. couperi* from the Highlands study site. However, two females developed externally visible infections around their transmitter implantation sites within 4 mo, and another male and female lost 23–31% of their body weight within 6 mo after receiving their transmitters. Therefore, we conducted all analyses with and without these four subjects and found that including them did not alter the overall patterns of our results. We nevertheless report the results of all analyses without these four subjects. We therefore included a total of 26 *D. couperi* from the Highlands site (18 males and 8 females) with mean number of fixes per individual of 110 (±55 SD) in the analyses of movement patterns.

Daily probability of movement calculated across all individuals was 0.40 and overall DPM for males and females was also 0.40. Males and females moved at similar frequencies throughout the year except for two brief periods (Fig. 1). Females moved more frequently than males during March and April, whereas males moved more frequently during November.

Median daily movement rate during the breeding season was 234 m/d (95th quantiles = 1.7–990.9 m/d) and 114 m/d (95th quantiles = 3.3–587.9 m/d) for males and females, respectively. During the nonbreeding season, these values were 185 m/d (95th quantiles = 4.4–745.0 m/d) and 140 m/d (95th quantiles = 8.2–571.8 m/d) for males and females, respectively. Overall, males exhibited longer daily movements than females (Fig. 2). Males and females made similar daily movements during the nonbreeding season as evidenced by the overlapping CI around the scale parameter (Fig. 2). During the breeding season, male daily movement distances were greater, as evidenced by the higher estimates for the scale parameter of the GPD.

Annual and Seasonal Home-Range Size

We had sufficient data from 12 Highlands and 59 Brevard subjects to estimate annual home ranges and estimated 12 and 84 annual home ranges from each study area, respectively (Appendices I and II). We removed four Highlands 6-mo home ranges because we lost contact with those subjects throughout their respective seasons and therefore estimated 36 6-mo home ranges from 19 Highlands snakes. We estimated 128 6-mo home ranges from 59 Brevard snakes. After removing 3 3-mo ranges on account of having lost contact with those subjects, we estimated 70 3-mo home ranges from 24 Highlands snakes. Males were larger than females for the pooled (male SVL = 173.4 ± 3.5 cm, female SVL = 163.9 ± 3.0 cm; $t = -2.07$, $P = 0.04$), Brevard (male SVL = 177.8 ± 4.3 cm, female SVL = 166.6 ± 2.8 cm, $t = -2.20$, $P = 0.03$), and Highlands data (male SVL = 155.3 ± 4.7 cm, female SVL = 139.5 ± 4.9 cm, $t = -2.33$, $P = 0.03$).

Models including sex were the best-supported models for all four home-range analyses (Table 1). Males consistently had larger home ranges than females (Fig. 3), although the model-averaged parameter estimate for sex overlapped zero
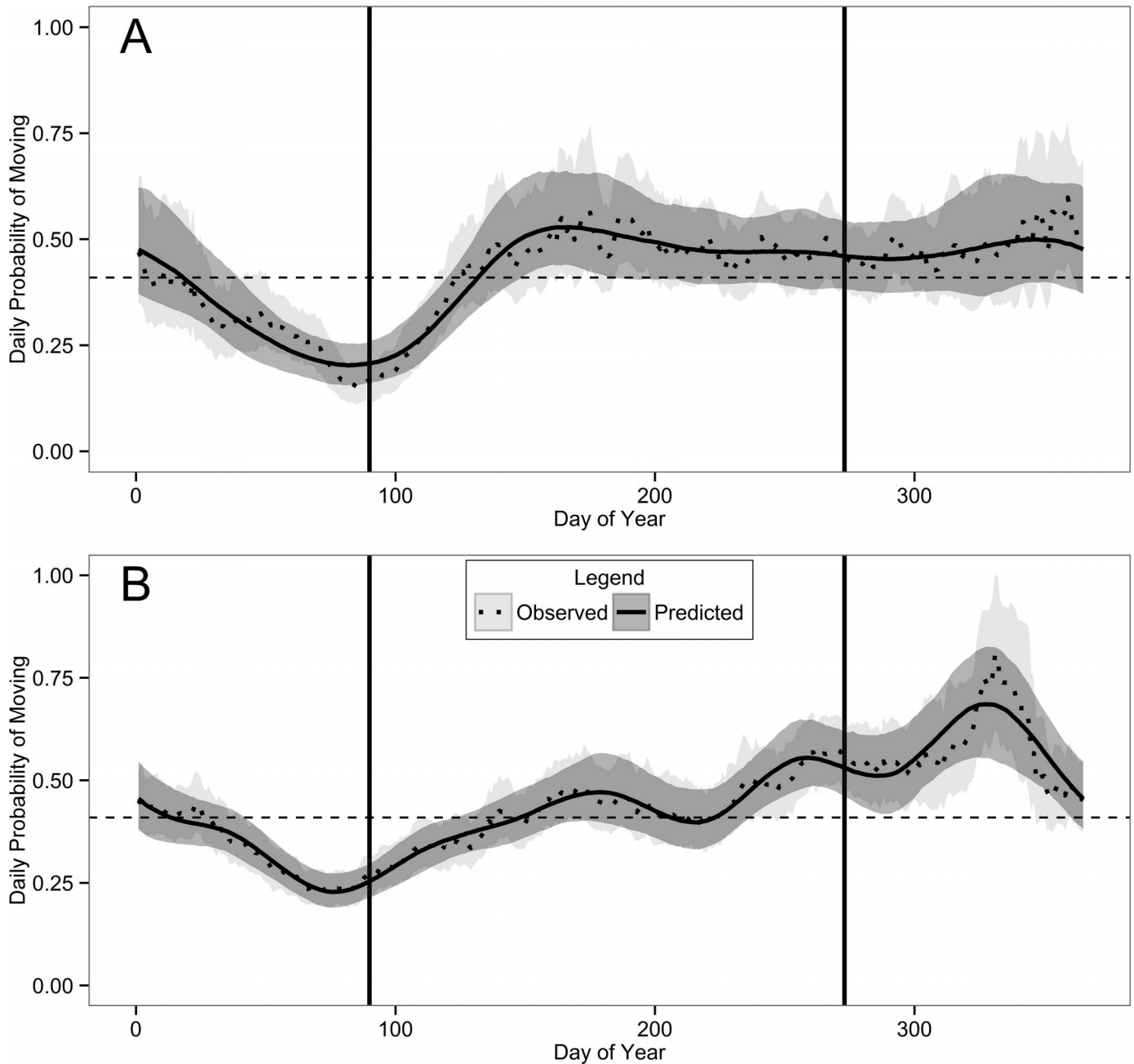
Fig. 1.—Seasonal change in daily probability of moving for female (A) and male (B) *Drymarchon couperi* in Highlands County, Florida. The dotted lines and light shaded ribbons represent the observed values with their bootstrapped 95% confidence intervals (CI) and the solid lines and dark shaded ribbons represent the predicted values and their bootstrapped 95% CI from generalized additive models fit separately to each sex. The horizontal dashed line is the overall daily probability of moving (DPM) across the entire study with both sexes (0.40). The leftmost vertical line is the start of the nonbreeding season (March 1) and the rightmost vertical line is the start of the breeding season (October 1).

for the Highlands 6-mo home ranges (Table 2). However, SVL was positively correlated with 6-mo home-range size in the Highlands subjects. Size only had a significant effect on Highlands 6- and 3-mo home-range sizes (Table 2). We found no support for differences in annual home-range size between study sites. However, the interactive effect of sex and season on 6-mo home-range size differed between Highlands (significant) and Brevard (nonsignificant, although the model-averaged 95% CI for the interactive term only slightly overlapped zero; Table 2). Male seasonal home ranges were larger in winter than in summer for Highlands,

while this trend was reduced in Brevard (Fig. 3). Male 3-mo home ranges from the Highlands data were also largest during the breeding season, whereas female 3-mo home ranges remained relatively invariant (Fig. 3).

Within-Individual Spatial Overlap

Within the Highlands and Brevard 6-mo data, we obtained 140 home-range dyads (58 males and 82 females) from 47 subjects. We obtained 74 home-range dyads (41 males and 33 females) from 19 subjects in Highlands 3-mo data. The volume of intersection was highly correlated with
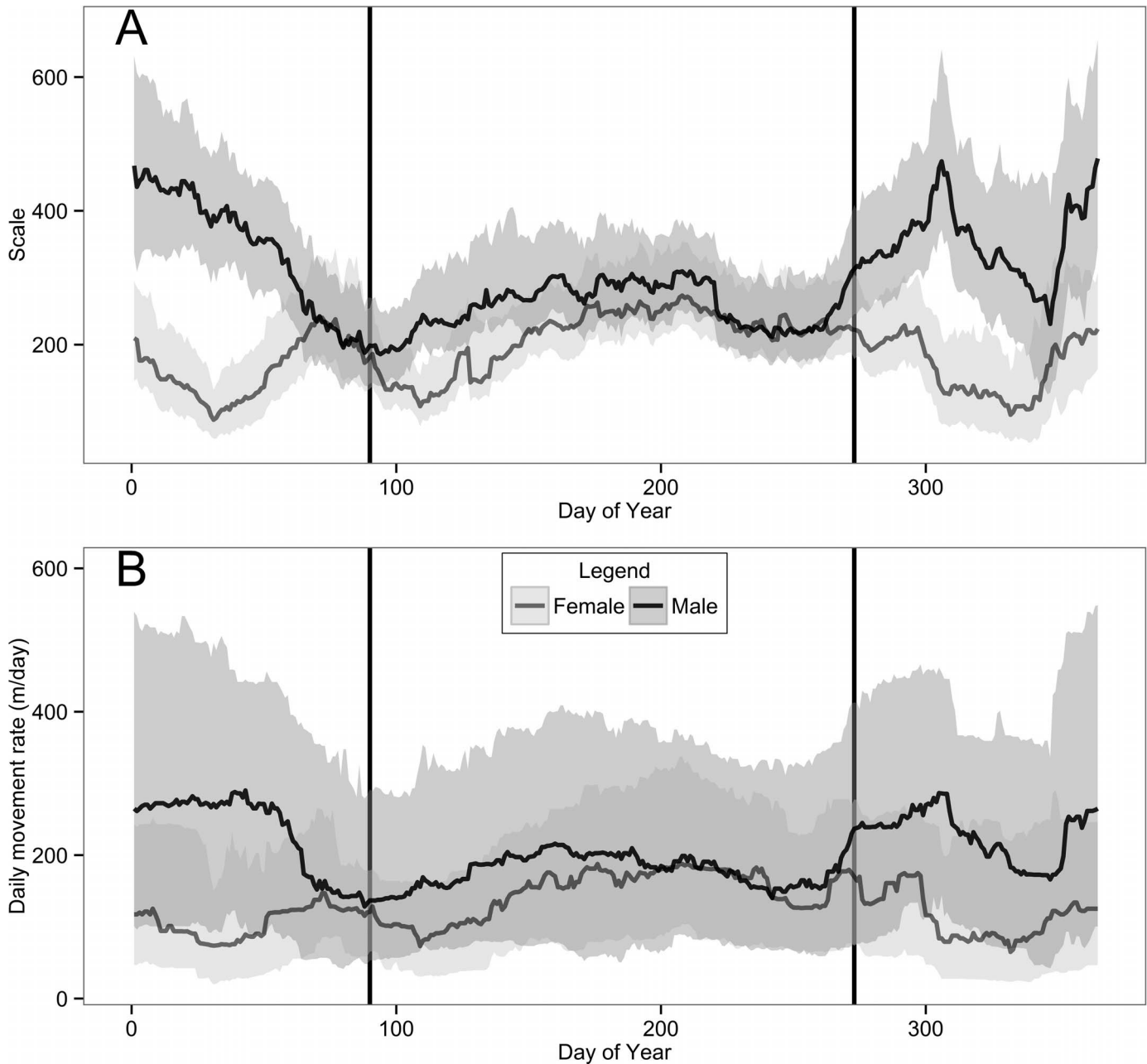
Fig. 2.—Movement distances and frequencies for *Drymarchon couperi* in Highlands County, Florida. (A) Estimates (solid lines) and bootstrapped 95% confidence interval (shaded ribbons) for the scale parameter from the generalized Pareto distributions (GPD) fit to subject daily movement distance for each day-of-year (DOY). Higher values of scale indicate a greater frequency of longer daily movement distances. (B) The median (solid lines) and inter-quartile range (25th and 75th percentiles, shaded ribbons) for daily movement rate (m/day). We do not present the estimates of the shape parameter from the GPD because it has a negligible effect on the overall form of the GPD distribution. The leftmost vertical line is the start of the nonbreeding season (March 1) and the rightmost vertical line is the start of the breeding season (October 1).

the percentage of home-range overlap ($r_s \geq 0.82$, $P < 0.0001$) and UDOI ($r_s \geq 0.96$, $P < 0.0001$), so we only report the results using VI. Mean VI across all dyads was 0.48 (range = 0.04–0.75) and 0.46 (0.13–0.75) for 6- and 3-mo dyads, respectively. Mean distance between centroids across all dyads was 296 m (11–3445 m) and 356 m (11–1469 m) for 6- and 3-mo dyads, respectively.

Models containing an effect of seasonal combination on VI between seasonal home ranges had high support for both 6- and 3-mo home ranges (Table 3). There was no strong support for an effect of sex on VI (Table 4). For 6-mo home

ranges, only the degree of overlap between breeding and non-breeding seasons separated by 12 mo (i.e., two seasons) was less than the degree of overlap between adjacent breeding and nonbreeding seasons (Fig. 4). The model-averaged 95% CI for seasonal combinations of 3-mo home ranges all overlapped zero for VI. Models containing an interactive effect of sex and season had very little support for both seasonal home ranges and overlap metrics ($w_i \leq 0.08$). We only observed two and three within-individual home-range dyads, from Brevard and Highlands, respectively (four male subjects), where the distance between home-range

TABLE 1.—Model selection results for annual, 6-mo, and 3-mo home-range sizes for *Drymarchon couperi* as a function of sex, size (snout–vent length), and study site (Study = Highlands or Brevard). Individual was included as a random effect in all analyses. Season in the 6-mo home-range models includes the breeding (October–March) and nonbreeding season (April–September); in the 3-mo model Season includes winter (January–March), spring (April–June), summer (July–September), and autumn (October–December). Number of fixes was included in all models. Deviance is $-2 \times$ log likelihood, k = number of parameters, and w_i = AIC$_c$ model weights. We report models for which the cumulative $w \geq 0.95$.

Model	Deviance	k	AIC$_c$	ΔAIC$_c$	w_i
Annual home range					
Sex + Size	−119.97	4	250.61	0.00	0.2470
Sex + Study + Size	−117.77	6	250.81	0.21	0.2228
Sex + Study	−119.07	5	251.09	0.48	0.1940
Sex	−119.19	5	251.32	0.71	0.1728
Sex × Study + Size	−117.56	7	252.77	2.16	0.0839
Sex × Study	−118.84	6	252.95	2.34	0.0768
Highlands 6-mo seasonal home range					
Sex × Season + Size	−30.04	8	81.41	0.00	0.6563
Sex × Season	−32.74	7	83.48	2.06	0.2342
Sex + Size	−35.84	6	86.58	5.17	0.0495
Sex	−37.53	5	87.07	5.65	0.0389
Brevard 6-mo seasonal home range					
Sex × Season	−141.34	7	297.62	0.00	0.4227
Sex × Season + Size	−141.09	8	299.38	1.76	0.1753
Sex + Season	−143.36	6	299.41	1.79	0.1731
Sex	−144.94	5	300.37	2.75	0.1069
Sex + Season + Size	−143.11	7	301.15	3.53	0.0723
Highlands 3-mo seasonal home range					
Sex × Season + Size	−55.64	12	140.76	0.00	0.7395
Sex × Season	−58.45	11	143.44	2.68	0.1932
Sex + Season + Size	−63.19	9	147.39	6.63	0.0269

TABLE 2.—Model-averaged betas (i.e., parameter estimates) and 95% confidence intervals (CI) for fixed-effects parameters from annual and seasonal models of home-range size for *Drymarchon couperi*. Parameter estimates for which model-averaged 95% CI did not overlap zero are displayed in bold. Reference levels are female (Sex), Brevard (Study), summer (6-mo season), and autumn (3-mo season).

| Parameter	Model-averaged β	95% CI
Annual home range		
Sex	**0.86**	**0.40 to 1.33**
Study	0.84	−0.63 to 2.31
Sex × Study	0.44	−0.90 to 1.78
Size	0.01	−0.00 to 0.02
Fixes	0.00	−0.02 to 0.01
Highlands 6-mo seasonal home range		
Sex	0.46	−0.40 to 1.32
Season	**−0.68**	**−1.31 to −0.05**
Sex × Study	**1.26**	**0.46 to 2.07**
Size	**0.02**	**0.00 to 0.04**
Fixes	**0.02**	**0.00 to 0.04**
Brevard 6-mo seasonal home range		
Sex	**0.80**	**0.30 to 1.30**
Season	**−0.30**	**−0.58 to −0.01**
Sex × Study	0.40	−0.00 to 0.79
Size	0.00	−0.01 to 0.02
Fixes	−0.01	−0.03 to 0.02
Highlands 3-mo seasonal home range		
Sex	**1.41**	**0.55 to 2.28**
Season (Spring)	0.02	−0.6 to 0.65
Season (Summer)	0.18	−0.41 to 0.78
Season (Winter)	−0.58	−1.17 to 0.01
Sex × Season (Spring)	**−0.93**	**−1.69 to −0.17**
Sex × Season (Summer)	**−0.94**	**−1.71 to −0.18**
Sex × Season (Winter)	0.06	−0.73 to 0.85
Size	**0.02**	**0.00 to 0.04**
Fixes	0.02	−0.00 to 0.04
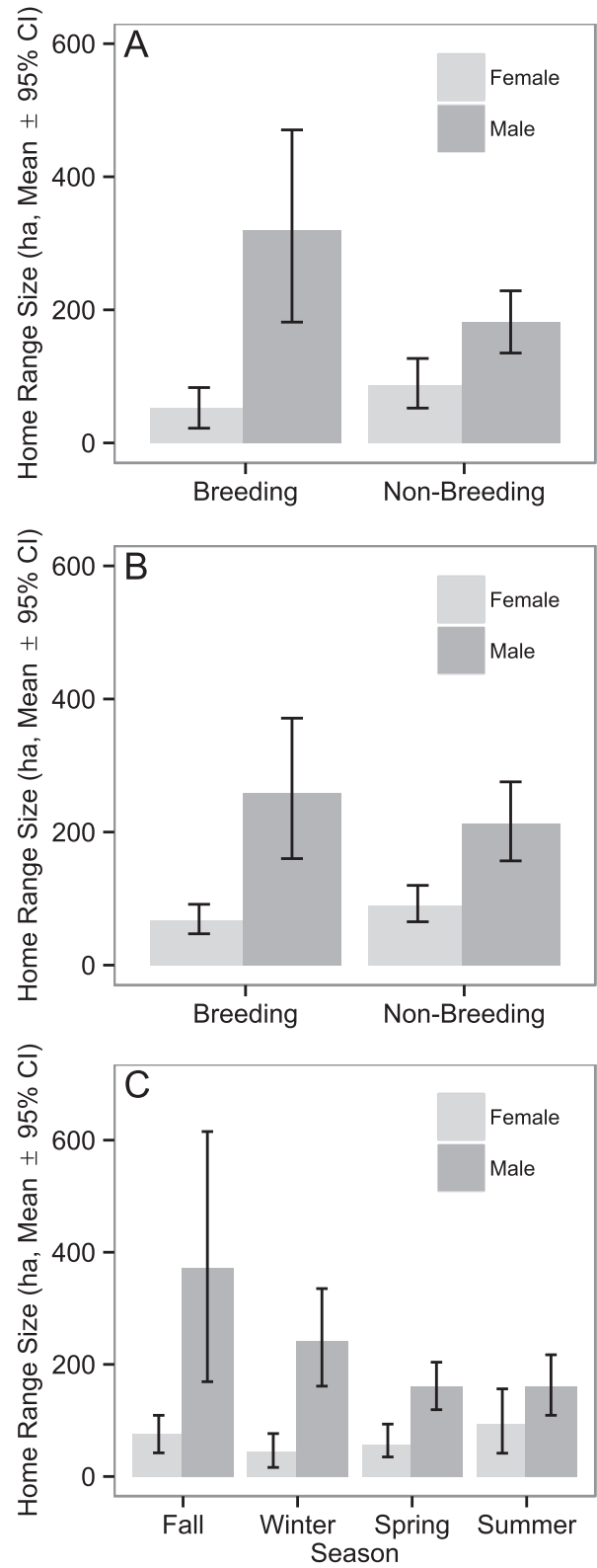
FIG. 3.—Seasonal home-range sizes (means ± bootstrapped 95% confidence interval [CI]) for *Drymarchon couperi* by sex and season. (A) Highlands 6-mo home ranges, (B) Brevard 6-mo home ranges, and (C) Highlands 3-mo home ranges. Home ranges were estimated with the use of 95% fixed-kernel utilization distributions with an unconstrained reference bandwidth matrix. Seasons for the 6-mo home ranges are breeding (October–March) and nonbreeding (April–September) and seasons for the 3-mo ranges are autumn (October–December), winter (January–March), spring (April–June), and summer (July–September).

TABLE 3.—Model selection results for *Drymarchon couperi* for factors influencing within-individual 6- and 3-mo home-range overlap. Season in the 6-mo home-range models includes the breeding (October–March) and nonbreeding season (April–September), whereas in the 3-mo model Season includes winter (January–March), spring (April–June), summer (July–September), and autumn (October–December). Deviance is $-2 \times$ log likelihood, k = number of parameters, and w_i = AIC$_c$ model weights. The null model contained only a random effect of individual. The reference levels for all models are females and a breeding–nonbreeding season with no intervening seasons (e.g., nonbreeding 2011–breeding 2011).

Model	Deviance	k	AIC$_c$	ΔAIC$_c$	w_i
Brevard and Highlands 6-mo					
Volume of intersection					
Season	57.02	6	−101.42	0.00	0.6150
Sex + Season	57.61	7	−100.38	1.04	0.3660
Sex × Season	57.92	10	−94.13	7.28	0.0161
Null	48.02	3	−89.85	11.56	0.0019
Sex	48.36	4	−88.42	13.00	0.0009
Distance between centroids					
Sex + Season	−171.77	7	358.40	0.00	0.5580
Sex	−175.48	4	359.25	0.85	0.3647
Sex × Season	−170.33	10	362.36	3.96	0.0769
Season	−181.06	6	374.75	16.36	0.0002
Null	−184.40	3	374.97	16.57	0.0001
Highlands 3-mo					
Volume of intersection					
Season	−62.50	6	−49.25	0.00	0.4396
Sex + Season	−63.33	7	−47.63	1.62	0.1956
Null	−53.87	3	−47.52	1.73	0.1854
Sex	−55.07	4	−46.49	2.76	0.1104
Sex × Season	−69.04	10	−45.55	3.71	0.0689
Distance between centroids					
Sex	169.30	4	177.88	0.00	0.8944
Sex + Season	168.07	7	183.76	5.88	0.0472
Sex × Season	160.39	10	183.88	6.00	0.0445
Null	180.00	3	186.34	8.46	0.0130
Season	178.65	6	191.90	14.02	0.0008

TABLE 4.—Model-averaged betas (i.e., parameter estimates) and 95% confidence intervals (CI) for fixed-effects parameters from *Drymarchon couperi* within-individual home-range overlap models. Parameter estimates for which model-averaged 95% CI did not overlap zero are displayed in bold. Reference levels are female (Sex) and breeding–nonbreeding (Season). The betas and CI for the interactive effect of Sex and Season are not reported because models with the interactive term had low support ($w_i \leq 0.07$) and the CI for the betas all overlapped zero.

	Model-averaged β	95% CI
Brevard and Highlands 6-mo		
Volume of intersection		
Season (breeding)	−0.04	−0.12 to 0.04
Season (nonbreeding)	0.00	−0.07 to 0.07
Season (breeding–nonbreeding 2)	**−0.18**	**−0.26 to −0.10**
Sex	−0.04	−0.12 to 0.04
Distance between centroids		
Sex	**0.93**	**0.52 to 1.34**
Season (breeding)	−0.03	−0.50 to 0.43
Season (nonbreeding)	0.25	−0.13 to 0.64
Season (breeding–nonbreeding 2)	**0.53**	**0.08 to 0.97**
Highlands 3-mo		
Volume of intersection		
Season (breeding)	0.09	−0.04 to 0.22
Season (nonbreeding)	0.10	−0.04 to 0.24
Season (breeding–nonbreeding 1)	−0.02	−0.11 to 0.07
Sex	−0.06	−0.19 to 0.07
Distance between centroids		
Sex	**1.15**	**0.49 to 1.81**
Season (breeding)	0.35	−0.44 to 1.15
Season (nonbreeding)	0.32	−0.61 to 1.25
Season (breeding–nonbreeding 2)	0.25	−0.23 to 0.73

centroids was >1 km (e.g., see Appendix S1, in the Supplemental Materials available online). For all but two subjects, there was substantial overlap between breeding and nonbreeding home ranges (i.e., VI ≥ 0.21, and % home-range overlap ≥ 0.40).

DISCUSSION

Our study supports that male and female *D. couperi* in peninsular Florida show different degrees of seasonal variation in movement patterns. Specifically, female *D. couperi* movement patterns were relatively invariant throughout the year, with the exception of a decrease in movement frequency in the late winter and early spring. In contrast, males increased their movement frequency, daily movement distances, and home-range sizes during the breeding season. These patterns are consistent with our hypothesis that male *D. couperi* undertake mate-searching movements during the breeding season. The timing of these increased movements are consistent with our observations of copulation (24 December 2012) and male–male combat (23 February 2013) among our Highlands subjects, and with reproductive behavior reported previously across the species' range (Speake et al. 1978; Moler 1992; Layne and Steiner 1996; Stevenson et al. 2003; Hyslop 2007).

Increased male movements during the breeding season are known from many snake taxa (Waldron et al. 2006; Cardwell 2008; Sperry and Weatherhead 2009b; Lelievre et al. 2012). Increased movements might increase male

reproductive success by increasing the number of females encountered (Madsen et al. 1993; Duvall and Schuett 1997; Glaudas and Rodriguez-Robles 2011; but see Smith et al. 2015). The spatial distribution of females can influence male mate-searching patterns (Duvall and Schuett 1997; Brown and Weatherhead 1999). For example, where females are widely distributed and spatially unpredictable, linear movements might maximize a male's chances of encountering a female (Duvall and Schuett 1997). At our study sites, both male and female movements throughout the year were nondirectional, indicating that female *D. couperi* were spatially predictable.

Females in many snake species also show an increase in movement during the breeding season (e.g., Cardwell 2008; Sperry and Weatherhead 2009b; Row et al. 2012), which might reflect travel to and from suitable oviposition sites (Blouin-Demers and Weatherhead 2002; Brown et al. 2005). Additionally, these movements might make females more accessible to males through the deposition of chemical cues (LeMaster et al. 2001; Jellen and Aldridge 2014; Jellen et al. 2014). In our study, however, female *D. couperi* did not increase their movements or home ranges during the breeding season and moved less frequently during the late winter and early spring. The late winter–early spring (i.e., March–April) decrease in daily probability of movement for females might be associated with gestation, as *D. couperi* oviposit in April–June (Moulis 1976; Speake et al. 1978; Newberry et al. 2009). Many female snakes reduce movements when gravid (Graves and Duvall 1993; Charland and Gregory 1995; Webb and Shine 1997; Carfagno and Weatherhead 2008). Interestingly, male *D. couperi* in our study exhibited a similar decrease in movement frequency during this period, indicating that the concurrent decrease in
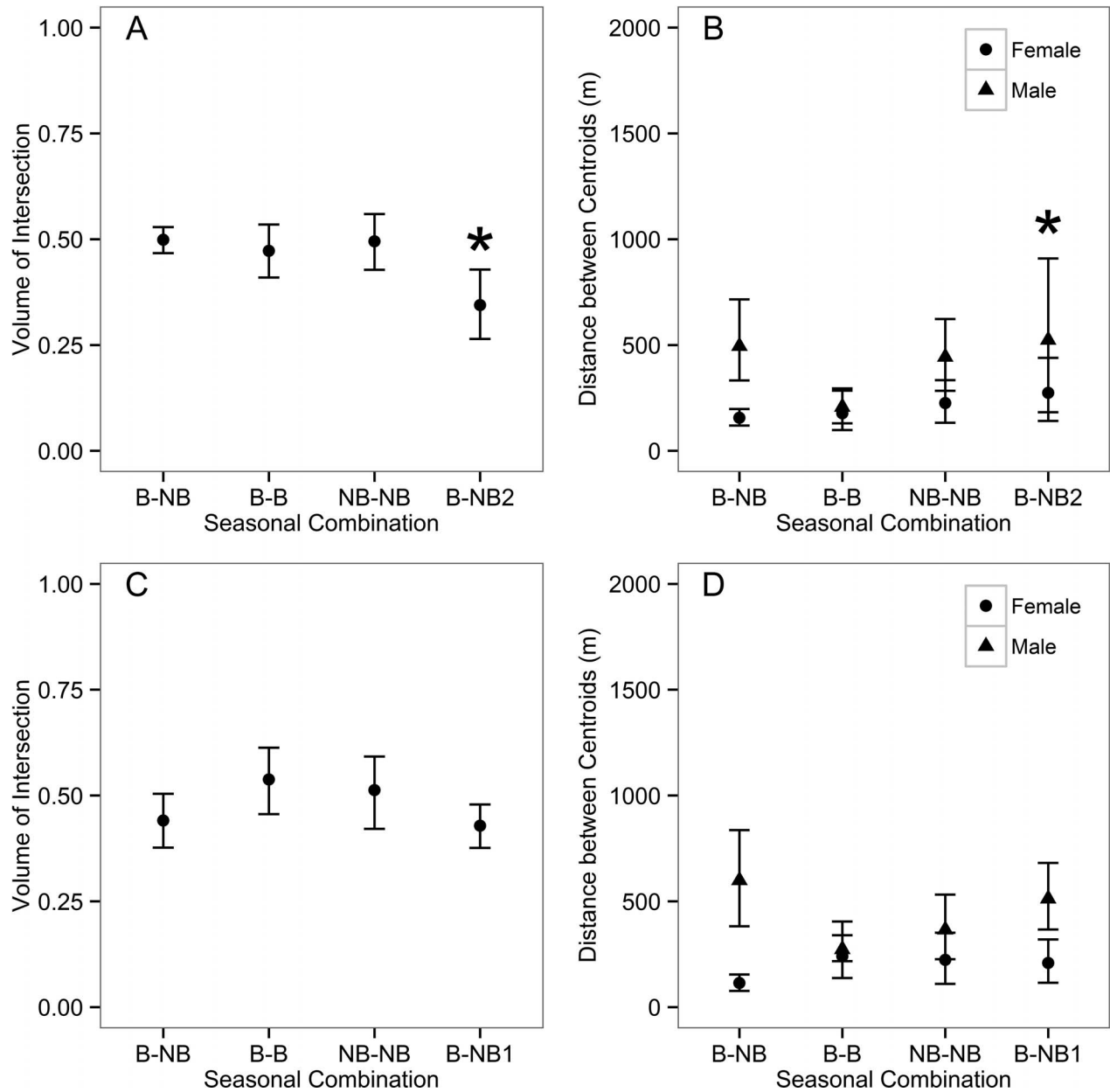
FIG. 4.—Within-individual seasonal overlap in home ranges of *Drymarchon couperi* measured in 6-mo (Brevard and Highlands sites combined, A and B) and 3-mo (Highlands only, B and C) intervals. Plotted values represent means ± bootstrapped 95% confidence interval (CI). Males and females were pooled for volume of intersection. Each 3-mo home range was reclassified into its respective 6-mo season (breeding or nonbreeding). The seasonal combination marked with an asterisk had a model-averaged parameter estimate for which the 95% CI did not overlap zero. Distance between home-range centroids differed between sexes for both the 6- and 3-mo data. See text for description of seasonal combinations.

female daily probability of movement might not be driven entirely by gestation. We are unsure of the causes behind this decrease in movement frequency. This time frame at our study sites is typically characterized by dry conditions that might reduce activity patterns among several reptilian and amphibian prey species of *D. couperi* (Stevenson et al. 2010). Lower movement frequencies during this time might therefore have been an energy-saving strategy. Dalrymple et al. (1991) found that road crossings of several snakes in southern peninsular Florida (Everglades National Park) remained relatively low through April and did not generally peak until May. Hyslop et al. (2014) found that the movement frequencies and distances of female *D. couperi*

in southern Georgia were lowest during December through April, although this might largely reflect *D. couperi* reliance on Gopher Tortoise burrows as cool-season shelter sites (Stevenson et al. 2003, 2009; Hyslop et al. 2009).

Drymarchon couperi in peninsular Florida remained surface active year-round. Many snake species in the southern portion of North America are surface-active during periods of warmer weather in winter, but these levels are generally much less than those observed during spring–autumn (Timmerman 1995; Cardwell 2008; Sperry and Weatherhead 2009b, 2012). Although studies have reported year-round snake activity in southern peninsular Florida (Dalrymple et al. 1991; May et al. 1996; cf. Bernardino and

Dalrymple 1992), activity levels still showed a decrease during the winter. With the exception of the late winter–early spring decrease in movement frequency, *D. couperi* at our study sites exhibited similar or increased activity levels during the winter months compared to the rest of the year. The pattern of winter breeding, and concurrent increases in male movements and home-range size, in *D. couperi* is different from spring and/or autumn breeding reported for most North American snakes (e.g., Aldridge and Duvall 2002). It is unclear why *D. couperi* show this divergent behavior. Dry-season (i.e., winter) breeding has been reported or inferred for several tropical species (Madsen and Shine 1996b; Aldridge and Duvall 2002; Brown and Shine 2002; Bertona and Chiaraviglio 2003; Fearn et al. 2005). The genus *Drymarchon* is found primarily in Mexico and Central and South America (Wuster et al. 2001), so winter breeding in *D. couperi* might reflect the tropical origins of this genus. However, some tropical species also breed during spring/summer months (Maciel et al. 2003; Marques et al. 2014) or show increased activity during spring–autumn compared to winter (Brown et al. 2005; Abom et al. 2012). Additionally, we note that our study did not examine the seasonality of other reproductive processes (e.g., vitellogenesis, ovulation).

The home ranges of male *D. couperi* were larger than those of female subjects during the nonbreeding season, although this difference was smallest during summer (July–September; mean values for males and females = 161.15 ha and 93.98 ha, respectively; β = 0.65, 95% CI = 0.03–1.28). This indicates that the larger annual home-range sizes we observed for males were not entirely attributable to male mate-searching movements. Similarly, Hyslop et al. (2014) found that mean spring–autumn home-range sizes for male *D. couperi* in southern Georgia were approximately 2–5 times larger than those of females. We are unsure why males would maintain larger home ranges outside of the breeding season, although other studies have also reported increased movements and/or larger home ranges for male snakes outside of the breeding season (Brown et al. 2005; Smith et al. 2009). This pattern might reflect the larger body sizes of male *D. couperi* (Layne and Steiner 1996; Stevenson et al. 2009). We found a positive effect of body size, but not sex, on seasonal home-range size at the Highlands site. However, we suspect this effect is attributable to low overlap in SVL between males and females (interquartile range, males = 145.0–162.9 cm vs. females = 126.3–141.5 cm), resulting in a high correlation between sex and SVL. Indeed, both of these covariates had similar effects on home-range size when examined separately. Hyslop et al. (2014) found that body size, in addition to sex, had a positive effect on *D. couperi* annual home-range size, and suggested that larger male home-range sizes were not attributable solely to greater resource needs of larger individuals. This hypothesis is supported by the effect of sex, but not size, on annual (Highlands and Brevard sites combined) and Brevard seasonal home-range size, despite males being larger.

Although our study was not designed to compare seasonal variation in *D. couperi* movement patterns between the southern and northern parts of their range directly, we note several qualitative differences between their movement patterns in peninsular Florida and southern Georgia (Hyslop et al. 2014). Consistent with results from Breininger et al.

(2011), *D. couperi* in peninsular Florida maintained smaller mean annual home ranges than those in southern Georgia (MCP: males, 149.12 vs. 510 ha; females, 48.97 vs. 102 ha; Hyslop et al. 2014). Although our annual home-range sizes were smaller than those reported by Breininger et al. (2011) this is likely because they reported home-range sizes with tracking durations of up to 2 yr. However, 3-mo home-range sizes, movement frequency, and distance were all lowest during winter (December–March) in southern Georgia, despite breeding occurring during that time (Speake et al. 1978; Stevenson et al. 2003, 2009; Hyslop et al. 2014). Mean 3-mo home-range size at that locality ranged from ≤10 ha for both males and females in winter to approximately 150–275 ha and 25–50 ha during spring–autumn for males and females, respectively (Hyslop et al. 2014). In contrast, mean winter 3-mo home ranges at our study sites were 100.58 ha and 16.10 ha for male and female subjects, respectively. Additionally, six males in the south Georgia study undertook lengthy (1.5–7 km) migrations between overwintering sites on sandhills and summer foraging habitat (Hyslop et al. 2014). These results contrast with the increased movement frequency, distance, and home-range size of *D. couperi* in peninsular Florida during the autumn–winter breeding season, and the lack of distinct migratory behavior.

Although our study cannot directly test hypotheses responsible for latitudinal variation in seasonal movement patterns of *D. couperi*, we suspect that this variation is driven by cooler winter temperatures in southern Georgia, which, in turn, might dictate *D. couperi* dependence on Gopher Tortoise burrows for winter shelter sites. In southern Georgia, >80% of autumn–winter shelter sites were in Gopher Tortoise burrows (Hyslop et al. 2009). In contrast, among the Highlands snakes monitored >105 d during the breeding season (*n* = 13), Gopher Tortoise burrows comprised a mean of 61% of shelter sites. Similarly, 29% of the Brevard snakes were never observed using a tortoise burrow for shelter (M. R. Bolt, personal observation).

In summary, we found that seasonal variation in *D. couperi* movements is influenced by differences in reproductive behavior between males and females, specifically male mate-searching. Our results also indicate differences in the movement and spatial ecology of *D. couperi* between the southern and northern edges of its distribution. We hypothesize that these differences are climatically driven, but additional research is needed to examine the contributing factors fully. Understanding latitudinal and seasonal variation patterns can also provide information useful for species management and conservation given the potential negative impacts of anthropogenic landscape changes on species movements at multiple spatiotemporal scales (Gillies et al. 2011; Beyer et al. 2013).

002-R). The comments of two anonymous reviewers and the Editor improved this manuscript.

Supplemental Material

Supplemental material associated with this article can be found online at http://dx.doi.org/10.1655/ Herpetplogica-D-15-00039.S1.

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APPENDIX I.—Sample sizes for estimation of annual and seasonal home ranges of male (M) and female (F) telemetered *Drymarchon couperi* in peninsular Florida. The mean (±1 SD), and range of number of fixes and number of days tracked (calculated across home ranges) are also presented.

	Number of snakes			Number of home ranges		Number of fixes		Number of days	
	Total	M	F	M	F	Mean ± SD	Range	Mean ± SD	Range
Annual, Highlands	12	9	3	9	3	103 ± 20	64–131	309 ± 47	255–365
Annual, Brevard	59	31	28	43	41	30 ±11	12–64	341 ± 53	255–365
6-mo, Highlands	19	12	7	21	15	56 ±11	35–84	160 ± 22	108–180
6-mo, Brevard	59	30	29	57	71	19 ± 4.9	11–34	161 ± 19.2	105–182
3-mo, Highlands	24	17	7	45	25	32 ± 7	18–49	86 ± 4	73–91

APPENDIX II.—Annual home-range size estimates (ha, mean ± 1 SD and range) and number of radio telemetry fixes for *Drymarchon couperi* in central Florida by sex and study location (Highlands and Brevard). Home-range estimators are the 100% minimum convex polygon (MCP) and the 95% volume contour of a fixed-kernel utilization distribution (FK UD). Utilization distributions were estimated with the use of the plug-in and reference bandwidths with unconstrained bandwidth matrices. For individuals with multiple annual home ranges we averaged their home-range sizes and then included this value in the final average.

Group	No. of snakes	No. of fixes Mean ± SD	MCP (ha)		95% FK UD (plug in) (ha)		95% FK UD (reference) (ha)	
			Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range
Highlands, males	9	99 ± 19	245.69 ± 138.95	27.71–456.17	272.76 ± 167.03	30.28–557.51	353.84 ± 202.44	39.16–456.17
Highlands, females	3	117 ± 19	60.71 ± 49.64	27.23–117.74	66.40 ± 59.65	23.70–134.55	84.41 ± 70.85	32.48–117.74
Brevard, males	31	31 ± 9	121.08 ± 97.49	6.18–371.58	220.97 ± 187.23	11.96–679.86	270.57 ± 227.89	14.32–818.13
Brevard, females	28	30 ± 12	47.72 ± 37.65	10.27–151.11	81.28 ± 75.32	13.01–315.44	101.77 ± 85.38	19.43–352.21
Males	40	45 ± 32	149.12 ± 118.53	6.18–456.17	232.62 ± 182.12	11.96–679.86	289.30 ± 222.70	14.32–818.13
Females	31	39 ± 28	48.97 ± 38.15	10.27–151.11	79.84 ± 73.23	13.01–315.44	100.09 ± 83.20	19.43–352.21
Total	71	43 ± 30	105.40 ± 104.65	6.18–456.17	165.90 ± 163.10	11.96–679.86	206.70 ± 198.82	14.32–818.13