Movement barriers, habitat heterogeneity or both? Testing hypothesized effects of landscape features on home range sizes in eastern indigo snakes

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Abstract

Animal home ranges are influenced by diverse intrinsic and extrinsic factors. For example, habitat heterogeneity may affect the spatial distribution of resources leading to larger home ranges where resources are spatially dispersed or, conversely, smaller home ranges where resources are concentrated or abundant. Other landscape features may lead to smaller home ranges by constraining or restricting animal movements. Understanding the relative importance of these two processes is increasingly important given the prevalence of anthropogenic features across contemporary landscapes. We test the relative importance of habitat heterogeneity and movement restriction on the home range size of a wide-ranging, habitat and dietary generalist, the federally threatened eastern indigo snake (*Drymarchon couperi*). We used data from 83 radio-tracked individuals in a multi-scale analysis of home range size as a function of multiple landscape features representing land cover and habitat heterogeneity. We found that home range size was negatively correlated to habitat heterogeneity (i.e., the standard deviation of normalized difference vegetation index [NDVI]) and urban intensity. Smaller home ranges in areas with high habitat heterogeneity and low urban intensity likely reflected reduced resource dispersion through the concentration of diverse foraging habitats. Home ranges were smallest in urban landscapes which, combined with previously documented avoidance of urban habitats by eastern indigo snakes, suggests that urban land cover restricts home range size. Our results demonstrate the importance of considering both the influence of resource dispersion and movement barriers in understanding animal space use. Moreover, we highlight the need to consider the potential role of anthropogenically subsidized resources (e.g., prey, shelter sites) to understand variation in eastern indigo snake home range sizes within urban areas.

Introduction

Animal movements may be thought of as spatially explicit outcomes from decisions reflecting benefits and costs of movement (Werner & Anholt, 1993; Bronmark et al., 2008). Benefits include the acquisition of food, water, mates, and shelter from predators and the abiotic environment, whereas costs include energetic expenditures, predation risk and exposure (Johnson et al., 2002; Fortin et al., 2005; Kie, Ager & Bowyer, 2005; Mitchell & Powell, 2007; Bartelt, Klaver & Porter, 2010). While intrinsic factors (e.g., sex, body size) can influence relative trade-offs of benefits and costs (Gehrt & Fritzell, 1998; Borger et al., 2006b; van Beest et al., 2011; Martin

et al., 2013), landscape characteristics may also influence these trade-offs and the resulting patterns of animal movement (Anderson et al., 2005; Karelus et al., 2017). Understanding the role of landscape features on animal movements is important both for understanding ecological processes (Collins & Barrett, 1997; Jetz et al., 2004; Fuller & Harrison, 2010) and developing effective conservation strategies (Chetkiewicz & Boyce, 2009; Zeller et al., 2017). The concept of an animal's home range as the area traversed by an individual in the course of its normal behavioral activities (Burt, 1943) provides an intuitive metric with which to understand the influence of landscape features on animal movements (Kie et al., 2010; Fieberg & Borger, 2012), particularly because a home range

should theoretically contain sufficient resources for such activities (Mitchell & Powell, 2004; Mitchell & Powell, 2007).

Landscape features influence animal home ranges through two non-exclusive processes. First, the spatial dispersion of resources often defines the extent of the area needed to obtain sufficient resources (Carr & Macdonald, 1986; Johnson *et al.*, 2002; Mitchell & Powell, 2004). High resource concentration, abundance or quality can result in smaller home ranges by reducing the spatial area required to obtain critical resources (Anderson *et al.*, 2005; Pejchar, Holl & Lockwood, 2005; Martin & Martin, 2007). For example, habitat heterogeneity may reduce home range size by increasing the spatial concentration of habitat-specific resources (Kie *et al.*, 2002; Di Stefano *et al.*, 2011; Mangipane *et al.*, 2018; Walter *et al.*, 2018). Conversely, habitat heterogeneity may increase home range size by fragmenting suitable habitat patches within a matrix of unsuitable habitats (Kapfer *et al.*, 2010; Hiller, Belant & Beringer, 2015; Ditmer *et al.*, 2018). The second process arises from differential costs of traversing certain landscape features (Proulx, Fortin & Blouin-Demers, 2014; Beyer *et al.*, 2016; Lomas *et al.*, 2019). These movement costs may reflect predation risk, insufficient resources or inhospitable abiotic conditions (Rothermel & Semlitsch, 2002; Ehlers, Johnson & Seip, 2014). Animals may therefore be unable or unwilling to circumvent these relatively high-cost habitats to access resources, thereby reducing home range size. Conversely, such habitats may indirectly increase home range size by increasing the spatial dispersion of essential resources.

Although both habitat heterogeneity, via resource concentration, and landscape impermeability may create similar patterns of home range size, the potential for differing population-level impacts makes it important to understand the mechanisms behind observed variation in home range size. For example, anthropogenically induced landscape changes may increase resource dispersion by fragmenting habitat patches within a semipermeable matrix. Although animals may still move among habitat patches, increased mortality within the matrix due to roads or human persecution (Tigas, Van Vuren & Sauvajot, 2002; Breininger *et al.*, 2012) may ultimately reduce population viability (Breininger, Legare & Bolt 2004, Fahrig, 2007; Revilla & Wiegand, 2008). Conversely, animals may exhibit reduced home range sizes in highly impermeable matrices or where habitat patches are highly isolated with potential consequences for resource acquisition, dispersal and genetic connectivity. Understanding the mechanisms behind variation in home range size in anthropogenic landscapes is therefore important for understanding species persistence in such landscapes.

In this paper, we test the relative influence of habitat heterogeneity and landscape impermeability on home range sizes of the federally threatened eastern indigo snake (*Drymarchon couperi*, hereafter DRCO). DRCO is the longest native snake in North America (>2 m) and endemic to the Coastal Plain of the south-eastern United States (Enge *et al.*, 2013). DRCO is an excellent focal species for evaluating the effects of landscape features on home range size because it is a wide-ranging species capable of moving up to 2 km in a single day with maximum home range sizes of 500–1500 ha (Breininger *et al.*, 2011; Hyslop *et al.*, 2014; Bauder *et al.*, 2016). In a previous

study in central peninsular Florida, Breininger *et al.* (2011) compared home range sizes between DRCO in suburban (i.e., developed) and natural landscapes and found that home ranges were smaller in suburban landscapes. Bauder *et al.* (2018) found that DRCO avoided urban land covers at multiple spatial scales, suggesting that suburban DRCO home ranges were smaller due to movement constraints imposed by urban development. However, because Breininger *et al.* (2011) did not quantify habitat heterogeneity, they could not evaluate its potential influence on DRCO home range size. Additionally, Breininger *et al.* (2011) classified DRCO home ranges on the basis of habitat features within the home range. Previous studies have found that home range size may be influenced by factors operating at multiple spatial scales (Kie *et al.*, 2002; Anderson *et al.*, 2005), including scales beyond the extent of the home range itself. Thus, a multi-scale analysis of the effects of landscape features on DRCO home range size is warranted to elucidate the mechanisms influencing those relationships. Therefore, we used multi-scale models of DRCO home range size to test two hypotheses arising from these previous studies: (1) Urbanization, by restricting DRCO movement, reduces DRCO home range size; and (2) habitat heterogeneity, by spatially concentrating different habitat types and the resources therein, reduces DRCO home range size.

Materials and methods

Study area

Our data were collected from four study areas across central peninsular Florida. The Cape Canaveral/Titusville (28.63°N, 80.70°W) and southern Brevard County (27.83°N, 80.58°W) study areas were located on Florida's Atlantic coast, whereas Avon Park Air Force Range (27.62°N, 81.32°W) and Highlands County (27.28°N, 81.35°W) were located in interior peninsular Florida. Xeric oak scrub, mesic pine flatwoods, hardwood hammocks, and forested and non-forested wetlands were presented in all four study areas, and maritime scrub and hammocks were presented in coastal study areas (Abrahamson *et al.*, 1984, Myers & Ewel 1990). Each study area also encompassed diverse anthropogenic habitats, including improved cattle pasture, unimproved pasture/woodlands, citrus groves, and rural and urban development. The Cape Canaveral/Titusville study area had the greatest urban development (Breininger *et al.*, 2011). Each study area contained varying proportions of public and private lands.

Radio telemetry data and home range estimation

Descriptions of radio telemetry procedures are described in Bauder and Barnhart (2014) and Breininger *et al.* (2011) and briefly recounted here. We captured DRCO primarily opportunistically in natural and anthropogenic habitats and had veterinarians surgically implant VHF radio transmitters (Reinert & Cundall, 1982; Hyslop *et al.*, 2009) into individuals weighing >500 g. We located individuals approximately weekly (Cape Canaveral/Titusville, southern Brevard County, Avon Park) or

every two days (Highlands County). Transmitter battery life ranged from 12 to 24 months, and select individuals had their transmitters replaced to extend tracking duration.

We estimated home range sizes using 95% volume contours from fixed kernel utilization distributions with unconstrained reference (REF) and plug-in (PI) bandwidth matrices (Bauder *et al.*, 2015) using the package κs (Duong, 2007; Duong, 2014) in R (R Core Team, 2017). We used snakes monitored for ≥255 consecutive days with ≥17 telemetry observations following Bauder *et al.* (2018). We calculated area-observation curves for each individual using the reference bandwidth as described in Bauder *et al.* (2016) to verify that we had a sufficient number of fixes for each individual to obtain a stable home range estimate (Harris *et al.*, 1990; Laver & Kelly, 2008). We retained the home range estimates for 83 individuals (45 males and 38 females; Cape Canaveral/Titusville: *n* = 36, southern Brevard County: *n* = 8, Avon Park: *n* = 21, Highlands County: *n* = 18) with 17–264 fixes (mean = 73, SD = 47). Although 17 fixes are a relatively small number, it is important to maximize the number of individuals in home range analyses because inter-individual variation is generally greater than variation due to sampling intensity (Borger *et al.*, 2006a). We statistically controlled for variation in sampling intensity in our analyses (see below).

Habitat covariates and hypothesized relationships

We considered 11 habitat covariates in our analyses. Details of data sources and habitat classifications are provided in Bauder *et al.* (2018) and briefly recounted here. Our land cover covariates were urban, undeveloped upland, wetland, pasture, citrus and canals because these have been found to influence multi-level habitat selection by DRCO (Hyslop *et al.*, 2014; Bauder *et al.*, 2018). Bauder *et al.* (2018) found that selection and avoidance by DRCO in peninsular Florida were strongest for undeveloped upland and urban, respectively, although DRCO tended to avoid wetland, pasture and citrus (Bauder *et al.*, 2018). Canals may also provide foraging opportunities for anurans, semi-aquatic snakes, and small mammals and mammal burrows for shelter (Ceilley et al. 2014). We also considered wetland edge because wetland–upland edges may represent additional foraging opportunities (Hyslop *et al.*, 2014).

We used multiple land cover data sources corresponding with the dates during which radio telemetry data were collected at each study area. These sources included the Cooperative Land Cover Map v. 3.0 (CLC, collected 2014) from the Florida Natural Areas Inventory and Florida Fish and Wildlife Conservation Commission (Knight, 2010; Kawula, 2014) and the St. John's (St. John's River Water Management District [SJRWMD] 2002), South Florida (South Florida Water Management District, 2004) and Southwest Florida Water Management District (Southwest Florida Water Management District, 2004). Wetland data were supplemented by the 2014 National Wetlands Inventory (NWI) data (U.S. Fish and Wildlife Service 2014). Canals were also identified using the National Hydrography Dataset's GIS flow line data at the 1:24 000

scale (U.S. Geologic Survey, 2014). All data were cross-walked into a common classification system following Knight (2010), and all GIS data were converted and/or resampled to 15-m pixel rasters.

Bauder *et al.* (2018) found that DRCO may avoid crossing paved roads. We used the 1998 U.S. Geologic Survey's 1:24 000 roads layer (U.S. Geologic Survey, 1990) (U.S. Geological Survey 1990, www.fgdl.org, accessed 1 Jun 2015) and combined all primary, secondary and tertiary roads following Bauder *et al.* (2018).

We also considered a measure of wetland–upland edge based on soil moisture. We obtained the available water storage (AWS) at 150 cm layer from the Soil Survey Geographic Database (SSURGO) accessed through the SSURGO Downloader (ESRI 2015). We then measured the standard deviation of AWS (SDAWS) using moving windows as described below.

Bauder *et al.* (2018) found that DRCO selected areas with high standard deviations of the normalized difference vegetation index (SDNDVI). They found that SDNDVI effectively captured heterogeneity in vegetation cover, particularly edges between vegetation and impervious surfaces and wetland–upland edges. We therefore considered SDNDVI as a proxy for habitat heterogeneity. We also considered NDVI itself to account for variation in vegetation cover within land cover classes. We calculated NDVI from LANDSAT 5 and 7 imagery converted to surface reflectance (Masek *et al.*, 2006) and downloaded from the U.S. Geologic Survey's Earth Explorer database (http://earthexplorer.usgs.gov/, accessed 15 May 2016). We compared the relationships between DRCO home range size and NDVI/SDNDVI calculated using winter (December–January) and spring (April–May) imagery and retained winter NDVI and SDNVI because they had greater empirical support (see also Bauder *et al.*, 2018).

We hypothesized that home range size would be negatively correlated with urban, roads and citrus due to restrictive effects (e.g., avoidance). We hypothesized that home range size would be negatively correlated with canals, wetland edge, SDAWS and SDNDVI owing to increased habitat heterogeneity. Because DRCO tends to avoid large wetland areas (Bauder *et al.*, 2018), we hypothesized a negative relationship with wetlands. We also hypothesized a negative relationship with pasture either through restrictive effects or because habitat heterogeneity within pastures is often, but not always, low. Finally, we hypothesized a positive relationship with undeveloped upland because large extents of a single land cover type may indicate reduced habitat heterogeneity.

Characterization of spatial scale

We measured each landscape covariate using a series of variable-radii circles centered on the mean of the x/y coordinates for each individual. We varied the radii from 50 to 3000 m using 100-m increments and measured the proportion or SD of each covariate within each circle after masking out open water. We identified the characteristic scale (sensu Holland, Bert & Fahrig, 2004) for each covariate using a pseudo-optimization

approach (McGarigal *et al.*, 2016) wherein we separately modeled home range size as a function of each covariate across the full range of scales. We included sex and number of days tracked in every model to control for previously documented sex-specific differences in DRCO home range size (Breininger *et al.*, 2011; Bauder *et al.*, 2016) and inter-individual variation in tracking intensity, respectively. We identified the characteristic scale as the scale with the greatest statistical support (see below) and created multi-scale models using combinations of covariates at their characteristic scales.

Statistical analyses

We report median home range sizes and the 2.5th and 97.5th quantiles. We modeled the log of home range size using linear models and ensured that assumptions of residual normality and homogeneity were met across candidate models (see below). We evaluated collinearity across landscape covariates at their best-supported scales. Urban and roads were highly correlated ($r = 0.89$), so we included these covariates in separate models. Urban, roads and undeveloped were moderately correlated with SDNDVI ($r = 0.63$, 0.66 and -0.60, respectively). All other pairwise correlations had $|r| \leq 0.59$ with the exception of canals and pasture ($r = 0.63$). Variance inflation factors were ≤ 2.00 and 2.29 for the REF and PI bandwidths, respectively.

We developed 28 candidate models with which to test how landscape features influenced DRCO home range size (Table 1). We controlled for sex and tracking intensity in each model, and our null model included only sex and number of days tracked. We evaluated support for each model using AIC adjusted for small sample sizes (AICc, Burnham & Anderson, 2002). Preliminary analyses suggested that the home range sizes for three males might be potential outliers with regards to urban and SDNDVI. For this reason, and because of the moderate collinearity among several covariates, we used a subsampling approach wherein we randomly selected 75% of our observations ($n = 62$), fit each model to the subsampled data and repeated this process 10 000 times. For each model, we calculated its mean rank, the proportion of times it was the top-ranked model (π), its median ΔAIC_c and its median R^2. We used this process to identify the characteristic scale of each covariate as the scale with the highest π. We then fit our 28 candidate models using each covariate at its characteristic scale. During each iteration, we used the remaining 21 samples as test data to evaluate each model's predictive ability. We quantified predictive ability using the root mean squared error (RMSE) and Lin's correlation concordance coefficient (CCC) between the observed and predicted test data (Lin, 1989). We report each model's median RMSE and CCC. We conducted a post hoc analysis by re-running our analyses with a 29th model containing an interactive effect between urban and SDNDVI. We evaluated the interactive relationship between home range size and urban and SDNDVI graphically using model-averaged predicted home range sizes averaged across the two models with additive and interactive effects of urban and SDNDVI.

To assess effect sizes of our covariates, we calculated model-averaged coefficient estimates after standardizing each

subsampled data set using partial standard deviations to account for collinearity (Cade, 2015) using the MuMIn package (Barton, 2015). Because we were specifically interested in effect sizes of particular covariates, we averaged coefficient estimates across models containing a given covariate following Grueber *et al.* (2011). We report the median and 2.5th–97.5th quantiles of the standardized model-averaged coefficient estimates.

We used lasso regression to evaluate covariate importance in the presence of collinearity (e.g., Olson *et al.*, 2018). Lasso regression estimates a shrinkage parameter (λ) that is applied to each covariate, resulting in covariates being 'shrunk' toward zero such that the estimates of less influential covariates are zero (Hastie, Tibshirani & Friedman 2009). We selected λ using 10-fold cross-validation using the *cv.glmnet* function and ran the lasso regression using the λ with the lowest cross-validation score with the *glmnet* function in the GLMNET package (v. 2.0-16, Friedman, Hastie & Tibshirani, 2010). For each covariate, we report the proportion of iterations where the lasso coefficient estimate was zero and the median and 2.5th–97.5th quantiles of the estimate.

We used hierarchical variance partitioning in the HIER.PART package (v. 1.0-4, Walsh & Mac Nally, 2013) to estimate the independent contribution of each covariate to the response variable (Chevan & Sutherland, 1991; Mac Nally, 2000). We specified the global model using all covariates except roads because HIER.PART can only accommodate ≤ 12 covariates. Because results from this package are sensitive to the order in which covariates are specified when using more than nine covariates (Olea, Mateo-Tomas & de Frutos, 2010), we randomly varied the order of all covariates during each of the 10 000 iterations. We report the median and 2.5th–97.5th quantiles of the independent contribution of each covariate.

Results

Characteristic scales and model rankings were very similar between the REF and PI bandwidths, and the top three models were identical between estimators (see Figure S1 and Tables S1–S2 for PI results). We therefore report results using the REF bandwidth. Median home range size was 143.8 ha (18.4–814.6 ha) across all individuals and 78.8 ha (18.8–361.7 ha) and 250.8 ha (20.5–1030.5 ha) for females and males, respectively. Six of our 11 landscape covariates had characteristic scales larger (≥ 1100 m) than the median home range size (radius = 677 m), and four covariates (roads, undeveloped, wetland and canals) had characteristic scales at the maximum scale we considered (Figure 1).

Models with SDNDVI made up eight of the nine top-ranked models (Table 1). The top three models (SDNDVI + urban, SDNDVI and SDNDVI + NDVI) had a cumulative subsampled model weight of 0.79 and relatively high predictive ability (median $R^2 = 0.53$–0.54, median CCC = 0.57). The standardized model-averaged and lasso coefficient estimates both indicated a negative relationship between home range size and SDNDVI (Figure 2), and the 2.5th and 97.5th quantiles for both metrics did not overlap zero (Table 2). We found a similar, but weaker, negative relationship with urban and NDVI although 35% of subsampled lasso regression models had $\beta_{NDVI} = 0$. Pasture had relatively high negative standardized model-averaged coefficient

Table 1 Model categories and support for 28 *a priori* candidate models relating eastern indigo snake home range size estimated using the unconstrained reference bandwidth to landscape covariates

Model	Mean Rank	Median ΔAIC$_c$	π	Median R^2	Median RMSE	Median CCC
SDNDVI + URB	2.57	0.86	0.3061	0.54	190.37	0.566
SDNDVI	2.88	1.17	0.2349	0.53	187.01	0.567
SDNDVI + NDVI	3.65	1.30	0.2538	0.54	185.59	0.565
SDNDVI + ROADS	5.43	2.70	0.0007	0.53	189.73	0.575
SDNDVI + UNDVL+WET + NDVI	5.59	3.36	0.0738	0.55	179.10	0.602
SDNDVI + CANALS	5.64	3.01	0.0127	0.53	183.79	0.572
SDNDVI + UNDVL +WET	7.02	4.28	0.0114	0.53	183.58	0.597
URB + CANALS	8.52	6.77	0.0466	0.49	217.66	0.498
SDNDVI + WETEDGE+SDAWS	8.88	4.99	0.0000	0.52	186.79	0.573
URB + PAST+CIT	9.72	7.67	0.0479	0.49	213.42	0.492
RDS + CANALS	12.01	9.49	0.0071	0.47	215.20	0.534
URB + UNDVL+WET + NDVI	12.69	10.19	0.0006	0.49	212.13	0.523
URB + UNDVL+WET	13.37	10.43	0.0000	0.47	218.23	0.516
URB	14.36	10.99	0.0000	0.45	239.05	0.442
UNDVL + WET+NDVI	14.90	11.80	0.0002	0.47	215.44	0.512
ROADS + PAST+CIT	15.17	11.55	0.0041	0.46	216.09	0.518
ROADS + UNDVL+WET + NDVI	17.06	12.77	0.0000	0.47	214.28	0.518
UNDVL + WET+PAST + NDVI	17.23	13.02	0.0001	0.47	210.06	0.517
ROADS + UNDVL+WET	18.45	13.65	0.0000	0.45	221.53	0.510
UNDVL + WET	18.61	14.02	0.0000	0.43	224.18	0.492
ROADS	19.37	14.62	0.0000	0.42	242.24	0.458
UNDVL + WET+CANALS	21.65	16.16	0.0000	0.42	221.96	0.495
UNDVL + WET+PAST	21.98	16.25	0.0000	0.42	223.60	0.491
UNDVL + WETEDGE+SDAWS + NDVI	24.93	21.69	0.0000	0.39	238.99	0.394
UNDVL + WETEDGE+SDAWS	25.07	21.90	0.0000	0.37	244.24	0.392
WETEDGE + SDAWS+CANALS	25.71	22.90	0.0000	0.36	245.27	0.421
WETEDGE + SDAWS	25.82	23.13	0.0000	0.35	256.78	0.389
Null	28.22	27.29	0.0000	0.27	288.27	0.318

CIT, citrus; PAST, pasture; SDAWS, standard deviation of available water storage; UNDVL, undeveloped upland; URB, urban; SDNDVI, standard deviation of normalized difference vegetation index; WET, wetland; WETEDGE, wetland edge.

Model metrics were calculated by randomly subsampling 62 home ranges from the full data set (*n* = 83) 10 000 times.

π is the proportion of times a given model was the top-ranked model. RMSE and CCC are the root mean squared error and Lin's (1989) concordance correlation coefficient, respectively, between the predicted and observed values for the remaining 21 home ranges.

All models, including the null model, contained sex and number of days tracked.

estimates, but 42% of subsampled lasso regression models had $β_{PASTURE} = 0$. Sex, SDNDVI and urban all had median proportions of independent contributions ≥0.15 (Table 2).

In the post hoc analysis testing for an interactive effect between SDNDVI and urban, the interactive model was ranked fourth but had a lower empirical support (median ΔAIC$_c$ = 1.90, π = 0.0701) than the aforementioned top three models (median ΔAIC$_c$ = 0.92–1.35, π = 0.22–0.27) with no appreciably greater predictive ability (Table S3). When using the PI bandwidth, the interactive model was ranked second and had similar empirical support as the model with additive effects of SDNDVI and urban (median ΔAIC$_c$ = 1.62 and 1.51, respectively, π = 0.19 and 0.16, respectively) with similar predictive ability (Table S3). The 2.5th–97.5th quantiles for the interactive coefficient estimates did not include zero for either bandwidth estimator (Table 3). A negative relationship between home range size and SDNDVI was presented across the observed range of urban values but was strongest in non-urban to low-urban landscapes (Figure 3).

Discussion

We found that SDNDVI had the strongest influence on DRCO home range size of the landscape features we evaluated, followed by urban. These strong influences were consistent across two home range estimators and multiple analytical approaches. Although other landscape covariates were included in highly ranked models, our results suggest that these covariates had relatively weak effects on DRCO home range size. The negative relationship between DRCO home range size and SDNDVI is consistent with our habitat heterogeneity hypothesis while the negative relationship between DRCO home range size and urban is consistent with our movement restriction hypothesis. However, urbanized landscapes also had relatively high SDNDVI values as the latter was highly effective in capturing the interface between vegetated and impervious surfaces. This makes it difficult to disentangle the effects of these two covariates within our study system. However, the presence of a strong interactive effect between SDNDVI and urban
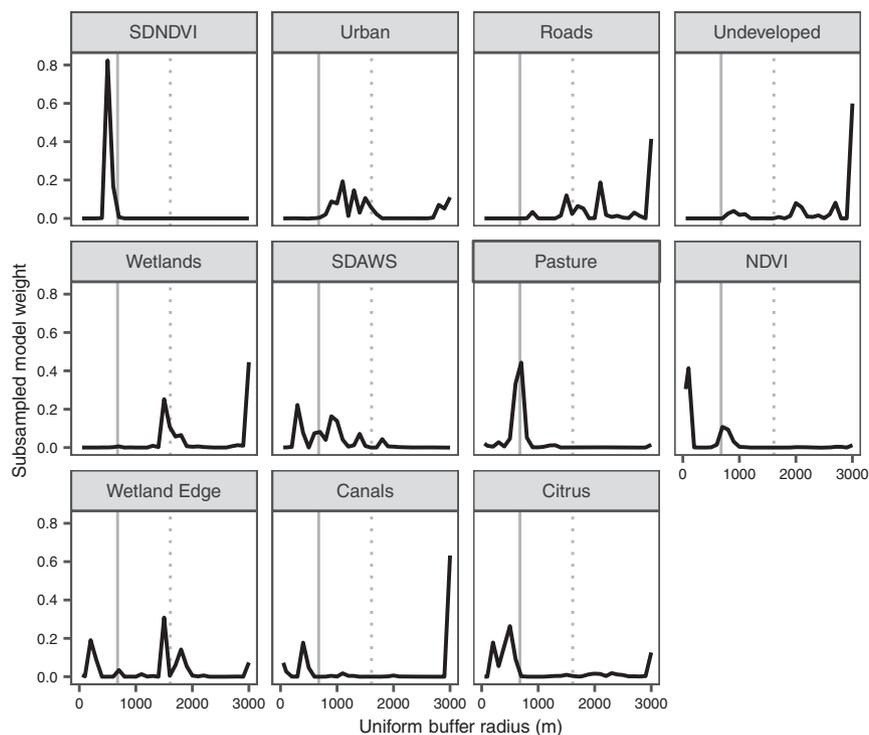
Figure 1 Characteristic scales of landscape covariates (see Table 1) influencing eastern indigo snake home range sizes estimated using the unconstrained reference bandwidth in central peninsular Florida. The y-axis values are the proportion of iterations where a given scale was the top-ranked scale using AIC_c across 10 000 iterations subsampling the full data set (n = 83) without replacement. The solid and dashed vertical lines represent the radii corresponding to the median (677 m) and 97.5th quantile (1610 m) of home range size, respectively.

suggests that both processes may influence DRCO home range size in different landscape contexts. The relationship between DRCO home range size and SDNDVI was strongest in landscapes with little or no urbanization, indicating that DRCO home range sizes in relatively undeveloped landscapes are smaller when heterogeneity in vegetation cover is high. This also suggests that the strong negative relationship between DRCO home range size and SDNDVI is not wholly driven by the correlation between SDNDVI and vegetated/impervious edge. SDNDVI also captures natural habitat edges, particularly wetland–upland edges, and heterogeneity in vegetation cover.

When resources occur in different habitats, the resource dispersion hypothesis (Macdonald, 1983; Johnson *et al.*, 2002) predicts that greater spatial concentrations of those habitats will result in smaller home ranges (Martin & Martin, 2007; Di Stefano *et al.*, 2011). Previous studies have noted negative relationships between habitat heterogeneity and home range size in ungulates (Kie *et al.*, 2002; Walter *et al.*, 2018), ursids (Mangipane *et al.*, 2018), raptors (Campioni *et al.*, 2013) and snakes (Hoss *et al.*, 2010). We hypothesize that habitat heterogeneity may increase the spatial concentration of resources for DRCO. DRCO are generalist predators that will take terrestrial and semi-aquatic prey (Stevenson *et al.*, 2010), and high habitat heterogeneity, particularly through wetland–upland edges, may correspond to greater foraging opportunities. Heterogeneous habitats may also increase the diversity and/or

concentration of retreat sites (Hyslop, Cooper & Meyers, 2009) and thermoregulating opportunities (Blouin-Demers & Weatherhead, 2001; Row & Blouin-Demers, 2006; but see Shine & Madsen, 1996). Bauder *et al.* (2018) found that DRCO selected high SDNDVI both within their home ranges and across the study area. Selection of heterogeneous habitats, including habitat edge, has been noted for a diversity of generalist predators (Marzluff *et al.*, 2004; Hoss *et al.*, 2010; Stewart *et al.*, 2013; Beatty, Beasley & Rhodes, 2014). However, additional research is needed to quantify the relationship between habitat heterogeneity and the spatial concentration of DRCO resources. Additionally, we only considered one aspect of habitat heterogeneity (i.e., variation in vegetation cover) but heterogeneity could be quantified using other approaches (Li & Reynolds, 1994).

Other studies found positive relationships between habitat heterogeneity and home range size (Tucker, Clark & Gosselink, 2008; McClintic *et al.*, 2014; Ditmer *et al.*, 2018). For example, Hiller *et al.* (2015) found that American black bear (*Ursus americanus*) home range size increased with increasing habitat diversity. This could reflect a process whereby patches of suitable habitat are increasingly dispersed within a matrix of less suitable habitat, thereby requiring a larger home range to acquire sufficient resources. Similarly, Kapfer *et al.* (2010) found that bullsnake (*Pituophis catenifer*) home range size increased with increasing amounts of avoided habitat
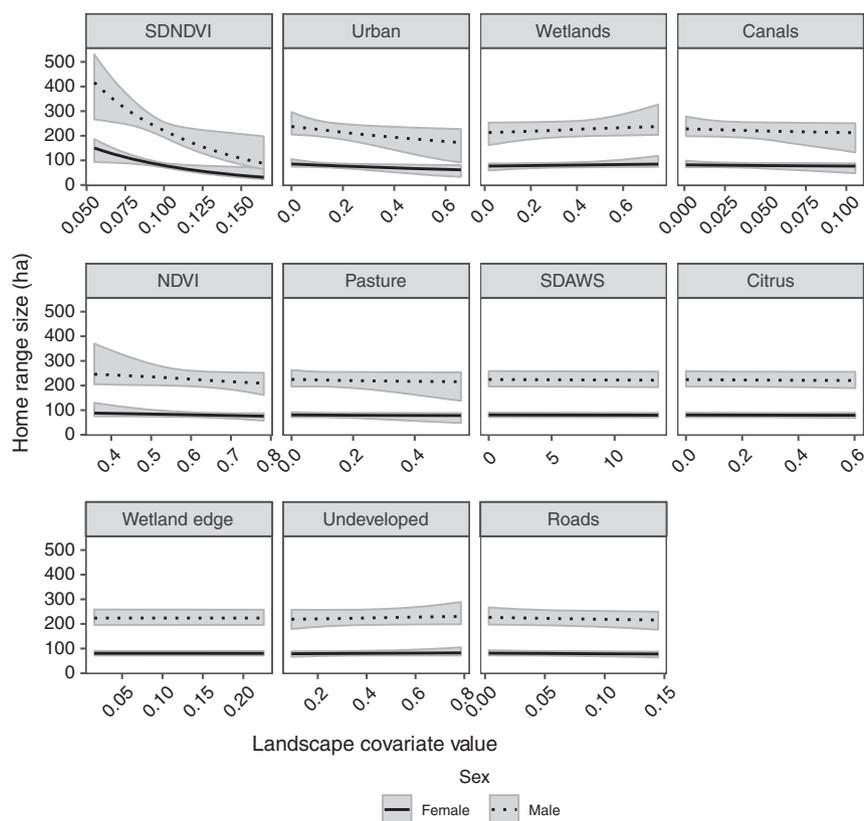
Figure 2 Model-averaged predicted eastern indigo snake home range sizes (median, 2.5th, and 97.5th quantiles across 10 000 subsampled data sets) estimated using the unconstrained reference bandwidth across landscape covariate values.

(agriculture and forest). Their observations indicated that these avoided habitats were still permeable to bullsnake movement and therefore did not constrain home range size. Testing whether agricultural land covers in our study areas simultaneously increase landscape heterogeneity and resource dispersion for DRCO would require additional analyses incorporating the spatial arrangement of different land covers. More generally, the nature of the relationship between habitat heterogeneity and resource concentration likely depends on the study species, landscape and metrics used to quantify habitat heterogeneity.

The relationship between SDNDVI and DRCO home range size was weakest in highly urbanized landscapes, where we observed the smallest DRCO home ranges consistent with Breininger *et al.* (2011). Our results are consistent with the hypothesis that smaller urban home ranges are caused by barriers or restrictions to DRCO movement, perhaps through behavioral avoidance of urban areas. Bauder *et al.* (2018) found that DRCO showed multi-scale avoidance of urban areas despite an apparent willingness to utilize them. Furthermore, DRCO suffer higher mortality in urban landscapes from both road mortality and human persecution (Breininger *et al.*, 2012). While DRCO appear to strongly avoid crossing large roads and highways, they readily cross small paved roads (Bauder *et al.*, 2018). This suggests that restrictive effects of urban areas are

not due entirely to a behavioral avoidance of roads, as suggested by the low empirical support for roads in our analyses. Urbanized areas could also be avoided through a perceived higher risk of mortality from humans or domestic animals. Mitrovich *et al.* (2009) found that coachwhips (*Coluber flagellum*), another relatively large-bodied (≥1 m), active foraging colubrid, had reduced home range size and home range overlap in habitat fragments bordered by urbanization. Lomas *et al.* (2019) reported that northern Pacific rattlesnakes (*Crotalus oreganus oreganus*) had smaller home ranges in habitats with varying anthropogenic disturbance compared to undisturbed habitats. Many studies of medium-sized mammalian carnivores have also reported negative relationships between home range size and urbanization (Gosselink *et al.*, 2003; Atwood, Weeks & Gehring, 2004; Gehrt, Anchor & White, 2009; but see Tigas *et al.*, 2002 and Riley *et al.*, 2003).

The negative relationship between DRCO home range size and urban could also result from reduced resource dispersion in urban areas through increased availability of urban-adapted prey (e.g., rodents) and anthropogenic retreat sites (e.g., brush piles, culverts). Some large-bodied herpetofauna may persist in urban environments by utilizing such resources in combination with secretive behaviors (Shine & Fitzgerald, 1996; Koenig, Shine & Shea, 2001). Tigas *et al.* (2002) suspected that

Table 2 Landscape covariate effects on eastern indigo snake home range size estimated using the unconstrained reference bandwidth

Covariate	Characteristic Scale (m)	Proportion of Lasso Zeros	Standardized Model-Averaged β	Lasso β	Proportion of Independent Contribution
Sex	NA	0.000	0.512 (0.422 to 0.600)	0.895 (0.613 to 1.119)	0.177 (0.103 to 0.276)
SDNDVI	500	0.001	−0.423 (−0.526 to −0.270)	−10.058 (−14.857 to −4.695)	0.169 (0.109 to 0.231)
Urban	1100	0.014	−0.192 (−0.469 to −0.069)	−0.877 (−1.702 to −0.211)	0.148 (0.101 to 0.203)
Wetlands	3000	0.121	0.147 (0.026 to 0.262)	0.450 (0.034 to 1.052)	0.072 (0.041 to 0.103)
Days	NA	0.196	0.145 (0.052 to 0.228)	0.000 (0.000 to 0.001)	0.038 (0.017 to 0.066)
Canals	3000	0.330	−0.106 (−0.301 to 0.018)	−3.281 (−8.899 to −0.190)	0.040 (0.019 to 0.069)
NDVI	100	0.351	−0.144 (−0.249 to −0.028)	−1.230 (−2.494 to −0.113)	0.036 (0.016 to 0.066)
Pasture	700	0.424	−0.234 (−0.340 to −0.079)	−0.754 (−1.952 to −0.006)	0.044 (0.021 to 0.071)
SDAWS	300	0.532	−0.087 (−0.156 to −0.017)	−0.016 (−0.055 to −0.001)	0.082 (0.055 to 0.111)
Citrus	500	0.606	−0.045 (−0.094 to 0.044)	−0.312 (−1.598 to 0.366)	0.043 (0.021 to 0.072)
Wetland Edge	1500	0.870	0.000 (−0.082 to 0.078)	0.005 (−2.029 to 1.914)	0.050 (0.025 to 0.077)
Undeveloped	3000	0.890	0.062 (−0.076 to 0.194)	0.018 (−1.508 to 0.488)	0.089 (0.062 to 0.122)
Roads	3000	0.959	−0.109 (−0.429 to −0.003)	−0.473 (−4.491 to 12.796)	—

SDAWS, standard deviation of available water storage; SDNDVI, standard deviation of normalized difference vegetation index.
Median and 2.5th and 97.5th quantiles of linear model and lasso regression coefficient estimates (β) and independent contribution across 10 000 data sets subsampled without replacement. Model-averaged coefficient estimates were calculated using partial standard deviations.
The proportion of lasso zeros are the proportions of iterations where a given covariate was shrunk to zero.

Table 3 Median and 2.5th and 97.5th quantiles of standardized model-averaged coefficient estimates (β) across 10 000 data sets subsampled without replacement for standard deviation of normalized difference vegetation index (SDNDVI), urban and their interactive effect (*) for eastern indigo snake home ranges estimated with unconstrained reference (REF) and plug-in (PI) bandwidths

Covariate	Bandwidth	Standardized Model-Averaged β
SDNDVI	REF	−0.412 (−0.515 to −0.268)
Urban	REF	−0.180 (−0.447 to −0.083)
SDNDVI * Urban	REF	0.112 (0.033 to 0.174)
SDNDVI	PI	−0.416 (−0.525 to −0.255)
Urban	PI	−0.246 (−0.571 to −0.119)
SDNDVI * Urban	PI	0.137 (0.044 to 0.203)

Standardized model-averaged coefficient estimates were calculated using partial standard deviations.

increased resource availability in urban areas resulted in no statistical difference for bobcat (*Lynx rufus*) and coyote (*Canis latrans*) home range sizes between fragmented and unfragmented landscapes. Anguiano & Diffendorfer (2015) found that California kingsnake (*Lampropeltis californiae*) home range size was unaffected by urbanization, likely because of their relatively small home range sizes (<10 ha). It is possible that smaller urban DRCO home ranges are in part the result of their ability to utilize a diversity of prey and retreat sites. Males of many snake species, including DRCO, increase their home ranges during the breeding season to locate females (Waldron, Lanham & Bennett, 2006; Bauder *et al.*, 2016). While estimates of DRCO densities are lacking, higher female densities in urbanized landscapes could potentially contribute to smaller male home range sizes. Fully understanding the causes behind smaller urban DRCO home ranges requires a more detailed evaluation of resource dispersion and utilization within urban landscapes.

Our results also highlight the importance of considering the effects of spatial scale in analyses of home range size (Kie *et al.*, 2002; Anderson *et al.*, 2005). While the conclusions of our multi-scale analyses regarding the effects of urban on DRCO home range size were the same as those of Breininger *et al.* (2011) using a home range-based classification, we found that landscape features most strongly influenced DRCO home range size at different spatial scales. For example, SDNDVI had the strongest effect at a scale smaller than an average DRCO home range size, suggesting that DRCO responded most strongly to within-home range habitat heterogeneity. This may reflect higher SDNDVI representing higher resource concentrations and influencing within-home range selection of those resources. In contrast, urban had the strongest effect at a scale larger than an average DRCO home range. This may be consistent with DRCO home range selection whereby DRCO select home ranges so as to reduce the amount of urban environments within their home range.

Our results corroborate the potential for urban environments to negatively affect DRCO spatial ecology and survival (Breininger *et al.*, 2011; Breininger *et al.*, 2012; Bauder *et al.*, 2018). While DRCO may persist in urban environments and potentially capitalize on anthropogenically derived resources,
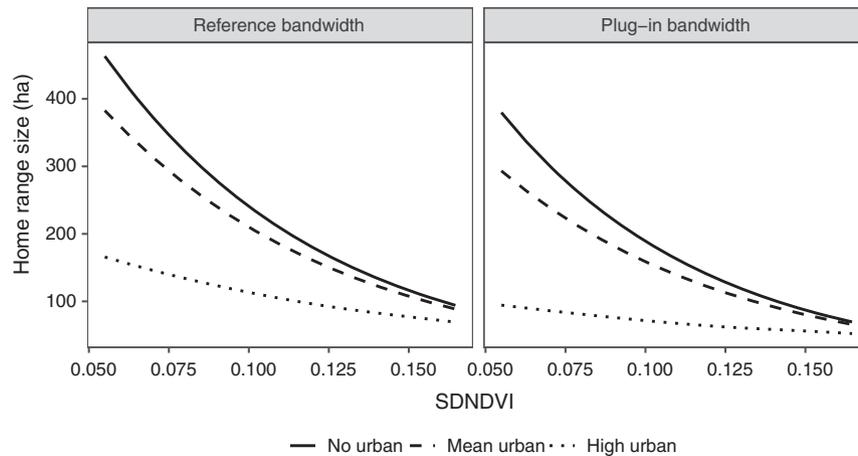
Figure 3 Model-averaged predicted male eastern indigo snake home range size (estimated using the unconstrained reference and plug-in bandwidths) as a function of the standard deviation of normalized difference vegetation index (SDNDVI) at three different levels of urbanization. Mean urban represents the mean value of urban while high urban approximates the 97th percentile of observed urban values. Only predicted values for males are shown for clarity.

such environments may have dubious value for the conservation of this species given high mortality rates for urban individuals (Breininger, Legare & Bolt 2004, Breininger *et al.*, 2012). Comparisons of DRCO body condition and density between undeveloped and urban environments could help further elucidate the condition of urban DRCO populations. We encourage additional research relating to two aspects of DRCO ecology and conservation with regard to urbanization. First, conservation programs may benefit from estimates of the minimum area needed for population persistence (e.g., Moler, 1992) under different landscape conditions, particularly estimates based on empirical estimates of DRCO space use, habitat selection and demographic parameters. Second, the consequences of urbanization for DRCO connectivity, particularly genetic connectivity, are poorly understood yet important when designing and evaluating range-wide conservation programs.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Model categories and support for 28 *a priori* candidate models relating eastern indigo snake home range size estimated using the unconstrained plug-in bandwidth to landscape covariates.

Table S2. Landscape covariate effects on eastern indigo snake home range size estimated using the unconstrained plug-in bandwidth.

Table S3. Model categories and support from a post hoc analysis testing for an interactive effect (*) of SDNDVI and urban on eastern indigo snake home range size.

Figure S1. Characteristic scales of landscape covariates influencing eastern indigo snake home range size in central peninsular Florida for home ranges estimated using the unconstrained plug-in bandwidth.