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RESEARCH ARTICLE

Multi-level, multi-scale habitat selection by a wide-ranging, federally threatened snake

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Abstract

Context Although multi-scale approaches are commonly used to assess wildlife-habitat relationships, few studies have examined selection at multiple spatial scales within different hierarchical levels/orders of selection [sensu Johnson's (1980) orders of selection]. Failure to account for multi-scale relationships within a single level of selection may lead to misleading inferences and predictions.

Objectives We examined habitat selection of the federally threatened eastern indigo snake (*Drymarchon couperi*) in peninsular Florida at the level of the home range (Level II selection) and individual telemetry location (Level III selection) to identify influential habitat covariates and predict relative probability of selection.

Methods Within each level, we identified the characteristic scale for each habitat covariate to create multi-scale resource selection functions. We used home range selection functions to model Level II selection and paired logistic regression to model Level III selection.

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Results At both levels, EIS selected undeveloped upland land covers and habitat edges while avoiding urban land covers. Selection was generally strongest at the finest scales with the exception of Level II urban edge which was avoided at a broad scale indicating avoidance of urbanized land covers rather than urban edge per se.

Conclusions Our study illustrates how characteristic scales may vary within a single level of selection and demonstrates the utility of multi-level, scale-optimized habitat selection analyses. We emphasize the importance of maintaining large mosaics of natural habitats for eastern indigo snake conservation.

Keywords Home range selection function · Habitat selection · Scale · Urbanization · Second-order habitat selection · Hierarchical habitat selection · Radio telemetry · Road crossing

Introduction

Ecological patterns and processes are influenced by factors operating at multiple spatial scales (Wiens 1989; Bowyer and Kie 2006; Martin et al. 2016). For example, species often respond to habitat features at multiple spatio-temporal scales (Boyce 2006; Mayor et al. 2009; Wheatley and Johnson 2009) or even show multi-scale responses to specific habitat features (Thompson and McGarigal 2002; Leblond et al. 2011; Shirk et al. 2014). Assessing habitat selection at one or a few spatio-temporal scales, even based on biologically-relevant criteria, may result in weak or misleading inferences regarding species-habitat relationships (e.g., Grand and Cushman 2004; McClure et al. 2012). Multi-scale habitat models often outperform single-scale models (Graf et al. 2005; Martin and Fahrig 2012; Timm et al. 2016). Characteristic scales (sensu Holland et al. 2004) may vary seasonally (Boyce et al. 2002; Zweifel-Schielly et al. 2009; Leblond et al. 2011), by sex, and behavioral state (Zeller et al. 2014). Despite the growing awareness of spatial scale in wildlife-habitat relationships, many studies fail to consider multi-scale relationships or do so at too few scales (McGarigal et al. 2016).

In their review of multi-scale habitat selection modeling, McGarigal et al. (2016) identified two non-exclusive approaches for assessing multi-scale

wildlife-habitat relationships. The first and most common approach assessed selection at hierarchically nested levels reflecting different behavioral processes (Johnson 1980; Meyer and Thuiller 2006; Mayor et al. 2009). For example, researchers might examine home range selection within a study area (i.e., Johnson's (1980) second order of selection) and selection of resource patches within a home range (i.e., Johnson's third order of selection). While levels vary in their spatial extent, and therefore scale, these extents vary among species or populations. The second approach assesses multi-scale selection by varying the spatial size (i.e., grain) of the observation unit and/or extent of analysis (e.g., Leblond et al. 2011). While scales may be selected to correspond to particular behavioral processes (e.g., home range selection), multi-level analyses explicitly link selection with different behavioral processes occurring over different spatial extents. Although multi-level studies are implicitly multi-scale (but see Wheatley and Johnson 2009), habitat covariates within each hierarchical level are predominately measured at a single spatial scale (e.g., Johnson et al. 2004). Yet multi-scale relationships may still be present within a given hierarchical level (e.g., DeCesare et al. 2012; Shirk et al. 2014; Zeller et al. 2017). Because characteristic scales may differ among covariates, using a single a priori scale for each covariate and each level may lead to misleading inferences. An alternative, and arguably more ideal, approach is to assess selection for each covariate at each level across a gradient of scales to identify the characteristic scale of each covariate at each level (e.g., Leblond et al. 2011; Bellamy et al. 2013). McGarigal et al. (2016) described this approach as a "multi-level scale optimized" approach. Despite its advantages, multi-level scale-optimized studies remain a minority among habitat selection studies (but see Zeller et al. 2017).

We examine multi-level scale-optimized habitat selection by the federally threatened eastern indigo snake (EIS, *Drymarchon couperi*). Endemic to the southeastern Coastal Plain of the U.S.A. (Enge et al. 2013), the EIS has declined throughout its range primarily due to anthropogenically induced habitat loss and fragmentation (U.S. Fish and Wildlife Service 2008). Its large body size (> 2 m), large home range sizes (Breininger et al. 2011; Hyslop et al. 2014), and year-round active foraging behavior, particularly in peninsular Florida (Bauder et al. 2016), increase its

vulnerability to anthropogenic landscape changes. Quantitative data on EIS habitat selection within peninsular Florida are lacking. Anecdotal observations suggest that EIS in peninsular Florida use a variety of natural and anthropogenically-disturbed habitats including rural and suburban development (Steiner et al. 1983; Moler 1992; Breininger et al. 2011; Enge et al. 2013). While flexible habitat use may mitigate population-level effects of anthropogenic landscape changes (e.g., Knopff et al. 2014), disturbed habitats may also act as population sinks (Mumme et al. 2000; Breininger et al. 2004), particularly if individuals select anthropogenic landscape features that increase mortality. Many snake species regularly cross roads (Andrews and Gibbons 2008) and selection for habitats containing roads combined with high road crossing rates may negatively impact population viability and connectivity (Row et al. 2007; Fahrig and Rytwinski 2009). Multi-level, multi-scale assessments of EIS habitat selection are therefore needed to better understand the impacts of anthropogenic landscape changes.

Our goal was to evaluate EIS second- and third-order selection (hereafter Level II and Level III, respectively) to provide a multi-level, scale-optimized assessment of EIS habitat selection in central peninsular Florida. We also estimated the probability of EIS road crossings to provide a fine-scale assessment of EIS responses to roads. We predicted that EIS would show negative associations with anthropogenic development and low probabilities of road crossing (Breininger et al. 2011, 2012; Hyslop et al. 2014). While EIS in peninsular Florida are surface-active year-round, they nevertheless utilize a variety of winter retreat sites, including gopher tortoise (*Gopherus polyphemus*) burrows (Bauder et al. 2016). Because tortoises primarily occupy terrestrial upland habitats (Auffenberg and Franz 1982; Castellon et al. 2015), mosaics of wetland and upland habitats may increase resource concentrations for EIS. We therefore predicted that EIS would show positive selection for natural habitat heterogeneity (e.g., Hoss et al. 2010; Steen et al. 2012) and comparatively stronger selection for upland habitats compared to wetlands during the winter. We predicted that males and females would show seasonally-variant patterns of Level III selection resulting from differences in breeding season (i.e., winter) reproductive behavior between males and females (Bauder et al. 2016).

Methods

Study areas

We used VHF telemetry data from two EIS studies occurring in a similar suite of habitats across central peninsular Florida. The Brevard study (1998–2002) encompassed Cape Canaveral/Titusville (28.63°N, 80.70°W; datum = WGS84 in all cases), southern Brevard County (27.83°N, 80.58°W), and the Avon Park Air Force Range (27.62°N, 81.32°W). The Highlands study (2011–2013) took place in central and southern Highlands County (27.28°N, 81.35°W). Natural habitats included xeric oak scrub, mesic pine flatwoods, hardwood hammocks, maritime scrub and hammocks, and various wetland habitats. Anthropogenic habitats present included improved cattle pasture, unimproved pasture/woodlands, citrus groves, commercial agriculture, and rural and urban development. Additional descriptions of the study areas and these habitats are provided elsewhere (Abrahamson et al. 1984; Myers and Ewel 1990; Breininger et al. 2011; Bauder and Barnhart 2014).

Telemetry data

Descriptions of telemetry data collection procedures are provided in Bauder and Barnhart (2014) and Breininger et al. (2011) and briefly recounted here. We monitored a total of 137 snakes (Highlands: $n = 30$, Cape Canaveral: $n = 71$, southern Brevard: $n = 12$, Avon Park: $n = 25$). Most snakes (> 90%) were captured opportunistically although a small number were captured through road-cruising, visual encounter surveys, or constant-effort trapping. Radio transmitters were surgically implanted into adult snakes weighing ≥ 500 g by professional veterinarians following standard surgical procedures (Reinert and Cundall 1982; Hyslop et al. 2009). Transmitter battery duration ranged from 12–24 months and a subset of individuals was recaptured and received new transmitters to extend their tracking duration. We located individuals approximately weekly in the Brevard study and once every two days in the Highlands study. We visually confirmed each snake's location for the majority of telemetry fixes and estimated the remaining [113 of 3219 (3.5%)] using triangulation (White and Garrott 1990), retaining only those with predicted linear error ≤ 150 m (Bauder and Barnhart 2014).

Home range estimation

We estimated "total" home ranges using all telemetry locations from each snake using the 95% volume contour polygon of a fixed kernel utilization distribution. Given that our data were collected at relatively infrequent intervals, we used the unconstrained reference bandwidth to provide a relatively high degree of smoothing and account for the uncertainty of an individual's location between telemetry fixes (Bauder et al. 2015). We estimated bandwidths using the package ks (Duong 2007, 2014) in R (R Core Team 2017). We used snakes that were monitored for $\geq$ 255 consecutive days because this duration provides an unbiased estimate of annual home range size (Bauder et al. 2015). However, some individuals meeting this criterion from the Brevard study had as few as 10 fixes. We therefore calculated area-observation plots to determine the number of fixes needed to reach a stable estimate of home range size (Bauder et al. 2016). Of the individuals from the Brevard study with $\geq$ 20 fixes, 90% (57 of 63) reached 90% of their observed home range size with < 17 fixes. We therefore assumed that $\geq$ 17 fixes would provide a reasonable estimate of the home range while still maximizing the number of individuals included in our analyses. We therefore estimated home ranges for 83 individuals (Highlands: n = 18, Cape Canaveral: n = 36, Indian River: n = 8, Avon Park: n = 21). Most variation in home range size is due to interindividual variation rather than variation in sampling intensity making it important to maximize the number of individuals (Borger et al. 2006). Additionally, other studies have found that < 20 fixes can still provide unbiased fixed kernel home range estimates (Said et al. 2005; Borger et al. 2006).

Habitat covariates

We used several habitat covariates that we predicted would influence EIS habitat selection (Table 1). Although we used land cover data from multiple sources and years, we took steps to ensure our habitat data were representative of conditions during each telemetry study period. We used 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) for the Highlands study area and

protected conservation areas in the remaining study areas. We used the St. John's (2000), South Florida (2004), and Southwest Florida Water Management District (2004) land cover data for remaining areas (additional details provided in Online Appendix 1). We also used the 2014 National Wetlands Inventory (NWI) data (U.S. Fish and Wildlife Service 2014) after visually confirming that the NWI data reflected land cover conditions when the telemetry data were collected in each study area. We classified a pixel as wetland if it was mapped as a wetland by any data source. We combined and reclassified the CLC and WMD data following Knight (2010) and considered five land cover types in our analyses: urban, undeveloped, wetlands, citrus, and improved pasture (Online Appendix 2). We considered urban, wetland, and citrus edge as additional land cover types. We also included paved roads (data collected 1998), linear wetland features (i.e., rivers, streams, canals, and ditches < 15 m wide, hereafter "canals"), soil moisture (available water storage (AWS) at 150 cm), and winter and spring normalized differenced vegetation index (NDVI) as habitat covariates (Online Appendices 3, 4). We calculated NDVI using imagery concurrent with our telemetry data. Lastly, we also calculated the standard deviation (SD) of AWS and NDVI to represent habitat heterogeneity. All GIS data, except NDVI, were obtained in vector format and converted to 15-m rasters. We assigned different weights to different road classes, urban densities, and undeveloped land covers to test if EIS responded differently to different development intensities (Table 2).

Characterization of spatial scale

To characterize scale-specific responses to our habitat covariates, we used Gaussian kernels to calculate the amount of each habitat covariate within ecological neighborhoods of varying sizes (Addicott et al. 1987). We used Uniform kernels to calculate the SD of AWS and NDVI as measures of habitat heterogeneity. We systematically varied the Gaussian bandwidth from 15–75 m using 15-m increments and from 100 to 2000 m using 100-m increments (e.g., DeCesare et al. 2012; Shirk et al. 2014). We varied the uniform kernel radii from 30 to 150 m using 30-m increments and from 200–4000 m using 200-m increments. We masked out open water pixels prior to smoothing our

Table 1 Habitat covariates used to assess multi-level, multi-scale eastern indigo snake (*Drymarchon couperi*) habitat selection in central peninsular Florida

Class	Covariate	Description	Source
Land cover	Undeveloped	Natural (e.g., scrub, flatwoods, dry prairie) and anthropogenic (e.g., unimproved pasture/woodland, rural)	CLC (Knight 2010; Kawula 2014) and WMD land cover
Land cover	Wetlands	Forested and unforested wetland	CLC and WMD land cover, Archbold Biological Station wetlands map (unpublished data), National Wetlands Inventory (USFWS 2014)
Land cover	Urban	High, medium, and low density urban	CLC and WMD land cover
Land cover	Citrus	Citrus groves	CLC and WMD land cover
Land cover	Pasture	Improved pasture	CLC and WMD land cover
Land cover	Canals	Permanent and intermittent canals and ditches ≤ 15 m wide	1:24,000 scale National Hydrography flowline data (USGS 2014)
Land cover	Roads	Paved roads (primary, secondary, tertiary)	1998 1:24,000 roads layer (USGS 1990)
Habitat edge	Wetland Edge	Wetland pixels adjacent to other land covers	CLC and WMD, Archbold Biological Station wetlands map (unpublished data), National Wetlands Inventory (USFWS 2014)
Habitat edge	Urban Edge	Urban pixels adjacent to other land covers	CLC and WMD land cover
Habitat edge	Citrus Edge	Citrus pixels adjacent to other land covers	CLC and WMD land cover
Soil moisture	AWS	Available water storage at 150 cm	Soil Survey Geographic Database (ESRI 2014)
Vegetation cover	Spring NDVI	Normalized differenced vegetation index (NDVI, Apr-May)	USGS Earth Explorer (http://earthexplorer.usgs.gov/)
Vegetation cover	Winter NDVI	NDVI (Dec-Jan)	USGS Earth Explorer

See Online Appendices 1–4 for additional details

CLC Florida Natural Areas Inventory and Florida Fish and Wildlife Conservation Commission Cooperative Land Cover Map, *WMD* Florida Water Management District, *USFWS* U.S. Fish and Wildlife Service, *USGS* U.S. Geological Survey

continuous raster surfaces and following the smoothing of all raster surfaces.

Measuring habitat use and availability

For our Level II analyses, we estimated home range selection functions (HRSF, Zeller et al. 2012). We measured habitat use by taking the home range-wide average of each habitat covariate measured at each scale and habitat availability by randomly shifting and rotating each home range 250 times within each snake's respective study area. We defined the extent of our study areas by buffering all telemetry fixes and then merging all the buffers within each study area. To select the buffer radius, we measured the maximum distance between the telemetry fixes for each individual as an approximation of home range width. We used

the 95th percentile of this distribution as our buffer radius (3860 m). We down-weighted each random UD so that the sum of the weights of the used UD equaled the sum of the weights of the available UD, ensuring a 1:1 ratio of used to available observations (Barbet-Massin et al. 2012; Squires et al. 2013).

For the Level III analyses, we evaluated how individuals selected locations relative to available habitats conditional upon the individual's current location and movement potential. We deemed it best to treat our data as points given our relatively low tracking intensity and therefore estimated point selection functions (PSF, Zeller et al. 2012) implemented conceptually as step-selection functions (Johnson et al. 2004; Thurfjell et al. 2014). We measured an individual's habitat use at time *t* and paired that value with a measure of the habitat available to that

Table 2 Weighting scenarios for different road classes and urban and undeveloped land covers

	Equal weights	Strong differences	Weak differences	Strong effect	Weak effect	No rural
Roads						
Primary	1	5	3	5	2	NA
Secondary	1	2.5	2	5	2	NA
Tertiary	1	1	1	1	1	NA
Urban/urban edge						
High density	1	5	3	5	2	NA
Medium density	1	2.5	2	5	2	NA
Low density	1	1	1	1	1	NA
Undeveloped upland						
Undeveloped	1	NA	NA	5	2	1
Rural	1	NA	NA	1	1	0

Weights were assigned to each class/category prior to Gaussian smoothing. Undeveloped includes sandhill, scrub, flatwoods, hammock, and dry prairie land covers while rural includes unimproved pasture, mixed rangeland, and rural land covers. See Online Appendices 2 and 4 for additional details

individual at time $t - 1$, thereby comparing habitat use to what an individual could have used. We measured use at each individual's unique telemetry location. For triangulated locations, we centered a Uniform kernel on the estimated location with a radius equal to that location's predicted linear error (Bauder and Barnhart 2014) and took the mean habitat value within that kernel. We measured availability using empirically-derived generalized Pareto distribution (GPD) kernels centered on the location at $t - 1$ (Zeller et al. 2014). Because the durations between successive telemetry locations varied, we allowed the size of the GPD kernel to increase as step duration increased. We modeled the relationship between the scale parameter of the GPD and the duration (i.e., number of days) between successive telemetry locations which showed scale increasing asymptotically with increasing duration (Online Appendix 5). We estimated separate PSFs for each sex and each 6-month season (breeding, Oct.–Mar., and non-breeding, April–September, Bauder et al. 2016). We used data from individuals monitored ≥ 105 days during a given season ($n = 80$), following Bauder et al. (2016), because our home range estimates are unbiased at these sampling durations (Bauder et al. 2015) and to ensure the seasonal home range was adequately sampled. This resulted in 728 observations for breeding season females ($n = 34$), 969 observations for non-breeding season females ($n = 28$), 841 observations for breeding season males

($n = 28$), and 983 observations for non-breeding season males ($n = 37$).

Resource selection analysis

We used a pseudo-optimization approach (McGarigal et al. 2016) to identify the characteristic scale for each covariate by fitting a series of single-variable models for each covariate across all scales and then retaining the scale with the lowest AIC as the characteristic scale (sensu Holland et al. 2004). For covariates with multiple weighting scenarios (Table 2) we retained the lowest-AIC scenario. We combined all covariates at their characteristic scales to create a multi-variable, multi-scale model for each level. We used a non-parametric Kruskal–Wallis test to test for differences in Level III characteristic scales among sex × season groups.

We constrained the range of scales considered for Level III to avoid confounding the effects of Level II and Level III selection. We defined the maximum scale for each sex × season group by taking the lower 5th percentile of seasonal home range size (HR5) for each group and then calculating the radius of a circular home range whose area equaled HR5. We then selected the maximum Gaussian bandwidth (h) such that $2 \times h$ equaled the radius of the circular home range and the maximum Uniform kernel radius equaled the radius of the circular home range. The

size of HR5 was 12.07 ha (females—breeding season), 23.41 ha (females—non-breeding season), 46.44 ha (males—breeding season), and 35.10 ha (males—non-breeding season), which corresponded to maximum h's of 105, 135, 195, and 165 m, respectively, and maximum radii of 210, 270, 390, and 330 m, respectively. We identified the characteristic scale as the scale with the lowest AIC that was not part of a monotonic decrease extending beyond the maximum scale. We tested for collinearity among covariates at their characteristic scales using Pearson's correlation coefficients (r). If two variables had $|r| > 0.60$ we retained the variable with the lowest AIC. Because urban and roads were moderately correlated with SD of NDVI at Level II ($r = 0.63$–0.68), we evaluated their effects post hoc by rerunning the analyses (see below) including urban or roads while excluding one or more other covariates to reduce collinearity. Variance inflation factors were ≤ 1.86 and ≤ 2.52 for the Level II and Level III analyses, respectively.

We estimated HRSFs using fixed-effects generalized linear models in R's glm function. We estimated PSFs using paired logistic regression (Compton et al. 2002; Zeller et al. 2014) and weighted each pair of used and available locations by the number of telemetry fixes observed at that location (median = 1, range = 1–10). We controlled for within-individual autocorrelation by grouping all observations by individual and computing robust (i.e., empirical) standard errors (Nielson et al. 2002; Hardin and Hilbe 2003; Fortin et al. 2005) using the coxph function in the R package survival (v. 2.38, Therneau 2015).

We fit all combinations of our covariates for both Level II and Level III because all covariates reflected a priori hypotheses, yet we had no reason to consider any particular combination of our covariates. We ranked models using AIC and used AIC parameter weights to assess relative variable importance (Burnham and Anderson 2002; Giam and Olden 2016). We standardized our data by subtracting the median from each observation and dividing it by its 0.05–0.90 quantile range. We report model-averaged standardized beta estimates, following Lukacs et al. (2010), across models whose cumulative weight summed to > 90% and deemed effects "significant" if their model-averaged 95% CI did not include zero.

Predicted surfaces

When creating predicted surfaces (e.g., Boyce et al. 2002), the data used to create each surface must be of the same type (i.e., have the same interpretation) as the data used to estimate the RSF (e.g., Zeller et al. 2016; Holbrook et al. 2017). For our Level II analyses, we therefore re-smoothed our Gaussian/Uniform kernel-smoothed rasters using a Uniform kernel equal in area to the median EIS home range (677 ha). Studies using paired logistic regression typically calculate predicted surfaces using the parameter estimates from paired logistic regression in an unpaired framework by applying the parameter estimates to habitat data without first differencing used and available data (Zeller et al. 2016). Thus, to create Level III predicted surfaces, we followed Zeller et al. (2016) to create raster surfaces representing the differences between habitat use and context-dependent availability. We used the GPD kernel corresponding to a 1-day step duration and applied it to every pixel in our kernel-smoothed raster surfaces. We then differenced these GPD kernel-smoothed surfaces (representing availability) from the original Gaussian/Uniform kernel-smoothed surfaces (representing use). We created Level III predicted surfaces for each sex × season group. We created model-averaged predicted surfaces using the models in the 90% model set. We also calculated the proportion of deviance explained (D^2) for each model.

We evaluated the predictive performances of our Level II and Level III RSF using Johnson et al.'s (2006) v-fold cross-validation procedure. Briefly, this approach divides relative probability of selection into equal-interval bins and compares the proportion of used observations within each bin to the area-weighted expected proportion of available points within each bin. We quantified the relationship between used and expected proportions using Lin's (1989) concordance correlation coefficient (CCC) following Zeller et al. (2014). Because we were interested in applying the results of our models beyond our study areas, we cross-validated our models across study sites ($v = 4$) such that for $v = i$, the ith site was used as testing data and the remaining sites as training data. For the Level III models, we created our available data by sampling our differenced raster surfaces using random points drawn from each study area at a density of 2.5 points/ha. For breeding season females, most training models

did not converge when cross-validating by site so we used 4-fold cross-validation without regard to site.

We multiplied our Level II and Level III predicted surfaces to create a multi-level, scale-optimized predicted surface of EIS relative probability of selection (Johnson et al. 2004). While not truly conditionally nested (DeCesare et al. 2012), our hierarchical multi-level design ensures that our surfaces are conceptually hierarchically nested (e.g., Johnson et al. 2004; Zeller et al. 2017).

Road crossing analysis

We modeled the daily probability of crossing a road as a binomial probability using the straight-line distance between consecutive telemetry fixes (i.e., one movement step) as the sample, trial size equal to step duration (i.e., the number of days between consecutive telemetry locations), and number of successes per sample as the number of observed road crossings for each step. We only used steps where an individual had moved (i.e., step length > 0). We assumed that we observed the true number of road crossings within each step and that no more than one crossing occurred per day. Because the validity of these assumptions decreases with increasing step duration, we only considered steps with 2–3 day durations to balance the accuracy of our observations with maximizing the number of individuals and steps included. We fit separate models for each sex × season group using road class (primary, secondary, tertiary) and Euclidean distance from road as covariates. If the snake did not move during the step, we measured the distance to the nearest road. We only included distances that were less than the diameter of a circular home range equal in area to the median seasonal home range for each group. To account for uncertainty due to maximum step duration, we fit two models for each group, one using 2 days and another 3 days as the maximum step duration. We then calculated D^2 for each model and used the normalized D^2 to calculate weighted average predicted probabilities of road crossing.

Results

Level II

The characteristic scales of 13 of our 18 covariates (including quadratic effects) were ≤ 100 m (Table 3). Among the remaining five covariates, model support for a single characteristic scale was weak (max. ΔAIC ≤ 0.90, e.g., AWS in Fig. 1). The best supported weighting scenarios for undeveloped and urban land covers and urban edge was the equal weights scenario while the best supported scenario for roads was the strong effect scenario (Table 3). Model support was equivocal across all scenarios (max. ΔAIC ≤ 2.84, Online Appendix 6).

At Level II, SD of spring NDVI (radius = 60 m), urban edge ($h = 1100$ m), and undeveloped ($h = 60$ m) received the strongest support (parameter weights ≥ 0.84) and had model-averaged 95% CI that did not or slightly overlapped zero (Table 4, Fig. 2). Post-hoc analyses including urban and roads indicated moderate to low support for these covariates (parameter weights = 0.48 and 0.32, respectively). The predictive performance of the top model was high (CCC = 0.96, 0.77–0.99) when cross-validating by site and $D^2 = 0.13$. Model-averaged CCC and D^2 across the 90% model set ($n = 164$) was 0.90 (range = 0.47–0.99) and 0.13 (range = 0.04–0.15), respectively.

Level III

Although Level III characteristic scales spanned nearly the entire range of scales we considered, the 15-m bandwidth was the most common across all groups (53%, Table 3, Fig. 3). This percentage was similar when we only considered significant covariates (55%) and covariates with parameter weights > 0.90 (62%). There was no significant difference in characteristic scales among groups (significant covariates only, $\chi^2 = 0.68$, $P = 0.88$). Model-averaged D^2 across the 90% model set was 24, 20, 32, and 22% for breeding and non-breeding season females and males, respectively.

Three covariates (SD of NDVI, undeveloped, and urban) received consistently strong support ($w = 1.00$) across all groups (Table 5). While not significant in each group, all groups selected increasing SD of NDVI and undeveloped and decreasing urban (Fig. 4). The

Table 3 Characteristic scales (m) for Level II and III selection for 18 habitat covariates

	Level II	Level III			
		Males		Females	
		Non-breeding	Breeding	Non-breeding	Breeding
Terrestrial	45[a]	15[b]	15[a]	15[b]	15[d]
Urban	15[a]	15[a]	15[a]	15[d]	15[c]
Spring NDVI	60	15	15	15	75
Winter NDVI	60	15	15	15	90
Citrus	15	15	15	15	15
Pasture	15	15	15	15	15
Canals	1200	15	60	15	45
Wetland edge	15	45	135	30	75
Wetland edge[†]	15	NA	NA	NA	NA
AWS	800	15	30	15	45
Roads	15[c]	15[d]	180[d]	30[c]	30[c]
Citrus edge	1400	60	15	15	15
Urban edge	1100[a]	135[a]	15[a]	75[a]	60[a]
Wetlands	400	90	15	30	15
Wetlands[†]	100	NA	NA	NA	NA
SD of spring NDVI*	60	45	15	75	75
SD of winter NDVI*	60	60	225	90	90
SD of AWS*	60	150	90	105	150

*Scales refer to Uniform kernel radius

[†]Wetlands and wetland edge were evaluated using linear and quadratic effects. Superscripts denote the following weighting scenarios (Table 2): [a]equal weight, [b]weak differences, [c]strong effect, [d]strong differences

degree and direction of selection for the remaining covariates varied among groups. Citrus and NDVI received strong support among three groups, with avoidance of the former and positive selection for the latter. Both sexes avoided pasture, especially during the breeding season (Table 5, Fig. 4). Males selected wetland edge while females tended to select urban edge and increasing SD of AWS while showing neutral selection for roads. While breeding season males showed broad scale ($h = 180$ m) selection for roads (Fig. 4) they also exhibited a secondary characteristic scale ($h = 15$ m, Fig. 3) and post hoc analyses indicated avoidance at this finer scale (model-averaged beta $= -0.16$, 95% CI -0.54 to 0.23, $w = 0.85$). Breeding season males appeared most selective of their habitat use showing significant selection for 7 of 12 covariates included in their analysis (Table 5).

Predictive performance varied across groups. We initially included pasture in our analyses for non-breeding season females and males but doing so reduced the model-averaged CCC from 0.70 to 0.67 and 0.81 to 0.68, respectively. Because the parameter weights for pasture were low ($w = 0.28$ and 0.39,

respectively) and the model-averaged 95% CI included zero ($\beta = -0.01$, 95% CI -0.29–0.27, $\beta = -0.09$, -0.72 to 0.54, respectively), we removed pasture from our final analyses of non-breeding season females and males. Model-averaged CCC was 0.62 (0.56–0.68), 0.70 (0.57–0.79), 0.89 (0.87–0.96), and 0.81 (0.73–0.89) for breeding and non-breeding season females and males, respectively.

Road crossing

The probability of road crossing decreased with increasing distance from road and differed among groups and road classes (Fig. 5). All groups had a near-zero probability of crossing primary roads and males had a near-zero probability of crossing secondary roads. Probability of crossing tertiary roads was 0.23–0.35 when an individual was adjacent to a road and became ≤ 0.01 when distance from road exceeded 340 m for breeding season females, 400 m for non-breeding season females, 1160 m for breeding season males, and 880 m for non-breeding season males.

Fig. 1 Change in ΔAIC across scales for select Level II covariates. Undeveloped includes rural land covers. Urban and urban edge use the equal weights scenario
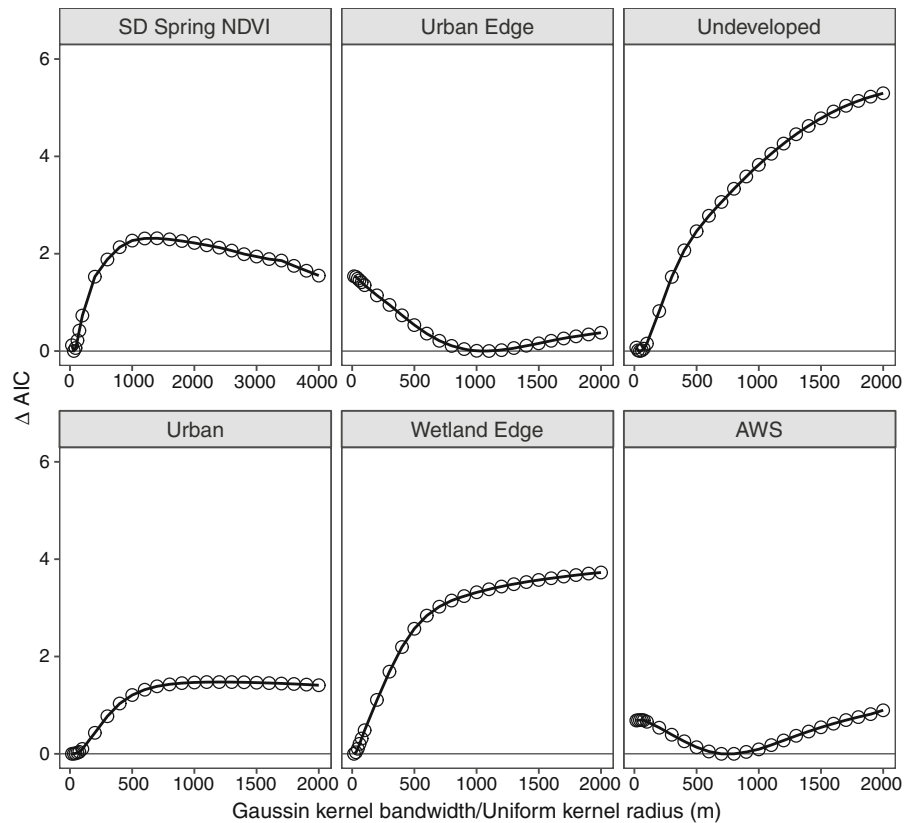

Table 4 Model-averaged standardized beta estimates, 95% CI, odds ratios, and AIC weights (*w*) for Level II covariates

|	Betas	95% CI	Odds ratio	*w*
SD Spring NDVI	2.64	0.52 to 4.76	14.01	0.89
Urban Edge	− 1.97	− 4.15 to 0.21	0.14	0.84
Undeveloped	1.60	− 0.06 to 3.26	4.95	0.84
Wetland Edge	0.31	− 0.81 to 1.43	1.36	0.39
AWS	− 0.22	− 1.36 to 0.92	0.80	0.37
Citrus	− 0.10	− 1.07 to 0.87	0.90	0.30
SD AWS	0.20	− 0.76 to 1.16	1.22	0.30
Winter NDVI	0.09	− 0.74 to 0.92	1.09	0.29
Pasture	0.03	− 0.75 to 0.81	1.03	0.28
Urban*	− 1.02	− 3.61 to 1.57	0.36	0.48
Roads*	− 0.12	− 0.92 to 0.68	0.89	0.32

*Estimates obtained via post hoc analyses (see text for details). Data were standardized by subtracting the median from each observation and dividing it by the 0.05–0.90 quantile range. Estimates were model-averaged across the 90% model set

Discussion

Our results indicate that EIS in central peninsular Florida showed consistent scale-specific responses to habitat selection within two hierarchical levels of selection. Within each level, the characteristic scales of selection were predominately the finest scales we considered. Because we used the home range as the

Fig. 2 Model-averaged predicted relative probabilities of selection and 95% CI for Level II using the 90% model set. Values for urban and roads were obtained via post hoc analyses. Covariates were standardized by subtracting the median from each observation and dividing it by the 0.05–0.90 quantile range
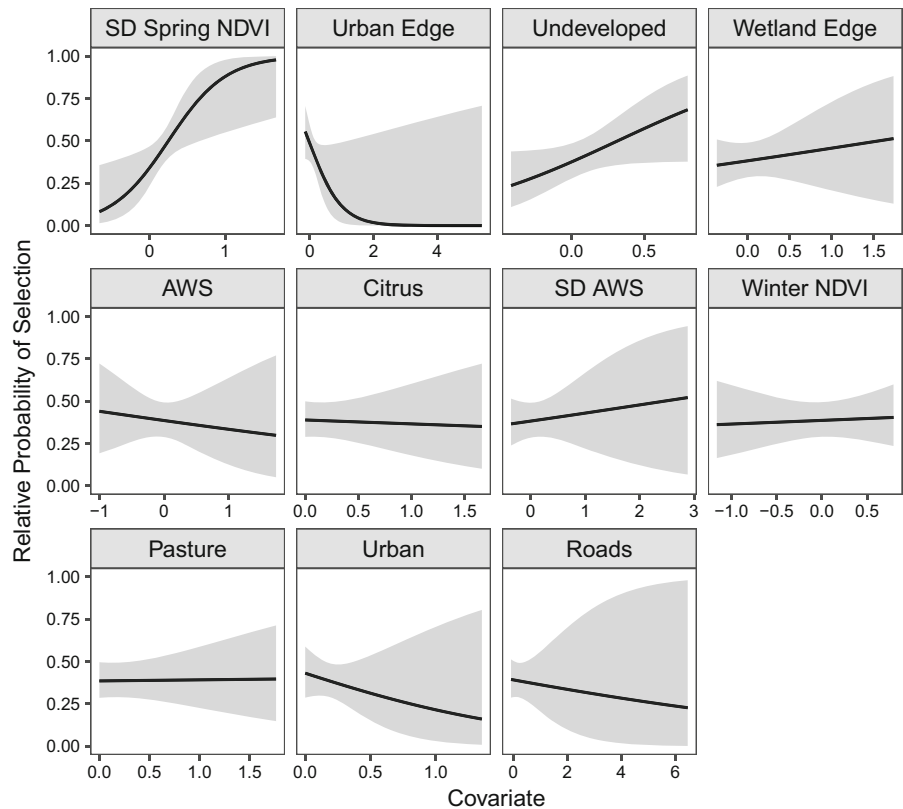

observation unit in the Level II analysis, selection at fine scales suggests that EIS respond most strongly to covariates across and slightly beyond the extent of their home range. The strongest exception to this trend was urban edge which, despite equivocal support (ΔAIC < 2) across all scales, showed the strongest association at a relatively large scale. This equivocal support across scales in our Level II analysis may suggest that a multi-scale approach using the home range as the observation unit was unnecessary. However, we still recommend that researchers conduct multi-scale Level II analyses because species may respond to habitat features beyond the extent of their home range (Kie et al. 2002; Anderson et al. 2005; Zeller et al. 2017). This may be particularly important if Level II selection is assessed using telemetry locations rather than home ranges as the observation units.

In contrast, we observed markedly different support across scales for some covariates in our Level III analysis. For example, ΔAIC between the 15- and 30-m bandwidth for undeveloped land cover ranged from 6.51–16.00. These results caution against using

single-scale analyses of habitat selection and highlight the importance of scale optimization for all covariates within a given hierarchical level. We recommend that researchers constrain the range of potential scales to correspond to a particular hierarchical level to avoid confounding selection across hierarchical levels. The broad (i.e., $h > 200$ m) characteristic scales we observed in our Level III analyses likely reflect confounding effects of second- and third-order selection. These confounding effects can be minimized by using observation units whose grain (i.e., spatial extent) corresponds to the hierarchical level of interest (e.g., assessing Level II selection using home ranges as the observation unit, Meyer and Thuiller 2006; Meyer 2007). Such an approach also ensures that relative probabilities of selection from each level are conditionally nested, thereby allowing selection at multiple hierarchical levels to be incorporated into a single predicted surface (Fig. 6).

The need to consider habitat selection at multiple spatial scales is widely recognized and many wildlife habitat selection studies employ either multi-level single-scale or single-level multi-scale analyses.

Fig. 3 Change in ΔAIC across scales for select Level III covariates by sex and season. ΔAIC for each group is rescaled so zero represents that group's characteristic scale. Undeveloped, urban, urban edge, and roads use the lowest-AIC weighting scenario (see text for details)
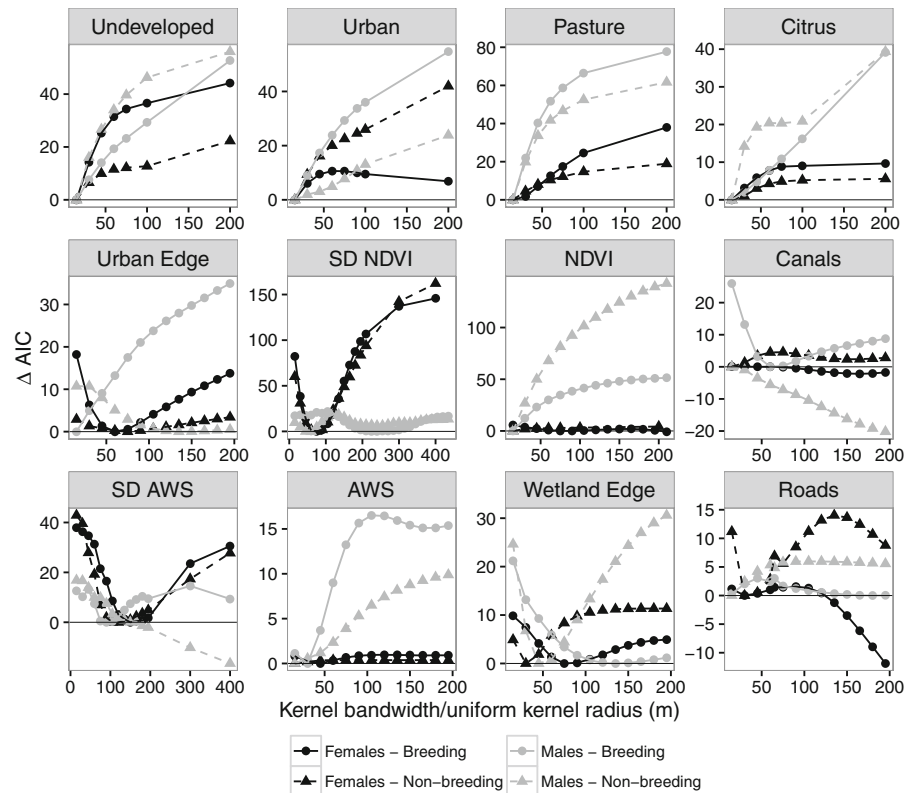
However, McGarigal et al. (2016) found that out of 173 "multi-scale" studies, only 8 were multi-level and scale-optimized. Multi-level, scale-optimized studies may be implemented in various ways depending on the study's particular objectives (e.g., Leblond et al. 2011; McNew et al. 2013). For example, researchers may optimize scale for a subset of covariates at each hierarchical level, particularly if previous research can inform the appropriate scale for the remaining covariates (Polfus et al. 2011; DeCesare et al. 2012). Alternatively, measuring covariates at a single scale within one hierarchical level while optimizing scale for covariates at other hierarchical levels may be appropriate in some applications, such as evaluating the importance of nest- or location-level factors relative to landscape-level factors (Irvin et al. 2013). However, we suggest that, for many research questions, scale-optimization across all covariates within each hierarchical level (Zeller et al. 2017) will lead to the strongest inferences and predictive abilities.

Multi-level selection of anthropogenic versus undeveloped habitats

Eastern indigo snakes also showed consistent patterns of habitat selection across levels, selecting undeveloped upland habitats and habitat edge (measured using SD of NDVI) and avoiding urbanized areas. Furthermore, EIS generally avoided citrus and pastures and selected increasing NDVI at Level III. The greater support for the equal weights scenario for urban edge (Level II) and urban (Level III) suggest that EIS consistently avoid urbanized habitat regardless of development intensity. The large Level II characteristic scale ($h = 1100$ m) for urban edge resulted in the predicted avoidance of relatively large patches of urban land cover rather than urban edge per se. This is consistent with Level II avoidance (albeit non-significant) of urban land cover. These results are consistent with our prediction that EIS would avoid anthropogenic development. However, the best supported weighting scenario for undeveloped upland for Level II included natural and rural land covers, suggesting that EIS select upland habitats with relatively low

Table 5 Model-averaged standardized beta estimates, 95% CI, odds ratios (OR), and AIC weights (*w*) for Level III covariates

	Non-breeding				Breeding			
	Betas	CI	OR	*w*	Betas	CI	OR	*w*
Males								
SD winter NDVI	1.52	0.91 to 2.13	4.57	1.00	1.93	0.60 to 3.25	6.87	1.00
Urban	− 1.13	− 2.39 to 0.14	0.32	1.00	− 1.80	− 3.25 to − 0.35	0.17	1.00
Undeveloped	0.89	− 0.23 to 2.00	2.43	1.00	1.16	0.17 to 2.14	3.18	1.00
Citrus	− 1.75	− 2.52 to − 0.97	0.17	1.00	− 1.51	− 3.26 to 0.24	0.22	1.00
Winter NDVI	2.19	1.02 to 3.36	8.95	1.00	1.49	0.47 to 2.50	4.42	1.00
Pasture	− 0.09*	− 0.72 to 0.54	0.92	0.39	− 0.48	− 1.48 to 0.52	0.62	0.79
Canals	0.12	− 0.35 to 0.59	1.13	0.46	1.49	0.32 to 2.66	4.45	1.00
SD AWS	0.09	− 0.42 to 0.61	1.10	0.39	0.21	− 0.71 to 1.12	1.23	0.58
Wetland edge	0.79	0.12 to 1.46	2.20	1.00	1.43	0.33 to 2.53	4.17	1.00
AWS	− 0.05	− 0.63 to 0.53	0.95	0.32	− 2.03	− 3.85 to − 0.21	0.13	1.00
Roads	− 0.17	− 0.60 to 0.25	0.84	0.68	0.43	− 0.09 to 0.96	1.54	0.89
Urban edge	− 0.18	− 1.25 to 0.88	0.83	0.54	NA	NA	NA	NA
Wetland	− 0.19	− 1.15 to 0.77	0.83	0.46	NA	NA	NA	NA
Citrus edge	NA	NA	NA	NA	0.14	− 0.07 to 0.36	1.15	0.98
Females								
SD winter NDVI	NA	NA	NA	NA	3.11	1.53 to 4.69	22.47	1.00
SD spring NDVI	2.97	1.91 to 4.04	19.57	1.00	NA	NA	NA	NA
Urban	− 1.42	− 2.64 to − 0.21	0.24	1.00	− 1.10	− 2.30 to 0.09	0.33	1.00
Undeveloped	1.30	0.32 to 2.29	3.68	1.00	1.33	0.19 to 2.46	3.78	1.00
Citrus	− 0.07	− 0.76 to 0.62	0.93	0.40	− 0.55	− 2.18 to 1.08	0.58	1.00
Winter NDVI	1.10	0.29 to 1.90	3.00	1.00	0.17	− 1.63 to 1.98	1.19	0.37
Spring NDVI	NA	NA	NA	NA	NA	NA	NA	NA
Pasture	− 0.01*	− 0.29 to 0.27	0.99	0.28	− 0.62	− 1.72 to 0.48	0.54	1.00
Canals	0.52	− 0.13 to 1.17	1.68	0.99	0.18	− 1.07 to 1.42	1.19	0.51
SD AWS	0.70	− 0.07 to 1.46	2.01	0.93	1.57	− 0.07 to 3.21	4.81	1.00
Wetland edge	0.01	− 0.33 to 0.35	1.01	0.28	0.01	− 0.83 to 0.84	1.01	0.27
AWS	− 0.07	− 0.60 to 0.46	0.93	0.34	− 0.18	− 1.19 to 0.82	0.83	0.46
Roads	0.03	− 0.20 to 0.25	1.03	0.33	0.08	− 0.29 to 0.46	1.08	0.50
Urban edge	0.13	− 0.54 to 0.80	1.14	0.45	1.05	0.22 to 1.88	2.86	1.00
Citrus edge	NA	NA	NA	NA	0.01	− 0.06 to 0.07	1.01	0.32

*Estimates obtained via post hoc analyses (see text for details) and were not included in the final model set. Data were standardized by subtracting the median from each observation and dividing it by the 0.05–0.90 quantile range. Estimates were model-averaged across the 90% model set

levels of anthropogenic disturbance. Multiple studies of medium-bodied mammalian carnivores in urbanized landscapes have also reported fine-scale avoidance of urban habitats (Riley et al. 2003; Gehrt et al. 2009; Gross et al. 2012). The fine-scale Level III avoidance of urban land cover may allow EIS to utilize relatively small patches of natural habitats within a matrix of urban land covers, a pattern seen in other snakes in urban landscapes (Mitrovich et al. 2009; Anguiano and Diffendorfer 2015). Breininger et al. (2011) found that EIS home ranges in suburban landscapes were significantly smaller than those in natural landscapes, a pattern consistent with our results.

Fig. 4 Model-averaged predicted relative probabilities of selection for Level III by sex and season using the 90% model set. Covariates were standardized by subtracting the median from each observation and dividing it by the 0.05–0.90 quantile range. Missing covariates were excluded from final analyses due to multicollinearity


— Female – Breeding   — Male – Breeding

-- Female – Non–breeding   -- Male – Non–breeding
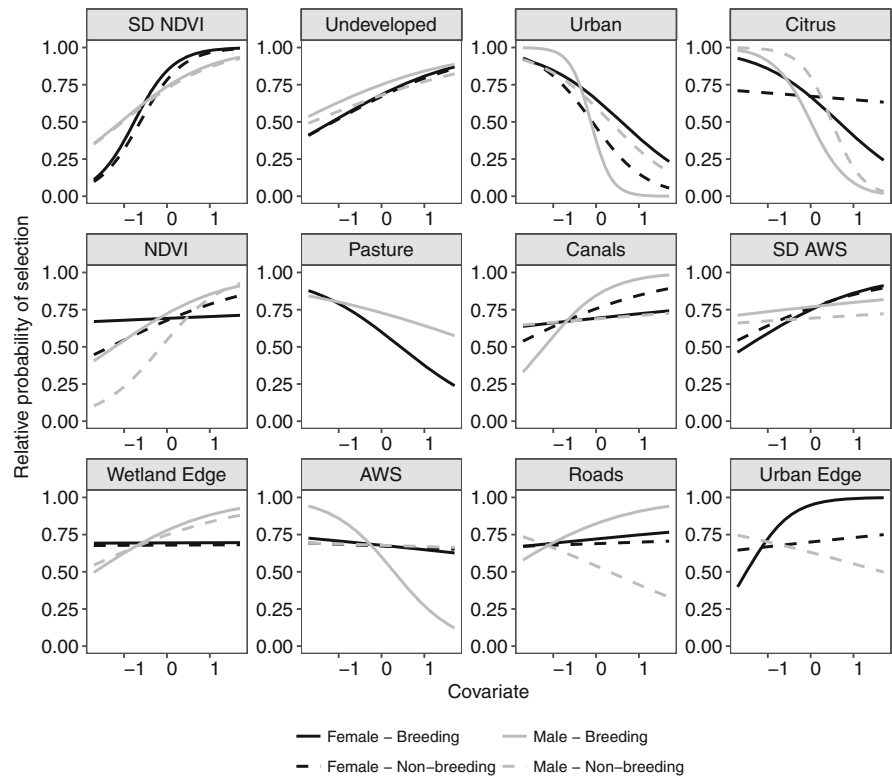
We are limited in our ability to discern the mechanisms responsible for EIS avoidance of anthropogenic habitats. While it could reflect scarcity of resources, anthropogenic habitats often support numerous potential prey and shelter sites (Koenig et al. 2001; Kwiatkowski et al. 2008; Pattishall and Cundall 2009). Like other researchers (Enge et al. 2013), we have observed EIS in all three urban development classes as well as citrus and pasture. Avoidance of anthropogenic habitats may also reflect risk avoidance behavior and/or cumulative effects of road mortality and human persecution (Breininger et al. 2012). However, EIS appeared to avoid urban more strongly than roads. Only non-breeding season males avoided roads (albeit non-significantly) and all groups had relatively high daily probabilities (≥ 0.23) of crossing adjacent tertiary roads.

Selection for habitat heterogeneity

Eastern indigo snakes also selected increasing SD of NDVI at both levels, which represents selection for habitat edges, either between vegetation communities or between vegetated and impervious surfaces (e.g.,

roads, urban development). Wetland edge and SD of AWS were also significantly selected at Level III by males and females, respectively. These results are also consistent with our prediction of selection for natural habitat heterogeneity. We offer several hypotheses to explain these patterns. First, heterogeneous habitats may spatially concentrate resources and compress home range sizes (Law and Dickman 1998; Kie et al. 2002; Hoss et al. 2010). Second, EIS are dietary generalists (Stevenson et al. 2010) and habitat edges may increase the diversity and abundance of potential prey species. Edge selection has been noted for dietary generalists in many mammalian and avian taxa (Marzluff et al. 2004; Stewart et al. 2013; Beatty et al. 2014). Third, habitat edges may increase opportunities for thermoregulation, a pattern noted in many north-temperate snakes (Blouin-Demers and Weatherhead 2001a; Row and Blouin-Demers 2006). However, ectotherms in mild climates may be more flexible in their thermoregulation (Shine and Madsen 1996) and therefore less reliant on edges or habitat openings for thermoregulation (Anderson and Rosenberg 2011). We did not observe a consistent increase in selection for SD NDVI during the winter breeding

Fig. 5 Predicted probability of road crossing by sex and season as a function of Euclidean distance from road and road class. Probabilities were obtained using D^2-weighted averages of predicted values using 2 and 3 day step durations
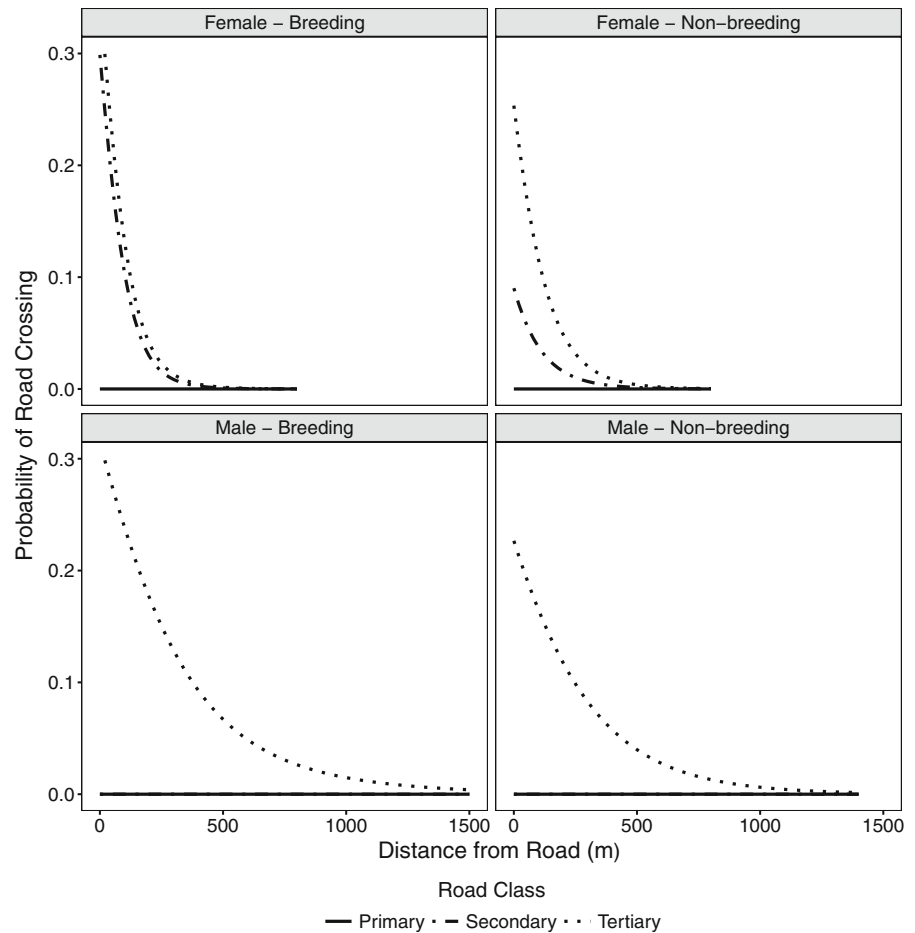
season, although the resolution of our land cover data may be poorly suited for testing this thermoregulatory hypothesis.

Our predicted surfaces often showed strong selection along road and urban edges reflecting high SD NDVI values. Given that EIS will readily cross tertiary roads, selection for anthropogenically-induced habitat edges may prove maladaptive (e.g., Mumme et al. 2000). Because EIS are active foragers with large home ranges and high movement potential (Breininger et al. 2011; Bauder et al. 2016), selection for these edges likely increases their risk of road mortality and human persecution (Whitaker and Shine 2000; Andrews and Gibbons 2008). In particular, male EIS, despite their near-zero probability of crossing primary and secondary roads, may be at greater risk of road mortality than females because of their greater movement potential and positive selection for roads at broader scales, which may lead to a greater absolute number of attempted road crossings over tertiary roads.

Seasonal variation in habitat selection

We found little evidence to support our prediction that the strength of selection for undeveloped uplands increased relative to that of wetlands during the breeding season. Level III selection for uplands was consistently strong year-round, whereas only males avoided areas with high soil moisture during the breeding season. However, some individuals in the Cape Canaveral study area used large expanses of salt marshes during the summer and predominately used uplands during the winter. We were unable to directly evaluate Level III selection for wetland in most groups because of multicollinearity. While the wetland parameter estimates from single-variable models were consistent with our prediction, these estimates were

Fig. 6 Multi-level scale-optimized predicted surfaces from the Cape Canaveral study area. **a** Level II predicted surface, **b–d** the normalized products of Level II and III predicted surfaces (rescaled from 0–1) for breeding season females, non-breeding season males, and breeding season males, respectively
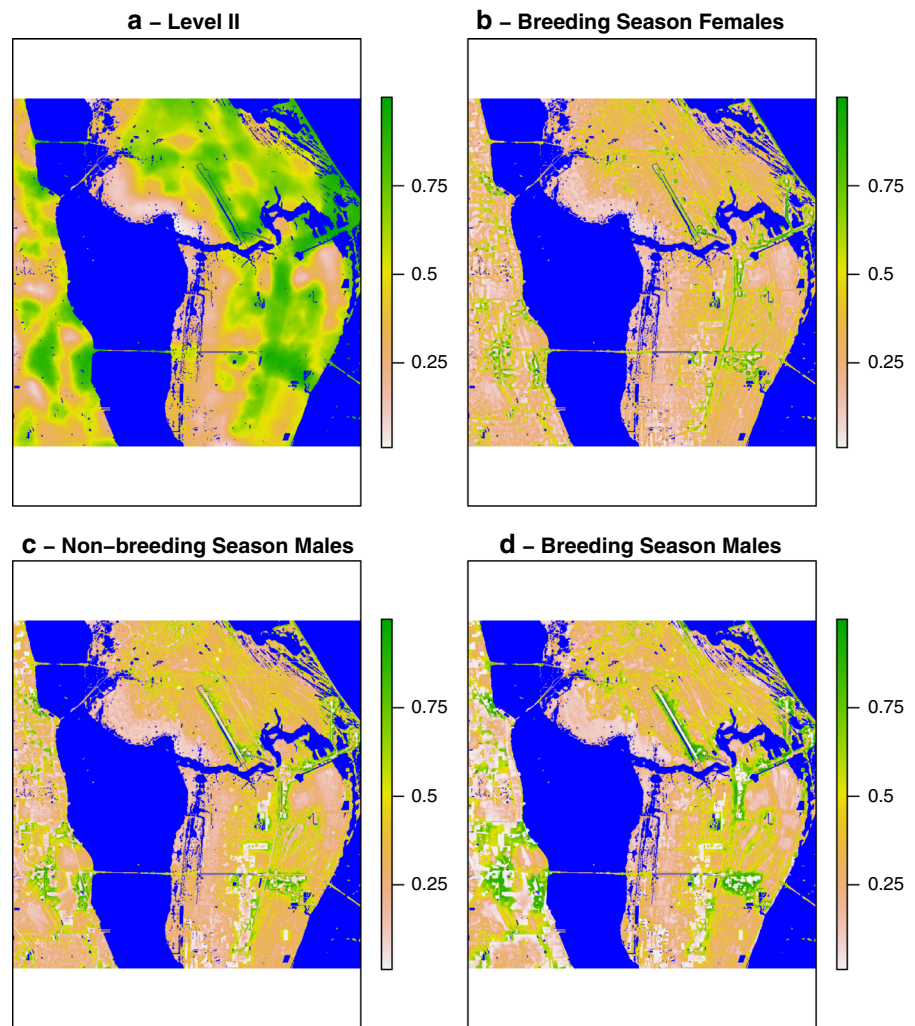
non-significant ($P \geq 0.152$). This lack of consistent seasonal variation in Level III selection differs from patterns of EIS habitat selection at the northern edge of their range (i.e., southern Georgia). During the winter, EIS in southern Georgia showed near-exclusive use of xeric sandhills supporting gopher tortoise burrows (Speake et al. 1978; Stevenson et al. 2003; Hyslop et al. 2014). During the summer, EIS used a greater diversity of habitats particularly wetlands where most foraging events were observed (Hyslop et al. 2014). The lack of distinct seasonal differences in habitat selection by EIS in central peninsular Florida may be driven, at least in part, by relatively mild winter temperatures that allow them to use a greater diversity of winter shelter sites (Bauder et al. 2016).

Inter-sex differences in habitat selection

Inter-sex differences in habitat selection can result from differences in reproductive behavior, selection of suitable gestation, nesting, or birthing sites, and/or differences in resource needs (e.g., Charland and Gregory 1995; Blouin-Demers and Weatherhead 2001b; Harvey and Weatherhead 2006). Patterns of selection for the most influential covariates (undeveloped upland and urban land covers, SD of NDVI) were consistent between sexes, highlighting the importance of these features. The greatest difference in patterns of Level III selection between sexes was the greater degree of selection by breeding-season males, for which all but one covariate was either significant or strongly supported ($w > 0.90$). We suspect this is due

to larger male home ranges and movement potential during the breeding season (Bauder et al. 2016) which may therefore entail a greater degree of selective use of both preferred and avoided habitats. Varying patterns of selection as a function of home range size have been reported in other taxa (Herfindal et al. 2009). Breeding season males strongly selected the weighting scenario for undeveloped upland that included rural land covers and selected roads at broad scales. This may be due to males' priority in locating females during the breeding season, which may lead them to traverse a greater diversity of habitats even if those habitats may be less suitable for other activities (e.g., foraging). Variation in home range size may explain other inter-sex differences in Level III selection. For example, males selected wetland edge in both seasons whereas females exhibited neutral selection of wetland edge and roads. This may reflect a hierarchical process of habitat selection wherein smaller female home ranges are selected in areas with optimal densities of wetland edge and roads, thereby resulting in neutral selection of these features within the home range.

Scope, limitations, and conclusions

We acknowledge limitations in our study that may influence our results and inferences. Several factors may have influenced the accuracy of our GIS data. First, there may have been some degree of temporal mismatch between our telemetry data and GIS data, although we attempted to minimize this by using GIS data contemporaneous with our telemetry data. Visual inspections of our GIS data using aerial imagery indicated that our GIS data accurately reflected land cover conditions when our telemetry data were collected. Second, within-class heterogeneity in land covers may have limited our ability to detect relationships (Gaston et al. 2017). Vegetation cover and building densities within urban and rural land covers were highly variable; however, our use of multiple weighting scenarios and other covariates (AWS, NDVI) should have mitigated this variability. Use of multiple land cover data sources may have introduced additional variability, although our reclassification of land cover into five classes should also have reduced this variability. Finally, combining different data types with different minimum mapping units may have also obscured Level III relationships. However, our use of

kernel-smoothed surfaces should have reduced this effect by effectively increasing grain size. Moreover, the strong Level III relationships we observed suggest that insufficient data resolution was not a primary cause of weak relationships. Logistical constraints prevented us from assessing selection for field-based microhabitat features (e.g., shrub cover, retreat site abundance). Many snake studies have demonstrated selection for microhabitat features (Reinert 1984; Moore and Gillingham 2006; Martino et al. 2012; Croak et al. 2013) which may be more important than selection for broader-scale habitat features (Harvey and Weatherhead 2006). The moderate predictive performances of our models may reflect our inability to model EIS responses to microhabitat features. While it is possible that large home range sizes and high movement potential cause EIS to respond more strongly to relatively broad-scale habitat features compared to microhabitat features, our study was unable to test this hypothesis.

Large tracts of undeveloped upland habitats containing a mosaic of natural habitats, particularly wetland-upland mosaics, are likely to prove essential for EIS conservation. While EIS exhibit flexible habitat use at multiple levels, our results corroborate previously noted negative impacts of habitat loss and fragmentation (Moler 1992; Breininger et al. 2004). In particular, despite avoidance of urban land covers, EIS will readily cross small paved roads and potentially select roadside habitats which may increase road mortality. While conservation of "rural" land covers may benefit EIS, such benefits are likely contingent upon low road densities and low rates of road-induced mortality. Nevertheless, even infrequent road mortality may still contribute to population-level declines (Mumme et al. 2000; Row et al. 2007; Fahrig and Rytwinski 2009). Given the development pressures on upland habitats within peninsular Florida (Turner et al. 2006; Swain and Martin 2014) maintaining and expanding existing conservation networks will likely benefit EIS conservation. We encourage additional research to determine the spatial requirements for viable EIS populations and the degree of EIS connectivity among protected lands within peninsular Florida.

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