



# Incorporating habitat suitability, landscape distance, and resistant kernels to estimate conservation units for an imperiled terrestrial snake

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## Abstract

**Context** Wildlife distributions are often subdivided into discrete conservation units to aid in implementing management and conservation objectives. Habitat suitability models, resistance surfaces, and resistant kernels provide tools for delineating spatially explicit conservation units but guidelines for parameterizing resistant kernels are generally lacking.

**Objectives** We used the federally threatened eastern indigo snake (*Drymarchon couperi*) as a case study for calibrating resistant kernels using observed movement data and resistance surfaces to help delineate habitat-based conservation units.

**Methods** We simulated eastern indigo snake movements under different resistance surface and resistant kernel parameterizations and selected the scenario that produced simulated movement distances that best approximated the maximum observed annual movement distance. We used our calibrated resistant kernel to model range-wide connectivity and compared delineated conservation units to Euclidean distance-based population units from the recent eastern indigo snake species status assessment (SSA).

**Results** We identified a total of 255 eastern indigo snake conservation units, with numerous large (2500–5000 ha of suitable habitat) conservation units across the eastern indigo snake distribution. There was substantial variation in the degree of overlap with the SSA population units likely reflecting the spatial heterogeneity in habitat suitability and landscape resistance.

**Conclusion** Our calibration approach is widely applicable to other systems for parameterizing biologically meaningful resistant kernels. Our conservation units can be used to prioritize future eastern indigo snake conservation efforts, identify areas where more survey work is needed, or identify small, isolated populations with high extinction risks.

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## Introduction

Delineating species distributions into discrete conservation units is a critical step in wildlife management. Spatially delineated units can be used for a variety of applications, including managing sustainable harvest (Swihart et al. 2020), implementing and evaluating recovery efforts for imperiled species (Fedy et al. 2017; Weckworth et al. 2018), informing translocation efforts (Moritz 1999), and maintaining adaptive potential within dynamic landscapes and climates (Crandall et al. 2000). A consistent theme when delineating conservation units is the presence of limited connectivity, thereby resulting in some degree of ecological, genetic, and/or demographic distinctiveness (Waples and Gaggiotti 2006; Lowe and Allendorf 2010; Weckworth et al. 2018). Connectivity is often evaluated using genetic data alone (Taylor and Dizon 1999; Palsboll et al. 2007; Lowe and Allendorf 2010) or in combination with movement or demographic data to evaluate the degree of demographic independence (Lowe and Allendorf 2010) among putative units (Olsen et al. 2014; Mee et al. 2015; Yannic et al. 2016; Fedy et al. 2017). However, collecting sufficient genetic or demographic data over the broad spatial scales at which management decisions are often implemented may be challenging, particularly for rare or cryptic species.

An alternative approach for delineating conservation units is to identify potentially suitable habitat patches and then use resistance (i.e., cost) surfaces to model inter-patch connectivity and define inter-connected patches as conservation units (Fajardo et al. 2014; Jackson et al. 2016; Zeller et al. 2017; Maiorano et al. 2019). Assigning resistance values remains an ongoing challenge in connectivity modeling (Spear et al. 2010; Zeller et al. 2012) as resulting estimates of connectivity may be sensitive to the range of resistance values (Rayfield et al. 2010; Koen et al. 2012) and landscape structure (Gonzales and Gergel 2007). Habitat suitability surfaces can be used to empirically parameterize resistance surfaces (Zeller et al. 2018) yet the relationship between habitat suitability and resistance is often non-linear and may vary depending on an individual's behavioral state (Elliot et al. 2014; Keeley et al. 2017). However, many studies have found that a negative exponential transformation provides a biologically realistic relationship between habitat suitability and resistance (Trainor et al. 2013;

Keeley et al. 2016; Zeller et al. 2018). Habitat suitability models may be developed from multiple sources of species occurrence data (e.g., opportunistic or community science data, systematic monitoring surveys), which are often readily available across broad spatial extents (Jones 2011; Crum et al. 2017; Bradter et al. 2018). Finally, modeling inter-patch connectivity can identify potential corridors among discrete habitat patches, which may themselves be of high conservation importance (Chetkiewicz and Boyce 2009; Zeller et al. 2017).

Many terrestrial wildlife are dispersal limited and connectivity thresholds based solely on Euclidean distance may overestimate connectivity in resistant landscapes. Multiple approaches exist for modeling connectivity that incorporate landscape resistance including least-cost paths (Adriaensen et al. 2003), circuit theory (McRae and Beier 2007), and individual-based models (Day et al. 2018; Zeller et al. 2020). Resistant kernels provide another approach for integrating landscape resistance and dispersal distance to model connectivity. Resistant kernels combine a probability distribution (i.e., standard kernel) representing an individual's movement potential in a non-resistant landscape with a resistance surface to measure the cost-distance from a focal pixel to every other pixel within a maximum distance threshold (Compton et al. 2007; Cushman et al. 2010, 2013). These kernels are built around source points representing the potential distribution of individuals or populations and then summed to create a connectivity surface. Resistant kernels require no specification of source–destination points or assumption that animals have complete knowledge of the landscape (Cushman et al. 2012a; Zeller et al. 2018). The shape of the standard kernel strongly influences the connectivity surface (Cushman et al. 2010; Ash et al. 2020) and is typically parameterized using observed movement distances (Compton et al. 2007; Cushman et al. 2012b, 2013; Zeller et al. 2017). However, if observed movement distances come from resistant landscapes (e.g., human-modified landscapes), this approach may underestimate the spread of resistant kernels because movements in resistant landscapes will not represent a species' maximum movement potential in low-resistance landscapes (e.g., Zeller et al. 2020). Alternatively, one can calibrate the resistant kernel by simulating connectivity under different standard kernels and selecting the kernel whose simulated movements

best approximate observed movements from the study landscape (e.g., Wiegand et al. 2003; Rossmann et al. 2007). A similar approach could also be used to empirically estimate the functional (e.g., non-linear) relationship between habitat suitability and landscape resistance (Trainor et al. 2013; Keeley et al. 2017; Zeller et al. 2018).

In this paper, we used the federally threatened eastern indigo snake (*Drymarchon couperi*, hereafter DRCO) as a case study illustrating how calibrated resistant kernels can be used to delineate habitat-based conservation units. DRCO is endemic to the southeastern United States, with naturally occurring populations found only in southern Georgia and peninsular Florida (Enge et al. 2013; U. S. Fish and Wildlife Service 2019). Current efforts to define conservation units for species recovery have been hampered by data limitations because of this species' cryptic nature (U. S. Fish and Wildlife Service 2019). Anthropogenic landscape alterations, including urban development and agriculture, likely reduce landscape connectivity (Breininger et al. 2012; Bauder et al. 2018, 2021), potentially contributing towards reduced population viability (Breininger et al. 2004). While Folt et al. (2019) reported range-wide spatial genetic structure for DRCO using microsatellite DNA, the presence of numerous sampling gaps continues to limit our understanding of DRCO population structure. Furthermore, defining conservation units solely on genetic data may fail to prioritize local, yet important, populations (Taylor and Dizon 1999). Chandler et al. (2022) published a range-wide multi-scale habitat suitability model for DRCO that accounts for known latitudinal differences in habitat associations (Hyslop et al. 2014; Bauder et al. 2018), which could be used to define inter-connected habitat-based conservation units.

Our objectives were to: (1) use the habitat suitability model of Chandler et al. (2022) and empirical DRCO movement data to calibrate a resistance surface and resistant kernel reflecting annual non-dispersing movements of adult DRCO, (2) use resistant kernels to create a range-wide DRCO connectivity surface, (3) threshold this connectivity surface to identify potential corridors and delineate habitat-based conservation units, and (4) compare our habitat-based conservation to the population units identified in the DRCO species status assessment (SSA; U. S. Fish and Wildlife Service 2019).

## Methods

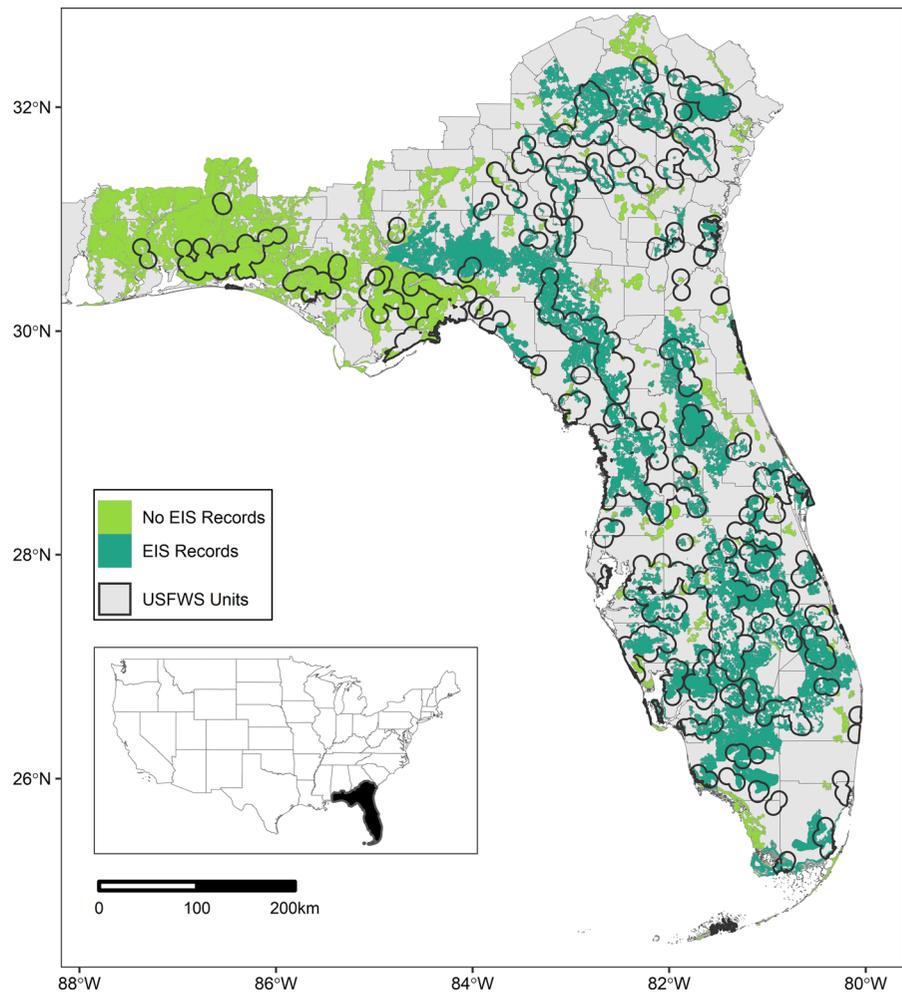
### Study area

We evaluated DRCO connectivity across the species' potential historical distribution including Florida, southern Georgia, and extreme southern Alabama (Fig. 1), excluding areas west of Mobile Bay, Alabama (e.g., southern Mississippi, Enge et al. 2013; U. S. Fish and Wildlife Service 2019). The habitat suitability model we used was developed over the approximate contemporary distribution of DRCO in south-central and southeast Georgia and peninsular Florida as described in Chandler et al. (2022). Our study area included a diversity of natural vegetation communities, including xeric sandhill and scrub, mesic pine flatwoods, hardwood hammocks, coastal hammocks and dunes, and forested and non-forested wetlands. Land cover types substantially modified by human activities were widespread and included urban and rural developments, agriculture, improved pasture, citrus, and commercial forest stands. Vegetation communities unique to southern Florida included mangrove swamps, Everglades marshes and stormwater control wetlands, and sugar cane. Additional information on these vegetation communities is available in Myers and Ewel (1990) and Ambrose et al. (2013).

### Resistance surface and resistant kernel

We derived our resistance surfaces from the habitat suitability surface of Chandler et al. (2022) whose values ranged from 0 to 1. We assumed that suitability was inversely related to resistance and used our calibration process to define the shape of this relationship (see below). Chandler et al. (2022) estimated lower suitability in wetlands, which resulted in high resistance for wetlands. However, DRCO forage in and around wetlands and are capable of moving through wetlands (Hyslop et al. 2014; Metcalf et al. 2021). We therefore added a constant to the suitability values for all wetland pixels, identified using the 2016 National Land Cover Data (available at <https://www.mrlc.gov>), to lower their resistance (Supplementary Material, Fig. S1). Adjusted suitability values > 1 were set to one. We then converted suitability to resistance on a scale from 1 to 100 using either a negative linear or exponential transformation following Trainor et al. (2013). We used the calibration approach described

**Fig. 1** Conservation units (shaded polygons) for eastern indigo snakes (EIS, *Drymarchon couperi*) across their historical distribution. Units with and without recent (2000–2020) eastern indigo snake records are denoted. Open polygons represent eastern indigo snake population units identified in the U.S. Fish and Wildlife Service’s (USFWS) Species Status Assessment



below to select the wetland constant and the shape of the transformation.

We also adjusted the resistance values for roads and open water. Major highways may restrict DRCO movement, both behaviorally (Bauder et al. 2018) and through mortality (Breininger et al. 2012). However, Chandler et al. (2022) evaluated DRCO suitability at spatial scales exceeding or equal to DRCO home range sizes so roads were not explicitly represented in the habitat suitability surface. We therefore used the 2016 TIGER roads layer (U. S. Census Bureau 2016) to identify major roads (interstates, state, and federal highways, TIGER RTTYP=I, S and U, respectively) and increase their resistance values (see below). We did not adjust resistance values of other road classes. Finally, we assigned all open water pixels  $\leq 270$  m from shore the maximum resistance value (100)

based on the maximum observed water crossing by a DRCO (263 m, D. Breininger, NASA, unpublished data). All other water pixels  $> 270$  m from shore were considered complete barriers (resistance = 9999).

We used half-normal resistant kernels to approximate the movement potential of an individual adult DRCO during routine annual movements within its home range, excluding extreme long-distance dispersal (Stevenson and Hyslop 2010) but including seasonal migrations between overwintering and summer habitats (Hyslop et al. 2014). This was conceptually consistent with on-going DRCO recovery planning efforts (U. S. Fish and Wildlife Service 2019). Hyslop et al. (2014) reported that male DRCO in southeast Georgia made directional movements of up to 7.5 km (straight-line displacement) during late spring between overwintering sites and summer foraging

areas. While other distributions may better approximate potentially right-skewed movement data (e.g., Zeller et al. 2014), more detailed data were unavailable for our study. We therefore used a half-normal kernel because its single parameter (bandwidth or  $\sigma$ ) facilitated calibration with limited data (see below). We based our resistant kernel on male movement distances because our primary goal was to identify inter-connected habitat patches based on the maximum biological movement potential of DRCO and for consistency with the conceptual framework used by the U.S. Fish and Wildlife Service in the current SSA (U.S. Fish and Wildlife Service 2019).

#### Calibrating the resistance surface and resistant kernel

We used a calibration approach analogous to model calibration in pattern-oriented modeling (Wiegand et al. 2003; Grimm and Railsback 2012) to select the wetland constant for wetland resistance, the shape of the relationship between habitat suitability and resistance, and the resistant kernel bandwidth. We evaluated all combinations of wetland constant values of 0 (no change), 0.10, 0.20, 0.30, and 0.50, linear and negative exponential relationships with parameter values of 2, 4, and 8 (Keeley et al. 2016; Zeller et al. 2018), and bandwidth from 250 to 10,000 m at 125 m increments. Major roads were poorly represented in our calibration area and preliminary tests indicated that our calibration approach could not identify an optimal resistance value for major roads. Preliminary comparisons with DRCO radio telemetry data indicated that assigning highways our maximum resistance value (100) overestimated their resistive effect and tended to overly split conservation units. We therefore assigned major roads a resistance value of 50 and made no adjustments to resistance values for smaller roadways. We also created a second connectivity surface using a resistance value of 75 for major roads for comparison.

We conducted our calibration using the approximate footprint of Fort Stewart (>110,000 ha) in southeast Georgia (excluding urban areas around the base's primary installations; Supplementary Material, Fig. S1) to represent a landscape with minimal anthropogenic sources of resistance and where annual DRCO movements should approximate their maximum biological potential. The observed DRCO movement data used for our calibration was also

collected at Fort Stewart. We randomly selected 1000 source points within the calibration area that were > 1 km from the edge of the calibration area. We assigned all pixel values outside of our calibration area a value of 9999 to ensure that the resistant kernel only spread within our calibration study area to avoid any confounding effects of more disturbed landscapes beyond Fort Stewart.

Our objective was to identify potentially inter-connected habitat patches, rather than identify the potential distance DRCO could move from any single habitat patch. We therefore realized that using 7.5 km as our calibration data point would overestimate the degree of inter-patch connectivity in landscapes with minimal resistance. For example, two patches separated by 15 km ( $7.5 \text{ km} \times 2$ ) could have overlapping resistant kernels in minimally resistant landscapes, yet this inter-patch distance is beyond the maximum annual movement distance reported for DRCO. We therefore used 3.75 km ( $7.5 \text{ km} \times 0.50$ ) as our calibration data point.

For each unique parameter combination, we created a unique resistance surface for Fort Stewart as described above and then built resistant kernels around all source points specifying a maximum kernel radius of  $3 \times \sigma$ . We normalized each resistant kernel to sum to one and then identified all pixels whose values were  $9.75\text{th} \leq x \leq 10.25\text{th}$  percentiles (i.e., the 10th percentile; Supplementary Material, Fig. S2). We assumed that these pixels represented the approximate upper bound of DRCO movement potential from that source point for a given parameter combination. We then calculated the Euclidean distance of these pixels to the source point. Finally, for each source point, we calculated the root mean squared error (RMSE) between the observed distances and an equal length vector of values equal to our calibration data point. We selected the parameter combination with the lowest median RMSE across all 1000 source points to use in creating our connectivity surface.

#### Creating connectivity surfaces

We placed source points for our resistant kernels within potentially suitable habitat patches to explicitly model connectivity among patches. We used only the high suitability class defined in Chandler et al. (2022). We assumed that habitat patches were homogenous with respect to DRCO habitat suitability

and therefore systematically placed points 500 m apart within all habitat patches and at the centroid of each patch's polygon to ensure small or highly irregular patches were included. We made no assumptions regarding the actual occupancy status or distribution of DRCO within habitat patches. We then built resistant kernels around each source point, summed all resistant kernels together, and linearly rescaled the resulting connectivity surface from 0 to 100. We defined potential corridors among habitat patches by subsetting connectivity surfaces at the 25th quantile (Zeller et al. 2017) of all non-zero connectivity values. To compare our connectivity surfaces with resistance values for major roads specified as 50 versus 75, we randomly selected 345,000 points directly on major roads or within a 500 m buffer around all major roads and then compared the proportion of random points that were less than or greater than their respective connectivity surfaces 25th quantile.

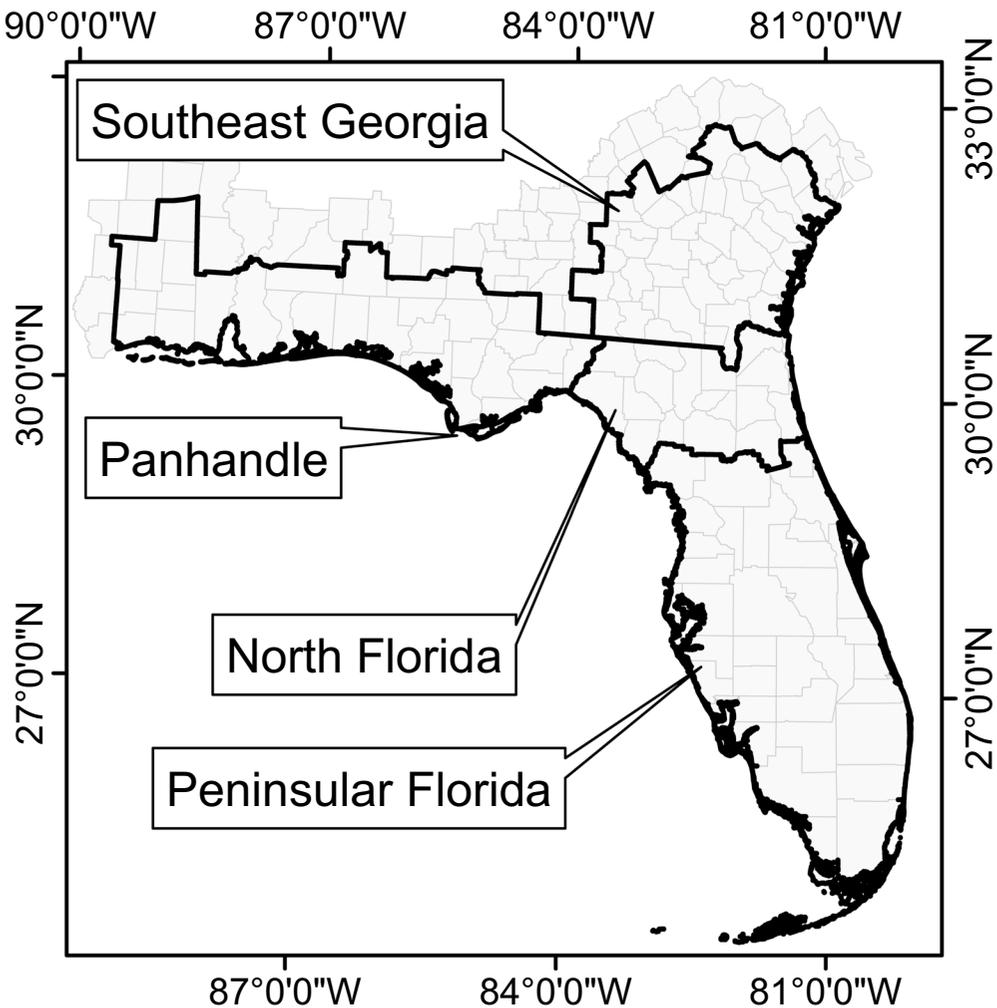
#### Defining conservation units and comparing with SSA

To define conservation units, we first merged our habitat patch and corridor polygons to ensure that conservation units captured all suitable habitat and potential movement corridors. We then split these initial conservation units using interstate highways (TIGER RTTYP=I) and major rivers throughout our study area, which we considered complete barriers to annual DRCO movement (Bauder et al. 2018). While DRCO are likely capable of crossing large rivers during dispersal movements, extensive (> 20 years) mark-recapture data from Georgia populations (Chandler, unpublished data) and radio telemetry data in both Georgia and peninsular Florida suggest that such river crossings during annual movements are rare. To identify major rivers, we selected all polyline segments with a stream order  $\geq 5$  in the National Hydrography Plus Dataset, Version 2 (McKay et al. 2014). The Caloosahatchee River/Canal was a smaller order (stream order=4), but we also considered it a barrier based on its comparable size to other large rivers.

We then filtered the conservation units using the following criteria. We retained all conservation units containing  $\geq 1$  recent (2000–2020) DRCO

observation from a verified source (see Chandler et al. 2022 for a detailed description of data sources). For units without recent DRCO records, we only retained units containing  $\geq 250$  ha of suitable habitat. We considered 250 ha as a minimum habitat patch area based on male DRCO home range sizes from peninsular Florida (Bauder et al. 2020) and observations of male–female home range overlap (Bauder et al. 2016b). Finally, we excluded habitat patches that likely never supported DRCO or where DRCO were likely extirpated due to habitat fragmentation (Breininger et al. 2004). This included patches that were on Georgia barrier islands not known to be occupied by DRCO, were completely surrounded by urban development and had no recent DRCO observations, or were in areas outside of the historical DRCO range and not directly adjacent to occupied patches.

We summarized our results to identify conservation units potentially capable of supporting viable DRCO populations. Estimates of the minimum area needed to support a viable DRCO population vary from, 1000 ha (Moler 1992) to > 8000 ha (Bauder 2019). We therefore considered polygons whose total area of habitat patch and corridor was  $\geq 2500$  and  $\geq 5000$  ha, respectively, as conservation units likely capable of containing viable DRCO populations. We calculated the number of conservation units, the proportion of each unit that was habitat patch or corridor, and the total area of each unit (habitat patch or corridor combined), summarizing these metrics across the four U.S. Fish and Wildlife Service Eastern Indigo Snake Representative Units (i.e., Southeast Georgia, North Florida, Panhandle, and Peninsular Florida; Fig. 2; U.S. Fish and Wildlife Service 2019). We also calculated the overlap between conservation units and protected lands using the U.S. Geological Survey Protected Areas Database (U.S. Geological Survey 2020). Finally, we also calculated the amount of overlap between each conservation unit and the population units defined in the SSA. The current DRCO SSA defined populations (i.e., conservation units) based on overlapping uniform kernels with 8 km radius buffers (Hyslop et al. 2014) around at least



**Fig. 2** U.S. Fish and Wildlife Service eastern indigo snake (*Drymarchon couperi*) Representative Units

two contemporary (2001–2017) DRCO observations (U. S. Fish and Wildlife Service 2019). While this radius was also based on annual non-dispersal movements of adult DRCO, this approach did not account for variation in landscape resistance or habitat suitability nor the potential presence of DRCO in areas lacking contemporary observations.

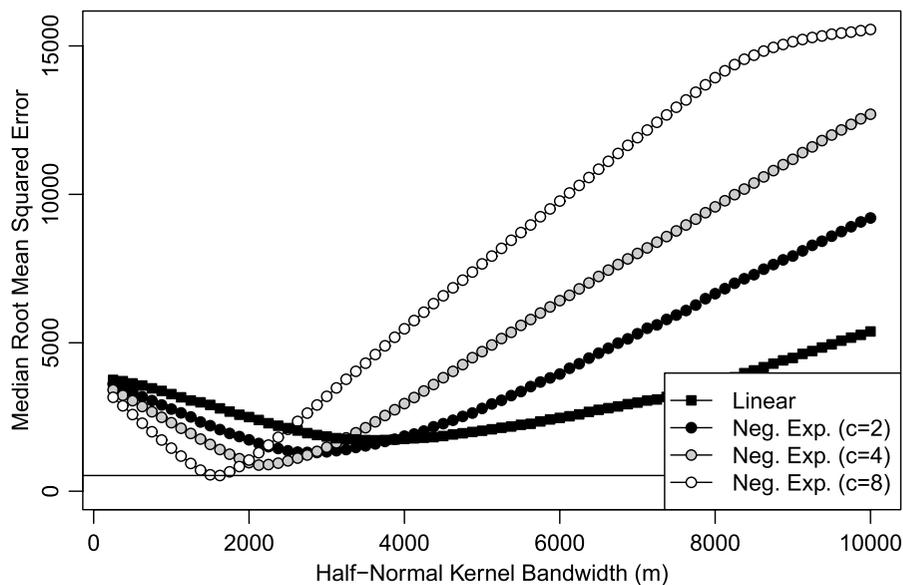
## Results

### Resistance surface and resistant kernel calibration

The functional relationship between habitat suitability and resistance had a strong effect on the performance

of different calibration scenarios with negative exponential relationships strongly outperforming linear relationships (Fig. 3). The optimal bandwidth for each negative exponential relationship decreased with the value of the negative exponential parameter. In contrast, the wetland constant had relatively little effect on scenario performance (Supplementary Material, Fig. S3). The parameter combination with the lowest median RMSE across all 1,000 calibration points included a bandwidth of 1625 m, a wetland multiplier of 0.50, and a negative exponential parameter of  $c=8$  (Fig. 3; Supplementary Material, Fig. S3). Increasing the resistance value of major roads from 50 to 75 changed the proportion of random points on or  $\leq 500$  m from major roads that were greater than or equal

**Fig. 3** Median root mean squared error (RMSE) plotted against the bandwidth ( $\sigma$ ) of a half-normal standard kernel under linear and negative exponential functional relationships between habitat suitability and resistance for eastern indigo snakes (*Drymarchon couperi*) on Fort Stewart, Georgia, USA. The exponential parameter is given as  $c$ . Results are presented for wetland constant = 0.50 (see Supplementary Material, Fig. S3 for all results). The horizontal black line represents the lowest median RMSE across all scenarios



to the 25th quantile of their respective connectivity surfaces from 0.109 to 0.060 and 0.295 to 0.283, respectively.

#### Eastern indigo snake conservation units

We identified a total of 255 DRCO conservation units across the species distribution, including 53 units in Georgia, 29 in North Florida, 41 in the Panhandle, and 132 in Peninsular Florida (Table 1; Fig. 1). Conservation units ranged in size from 175–1,137,920 ha and included 7–545,932 ha of potentially suitable DRCO habitat (22 units with less than 250 ha of suitable habitat retained because of DRCO records). There were 71 and 47 conservation units that contained at least 2500 or 5000 ha of potential DRCO habitat, respectively (Table 1). The proportion of conservation unit overlapping protected land varied from almost none to almost complete overlap ( $\geq 2500$  ha: median = 0.25, range = 0.00–1.00;  $\geq 5000$  ha: median = 0.23, range = 0.00–0.98). Approximately 36% (93 of 255) of conservation units included at least one contemporary DRCO record. The percentage of conservation units with contemporary records was highest in Georgia (42%) and Peninsular Florida (47%) and lowest in North Florida (28%) and the Panhandle (2%) Representative Units. On average, 37% of the conservation units overlapped a population unit

from the SSA, and, similar to the above results, this percentage was highest in the Georgia and Peninsular Florida Representative Units (Table 1).

The largest conservation units were typically located in landscapes with substantial amounts of protected land (e.g., the Florida Panhandle), while the smallest units (including many of those with less than 250 ha of potentially suitable habitat) were found on islands in western and southern Florida (Fig. 1). In Georgia, the largest conservation units were located on Fort Stewart, along the Altamaha River, and along the Alapaha River (Fig. 1, Fig. S4). In Florida, significant protected areas overlapping conservation units included Ocala National Forest, Green Swamp Wildlife Management Area, and Avon Park Air Force Range and Kissimmee Prairie Preserve State Park in central Florida, and Big Cypress National Preserve, Picayune Strand State Forest, Rookery Bay National Estuarine Research Reserve, and Everglades National Park in southern Florida (Fig. 1, Fig. S4). Large conservation units were also located on Eglin Air Force Base and Apalachicola National Forest in the Florida Panhandle although these sites lack confirmed contemporary DRCO records. Importantly, the Alapaha River drainage was the most prominent and only contiguous corridor between DRCO populations in the Georgia and North Florida Representative Unit (Fig. 4D).

**Table 1** Characteristics of eastern indigo snake (*Dymarchon couperi*) conservation units (CUs) across their historical distribution, summarized by U.S. Fish and Wildlife Service (USFWS) Eastern Indigo Snake Representative Units

USFWS representative units	Min habitat area (ha)	# of conservation units (CUs)	# CUs with EIS records	Percent habitat	Perimeter to area ratio	Proportion protected area	Proportion SSA unit
All	–	255	93	0.23 ± 0.18	22.6 ± 16.9	0.34 ± 0.32	0.37 ± 0.40
Georgia	–	53	22	0.14 ± 0.08	18.6 ± 6.7	0.16 ± 0.25	0.41 ± 0.41
North FL	–	29	8	0.17 ± 0.11	18.0 ± 9.4	0.34 ± 0.29	0.29 ± 0.39
Panhandle	–	41	1	0.29 ± 0.14	16.0 ± 6.2	0.23 ± 0.28	0.11 ± 0.24
Peninsular FL	–	132	62	0.26 ± 0.21	27.4 ± 21.3	0.45 ± 0.33	0.45 ± 0.41
All	250	233	71	0.24 ± 0.17	21.8 ± 16.7	0.33 ± 0.32	0.33 ± 0.38
Georgia	250	48	17	0.15 ± 0.08	17.7 ± 6.1	0.15 ± 0.22	0.35 ± 0.38
North FL	250	27	6	0.18 ± 0.11	18.2 ± 9.8	0.32 ± 0.28	0.27 ± 0.38
Panhandle	250	41	1	0.29 ± 0.14	16.0 ± 6.2	0.23 ± 0.28	0.11 ± 0.24
Peninsular FL	250	117	47	0.27 ± 0.20	26.3 ± 21.5	0.45 ± 0.33	0.40 ± 0.40
All	2500	71	39	0.29 ± 0.12	13.3 ± 6.4	0.31 ± 0.28	0.38 ± 0.33
Georgia	2500	14	10	0.23 ± 0.08	12.8 ± 3.2	0.12 ± 0.22	0.49 ± 0.36
North FL	2500	7	4	0.30 ± 0.08	15.8 ± 9.8	0.33 ± 0.26	0.26 ± 0.29
Panhandle	2500	20	1	0.36 ± 0.13	13.4 ± 6.6	0.22 ± 0.26	0.19 ± 0.30
Peninsular FL	2500	30	24	0.27 ± 0.12	12.9 ± 6.6	0.45 ± 0.25	0.48 ± 0.29
All	5000	47	30	0.30 ± 0.13	11.7 ± 5.6	0.29 ± 0.25	0.41 ± 0.29
Georgia	5000	10	8	0.22 ± 0.07	12.5 ± 3.6	0.17 ± 0.24	0.52 ± 0.31
North FL	5000	5	3	0.27 ± 0.08	13.2 ± 6.5	0.19 ± 0.10	0.30 ± 0.32
Panhandle	5000	13	1	0.40 ± 0.13	10.7 ± 5.9	0.19 ± 0.22	0.20 ± 0.27
Peninsular FL	5000	19	18	0.29 ± 0.13	11.5 ± 6.3	0.44 ± 0.24	0.53 ± 0.20

Units spanning multiple regions were assigned to the region containing a majority of the area. Minimum habitat area refers to the potentially suitable eastern indigo snake habitat within each conservation unit (i.e., not including corridor). Species status assessment (SSA) population units were delineated using uniform kernels around confirmed eastern indigo snake observations

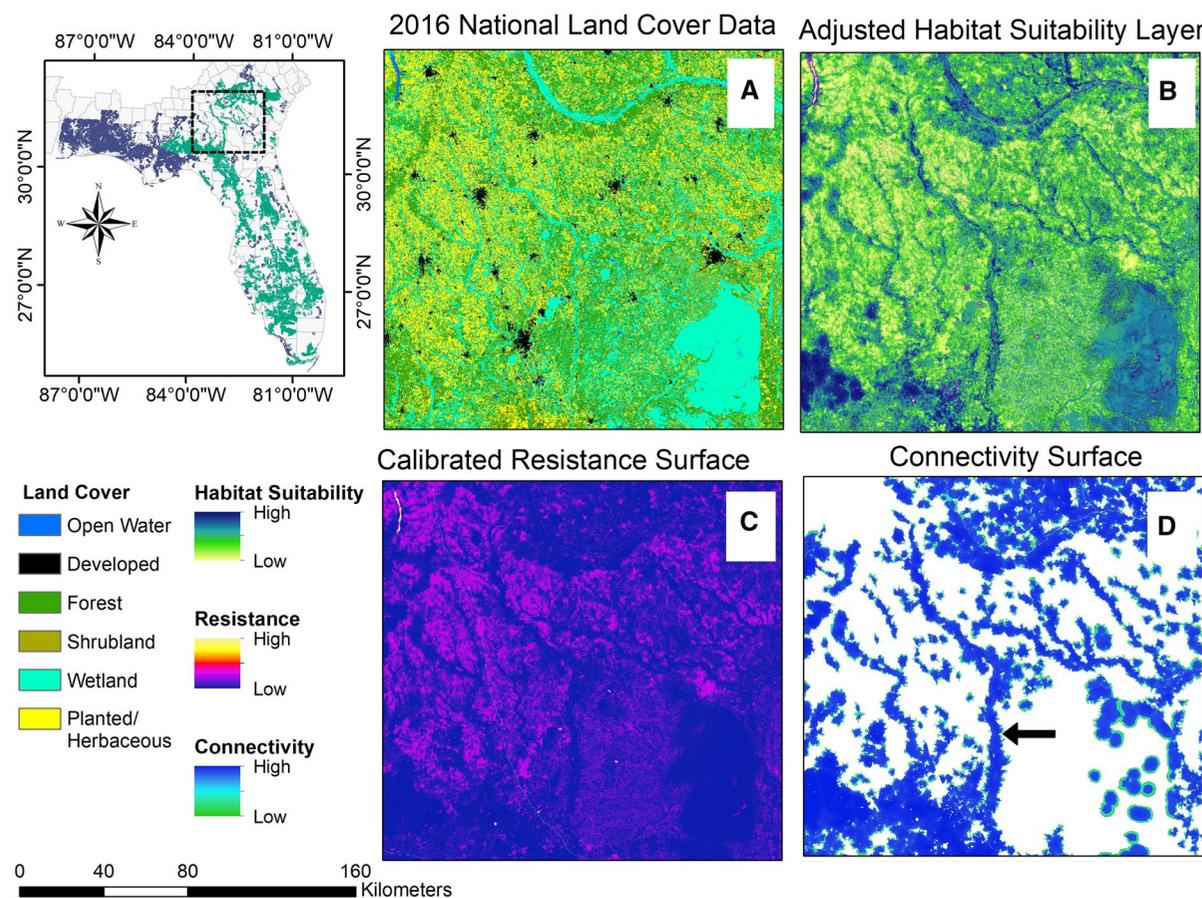
Unless indicated otherwise, values represent means ± standard deviations

## Discussion

We applied an empirical approach to delineate conservation units across the historical range of the imperiled DRCO, integrating a previously created habitat suitability model with empirical estimates of landscape resistance and species-specific movement data. We identified 255 conservation units across Florida, southern Georgia, and southern Alabama, including several large (>2500 ha) units that are likely capable of supporting viable populations. Many conservation units were associated with large tracts of protected lands that have been previously identified as important for DRCO conservation (e.g., Fort Stewart, Ocala National Forest, Altamaha River Corridor) (Enge et al. 2013; Stevenson and Chandler 2017). Yet substantial portions of many conservation

units are not protected, highlighting the importance of landscape-scale conservation planning for wide-ranging terrestrial vertebrates (Larkin et al. 2004; Nandintsetseg et al. 2019). Furthermore, our results emphasize the importance of the Apalaha River sandhills as the only remaining corridor potentially connecting DRCO populations in Georgia and Florida. Yet protected lands in the Apalaha River region are relatively scarce, especially when compared to the Altamaha River corridor (Stevenson and Chandler 2017). Future research is therefore needed to evaluate the distribution and status of DRCO within the Apalaha River region and to determine the degree of connectivity between DRCO populations in Georgia and Florida.

The degree of overlap between our habitat-based conservation units and the Euclidean distance-based



**Fig. 4** Conservation units for the eastern indigo snake (*Drymarchon couperi*) were delineated from a habitat suitability surface (A). The habitat suitability surface was modified to better account for snake use of wetlands and the potential bar-

rier effects of roads (B), and this modified surface was then used to create a resistance surface (C). Landscape connectivity was modeled using this resistance surface (D). The black arrow in Fig. 4D highlights the Alapaha River corridor

SSA population units was variable. There was relatively high concordance in Georgia and Peninsular Florida, regions where the distribution of DRCO populations has been relatively well documented through multiple research and monitoring projects (e.g., Stevenson et al. 2009; Breininger et al. 2011; Ceilley et al. 2014; Bauder et al. 2017; Metcalf et al. 2021) and opportunistic sightings (Enge et al. 2013). Concordance among our conservation units and SSA populations was lower in the North Florida and Panhandle regions. The contemporary distribution of DRCO is less well understood in North Florida, potentially due to inadequate survey effort, local extirpations, or both, whereas DRCO have been regionally extirpated from the Panhandle since approximately the 1990s (Enge et al. 2013). Our results also strongly suggest

that the Euclidean distance-based SSA populations often extend into landscapes unlikely to serve as habitat or as movement corridors for DRCO, especially along river corridors in southern Georgia. Conversely, there were also many cases where boundaries of SSA population units did not include potentially suitable habitat contiguous with potentially suitable habitat within the population unit. These differences highlight the importance of accounting for landscape heterogeneity and its potential effects on species movement when delineating conservation units (With et al. 1997; O'Brien et al. 2006; Macdonald et al. 2019).

Our results illustrate the potential for habitat suitability data to inform landscape-scale connectivity modeling using resistant kernels. Although parameterizing resistant kernels may be challenging if

movement data from low-resistant landscapes are unavailable (e.g., Compton et al. 2007), calibration can be used to parameterize the resistant kernel in a biologically meaningful manner. Furthermore, resistant kernels can accommodate different probability distributions (Cushman et al. 2012b; Zeller et al. 2020), depending on the desired distance-decay function. For example, Zeller et al. (2020) used a resistant kernel based on a generalized Pareto distribution (GPD) to simulate daily movements of American black bear (*Ursus americanus*). They found that simulated movements were consistently shorter than their observed movements and therefore multiplied the shape parameter of the GPD by a constant to produce more realistic distributions of simulated movements. Similarly, Bauder (2019) calibrated a GPD-based resistant kernel by comparing simulated DRCO daily movements from multiple constants to the observed distribution of movements. Our results also suggest that calibration may still be preferable even when movement data from non-resistant landscapes are available. For example, a bandwidth of approximately 2280 m would be needed for a two-dimensional half-normal kernel to have a 90th percentile of 3750 m yet our calibrated bandwidth (1625 m) for a three-dimensional half-normal kernel with an identical 90th percentile was approximately 29% less. Furthermore, the calibration approach we illustrate mitigates some of the limitations in modeling resistance/connectivity as a function of habitat suitability by allowing observed data to inform the relationship between suitability and resistance. Our approach is readily expandable to other data sources including telemetry data or dispersal distances estimated from mark-recapture or genetic data. We therefore recommend that researchers employing cost-distance thresholds in connectivity modeling calibrate their thresholds using observed movement data.

Our results are dependent upon our use of a half-normal kernel to describe DRCO movement potential, the quality of the habitat suitability model, and the assumption of a spatially constant relationship between habitat suitability and resistance. The half-normal kernel may have overestimated connectivity compared to right-skewed distributions, which often describes animal movements (Zeller et al. 2014; Keeley et al. 2016; Bauder et al. 2018). However, the half-normal distribution's single parameter makes

it ideal when calibrating to sparse data and the connectivity surface could be subset at lower quantiles to obtain a more conservative connectivity estimate. Our resistant kernel was also based on male DRCO movement distances which are greater than female movements (Hyslop et al. 2014; Bauder et al. 2016a). While our connectivity estimates are based on maximum DRCO movement potential, shorter female movement distances should be considered when using our conservation units to infer population viability. Additionally, our calibration approach was unable to identify an optimal resistance value for major roads, which introduces additional uncertainty into our results. We re-created our connectivity surface using a major roads resistance value of 75, which generally returned similar conservation units but also split peripheral areas of some units. Understanding the sensitivity of our conservation units to major roads resistance for particular areas may therefore require reevaluating our connectivity surfaces under multiple scenarios to fully understand the range of variability in connectivity estimates.

Our habitat suitability model accounted for spatial variation in DRCO habitat suitability relationships (Chandler et al. 2022), although data on spatial variation in landscape resistance beyond our habitat suitability model were unavailable. Predictive performance of our habitat suitability model was higher in Georgia than in southern Peninsular Florida (Chandler et al. 2022), presumably reflecting more restrictive habitat requirements by DRCO in cooler climates due to their reliance on gopher tortoise (*Gopherus polyphemus*) burrows (Hyslop et al. 2009; 2014). While the habitat suitability model in Georgia had some bias towards DRCO winter habitat, this bias was mitigated in our connectivity analysis because our resistant kernels included seasonal migrations between over-wintering and summer habitat (Hyslop et al. 2014). An additional assumption is that we opted to retain a geographically constant DRCO movement potential, despite geographic variation in DRCO spatial ecology (Jackson 2013; Hyslop et al. 2014; Bauder et al. 2016a; Metcalf et al. 2021), for consistency with the DRCO SSA (U. S. Fish and Wildlife Service 2019). Furthermore, we wanted our resistant kernels to capture the maximum biological DRCO movement potential because conservation units should arguably protect all individuals including

individuals with more extreme movements. Basing conservation units on mean/median movement distance could exclude such individuals.

In contrast, the habitat suitability model's poorer predictive performance in southern Peninsular Florida, likely due to increasingly diverse DRCO habitat use in milder climates (Moler 1992; Breininger et al. 2011; Ceilley et al. 2014; Bauder et al. 2018; Metcalf et al. 2021), may have resulted in overestimating connectivity in this region despite a lower prevalence of potentially suitable habitat. In this region DRCO will use agriculturally modified landscapes, particularly canals traversing sugar cane or abandoned citrus groves (Enge et al. 2013; Jackson 2013, this study), yet it is unclear if such landscapes do indeed promote connectivity. Predicted habitat suitability was often relatively high in citrus groves, which were classified as agriculture within our GIS data (Chandler et al. 2022), despite evidence that DRCO avoid active citrus (Bauder et al. 2018). Additional data on DRCO movement and habitat ecology in agriculturally dominated landscapes is needed to better understand the potential conservation value of such landscapes for DRCO. We ultimately suggest caution when using our modeling results within southern Peninsular Florida.

It is important to emphasize that our habitat suitability and connectivity models do not indicate DRCO presence or absence, and we strongly caution against inferring DRCO absence from our results as DRCO are difficult to detect due to their cryptic behavior, low densities, and large home range sizes. DRCO may be absent from potentially suitable habitats for at least two reasons. First, DRCO populations in suitable habitat may have been extirpated due to cumulative long-term effects of anthropogenic mortality, particularly from roads (Breininger et al. 2004; Maiorano et al. 2019), or declining gopher tortoise populations (U. S. Fish and Wildlife Service 2019). Second, historical landscape changes (e.g., timber harvest, agriculture) or human activities (e.g., over-collection of DRCO and/or gopher tortoises) may have extirpated DRCO in areas that now appear to contain suitable habitat. We suspect this is true in the Florida Panhandle Representative Unit where large tracts of potentially suitable habitat exist without contemporary DRCO records (Enge et al. 2013). Many other species also show signatures of past landscape conditions in their contemporary distributions (Lindborg and

Eriksson 2004; Waldron et al. 2008; Halstead et al. 2014) and other studies have noted lags in population responses to past landscape changes (Tilman et al. 1994; Metzger et al. 2009).

Spatially explicit conservation units for DRCO have several direct applications to future conservation and management of this imperiled species. First, the importance of additional inventory surveys for DRCO is widely recognized (U. S. Fish and Wildlife Service 2019) and our results can serve to prioritize future survey efforts. Second, results can be used to guide land protection efforts, particularly in combination with existing conservation efforts within the southeastern United States (Swain and Martin 2014). Third, while our results do not inform the realized intra- and inter-unit connectivity, habitat-based conservation units can still play an important role in guiding and quantifying species recovery efforts. For example, identifying small, isolated DRCO populations that may be especially vulnerable to urban expansion or sea level rise (U. S. Fish and Wildlife Service 2019) can be used to guide management actions to improve population resilience. Finally, our results can serve as a foundation for future work attempting to model spatially explicit DRCO population viability across the species' distribution.

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**Code availability** R script used in these analyses are available from the corresponding author upon reasonable request.

## Declarations

**Conflict of interest** The authors have no conflicts of interest to declare.

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