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Coyote Ecology and Management on the Barrier Islands of North Carolina

Estimating Population Dynamics, Investigating Movement, and Evaluating Fladry as a Targeted Deterrent to Protect Shore-Nesting Birds and Sea Turtles

A coyote on Shackleford Banks.
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Coyote Ecology and Management on the Barrier Islands of North Carolina: Estimating Population Dynamics, Investigating Movement, and Evaluating Fladry as a Targeted Deterrent to Protect Shore-Nesting Birds and Sea Turtles

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Abstract

Over the past two decades, coyotes have colonized North Carolina's barrier-island chain where they have been documented depredating protected shore-nesting birds and sea turtles. Following their arrival, federal agencies have trapped and removed >170 coyotes, yet the species persists. We combined non-invasive genetic mark-recapture with GPS tracking to describe coyote population and behavior within Cape Hatteras and Cape Lookout National Seashores and Pea Island National Wildlife Refuge. We implemented a multistate robust design model to provide estimates of island-specific abundance, apparent survival, inter-island movement, and detection probability. Average site densities ranged from 0.05 to 0.86 coyotes/km^2, with Bodie having the highest average density, followed by Pea Island, Shackleford Banks, South Core Banks, Hatteras, Ocracoke, and North Core. We used tracking data to quantify space use, characterize inter-island movement, and evaluate the efficacy of fladry, a non-lethal deterrent, at reducing entry in sensitive nesting areas. While most monitored coyotes remained on the island where they were first detected, we documented inter-island movement with both datasets: genetic recaptures revealed a resident female moving from North Core Banks to Ocracoke and back (~4 km), and another female on Cape Lookout made >50 crossings among Shackleford Banks, Morgan Island, and South Core Banks, predominately at night and often near low tide. While these events are uncommon, they demonstrate functional connectivity which appears to be at a level sufficient to refill vacancies caused by lethal removal. Additionally, pack sizes on Hatteras and Bodie remained stable across seasons despite over a dozen animal removals. Furthermore, we did not find clear population reduction in our population due to removal. Our model showed that apparent survival tended to be lower where predator management occurred, but the effect size was small and highly uncertain with credible intervals overlapping zero, and abundance did not consistently decline following culling events. The fladry experiment coincided with an 83% reduction in crossings by the individual that most frequently used the protected area prior to deployment, demonstrating its ability to reduce incursions into sensitive nesting areas. Overall, our results demonstrate that sustained suppression or eradication of coyote populations on the Outer Banks is unlikely, and that management aimed at modifying their behavior has a greater potential to reduce their impacts on vulnerable nesting species.

Introduction

Non-native predators can drive severe biodiversity losses by depressing native populations (Doherty et al. 2016; Salo et al. 2007), introducing novel pathogens (Chinchio et al. 2020), and altering community dynamics (Croll et al. 2005; Savidge 1987). These impacts are often most acute on islands where naïve prey, simplified food webs, and geographic isolation amplify predator effects (Courchamp et al. 2003). Because these negative impacts generally scale with predator density (Yokomizo et al. 2009), managers need reliable estimates of population size to set realistic objectives for eradication or control. Eradication of invasive mammals has been particularly successful on islands where populations of invasive species can be more effectively controlled due to geographic isolation (Veitch and Clout 2002). The most successful programs have completely eradicated invasive species from island ecosystems, restoring balance to native ecosystems (Howald et al. 2007; Jones et al. 2016; Nogales et al. 2004). However, these eradication efforts are costly, logistically challenging, and require insights into the species' behavior and movement ecology to inform effective management and removal efforts (Holmes et al. 2015). Furthermore, the cost-benefit analysis of full eradication programs changes substantially if there is a high probability of the species re-colonizing.

Coyotes (*Canis latrans*) are highly mobile, generalist mesopredators capable of exploiting a wide range of food sources (Patterson et al. 1998). Their range expansion, facilitated by the extirpation of large carnivores and forest fragmentation, has reached most of North America, including multiple island systems (Hody and Kays 2018; Prugh et al. 2009). On the U.S. East Coast, coyotes have colonized barrier-island systems via swimming and highway bridges (Way 2009; Weckel et al. 2015). As newly established apex predators in coastal settings (Crosby et al. 2024), there is concern that coyote predation could jeopardize the endangered shore-nesting sea turtles and numerous bird species that rely on offshore islands as critical nesting habitat. While a system-wide assessment of their impact on these two groups has not been conducted, site-level studies have confirmed coastal coyotes are indeed eating a variety of seabirds and depredating turtle nests (Etheredge et al. 2015; Lovemore et al. 2020; Whitaker et al. 2015).

The Outer Banks of North Carolina were colonized by coyotes within the last two decades. Along the northern chain within Cape Hatteras National Seashore (CAHA), a unit of the National Park Service (NPS), and Pea Island National Wildlife Refuge (PINWR), the first documented observations of coyote sign and/or predation impacts on managed beaches progressed southward from Bodie Island (2008) to Pea Island (2014–2015), Hatteras Island (2015), and most recently Ocracoke Island (2023; personal communication from CAHA/PINWR, September 2025). In Cape Lookout National Seashore (CALO), another unit of the NPS, coyotes were first detected on North Core Banks (2013), followed by South Core Banks and Shackleford Banks (2014), consistent with a separate colonization pathway. Since arriving on these barrier islands, coyotes have been documented predating nests of birds and sea turtles (Altman 2023; Altman and Stephenson 2023; Doshkov et al. 2019; Thompson et al. 2019) and are recognized as a cause of sea turtle nest failures across CAHA and CALO (Altman 2023; Thompson et al. 2019).

Management has largely emphasized lethal removal (CAHA since 2009; CALO since 2017; PINWR since 2023), with 173 coyotes removed across the system (personal communications from CAHA 28 Aug 2025; CALO 18 Aug 2025; PINWR 2 Aug 2025). Removal efforts were largely ongoing during the study period and were implemented independently by each management unit (CAHA, CALO, and PINWR). Methods vary among units with NPS units employing foothold traps via contracted trappers whereas PINWR uses firearms. The primary deviation from regular management activities occurred at CALO, where some coyotes captured as part of regular coyote management were collared for this study and released rather than euthanized. However, the effectiveness of this approach is in question as coyotes persist, and predation of shore-nesting birds and sea turtles continues. Past research has shown that culling as a means of coyote population control often fails because of compensatory responses such as immigration into removal areas and shifts toward earlier or higher reproduction (Kierepka et al. 2017; Kilgo et al. 2017; Knowlton et al. 1999). Across mainland North America studies actually find higher abundance where hunting pressure is greatest (Kays et al. 2017; Moll et al. 2025). Given these challenges, non-lethal management strategies are being explored elsewhere to curb unwanted coyote behavior, rather than population size, and some examples of such methods include sprinkler systems, hazing, and fladry (McLellan and Walker 2021; Young, Draper et al. 2019; Young, Hammill et al. 2019). We chose to study fladry, a non-lethal deterrent made up of evenly spaced flags that create a novel visual and auditory barrier coyotes are wary of. Relative to sprinkler systems (which require installation and maintenance) and hazing (which requires active human involvement), it is a comparatively inexpensive, low effort, passive method that can be deployed quickly, and it has been piloted in other coastal systems to protect shore-nesting birds (Davis and Heiser 2024).

This study will focus on inventorying the current coyote population, investigating coyote movement patterns, and testing the effectiveness of fladry as a non-lethal deterrent. Within this context, our project integrates two main goals:

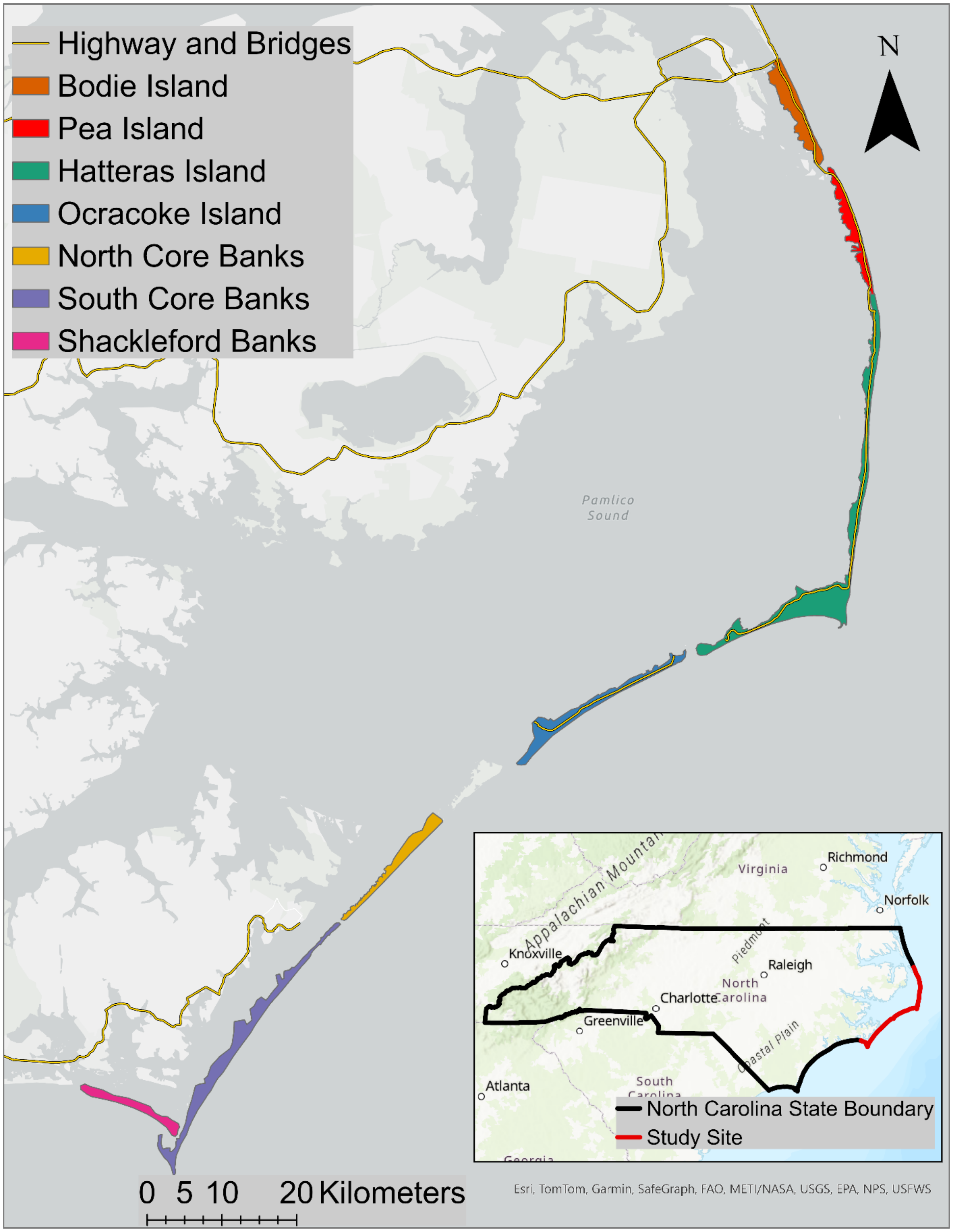
1. Conduct noninvasive genetic surveys to estimate island-specific abundance, apparent survival, inter-island movement, and detection probability to describe the population.
2. Deploy high resolution GPS tracking collars on coyotes to quantify space use, characterize inter-island connectivity, and test fladry’s effectiveness as a non-lethal deterrent to protect shore-nesting birds and sea turtles by reducing entry into protected areas.

Together, these two approaches allow us to provide both the demographic and behavioral insight natural resource managers need to understand the Outer Banks coyote population and set realistic objectives, both for protecting shore-nesting birds and sea turtles as well as planning future coyote control efforts.

Methods

Study Area

The Outer Banks are a chain of narrow barrier islands (~200 km long) that line most of North Carolina's coastline. We surveyed seven sites in total (see Figure 1): three in CAHA (Bodie, Hatteras, and Ocracoke Islands), three in CALO (South Core, North Core, and Shackleford Banks), and PINWR. It is important to note that Bodie Island is not a true island; it is a peninsula extending out from the mainland. Furthermore, Pea Island, a wildlife refuge managed by the US Fish and Wildlife Service, is located between Bodie Island to the north and is physically connected to Hatteras Island to the south. Hatteras Island and Pea Island form one landmass. These four northern sites (3 CAHA and Pea Island) are separated from the mainland by the Pamlico Sound (~24–32 km of open water), the largest lagoonal estuary in the United States (Paerl et al. 2001). Our study sites in CALO (n = 3 islands) are south of Ocracoke Island, and are separated from the mainland by the Core Sound (~3–5 km). Much of the northern islands (e.g., Bodie, Hatteras, and Pea Islands) are connected to the mainland by highway bridges while the southern four islands (Ocracoke Island of CAHA as well as North Core, South Core, and Shackleford Banks of CALO) are separated by wide sounds. See Table 1 for more details on island specific details.



Esri, TomTom, Garmin, SafeGraph, FAO, METI/NASA, USGS, EPA, NPS, USFWS

Figure 1. Study area showing the seven sites we surveyed for coyote scat collection. Highways and bridges are displayed to show the physical connection the northern three sites have with one another and the mainland.

NPS / DANIEL SOSSOVER

Table 1. Detailed table describing each island in our study, its size, human presence, access, details on its isolation, who manages the island, and what we predict coyote abundance will be.

Island	**Size (km^2)**	**Human Presence/Use**	**Roads & Access**	**Isolation**	**Management**	**Predicted Coyote Abundance**
Bodie	~28	Permanent residents; Developed	Accessible by car via NC Hwy 12	Not true island, actually a peninsula physically connected to mainland	NPS-CAHA	Medium: anthropogenic food subsidies, connectivity to mainland
Pea	~21	Bird Sanctuary; Uninhabited	Accessible by car via bridge/highway connected to Bodie/mainland	Separated from Bodie Island/mainland by Oregon Inlet (~1.3km wide). Pea Island and Hatteras Island form one landmass.	United States Fish and Wildlife Service (USFWS) – Wildlife Refuge	Medium: no anthropogenic food subsides but year-round bird community likely provides stable food source, connected to Hatteras
Hatteras	~74	~4,000 permanent residents; Developed	Accessible by car from mainland via bridge from Bodie to Pea Island.	Physically connected to Pea and forms one landmass; separated from Bodie/mainland by Oregon Inlet (~1.3km wide); separated from Ocracoke Island by Hatteras Inlet (~4km wide)	NPS-CAHA	High: anthropogenic food subsidies, largest island in study system, connected to Pea
Ocracoke	~28	~700 permanent residents; Developed	Accessible only by ferry/boat	Highly isolated; separated by Hatteras & Ocracoke Inlets (~4km wide)	NPS-CAHA	Low/Medium: anthropogenic food subsidies but isolated
North Core	~32	Uninhabited	Accessible only by ferry/boat; segmented sand-based road system	Separated from Ocracoke by Ocracoke Inlet (~4km wide) and separated from South Core by Ophelia Inlet (~800m)	NPS-CALO	Low: isolated, no anthropogenic food subsidies
South Core	~38	Uninhabited	Accessible only by ferry/boat; sand-based road system	Separated from North Core by Ophelia Inlet (~800m) and Shackleford by Barden Inlet (~800m)	NPS-CALO	Low: isolated, no anthropogenic food subsidies
Shackleford	~8	Uninhabited; ~120 wild horses	Accessible only by ferry/boat; no roads of any kind	Surrounded by multiple islands including Bogue Banks (~2.4km away), Harker's Island (~3.2km away), Morgan Island (~1.5km away), South Core Banks (800m), and Rachel Carson Reserve (~1.5km away).	NPS-CALO	Low: isolated, no anthropogenic food subsidies

Custom-Made Island Boundaries

Because the boundaries of these islands shift frequently and the movement analyses and density estimates require precise location data we created custom made island boundaries. This was done by combining NPS provided shapefiles, satellite imagery, and new spatial data we collected using handheld GPS during the duration of our study. We used these shapes to convert abundance estimates to density and to define island extent for our movement analyses. Polygons traced the shoreline (excluding offshore shoals or sandbars) and were validated by overlaying GPS points we took in the field. Although PINWR and Hatteras form one continuous landmass, we treated them separately because they function as distinct management units managed by different agencies (USFWS vs. NPS) which necessitated separate density estimates.

Noninvasive Genetics: Sampling, Lab Protocols, and Population Modeling

Field Sampling Protocol

We conducted scat surveys during three field seasons: Winter 2024 (Feb 1–Mar 8), Summer 2024 (July 8–August 20), and Winter 2025 (February 10–March 20). We surveyed each site (making up one "survey round") four times per field season with roughly one week between each survey round in a field season. We surveyed six of the seven sites/islands during all three field seasons, except Bodie Island which had two survey rounds as it was added after the first field season. We used a combination of vehicle-based and on-foot methods to conduct surveys. We surveyed all roads and sound-side and oceanside beaches accessible to vehicles by vehicle and we conducted foot surveys on publicly accessible trails. We covered approximately 250 km per survey round across the seven sites/islands.

We collected scats in the field using 50 mL Falcon tubes filled with 100% molecular grade ethanol, and we labeled them with GPS coordinates, date of collection and island name. We stored samples in a cooler in the field and later transferred them to a −20°C freezer until DNA extraction.

Laboratory Methods

We extracted all fecal samples using Zymo Soil/Microbe Miniprep kits with a final elution of 55 µL. We performed all extractions in a dedicated clean room away from spaces with high quality DNA. After completing extractions, we amplified all samples in two multiplexes. The first multiplex contained a microsatellite locus (FH3725, Guyon et al. 2003; De Barba et al. 2014) species identification set (forward primer SIDL and two reverse primers H16145 and H3R), and the sex-linked zinc-finger (ZF) protein gene (Forward: ZFKF 203L, Reverse: ZFKF 195H; Ortega et al. 2004). The second multiplex included eight microsatellite loci (Cxx119, Holmes et al. 1995; Cxx173, Ostrander et al. 1993; FH2001, FH2054, FH2088, and FH2137, Francisco et al. 1996; FH2611, Eichmann et al. 2004; and FH2670, Guyon et al. 2003).

We used Qiagen Multiplex kits (1X Mastermix, 0.5X Q solution) to conduct polymerase chain reactions (PCR; 13 µL total) that contained 4 µL of extracted DNA and 0.25 µM of each primer except ZF (0.05 µM) and species identification (0.30 µM SIDL). We amplified both multiplexes under the same conditions on a multi-step touchdown protocol. The touchdown conditions included an initial denaturation at 95°C for 5 min, 4 cycles of denaturation at 95°C for 45 s, touchdown annealing temperatures from 68°C to 60°C for 5 min, and extension at 75°C for 1 min. We then ran a single touchdown cycle of annealing at 58°C to 56°C for 2 min, and extension at 72°C for 1 min followed by 31 cycles of denaturation at 95°C for 45 s, annealing 54°C for 2 min, and extension at 72°C for 1 min with a final extension of 72°C for 10 min. We analyzed PCR products using an Applied Biosystems Sequencer 3500 and sized via LIZ size standard (Applied Biosystems Inc). We called allele sizes in the program Geneious Prime (Kearse et al. 2012).

Quality Control and Individual Matches

Fecal samples often contain low quality and quantity of DNA, which requires strict quality control to ensure accurate genotypes. First, we amplified all samples in duplicate to ensure matching genotypes, and when mismatches occurred, we amplified them a third time to reach a consensus. Two types of genotyping errors occur: allelic dropout and false alleles. Allelic dropout occurs more frequently, and results from a heterozygous genotype being called a homozygote due to low or no amplification of a second allele. False alleles occur in the opposite case, where a true homozygote is called a heterozygote due to non-specific amplification. We defined allelic dropout when two duplicates mismatched, and the third amplification confirmed a heterozygote whereas the opposite was counted as a false allele. We also ran negative PCR controls on all plates to identify any contamination. Finally, we calculated the probability of identity (P_{ID}) and siblings (P_{sib}) to ensure our microsatellite dataset contained sufficient power to accurately differentiate unrelated individuals and siblings.

To identify matching genotypes, we used the function “Matches” in Genalex 6.2 (Peakall and Smouse 2006). This function produces a list of matching individual genotypes as well as highly similar ones (1–3 alleles different). For genotypes that were 1–3 alleles different, we re-inspected the electropherograms in Geneious, and if ambiguous, we re-ran both individuals to confirm a similar or matching genotype. We then summarized all unique individuals into a single genotype (i.e., consensus genotype), and identified any repeated genotypes (i.e., recaptured individuals).

Population Model

Overview & Terminology

We estimated coyote abundance, apparent survival, per-capita recruitment, inter-island movement, and detection probability using a multistate robust design mark-recapture model (Kendall and Nichols 2002; Kéry and Schaub 2012; Pollock 1982). In this framework, populations are demographically closed (no additions or subtractions) within each primary period and open (allows for births, deaths, immigration, and emigration) between primary periods. Our sampling comprised three primary periods, Winter 2024, Summer 2024, and Winter 2025, each with four secondary occasions. Secondary occasions are the repeated survey rounds within a primary period. We use the terms primary period and secondary occasion throughout this next section.

Data and Capture Histories

The genotypes from our scats provided individual identification and island of detection for each secondary occasion. For each identified individual, we constructed encounter histories by island × secondary occasion within each primary period. Islands with no survey effort in a given primary period (only Bodie in Winter 2024) were coded explicitly as zero survey effort in a binary survey-effort matrix so that non-detections there do not imply absence of coyotes.

To account for undetected individuals, we employed data augmentation, a process of adding a set of all-zero encounter histories to represent potential undetected individuals. The model estimated each individual's latent state z[i,j], indicating whether they were alive and available for detection in each primary period. This process allowed us to estimate abundance including undetected animals as well as our genetically identified individuals. These all-zero encounter histories were added to our capture histories constructed from our genotyped fecal samples. This augmented capture history was the dataset we used for subsequent population modeling.

Latent States

We defined nine discrete states for each coyote:

- not yet entered the system (coded as 1, animal is not born yet or has not reached the islands),
- alive/present on one of seven islands (coded by island 2–8: Bodie, Pea, Hatteras, Ocracoke, North Core, South Core, and Shackleford),
- or dead/permanently emigrated (9).

These were encoded in the latent state matrix z[I,j], capturing transitions between islands or out of the system. Although Bodie Island was not surveyed in the first primary period abundance was estimated using subsequent data in primary periods 2 and 3.

Model Parameters

Detection probability was modeled as a function of two binary covariates:

1. **Survey effort:** whether an island was surveyed during a primary period.
2. **Road-based effort:** whether surveys included roads, which likely increased detection rates.

Road-based surveys were conducted on Hatteras (inter-dunal roads), North Core (segmented road-system), and South Core (defined sand road along island's entire length) while we did not define the other islands as having road-based surveys. The rest were primarily surveyed on beaches and trail systems when available. Since coyotes use roads and trails we believe the islands where we had this additional survey factor might influence our detection probability, though we didn't explicitly impose one. No evidence suggested detection differed by sex or other individual characteristics.

Apparent survival (ϕ) was modeled as a function of lethal predator control using a binary covariate representing presence or absence of culling between primary periods:

$$\text{logit}(\phi_{s,j}) = \beta_0 + \beta_1 \times \text{predMgmt}_{[s,j]}$$

Where:

$\phi_{s,j}$ = apparent survival probability for coyotes on island s during interval j (probability of being alive and still present in the system at j+1)

logit() = logit link function, transforming probabilities (0–1) to the continuous real scale

β_0 = intercept (baseline logit survival when no predator management occurred)

β_1 = regression coefficient representing the effects of predator management (lethal control)

$predMgmt_{[s,j]}$ = binary covariate coded as 1 if predator control occurred between intervals j and j+1 on island s, and 0 if not

This formulation does not distinguish between permanent emigration and death because the net effect on the population is the same (i.e., loss of an individual from the island). Meaning individuals that either died or permanently emigrated out of our study system between primary periods are not distinguishable in the model.

Recruitment (number of new individuals entering the population between survey periods) was estimated as a per-capita rate (f):

$$\hat{R}_{s,j} = f \cdot \hat{N}_{s,j-1}$$

Where:

$\hat{R}_{s,j}$ = estimated number of new recruits on island s during season j

f = per-capita recruitment rate (average number of new individuals per existing individual)

$\hat{N}_{s,j-1}$ = estimated abundance on island s in the previous season (j−1)

New individuals are defined as those not present in the population in the previous primary period. Recruitment includes both locally born coyotes and immigrants arriving to the island, but cannot distinguish between these sources as new individuals were entered as “not yet entered” as a latent state. Our model applies a single f across all islands and seasons, so the estimate represents an average recruitment rate for the study area.

Movement between islands was modeled as a first-order Markov process, meaning the location of an individual coyote in one season depends only on the island it occupied in the previous survey period. Transitions were only allowed between geographically adjacent islands; all other movements, such as Bodie to South Core, were not allowed. We included the ability for individuals to move between islands (states) because both our genetic and GPS data detected inter-island movement. Further, this allowed the uncertainty associated with inter-island movements to propagate into estimates of survival, recruitment, abundance, entry probability, and detection probability.

Model Implementation

We implemented the multistate robust design model in JAGS (Plummer 2003) using the jagsUI package in R (Kellner 2015). To achieve stable reliable posterior estimates, we ran three parallel MCMC chains for a total of 1,200,000 iterations per chain with the first 200,000 iterations discarded as burn-in. We applied a thinning interval of 10, resulting in 100,000 retained posterior samples per chain and 300,000 total.

This high iteration count, long burn-in, and thinning were necessary because the lack of survey effort on Bodie Island in the first primary period caused parameters related to Bodie in the first survey period to mix poorly. This caused a high level of uncertainty particularly for Bodie Island's estimated abundance in Winter 2024. This uncertainty propagated into several of Bodie's connected and derived parameters which had low effective sample sizes and required additional iterations and a high-level of thinning to reduce autocorrelation as a result of poor mixing to achieve stable posterior estimates.

Model Priors

We used weakly informative priors for all key model parameters (detection probability, apparent survival, per capita recruitment, and movement) to constrain estimates to realistic biological values while allowing the data to drive inference. Survival regression coefficients (β_0, β_1) were assigned Normal(0, 0.1) priors on the logit-scale which allow for a wide range of positive or negative effects without assuming a directional influence of covariates like predator management. Detection probability was assigned a Beta(1,1) prior (i.e., uniform over [0,1]) and grouped by whether road-based surveys were conducted (road_det) to account for expected differences in detectability. We didn't impose any assumption that islands with road-based surveys would be higher or lower. The per capita recruitment rate was assigned a Gamma (0.1, 0.1) prior, which constrains this parameter to be positive while remaining flexible for either low or high recruitment rates. Transition probabilities between islands were assigned uninformative Dirichlet priors, which allows equal probability of remaining on an island or moving to adjacent islands, constrained by the reality of geography.

Model Assumptions & Convergence

The multistate robust design model relies on the following assumptions about recruitment: 1) demographic closure within primary periods (i.e., surveying period) and 2) open population dynamics between primary periods (i.e., immigration/emigration, births/deaths occur between surveys). Essentially, no population size changes occur during primary periods, only between. This model also requires that the augmented number of individuals (i.e., undetected individuals) exceeds the true observed unique individuals. Finally, the model assumes all individuals, regardless of sex, have equal detection probability within each modeled group. Because we conducted road-based surveys on some islands and not on others, we anticipated that detection probability might differ between islands as increased survey effort along roads could increase detection probability. We do not have any evidence that detection probability varied by sex or other factors so the assumption of equal detection probability within each survey group probability is the most biologically realistic for this system.

We evaluated the convergence of our model using standard MCMC diagnostics provided by the jags() function in the jagsUI package in R (Kellner 2015). All monitored parameters had R_hat values extremely close to 1.00 (range: 0.99999–1.00049) indicating convergence across chains.

Spatial Considerations

Although Pea Island and Hatteras Island form one continuous landmass, we modeled them as separate states due to their differing human densities and management practices. Pea Island has no permanent residents, so it experiences less human disturbance and is not fragmented by development to the same extent as Hatteras. Furthermore, each area is managed by different agencies (U.S. National Park Service vs. U.S. Fish and Wildlife Service), which necessitates providing separate densities to each stakeholder.

Density Calculations

Density was calculated post hoc from island-specific abundance estimates and island area (density = abundance/island area).

Pack Structure

To assess potential packs, we analyzed the spatial distribution of genotyped coyotes on each island. Packs were inferred from spatially segregated groups of individuals, with recaptures providing the strongest evidence of movement and territory use. Individuals that were recaptured at widely separated locations across an island were interpreted as belonging to a single pack that ranges broadly over the entire area. In contrast, when recaptured individuals were repeatedly detected only within a limited portion of an island and never elsewhere, this pattern suggested the presence of multiple, spatially distinct packs. Single detections were assigned to the nearest overlapping group.

Movement Ecology: From Capture to Analysis

Animal Capture

We collaborated with U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services (USDA-APHIS-WS) to capture coyotes for GPS collaring. In September 2023, trapping was conducted on South Core Banks over a 29-day period, totaling 1,044 trap nights, which resulted in the capture of six individual coyotes (USDA 2023). Of these, two males (one adult "Rahzar" and one subadult "Ed") were collared and released, while the remaining four were euthanized. A second trapping effort took place over the course of 21 days between April and May of 2024, with 568 trap nights conducted across South Core Banks and Shackleford Banks (USDA 2024). This effort resulted in the capture of four coyotes: one adult female on South Core ("Martha"), and two adult females ("Cruella" and "Azula") and one adult male on Shackleford Banks. All but the adult male were collared and released. Coyotes were captured using foothold traps, and all handling procedures were conducted by USDA-APHIS-WS and approved by the Institutional Animal Care and Use Committee (23-234). Towards the end of our project USDA-APHIS-WS conducted another round of trapping across CALO in April of 2025 as part of ongoing coyote management efforts. During this, Rahzar and Azula were caught and killed; we obtained their collars from trappers.

Collar Configuration, Data Retrieval, and Performance Assessment

All coyotes were fitted with accelerometer-informed GPS collars (AIGPS) developed by e-obs GmbH (1D model, e-obs, Munich, Germany). Each collar weighed 275 g, representing less than 3% of coyote body mass, and was equipped with a leather breakaway link designed to degrade over time and ensure they'd eventually detach from the animal. These collars integrate GPS with tri-axial accelerometers, reducing the typical trade-offs between fix frequency and battery longevity seen in traditional collars, which record GPS locations at fixed intervals regardless of what the animal is doing (Brown et al. 2012). The accelerometer records movement along the X, Y, and Z axes, and uses a real-time thresholding system based on raw acceleration variance to classify the animal's current behavioral state (Nathan et al. 2012).

The collars were programmed to collect GPS fixes every three minutes when the animal was classified as active (after three consecutive readings above a variance threshold of 5000 [unitless variance score]) and would revert to taking a GPS fix every five hours during periods of inactivity (after three consecutive readings below the threshold). This dynamic setup allowed us to conserve battery during periods of inactivity while getting fine-scale spatial data once the animals were active. At each fix, our collars recorded GPS coordinates (latitude and longitude), timestamp, and a host of environmental and diagnostic metadata including satellite count, battery voltage, and temperature. A summary of all the variables the collars recorded is provided below in Table 2.

Table 2. Detailed explanation of every data category our GPS collars collected during the duration of our study. Every row in our collar dataset has these data types.

Column Name	Description
event-id	Unique identifier for each recorded event.
visible	Indicates whether the data point is visible/usable.
timestamp	Time the event was recorded.
location-long	Longitude of the GPS location.
location-lat	Latitude of the GPS location.
bar:barometric-pressure	Barometric pressure recorded by the collar.
data-decoding-software	Version of the software used to decode the data.
eobs:acceleration-axes	Axes measured by the accelerometer (X, Y, Z).
eobs:acceleration-sampling-frequency-per-axis	Sampling frequency per axis of the accelerometer.
eobs:accelerations-raw	Raw acceleration values from the tri-axial accelerometer.
eobs:activity	Activity level calculated by the collar.
eobs:activity-samples	Number of activity samples used to calculate activity level.
eobs:battery-voltage	Battery voltage at the time of data recording.
eobs:fix-battery-voltage	Battery voltage at the time of GPS fix.
eobs:horizontal-accuracy-estimate	Estimated horizontal accuracy of the GPS fix (m).
eobs:key-bin-checksum	Checksum for data integrity verification.
eobs:speed-accuracy-estimate	Estimated error in speed measurement.
eobs:start-timestamp	Timestamp marking the beginning of a GPS burst.
eobs:status	Status code of the collar at the time of fix.
eobs:temperature	Ambient temperature recorded by the collar.
eobs:type-of-fix	Type of GPS fix (e.g., 2D, 3D).

Table 2 (continued). Detailed explanation of every data category our GPS collars collected during the duration of our study. Every row in our collar dataset has these data types.

Column Name	**Description**
eobs:used-time-to-get-fix	Time it took to acquire the GPS fix.
gps:dop	Dilution of Precision (DOP) value indicating GPS accuracy.
gps:satellite-count	Number of satellites used to obtain GPS fix.
ground-speed	Ground speed of the animal based on GPS data (m/s).
heading	Direction of travel in degrees from north.
height-above-ellipsoid	Height above the ellipsoid (altitude estimate).
import-marked-outlier	Whether the data point was manually marked as an outlier.
mag:magnetic-field-raw-x	Raw magnetic field data from the X-axis.
mag:magnetic-field-raw-y	Raw magnetic field data from the Y-axis.
mag:magnetic-field-raw-z	Raw magnetic field data from the Z-axis.
manually-marked-outlier	Indicates whether the point was manually flagged as an outlier.
orientation:quaternion-raw-w	Raw W component of the quaternion representing orientation.
orientation:quaternion-raw-x	Raw X component of the quaternion representing orientation.
orientation:quaternion-raw-y	Raw Y component of the quaternion representing orientation.
orientation:quaternion-raw-z	Raw Z component of the quaternion representing orientation.
sensor-type	Type of sensor used (e.g., GPS).
individual-taxon-canonical-name	Scientific name of the tracked individual.
tag-local-identifier	Local identifier of the tag used.
individual-local-identifier	Identifier assigned to the tracked animal.
study-name	Name of the study in which the data were collected.

We used Yagi antennas to periodically locate the coyotes, approach within 100–200 m, and download the data from each animal, which was then uploaded to the MoveBank repository (Kays et al. 2022). We evaluated collar performance using the “eobs:type-of-fix” field from the e-obs tracking data, which indicates what type of fix was recorded (3 = 3D fix, 2 = 2D fix, 1 = no fix). We considered both 2D and 3D fixes as successful whereas a value of 1 was treated as a failed fix (MoveBank Attribute Dictionary 2025).

Fladry Experiment

Fladry is a non-lethal predator deterrent that uses a suspended line of evenly spaced flags to create a novel visual and auditory barrier. The movement of the flags in the wind discourages predators, including coyotes (Young et al. 2019), from crossing into sensitive/protected areas. Although originally designed to protect livestock from wolf predation, fladry has been tested in a variety of ecological and management contexts, including other coastal ecosystems, most relevantly by state managers to protect shore-nesting birds and turtles (Davis and Heiser 2024). Generally, fladry’s effectiveness depends on the duration of deployment, as animals eventually habituate to the novel barrier and it’s no longer effective. Fladry has been shown to be effective for around 60 days (Windell et al. 2022; Young et al. 2019); therefore, less than two months is the ideal timeline where we can get the discouraging effects without the animals habituating to the stimuli.

We installed a fladry barrier near the northern terminus of South Core Banks (34.8141441, −76.3605699) to protect a large NPS managed nesting area for shorebirds and sea turtles. The fladry line extended across the entire width of the island to deter coyotes from entering the protected nesting area just north of the fladry line. Young et al. (2019) found that smaller gaps between flags increase efficacy, so we spaced our 18-24 inch long flags only 6–8 inches apart. The line was mounted on posts set in sand that allowed the flags to lay on the ground or hang as much as six inches off the ground. Deployment ran from June 17th to August 16th with NPS staff inspecting the line weekly to untangle flags that wrapped around the line. To document what the coyotes did once they encountered the barrier, we placed four motion-activated camera traps along the length of the fladry line. Furthermore, we assessed whether coyotes reduced their use of the north side of South Core Banks following fladry deployment with the GPS collar data from our three South Core Banks resident individuals (Ed, Martha, and Rahzar). Each of their GPS fixes were classified as occurring on the north or south side of the fladry line. South-to-north transitions were identified by comparing successive fixes with each fix above the line assigned as “north” and each below as “south.” Then, for each individual, we calculated the number of S → N transitions and the total monitoring effort (hours) within each period (pre-deployment, during deployment, and post-deployment). Crossing rates were summarized as the number of transitions per 24 hours at both the group and individual level.

To test for statistically significant changes in crossing rates between the pre-deployment and deployment periods, we used Poisson exact tests. This test allows us to evaluate whether coyotes crossed north of the fladry line less frequently during deployment than before. Post-deployment rates were also summarized and are reported descriptively to provide additional context but were not included in the formal statistical tests. Tests were conducted on an individual level as well as pooled (all three animals’ data combined).

Activity

Coyotes are known to be more active nocturnally in areas with high human activity (Soccorsi and LaPoint 2023) and shift toward nocturnality with increased human activity (Reilly et al. 2017). Further, they’ve been shown to take advantage of seasonal resource pulses (Jensen et al. 2024). Therefore, to investigate whether coyote activity patterns varied with changes in prey availability and human recreation, we divided the year into two biologically and management-relevant periods. We defined April through September as the nesting/visitor season, which coincides with beach-nesting shorebird breeding activity (nesting, incubation, chick-rearing, and fledging) and sea turtle nesting and hatchling emergence, as well as peak human visitation (see Figure 2). We defined October through March as the off-season, when beach-nesting shorebird breeding activity and sea-turtle nesting/hatchling emergence are absent, and overall visitation is substantially lower than April–September.

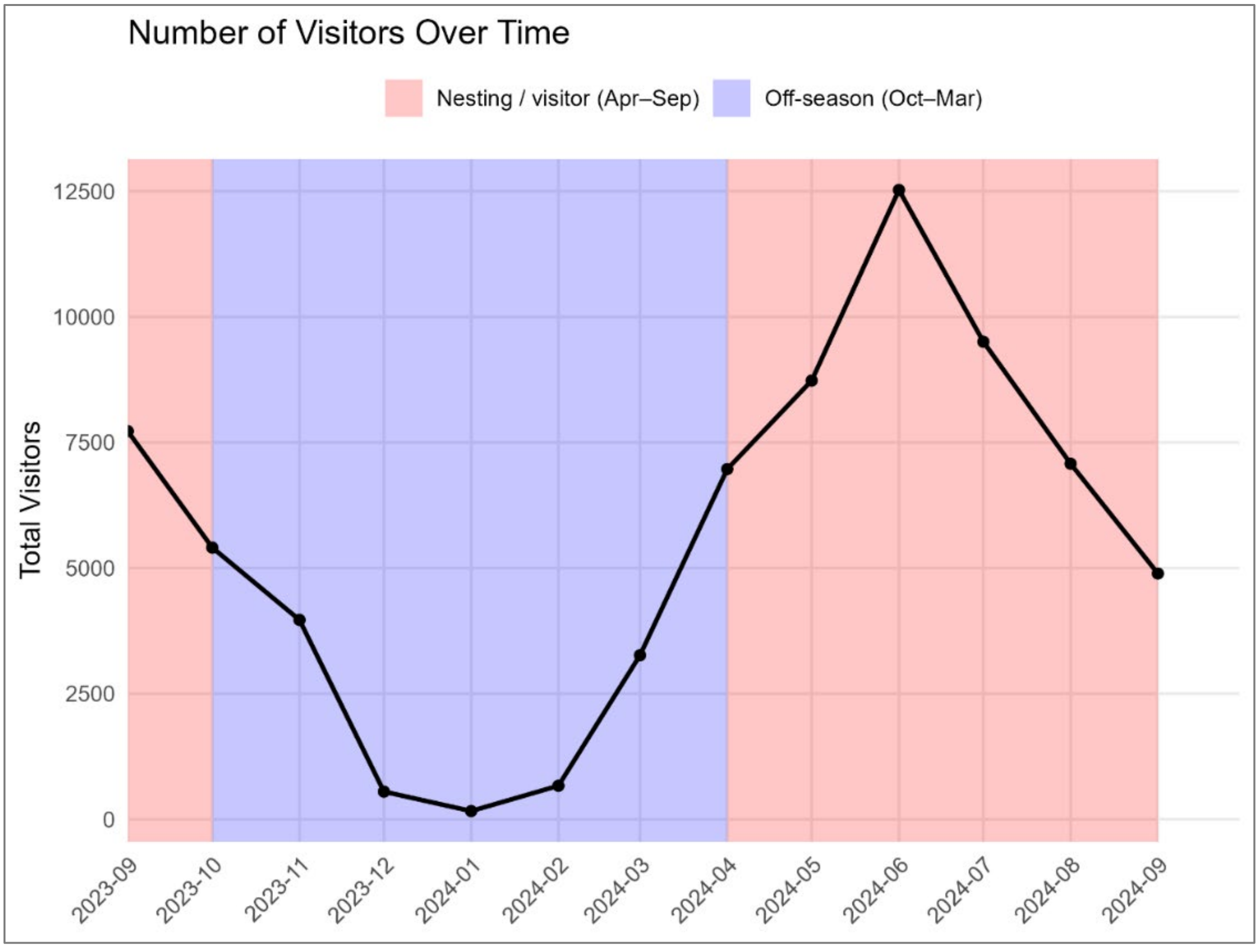


Figure 2. Monthly ferry visitation to South Core and Shackleford (Sep 2023–Sep 2024). Shaded bands: Apr–Sep = nesting season for shore-nesting birds & sea turtles and peak visitation; Oct–Mar = off-season (data: Cape Lookout NS).

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We quantified activity using the accelerometer bursts collected from our GPS collars by calculating Vectorial Dynamic Body Acceleration (VeDBA) for each sample using this formula:

$$\mathrm{VeDBA}_i = \sqrt{(X_i - \bar{X})^2 + (Y_i - \bar{Y})^2 + (Z_i - \bar{Z})^2}$$

Where:

X_i, Y_i, Z_i are the raw acceleration values

$\bar{X}$, $\bar{Y}$, $\bar{Z}$ are the average values of each axis in the burst

This approach is widely accepted in movement ecology as a reliable measure of animal activity and as a proxy for energy expenditure (Gleiss et al. 2011; Qasem et al. 2012).

Distance

We measured daily movement as the sum of straight-line distances between consecutive GPS fixes within each calendar day. Given the high resolution of our data compared to typical coyote studies, we use a scale-insensitive approach (Noonan et al. 2019) to estimate the distance moved by animals from several published GPS datasets: Albany Pine Bush, NY (Bogan and Kays 2019), northern Washington, WA (Prugh et al. 2023), and Fishlake NF, UT (Mahoney 2017).

Home Ranges & Core Areas

We estimated seasonal core areas (50%) and home ranges (95%) using autocorrelated kernel density estimation (AKDE) using the ctmm R package (Calabrese et al. 2016; Fleming et al. 2015; Silva et al. 2022). First, we partitioned each coyote's tracking data by season (Spring, Summer, Fall, Winter). Then, for each individual-season dataset, we fit a continuous time movement model using variograms and maximum-likelihood estimation and then generated AKDE utilization distributions and extracted 50% (core area) and 95% (home range) contours with 95% confidence intervals.

Identification of Resting and Feeding Sites

To investigate coyote resting and feeding sites, we used the MoveApps platform, a cloud-based, no-code environment for analyzing animal movement by building modular workflows (Kölzsch et al. 2022). Our workflow included four MoveApps modules: the *Movebank Location* (Kölzsch et al. 2024a), *Filter/Annotate Day or Night* (Kölzsch 2024b), *Multiple Animal Cluster Detection* (Kölzsch and Kendall 2024), and *WriteCSV* (Kölzsch and Scharf 2024).

Coyote Space Use Before and During Turtle Nesting Season

We used a resource selection function approach to compare the characteristics of sites used by coyotes against a set of random points as a test of their habitat selection. Specifically, we tested whether coyotes selected areas near turtle nest areas specifically, versus showing a general affinity for ocean-facing beaches. We used GPS movement data from three resident coyotes who overlapped most with turtles: one adult female on Shackleford Banks and two males on South Core Banks.

We filtered individuals' GPS data to include only active movement (i.e., <5 min between fixes due to high accelerometer movement). We then split these filtered datasets into two periods, PRE (on or before May 20th, 2024) and DURING (May 21st to Aug 31st, 2024), matching the start and end dates of the 2024 sea turtle nesting dataset provided by the NPS. Within each period, GPS fixes were treated as used locations. Availability was represented by a 10:1 ratio of random points drawn from the area each animal used in that period, defined as the convex hull of its GPS fixes intersected with the island barrier polygon. At all points (used and available), we calculated two covariates: (1) distance to the nearest turtle nest and (2) a binary indicator (in_beach50) for whether the point fell within a 50-m buffer of the ocean-facing beach. Distances to the nearest turtle nest were z-standardized across periods.

We fit three logistic use-availability models per individual, each including period (PRE & DURING) interactions:

Model A: Nest proximity only (z_dist_turtle x period)

Model B: Beach use only (in_beach50 x period)

Model C: both effects jointly (z_dist_turtle x period + in_beach50 x period)

Where z_dist_turtle represents the standardized distance to the nearest nest, in_beach50 is a binary indicator of whether the point fell within 50 m of the ocean-facing beach, and period distinguishes between the two periods. Model fit was assessed by Akaike's Information Criterion (AIC).

Investigating Inter-Island Movement

To investigate inter-island movement, we assigned each GPS fix to an island (South Core Banks, Shackleford Banks, or Morgan Island) with a point-in-polygon overlay (using the st_within function of the sf R package). Fixes that did not fall inside any island polygon were labeled as "Ocean". To be able to quantify residency and identify crossing events, movement data was partitioned into bouts. We defined a bout as a stream of consecutive/sequential GPS fixes labeled with the same island. A bout began at the first fix immediately following an island label change and ended at the last fix prior to the next island label change. For each bout we recorded the island label, start and end timestamps, duration (end − start; in minutes), and the number of fixes. After creating the bouts, to ensure brief near-shore excursions weren't misclassified as inter-island movement, sequences in the form Island A → Ocean → Island A were collapsed by relabeling the intermediate Ocean fixes as Island A and recomputing the bout IDs. This process was sequence-based and did not add or remove fixes.

For residency summaries, we calculated the time between consecutive fixes, summing these intervals by island to estimate total time spent per island. We also noted the number and proportion of fixes per island, and summarized how long coyotes stayed on each island in a bout, reporting minimum, median, mean, and maximum bout durations along with the number of bouts per island. Inter-island movement events (i.e., water crossings) were identified/defined as an Ocean bout bracketed by two different islands (e.g., Island A → Ocean → Ocean…… → Island B). For each crossing, we recorded departure, arrival, duration (mins), and route (origin → destination). We then took this list of crossing events and summarized crossing events by route and duration.

To assess whether crossings were associated with low tides, we obtained predicted high/low tide times from the nearest NOAA CO-OPS station (Beaufort, NC; Duke Marine Lab; Station ID 8656483). For each crossing event, we matched the coyote's departure time to the nearest predicted low tide and calculated the difference in minutes, flagging events that occurred within ± 1 hour of low tide. Because the time of low tide shifts daily, this nearest low matching analyzes relative tidal phase rather than absolute clock time; in other words, we tested whether crossings occurred closer to low tide than expected by chance, not whether they clustered at the same time of day. Under the null hypothesis we'd expect that departure times would be uniformly distributed with respect to tidal phase. The expected proportion of crossings within a ± 1 hour window is: $p_0 = 2w/T$, where w is window length (1h) and T is the mean semidiurnal tidal period (~12.42 h). We then tested whether the observed proportion exceeded this null expectation using a one-sided binomial test and report Wilson 95% confidence intervals.

Results

Scat Collection & Genotyping

Results of Surveying Effort

In total, we collected 387 fecal samples across our three sampling periods (see Table 3). We eliminated 77 (20.10%) of these samples due to low DNA amplification as we retained only samples that produced successful genotype at 7 or more loci for further analysis. Four samples were not scat (hairs/organs). The remaining 306 samples consisted of 247 coyotes and 59 dogs. In both species' identification markers, dogs and coyotes amplify non-overlapping sized products (~4bp difference between species), allowing for non-ambiguous species assignment. Genotyping errors remained low overall, with all errors classified as allelic dropout (16 cases out of 5,508 total reactions for 306 fecal samples; 0.29%). The probability of assigning two unrelated individuals ($P_{ID} = 1.0 \times 10^{-12}$) or siblings ($P_{sib} = 7.8 \times 10^{-5}$) as the same individual were both low; therefore, we had confidence in using Matches analysis for individual identification. We identified a total of 62 (20 M, 42 F) coyotes across 7 islands, each captured between 1 and 34 times. We detected a 2:1 ratio of females to males.

Table 3. Summary of scat collection and coyote genotyping by island and season. Island cells are formatted as follows: scats collected / genetically ID'd coyote scats / unique coyotes. Across all islands, 306/387 successfully amplified at ≥7 loci. Of those, 247 were identified as coyote with 62 unique individual coyotes across the entire study.

Island	Winter 2024	Summer 2024	Winter 2025	Total
Bodie	N/A	23 / 17 / 13	31 / 29 / 11	54 / 46 / 19
Pea	23 / 13 / 3	0 / 0 / 0	17 / 14 / 5	40 / 27 / 6
Hatteras	52 / 31 / 9	21 / 10 / 6	22 / 12 / 7	95 / 53 / 17
Ocracoke	10 / 2 / 2	7 / 1 / 1 [A]	5 / 1 / 1	22 / 4 / 3
North Core	24 / 19 / 2	17 / 1 / 1 [A]	17 / 8 / 1	58 / 28 / 2
South Core	40 / 33 / 7	33 / 19 / 5	35 / 29 / 7	108 / 81 / 13
Shackleford	8 / 7 / 2	0 / 0 / 0	2 / 1 / 1	10 / 8 / 3
Total (all islands)	157 / 105 / 25	101 / 48 / 25	129 / 94 / 33	387 / 247 / 62

[A] The single unique individual detected in Summer 2024 on Ocracoke and North Core is the same individual/genotype (i.e., one coyote detected on both islands that season).

Key Population Parameter Estimates

The multistate robust design mark-recapture model we used to analyze coyote individuals detected in our fecal DNA analysis not only allowed us to estimate coyote abundance, but also apparent survival, per-capita recruitment, inter-island movement, and the probability of detecting an individual in our survey. We present a summary of those parameter results here, and then go into the details of abundance more in subsequent sections.

- Detection probability (per secondary occasion, given the alive/present):
    - Islands without road-based surveys = 0.208 (95% CI 0.131–0.298)

    - Islands where road-based surveys were conducted = 0.376 (95% CI 0.287–0.465)
    - Interpretation: Detection probabilities were indeed statistically significantly higher when island surveys included road-based surveys.
- Apparent survival (between primary periods):
    - No predator management = 0.631 (95% CI 0.431–0.823)
    - With predator management = 0.544 (95% CI 0.274–0.876)
    - Effect of management on survival (logit scale β_1): posterior mean −0.33, 95% CI −1.85 to +1.50, SD 0.88; 69.6% of posterior samples were less than 0.
    - Interpretation: Trends towards lower survival with predator management, but with high uncertainty and the credible interval overlaps 0.
- Per-capita recruitment:
    - Applied uniformly across all islands and seasons, average per-capita recruitment was 0.27 (95% CI 0.093–0.471, SD 0.097).
    - Interpretation: Per-capita recruitment rate of 0.27 over five months indicates moderate levels of new individual additions to the population.
- Movement between islands
    - Most individuals were predicted to remain on their initial island across seasons. Example “stay” probabilities: Bodie = 0.93 (95% CI 0.76–0.99).
    - Movement to neighboring islands were generally estimated to be low but non-zero with the strongest signal from Shackleford → South Core = 0.52 (95% CI 0.03–0.97).
    - Most estimates had wide credible intervals indicating these are best treated as movement potential, NOT actual precise rates of movements between islands.
    - Interpretation: Movement between islands was low.

Abundance and Density

Estimates of abundance from our robust design were under 11 animals at each island except for Bodie Island (Table 4).

Bodie Island is connected to the mainland and had the highest abundance (Summer 2024: 24.2, 95% CI: 17–35 animals; Winter 2025: 16.9, 95% CI: 12–26 animals). As expected, the unsampled Winter 2024 period had a high estimate with wide confidence intervals (32.1, 95% CI: 16–60). When converted to densities, Bodie Island still had the highest density (Figures 3 and 4, Table 5) whereas Pea Island had the highest among the remaining six (0.232–0.381 coyotes/km^2). The lowest densities were on Ocracoke Island (southernmost CAHA island; 0.082–0.111 coyotes/km^2) and North Core Banks, the northernmost island in CALO (0.040–0.069 coyotes/km^2).

Table 4. Posterior abundance estimates (posterior mean; 95% credible interval) for coyotes by island and primary sampling period (Winter 2024, Summer 2024, Winter 2025), from the multistate robust-design model fit to our genetic mark-recapture data from our noninvasive scat collection. Islands are listed north-to-south.

Island	**Winter 2024**	**Summer 2024**	**Winter 2025**
Bodie	32.1 (16.0–60.0)	24.2 (17.0–35.0)	16.9 (12.0–26.0)
Pea	5.0 (3.0–10.0)	4.6 (2.0–10.0)	8.2 (5.0–14.0)
Hatteras	10.7 (9.0–14.0)	8.9 (6.0–13.0)	8.0 (7.0–11.0)
Ocracoke	3.2 (2.0–7.0)	2.5 (0.0–7.0)	2.3 (1.0–6.0)
North Core	2.3 (2.0–4.0)	1.5 (1.0–3.0)	1.3 (1.0–3.0)
South Core	8.1 (7.0–11.0)	6.5 (5.0–10.0)	7.9 (7.0–10.0)
Shackleford	3.3 (2.0–7.0)	1.4 (0.0–5.0)	2.2 (1.0–5.0)

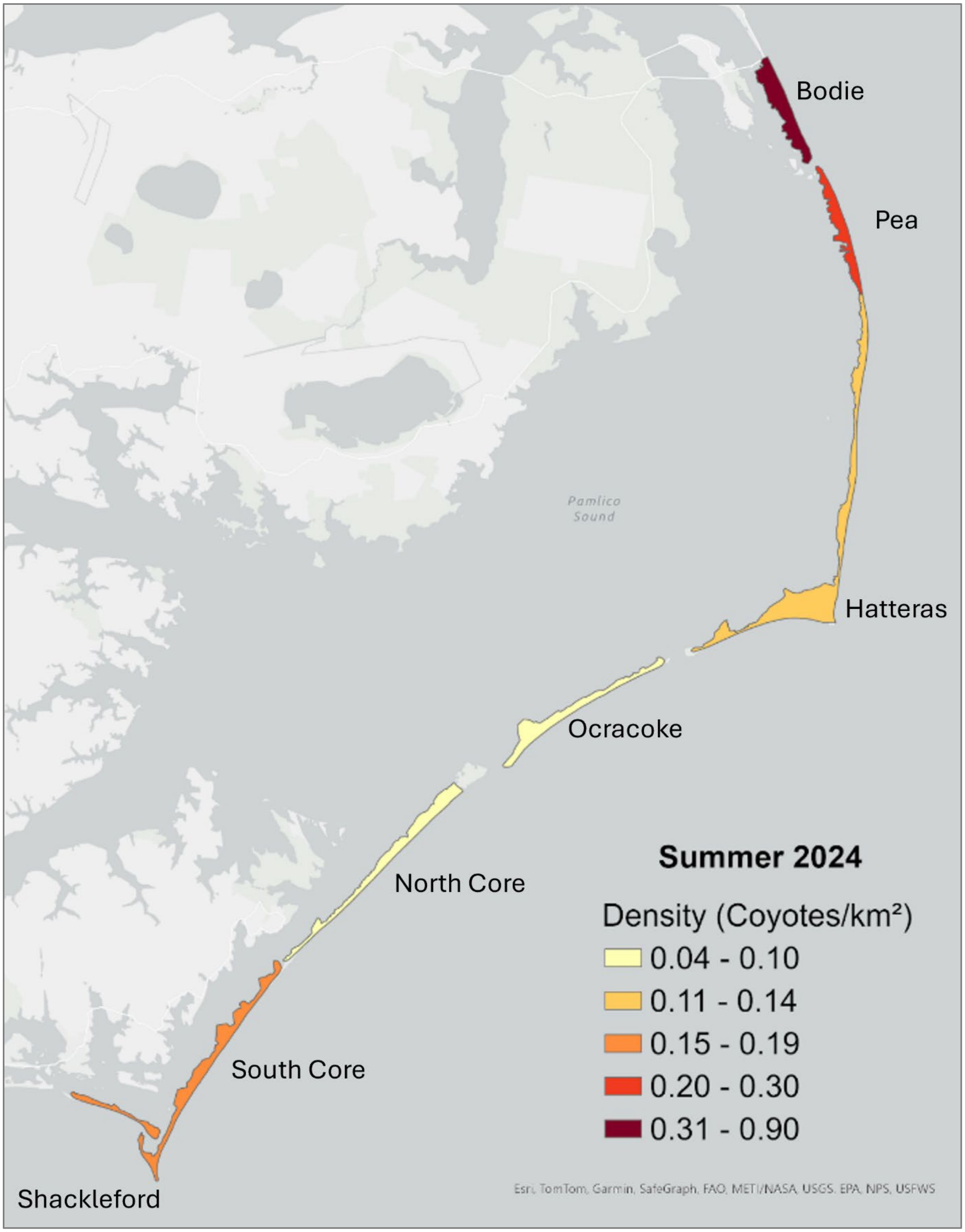

Figure 3. Estimated coyote density by island for Summer 2024. Bodie has the highest density, followed by Pea, South Core Banks and Shackleford, then Hatteras, and finally Ocracoke and North Core Banks. These density classes were chosen to highlight the trends.

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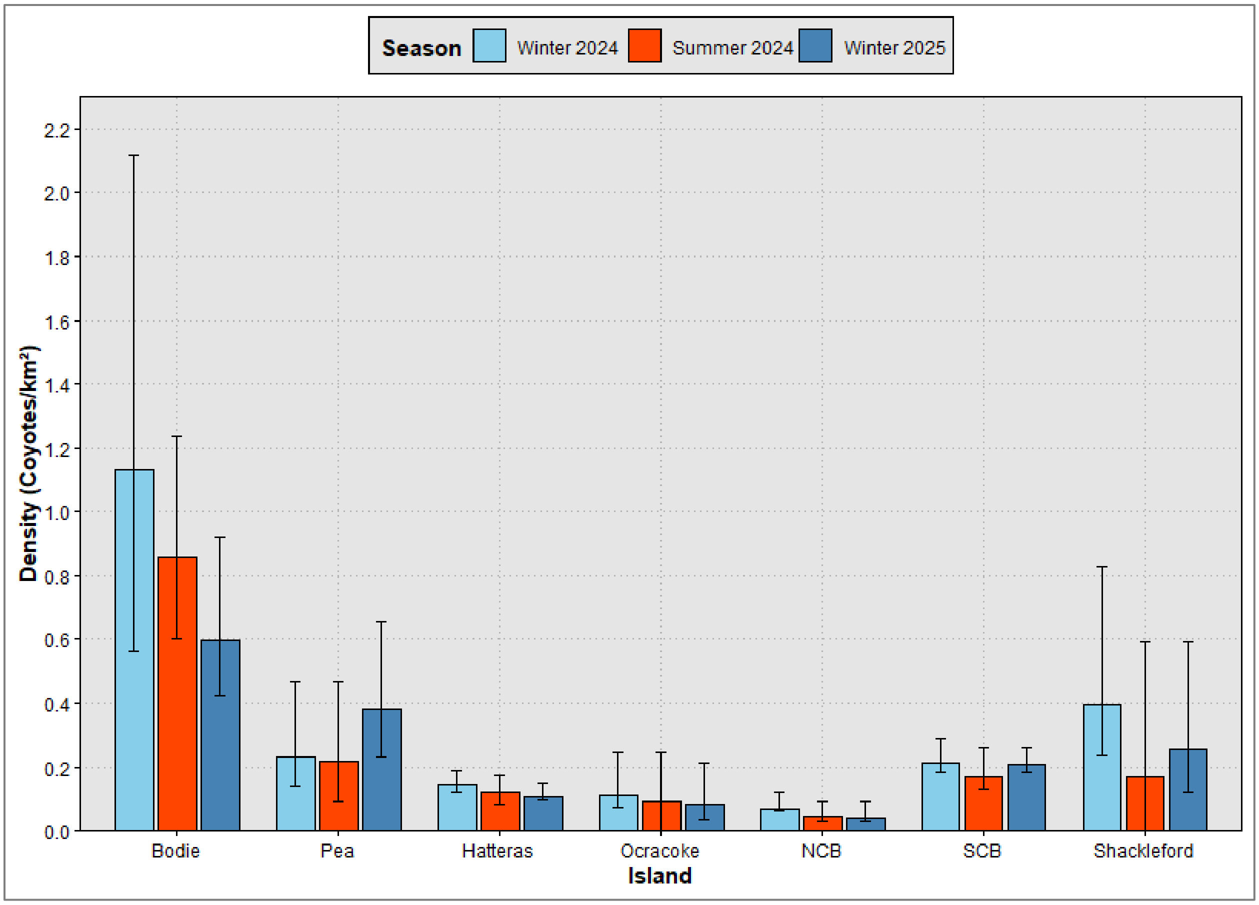

Figure 4. Seasonal coyote density trends across all islands estimated by island and season (Coyotes/km^2). Bars show per-island density estimates with 95% CI displayed as error bars. Density = abundance estimate for each island / island area.

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Table 5. Island-level mean coyote density across the seven islands we surveyed. Density = abundance estimate for each island / island area.

Island	Average Density (coyotes/km^2)
Bodie	0.86
Pea	0.28
Shackleford	0.27
South Core	0.20
Hatteras	0.12
Ocracoke	0.09
North Core	0.05

Values in Table 5 are posterior mean densities per island, calculated as posterior abundance divided by island area and averaged across the three primary periods sampled (Winter 2024, Summer 2024, Winter 2025). Islands are ordered from highest to lowest density. Bodie shows the highest average density (0.86 coyotes/km^2), while North Core and Ocracoke are lowest (0.05 and 0.09 coyotes/km^2). Densities are rounded to two decimals. Our abundance posteriors come from the multistate robust-design mark-recapture model we developed.

Although no coyote scats were detected on Ocracoke (the one female we identified had swam from North Core Banks which was a direct violation of our model's assumption of closure during a field season so the detection history matrix we fed our model did not include this detection, essentially treating the detection as if it had not happened) and Shackleford Banks during the Summer 2024 season, both islands were still surveyed during that period. Because detection is modeled explicitly and the absence of detections still informs parameter estimation, the resulting abundance estimates remain valid.

Tracking Data

The five collars attempted a total of 175,940 GPS fixes and were successful at a rate >99%, providing 26,957–38,979 fixes and 43,447–137,309 accelerometer readings per animal (Table 6).

Table 6. Performance of accelerometer-informed GPS collars by individual. Parameters shown include Collar ID, Animal ID (sex), total # of GPS fixes, % of GPS fixes that were successful, total # of acceleration records, start/end date of the deployment, and reason for end.

Collar ID	**Animal ID (sex)**	**# of GPS Fixes**	**% of GPS Fixes that were Successful**	**# of Acceleration Measures**	**Start Date**	**End Date**	**Reason for End**
12541	Rahzar (m)	34450	99.91%	51280	09/14/2023	09/04/2024	Trapped by USDA w/battery dead
12543	Ed (m)	36722	99.86%	48343	10/02/2023	09/01/2024	Battery died
12539	Martha (f)	38745	99.88%	45441	05/16/2024	03/27/2025	Awaiting retrieval
12547	Azula (f)	26957	99.89%	137309	04/17/2024	05/03/2025	Trapped by USDA
12542	Cruella (f)	38979	99.76%	43447	04/22/2024	02/17/2025	Awaiting retrieval

Inter-Island Movement

Movement Identified via Scat

The only case of inter-island movement detected with our fecal surveys was during Winter 2024 where a single female moved between North Core Banks and Ocracoke Island. We first detected her on North Core Banks in the first round of sampling in Winter 2024 and subsequently recaptured her 17 times on the island, which indicates residency. In our second round of sampling in Summer 2024, we again found her scat on North Core Banks, but then also on Ocracoke Island, which is direct evidence of an inter-island movement event. In the third survey period (Winter 2025), we again detected her only on North Core Banks. These two movements (North Core → Ocracoke → North Core) correspond to a rough probability of 1.1% across all 185 genetic recapture events (excluding singletons) in our study, or 2.9% of the 34 recaptured coyote individuals.

Movement Identified via GPS Collars

We documented 54 inter-island crossings from one individual, Azula (see Figure 5). Movements between Shackleford Banks (SB) and Morgan Island (MI) accounted for 41/54 (76%) of all crossings: SB → MI (n = 24; 44%) and MI → SB (n = 17; 31%). The remaining crossings connected MI → South Core Banks (SCB; n = 7; 13%) and SCB → SB (n = 6; 11%). We did not observe a direct SB → SCB crossing; she always traveled to MI first. While moving between these three islands, she regularly utilized a series of small islets as resting sites, which included Blinds Hammock, Great Marsh Island, and Sheep Island when en route from SB → MI and Whitehurst Island when traveling from MI → SCB. When swimming from SCB → SB, she swam the gap directly, typically leaving from Power Squadron Spit and once crossing Barden Inlet (see Figure 5). Crossing durations were generally short, on the order of tens of minutes in length (see Table 7). SB → MI had a median of 28.5 min (range 12–153; mean 37.6); the 153-minute outlier reflected longer pauses/breaks on the stepping-stone islands along her route. MI → SB median duration was 33.0 min (18–48; mean 34.1) whereas MI → SCB was 30.0 min (24–48; mean 34.3). SCB → SB was the quickest at 13.5 min (9–18; mean 14.0). We also documented 168 short near-shore excursions, most representing brief steps just outside our island boundary (range 0–99 mins); the 99-min maximum reflects an attempt to swim to Baregrass Island.

Figure 5. Inter-island crossing routes taken by a collared female coyote (“Azula”) across Cape Lookout National Seashore. One example of each observed route/direction is shown and meant to illustrate typical crossing pathways, rather than a single trip.

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Table 7. Inter-island crossing routes and durations for a GPS-collared female coyote ("Azula") across Cape Lookout National Seashore. Duration is measured from the last GPS fix on the origin island to the first fix on the destination island.

Origin	Destination	n_crossings	mean_minutes	median_minutes	min_minutes	max_minutes
Shackleford Banks	Morgan Island	24	37.62	28.49	12.00	153.00
Morgan Island	Shackleford Banks	17	34.06	33.00	18.02	48.00
Morgan Island	South Core Banks	7	34.29	30.00	24.00	48.00
South Core Banks	Shackleford Banks	6	14.00	13.50	9.00	18.00

Azula split her time among MI (61.7%), SCB (20.9%), and SB (17.4%) (Tables 8 and 9, Figure 6). On Morgan, bouts were frequent and long (n = 24; median = 8.06 days; max ~33 days) with Shackleford bouts being shorter (n = 24; median = 1.15 days; max ~16.6 days) while South Core had fewer but often much longer bouts (n = 7; median = 7.96 days; max ~35.0 days). Her longest (33 d) continuous stay (31 Oct–3 Dec 2024) on Morgan Island is notable given its small size (~0.13 km^2) and lack of a fresh water source.

Table 8. Island residency for a GPS-collared female coyote ("Azula") by fixes and time on Cape Lookout National Seashore from 2024–2025.

Island	Fixes	prop_fixes	time_days	prop_time
Morgan Island	10099	0.38	234.44	0.62
South Core Banks	9430	0.36	79.33	0.21
Shackleford Banks	6808	0.26	65.99	0.17

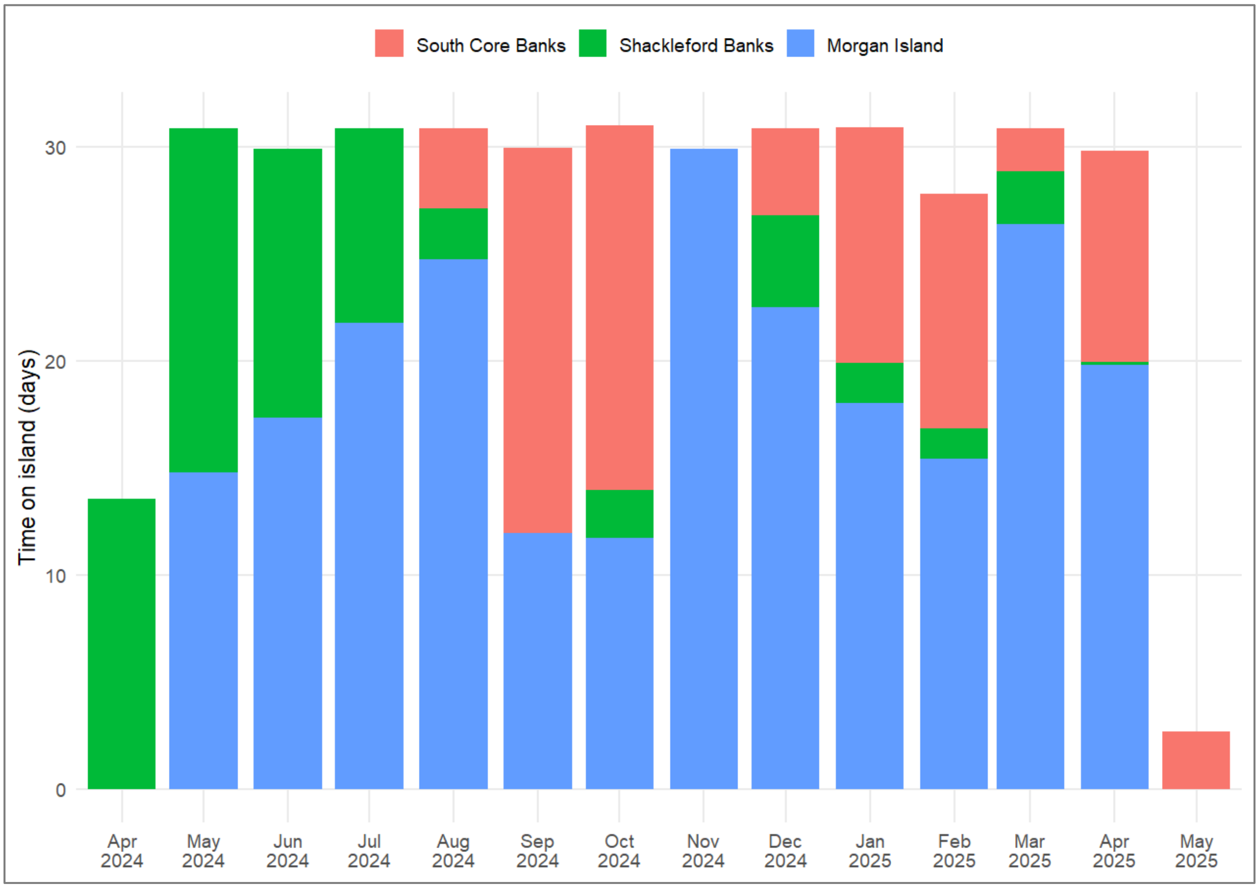

Figure 6. Monthly island residency for a GPS collared female coyote ("Azula"), April 2024–May 2025. Bars sum to the number of days in each month.

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Table 9. Stay lengths ("bouts") by island for a GPS-collared female ("Azula") in days.

Island	**n_bouts**	**min_bout_days**	**mean_bout_days**	**median_bout_days**	**max_bout_days**
Morgan Island	24	2.98	9.76	8.06	32.96
Shackleford Banks	24	0.03	2.73	1.15	16.64
South Core Banks	7	3.69	11.32	7.96	34.99

Across Azula's 54 inter-island crossings, most (50/54, 92.6%) occurred nocturnally (between 20:00–05:59 local time). Further, 22 of the 54 (40.7%) began within 1 hour of low tide (95% CI: 28.7–54.0%; see Figure 7). Under the null expectation, departure time would be independent of tidal phase. If po is the probability that a randomly timed departure falls within 1 hour of low tide during a semidiurnal cycle of length T = 12.42 h, and the window (w) is 2 h, then po = w/T = 2 / 12.42 = 0.161 (16.1%). The observed fraction near low tide (22/54 = 40.7%) is ~2.5 times greater than what we'd expect under a uniform-time departure (po).

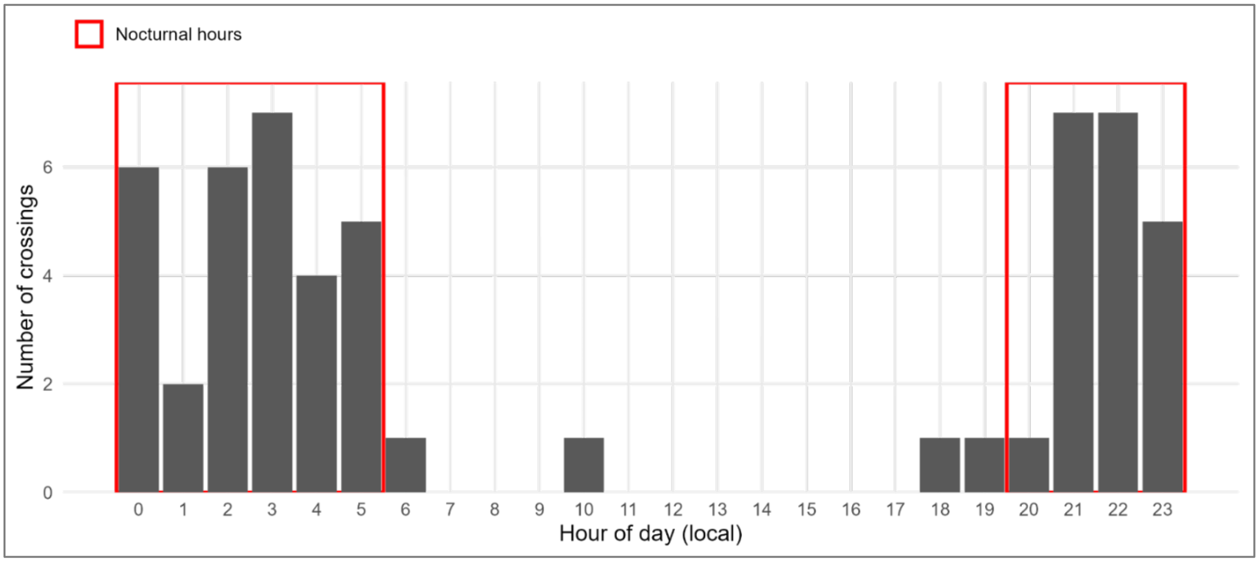

Figure 7. Histogram of crossing start times for a GPS-collared female coyote ("Azula"). Red boxes denote nocturnal hours (20:00–05:59).
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All other coyotes remained residents on the island we originally trapped and collared them on. Ed, our young, collared male, explored Shark Island once, an emergent shifting sandbar off Cape Lookout Point that connects to South Core during low tide but is otherwise isolated (see Figure 8). On April 11th, 2024, he crossed from South Core Banks to nearby Shark Island (3:00–6:15 EDT, 66 fixes). The crossing began before the morning low tide (~04:22 EDT) and finished after the flood had begun, according to NOAA Tides & Currents, Station 8656841 (Cape Lookout Bight).

Figure 8. Single exploratory crossing by a GPS-collared male coyote ("Ed") from South Core Banks to Shark Island on April 11th 2024. The inset panel enlarges the Shark Island segment.

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Home Range and Core Area

Like all other kernel-based methods, AKDE assumes that space is continuous and homogeneous in all directions; in our case, around each GPS fix (Fleming et al. 2015). Given that our study system is made up of long, narrow linear barrier islands, this assumption is violated and resulted in all our contours extending into the open ocean (Figure 9).

Since most coyotes didn't utilize the open ocean and the contours often extended into islands the coyote had never been recorded visiting, leaving them unmodified would result in unrealistic and inflated estimates. To constrain estimates to available land, we clipped each individual's AKDE polygons (50% and 95%; low/mean/high CIs) to island boundaries according to the island each coyote occupied using spatial intersections in the sf R package (Pebesma 2018). For individuals that used multiple islands, we merged the relevant island polygons and applied the same clipping to all confidence surfaces. This modification produced estimates of core area and home range to usable terrestrial habitat.

AKDE summaries (Figures 10–12; Table 10) show clear individual and season-dependent variation.

Figure 9. Example of our original 50% AKDE contour compared to our land-constrained AKDE for Rahzar in Winter.

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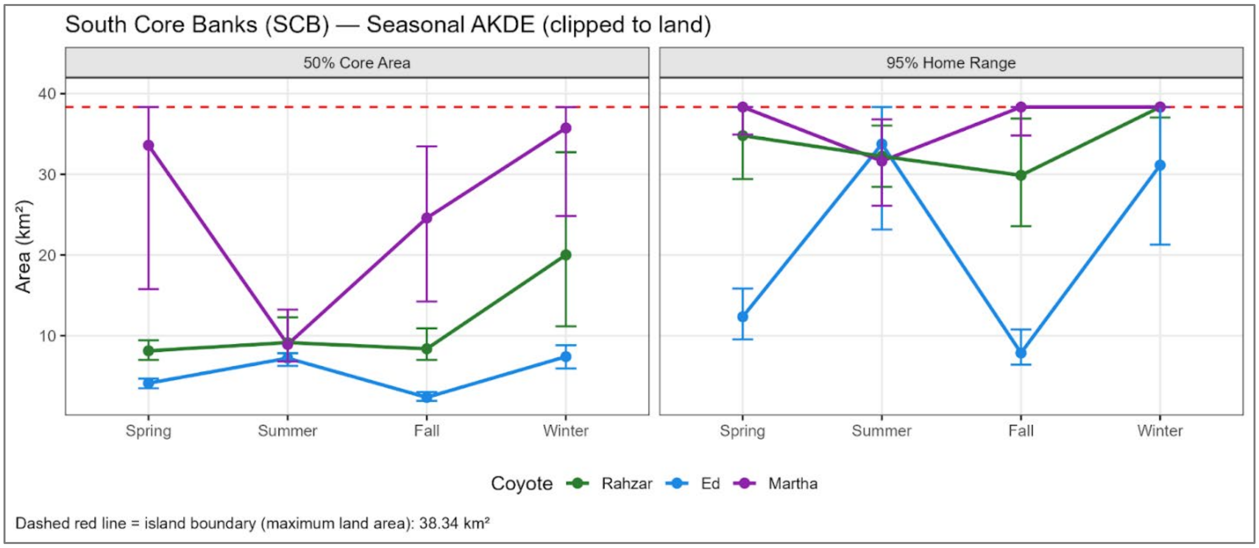

Figure 10. Seasonal core area and home ranges for South Core Banks residents (Martha, Ed; Rahzar).
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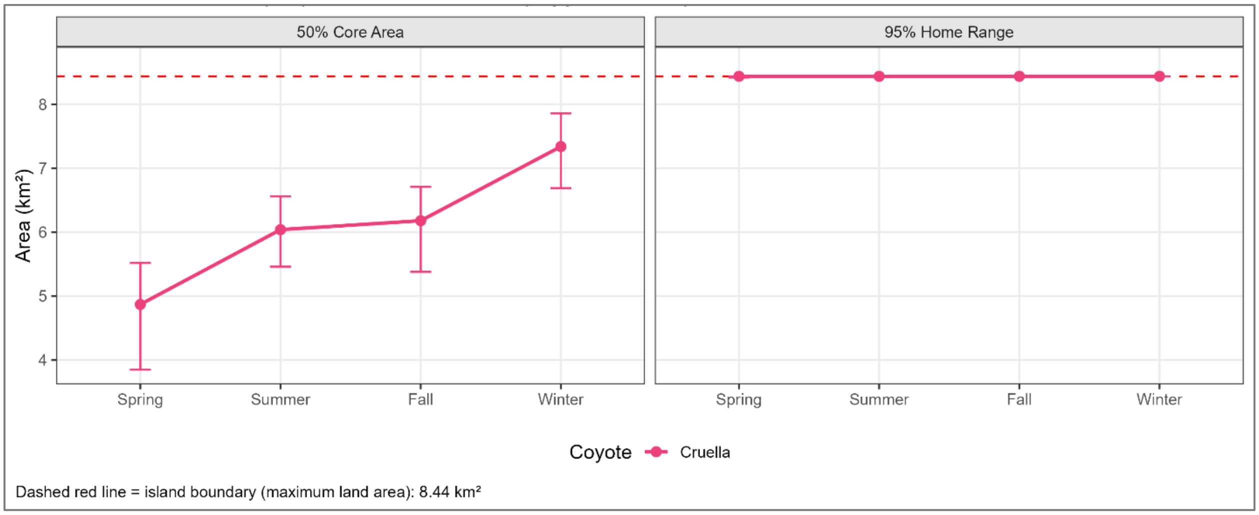

Figure 11. Seasonal core area and home ranges for Shackleford Banks resident (Cruella).
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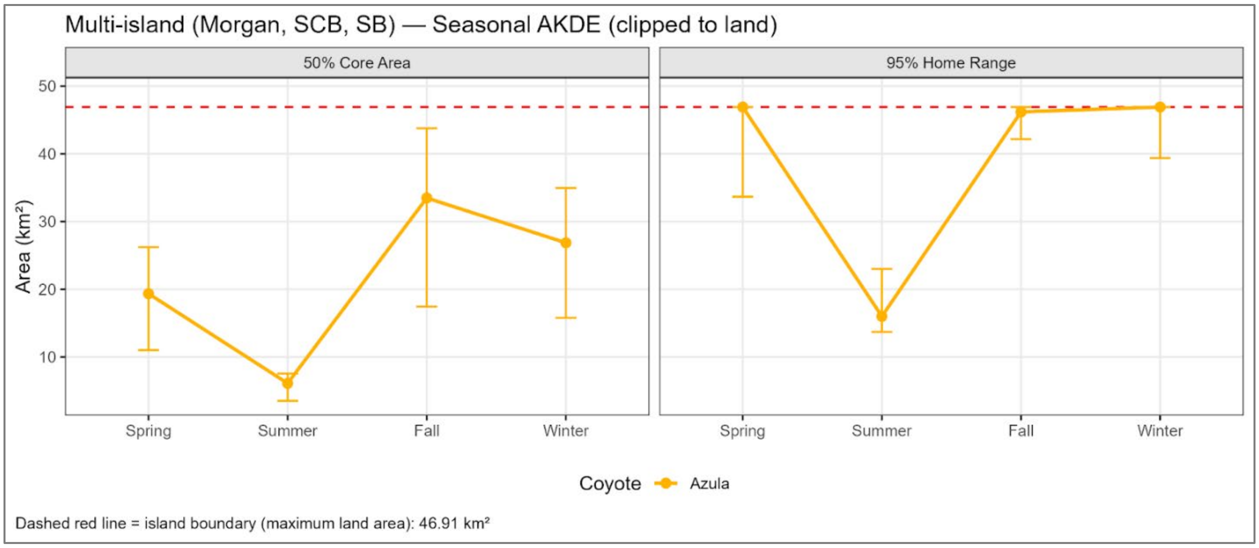

Figure 12. Seasonal core area and home ranges for “Azula”, our multi-island traveler.
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Table 10. Autocorrelated kernel density estimates of core area (50% utilization distribution, UD) and home range (95% UD) by individual and season, with the number of corresponding GPS fixes for that season and island area.

Individual	Season	GPS fixes (n)	Island area (km^2)	UD50 (km^2) [95% CI]	UD95 (km^2) [95% CI]
Rahzar	Spring	23647	38.34	8.13 [7.01–9.43]	34.8 [29.41–38.34]
Rahzar	Summer	25409	38.34	9.15 [7.83–12.28]	32.24 [28.44–36.04]
Rahzar	Fall	15944	38.34	8.38 [7.01–10.92]	29.88 [23.58–36.91]
Rahzar	Winter	20760	38.34	20.02 [11.16–32.75]	38.34 [37.04–38.34]
Ed	Spring	23418	38.34	4.12 [3.49–4.68]	12.35 [9.55–15.85]
Ed	Summer	25037	38.34	7.22 [6.27–7.84]	33.76 [23.17–38.34]
Ed	Fall	13792	38.34	2.36 [1.93–3.01]	7.86 [6.42–10.78]
Ed	Winter	22868	38.34	7.41 [5.94–8.83]	31.14 [21.29–38.34]
Martha	Spring	10553	38.34	33.6 [15.77–38.34]	38.34 [34.92–38.34]
Martha	Summer	24526	38.34	8.92 [6.82–13.24]	31.64 [26.12–36.82]
Martha	Fall	24202	38.34	24.59 [14.24–33.47]	38.34 [34.81–38.34]
Martha	Winter	24952	38.34	35.74 [24.83–38.32]	38.34 [38.33–38.34]
Cruella	Spring	11129	8.44	4.87 [3.85–5.52]	8.44 [8.42–8.44]
Cruella	Summer	26877	8.44	6.04 [5.46–6.56]	8.44 [8.44–8.44]
Cruella	Fall	25258	8.44	6.18 [5.38–6.71]	8.44 [8.44–8.44]
Cruella	Winter	19254	8.44	7.34 [6.69–7.86]	8.44 [8.44–8.44]
Azula	Spring	56220	46.91	19.35 [11.02–26.21]	46.91 [33.66–46.91]
Azula	Summer	38881	46.91	6.11 [3.52–7.56]	16 [13.7–23]
Azula	Fall	39702	46.91	33.48 [17.45–43.77]	46.19 [42.18–46.91]
Azula	Winter	40344	46.91	26.86 [15.78–34.94]	46.91 [39.38–46.91]

Spatially, the core areas of all three South Core residents were concentrated in the southern portion of the island in the maritime forest surrounding Cape Lookout Village Historic District and Lighthouse. Notably, Martha's core areas often extended farther north than those of the two males, but all three overlapped substantially in the southern portion across every season. On Shackleford Banks, Cruella's core area was distributed as a broad band across the island's width, with only its size changing through time. For Azula, her core area overlapped directly with all other coyotes in every season.

Together, these results show strong overlap among residents on South Core Banks, steady expansion by Cruella on Shackleford, and pronounced summer contractions by Martha and Azula. On SCB, males generally maintained smaller, more stable core areas through spring and summer, with Rahzar expanding only in winter and Ed exhibiting the smallest observed core in our dataset (2.36 km^2 in fall). All island-season datasets were best fit by anisotropic Ornstein-Uhlenbeck foraging (OUF) movement models (Table 10).

Distance Moved

Across 1,698 coyote-days of GPS data, the daily straight-line distance traveled averaged 14.7 ± 9.40 km/day overall and spanned 0.02–54.62 km/day. Cruella moved the most on average across the year, followed by Rahzar, Martha, Ed, and Azula (Table 11).

Table 11. Straight-line daily distance (km/day) summarized across the entire study period for each collared coyote. Shown are mean, minimum, and maximum daily totals that were calculated as the sum of straight-line steps between successive GPS fixes within each calendar day.

Individual	Mean Distance (km/day)	Minimum (km/day)	Maximum (km/day)
Azula	8.35	0.02	52.80
Cruella	21.80	2.55	46.94
Ed	13.35	1.95	34.88
Martha	15.47	0.19	37.06
Rahzar	16.20	0.02	54.62

Seasonally, patterns were consistent for the males and split among the females. Rahzar and Ed traveled the farthest, on average, in summer and the least in fall (Figure 13). Among the females, Martha and Azula were highest in the winter, while Cruella peaked in summer. The longest single-day distance moved (54.62 km, summer) was Rahzar where he ran from the south end of South Core Banks to the north end and back south in one day. Similarly, Azula's maximum (52.80 km, winter) started near the north end of South Core Banks, where she ran the entire length of the island, swam across Power Squadron Spit to Shackleford, and continued with back-and-forth treks along the east and west ends. Although there was great individual variability in distance moved per day (Table 11) there was no difference between the average value for males (14.82 ± 8.51 km/day) and females (14.63 ± 9.93 km/day).

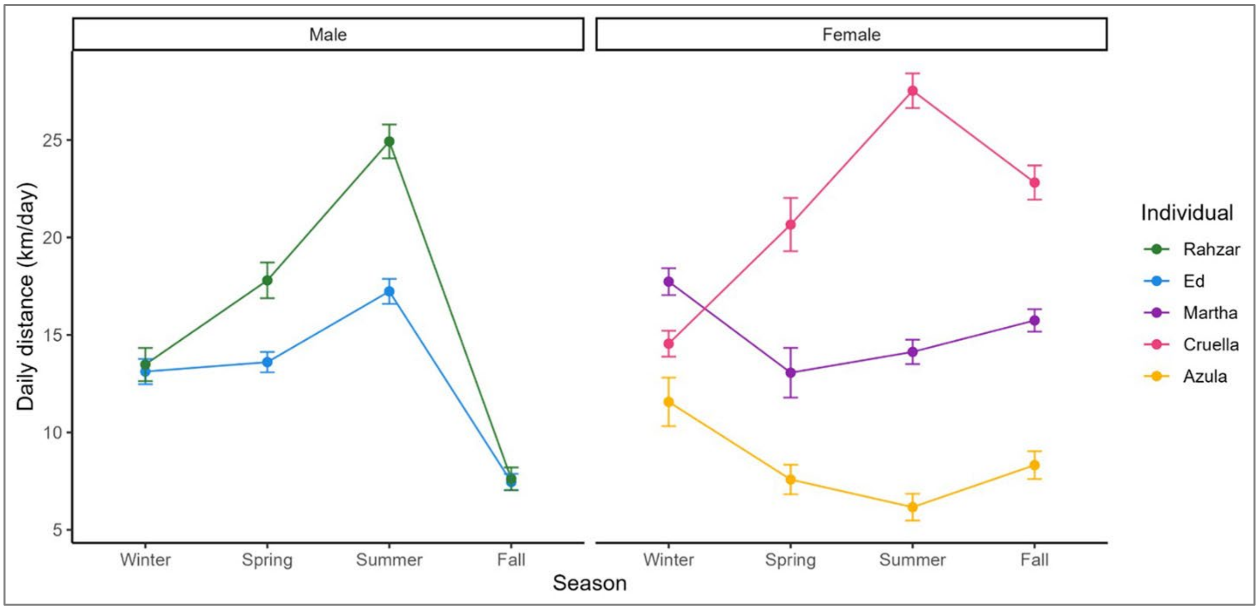

Figure 13. Seasonal daily distance (mean ± standard error) by individual, faceted by sex.
NPS / DANIEL SOSSOVER

Spatial Patterns of Resting and Feeding Sites

Overall, coyotes used their habitats so completely that their GPS fixes effectively trace the outline of the islands they live on (Figure 14a). Daytime resting sites were distributed across the full length of South Core Banks with clear clustering at the southern end around the Cape Lookout Historic District and a second cluster just south of Great Island Cabin Camp (Figure 14c and Figure 15). These resting hotspots were shared by multiple individuals, sometimes concurrently, and even Azula, during visits to South Core Banks, slept in the same patches used by the residents. On Shackleford Banks, daytime resting sites were distributed across the island with slight clustering toward the easternmost and westernmost ends. These patterns demonstrate that coyotes do not appear to be confining their resting to a single corner or end of the islands. Nighttime feeding clusters were island-wide on both SCB and SB (Figure 14b and Figure 16). On SCB, feeding points formed a continuous strand along the ocean beach; sound-side was sparse north of the Les and Sally Cabins but common south of that area. In summer, when visitation peaks, feeding is mostly concentrated south of Great Island Camp; in other seasons, clusters were more broadly distributed. On Shackleford Banks, feeding clusters occurred both on the ocean-side and sound-side beaches, creating two coastal bands that wrap around the island. Notably, we did not identify any feeding clusters on the small islands/islets Azula used to cross between Shackleford Banks ↔ Morgan Island ↔ South Core Banks.

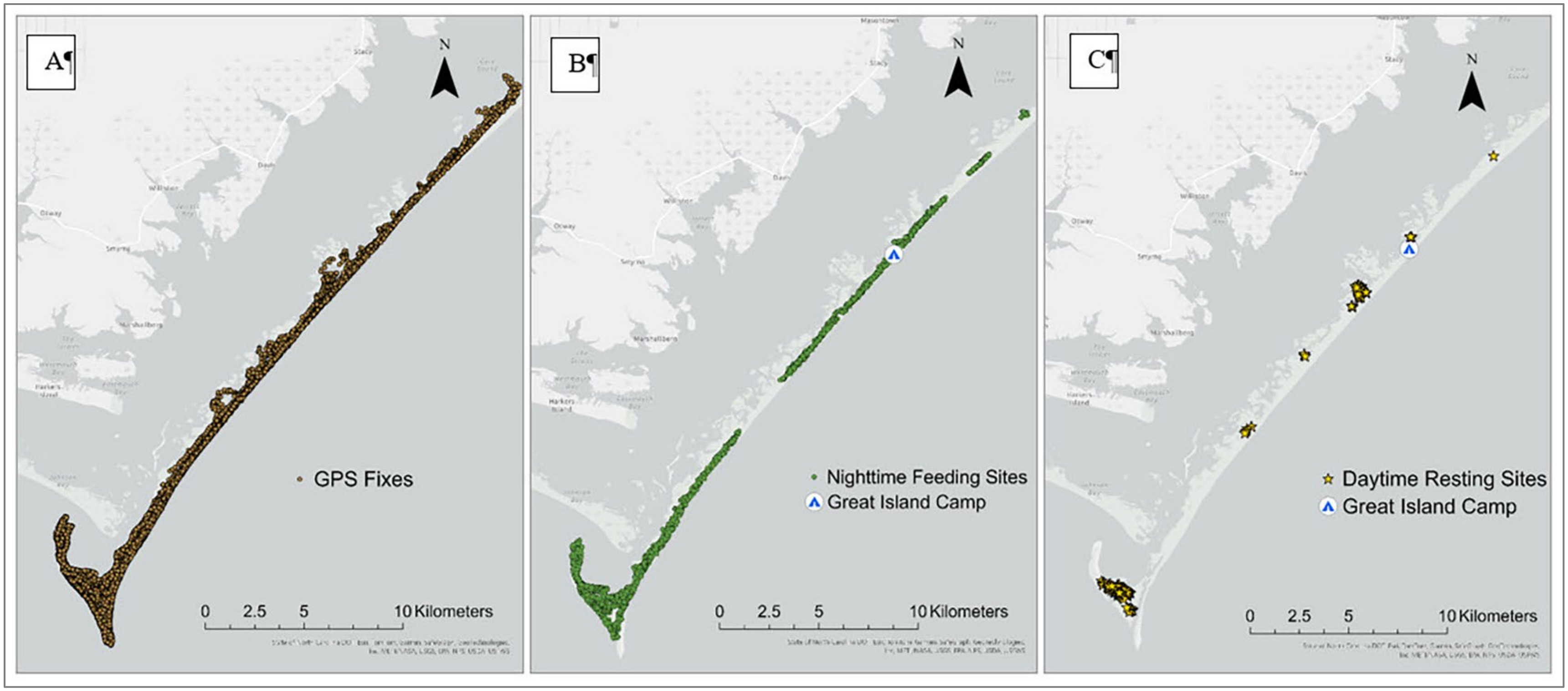

Figure 14. Spatial distribution of GPS fixes (A), nighttime feeding sites (B), and daytime resting sites (C) for South Core Banks resident male “Rahzar.” Together, these maps illustrate the typical pattern we observed for our South Core resident coyotes.

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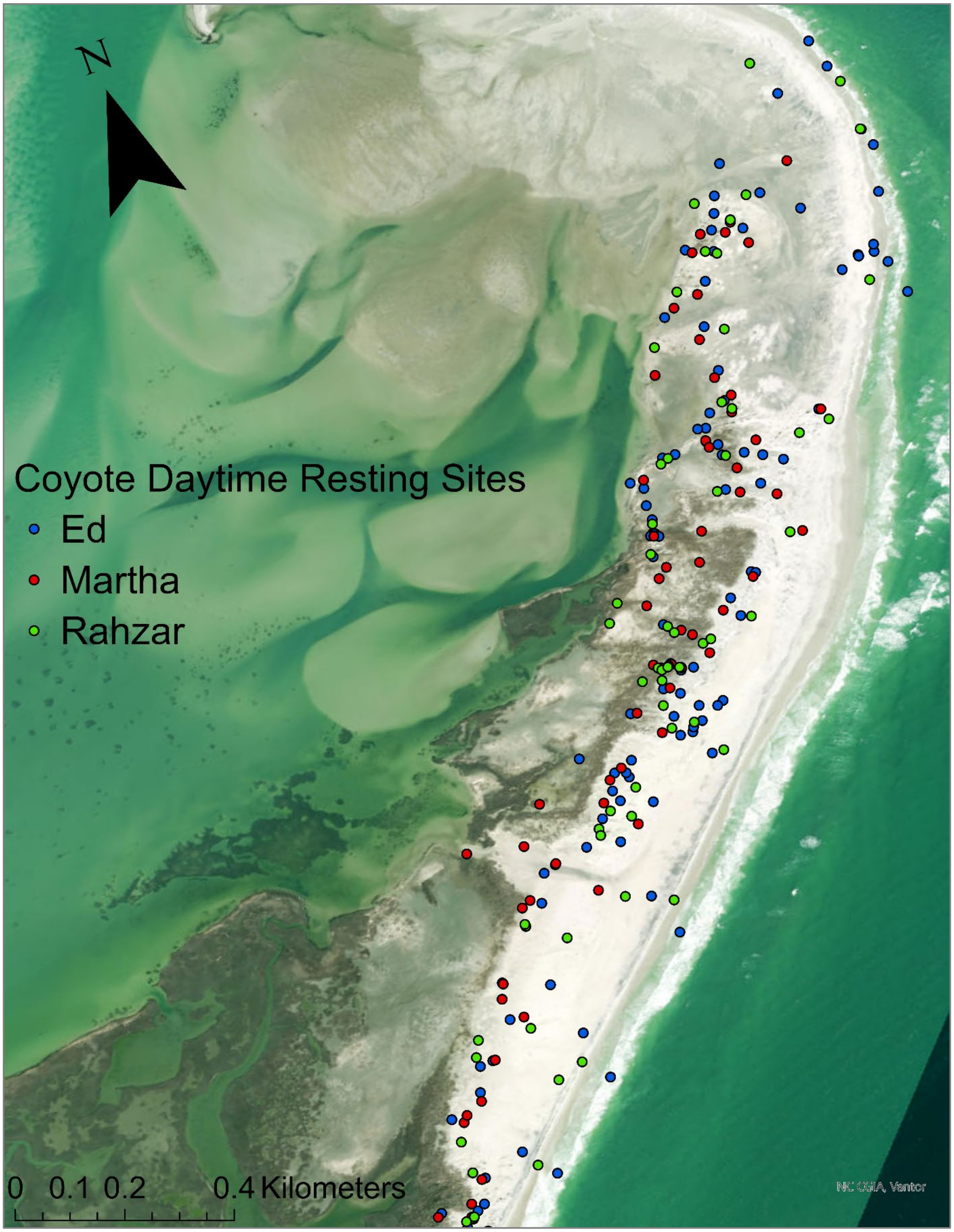

Figure 15. Spatial distribution of inferred daytime resting sites for three resident coyotes on the northern end of South Core Banks during the shorebird nesting season (data spans Apr 1–Sep 15, 2024).
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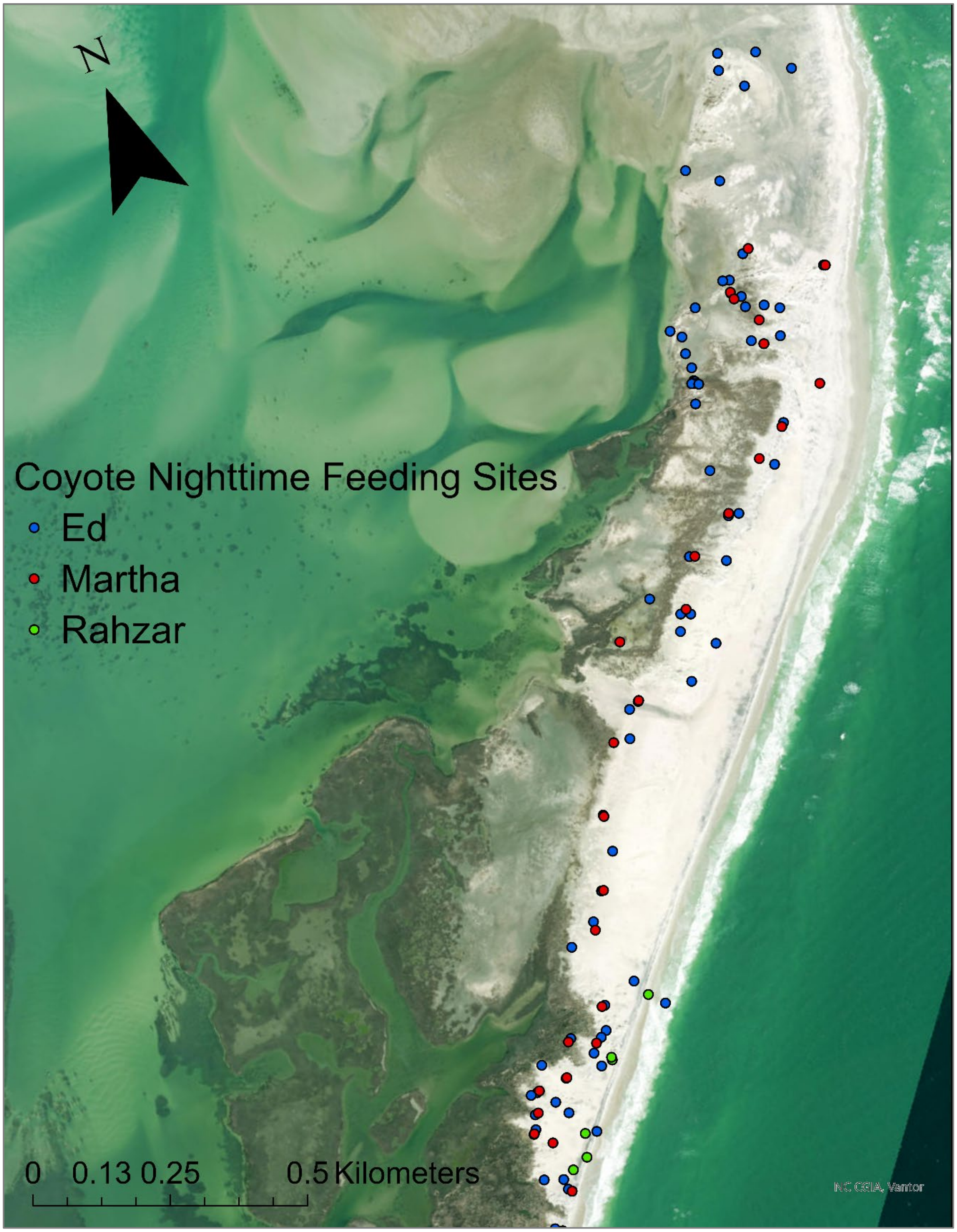

Figure 16. Spatial distribution of inferred nighttime feeding sites for three resident coyotes on the northern end of South Core Banks during the shorebird nesting season (data spans May 1–Sept 1, 2025).
NPS / DANIEL SOSSOVER

Activity

Coyotes exhibited a consistent nocturnal activity pattern across all seasons. The actogram for Martha (Figure 17) illustrates the typical pattern with low VeDBA during daylight hours, increasing rapidly at sunset, and remaining elevated throughout the night before declining near sunrise. This diel structure was observed for every collared individual, so we summarize pooled patterns below (Figure 18) that show activity was concentrated during nighttime hours with low VeDBA values during the day. This diel pattern was consistent across all individuals and throughout the year, with activity times shifting to match seasonal variation in sunrise/set.

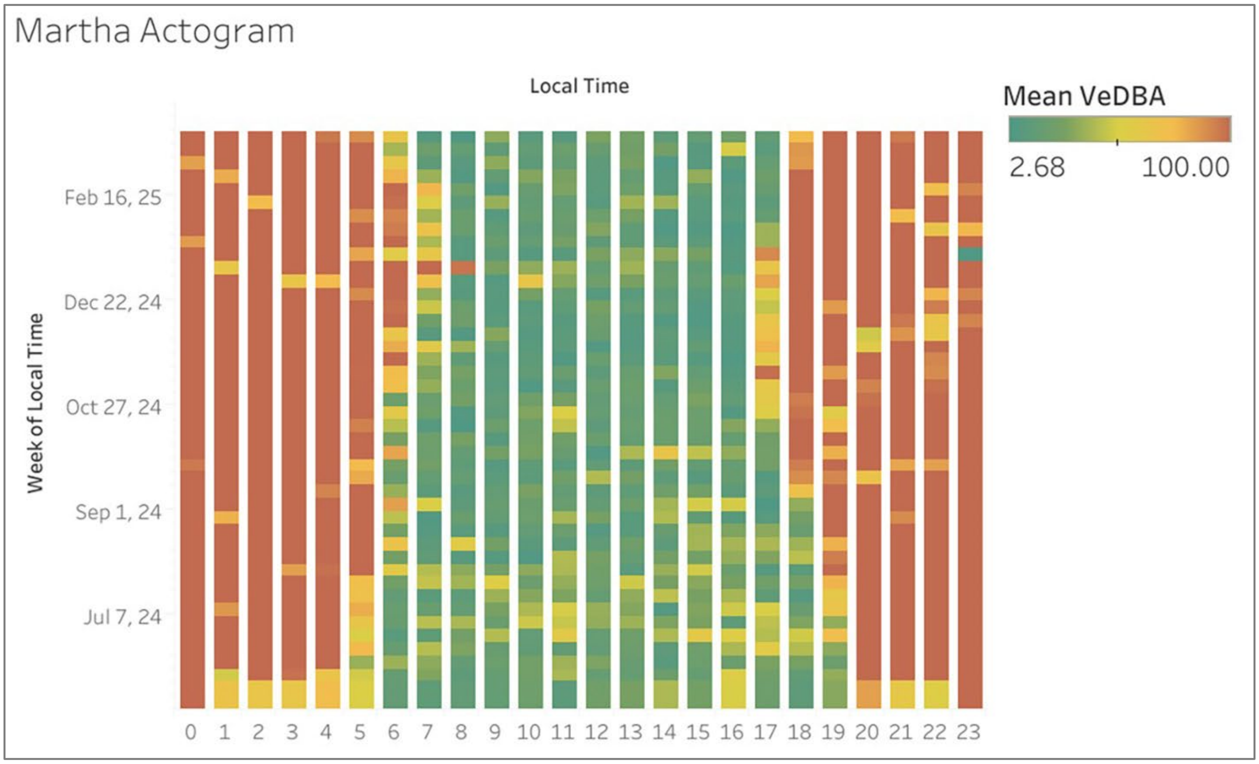

Figure 17. Weekly actogram of hourly activity (VeDBA) for the resident female on South Core Banks "Martha" from June 2024–March 2025. VeDBA values are aggregated to hourly means from tri-axial accelerometer records.

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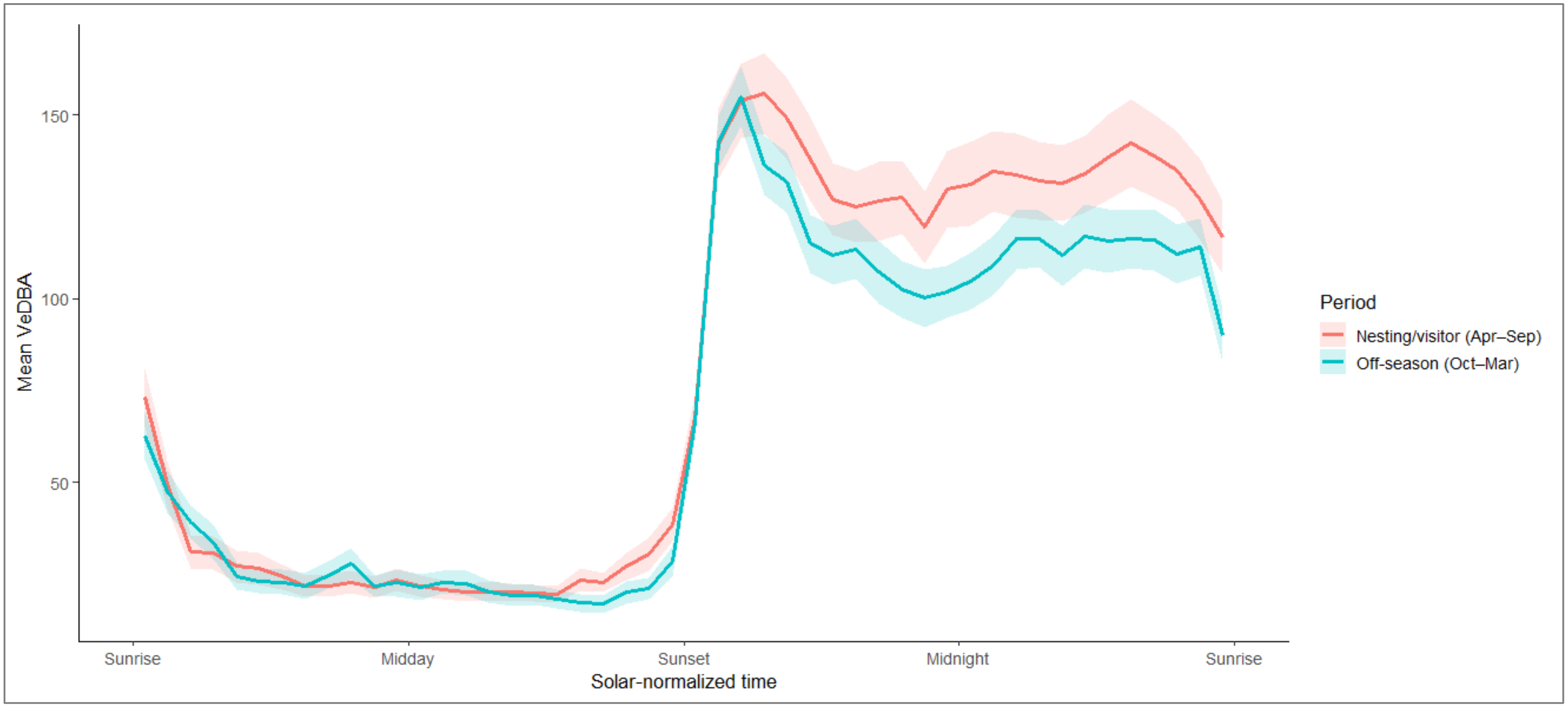

Figure 18. Solar-normalized diel activity (VeDBA) pooled across all collared coyotes: nesting/visitor season (Apr–Sep) vs. off-season (Oct–Mar). *NPS / DANIEL SOSSOVER*

Solar-normalized activity curves (pooled across all individuals) show the same sharp rise immediately at sunset, sustained high activity throughout the night, and low activity during daylight hours. Nighttime activity (sunset–sunrise) was higher during the nesting/visitor period than during the off-season, with largely non-overlapping 95% confidence intervals. Restricting the comparison to sunset → sunrise on the solar axis, we found the pooled mean night VeDBA was 132 during the nesting/visitor period (95% CI: 126–138; n = 234 nights) and 113 in the off-season (95% CI: 110–116; n = 365 nights), a difference of 18.6 VeDBA units (95% CI: 12.0–25.1). As a percentage, this corresponds to a 16.4% (95% CI: 10.6–22.2%) increase in nighttime activity during the nesting/visitor season relative to the off season VeDBA mean. Further, the visitor/nesting season activity curve also shows overall higher VeDBA just before sunset with mostly non-overlapping confidence intervals. Daytime VeDBA was low in both periods.

Pack Structure

The spatial patterns of individuals mapped from scat collection provided evidence for multiple packs on Bodie and Hatteras Islands, whereas all other islands supported a single pack. Our animal tracking work on CALO corroborates this interpretation/pattern.

Genetics

Based on the spatial clustering of scat recaptures, on both Bodie and Hatteras, individuals were consistently detected in either the northern or southern portion of the island but never both (see Figures 19–20), indicating clear north–south spatial partitioning that persisted across all sampling periods. Despite removals on Bodie (n = 9) and Hatteras (n = 5) in 2024, overall pack sizes remained relatively stable (see counts in Table 12).

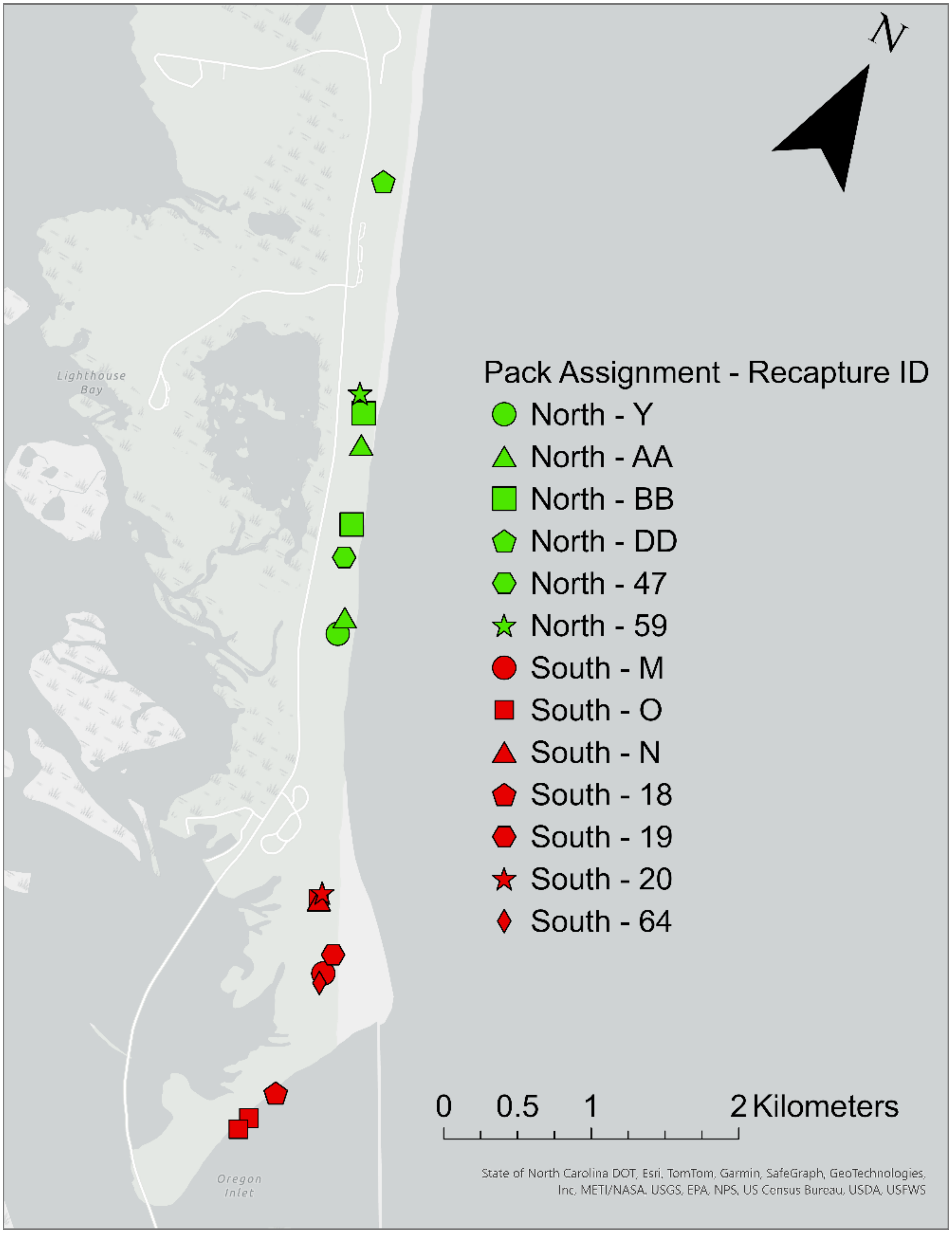

Figure 19. Pack structure inferred from the spatial distribution of genetic recapture on Bodie Island (North vs. South packs). Each point represents a scat location, and each unique individual coyote was assigned a unique color-symbol combination.

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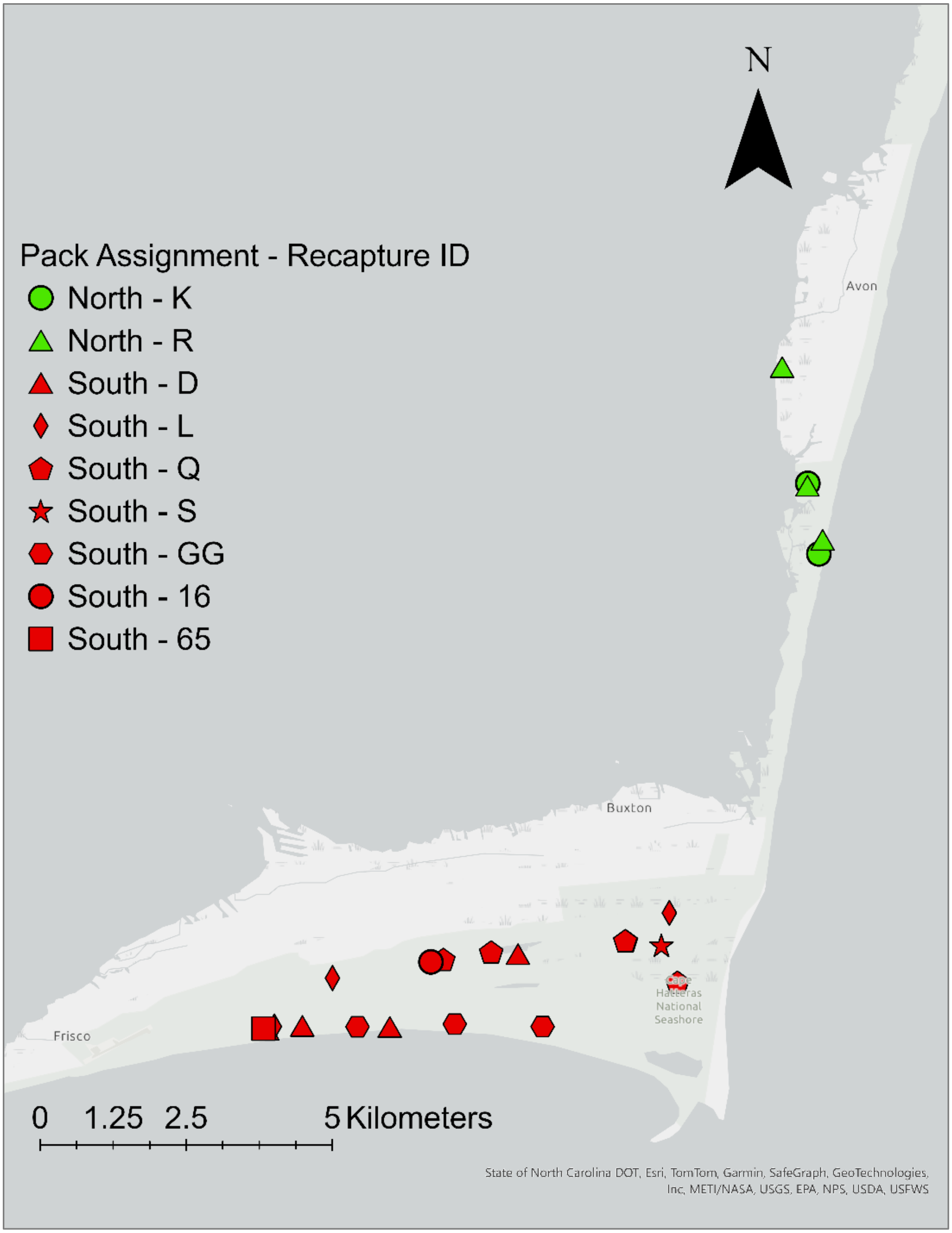

State of North Carolina DOT, Esri, TomTom, Garmin, SafeGraph, GeoTechnologies, Inc, METI/NASA, USGS, EPA, NPS, USDA, USFWS

Figure 20. Pack structure inferred from the spatial distribution of genetic recapture on Hatteras Island (North vs. South packs). Each point represents a scat location, and each unique individual coyote was assigned a unique color-symbol combination.

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Table 12. Pack composition by island and sampling period (unique genotyped individuals and sex). Packs were delineated by the spatial clustering of individuals' detections (see pack maps above), not by genetic relatedness or social observations.

Site	Packs	Sampling Period	Total	Male	Female
Bodie	BI_north	Summer 2024	6	2	4
Bodie	BI_north	Winter 2025	6	1	5
Bodie	BI_south	Summer 2024	7	1	6
Bodie	BI_south	Winter 2025	5	1	4
Hatteras	CL_north	Winter 2024	2	1	1
Hatteras	CL_north	Summer 2024	2	1	1
Hatteras	CL_north	Winter 2025	3	1	2
Hatteras	CL_south	Winter 2024	7	2	5
Hatteras	CL_south	Summer 2024	4	2	2
Hatteras	CL_south	Winter 2025	4	1	3

Tracking

Tracking data corroborated one pack per island on the CALO islands we monitored. On SCB, residents (Rahzar, Ed, and Martha) showed substantial overlap among 50% AKDE cores across all seasons, sharing daytime resting sites (sometimes concurrently) distributed across the length of the island in patterns consistent with a single pack sharing space. On Shackleford Banks, the resident female (Cruella) maintained an island-spanning core area that varied in size seasonally and her movement data showed no evidence of her avoiding a part of the island which would've suggested a second pack. Azula, our multi-island traveler, had a core area that overlapped every collared coyote we had in our study.

Coyote Space Use Before and During Sea Turtle Nesting Season

Our resource selection functions with tracking data from three animals allowed us to test if each one preferred using the beach vs. other habitat, preferred using areas near known turtle nests, and whether this varied before and during nesting season. Across our three individuals, the combined interactive model (Model C: used~ z_dist_turtle × period + in_beach50 × period) provided the best fit to the use-availability data, showing that coyotes preferred to use the beach and areas near turtles, but that this varied seasonally (ΔAIC (C - additive): Cruella = −141; Ed = −208; Rahzar = −536). Used locations were consistently closer to nest sites than available points in both periods for every individual, but the seasonal change varied by animal with no overall trend. For example, the Shackleford female's median distance to nearest nest increased from 308 m (pre-nesting season) to 377 m (during), and the odds ratio moved toward 1 (0.71 pre-nesting season to 0.85 during), showing that she did not intensify nest-area selection when the turtles were actually there. Of the three individuals, Ed was the only individual whose median distance to nest decreased (i.e., was closer to nests) during nesting season compared to pre-nesting season. In both periods, beach use exceeded availability for all three coyotes: Ed (PRE used 7.34% vs. available 6.07%; DURING 12.35% vs. 5.70%), Rahzar (PRE 11.68% vs. 5.56%; DURING 21.04% vs. 6.28%), and Cruella (PRE 13.5% vs.

8.12%; DURING 21.0% vs. 8.06%). The largest difference between pre and during nesting season was for Rahzar (+8.64 percentage points). Taken together these results show that coyotes prefer the ocean-facing beach, with beach selection increasing during the nesting period. However, after accounting for this general beach affinity, coyotes did not show a consistent increase in selection for areas nearer to active turtle nests. Because the nesting period overlaps peak human visitation, these patterns may be confounded by human activity.

Fladry Experiment

Our camera traps only recorded one instance of a coyote approaching the fladry line. The individual approached the barrier at 1:10 am on July 3rd, and walked along it until it left the cameras' viewshed at the point where the line ended at the ocean surf. Our cameras also captured one video of a deer approaching the fladry line and jumping over it. Based on the GPS data retrieved from our three collared coyotes on South Core Banks, they each "breached" the line once by swimming around the line's sound-side terminus in the marshes. These events were not captured by our cameras.

In aggregate, for the three South Core Banks residents, northbound crossings occurred at a rate of 0.11 events per 24 h pre-deployment (4,995 h), 0.04 during fladry deployment (1,921 h), and 0.48 post-deployment (2,593 h). A Poisson exact test comparing pre and during deployment yielded a rate ratio of 0.34 (95% CI 0.07–1.12; p =0.079) which would indicate a substantial (but not statistically significant) reduction in crossing rate while fladry was deployed. However, there was considerable variability at the individual level that complicates this pooled interpretation (Table 13).

Table 13. Individual crossing rates (events per 24 h) before, during, and after fladry deployment period. Events are the number of northbound crossings into the island's north section (past the fladry line).

Individual	Period	Hours	Events	Rate per 24 h
Ed	Pre	2513.9	2	0.02
	During	641.1	1	0.04
	Post	146.3	2	0.33
Martha	Pre	207.0	0	0
	During	642.5	1	0.04
	Post	2285.5	50	0.53
Rahzar	Pre	2274.2	21	0.22
	During	637.8	1	0.04
	Post	161.7	0	0

At the individual level, patterns diverged: crossing rates (events/24 h) into the island's north section were low for Ed, ambiguous for Martha, and clearly suppressed for Rahzar. Ed crossed only five times total: 0.02 pre-deployment (2 events, 2,514 h), 0.04 during (1 event, 641 h), and 0.33 after removal (2 events, 146 h)—so he's a weak test case; a Poisson exact test comparing pre vs. during showed no meaningful difference (p = 0.49; 95% CI: 0.03–37.7). Martha had little pre-data (0 events, 207 h); she crossed at 0.04 during deployment and jumped to 0.53 after removal, suggesting a barrier effect but preventing formal pre–during inference. Rahzar provided the strongest evidence: 0.22 pre (21 events, 2,274 h) dropping ~83% to 0.04 during (1 event, 638 h), a reduction that approached statistical significance ($p = 0.066$), indicating fladry likely suppressed his crossings while active.

Discussion

Coyote Density in Context of Coastal and Mainland Systems

Our model estimates that coyote densities across the Outer Banks range from 0.05 to 0.86 coyotes/km^2, with most islands having slightly lower densities than recent coyote density estimates from four coastal counties bordering our study area (Currituck, Dare, Hyde, and Carteret) which were in the 0.2–0.4 coyotes/km^2 range (Parsons et al. 2024). All but one of our island estimates fall within or below that adjacent-county range. The exception is Bodie at 0.86 coyotes/km^2, roughly two to four times higher than those adjacent coastal communities and 1.9× the statewide mean reported by Parsons (0.46 coyotes/km^2; 95% CI: 0.02–1.45). Our estimated average densities for Pea Island, Shackleford Banks, and South Core Banks fall within the mapped predicted-density class for the coastal counties adjacent to our study area (0.2–0.4 coyotes/km^2), while Hatteras, Ocracoke, and North Core Banks are below it. This range of density estimates from below adjacent mainland levels, to similar, to well above them, highlights an interesting spatial gradient.

Variation in Density Across Islands

Coyote density across the Outer Banks declined with increasing island isolation, while total abundance was generally higher on larger islands but did not scale directly with island size. These patterns likely reflect a combination of recent colonization, ongoing lethal control, and limited movement to more isolated islands, suggesting that populations have not reached equilibrium. In addition to isolation, variation in density is probably also shaped by human presence, resource availability, habitat quality, and management intensity. Although our sample of eight islands is too small for formal statistical analysis, comparing their differences highlights how these factors interact and informs recommendations for managing coyote populations in island systems.

Bodie Island

Coyotes were first documented on Bodie in 2008, making it the earliest colonized site in the system with trapping beginning in 2009. This long history of occupancy and removal in conjunction with it being physically connected to and part of the mainland likely explains why it had by far the highest density estimates across all seasons (average = 0.86 coyotes/km^2). This pattern suggests strong immigration potential from mainland source populations. Our seasonal abundance estimates ranged from 16.9 to 32.1 individuals on this island, the highest in our study. Consistent predator removal occurs on Bodie, so its consistent high abundance suggests that its connection to the mainland is facilitating compensatory immigration. Counterintuitively, the removal of resident individuals can result in higher coyote abundance because it creates opportunities for transient coyotes to move in; the loss of one territory holding animal could attract multiple transients, at least temporarily. Eventually pack dynamics would reestablish and exclude transients, but with the continuous removal of resident individuals seen at Bodie Island, this equilibrium is unlikely to occur.

Bodie supports relatively high-quality habitat because it contains large, contiguous forest patches on the sound side that could provide denning sites and shelter, while also being adjacent to developed areas that offer anthropogenic food subsidies (roadkill, pets, garbage, etc.). This combination of natural cover adjacent to human development creates a habitat mosaic that coyotes often exploit with great success. GPS-based studies show coyotes select for areas where natural habitat features (parks, vegetation) overlap with human activity, which offers both shelter and access to anthropogenic food sources (Zepeda et al. 2025). This combination of direct mainland connectivity, ongoing removal of resident coyotes, and high-quality habitat likely explains both the high densities/abundances and persistence of coyotes on this site/island.

Pea Island

Coyotes were first detected on Pea Island in 2014–2015, making it the second site/island along the northern chain to be colonized. Pea Island held the second-highest average density across all seasons (0.28 coyotes/km^2) and comparatively lower abundance estimates (4.6 to 8.2 individuals depending on the season). While it is separated from Bodie Island by Oregon Inlet, the gap is only about 1 km wide and is covered by a bridge, and we presume this is not a substantial barrier. Coyotes have been documented using man-made highway bridges to cross other, larger water bodies elsewhere (Way 2009; Weckel et al. 2015). Additionally, this inlet distance is considerably shorter than Ocracoke Inlet (~4 km), which we documented a coyote crossing twice. This proximity to Bodie and its physical connection to Hatteras to the south forming one larger landmass reduces the effect of isolation. Pea Island differs from Hatteras to its south in many significant ways: it has no permanent residents, is managed by the U.S. Fish and Wildlife Service, and functions as a critical bird sanctuary that hosts tens of thousands of migratory and wintering waterfowl which could provide substantial and predictable prey for coyotes. Pea Island's landscape has little human disturbance and habitat fragmentation. Aside from Highway 12, which bisects the island, the landscape remains largely undeveloped. Predator control on Pea Island is recent, starting in 2023, and is conducted sporadically using firearms rather than having full-time staff members dedicated to trapping coyotes as is done on Bodie and Hatteras. These factors (moderate connectivity, contiguous forested habitat along the sound side across the island, high prey base, and removals being recent and intermittent) likely help explain why we observed relatively higher coyote densities here compared to Hatteras.

Shackleford Banks

Shackleford Banks was colonized by coyotes in 2014 and had the third-highest average density (0.27 coyotes/km^2), nearly matching Pea Island. This relatively high density is likely, in part, driven by its close proximity to multiple adjacent islands, Harker's Island, Rachel Carson Reserve, Bogue Banks, and South Core Banks, which functionally reduces its isolation. Seasonal abundance estimates were consistently low ranging from 1.4 to 3.3 individuals, but given the small island size (8 km^2), this resulted in a relatively high density. In Summer 2024 no coyote scat was found. We were still able to provide estimates informed by Winter 2024 estimates and recruitment (i.e., "surveyed and didn't find anything" is different from "did not survey so we do not know anything"). Shackleford Banks is also home to more than one hundred wild horses. While no predation events on foals have been documented, coyotes have been photographed eating horses that died of natural causes (Dr. Sue Stuska, personal communication, September 8th, 2025). While infrequent, it could supplement the coyote diet. Furthermore, we confirmed that coyotes can travel between Shackleford and South Core Banks, with one female documented swimming the shallow waters between Barden Inlet and Power Squadron Spit seven times. This functional connectivity to South Core Banks and infrequent predator removal likely explains the relatively high coyote densities.

South Core Banks

South Core Banks was also colonized by coyotes in 2014 and lies immediately east of Shackleford but is much larger (~38 km^2). It had the fourth-highest coyote density (0.20/km^2) with moderate seasonal abundance estimates ranging between 6.5 to 8.1 individuals. Its density was lower than Pea and Shackleford, likely due to the distribution of suitable cover. Most of South Core consists of open dunes, beaches, and flats with some forested areas. Cape Lookout National Seashore predator removal efforts are mostly focused on South Core Banks due to high levels of nest predation. While these control efforts **may** be suppressing the coyote population, functional connectivity with Shackleford Banks could provide demographic buffering through compensatory immigration.

Hatteras Island

Hatteras Island, physically connected to and directly south of Pea, is the largest management unit in the Outer Banks chain (~73 km^2), and was colonized by coyotes in 2018, but supported relatively low densities (0.12/km^2) with seasonal abundance estimates ranging from 8.0 to 10.7 individuals. The combination of recent arrival and continued removal efforts likely explain why densities remain lower than expected given the island's size and connectivity. Often, urban environments supplement coyote populations by providing anthropogenic food resources resulting in inflated coyote populations relative to non-urban environments. We do not see that effect on Hatteras, suggesting that the population may not have reached equilibrium. Further, the removal of five coyotes on Hatteras in 2024 did not reduce pack size. The likely explanation is that its direct connection to Pea Island is facilitating compensatory buffering.

Ocracoke Island

Ocracoke is the most isolated island in our study and was the last island to be colonized by coyotes, with their arrival documented in 2023. Unsurprisingly, it had among the lowest densities (0.09 coyotes/km^2) and seasonal abundances of only 2.3 to 3.2 individuals. Its geographic isolation and very recent colonization likely explain these patterns. While Ocracoke has permanent residents, human development is limited and mostly clustered in Ocracoke Village, with Highway 12 bisecting the island separating the marshes from the open beach. This leaves large portions of the island as continuous habitat. Therefore, it's likely that without a sustained culling effort here coyote densities will increase over time.

North Core Banks

Coyotes were first documented on North Core Banks in 2013, giving the population a little over a decade to establish. Despite this, North Core (~33 km^2) had the lowest average density in the study (0.05 coyotes/km^2), with seasonal abundance estimates ranging from only 1.3 to 2.3 individuals. The island is among the most remote in our study system, and habitat here is more open with less forest. Predation on shore-nesting birds and turtles has remained relatively low and unproblematic here so CALO has not prioritized North Core in its predator management program, instead focusing removal efforts on South Core and Shackleford where predation is high. Its relatively poor habitat and geographic isolation likely explain why coyote densities on North Core remain the lowest in the system, even after presumably a decade of continued occupancy. It's possible that there are a couple resident coyotes living here year-round and the absence of coyote removal helps them maintain their territoriality and exclude transients arriving to the island to establish.

Fladry

Our fladry experiment across the northern section of SCB coincided with a particularly notable strong effect for the one coyote that frequently used the northern section of the island before the fladry was installed. Another resident rarely used the northern section regardless of treatment (Ed), and one female had too little pre-deployment data for us to make a comparison of space use. Furthermore, our camera traps did not document any coyotes, collared or uncollared, crossing the fladry line. Instead, our tracking data showed crosses by collared animals swimming on the sound side, and our cameras showed one uncollared animal crossing the line via the surf. Thus, our pilot study results are consistent with short-term deterrence and shows the promise of fladry as a non-lethal management tool to reduce coyote intrusion into protected nesting sites. For future nesting-season protection planning, existing perimeter string on nest enclosures should be replaced with pre-made fladry, essentially encircling nesting sites as ranchers do to protect calving pastures. We suggest that fladry be incorporated as a part of the suite of tools available to coastline land managers responsible for protecting shore-nesting birds and sea turtles. However, it must be used conservatively, as coyotes can become habituated if improperly designed (flag spacing is insufficient), maintained (flags must be untangled regularly to ensure deterrence), or left up for long enough that coyotes habituate.

General Behavior of Island Coyotes

Island coyotes in our system exhibit strong nocturnality, travel along ocean-side beach (and roads where present), and rest in forested areas during the day. They also scale their space use to encompass the entirety of the islands on which they inhabit.

Across 1,698 coyote-days, mean travel was ~14.7 km/day with individuals capable of making entire island-length loops and traveling up to ~54.6 km in a day. Despite considerable individual and seasonal variability, sex-averaged means across the full study period were nearly the same, and roughly similar to the average values we calculated for other datasets from mainland animals in NY, WA, and UT. Although our daily totals are based on straight-line step sums rather than movement models, the very short GPS fix intervals for moving animals in our study minimizes path distance underestimation and yields values comparable to ctmm-based distances (Rowcliffe et al. 2012).

During the spring-summer nesting/visitor season, coyotes showed higher nighttime activity than in the off-season, aligning with findings elsewhere that overall nocturnal activity increases with increasing levels of human recreation (Farmer and Allen 2019). Interestingly, we did not detect a shift towards crepuscular or diurnal activity as human recreation subsided in the winter—coyotes continued to be highly nocturnal.

Across individuals, 95% home ranges varied from 8.44–46.91 km^2. Azula reached 46.91 km^2 in all seasons except summer, the full extent of South Core, Shackleford, and Morgan, whereas, in contrast, Cruella remained fixed at 8.44 km^2 year-round, matching the exact geographic boundary of

Shackleford. Notably, our 95% home range sizes are similar to estimates from nearby coyotes on the mainland (13–47 km^2; Hinton et al. 2015), indicating island coyotes exhibit typical mainland-like home range size.

Given the extensive, persistent, spatial overlap of all our coyotes on South Core Banks and the fact our traveler Azula's core area also overlapped the SCB residents and the Shackleford female Cruella, these individuals are likely closely related. On the mainland, when multiple packs co-inhabit an area, they typically segregate spatially by family groups, excluding unrelated and transient coyotes from their home ranges. Our configuration of island-wide 95% home ranges with overlapping 50% core area indicates a single-family group occupying SCB at a time, rather than multiple territorially segregated packs. Core areas, generally, were stable across seasons with two out of our three females' cores shrinking in summer and expanding in winter.

Nighttime feeding sites were broadly spread across ocean beach (plus a sound-side band on Shackleford), while daytime resting sites were concentrated in maritime forest/hammocks with clear clustering across individuals near Cape Lookout Historic District and just south of Great Island Camp. Regarding sea turtle activity, coyotes were closer to nests than random both before and during nesting, but we did not find a uniform increase in nest selection during the turtle breeding season that you would expect if coyotes were, in fact, focusing on the nests themselves. Ed strengthened selection for these sites during nesting season whereas Rahzar and Cruella weakened. This suggests that the proximity to nests reflects a shared use of the shoreline by turtles and coyotes rather than explicit nest-targeting. Coyotes exhibit individual dietary specialization even within the same landscape, where some individuals repeatedly exploit particular food types while neighboring coyotes do not (Caspi et al. 2025; Larson et al. 2020; Newsome et al. 2015). Although our sample size is low (n = 3 individuals), our results suggest that a subset of coyotes may be increasingly efficient at locating and exploiting sea-turtle nests, rather than a population-wide pattern of nest targeting.

Inter-Island Connectivity and Recolonization Risk

We detected inter-island coyote movement with both datasets. Genetic recaptures identified one individual moving from North Core Banks to Ocracoke and back (~4 km across Ocracoke Inlet), representing ~2.9% of the total individuals we detected at least twice. Animal tracking showed one of our five collared animals completing 50+ crossings among Shackleford, Morgan, and South Core, predominantly at night and often near low tide, routinely bridging ≤0.8 km water gaps via shoals, sandbars, and islets. Together, these results show that even the most isolated islands exchange animals and that adjacent islands can be linked through regular movement. While movement events for some islands may be uncommon, they appear to be sufficient to refill vacancies, so island-specific removals are prone to rapid backfilling from neighbors. Although our observed movement rate was low on monthly or annual time scales, it only takes a pair of dispersers to re-establish a population, so recolonization risk remains high over management-relevant time frames for all islands on the Outer Banks. This risk is also higher today than a decade ago when they first colonized because surrounding source areas now support more coyotes, increasing immigration pressure.

Management Implications

When an invasive predator first arrives on isolated islands the first obvious management action is to attempt to eradicate them. Our finding of high or typical densities, relative to the adjacent mainland population, after 16 years of removing 173 coyotes suggest that this goal is likely impossible. Coyote eradication is especially futile on the more connected islands like Bodie, Hatteras, and Pea, because immigration and reproduction immediately offset removals. In theory it might be possible to remove all of the animals we estimate to live on the more isolated North Core (1–4 coyotes) and Ocracoke islands (1–7). However, this would require very intense trapping effort, and our movement data suggest it would be a short-lived success as coyotes would recolonize eventually. After accepting that coyotes are here to stay, the next strategy is to try and reduce their population size. Our model results suggest that lethal removal has not substantially reduced coyote numbers on the Outer Banks, likely due to compensatory immigration and/or reproduction. Our results finding little or no reduction in coyote abundance after removal is consistent with other mainland studies, but it is noteworthy that it is also occurring on this isolated island chain where immigration is more difficult. Given the incredible ability of coyote populations to compensate for removal, we suggest managers instead focus on trying to affect coyote behavior. While lethal removal may not be significantly reducing the population size, it may provide indirect benefits by reinforcing coyote wariness around humans (Brooks et al. 2020), which could help prevent human-coyote conflict in the future. This is particularly relevant for places like Oregon Inlet Campground, where coyotes have already been observed approaching people and tents (Personal communication from Oregon Inlet Campground, 14 August 2024). However, targeting coyotes near people is complicated by risk of tourists or their dogs being unintentionally caught in the foot-hold traps. Therefore, to reduce nest predation, we suggest management actions designed to temporarily deter coyotes. The NPS already protects turtle nests from coyotes by placing a grate over the top as soon as nests are detected, which has proven effective (Jobe et al. 2023; Lavelle 2023; Lovemore et al. 2020). Bird nests cannot be physically protected in the same way, but coyotes might be temporarily kept out of nesting colonies with fladry. Our tracking and camera data suggest fladry can be effective in this environment. We suggest future applications encircle areas of high nest concentration with fladry, with attention to coyote specific recommendations on flag spacing, designs to deter flag furling, and using <2 month deployments to prevent habituation. Taken together, our results demonstrate that sustained population suppression or eradication of coyotes on the Outer Banks is unlikely. Instead, we suggest that the most promising management approaches aim to strategically modify coyote behavior to reduce their impacts on vulnerable nesting species and prevent future conflict with humans.

Limitations of Our Study

A longer, multi-year study would be required to formally evaluate how predator management actions impact coyote population dynamics as our 1.5-year study cannot fully disentangle management effects from natural population processes such as immigration, recolonization, and interannual variation in reproduction and recruitment. While we documented inter-island movement in both our datasets and demonstrated functional connectivity, evaluating whether movement rates or demographic parameters vary across years, and how these patterns respond to sustained management pressure, would require monitoring over multiple reproductive cycles.

Future Coyote Monitoring

The methods we employed in this study could be continued for coyote monitoring. The fecal DNA approach gives the most precise estimates of population size, and with the proper sample design, can also provide demographic information on dispersal, survival, and reproduction. However, the field and laboratory work needed to acquire these data are substantial and may not be sustainable for longer term monitoring at the full scale of our study. Although, continuing this at a smaller scale on fewer study sites might be feasible. Similarly, more animals could be tracked with GPS collars to provide information on inter-island movement, survival, dispersal, and individual coyote behavior. We would suggest collars with satellite or cell-phone data transmission to reduce the required field work and ensure off-island movements can be detected.

Camera traps are another monitoring approach that might be more sustainable for longer term monitoring. Because individual coyotes can’t be identified from images, we cannot get survival and dispersal information from camera traps. However, new AI tools and statistical models have enabled density estimation from camera traps. Thus, an array of cameras could be used to estimate the density of coyotes, and other species, on each island. Camera traps can also be used to measure fine-scale space use of coyotes, which could be useful for testing the effectiveness of fladry for keeping coyotes out of nesting areas.

Other less expensive survey methods are not appropriate for monitoring coyote populations. Tracks in the sand are too difficult to survey in standardized ways due to variable weather, and can be affected by coyote movement rate, as well as abundance. Citizen science observation (i.e., from iNaturalist) are opportunistically collected, and thus not useful for abundance estimation at fine scales. We also tested if we could get coyotes to defecate on a scent lure, as they are sometimes known to over-mark the scent of an unknown coyote, and this would facilitate the collection of fecal samples. Unfortunately, Outer Banks coyotes were not interested in defecating where we wanted them to.

In summary, the fecal DNA and tracking collaring work we did for this study could be continued to monitor coyote populations, although it would require a large effort. Camera trap approaches might be less work, and thus more sustainable, and could provide long term density estimates, but not information on survival, immigration, or reproduction.

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