ABSTRACT

SOSSOVER, DANIEL. Coyote Ecology and Management on the Barrier Islands of North Carolina. (Under the direction of Drs. Roland Kays and Elizabeth Kierepka)

Over the past two decades, coyotes colonized North Carolina's barrier-island chain where they have been documented depredating protected shore-nesting birds and sea turtles. Since 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 the coyote population and their behavior. We implemented a multistate robust design model to provide estimates of island-specific abundance, apparent survival, inter-island movement, and detection probability. Average island densities ranged from 0.05 to 0.86 coyotes/km², 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 overall reduction in boundary crossings (rate ratio ~ 0.34; not statistically significant) 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.

Coyote Ecology and Management on the Barrier Islands of North Carolina

by
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BIOGRAPHY

Before joining NC State, Daniel Sossover graduated from SUNY ESF Ranger School in 2020 with an Associate's of Applied Science in Environmental and Natural Resources Conservation. He then went on to graduate from Cornell University in 2022, with a Bachelor of Science in Environment and Sustainability, having concentrated in Environmental Biology and Applied Ecology. There, he led and then published his first wildlife research study where he used audio recording units and machine learning algorithms to study wolves and coyotes in California. His passion for conducting field-based research that informs real-world wildlife management brought him to NC State to lead the first ever coyote inventory project on the barrier islands of North Carolina to study island coyote behavior, population dynamics, and explore non-lethal management tools to protect shore-nesting birds and sea turtles. At NC State, he graduated with an M.S. in Fisheries, Wildlife, and Conservation Biology, along with a minor in Statistics and a graduate certificate in Geographic Information Systems.

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COYOTE POPULATION DYNAMICS ACROSS NORTH CAROLINA’S BARRIER ISLANDS

ABSTRACT

Coyotes (*Canis latrans*) recently colonized the barrier islands of North Carolina's Outer Banks where they have been documented depredating protected shore-nesting birds and sea turtles. In response, federal agencies have conducted intensive culling since 2009, removing >170 individuals across Cape Hatteras National Seashore, Cape Lookout National Seashore, and Pea Island National Wildlife Refuge. Despite over a decade of lethal control, coyotes persist, raising questions about efficacy of eradication. Further, no population estimates or demographic data exist to inform management strategies. To address this knowledge gap, we conducted noninvasive fecal surveys across seven barrier islands (Bodie, Pea, Hatteras, Ocracoke, North Core Banks, South Core Banks, and Shackleford Banks) during three seasons (Winter 2024, Summer 2024, Winter 2025), completing four survey rounds per island per season. We collected 387 samples and identified 62 unique individuals (20M:42F). We then fit a multistate robust design mark-recapture model to estimate island-specific abundance, apparent survival, recruitment, inter-island movement, and detection probability. Densities ranged from 0.05–0.86 coyotes/km^2 and generally declined with distance from the mainland from Bodie through Pea, Hatteras, Ocracoke, and North Core Banks, then increased again on South Core Banks and Shackleford Banks. This gradient likely reflects the combined effects of island size, geographic isolation, culling intensity, and anthropogenic resource availability. Apparent survival was lower on islands with active predator management (0.544 vs. 0.631), but the management effect’s 95% credible interval overlapped zero, indicating high uncertainty. We detected one inter-island movement where a female swam from North Core Banks to Ocracoke Island and back, crossing the system’s second widest inlet (~3.2km) between its two most geographically isolated islands. Our results demonstrate that sustained suppression or eradication of coyotes on the Outer Banks is unlikely. If the objective of coyote management is to reduce nest depredations during the breeding season, our results suggest that behavior-focused strategies such as fladry may offer a better mitigation of predation pressure than coyote removal.

INTRODUCTION

Non-native predators can have severe impacts on ecosystems by causing declines of native species (Doherty et al., 2016; Salo et al., 2007) introducing novel diseases (Chinchio et al., 2020), and altering community dynamics (Croll et al., 2005; Savidge, 1987). The most dramatic consequences of non-native predators are often observed on islands with highly adaptable, generalist mammalian mesopredators (e.g., foxes, stoats, mongoose) because islands are isolated from large mainland populations that could help compensate for increased mortality rates (Courchamp et al., 2003). The severity of these impacts are often density dependent where large numbers of predators create more severe declines in naive prey (Yokomizo et al., 2009). Therefore, knowing the population size of non-native predators is important for effective management to mitigate their negative impacts on native species.

Coyotes (*Canis latrans*) have expanded their geographic range largely due to the widespread extirpation of large predators such as wolves (*Canis lupus*) and forest fragmentation, and are now established across most of North America including multiple island systems (Hody & Kays, 2018). Most recently, they have reached eastern barrier islands by swimming and traveling along highway bridges (Way, 2009; Weckel et al., 2015). Coyotes are adaptable generalist predators, taking advantage of whatever prey is most abundant in a given area (Patterson et al., 1998). On barrier islands, there is concern that coyotes are endangering sea turtles and shore-nesting birds. Indeed, recent work has confirmed that island coyotes predate both seabirds and turtle nests (Etheredge et al., 2015; Lovemore et al., 2020). Therefore, there have been calls for the management of coyote populations across numerous island ecosystems to prevent declines of sensitive bird and turtle species.

Management for coyotes typically involves killing individuals to reduce their population size, although the efficacy of this approach is questionable. Coyotes are capable of high reproductive output, and can alter their reproductive strategies when faced with removal (e.g., breed younger; Kilgo et al., 2017). Additionally, they are highly mobile, resulting in compensatory immigration of new animals to replace those that are removed (Kierepka et al., 2017). The result, at least in mainland populations, is that coyote abundance can actually be higher in places where they are hunted (Kays et al., 2017). Coyote removal could be more effective on islands where coyote immigration would be more difficult, but there have been no estimates of coyote population sizes on islands, so the number of animals that would need to be killed to achieve eradication is unknown.

Coyotes have become established on the Outer Banks of North Carolina over the past two decades, arriving from either the mainland or adjacent islands presumably by a mix of swimming across inlets to isolated islands and crossing man-made bridges where they exist. Along the northern chain, colonization progressed southward: Bodie Island (2008) -> Pea Island (2014-2015) to Hatteras Island (2018) to Ocracoke Island (2023; Cape Hatteras National Seashore/Pea Island National Wildlife Refuge pers. comm., Sept 2025). In contrast, Cape Lookout National Seashore shows a separate timeline with coyotes first detected on North Core Banks (2013) followed by South Core Banks and Shackleford Banks (2014). This timeline is consistent with two independent colonization events.

Since their arrival, coyotes have been documented preying on both shorebird and sea turtle nests at Cape Hatteras (CAHA) and Cape Lookout (CALO) National Seashores. At CAHA, depredation was the leading cause of sea turtle nest failure in 2018, with coyotes identified as the primary predator (Thompson et al., 2018); they were also documented depredating shorebird nests (Doshkov et al., 2018). At CALO, the 2023 annual reports note that coyotes accounted for the majority of turtle nest losses and were identified as the primary predator of shorebird nests (Altman, 2023; Altman & Stephenson, 2023). To address this nest predation federal agencies have conducted regular coyote removals began on CAHA (2009), CALO (2017), and Pea Island National Wildlife Refuge (2023; PINWR), totaling 173 coyotes across all sites. The effectiveness of these removals remains uncertain as coyote populations persist and nest predation continues to threaten native birds and turtles. Because there are no local estimates of coyote abundance, managers have no information of how many animals remain or how quickly they are breeding or recolonizing. Coyote population estimates would help managers gauge the scale of the challenge, evaluate whether current removal efforts are sufficient, and design more targeted and effective management strategies for protecting vulnerable nesting species.

To estimate densities of coyotes on the Outer Banks, we collected fecal samples across seven islands that make up CAHA, CALO, and PINWR. These islands vary in four factors that likely contribute to coyote density. Larger islands are expected to support more animals, while greater isolation is expected to limit dispersal and immigration. The intensity of lethal control may also reduce densities, particularly on more isolated islands where compensatory immigration is less likely. Finally, the availability of resources differs substantially across these islands. For example, inhabited islands provide anthropogenic food subsidies such as roadkill, pets, and garbage while coyotes on uninhabited islands rely more heavily on natural prey or allochthonous inputs (e.g. stranded fish and washed-up birds). Overall, this study will provide critical population density information for coyote control, and potentially identify factors that predict density across the Outer Banks and other island systems.

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 islands in total (see Figure 1): three in CAHA (Bodie, Hatteras, and Ocracoke Islands), three in CALO (South Core, North Core, and Shackleford Banks), and Pea Island National Wildlife Refuge (hereby called Pea Island). Pea Island, a wildlife refuge managed by the US Fish and Wildlife Service, is located between Bodie Island to the north and Hatteras Island to the south. These four northern islands (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 individual island characteristics.

Landscapes on all these islands are a mix of open beaches backed by dunes to grassy habitats that transition to salt marshes and maritime forest patches (i.e., hammocks). Beach habitats are important for many shore nesting species, but coyote predation is particularly concerning for imperiled populations of American oystercatchers (*Haematopus palliatus*), piping plovers (*Charadrius melodus*), and nesting sea turtles such as loggerheads (*Caretta caretta*) and greens (*Chelonia mydas*). The U.S. National Park Service uses multiple mitigation methods to protect these species during spring and summer nesting seasons including physical barriers to prevent animals from digging up for sea turtle nests and temporarily closing sections of the beaches to vehicles.

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 (Outer Banks, NC). We predict higher connectivity and potential for human supplementation will result in higher coyote abundances whereas isolation will likely result in lower abundance.

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	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	Separated from Bodie by Oregon Inlet (~1km wide) but highway bridge connects them. Physically connected to Hatteras	USFWS Wildlife Refuge	Medium - no anthropogenic food subsidies but year-round bird community likely provides stable food source, connected to Hatteras
Hatteras	~74	~4,000 permanent residents; Developed	Accessible by car from Pea Island	Physically connected to Pea; Separated from Bodie by Oregon Inlet (~1km wide); Separated from Ocracoke by Hatteras Inlet (~4km wide)	NPS-CAHA	High - anthropogenic food subsidies, largest island in study system, connected to Pea

Table 1 (continued).

Ocracoke	~28	~700 permanent residents; Developed	Accessible only by ferry/boat;	Highly isolated; separated by Hatteras (~4km) & North Core by Ocracoke Inlet (~3.2km wide)	NPS-CAHA	Low/Medium - anthropogenic food subsidies but isolated
North Core	~32	Uninhabited	Accessible only by ferry/boat; Sand-based road system	Highly isolated; Separated from Ocracoke by Ocracoke Inlet (~3.2km 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 boat; Segmented 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 boat; No roads of any kind	Surrounded by multiple islands: Bogue Banks, Harker's Island, South Core Banks, and Rachel Carson Reserve.	NPS-CALO	Low - isolated, no anthropogenic food subsidies

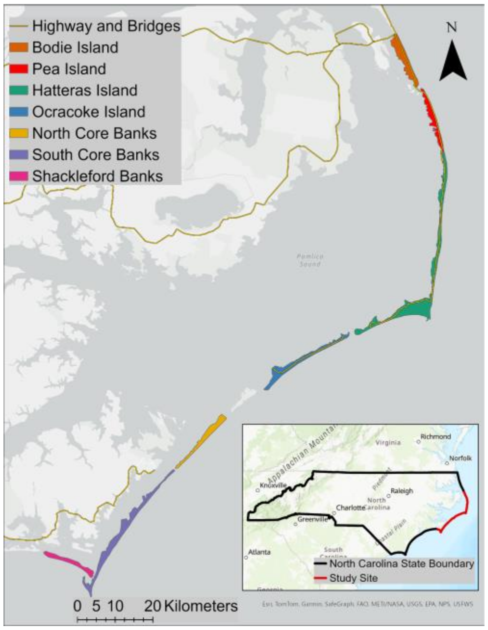

Figure 1. Study area showing the seven barrier islands we surveyed for coyote scat collection. We worked across Cape Hatteras National Seashore (Bodie, Hatteras, Ocracoke), Pea Island National Wildlife Refuge, and Cape Lookout National Seashore (North Core, South Core, Shackleford). Surveys for scat combined on-foot transects and vehicle-based transects. Survey seasons were Winter 2024, Summer 2024, and Winter 2025. There are bridge or land connections between Bodie, Pea and Hatteras islands, but the four southern islands have no physical connection to each other or to the mainland. Connectivity differs sharply between these islands (bridge north vs isolated south).

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 island four times per field season with roughly one week between repeated surveys. We surveyed six of the seven islands during all three seasons, as Bodie Island was added after the first field season. We used a combination of vehicle-based and on-foot methods to conduct surveys. We surveyed all vehicle accessible roads, beaches (sounds and ocean sides), and conducted foot surveys on publicly accessible trails. We covered approximately 250 km per survey round across the seven islands.

We collected scats with clean gloves in the field and placed each sample into a 50 mL Falcon tube filled with 100% molecular grade ethanol. Each tube was labeled 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 uL. 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)'s 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 45s, 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 45s, annealing at 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, 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 we counted the opposite case 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 contains sufficient power to accurately differentiate unrelated individuals and siblings.

To identify matching genotypes, we used the function “Matches” in Genalex 6.2 (Peakall & Smouse, 2006). This function produces a list of matching individual genotypes as well as highly similar (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

Definitions

i = individual unique coyote
j = primary period (season: Winter 2024, Summer 2024, Winter 2025)
k = secondary occasion (within-season survey round; four per primary period)
s = island index (spatial state)

Data

We used genetic IDs to build a capture-history matrix in which each row is a unique individual and each column is a secondary occasion (four per primary period). Each cell records 0 if the individual was not detected in that round, or 1-7 to indicate the island where it was detected (1 = Bodie, 2 = Pea, 3 = Hatteras, 4 = Ocracoke, 5 = North Core, 6 = South Core, 7 = Shackleford). This capture-history matrix is the observed input to the population model.

Model Overview

We implemented a multistate robust design mark-recapture model (Pollock, 1982; Kendall & Nichols, 2002; Kéry & Schaub, 2012) to estimate abundance, apparent survival, recruitment, inter-island movement, and detection probability. The model translates observed detection history (our capture-history matrix) into a latent state matrix that includes unobservable states. We defined nine discrete states for a focal coyote: not yet entered the system (coded as 1, animal is not born yet or reached the islands), 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).

We coded these values into the latent state matrix (z[i,j]) where the state of each individual i during primary period j represents their geographic location (which island they occupied) as determined from genetically identified scat samples. When an individual is detected on island X in the capture-history matrix (coded 1 - 7), the model sets the latent state for that primary period to the corresponding island/state (2 - 8); when the entry is 0 (not detected) the model allocates probability across island states and the unobservable states (1 = not yet entered; 9 = dead/permanently emigrated). The latent state matrix captures transitions between islands across survey periods. For example, if individual 3's scat was detected on South Core Banks during primary period 2 and on Shackleford Banks during primary period 3, this would reflect a state transition between z[3,2] = 7 (South Core, latent state 7) and z[3,3] = 8 (Shackleford, latent state 8). Unless otherwise stated, we report posterior means (± posterior SD) with equal-tailed 95% credible intervals.

Parameters

The robust design estimates apparent survival, recruitment, and movement between surveys (i.e., after Winter 2024 - before Summer 2024 surveys and after Summer 2024 - before Winter 2025). Within each primary period, detection probability, and abundance are estimated from the repeated within-season rounds (secondary periods) using the capture history matrix, with islands grouped by whether road-based surveys were conducted.

Detection

Detection probability is a core parameter for abundance estimation as it represents the conditional probability of detecting an individual given that it is alive and present on an island during a secondary occasion. We modeled detection probability as a function of survey effort (whether we surveyed an island on a given primary period) and road-based survey effort (i.e., if surveys were conducted on a road system within a vehicle). The covariate road_det[s] is binary: islands where road-based surveys were conducted = 1 (Hatteras, North Core, and South Core) and non-road surveyed islands = 0 (Shackleford, Ocracoke, Pea, and Bodie). Detection probability was also adjusted by a binary survey-effort covariate, with zero effort (no surveys conducted) coded explicitly for Bodie Island in the first primary period. We do not believe any coyote-specific factors (e.g., sex, age) impacted detection probability during our survey periods, but survey methods are likely to impact our ability to find coyote scats.

Apparent Survival

Estimated between primary periods:

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

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). Each between-survey interval had its own apparent survival estimate based solely on whether culling was conducted between our surveys.

Recruitment

We estimate a single global per-capita recruitment rate f across islands and seasons; expected recruits to island s at period j was calculated:

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

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. Since our model applies a single f across all islands and seasons, the estimate represents an average recruitment rate for the study area.

Movement

We modeled transitions 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. We allowed transitions only between geographically adjacent islands; all other movements such as Bodie to South Core were fixed to zero. We included the ability for individuals to move between islands (states) because both our genetic and telemetry data (Chapter 2) detected inter-island movement. We retained movement parameters (θ) in the model so that uncertainty associated with inter-island movements could propagate into estimates of survival, recruitment, abundance, entry probability, and detection probability. Each island had its own movement probability calculated between each survey interval. These values represent the likelihood of an individual staying on the island they were last detected versus the likelihood of them moving to an adjacent island.

Implementation

Data Augmentation & Superpopulation

To account for imperfect detection (undetected individuals), we used data augmentation. The superpopulation is the set of all coyotes that could have occupied the study area at some point during the study period, whether or not they were detected. The number of rows in our original capture-history matrix is n (the number of unique coyotes identified from our genotyped scat samples) and we expanded this matrix to a fixed size of M = 150 by appending M - n all zero capture-histories representing potentially real but undetected individuals. Therefore, M equals the total number of histories after augmentation and serves as the upper bound on the superpopulation considered by the model. The model infers how many of those M histories correspond to real animals.

Priors

We specified priors to keep parameters within biologically plausible ranges without imposing strong directional assumptions which allows data-driven 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. We assigned a Beta(1, 1) prior to detection probability and grouped it by whether we conducted road-based surveys (covariate named: “road_det”) to account for expected differences in detectability. We did not impose any assumption that islands with road-based surveys would be higher or lower. Per-capita recruitment was assigned a Gamma(0.1, 0.1) prior, which constrains this parameter to be positive while remaining flexible allowing for either low or high recruitment rates. Transition probabilities or movement 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.

MCMC & Convergence

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. Because Bodie Island wasn't sampled in Winter 2024, parameters tied to that island/period mixed slowly so longer runs and thinning ensured effective sample sizes. We verified convergence using Gelman-Rubin diagnostic values and all parameters were <1.1.

Model Assumptions

General Overview

The multistate robust design model relies on the following assumptions about recruitment: 1) demographic closure within each primary period (i.e., within-season) and 2) open population dynamics between primary periods (i.e., immigration/emigration, births/deaths occur). Essentially, no population size changes occur during a primary period, only between. Data augmentation requires setting an augmented size *M* that comfortably exceeds the true (unknown) superpopulation (N*); the model estimates N* and we set M = 150. 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.

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. We calculated density 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. We interpreted individuals that were recaptured at widely separated locations across an island 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 indicates the presence of multiple, spatially distinct packs. Single detections were assigned to the nearest overlapping group.

Population Growth Rate Calculations

We estimated system-wide seasonal population growth rate (λ) using two approaches. First, we calculated empirical growth rates from model-derived system-wide mean abundance estimates across seasons using the ratio $\lambda = N_{t+1}/N_t$, where N_t and N_{t+1} are estimated total abundances across all islands for consecutive seasons/primary periods. Second, we estimated growth rate from our mean estimated demographic parameters using $\lambda = \phi + f$, where ϕ is apparent survival and f is per capita recruitment. This demographic approach assumes no emigration and treats recruitment as a combination of both reproduction and immigration, consistent with our modeling framework. Because ϕ and f reflect seasonal change, and not annually, both abundance and vital-rate based λ estimates represent seasonal population growth, not annual.

RESULTS

Scat Collection and Genotyping

In total, we collected 387 fecal samples across our three sampling periods (Table 2). Spatial locations of scats on each island per season are shown in Figures 2.1-2.7.

We eliminated 77 fecal samples due to low amplification (20.10%) as we retained only samples that produced successful genotype at 7 or more loci for further analysis. The remaining 306 samples consisted of 247 coyotes and 59 dogs. 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 2. Summary of scat collection and genotyping results by island and season. Counts of scats collected in each surveying season are partitioned by amplification success, species ID, and the number of unique coyotes identified. Data comes from repeated within-season rounds using standardized transects across the Outer Banks. The count of unique coyotes per survey reflects the number of individuals detected in each survey considered independently, without removing between-survey recaptures.

Island	Winter 2024	Summer 2024	Winter 2025	Total
Bodie	N/A	23	31	54
Pea	23	0	17	40
Hatteras	52	21	22	95
Ocracoke	10	7	5	22
North Core	24	17	17	58
South Core	40	33	35	108
Shackleford	8	0	2	10

Table 2 (continued).

Total Scat Collected	157	101	129	387
Total Scat Amplified (≥7 loci)	134	71	101	306
Genetic ID as Coyote	105	48	94	247
Unique Coyotes Per Season	25	25	33	*
Total Unique Coyotes (Across All Seasons)	*	*	*	62

Figure 2.1 Locations of all scat collected during seasonal surveys on Bodie Island, North Carolina. Points represent scat samples collected during noninvasive surveys in Summer 2024 (orange; n = 23) and Winter 2025 (n = 31), totaling 54 samples. Major roads and bridges are shown in yellow. Bodie was not surveyed in Winter 2024. Detections are numerous, but clustered near the southern end of the island.

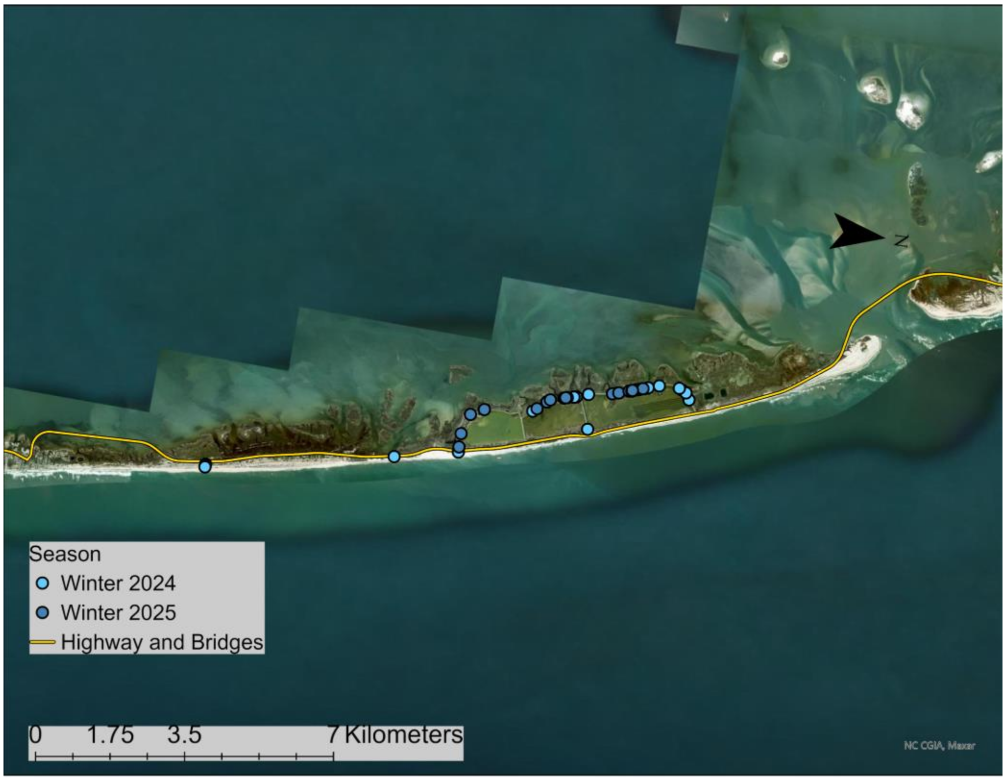

Figure 2.2 Locations of all scat collected during seasonal surveys on Pea Island National Wildlife Refuge, North Carolina. Points represent scat samples collected during noninvasive surveys in Winter 2024 (n = 23) Summer 2024 (n = 0), and Winter 2025 (n = 17), totaling 40 samples. Major roads and bridges are shown in yellow. Pea Island was surveyed in Summer 2024, but no scats were found.

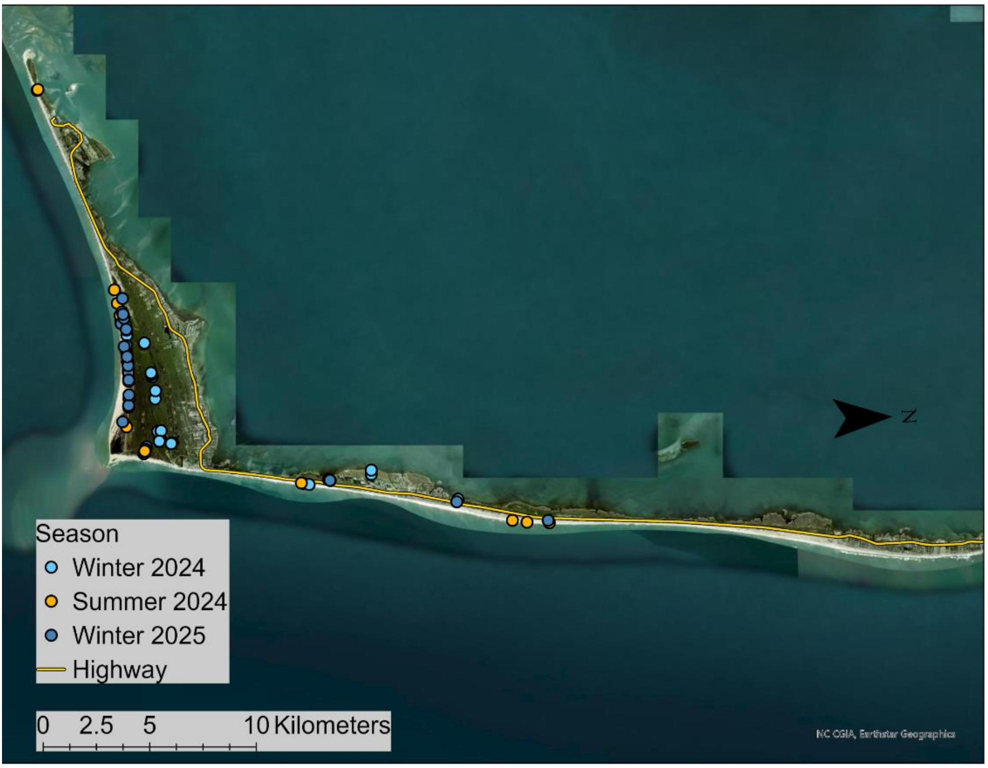

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Figure 2.3 Locations of all scats collected during seasonal surveys on Hatteras Island, North Carolina. Points represent scat samples collected during noninvasive surveys in Winter 2024 (light blue; n = 52) Summer 2024 (orange; n = 21), and Winter 2025 (dark blue; n = 22), totaling 95 samples. The major highway is shown in yellow. No scats were found on the northern section of Hatteras Island.

Figure 2.4 Locations of all scats collected during seasonal surveys on Ocracoke Island, North Carolina. Points represent scat samples collected during noninvasive surveys in Winter 2024 (n = 10) Summer 2024 (n = 7), and Winter 2025 (n = 5), totaling 22 samples. The major highway is shown in yellow.

Figure 2.5 Locations of all scats collected during seasonal surveys on North Core Banks, North Carolina. Points represent scat samples collected during noninvasive surveys in Winter 2024 (n = 24) Summer 2024 (n = 17), and Winter 2025 (n = 17), totaling 58 samples.

Figure 2.6 Locations of all scats collected during seasonal surveys on South Core Banks, North Carolina. Points represent scat samples collected during noninvasive surveys in Winter 2024 (n = 40) Summer 2024 (n = 33), and Winter 2025 (n = 35), totaling 108 samples.

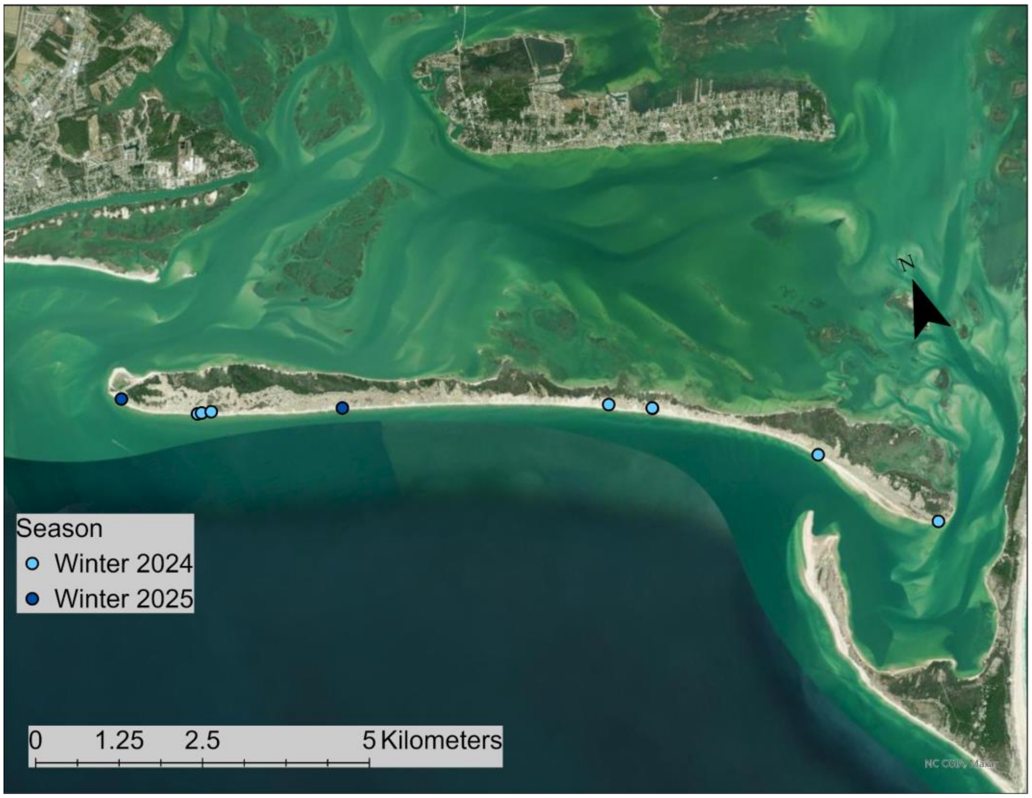


Figure 2.7 Locations of all scats collected during seasonal surveys on Shackleford Banks, North Carolina. Points represent scat samples collected during noninvasive surveys in Winter 2024 (n = 8) Summer 2024 (n = 0), and Winter 2025 (n = 2), totaling 10 samples. Shackleford was surveyed in Summer 2024, but no scats were found.

Inter-Island Movement

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. This movement violated our demographic-closure assumption within the primary periods (Winter 2024, Summer 2024, Winter 2025). To preserve closure, we set her s12

(Summer 2024, round 2) Ocracoke detection to zero in the capture history so she was not modeled as available on two islands in the same period.

Population Modeling

Key Model Parameter Estimates

Detection probability varied based on whether road-based surveys were conducted. The model estimated a mean detection probability of 0.208 (95% CI: 0.131 - 0.298) for islands without road surveys and 0.376 (95% CI: 0.287 - 0.465) on islands with road surveys. Therefore, detection probabilities were higher when surveys were conducted via a vehicle on a road. These detection probability estimates refer to the average probability of detecting an individual coyote during a single secondary survey occasion, conditional on the fact that the individual was present and alive.

Apparent survival between primary periods was estimated to be 0.631 (95% CI: 0.431 - 0.823) in the absence of predator management and 0.544 (95% CI: 0.274 - 0.876) when predator management was present - thus survival was lower where coyotes were being targeted by trappers but not significantly different from where they were not. The posterior distribution for B1 (the effect of predator management on survival) was -0.33 but overlapped with zero on the logit scale (posterior mean = -0.33, 95% CI: -1.85 to +1.50, SD = 0.88) - **i**ndicating that predator management may reduce coyote survival, but the wide credible interval indicates the effect is highly uncertain. Approximately 0.696 of the posterior samples supported lower apparent survival when predator management was present. The estimated per capita recruitment rate (f) was 0.27 (95% CI: 0.093-0.471, SD = 0.097). Our model applies a single f across all islands and seasons, so this value represents the average per capita recruitment rate for the Outer Banks during the study period.

Finally, our model estimated movement probabilities between adjacent islands, but the posterior distributions were wide. Overall, our movement estimates indicate that most individuals remain on the island they were detected on first across seasons. For example, the probability of remaining on Bodie Island (posterior mean = 0.93, 95% CI: 0.76-0.99) was high, and similarly high on South Core Banks (posterior mean = 0.75, 95% CI: 0.66-0.86). Movement probabilities to neighboring islands were generally low but not zero. The strongest inter-island movement signals came from Shackleford Banks to South Core Banks (posterior mean = 0.52, 95% CI: 0.03-0.97). Given the wide credible intervals, these transition probabilities are imprecise and should be interpreted cautiously.

Abundance and Density Estimates

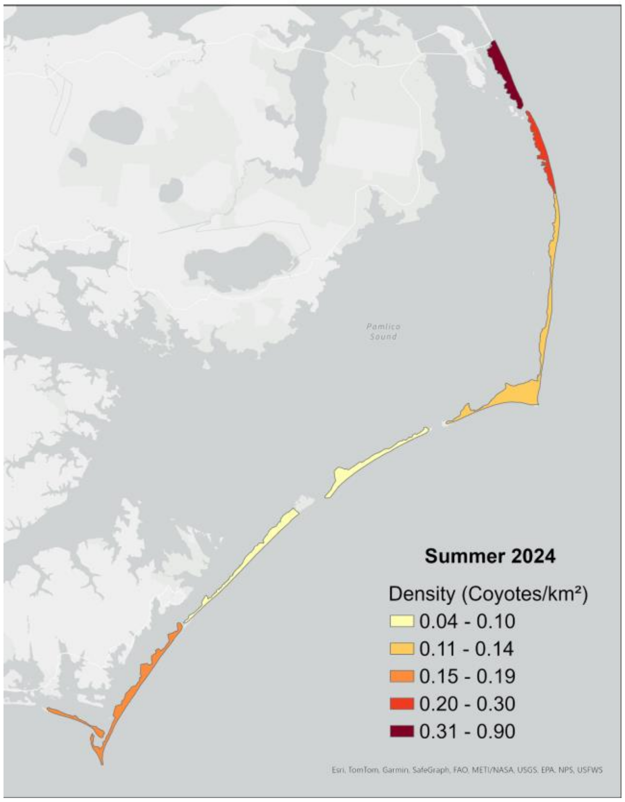
Mean estimates of abundance from our robust design were under 11 animals at each island except for Bodie Island (Table 3).

Table 3. 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. Abundance is greatest on Bodie and Hatteras and lowest on Ocracoke and North Core.

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)

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 had a high estimate with wide credible intervals (32.1, 95% CI: 16-60). When converted to densities, Bodie Island still had the highest density (Figure 3 and 4, Table 4) 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).



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

Figure 3. Summer 2024 coyote density by island (coyotes/km^2). Island-level densities were estimated with our multistate robust-design genetic mark-recapture model and calculated as posterior mean abundance divided by mapped island area. Scats were collected in four within-season rounds using standardized vehicle-based and foot-based transects. The choropleth shows a connectivity gradient as Bodie > Pea > Hatteras > Ocracoke > North Core with densities rising again on South Core and Shackleford. Class breaks in the legend were chosen to emphasize these trends.

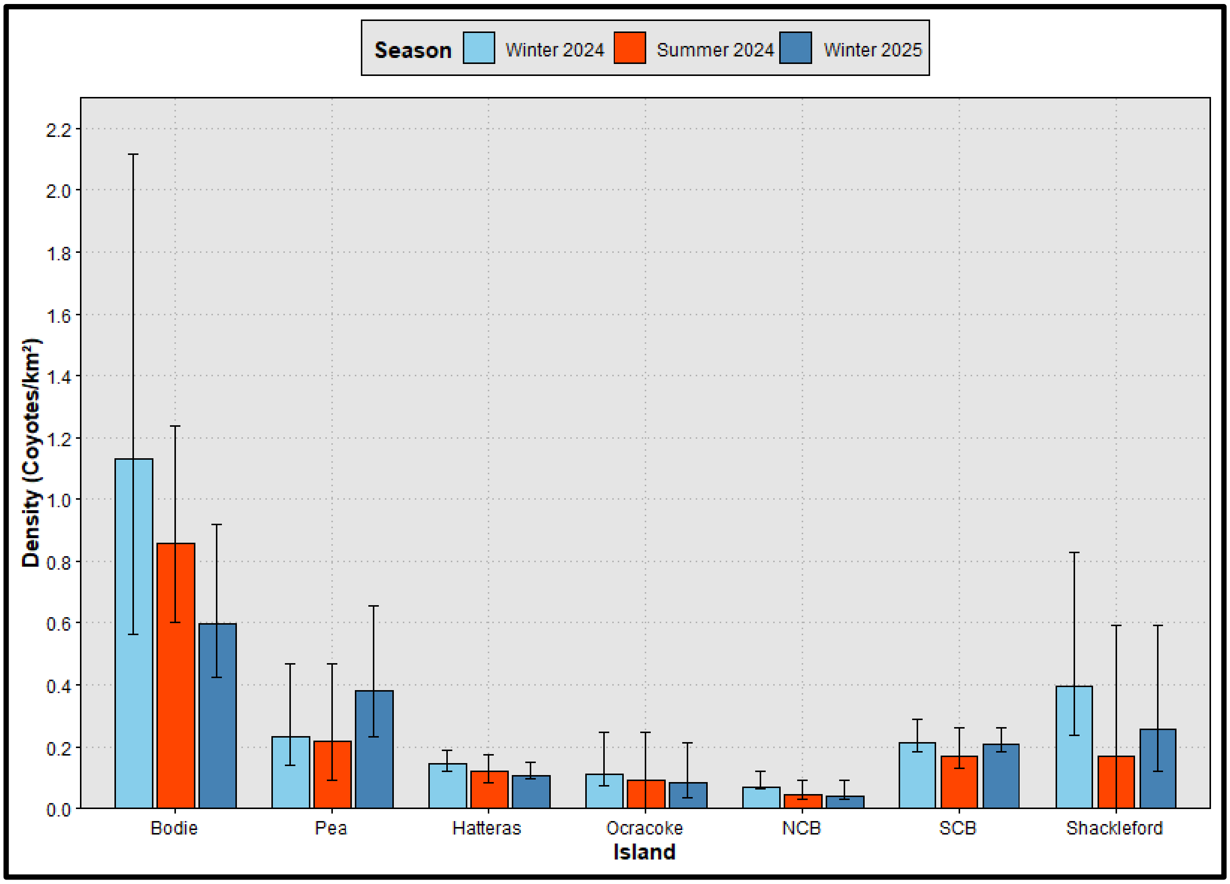


Figure 4. Seasonal coyote density by island (coyote/km^2) with 95% CI displayed as error bars. Bars show island-season densities for Winter 2024 (light blue), Summer 2024 (orange), and Winter 2025 (dark blue), calculated as posterior mean abundance from the multistate robust-design genetic mark-recapture model we developed divided by mapped island area. Bodie was not surveyed in Winter 2024, contributing to wider uncertainty. Across the bridged northern chain, density declines with distance from the mainland Bodie > Pea > Hatteras > Ocracoke > North Core and then increases again toward South Core and Shackleford.

Table 4. Island-level mean coyote density across the seven islands we surveyed. Values are calculated as posterior abundance divided by island area and averaged across the three primary periods sampled (Winter 2024, Summer 2024, Winter 2025). Our abundance posteriors come from the multistate robust-design mark-recapture model we developed. 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).

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

Although no coyote scats were detected on Ocracoke 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.

Population Growth Rate

We calculated system-wide seasonal population growth rates (λ) using both abundance-based and demographic-based approaches. Based on posterior mean abundance estimates, λ was 0.91 between Winter 2024 and Summer 2024, and 0.90 between Summer 2024 and Winter 2025, yielding a mean seasonal λ of 0.905. Using our estimated mean apparent survival ($\phi = 0.638$) and per capita recruitment ($f = 0.27$), we obtained a vital-rate-based λ of 0.908. Both estimates are below 1, suggesting that the population was nearly stable but slightly declining over the course of our study.

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. 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 Figs. 5-6), indicating clear north–south spatial partitioning that persisted across all sampling periods. Despite targeted removals on Bodie (n = 9) and Hatteras (n = 5) in 2024, overall pack sizes remained relatively stable (see counts in Table 5).

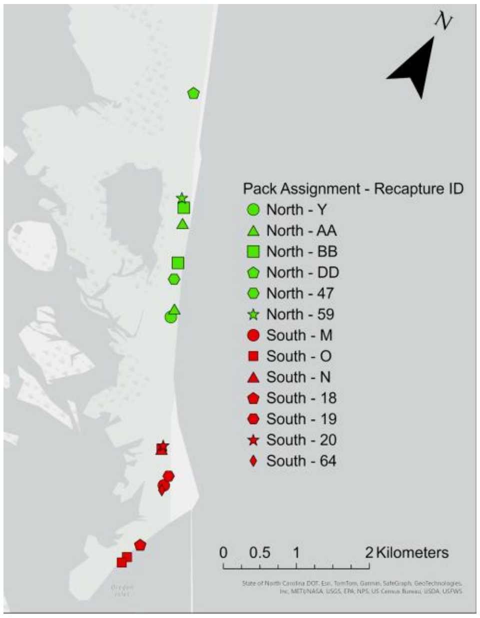


Figure 5. Pack structure inferred from the spatial distribution of genetic recaptures on Bodie Island. Clusters of recaptures were identified by mapping repeat detections of the same individuals through time. Each point represents a scat location and each unique individual coyote was assigned a unique color symbol combination. Recaptures clustered on either end of the island across all seasons which indicates two spatially segregated packs.

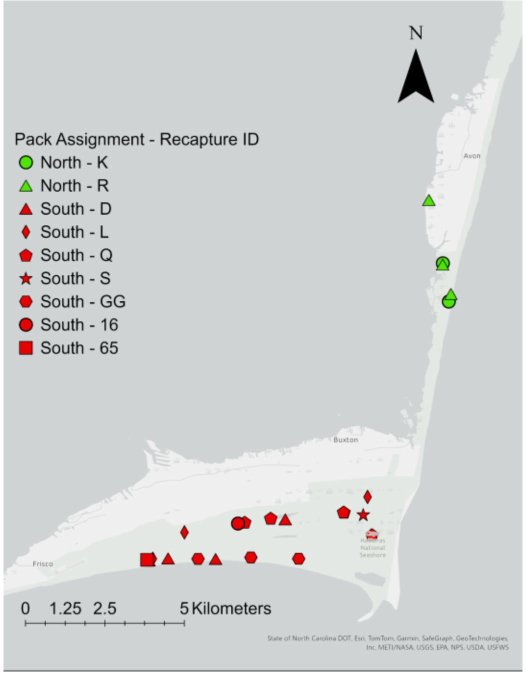


Figure 6. Pack structure inferred from the spatial distribution of genetic recaptures on Hatteras Island. Clusters of recaptures were identified by mapping repeat detections of the same individuals through time. Each point represents a scat location and each unique individual coyote was assigned a unique color symbol combination. Recaptures clustered on either end of the island across all seasons which indicates two spatially segregated packs.

Table 5. Pack composition by island and sampling period. Packs were delineated by the spatial clustering of individuals' detections (see pack maps above), not by genetic relatedness or social observations. Pack membership counts (by island, season, and sex) are summarized below. Two packs persist on Bodie and Hatteras throughout our study period and pack sizes remain stable despite ongoing removals (n = 9 for Bodie; n = 5 for Hatteras).

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

Table 5 (continued).

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

DISCUSSION

General Overview

Coyotes are highly adaptable carnivores whose recent expansion into barrier island ecosystems raises both ecological and management challenges. In this study, we used genetic data to estimate coyote densities, pack structure, movement, and demographic parameters across the Outer Banks of North Carolina, a system where predator control is ongoing due to concerns over bird and sea turtle nest predation. We found that coyote densities were mostly well below mainland levels, excepting the higher densities in the most connected, and most disturbed site (Bodie island). The density differences between islands reflect the effects of island size, isolation, habitat quality, and management intensity. We found multiple packs on Hatteras, the largest island in the system, and on Bodie, the most connected to the mainland while smaller or more isolated islands had a single pack. Coyote survival was only slightly lower on islands with active predator removal, though the effect was not statistically significant, suggesting that immigration and reproduction largely compensates for this management effort. Finally, we found that while inter-island movement was rare, it does occur, highlighting the potential for demographic and genetic connectivity even across substantial water gaps. Together, these findings underscore the complexity of managing a recently established predator in a dynamic coastal landscape and highlight that effective control strategies will need to account for island-specific conditions: high immigration pressure on connected islands, the persistence of multiple packs on larger islands, compensatory dynamics under predator removal, and the potential for rare but important inter-island movements that can undermine eradication efforts.

Coastal versus Mainland Coyote Densities

Our model estimates that coyote densities across the Outer Banks range from 0.05 to 0.86 coyotes/km^2, with most islands being slightly lower 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 seven 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 island in the system with trapping beginning in 2009. This long history of occupancy and removal in conjunction with it being physically connected to 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 island.

Pea Island

Coyotes were first detected on Pea Island in 2014-2015, making it the second 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 1km 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 (~3.2km), which we documented a coyote crossing twice. This proximity to Bodie and its physical connection to Hatteras to the south 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 (~8km^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 (~38km^2). It had the fourth-highest coyote density (0.20/km^2) with moderate seasonal abundances 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, directly south of Pea and the largest in the Outer Banks chain (~73 km^2), 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 coyotes on Hatteras during our study period did not reduce pack size. The likely explanation is 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 abundance 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 does not include North Core in its predator management program, instead focusing removal efforts on South Core and Shackleford. 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’s 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.

Pack Structure

Pack structure provides a social lens for interpreting the density patterns observed across the islands. Using spatial clustering of genotyped recaptures, we identified discrete north–south partitions on Bodie and Hatteras Islands, where individuals were consistently detected in only one section of the island across all seasons. Pack sizes were relatively stable through time, despite ongoing removals. In contrast, all other islands showed detections distributed throughout their length, consistent with a single pack using the entire island. Multiple packs thus appear to occur only where area, food resources, and connectivity are greatest. The large but remote islands might have enough resources to support multiple packs, but be limited by such reduced immigration. These findings mirror broader patterns of coyote social ecology, where territories are typically exclusive and may be compressed in human-influenced environments (Bekoff & Wells, 1980; Atwood et al., 2004; Gehrt et al., 2009). For management, this suggests that control on multi-pack islands must consider territorial boundaries and the potential for transients to quickly occupy vacated spaces, while on single-pack islands, whole-island strategies may be more feasible. These pack structures are also important because they could have impacts on population parameters such as detection, recruitment, and apparent survival.

Population Parameters

Recruitment and Apparent Survival

By identifying individual coyotes across three seasons we were able to provide the first estimates of recruitment (addition of new animals) and apparent survival (probability that an individual alive in one season is alive and still in the study area in the next) for coyotes on the Outer Banks. While our model did not distinguish between reproduction and immigration, and our recruitment estimate was averaged across all islands, our results provide an important first approximation of the demographic processes at work in this kind of system.

We estimated both abundance-based and vital-rate-based measures of population growth (λ) across the Outer Banks. In both cases, with, and without predator management, λ was less than one. These results would suggest that populations would decline over time. However, this result should be interpreted very cautiously. Coyote life history allows for rapid rebound and recolonization, and, in reality, despite over a decade of culling, they persist in this system. Furthermore, our data comes from only a relatively short timespan for such a long-lived species (5+ years in the wild). One and a half years provides not only **very** limited statistical power but also cannot capture inter-annual variability in reproduction, mortality, or dispersal. To truly estimate population growth rate, a multi-year study would be required to evaluate changes in abundance.

While the same may be true regarding formally evaluating lethal removal efforts on this population, extensive research shows that coyote eradication is made practically impossible due to their compensatory strategies. These coyote populations are heavily persecuted in an effort to control their populations, with 173 removed over 15 years. This has been most intense in Bodie island where 71 coyotes have been removed since they arrived back in 2009. Apparent survival was estimated to be lower on islands with active predator removal (54.4%) compared to islands without (63.1%). However, the difference was not statistically significant, with wide credible intervals overlapping zero. These results suggest that while removals may reduce survival locally, compensatory processes such as reproduction and immigration maintain populations. Despite their isolation, these populations are being sustained by immigration. This is most obvious on Bodie where it is connected. The fact that coyotes are still present on islands like Ocracoke and North Core, despite isolation and low densities, suggests either: occasional immigration events or low levels of reproduction that are enough to maintain very small populations in the short term, but probably not indefinitely without new arrivals. As a result of only having a global recruitment estimate, we can't separate these processes. But the pattern of persistence on remote islands, despite low density and intermittent removals, implies that even rare immigration may play an outsized role in keeping them occupied.

On the Outer Banks, our results suggest that sustained coyote control is most likely to succeed on the smaller, more isolated islands where immigration is rare, but might fail even there. On larger islands or those connected to the mainland, our results indicate that coyote persistence despite removal is likely due to continued dispersal and demographic compensation. If coyote populations can persist under sustained removal even in isolated island systems, this highlights the futility of expecting long-term population reduction from lethal control in highly connected mainland landscapes.

Movement

Immigration through movement is likely a critical process that allows coyotes to persist on the Outer Banks. More broadly, movement is central to how coyotes and other generalist mesopredators expand into new regions, with even rare dispersal events sustaining populations and enabling colonization of novel habitats.

Our scat collection documented two movements, by the same animal, from North Core Banks to Ocracoke, and then back again. This is especially noteworthy because these are the two most geographically isolated islands in the system, separated by the second widest inlet in the system (~3.2 km wide), with Ocracoke being the last island to be colonized by coyotes in 2023. These two movements correspond to a rough probability of 1.1% across 185 genetic recapture events (excluding singletons), or 2.9% of the 34 recaptured coyotes. Our model corroborates this finding by estimating high within-site fidelity and generally small, nonzero movement probabilities between neighboring islands. Further highlighting this connectivity, in related GPS tracking work Sossover et al (in prep) found one of five collared animals moving between islands, with a female crossing between Shackleford Banks, Morgan Island, and South Core Banks on 54 occasions. These islands are separated by narrower inlets than North Core and Ocracoke, but this reinforces that movement among these barrier islands though infrequent does occur.

While recent work has documented a single one-way inter-island movement by a coyote (800m; Spicer & Leberg, 2025), our study provides the first instance of bidirectional movements between islands and confirms the longest recorded inter-island crossing (~3.2km). These findings demonstrate connectivity within a barrier island system. Previous research has shown coyotes dispersing across aquatic or marine barriers in other contexts, including swimming across rivers and lakes as well as crossing water bodies via man-made bridges (Way, 2002, 2009; Hinton et al., 2012, 2015). The presence of coyotes on isolated barrier islands is itself proof they can traverse significant geographic barriers such as sounds and inlets. Therefore, if management ever happens to eradicate them from an island, they would likely recolonize within a few years. Furthermore, movement provides a method for demographic rescue and increasing genetic diversity for isolated islands experiencing lethal removal.

Management Implications

When an invasive predator first arrives on isolated islands the first obvious management action is to eradicate them. Our findings that coyote populations persist at densities similar to or only slightly lower than adjacent mainland populations after 16 years of removals (n = 173) indicates eradication is difficult or impossible. While reproduction is likely the primary driver of population persistence across all islands, immigration also occurs, and is presumably higher on the mainland-connected northern islands (Bodie, Pea, and Hatteras), making eradication especially difficult there. 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 data suggest it would be a short-lived success as coyotes would recolonize from adjacent islands.

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 reproduction and/or immigration. On the smaller, more isolated islands like North Core and Ocracoke, where abundance estimates are low, complete removal may still be feasible, at least temporarily, before recolonization/reimmigration occurs. Our results finding little or no reduction in coyote abundance after removal is consistent with other mainland studies, but is noteworthy that it is also occurring on this isolated island chain where immigration is more difficult. 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 reduce 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 with campers, Aug 14th, 2024).

Given the well documented ability of coyotes to compensate to removal, managers aiming to reduce nest predations might want to consider alternative strategies designed to alter coyote behavior, especially on the larger or more connected islands. These could include deterrents like fladry during sensitive periods or diversionary feeding during nesting season to reduce predation (Bamber et al., 2024). A recent pilot fladry study on the Outer Banks (Sossover et al., Movement Chapter) showed promise as a targeted seasonal deterrent, suggesting that it could help keep coyotes out of protected areas used by nesting shorebirds and sea turtles. Overall, our results indicate that sustained suppression or eradication of coyotes on the Outer Banks is unlikely due to recolonization and compensatory dynamics. If the management objective is to reduce impacts on vulnerable nesting species, incorporating behavior-focused tools alongside selective removal may provide more consistent protection than removal alone.

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CHAPTER 2

MOVEMENT AND BEHAVIOR OF COYOTES ON BARRIER ISLANDS

ABSTRACT

Invasive species, particularly predators, can have catastrophic effects on native wildlife and have been responsible for the decline and extinction of numerous island species. Coyotes (*Canis latrans*) have recently colonized North Carolina's barrier islands known as the Outer Banks, where they are depredating protected shore-nesting birds and sea turtles, creating an urgent management concern. Although coyote behavior and ecology is well studied on mainland systems, little is known about how they use coastal island systems, making management more difficult. To address these knowledge gaps, we used high-resolution, accelerometer-informed GPS collars to describe coyote movement and behavior. Five coyotes were monitored for 1,698 coyote-days (~176,000 GPS fixes). Coyotes were strongly nocturnal year-round, with nighttime activity (VeDBA) 16.4% higher (95% CI: 10.6 – 22.2%) during April – September which coincides with peak human visitation and nesting season for shorebirds and sea turtles compared to the off-season (October – March). Mean daily distance traveled was 14.7 ± 9.4 km (maximum 54.6 km). Daytime resting hotspots clustered in maritime forest, while nighttime foraging concentrated on beaches. Seasonal space use (95% AKDE) ranged 7.86 – 46.91km^2 and generally scaled to island geometry with home ranges often encompassing the full extent of the island they inhabited. Core areas (50% AKDE) averaged 13.99 ±11.08 km^2 (range 2.36 – 35.74 km^2) after clipping to land. Most individuals stayed on a single island across all seasons, but one female completed 54 inter-island crossings linking three islands and notably spent 62% of her time on a 0.13km^2 islet known as Morgan Island. Use-availability models (n = 3) showed coyotes concentrated on beaches and after controlling for that affinity, we did not detect a statistically significant, consistent increase in sea turtle nest site selection; only 1/3 increased, suggesting a subset of coyotes may be disproportionately responsible for nest depredations. To reduce incursions into a protected area with shorebird and sea turtle nests we installed a fladry line spanning the entire width of South Core Banks from the ocean to the sound. During deployment, northbound crossing into a protected nesting area fell by ~66% at the group level and ~83% for the primary user of that zone pre-deployment. Together, we provide the first description of island coyote movement and behavior on the Outer Banks, which likely can be helpful for managing

and understanding coyotes on other island systems, and demonstrate that fladry can effectively reduce predator access to sensitive nesting sites.

INTRODUCTION

Invasive species, particularly predators, can have catastrophic effects on native wildlife and have been responsible for the decline and extinction of numerous island species (Courchamp et al., 2003). Eradication programs are often implemented to mitigate these problems, and have been particularly successful on islands where populations of invasive species can be more effectively controlled due to geographic isolation (Veitch & Clout, 2002). The most successful programs have completely eradicated invasive species from island ecosystems, restoring balance to native ecosystems (Jones et al., 2016; Howald et al., 2007; Nogales et al., 2004). However, these eradication efforts are costly, logistically challenging, and require insights into the species' behavior and 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 adaptability has facilitated their range expansion across most of the United States following the widespread extirpation of larger carnivores, as well as forest loss and fragmentation (Prugh et al., 2009; Hody & Kays, 2018). Coyotes entering new areas as part of range expansion, or reaching higher abundance due to extirpated predators (i.e. mesopredator release (Prugh et al., 2009)), have been implicated in the declines of numerous threatened and endangered species, with the potential to reconfigure entire community structure (Ripple et al., 2013; Chow-Fraser et al., 2022). However, efforts to manage coyote populations through lethal removal are complicated by compensatory strategies (Knowlton et al., 1999) of immigration of new animals to areas experiencing removal (Kierepka et al., 2017), and increasing their reproductive output and breeding younger when faced with removal (Kilgo et al., 2017). Given these challenges, non-lethal management strategies are being explored to manage coyote behavior, rather than population size, and include sprinkler systems, hazing, and fladry (McLellan & Walker, 2021; Young et al., 2019; Young et al., 2019).

Coyotes have most recently colonized the coastal ecosystems along the eastern coast of the United States where they are the new apex predator (Crosby et al., 2024). This expansion appears to elevate predation pressure on ground-nesting shorebirds and sea turtles; while regional-scale impacts remain unresolved, site-level studies have documented threats to nesting outcomes (Lovemore et al., 2020; DeFelice et al., 2024). They have become established on the barrier islands of the Outer Banks of North Carolina within the last two decades, presumably by a mix of swimming across inlets and sounds as well as crossing man-made bridges where they exist. Since their arrival to these barrier islands they have been documented predating nests of birds and sea turtles (Altman & Stephenson, 2023; Altman, 2023; Doshkov et al., 2018; Thompson et al., 2018) and are recognized as the primary cause of sea turtle nest failures across Cape Hatteras and Cape Lookout National Seashores (Altman, 2023; Thompson et al., 2018). To combat this predation, coyote removals have been conducted annually on these barrier islands (CAHA since 2009, CALO since 2017, and PINWR since 2023). Although 173 coyotes have been removed across the Outer Banks (Personal Communications w/CAHA Aug 28th, 2025; CALO Aug 18th, 2025; & PINWR Aug 2nd, 2025 Staff) they remain a problem for park managers.

Although coyote behavior and ecology is well studied on mainland systems, little is known about how they use coastal systems, making management more difficult. In particular, local information about how they use the habitats would help managers target them for removal, or implement fine-scale management of their behavior around nesting sites. For example, fladry, a suspended line of evenly spaced flags, creates a novel visual and auditory barrier that can deter predators, including coyotes, from sensitive areas like nesting sites (Young, Draper, et al., 2019). Originally developed to protect livestock from wolves, it has also been deployed by state managers in coastal settings to protect shore-nesting birds and turtles with promising early results and plans for continued trials (Davis & Heiser, 2024). Because animals eventually habituate, effectiveness is short-lived (generally ≤60 days), making fladry best suited for targeted, breeding-season deployments around sensitive nesting sites (Young, Draper, et al., 2019; Windell et al., 2022). Additionally, local data about movement between islands would help inform the risk of recolonization after eradication. A recent Gulf barrier-island coyote study documented one case of inter-island movement but used coarse (1-4h) GPS fix intervals and covered only November-April (Spicer & Leberg, 2025). Accordingly, higher-resolution, year-round tracking data across the breeding and dispersal seasons is needed to reveal short-duration behaviors and test individual responses to non-lethal management strategies.

To address these knowledge gaps we investigated coyote movement and behavior using high-resolution tracking collars to describe movement patterns, activity hotspots, and explore fladry as non-lethal management strategy to protect shore-nesting birds and sea turtles. These insights hope to support more targeted and effective management interventions for this persistent invasive predator.

METHODS

Study Area

The Outer Banks are a chain of barrier islands along the coast of North Carolina comprising Cape Hatteras (CAHA) and Cape Lookout (CALO) National Seashore as well as Pea Island National Wildlife Refuge. This study was conducted on CALO, the southern portion of North Carolina's Outer Banks. CALO is a ~90km stretch of barrier islands between Ocracoke Inlet to the north and Beaufort Inlet to the south. The seashore consists of three primary National Park Service managed islands: Shackleford Banks, South Core Banks, and North Core Banks as well as several smaller islands such as Shark Island, Sheep Island, Morgan Island, Whitehurst Island, and Portsmouth Island.

Our study focused specifically on Shackleford Banks and South Core Banks, two large, undeveloped, and adjacent barrier islands that serve as critical habitat for shore nesting birds and sea turtles (Figure 1). Shackleford Banks (SB) is approximately 13km long and 8km^2, while South Core Banks (SCB) is about 37km in length and 38km^2. These two larger islands are separated from each other by Barden Inlet, a 800m wide channel, and are isolated from the mainland by shallow bodies of water. Back Sound (1 - 2m deep) is north of SB and separates it from the mainland, whereas SCB has Core Sound (2 - 3m deep) to the west. All islands in this system are only accessible by boat.

Both islands can be described as a mix of open beaches, dune systems, grasslands, salt marshes, maritime forests, and hammocks (NPS Cape Lookout National Seashore, 2023c). SB has the most extensive contiguous maritime forest within CALO (NPS Cape Lookout National Seashore, 2024). In contrast, SCB contains a patchy, planted forest near its southern end, with a narrow band of forest approximately 50 - 200m wide, extending northward along most of the island's length on the sound side. These islands support a range of ground-nesting birds such as the American Oystercatcher (*Haematopus palliatus*) and Piping Plovers (*Charadrius melodus*) as well as threatened and endangered sea turtles such as Loggerheads (*Carretta caretta*) and Kemp's ridley (*Lepidochelys kempii*). In addition to these species, the islands support a diverse mammal, reptile, amphibian, and bird community (NPS Cape Lookout National Seashore, 2023a, 2023b, 2023d, 2023e).

CALO geographic isolation once protected these breeding species from mainland predators, however, coyotes were first confirmed on NCB in November 2013, SCB in February 2014 and on SB in December 2014 (Personal Communication, NPS, Jon Altman, Aug 18th 2025). Coyotes are presumed to have reached these islands by swimming across shallow inlets and sounds, potentially using sandbars exposed during low tide. Since they colonized the seashore, park managers have documented increased predation on bird and sea turtle nests leading to declines in nesting success. Annual NPS reports note that coyotes accounted for the majority of turtle nest losses and were identified as the primary predator of shorebird nests (Altman, 2023; Altman & Stephenson, 2023). This predation pressure is so detrimental on SB, American Oystercatchers appear to have abandoned the island, either by not returning or returning but not nesting (Personal Communication, NPS, Jon Altman, 2024).

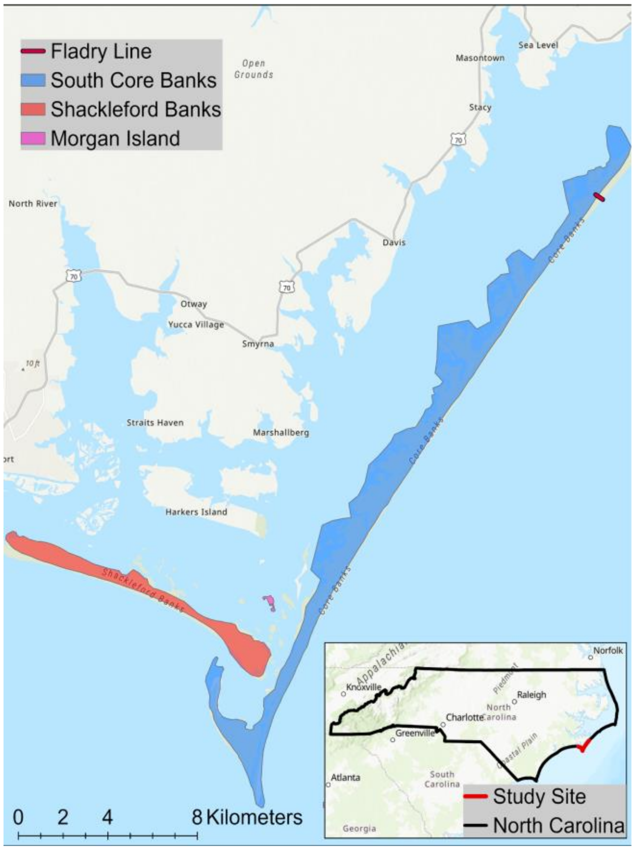


Figure 1. Study area in Cape Lookout National Seashore, North Carolina. South Core Banks is shown in blue, Shackleford Banks in red, and Morgan Island in pink. The short red line marks the location of the fladry barrier installed on South Core Banks in 2024. The inset locates the study system on the North Carolina coastline. This map shows the island's layout, fladry location, and highlights that these islands are adjacent to one another.

Animal Capture

CALO began contracting USDA-APHIS-Wildlife Services annually shortly after coyotes arrived to the park in 2013 to conduct predator removal across its islands, targeting coyotes as well as raccoons (*Procyon lotor*), opossums (*Didelphis virginiana*), feral cats (*Felis catus*), mink (*Neovison vison*), and nutria (*Myocastor coypus*). For our study we collaborated with the National Park Service and 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 APHIS Wildlife Services, North Carolina Program, 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 APHIS Wildlife Services, North Carolina Program, 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. During this trapping session, 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 275g, 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 score]) and would revert to taking a GPS fix every five hours during periods of inactivity (after three consecutive readings below our threshold). This dynamic setup allowed us to conserve battery during periods of inactivity while getting fine-scale spatial data once the animals were active.

We used Yagi antennas to periodically locate the coyotes, approach within 100-200m, 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 telemetry 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 (Max Planck Institute of Animal Behavior, 2024).

Fladry Experiment

We installed a fladry barrier near the northern terminus of South Core Banks (34.8141441, -76.3605699) to protect a large National Park Service (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 its efficacy, so we spaced our flags only 6-8 inches apart and 18-24 inches long. The line was mounted on posts set in sand that allows the flags to lay on the ground or 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.

We used tracking data to assess whether coyotes reduced their use of the north side of South Core Banks following fladry deployment. Each GPS fix in their dataset was 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.

Data Analysis

Animal Activity

Coyotes are known to be more active nocturnally in areas with high human activity (Soccorsi & 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.

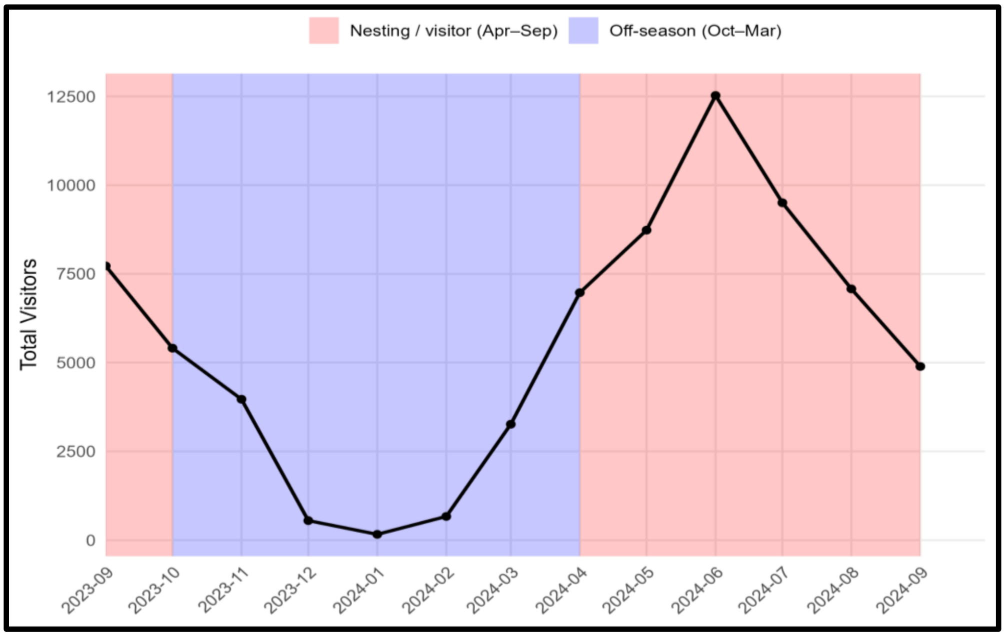


Figure 2. Monthly ferry visitation records to South Core and Shackleford Banks from Sep 2023 – Sep 2024. Total monthly visitors = Great Island Ferry (vehicles and walk ons to South Core Banks) + Shackleford Banks West End ferry passengers. Background bands mark Apr – Sep (nesting/visitor season) and Oct – Mar (off-season). Data was obtained from Cape Lookout National Seashore visitation records.

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:

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

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

We summarized each burst by calculating the mean VeDBA across all samples, producing a single activity value per 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). All data processing and VeDBA calculations were conducted in R. We combined the results from all our individuals into a single dataset, which included metadata for timestamp, individual ID, and burst characteristics (e.g., number of samples, sampling frequency, and duration). We used this single dataset to analyze patterns of activity.

Distance

We measured daily movement as the sum of straight-line distances 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 & Kays, 2019), northern Washington, WA (Prugh et al., 2023), and Fishlake NF, UT (Mahoney, 2017).

Home Ranges and 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., 2023/2024)*, Filter/Annotate Day or Night* (Kölzsch, 2021/2024), *Multiple Animal Cluster Detection* (Kölzsch & Kendall, 2021/2024), and *WriteCSV* (Kölzsch & Scharf, 2020/2024). Resting sites were identified by classifying daytime locations (sunrise to sunset, with +30 min after sunrise and -30 min before sunset as adaptation periods) and applying buffer clustering with overlap union. Settings included: a 50m cluster radius, a minimum of three GPS fixes, a minimum duration of 3h, and a maximum gap of 1d between fixes. Feeding clusters were identified from nighttime locations (sunset to sunrise, with -30 min after sunrise and +30 min before sunset as adaptation periods) using the same clustering method as before but adjusted for shorter trips: a 50m cluster radius, a minimum of five GPS fixes, a minimum duration of 15 mins, and a maximum gap of 30 mins.

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, 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 individual’s' GPS data to include only active movement (i.e. <5min 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 being the binary indicates of whether the point fell within 50m 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; Pebesma, 2018)). 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 tide, 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 (~12.42h). We then tested whether the observed proportion exceeded this null expectation using a one-sided binomial test and report Wilson 95% confidence intervals.

RESULTS

Tracking Data

The five collars attempted total of 175,940 GPS fixes (Table 1) and were successful at a rate >99% providing 26,957 - 38,979 fixes per animal, and 43,447 - 137,309 accelerometer readings (Table 2). Deployment durations varied by individual, with data retrieval ending due to battery depletion or USDA removal of the collared coyote.

Table 1. Performance of five accelerometer-informed GPS collars deployed on coyotes on Cape Lookout National Seashore. Individual deployment windows varied but span September 2023 – May 2025. Columns report 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. Collars achieved >99% fix success with long monitoring windows.

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

Fladry

Our camera traps only recorded one instance of a coyote approaching the fladry line. The individual approached the barrier at 1:10am on July 3rd, 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, the three South Core Banks residents, northbound crossings occurred at a rate of 0.11 events per 24h 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 indicates a substantial albeit 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 2).

At the individual level, patterns diverged: crossing rates (events/24 h) into the island's north section were low for Ed, Martha lacked sufficient data, 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.

Table 2. Northbound crossing rates for three GPS-collared resident coyotes at the South Core Banks fladry barrier, Cape Lookout National Seashore. The fladry line spanned the full width of the island from the ocean-side beach to the sound-side marsh. Rates were calculated by classifying each GPS fix as north or south of the line, counting south-to-north transitions between successive fixes, dividing by monitored hours in each period (pre-deployment, the deployment from June 17 to August 16, 2024, and post-deployment), and scaling to events per 24 hours. Rahzar showed a clear reduction during deployment, Ed remained low with little change, and Martha lacked a pre-deployment baseline (see pre-period monitoring hours) and increased after removal. During deployment, each coyote bypassed the fladry barrier once by swimming through the sound-side marsh around the line's western terminus rather than passing under or over the flags.

Animal	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
	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

Activity

Coyotes exhibited a consistent nocturnal activity pattern across all seasons. The actogram for Martha (Figure 3) 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 4) that 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.

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 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). This result 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.

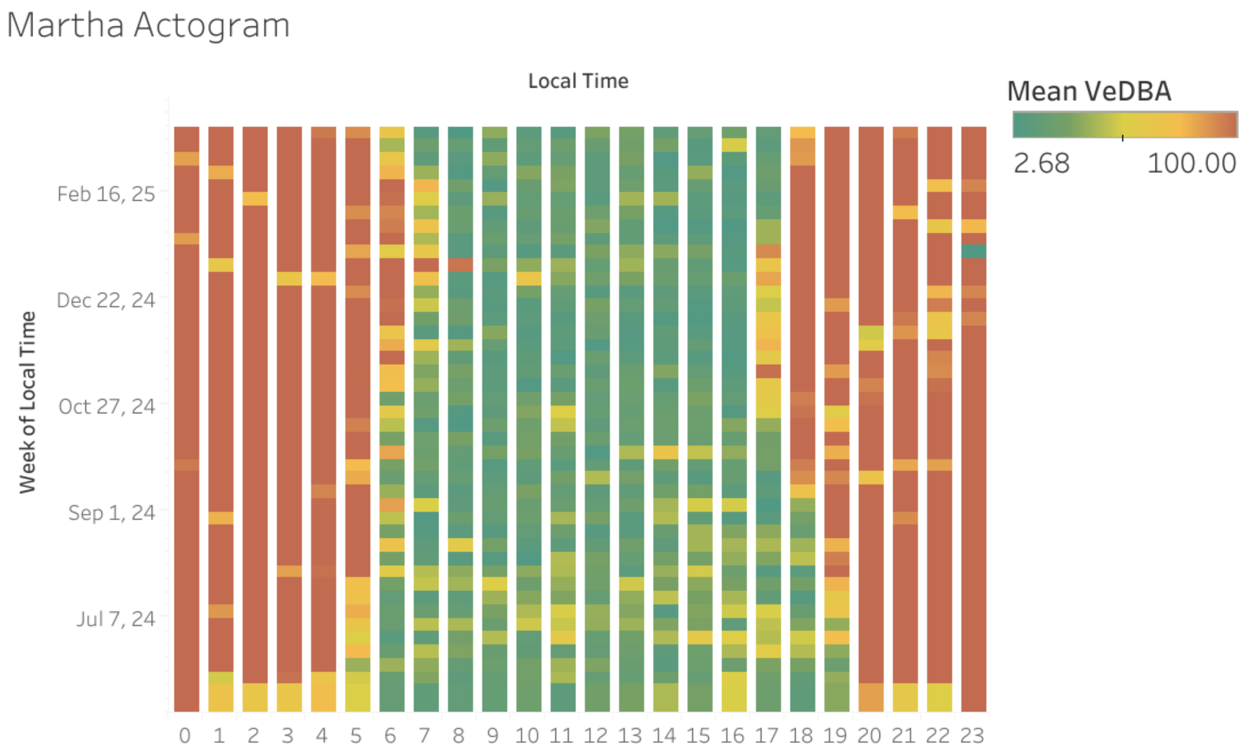


Figure 3. Weekly actogram of hourly activity measured in VeDBA for the resident female coyote on South Core Banks “Martha” from June 2024 – March 2025. VeDBA values are aggregated to hourly means from tri-axial accelerometer mounted on tracking collar and then averaged per week. Warmer colors indicate higher activity while greener colors indicate lower activity. Martha exhibited a strongly nocturnal activity pattern across seasons, with highest activity between ~20:00 - 05:00 and low daytime activity. The low-level activity during the first few days after capture likely reflects post-capture recovery. Overall, this pattern shows activity is strongly nocturnal year-round and we saw this for all five collared coyotes in our study.

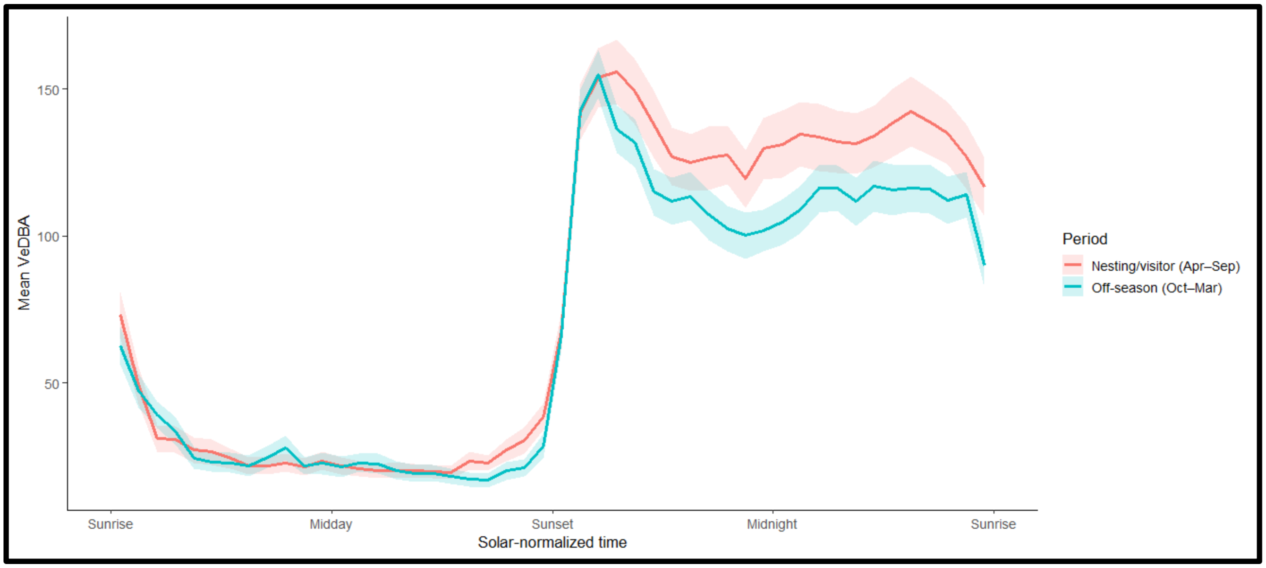


Figure 4. Solar-normalized mean VeDBA (±95% CI as shaded bands) for five collared coyotes, on Cape Lookout barrier islands, pooled by season: Nesting/visitor (Apr – Sep; bird and sea turtles nesting plus peak human visitation) vs Off-season (Oct – Mar). VeDBA was derived from tri-axial accelerometers on GPS collars, aggregated to hourly means by day and averaged across all individuals. Solar-normalization aligns sunrise and sunset across dates. Curves show a sharp rise at sunset, sustained nocturnal activity, and low daytime activity. The nesting/visitor curve is higher just before and after sunset compared to the off-season. Overall nighttime mean VeDBA (sunset to sunrise) was ~16% higher in the nesting/visitor season.

Home Ranges and Core Areas

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 (See Figure 5).

Figure 5. Example of raw (unclipped) versus land-constrained (clipped) 50% AKDE utilization distribution (UD) for an adult male coyote "Rahzar" in Winter on South Core Banks. The red polygon represents the original AKDE contour, which extends ~2km offshore into the Atlantic Ocean and overlaps Shackleford Banks. Rahzar did use these areas. This overextension reflects AKDEs' assumption of continuous open space in all directions. The yellow polygon shows the same contour clipped to the island boundary, restricting the estimate to the island Rahzar occupied and better representing his space-use. Clipping the AKDE contours allowed us to correct for inflated area estimates.

Since most coyotes did not 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 (Figs. 6-8; Table 3) show clear individual and season-dependent variation.

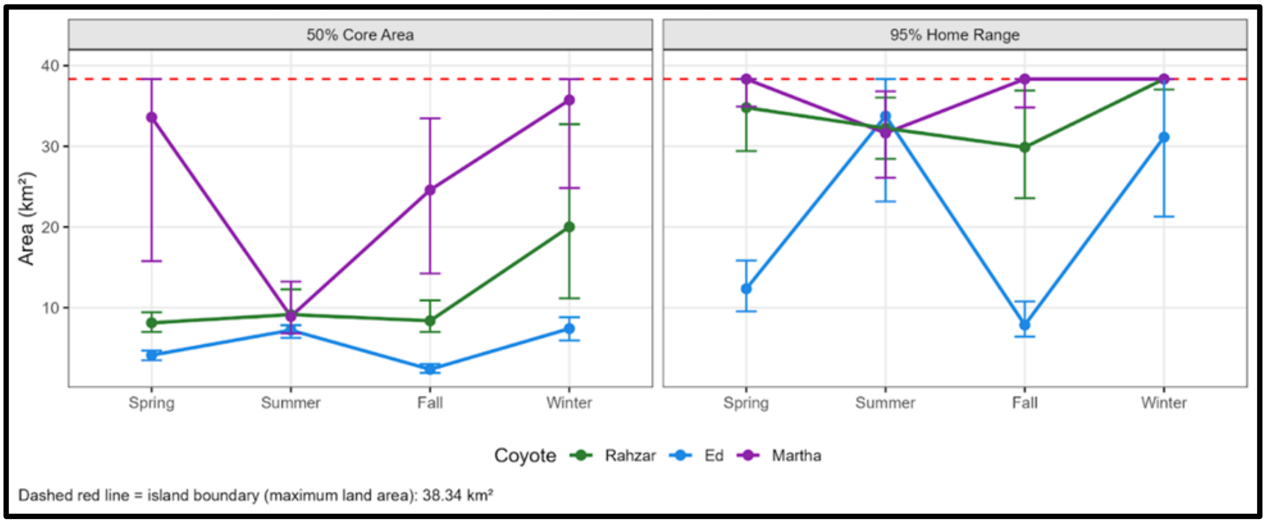


Figure 6. Seasonal AKDE core areas (50% UD) and home ranges (95% UD) for three resident coyotes on South Core Banks, Cape Lookout National Seashore. Data is from accelerometer informed GPS collars and spans Sep 2023 – Mar 2025. The two panels plot seasonal estimates for Ed (male, blue), Rahzar (male, green), and Martha (female, purple). Points are AKDE estimates with error bars showing ±95% confidence intervals from the model. Areas were clipped to the island boundary, the red dashed line marks the island's maximum land area (38.34 km^2). Deployment windows differed by individual with Ed from Sep 2023 – Sep 2024, Rahzar from Oct 2023 – Sep 2024, and Martha from May 2024 – Mar 2025. Ed and Rahzar maintained relatively stable core areas across seasons while Martha's core area were consistently larger. Core areas were generally smaller in summer and largest in winter. 95% UD often approached the island-size ceiling.

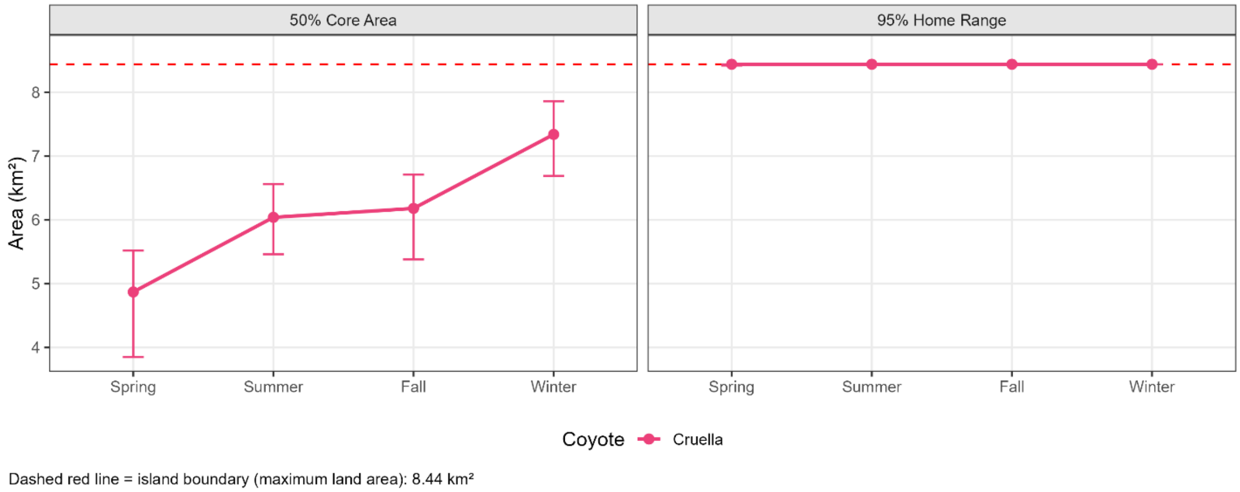


Figure 7. Seasonal AKDE core area (50% UD) and home ranges (95% UD) for “Cruella” an adult female resident coyote on Shackleford Banks, Cape Lookout National Seashore. Data is from accelerometer informed GPS collars and spans Apr 2024 – Feb 2025. The two panels plot seasonal estimates with ±95% Confidence intervals show as error bars. Areas were clipped to the island boundary; the red dashed line marks the island’s maximum land area (8.44 km^2). Cruella’s core area increased consistently each season from spring to winter while her home range equaled the island-size ceiling in all seasons.

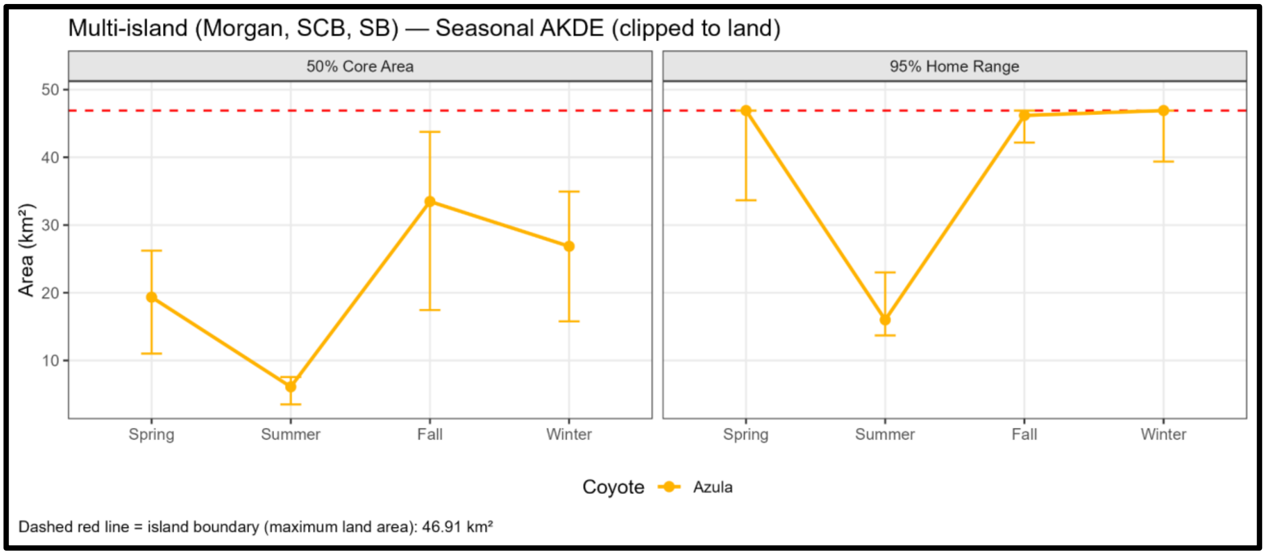


Figure 8. Seasonal AKDE core areas (50% UD) and home ranges (95% UD) for “Azula,” a multi-island traveling female coyote using Morgan Island, South Core Banks, and Shackleford Banks, Cape Lookout National Seashore. Data are from an accelerometer-informed GPS collars and span Apr 2024 – May 2025. The two panels plot seasonal estimates with point being AKDE estimates with error bars showing ±95% confidence intervals from the model. Areas were clipped to the combined land size of the three islands she used. The red dashed line marks the maximum land area available across those islands (46.91 km^2). Azula’s core area varied strongly by season with it being smallest in summer and largest in fall while her 95% UD reached the land-area ceiling in every season except summer.

Table 3. Autocorrelated-kernel density estimates of core area (50% utilization distribution) 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 (km²)**	**UD50 (km²) [95% CI]**	**UD95 (km²) [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]

Table 3 (continued).

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. 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 km² in fall). All island-season datasets were best fit by anisotropic Ornstein-Uhlenbeck foraging (OUF) movement models (Table 3).

Distance Moved

Across 1,698 coyote-days of GPS data, 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 4).

Seasonally (Figure 9), patterns were consistent for the males and split among the females. Rahzar and Ed traveled the farthest, on average in summer and lowest in fall. Among the females, Martha and Azula were highest in the winter, while Cruella peaked in summer. The longest single-day distance moved (54.62km, 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 (52.80km, 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 4) there was no difference between the average value for males (14.82 +- 8.51 km/day) and females (14.63 +- 9.93 km/day).

Using the ctmm framework, re-estimated means were Albany, NY 21.36 ± 3.32 km/day (n = 2), northern Washington 16.78 ± 4.38 km/day (n = 14), and Fishlake UT 18.71 ± 11.38 km/day (n = 6). Our overall mean (14.7 ± 9.40 km/day) falls within this ctmm-derived range, albeit towards the lower end.

Table 4. Daily movement distance by individual (mean, minimum, maximum; km/day) Straight-line daily distance (km/day) summarized across the entire study period for each collared coyote: mean, minimum, and maximum daily totals. We calculated daily distance as the sum of straight line steps between successive GPS fixes within each calendar day, computed in km, therefore, these values represent minimum path lengths. Individuals showed substantial variability: Cruella and Rahzar had the highest mean daily distances, while Azula had the lowest mean. Rahzar recorded the largest single-day total (54.62 km), upon inspection was a full-length traverse of South Core Banks from the southern end to the northern end and back.

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

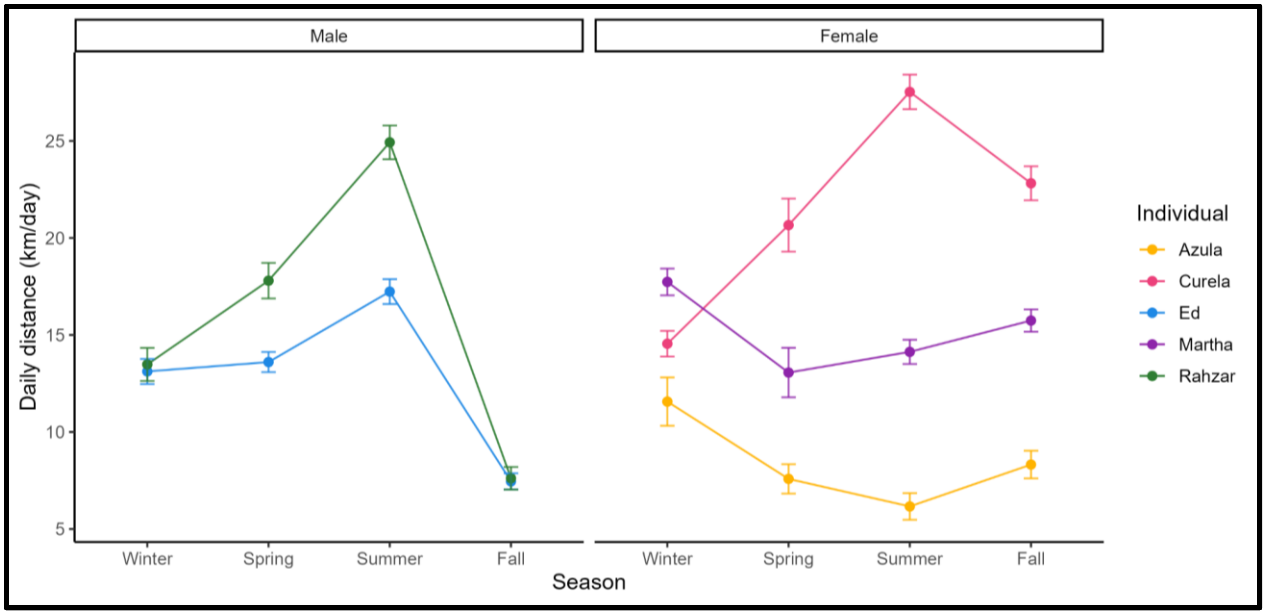
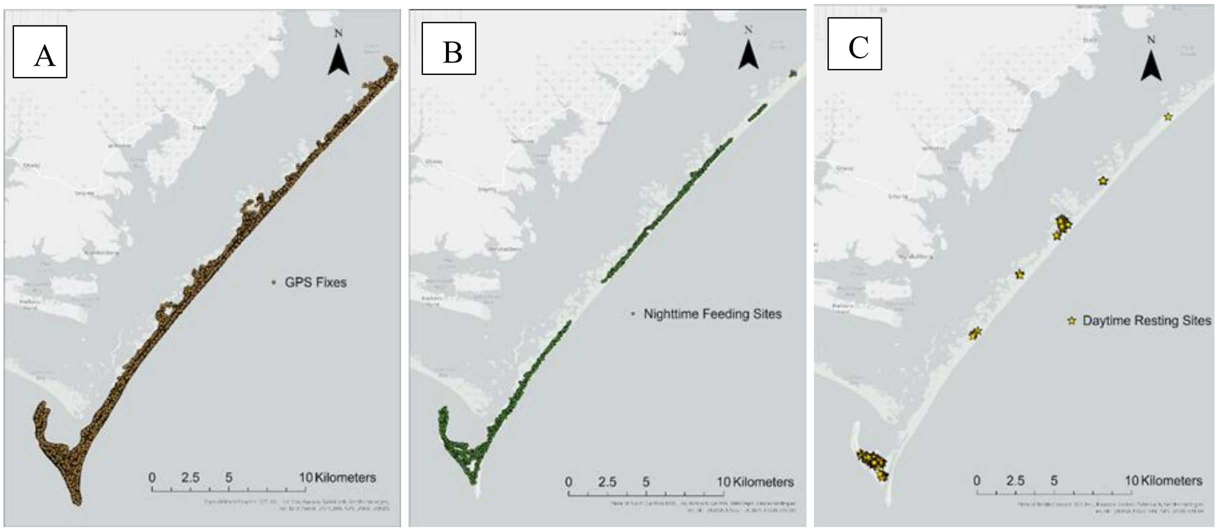


Figure 9. Seasonal mean daily straight-line distance (km/day ± standard error) by individual, faceted by sex, for five GPS-collared coyotes on Cape Lookout barrier islands. Individual deployment window lengths differ but range from Sep 2023 – May 2025. For each coyote, daily distance is the sum of straight-line (Euclidean) step lengths between successive GPS fixes within a calendar day. Lines connect seasonal means; points are means and error bars are ± 1 standard error computed from the distribution of daily distances within each individual x season. Males are in the left panel with Ed in blue and Rahzar in green showing summer peaks and fall lows. Females are in the right panel with Cruella shown in pink, Azula in yellow, and Martha in purple. Martha and Azula's mean daily distance are highest in winter, low in spring and summer, then rise again in the fall. Cruella, in contrast, peaks in summer and remains elevated into fall, aligning more with the pattern we see in the males then the other females.

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 10a). 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 10b). 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 10c). 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 10. Spatial distribution of GPS fixes, nighttime feeding sites, and daytime resting sites for South Core Banks GPS-collared resident male “Rahzar.” Three panels summarize one male resident’s space use on South Core Banks. (a) All GPS fixes (brown points) trace the entire island. (b) Nighttime feeding sites (green points; March 1-30, 2024) align primarily along the ocean beach, forming a near continuous strand of foraging locations. (c) Daytime resting sites (yellow points; March 1 - May 30 2024) occur across South Core Banks but show clear clustering in Cape Lookout Historic District at the southern top and a second cluster just south of Great Island Cabin Camp. These analyses were conducted using the MoveApps platform. Together, these maps illustrate the typical pattern we observed for our resident coyotes where their GPS fixes ranged broadly, fed mostly on the ocean side, and slept across the island with some clustering in particular area.



Coyote Space Use Before and During Turtle Nesting Seasons

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 rather this varied before and during nesting season. Across our three individuals, the combined interactive model (Model C: used~ z_dist_turtle x period + in_beach50 x 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 308m (pre-nesting season) to 377m (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 beach, but don't consistently spend more time near active turtle nests, once beach affinity is accounted for.

Island-Island Movement

We documented 54 inter-island crossings from one individual, Azula (Figure 11). Movements between Shackleford Banks (SB) and Morgan Island (MI) accounted for 41/54 (76%) of all crossings: SB to MI (n = 24; 44%) and MI to SB (n = 17; 31%). The remaining crossings connected MI to South Core Banks (SCB; n = 7; 13%) and SCB to SB (n = 6; 11%). We did not observe a direct SB to SCB crossing; she always traveled to Morgan Island 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 enroute from SB to MI and Whitehurst Island when traveling from MI to SCB. When swimming from SCB to SB, she swam the gap directly, typically leaving from Power Squadron Spit and once crossing Barden Inlet (See Figure 11.). Crossing durations were generally short, 10s of minutes (See Table 5). SB to 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 to SB median duration was 33.0 min (18-48; mean 34.1) whereas MI to SCB was 30.0 min (24-48; mean 34.3). SCB to 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 11. Inter-island crossing routes from a GPS collared female coyote "Azula" at Cape Lookout National Seashore. Dashed arrow show on example of each observed route/direction (Shackleford Banks -> Morgan Island, Morgan Island -> Shackleford Banks, Morgan Island -> South Core Banks, and two South Core Banks -> Shackleford routes via Power Squadron Spit and Barden Inlet. Lines connect sequential GPS fixes with arrowheads indicating direction and labels mark the stepping stone islets she used (Blinds Hammock, Great Marsh Island, Sheep Island, Whitehurst Island) and the names of relevant geographic locations. Examples come from different dates and are meant to illustrate crossing pathways, rather than a single trip.

Table 5. Inter-island crossing routes and durations for a GPS-collared female coyote "Azula" across Cape Lookout National Seashore. Data spans April 2024 – May 2025. Crossings were identified by assigning each GPS fix to an island polygon and detecting Island A -> Ocean -> Island B sequences with duration being the interval from the last fix on the origin island to the first fix on the destination island. Table below summarizes route-specific frequency and travel time. Movements were dominated by the Shackleford – Morgan route with trips typically lasting tens of minutes.

Origin	Destination	# of 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

She split her time among MI (61.7%), SCB (20.9%), and SB (17.4%). Absolute counts and proportion of fixes and time are in Table 6, and month-by-month residence is shown in Fig 12. Bout structure reflects her island use patterns (See Table 7). On MI, bouts were frequent and long (n=24; median 8.06 days; max of ~33 days) with SB bouts being shorter (n=24; median 1.15 days; max ~ 16.6 days) while SCB had fewer but often much longer bouts (n=7; median of 7.96 days; max ~35.0 days). Her longest continuous stay on MI (~0.13km^2) is notable, occurring over 33 days between October 31 2024 and December 3 2024. Across Azula's 54 inter-island crossings, 50/54 (92.4%) of crossing occurred nocturnally (between 20:00-05:59 local time; See Figure 13). Further, 22/54 of them (40.7%) occurred within + or - 1 hour of low tide (95% CI: 28.7-54.0%). Our null expectation is po = 2/12.42 = 16.1%. The observed rate is ~2.5x greater than what we'd expect under a uniform-time departure.

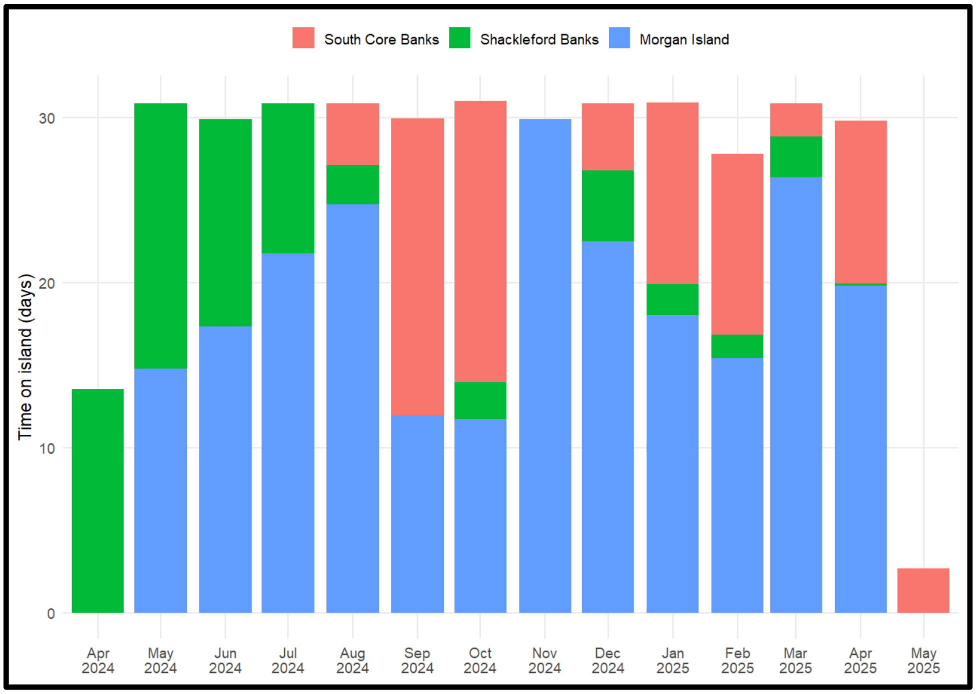


Figure 12. Monthly island residency for a GPS-collared female coyote “Azula” at Cape Lookout National Seashore from Apr 2024 to May 2025. Stacked bars show the number of days per calendar month spent on Morgan Island (blue), South Core Banks (red), and Shackleford Banks (green). Residency was assigned by intersecting GPS fixes with island polygons and summing time/days per island per month. Azula spent most of April and June 2024 on Shackleford. She then spent gradually more time on Morgan while still using SB through August. We first documented her visiting SCB in August and spent much of September and October there. She then returned to MI for all of November, then spent the remaining months mostly on MI with intermittent visits to SCB and occasional shorter visits to SB. This is notable as MI is only 0.13km^2. The record ends with her death in early May 2025.

Table 6. Island residency for a GPS-collared female coyote “Azula” at Cape Lookout National Seashore from April 2024 – May 2025. GPS fixes were assigned to island polygons and time was computed by summing intervals between successive fixes. The table reports GPS fix counts and proportions of fixes and days she spent on each island. Azula divided her time among the three islands but spent the most time on Morgan Island, with additional use of South Core Banks and Shackleford Banks.

Island	# of fixes	Prop of fixes	Time days	Prop of 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

Table 7. Amount of time a GPS-collared female coyote on Cape Lookout National Seashore spent on different islands. Data spans April 2024 – May 2025. Using the tracking data, we defined a bout as continuous residency on a single island (from the first fix after arrival to the last fix before departure) and summarized counts and durations for each island below. Visits to Morgan Island were frequent with moderate stay lengths (median ~8 d), with South Core Banks visits less frequent but similarly long (median ~8 d), and Shackleford Banks visits were frequent but generally short (median ~1.2 d).

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

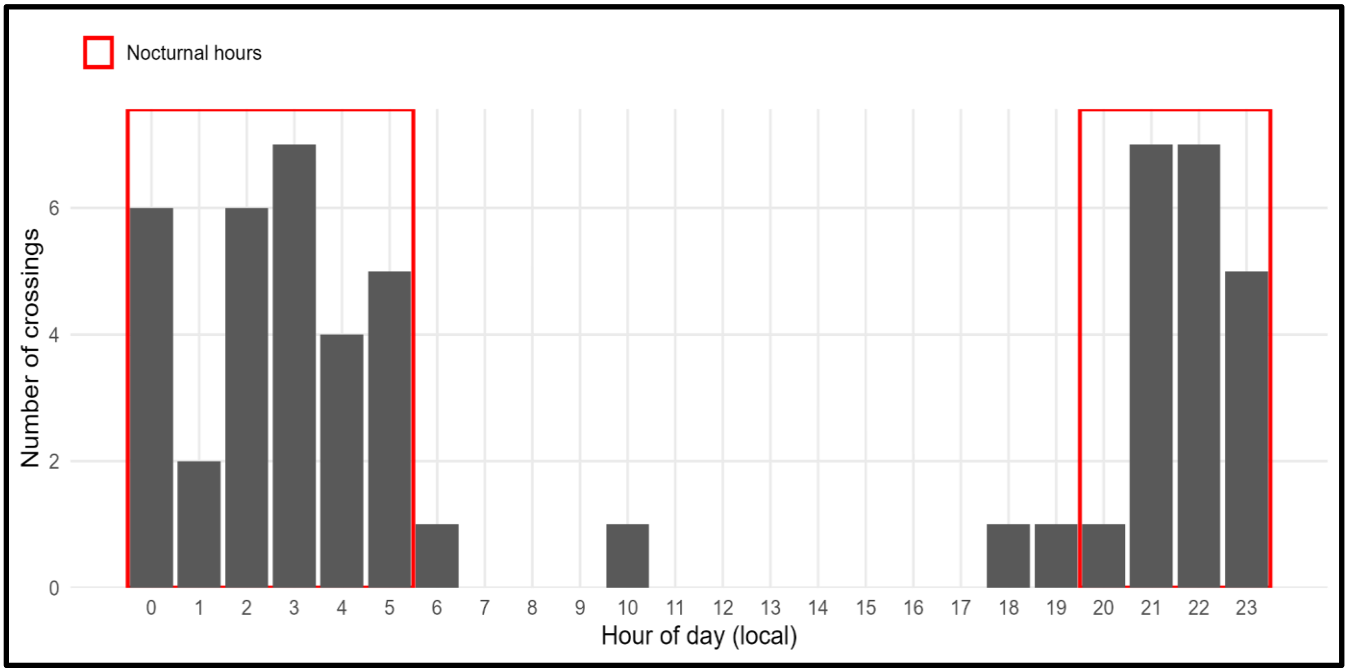


Figure 13. Departure times for inter-island crossings by a GPS-collared female coyote “Azula” at Cape Lookout National Seashore. Data spans April 2024 – May 2025. The histogram counts inter-island crossings by hour of local time (1-hour bins). Red boxes mark nocturnal hours (20:00 – 05:59). Crossings were identified from Island A -> Ocean -> Island B sequences from overlapping GPS fixes to island polygons and reviewing them sequentially. The departure time is the timestamp of the last fix on the origin island (start of the crossing). Most crossings occurred at night (50 of 54; 92.6%).

All other coyotes remained residents on the island we originally trapped and collared them on. Ed, our juvenile collared male, explored Shark Island once, a shifting sandbar off Cape Lookout Point that connects to South Core during low tide but is otherwise isolated (See Figure 14). 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 14. Single exploratory crossing by a GPS-collared male coyote “Ed” from South Core Banks to Shark Island on April 11th 2024. The main panel shows all of Ed’s GPS fixes for that day (n = 66). Between ~03:00 and 6:15 EDT he left South Core and crossed to Shark Island near the morning low tide (~04:22 EDT; NOAA CO-OPS Station 8656841), circled the island, and returned. Shark Island is a shifting sandbar off Cape Lookout Point that connects to South Core at very low tide making the distance between them shallow enough to walk across. The inlet zooms to Shark Island and shows his path here.

DISCUSSION

Our tracking data provides the first detailed movement of coyotes on the Barrier Islands of North Carolina, providing behavioral data relevant to reducing their threat to native nesting birds and turtles. Most animals remained on the same island during the study, covering nearly every square meter.

General Behavior of Island Coyotes

Island coyotes in CALO exhibit strong nocturnality, traveling along ocean-side beach (and roads where present), and resting in forested areas during the day. They also scale their home range to encompass the entirety of the islands in 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 (males = 14.8 km/day and females = 14.6km/day), and roughly similar to the average values we calculated for other datasets from mainland animals in NY, WA, and UT (16-21 km/day). Although our daily totals are based on straight-line step sums rather than movement models, the very short (3min) 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 (higher mean VeDBA from sunset to sunrise) than in the off-season, aligning with findings elsewhere that overall nocturnal activity increases with increasing levels of human recreation (Farmer & 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% UDs ranged from 8.44 to 46.91 km^2 (composite 26.89 ± 3.11 km^2), with pronounced individual variation in space use. 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% UD range falls within mainland estimates (13-47km^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 Azula's core area also overlapped the SCB residents and the Shackleford Banks 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, potentially as a result of denning/pup-rearing.

Nighttime feeding 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 result 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 (Newsome et al., 2015; Larson et al., 2020; Caspi et al., 2025). Although our sample size is low (n = 3), 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.

Movement Between Islands

We documented 54 inter-island crossings by one female (Azula) between Shackleford Banks, Morgan Island, and South Core Banks. Movements were predominately nocturnal (~92%) and often aligned with low tide (~41% within ±1h), when effective crossing distances are reduced due to exposed sandbars. Most crossings were short (tens of minutes) with movements between Shackleford Banks and Morgan Island comprising ~76% of crossing events. She regularly used small islets (e.g. Blinds Hammock, Great Marsh Island, Sheep Island, and Whitehurst Island) as stopovers. Residency bouts showed a remarkable week-long (up to ~33 days) occupancy on the tiny (0.13 km^2) Morgan Island and multi-day stays on Shackleford and South Core Banks (up to ~35 days) over our study period. She was presumably feeding on nesting birds at these sites, and must have been subsisting on rainwater, since there is no known source of ground water on Morgan Island. Thus, these movements were part of repeated, multi-island use over months.

Past work has documented the capacity of coyotes to cross water bodies via swimming (Spicer & Leberg, 2025) or utilizing man-made bridges (Sacks et al., 2006; Way, 2009). However, repeated inter-island commuting within a single barrier island system has not been documented. Our case of semi-routine, tide-aware, inter-island movements across a seemingly fragmented seascape of barrier islands, ephemeral sandbars, and shallow shoals shows the remarkable adaptability of coyotes. Azula effectively stitched together isolated islands into a single, stable, year-round territory supplementing her main base's (Morgan Island) tiny size with repeated multi-day residences on the larger islands. Presumably she did not breed as we did not observe denning behavior in April/May.

Fladry

Our fladry experiment across the northern section of SCB coincided with a ~66% reduction in northbound crossing at the group level and a notable dip for one coyote that frequently utilized 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. 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. If managers choose to use fladry during nesting season, then encircling nesting sites would be a more effective design. While our line design was effective in reducing coyote use, our GPS tracks show they were still able to access the other side by swimming around it on the sound side. Fladry can be incorporated as a part of the suite of tools available to coast-line 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.

Implications for Coyote Management

When coyotes first arrived in the Outer Banks and began to predate nests of sensitive species the first management response was to try to eradicate them. While this could be a solution if coyote colonization was very rare, new research is showing this is not the case. Our tracking results show that coyotes will readily explore newly formed islands and regularly swim between nearby islands. Even the most isolated islands separated by deep water can be crossed as other recent work documented a coyote swimming back and forth between Ocracoke Island and North Core Banks (Sossover et al in prep). In this interconnected landscape of barrier islands, shoals, and small islets, removal efforts on individual islands are likely offset by immigration from neighboring islands and occasional mainland dispersers, especially in the northern islands which are connected by bridges. Management by removal is further compounded by coyotes' evolved compensatory strategies which include increased reproduction under persecution (Knowlton et al., 1999), wide-ranging dispersal capacity (Harrison, 1992), and dietary flexibility (Jensen et al., 2022). Complete eradication from this barrier island system is therefore unlikely, and coyote removal may actually work against management goals by inducing higher coyote abundance due to accelerated immigration (Moll et al., 2025). However, some level of coyote trapping might be useful to prevent coyotes from becoming habituated to people and becoming a threat to people and pets (Timm et al., 2004; White & Gehrt, 2009). In this case, our movement data does reveal potential opportunities for more strategic trap placement. Daytime resting sites were utilized by multiple individuals across time, these locations could serve as strategic long-term trapping sites. Management efforts that incorporate a focus on curbing unwanted coyote behavior may be more successful than removals alone. Our preliminary results with fladry suggest that it could be useful for temporarily keeping coyotes out of sensitive nesting areas. Ultimately, the challenge posed by coyotes on the barrier islands is not much different than the mainland, this is still a connected landscape, and success depends less on eradication and more on shaping behavior to reduce conflict.

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