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Examining Internesting Habitat Use of Northwest Atlantic Leatherback Sea Turtles (*Dermochelys coriacea*)

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**EXAMINING INTERESTING HABITAT USE OF NORTHWEST ATLANTIC
LEATHERBACK SEA TURTLES (*DERMOCHELYS CORIACEA*)**

A Thesis

Presented to

The Faculty of Moss Landing Marine Laboratories

San José State University

California State University Monterey Bay

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

Christina I. Mauney

Summer 2024

CALIFORNIA STATE UNIVERSITY MONTEREY BAY

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EXAMINING INTERESTING HABITAT USE OF NORTHWEST ATLANTIC

LEATHERBACK SEA TURTLES (*DERMOCHELYS CORIACEA*)

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ABSTRACT

Examining Internesting Habitat Use of Northwest Atlantic Leatherback Sea Turtles (*Dermochelys coriacea*)

by

Christina I. Mauney

Master of Science in Marine Science
California State University Monterey Bay, 2024

Understanding the spatial ecology of highly migratory marine animals is essential for effective conservation strategies, particularly in the face of climate change and increasing anthropogenic pressures. This study investigates the nesting characteristics, habitat use, and behavior of leatherback sea turtles (*Dermochelys coriacea*) in the Northwest Atlantic population nesting at Sandy Point National Wildlife Refuge (SPNWR) in St. Croix, US Virgin Islands.

Ten female leatherbacks were studied during the internesting interval of the 2020 and 2021 nesting seasons. The study's objectives were to examine leatherback nesting characteristics, delineate critical internesting habitats, and characterize behaviors during the internesting interval. Data collection included a combination of nighttime beach surveys (direct observation) and deployment of Argos satellite-transmitting dataloggers (satellite tags), alongside analysis methods such as Autocorrelated Kernel Density Estimation (AKDE) and movement persistence models.

The average internesting tracking duration was 26 days, and during the internesting interval turtles traveled far offshore of SPNWR. Home range analysis revealed that critical habitats for leatherbacks during the internesting interval extend beyond the waters of existing Critical Habitat areas, and throughout the waters surrounding and between St. Croix, Puerto Rico, and Antigua. Behavioral analysis showed that leatherbacks consistently exhibited high move persistence, indicative of rapid and directed movement, potentially in response to predator risk. These home range and behavioral results highlight the importance of considering broader spatial scales for conservation efforts and of understanding predator-prey dynamics.

Reproductive output by leatherbacks in the study was relatively low compared to historic data. Leatherbacks nesting at SPNWR exhibited reduced reproductive philopatry, with 20% of turtles exhibiting straying behavior and nesting on multiple beaches besides Sandy Point including Vieques, Puerto Rico, Antigua, and the east side of St. Croix. This finding challenges the traditional view of leatherback fidelity and indicates potential adaptability to environmental changes. The analysis also highlighted instances of extended internesting intervals (up to 25 days), demonstrating that leatherbacks may skip a nesting event during the season and suggesting a shift in reproductive strategies, potentially linked to environmental stressors or changes in foraging opportunities. The average clutch frequency was 3.6 (± 1.9 nests). These reduced clutch frequencies and overall reproductive outputs compared to historical data indicate possible shifts in life history traits under changing climatic conditions.

The findings of this study enhance our understanding of the nesting and internesting behaviors of leatherback sea turtles. They highlight the importance of updating and refining conservation strategies to reflect these nuanced behaviors. The study suggests a need for

expanded critical habitat protections, increased regional collaboration, and further investigation into leatherback-predator interactions. These insights contribute to a comprehensive understanding of the leatherback sea turtles' adaptive strategies to environmental challenges at Sandy Point, underlining their resilience and dynamic ecological roles.

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INTRODUCTION

A robust knowledge of movement and habitat use is necessary to understand animal biology and relationship with the environment. Marine animal movement occurs in response to biotic and abiotic environmental factors such as predation (Wirsing et al. 2008), prey distribution (Womble et al., 2014), and ocean circulation (Afán et al., 2015; Nicol et al., 2000), as well as to individual-level choices and behaviors (Mueller and Fagan, 2008; Shaw, 2020). Examining drivers of movement and habitat use is critical for understanding and predicting both current and potential species distributions, as well as for considering how a species may respond to climate change. Knowledge about habitat use is essential to effectively manage threatened species via spatial approaches such as time-area closures (Armsworth et al., 2010), dynamic management (Hazen et al., 2017), and ship traffic modification (Vanderlaan and Taggart, 2009).

Movement studies are especially important for highly migratory species such as tunas (Block et al., 2005, 2001), cetaceans (Bailey et al., 2009), pinnipeds (Burton and Koch, 1999), and sea turtles (Plotkin, 2010), which occupy large geographic regions over space and time (Block et al., 2011). Sea turtles use different habitats during varied life stages – juveniles occupy large areas of oceanic waters (Carr, 1987; Gaspar et al., 2012; Shillinger et al., 2012), while adults frequent both oceanic and neritic environments (Dodge et al., 2014; Eckert et al., 2006; James et al., 2005). Leatherback sea turtles (*Dermochelys coriacea*) are particularly wide-ranging, making basin-wide annual migrations. For example, leatherbacks in the northern Atlantic travel from summer foraging grounds in the Northwest Atlantic to breeding grounds in Florida and throughout the Wider Caribbean (Dodge et al., 2014; Fossette et al., 2010; James et al., 2007, 2005), and Pacific leatherbacks undertake extensive migrations from the western Americas to the South Pacific (Benson et al., 2020, 2011, 2007a, 2007b).

As long-lived gigantotherms (Paladino et al., 1990), leatherbacks inhabit most of the world's oceans (except the Arctic and Southern Oceans) and survive in broad thermal conditions through adaptations such as countercurrent venous and arterial structures and behavioral thermoregulation (James and Mrosovsky, 2004; Paladino et al., 1990, p. 199). Leatherbacks generally forage at temperate and subtropical latitudes (Eckert et al., 2012), primarily consuming gelatinous zooplankton (including scyphozoan jellyfishes, hydromedusae, *Cyanea capillata*,

ctenophores, tunicates, siphonophores, and *Chrysaora quinquecirrha*) (Bjorndal, 1996; Dodge et al., 2011; James and Herman, 2001). Nesting beaches are located at tropical and subtropical latitudes (Eckert et al., 2012).

During the nesting season, female leatherbacks spend approximately 9-10 days at sea between egg-laying events while eggs develop in the oviduct, laying 5-6 clutches of eggs during a nesting season (Boulon et al., 1996; Eckert et al., 2012; Spotila and Tomillo, 2015). This period between nesting events, called the internesting interval, is a critical time in adult leatherback life. In the internesting interval, females spend time in nearshore waters, where they are vulnerable to anthropogenic influence such as shipping and interactions with nearshore fisheries (K. L. Eckert et al., 1989; Eckert, 2006; Shillinger et al., 2010). To quantify and mitigate these potential threats, a few studies have sought to understand the behavior and habitat use of internesting leatherbacks using animal-attached data loggers (Asada et al., 2022; Dodge et al., 2022; Eckert et al., 1986; Shillinger et al., 2010).

Previous studies have characterized internesting leatherback behavior using technologies such as Time Depth Recorders (TDRs) (Eckert, 2006; Eckert et al., 1986; S. A. Eckert et al., 1989; Fossette et al., 2007) and video loggers (Asada et al., 2022; Reina et al., 2005). During the internesting period, leatherbacks spend a large proportion of their time diving (Eckert, 2002), perhaps as a predator avoidance strategy (Asada et al., 2022, 2021; Eckert et al., 1986) or a behavioral thermoregulatory adaptation to cope with high sea surface and nesting beach temperatures (Eckert et al., 1986; Shillinger et al., 2010; Wallace et al., 2005). Some have theorized that leatherbacks forage (likely opportunistically) during the internesting interval (Asada et al., 2022; Casey et al., 2010; K. L. Eckert et al., 1989; Eckert et al., 1986; Fossette et al., 2009, 2008, 2007; Myers and Hays, 2006; Shillinger et al., 2010), while others have documented that feeding does not occur (Reina et al., 2005; Wallace et al., 2005). Spotila and Tomillo (2015) suggested that these differences in findings indicate behavioral plasticity; in other words, leatherbacks may alter their foraging behavior during the internesting interval in response to food availability.

Fewer studies have examined leatherback distribution and habitat use during the internesting interval. These investigations documented that leatherbacks preferentially reside in

nearby coastal habitats during the 10 days between egg-laying events (Eckert et al., 2006; Georges et al., 2007; Hitipeuw et al., 2007; Shillinger et al., 2010); however, some studies have reported leatherback use of offshore habits as well (Hitipeuw et al., 2007; Shillinger et al., 2010).

Leatherbacks are listed as Vulnerable worldwide (Wallace et al., 2013), and they are grouped into Regional Management Units (RMUs) based on genetics and geography for research and management (Wallace et al., 2010). Declines in Northwest Atlantic RMU populations since 2009 (Northwest Atlantic Leatherback Working Group, 2018) have revealed a need for knowledge on the location and physical properties of critical leatherback nesting habitats and the use of interesting habitats. Though habitat use has been studied for other life phases, few studies have examined movement specifically during the interesting interval (Benson et al., 2007c; Eckert et al., 2006; Fossette et al., 2008; Okuyama et al., 2016; Shillinger et al., 2010), and even fewer have examined the genetically distinct (Dutton et al., 2013) Northern Caribbean population (Puerto Rico and the US Virgin Islands) (Eckert, 2002; Eckert et al., 1986). Understanding key patterns and drivers of movement and distribution is critical to reaching species management goals, as improved understanding of reproductive strategies and habitat use can inform management strategies such as monitoring and protecting nesting beaches and in-water habitat.

Sandy Point National Wildlife Refuge (SPNWR), in St. Croix US Virgin Islands, has been the site of extensive leatherback (Northwest Atlantic RMU, Northern Caribbean population) monitoring and management since the late 1970s (Evans, 2010). Leatherback nesting at SPNWR has declined severely since the early 2010s (Garner et al., 2017; Northwest Atlantic Leatherback Working Group, 2018). As a result of these changes, critical management questions include: Why has leatherback nesting declined at SPNWR, and where are important interesting habitats for leatherbacks nesting at SPNWR?

The objective of this study was to use animal-borne telemetry data (satellite tag) to (1) examine leatherback nesting characteristics, (2) identify important interesting habitat areas, and (3) characterize leatherback behaviors (such as resting, rapid transiting, and slow transiting) during the interesting interval.

MATERIALS AND METHODS

Study Site

Data for this study were collected in St. Croix, US Virgin Islands, in the Northeast Caribbean Sea approximately 100 km southeast of Puerto Rico. St. Croix is a Caribbean island in the Lesser Antilles island arc, located southeast of the Greater Antilles and north of South America (Vacher and Quinn, 1997) (Figure 1). It is part of the elevated St. Croix Platform and surrounded by numerous oceanic trenches and basins.

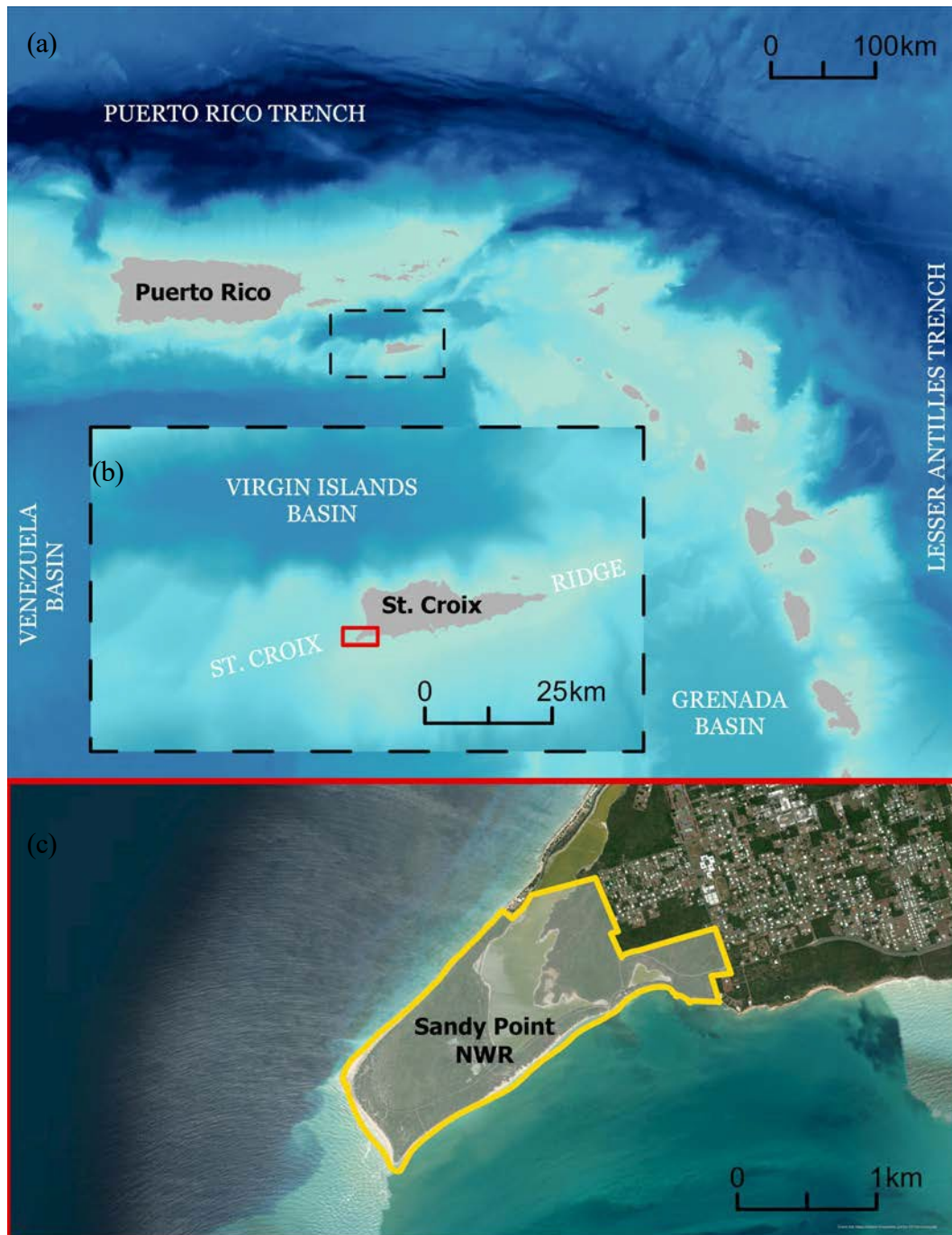


Figure 1. Bathymetric map (darker colors represent greater ocean depth) of (a) the US Virgin Islands and the Lesser Antilles and (b) St. Croix (Source: gridded bathymetry data downloaded from GEBCO (The General Bathymetric Chart of the Ocean; <https://www.gebco.net/>)). (c) Imagery map of Sandy Point NWR, at the southwest point of St. Croix (Sources: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community).

Sandy Point National Wildlife Refuge (SPNWR), located on the southwestern tip of St. Croix (Figure 1c), is a critically important nesting area for leatherback sea turtles (Boulon et al., 1996; Dutton et al., 2005). It was designated as Critical Habitat for leatherback sea turtle nesting both on land (by USFWS 1978) and in the adjacent waters (by NOAA National Marine Fisheries Service 1979), and it once had the densest nesting of leatherbacks in US jurisdiction (Boulon et al., 1996). Sandy Point NWR was established in 1983 as the first National Wildlife Refuge for the protection of leatherback sea turtle nesting habitat (Evans, 2010). Monitoring and management of leatherback nesting has been ongoing at Sandy Point since 1977, and the resultant dataset is the most comprehensive in the world (Evans, 2010), with detailed nesting histories for approximately 857 females.

Data Collection

Ten nesting female leatherback turtles were outfitted with Argos satellite-transmitting dataloggers (satellite tags) (Figure 2) during the 2020 and 2021 nesting seasons under appropriate permits (IACUC SWPI2021-03; DPNR DFW21084U; TE 697819-5) and using approved protocols (Dodge et al., 2015, 2014). To prevent corrosion and biofouling, tags were coated with Interlux anti-fouling primer and paint before deployment. Tags were programmed to archive and transmit data until battery exhaustion (or tag removal/failure). Tags were deployed after the first month of the nesting season to balance the early season risk of tag loss due to mating and predation with the late season risk of capturing fewer interesting days. Both first-time nesters (neophytes) and returning nesters (remigrants, identified from previously applied flipper or Passive Integrated Transponder (PIT) tags) were targeted to see the full range of nesting site choices.

Nighttime surveys were conducted using ATV and foot patrols in collaboration with USFWS and St. Croix Sea Turtle Project researchers and volunteers. To encounter all nesting female leatherbacks, the beach was surveyed every 30 minutes between 20:00 and 03:00 during April – June. When a nesting female was encountered, existing identification tags (a uniquely coded external flipper tag on the rear flipper and/or an internal Passive Integrated Transponder PIT tag) were checked and tags were applied to untagged neophyte females. Injuries were

catalogued and photographed. Morphometric data (such as body size, measured as Curved Carapace Length (CCL) and Curved Carapace Width (CCW) using a flexible tape measure) was collected. Turtles were assessed for satellite tag suitability based on nesting history, physical health, and nesting conditions such as the location and timing of the encounter.

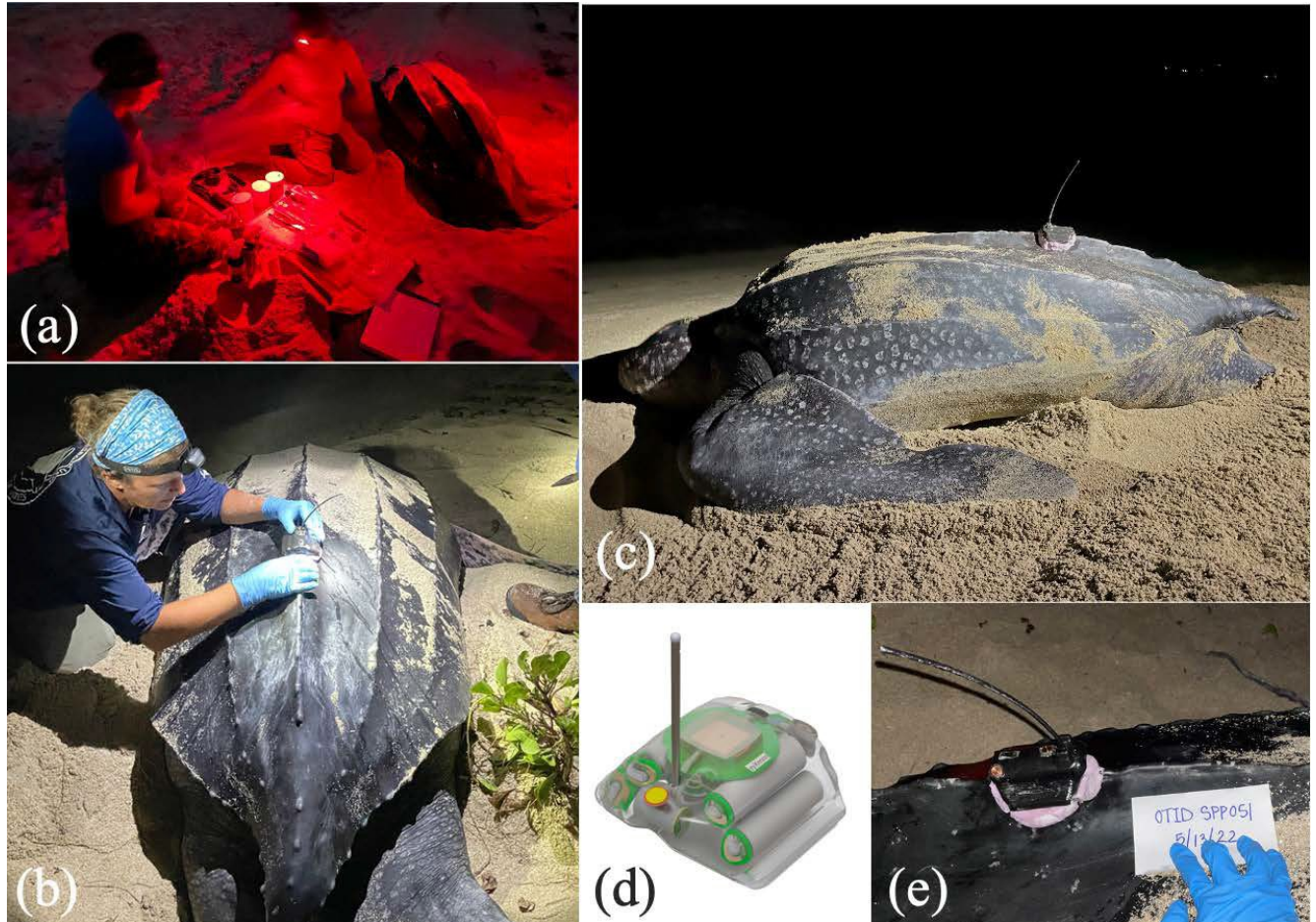


Figure 2. Satellite tag deployed on leatherback turtle via direct attachment method (photos: N. Mauney) (a) field work station setup for satellite tagging (b) C. Lombard finishes satellite tag deployment by completing final checks to attachment site (c) side view of satellite-tagged leatherback departing the beach (d) Wildlife Computers Inc. SPLASH10-F-294A tag (photo: Wildlife Computers Inc.) (e) satellite tag attachment site, with card identifying date and individual.

If a leatherback was encountered early in the nesting process and determined to be a suitable candidate based on the criteria above, a satellite tag was deployed using the direct attachment method (Dodge et al., 2015, 2014), which is the recommended leatherback satellite

tagging method (Jones et al., 2011). The satellite tag attachment process was initiated when the turtle entered her egg-laying trance, during oviposition, to avoid disturbance of the nesting process. The tag was mounted two-thirds of the way down the turtle's carapace along the dorsal ridge, to maximize potential contact with satellites during deployment, on a cushion of two-part cold-curing silicone putty (Figure 2). It was secured in place with antenna wire threaded through surgical tubing in two 4.5 mm holes.

Instrumentation

Turtles were outfitted with Wildlife Computers, Inc. (Redmond, WA) SPLASH10-F-294A (dimensions 86 x 91 x 26mm, mass 210g) Argos satellite-transmitting tags (Dodge et al., 2015, 2014). Tags were selected to balance optimal battery and location capabilities with small size to reduce drag (Jones et al., 2011). These dataloggers archived haul-out, Fastloc GPS, and environmental data and transmitted summarized data via the Argos satellite system. Additional locations were obtained from the Argos satellite system using a doppler shift method. The time interval between location points ranged from three minutes to 21 hours.

The satellite tag attempted to record and transmit an Argos location, at 15 second intervals, each time the SPLASH10 tag broke the water's surface using the Argos satellite system. Location accuracy was classified for each Argos-derived position using Location Classes (LC) ranked 3, 2, 1, 0, A, B, Z (highest to lowest accuracy) (Supplementary Table 1). A haul-out instance was recorded each time a tag's Wet/Dry sensor was sufficiently dry, defined as dry for at least 30 seconds each minute, for more than 20 consecutive minutes (or 40 seconds/ 10 minutes).

The tag attempted to record and transmit a Fastloc GPS (FastGPS) location every 10 minutes or each time the SPLASH10 tag broke the surface by documenting a snapshot of near-instantaneous GPS satellite signals and processing and compressing them onboard to reduce Argos transmission size (Costa et al., 2010; Wildlife Computers Inc., 2020). Each Fastloc GPS snapshot location consisted of a seed location, satellite ID numbers, their respective pseudo ranges, and a timestamp (Wildlife Computers Inc. 2020). Fastloc GPS records tag locations with

higher positional accuracy and lower uncertainty than Argos (Costa et al., 2010; Jonsen et al., 2013).

Data Analysis

All transmitted location data (Fastloc GPS and Argos-derived) were retrieved from the Argos satellite system via the Wildlife Computers Portal. Fastloc GPS data were post-processed in the portal using the Fastloc GPS Solver tool, which converted compressed snapshots into GPS coordinates (Wildlife Computers Inc. 2020). Argos locations in quality LC-Z, for which no error estimate was available, were removed (Hays et al., 2001). FastGPS locations with a Residual value greater than 35 were removed, as well as locations estimated using fewer than 4 satellites, as is standard practice (Dujon et al., 2014).

Individual tracks were subset to only include locations collected during the interesting interval, defined as the time between tag deployment and the beginning of the post-reproductive migration. The start of the post-reproductive migration was defined as the date of the last identified nesting location before migration, or the last possible nesting event (for turtles that remained in the nesting grounds for >10 days past the last documented nest).

Raw Argos and Fastloc GPS locations vary in their location error and sampling frequency. To reconstruct a realistic track for each individual, position estimates were improved, and the sample interval was regularized by fitting a continuous-time state-space model (SSM) to the location data using the *aniMotum* package (Jonsen et al., 2023) (formerly *foieGras* (Jonsen et al. 2020)) in R (*v* 4.2.2). Tracks were reconstructed using a correlated random walk model at a 3-hour time step, with a speed filter of 3.4 m/s, based on the maximum velocity of leatherbacks, to exclude outlier locations (Asada et al., 2022).

Although other leatherback movement studies have used a coarser time step of 6 - 24 hours in SSMs (Bailey et al., 2008; James et al., 2005; Shillinger et al., 2008), to suit the different goals of this study and the distribution of this data, I tested a range of time-steps (1, 3, 6, 12, 24-h) and gap lengths (up to 25-h) to select an appropriate parameter. I chose a time step of 3 hours due to the fine temporal resolution of our raw data (examined through using sample frequency distributions), the goals of our behavioral classification [Objective 3], and the short

duration of the interesting interval. After exploring the data, I chose to remove track sections where the gap was >15 hours (5 x the interpolated time step), to minimize the error associated with large data gaps (Bailey et al., 2012, 2008), as this struck a good balance between minimizing data removal and ensuring interpolation accuracy.

Summary statistics, such as maximum distance from SPNWR, total distance traveled during the interesting interval, and average travel rate, were computed from these interpolated tracks using the *sf* package (Pebesma, 2018) in R (v 4.2.2).

[Objective 1] Examination of nesting characteristics

Each tagged turtle's nesting events were inferred from nighttime survey, morning survey, and satellite tag data. To determine the approximate date and location of nesting events, the following criteria were considered: (a) direct observation (from nighttime survey), (b) indirect observation (meaning that the unidentified track from a beach survey aligned with an individual's track location and timing), (c) distance to shore (GPS or Argos LC3), (d) haul-out message, (e) time elapsed since last nesting event, (f) location quality, and (g) location frequency, as suggested by (Tucker, 2010). Due to limited data availability, I did not use genetic data or diving behavior to identify nesting (Hart et al., 2010; Tucker, 2010). Mean and standard deviation values are reported.

Several satellite tags failed prior to the beginning of migration. The full length and nesting characteristics for individuals whose tag failed are not fully captured.

[Objective 2] Delineation of high-use interesting habitats

Leatherback home range during the interesting interval was delineated with Autocorrelated Kernel Density Estimation (AKDE) analysis (Fleming et al., 2015) using the *ctmm* package (Calabrese et al., 2016) in R (v 4.2.2). The continuous-time movement model, AKDE, was chosen over traditional home range estimation methods (such as minimum convex polygon and Kernel Density Estimator) because it explicitly accounts for temporal autocorrelation and other biases that are inherent in satellite tag location data (Silva et al., 2022).

As the *ctmm* package is prepared to address data with location error and irregular time intervals, raw Fastloc GPS and Argos data exports from the Wildlife Computers Portal (with Argos LC-Z, FastGPS Residuals > 35, and FastGPS 4 satellites removed) were used instead of smoothed data.

To conduct an error-informed analysis, location errors must be quantified (Fleming et al., 2021). Argos location error was calibrated using a prior, or range of realistic Root Mean Squared User Equivalent Range Error (RMS UERE) values (C. Fleming, personal communication, February 13, 2023) and error ellipse information (error radius, error semi-major axis, error semi-minor axis, and error ellipse orientation) (Fleming et al., 2021). Uncalibrated Fastloc GPS location errors were assigned based on an informative prior (Fleming et al., 2021). A 10-meter RMS UERE was applied with 2 Degrees of Freedom (DOF) to construct the prior (Fleming et al., 2021). Outliers from all location data were removed using *ctmm*'s `outlie()` method (Calabrese et al., 2016).

To visualize the autocorrelation structure, I generated a variogram for each individual by plotting its squared distance traveled (semi-variance) as a function of time lag (Fleming et al., 2014). I examined each variogram and inspected it for range residency, which is an assumption of AKDE estimation. Range residency was confirmed when semi-variance reached an asymptote (leveled off) at large time-lag values (Fleming et al., 2014). For individuals whose variogram did not exhibit range residence, tracks were segmented or truncated until variograms suggested range residency. For example, one turtle (Spot) nested at Sandy Point three times before nesting in Antigua three times. To allow the data to meet the range residence assumption of the AKDE model, Spot's track was split into two sections to reflect her two effective home ranges.

Because the analysis of home range for each individual depends not only on the number of location observations (absolute sample size) but also the number of home range crossings, effective sample size was calculated and reported (Silva et al., 2022).

I fit several movement models for each individual to account for biases specific to the data. To mitigate biases associated with oversmoothing in small effective sample sizes, I used an area-corrected AKDE (AKDEc) (Fleming and Calabrese, 2017) model. To rectify autocorrelation estimation bias in small absolute and effective sample sizes, I used the

perturbative hybrid residual maximum likelihood (pHREML) (Fleming et al., 2019) method. The best movement model for each individual was selected based on AIC score. I recorded the home range crossing time, effective sample size (number of home range crossings), and absolute sample size (number of locations). To account for biases due to unrepresentative sampling in time (i.e., irregular time steps and absolute sample sizes among individuals), I used a weighted AKDE approach (wAKDE) (Fleming et al., 2018) with the best-fit model to estimate a core home range using the 50% AKDE contour and a full home range using the 95% AKDE contour (Chan et al., 2022) for each individual. I estimated a population core home range and full home range using the 50% and 95% contour of the *ctmm* `pkde()` hierarchical kernel density estimation function. Mean and standard deviation values are presented.

[Objective 3] Characterization of leatherback behaviors

To characterize leatherback movement behavior during the interesting interval, I used a movement persistence model (mpm) in the *aniMotum* R package (Jonsen et al., 2023) to calculate move persistence (γ_t). Move persistence, an index for behavior, ranges from 0 to 1 and is based on the autocorrelation between an animal's speed and direction. A low move persistence value is indicative of relatively slow and sinuous movement (or Area-Restricted Search, ARS), and a high move persistence value is indicative of rapid, directed movement (or transiting) (Florko et al., 2023; Jonsen et al., 2023; Vogel et al., 2023).

An mpm was selected over other behavioral analysis methods (such as Hidden Markov Models) because its resulting continuous-scale index (move persistence) allows for a more nuanced assessment of behavioral shifts than is provided by HMMs' resulting discrete behavioral states (Jonsen et al., 2023). Additionally, unlike the HMM, the mpm does not require prior assumptions or knowledge about the number of hidden behavioral states within the location data (Jonsen et al., 2023; McClintock and Michelot, 2018).

To compute move persistence, I used a move persistence model in state space form (`fit_ssm` with `model= mp`) to simultaneously estimate location and move persistence along each track separately. I first pre-processed the raw Argos and FastGPS data (same as Objective 1) and removed track sections where the gap was > 20 hours. I selected a larger gap length for this

analysis because the mp SSM deals well with location data that are irregularly timed and have large location errors (Jonsen et al., 2023). This novel method allows for the uncertainties associated with location error to be carried through to move persistence estimates (Jonsen et al., 2023), which is especially important in this study because we used both Argos and FastGPS data. I interpolated the data to a 3-hour time step and used a speed filter of 3.4 m/s (Asada et al., 2022). To more clearly visualize changes in movement behavior, I rescaled move persistence using min-max normalization.

The relationship between ocean depth and move persistence was assessed using linear regression. Outliers were removed based on Cook's distance, and move persistence values were transformed using a square root transformation to improve normality and homoscedasticity of residuals.

RESULTS

Satellite Tag Deployments

Ten female leatherbacks were tracked during their interesting interval in the 2020 and 2021 nesting seasons – three neophyte and seven remigrant turtles (Table 1). Tags were deployed in late April of 2021 (n=1) and early May of 2020 (n=3) and 2021 (n=6) (Table 1).

The average interesting tracking duration was 26 days (\pm 19 days) and totaled 265 days across all turtles (Table 1). The average number of interesting locations per individual was 456 (\pm 377), with a total of 5,016 locations among all ten individuals during the interesting interval (Table 1). Three individuals' satellite tags stopped transmitting before the end of the interesting interval (Ann, Cindy, and Tito), while the other tags ceased transmitting during or after migration (Table 1). The average time tracked after interesting was 202 days (\pm 148 days) (Table 1).

Table 1. Summary of satellite tag deployments. Flipper tag number, PTT ID, and Name are turtle identifiers. Tag Deploy Date refers to the date (UTC) the satellite tag was deployed. Internesting (IN) End Date denotes the date on which either (a) the tag stopped transmitting or (b) the individual began migrating. IN / Total Days refers to the number of interesting days tracked and total number of days tracked (including migration). IN locations reports the number of locations transmitted during the interesting interval (after erroneous location removal). Nesting Years denotes the years during which each individual has been documented nesting at Sandy Point. Max Distance refers to each individual's maximum distance from Sandy Point during the interesting interval. Total Distance represents the total distance traveled during the interesting interval. Avg. Travel Rate is the average distance traveled per day. Rows shaded in light blue correspond to neophyte turtles.

Flipper Tag Number	PTT ID	Name	Tag Deploy Date	IN End Date	IN / Total Days Tracked	IN LOCATIONS	First Tagged Year	Nesting Years	Curved Carapace Length	# nests	Max Dist. (km)	Total Dist. (km)	Travel Rate (km/day)
SPP002	181165	Ann	2021-04-20	2021-05-02	12 / 12	181	2011	2011, 2015, 2019, 2021	164.4	4	71	611	51.5
SPP088	181170	Barb	2020-05-08	2020-06-27	50 / 296	1057	2012	2012, 2015, 2020, 2022	162.7	7	138	2,166	43.5
SPP832	181172	Cindy	2021-05-04	2021-05-14	10 / 10	114	2021	2021	156.4	1	149	528	53.4
SPP846	200614	Leona	2020-05-10	2020-06-20	41 / 187	1247	2016	2016, 2020	156.5	4	188	2,163	52.9
SPP852	181169	Mona	2021-05-04	2021-05-20	16 / 356	228	2021	2021	151.3	1	125	903	55.7
SPP862	181168	Nellie	2021-05-04	2021-05-16	12 / 95	195	2021	2021	151.0	4	102	525	43.3
SPP319	181166	Spot	2021-05-02	2021-06-28	57 / 196	837	2015	2015, 2018, 2021	153.8	6	428	3,271	57.4
SPP380	181167	Sunshine	2021-05-04	2021-05-17	13 / 452	178	2017	2017, 2021	151.1	3	243	1,070	83.9
SPP353	181171	Tito	2021-05-01	2021-06-15	45 / 45	613	2016	2016, 2019, 2021	148.4	3	152	2,773	61.5
SPP421	200615	Winona	2020-05-05	2020-05-15	10 / 32	366	2018	2018, 2020, 2022	154.6	3	122	693	57.1

Track Overview

After nesting at Sandy Point, leatherbacks typically swam northwest toward the Virgin Islands Basin or southwest toward Muertos Trough before eventually returning to Sandy Point (or another beach) to nest again (Figure 3). Many leatherbacks swam along or passed through seafloor features such as trenches (deep seafloor depression with steep sides – such as Muertos Trench and Puerto Rico Trench), basins (seafloor depressions - such as Virgin Islands Basin, Vieques Basin, Whiting Basin, St. Croix Basin), escarpments (steep underwater cliffs), and passed through depths ranging from 0 m – 7,455 m (Figure 1, Supplementary Figure 1). Leatherbacks that nested on other beaches also moved toward seafloor features such as basins and troughs; however, they also spent time in low and medium-profile shelf environments.

The average interesting travel rate was 56.0 km/day (\pm 11.4 km/day) (Table 1). The average farthest distance from Sandy Point during the interesting interval was 172 km (\pm 101.3 km) (Table 1).

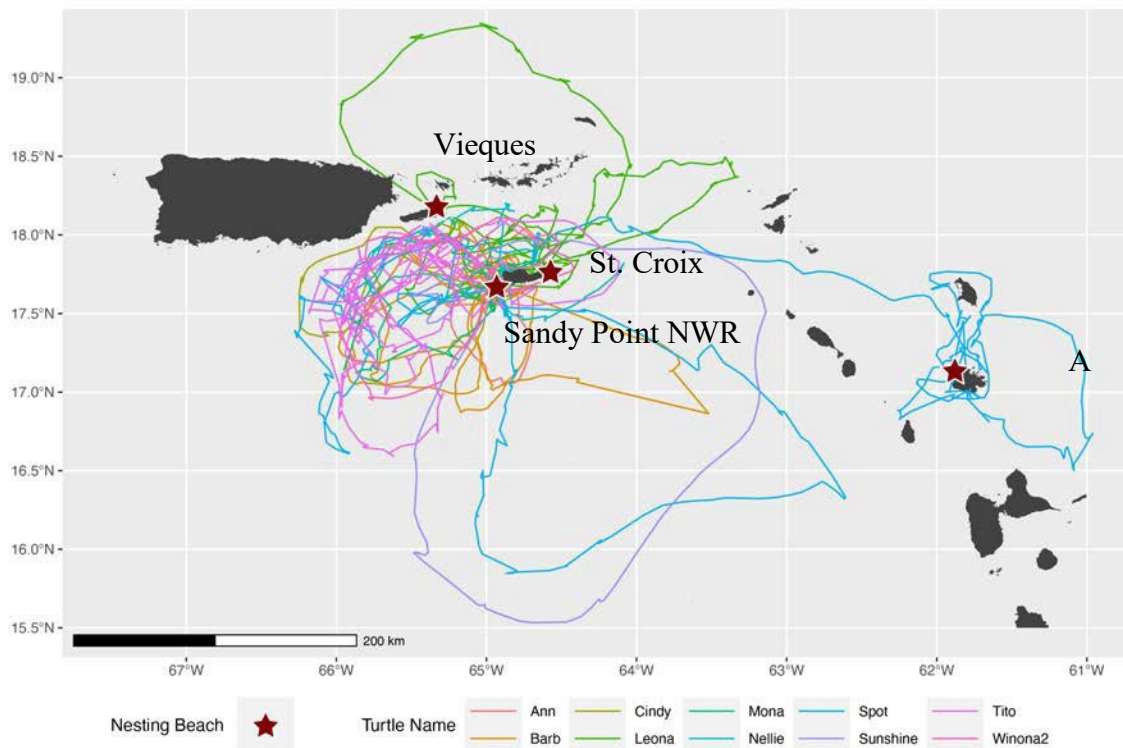


Figure 3. Leatherback tracks during the internesting interval based on SSM-derived locations, with each color representing an individual. Red stars represent nesting beaches (Sandy Point NWR, St. Croix, Vieques Puerto Rico, and Antigua).

Nesting Characteristics

During the 2020 and 2021 nesting season, satellite-tagged leatherbacks ($n=10$) nested a total of 36 times. They nested 30 times at Sandy Point (83.3%), three times in Antigua (8.3%), two times on the east side of St. Croix (5.5%), and once in Vieques, Puerto Rico (2.7%) (Figure 3). Eight of the 10 satellite-tagged turtles (80%) nested only at Sandy Point, and two (20%) nested on other beaches. Once a turtle nested on a different beach, she did not return to nest at the initial beach during the season. Leona nested once at Sandy Point, then twice on the east end of St. Croix, followed by once on Vieques, Puerto Rico. Spot nested three times at Sandy Point, then three times on Antigua.

Satellite-tagged turtles nested $3.6 (\pm 1.9)$ nests during the season (clutch frequency), including nests observed during nesting surveys (before and after satellite tag

deployment (Figure 4). Neophyte turtles nested 2.0 times (± 1.7 nests), and remigrant turtles nested 4.3 times (± 1.6 nests) (Figure 4).

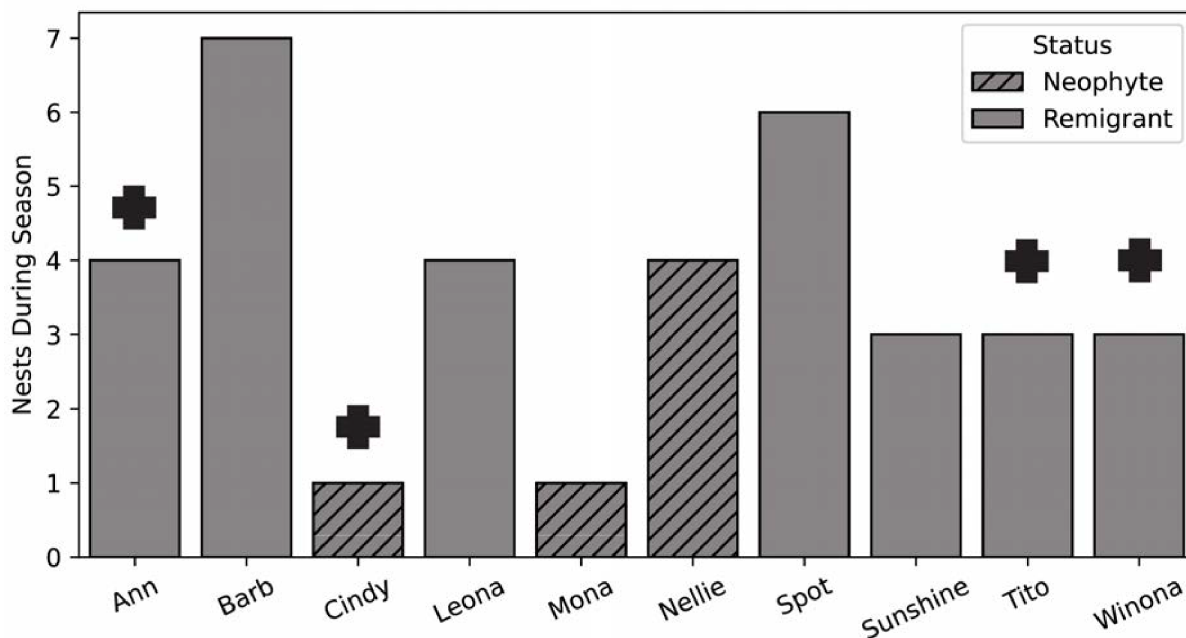


Figure 4. The number of nests laid by each turtle during the season. Neophyte turtles are indicated with hashed bars. Turtles with tags that failed prior to migration are indicated with a plus symbol.

Satellite-tagged leatherbacks nested every 12.2 days (± 5.3 days). This interesting interval length ranged from 7.9 days to 24.9 days (Figure 5). The frequency distribution of interesting intervals exhibited a bimodal distribution, with one peak around 10 days and another around 24 days (Figure 5). Ann, Nellie, Spot, and Tito each had one extended interesting interval of ~ 24 days.

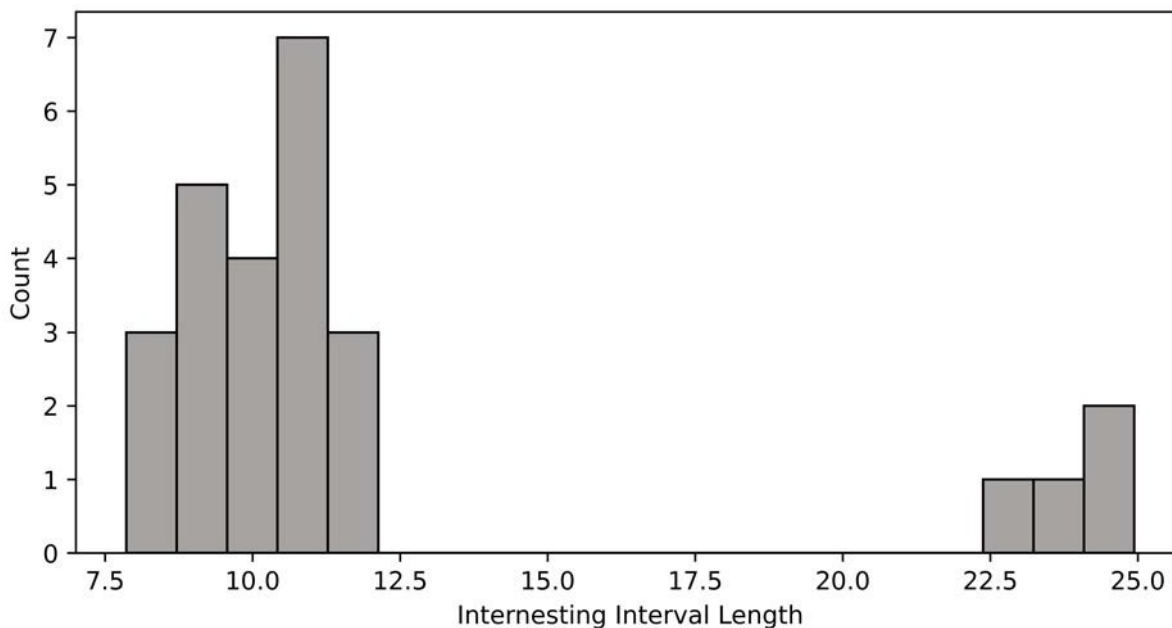


Figure 5. Interesting interval length (the number of days between subsequent nesting events).

Ann laid four clutches at Sandy Point, and her satellite tag was deployed during the second nesting event. She had an interesting interval of 25 days between the second and third nests (Figure 3; Figure 5). After satellite tag deployment, Ann spent 12 days in the waters around St. Croix, then swam back and lingered offshore of Sandy Point, where the satellite tag failed (Figure 3). Thirteen additional days later, when Ann reappeared to nest at Sandy Point, the satellite tag was missing and there were rake marks consistent with a shark predation event on the carapace near the attachment site. Nesting beach surveyors did not observe her nesting at Sandy Point in the 25-day interval between nests 2 and 3, though it is possible that she nested elsewhere during that time despite the likely predation event.

Nellie laid a total of four clutches at Sandy Point during the season, and her satellite tag was deployed during the third nesting event. Before satellite tag deployment, Nellie had an interesting interval of 23 days (based on Sandy Point NWR beach surveys) (Figure 5).

Spot had an interesting interval of 25 days between her third nest (at Sandy Point) and fourth nest (on Antigua) (Figure 3; Figure 5). During the expected nesting days (8-12 days after last nest), Spot was far offshore, between 40 km and 150 km from the nearest beaches on Puerto

Rico and St. Croix (Figure 6), respectively. Around day 13, Spot began swimming approximately 500 km to Antigua, where she subsequently laid 3 clutches (Figure 3).

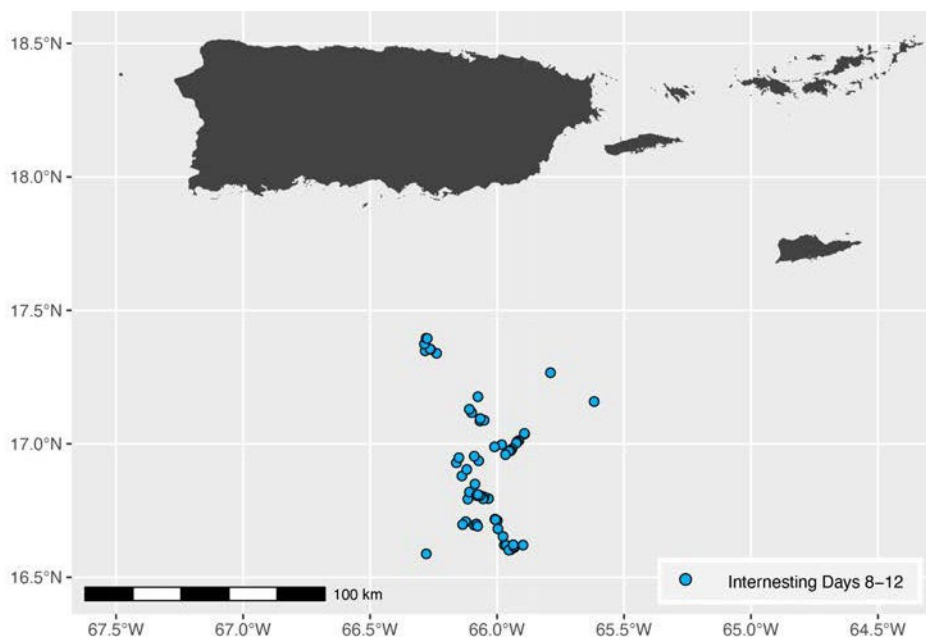


Figure 6. Raw locations of Spot between 8 and 12 days after nesting event (interesting days 8-12).

Tito had an interesting interval of 23 days between the second and third nest (Figure 3; Figure 5). Satellite tag pings 20 km offshore of Puerto Rico indicated that she could have nested on the south side of the island at Maunabo (Playa California); however, nesting was unlikely due to her large distance from shore and lack of a haul-out record (Figure 3).

Home Range Delineation

Core (50% AKDE) and full (95% AKDE) interesting home range area estimates varied across individuals (Table 2). The core individual interesting home range area averaged 18,172 km² (\pm 23,549 km²; range = 3,029 - 81,615 km²), and the full individual interesting home range area averaged 78,424 km² (\pm 97,542.4 km²; range = 13,251 - 336,093 km²) (Table 2). There was no significant difference in 50% core home range size for neophyte vs. remigrant turtles (neophyte average = 10,215 km² \pm 2,400 km² ; remigrant average = 21,156 km² \pm 27,446 km²). There was no difference in 95% full home range area for neophyte vs. remigrant turtles

(neophyte average = $42,258 \text{ km}^2 \pm 11,472 \text{ km}^2$; remigrant average = $91,986 \text{ km}^2 \pm 113,066 \text{ km}^2$) (Table 2). However, remigrants had much larger variability in both 50% core home range and 95% full home range size (Table 2).

Table 2. Estimated core individual home range (50% AKDE) and full individual home range (95% AKDE) areas in square kilometers for ten satellite tagged turtles identified by flipper tag, PTT ID and name. Effective sample size is an estimate of sample size that accounts for both the number of location observations and the number of home range crossings for each individual. Parenthesized numbers represent 95% confidence intervals.

Flipper Tag Number	Name	Effective sample size	Core individual home range (50% AKDE) (km ²)	Full individual home range (95% AKDE) (km ²)
SPP002	Ann	4.7	3,029 (939 - 6,320)	13,251 (4,108 - 27,652)
SPP088	Barb	2.7	8,734 (1,618 - 21,728)	42,259 (7,830 - 105,131)
SPP832	Cindy	2.0	10,283 (1,238 - 28,684)	44,286 (5,334 - 123,537)
SPP846	Leona	3.4	12,210 (2,889 - 28,122)	61,461 (14,542 - 141,556)
SPP852	Mona	3.1	7,781 (1,636 - 18,625)	29,908 (6,288 - 71,588)
SPP862	Nellie	1.8	12,580 (1,328 - 36,186)	52,580 (5,550 - 151,246)
SPP319	Spot_STX	1.7	81,615 (7,820 - 239,837)	336,093 (32,205 - 987,659)
	Spot_Antigua	19.8	3,938 (2,397 - 5,854)	19,870 (12,098 - 29,539)
SPP380	Sunshine	2.3	42,319 (6,111 - 112,819)	187,764 (27,112 - 500,565)
SPP353	Tito	6.9	8,840 (3,514 - 16,579)	36,280 (14,424 - 68,042)
SPP421	Winona	2.9	8562 (1728 - 20759)	38,908 (7,852 - 94,332)

Core individual home range area (50% AKDE) for most turtles was in the waters surrounding St. Croix and between St. Croix and Puerto Rico (Figure 7). The notable exception is Spot, whose core home range area extended to waters offshore of Antigua and Barbuda (Figure 7). Full individual home ranges (95% AKDE) spanned broader geographic areas than their core individual home ranges (Figure 7). Several of the full home ranges spanned not only St. Croix and the waters between St. Croix and Puerto Rico, but also waters farther offshore of St. Croix and to the northeast and southeast of Puerto Rico (Figure 7).

Aside from these general trends, there was variability in the size and location of core and total home ranges for Sandy Point leatherbacks. Some individuals, like Ann (Figure 7a), had a relatively small home range that was primarily offshore of Sandy Point and between Sandy Point and Puerto Rico. However, other individuals, such as Sunshine and Leona (Figure 7i; Figure 7d),

had home ranges that spanned a much larger area, covering most of St. Croix, stretching to the eastern side of Puerto Rico, and spanning farther south into waters in the Virgin Islands Basin that are even farther south than the two islands. Finally, Spot effectively had two separate home ranges: one large home range around St. Croix and Puerto Rico and one smaller home range around the islands of Antigua and Barbuda (Figure 7g; Figure 7h).

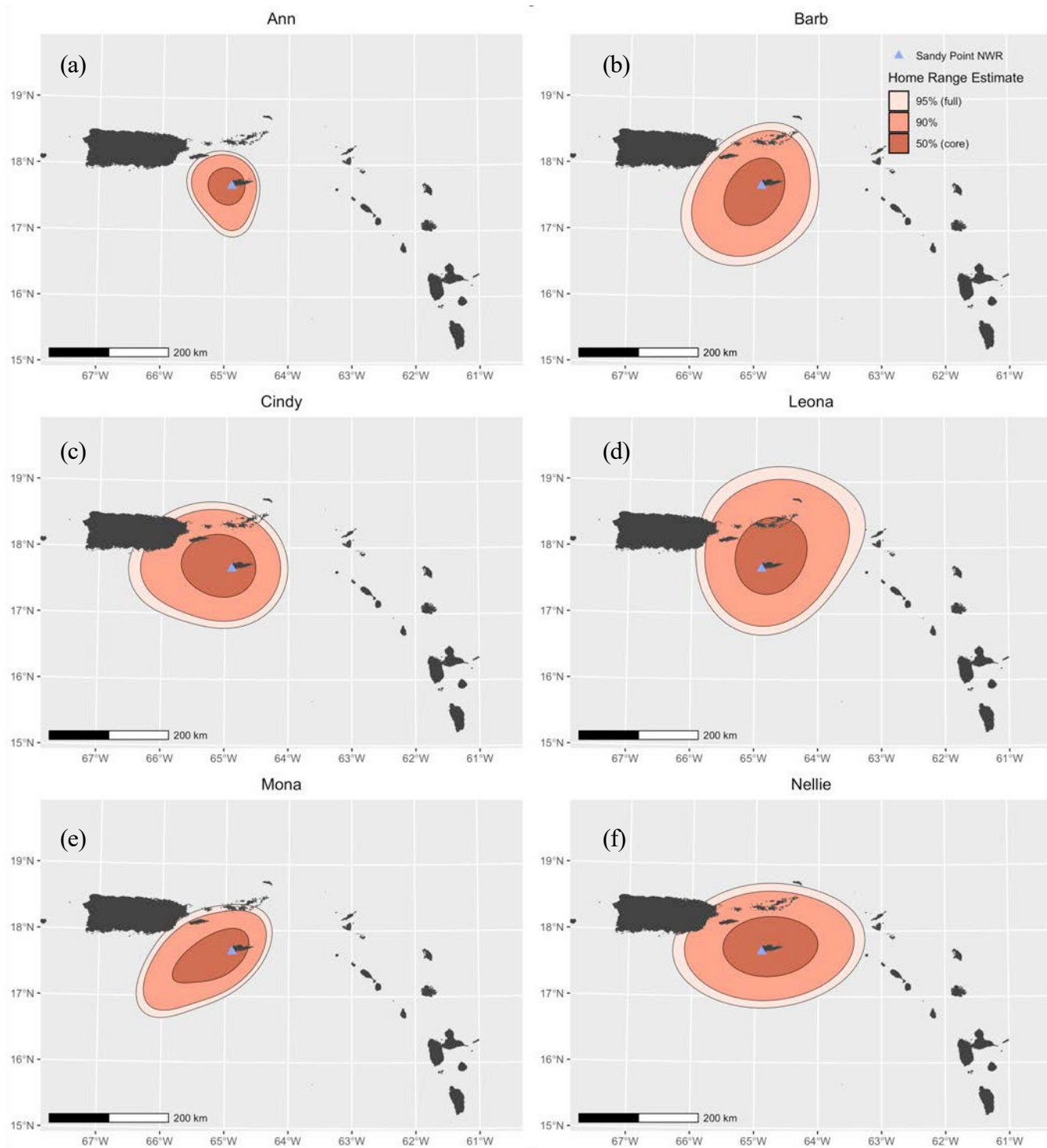


Figure 7. Delineation of 50% (core) (red), 90% (pink), and 95% (total) (light pink) individual AKDE home range for each satellite tagged leatherback (a) Ann, (b) Barb, (c) Cindy, (d) Leona, (e) Mona, (f) Nellie, (g) Spot (Antigua), (h) Spot (St. Croix), (i) Sunshine, (j) Tito, (k) Winona.

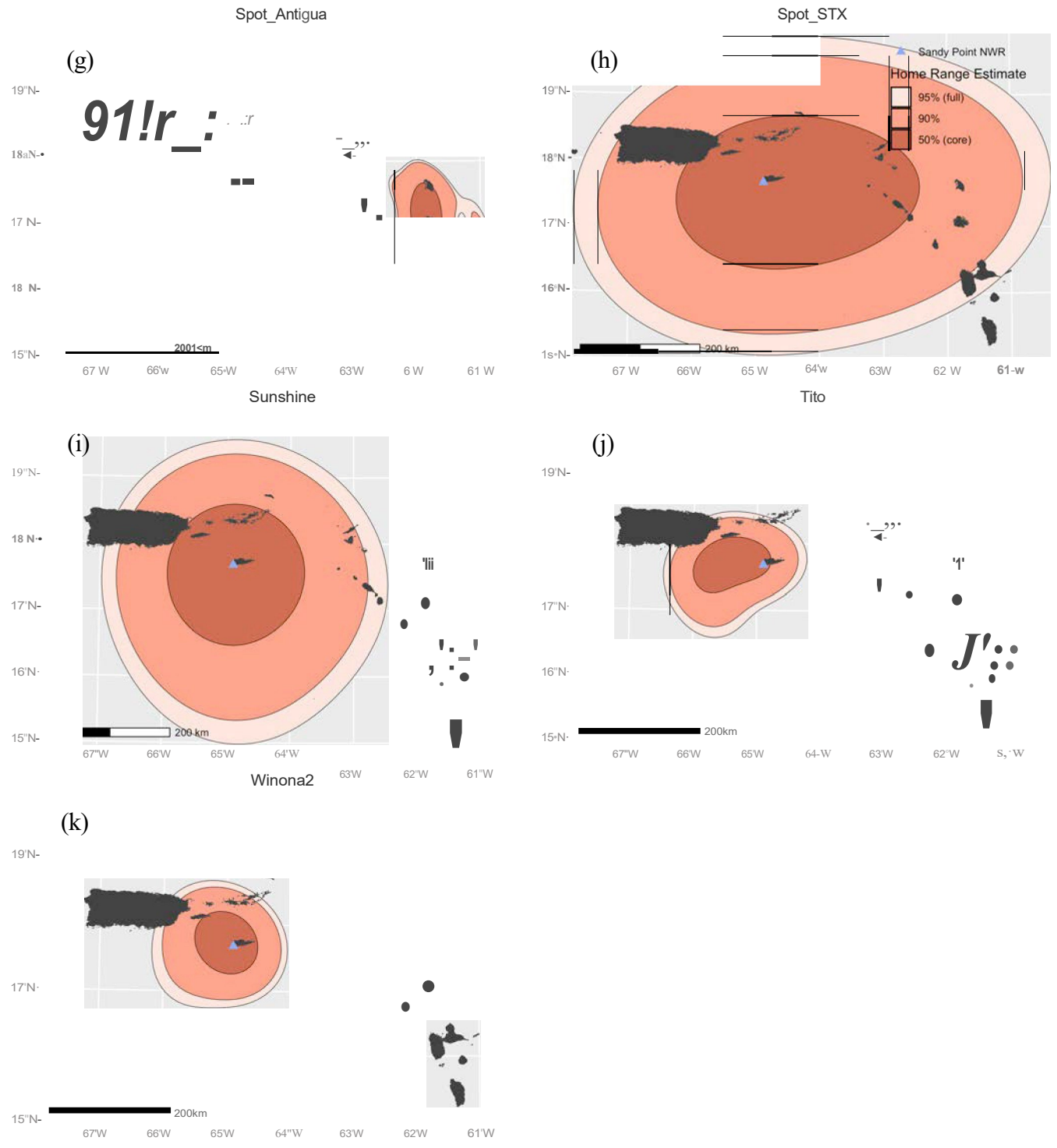


Figure 7, continued

The core population home range area (50% pKDE) estimate was 12,396 km² (95% CI 10,005 - 15,039 km²). The full population home range area (95% pKDE) estimate was 107,249 km² (95% CI 86,563 - 130,117 km²). The core population home range encompassed the waters surrounding St. Croix and between St. Croix and Puerto Rico (Figure 8). The full population home range included the waters surrounding St. Croix, in addition to nearby islands including St. Thomas, St. John, Vieques, the eastern half of Puerto Rico, Barbuda, and Antigua (Figure 8).

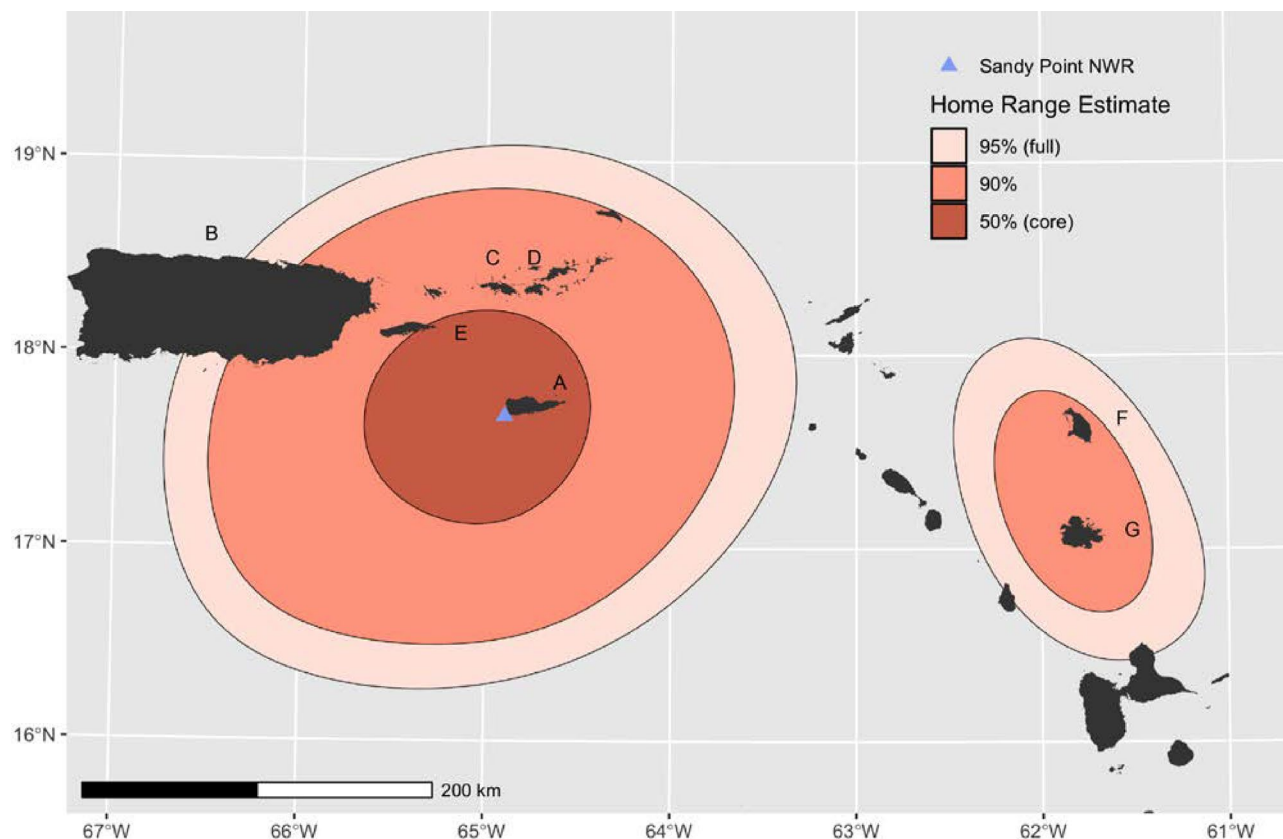


Figure 8. Estimates of 50% (red), 90% (orange), and 95% (pink) PKDE population home range, with Sandy Point NWR denoted with a purple triangle. Labeled islands correspond to St. Croix (A), Puerto Rico (B), St. Thomas (C), St. John (D), Vieques (E), Barbuda (F), and Antigua (G).

Behavioral Classification

All leatherbacks demonstrated relatively high move persistence throughout the interesting interval, which is indicative of primarily directed movement and rapid transit (mean = 0.80) (Figure 9). They did not exhibit a full range of move persistence values (range: 0.34 –

0.96) and had few instances of relatively slow and tortuous movement (Figure 9; Figure 10). Move persistence was positively correlated to depth, but the linear relationship was very weak, despite statistical significance ($t = 3.933$, $p < 0.01$, $R^2 = 0.0072$) (Supplementary Figure 1).

There was individual variability in relative move persistence over the course of the interesting interval. While some turtles exhibited relatively high move persistence upon departing from the nesting beach, others did not and had relatively high move persistence in the middle of the interesting interval (Figure 10). For example, Winona departed from the nesting beach with a high move persistence, and move persistence declined during the next few days of the interesting interval (Figure 10k). Similarly, some individuals returned to the nesting beach with relatively high move persistence, while others did not (Figure 10). Spot departed the nesting beach with a relatively low move persistence and had higher move persistence swimming between nesting events (Figure 10h).

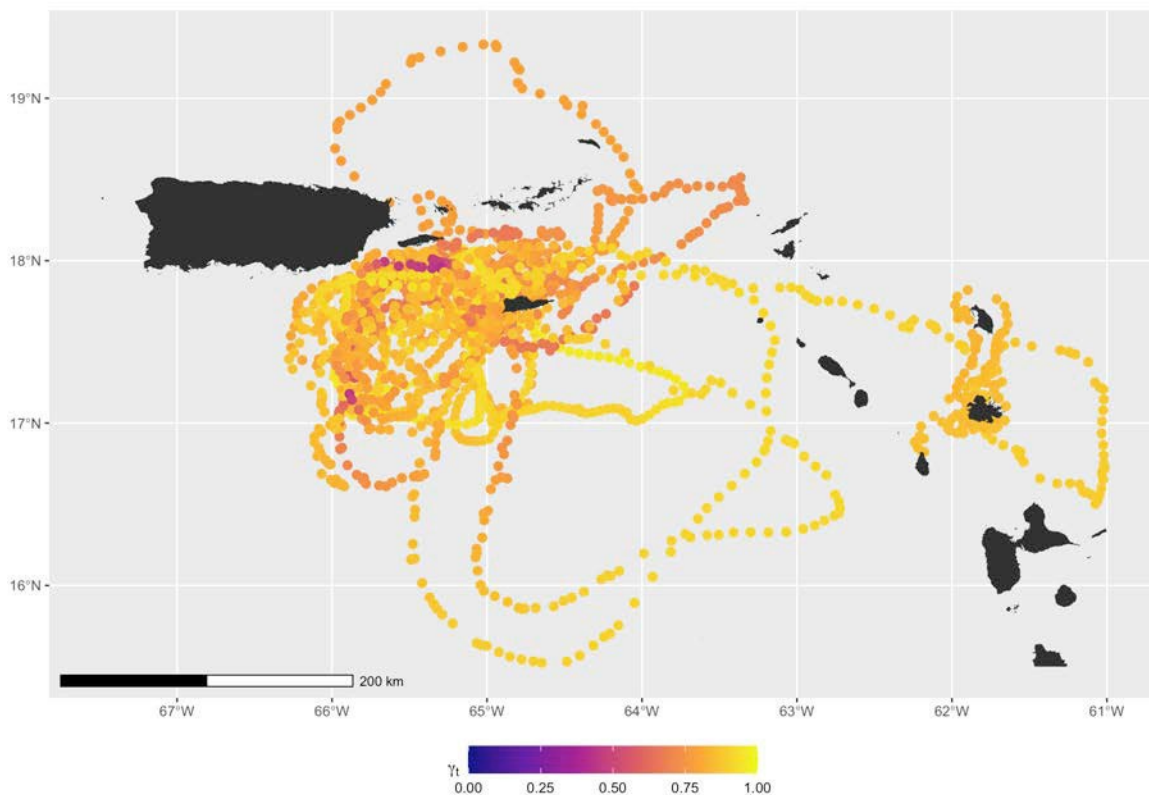


Figure 9. Leatherback locations (at 3-hour intervals) colored by move persistence (γt), ranging from a move persistence of 0 (representing Area-Restricted Search (ARS) behavior, in purple) to 1 (representing transit behavior, in yellow), on a scale of 0 to 1.

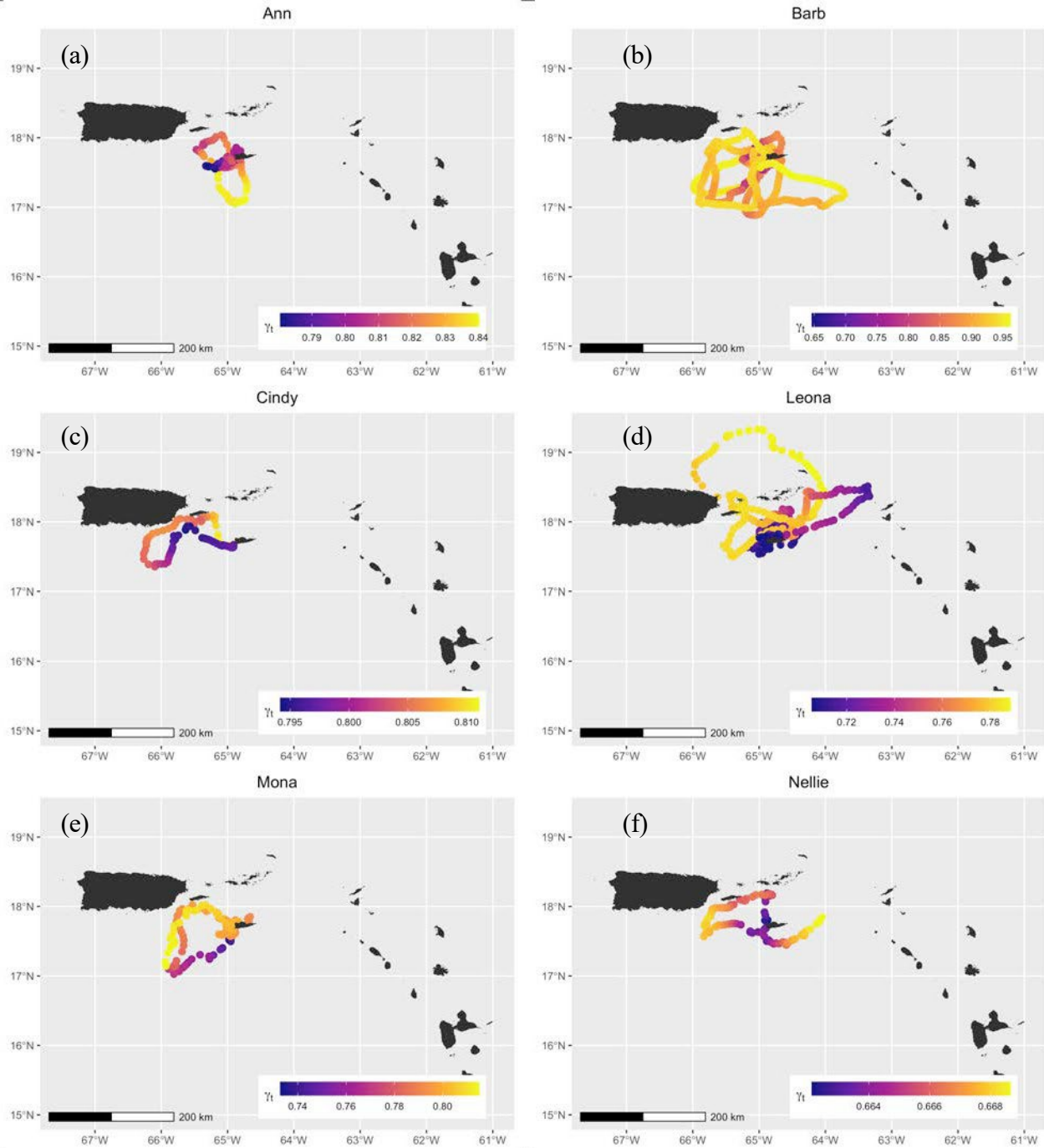


Figure 10. (a-k) maps of locations (at 3-hour intervals) for each individual turtle (a) Ann, (b) Barb, (c) Cindy, (d) Leona, (e) Mona, (f) Nellie, (g) Spot (Antigua), (h) Spot (St. Croix), (i) Sunshine, (j) Tito, (k) Winona on a normalized scale colored by move persistence (γ_t). Color scales (on a gradient of purple to yellow) represent area-restricted search and transit behavior respectively. Each color scale is scaled according to each individual's move persistence values. (l) frequency distribution of move persistence values.

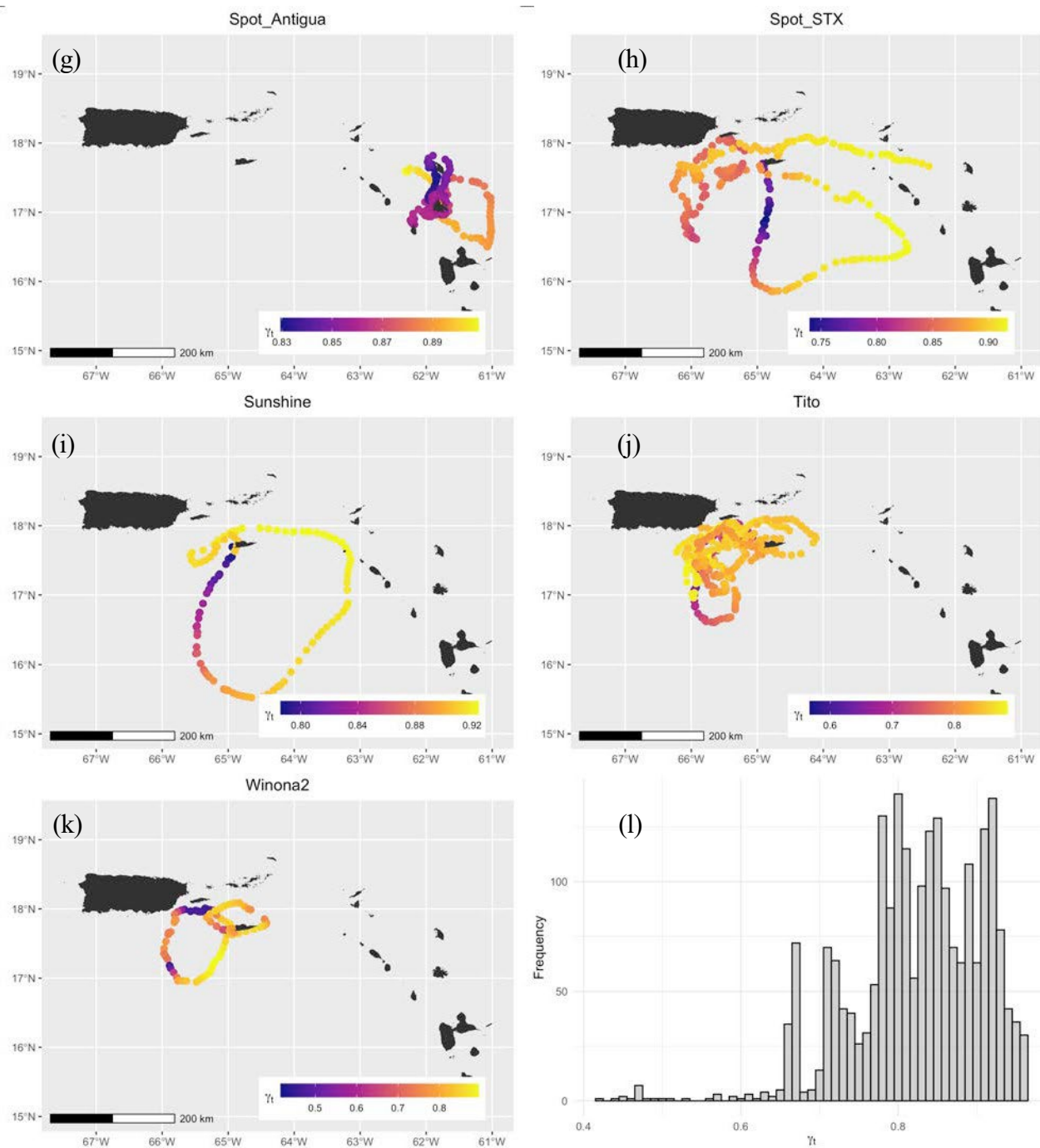


Figure 10, continued

DISCUSSION

Understanding the reproductive characteristics and important habitats of highly migratory marine animals is critical to their conservation and management. Leatherback sea turtles are especially essential to study due to their declining nesting numbers throughout the Wider Caribbean and at historically important beaches like SPNWR (Garner et al. 2017; Northwest Atlantic Leatherback Working Group 2018). Through this study, I successfully tracked 10 nesting female leatherbacks during the internesting interval using satellite tags. By documenting nesting characteristics, previously unknown important internesting habitats, and internesting behavior, this work advances our knowledge of leatherback life history and movement during a vulnerable and cryptic phase of life.

Nesting Characteristics

Beach Switching

While most satellite-tagged leatherback nests were laid at Sandy Point, turtles also nested on other beaches in St. Croix, Puerto Rico, and Antigua during the season. Though sea turtles natal homing (or reproductive philopatry) life history strategy suggests that leatherbacks should primarily return to nest at the beach of their hatching (Dutton et al., 1999; Kamel and Mrosovsky, 2004; Keinath and Musick, 1993; Pritchard, 1982), some turtles in this study used multiple nesting beaches.

This beach-switching, or “straying” (K. L. Eckert et al., 1989), in which leatherbacks exhibit inter-beach and inter-island migrations for nesting within a single season, has been reported previously in leatherbacks nesting at Sandy Point (Boulon et al., 1996; Dutton et al., 2005; K. L. Eckert et al., 1989; Garner et al., 2017; Keinath and Musick, 1993; NMFS and USFWS, 2013) and elsewhere in the Atlantic (NMFS and USFWS, 2013; Pritchard, 1973; Schulz, 1971; Stewart et al., 2014). However, the prevalence of straying (and nesting at multiple beaches) for the satellite-tagged leatherbacks in this study was greater than previously reported. Eckert and colleagues (1989) monitored three nesting beaches that leatherbacks were theorized to stray between – Sandy Point (St. Croix), Manchenil (St. Croix), and Culebra (Puerto Rico).

Through nighttime nesting beach surveys over three years (1984-1986), they found that 3.5% of leatherbacks (6 of 173 turtles) strayed from their initial nesting beach during the three years. And of the turtles that initially nested at Sandy Point, 4.3% strayed. By contrast, we found that 20% of satellite-tagged leatherbacks (2 of 10) strayed from the nesting beach at Sandy Point.

The higher percentage of leatherbacks that strayed from their initial nesting beach in this study may indicate that straying in leatherbacks nesting at Sandy Point is more prevalent than was previously known, that it has increased through time, or that it is due to sample size effects. With the implementation of satellite tagging methods, this study was able to identify nesting events on remote and unmonitored beaches that would not have been detected by nesting beach surveys, such as in Eckert (1989). However, if the difference in beach switching prevalence between studies is not entirely explained by differences in survey methods and sample size, then our results could suggest that Sandy Point may be a less favorable nesting habitat than it once was and this is supported by nesting numbers (Northwest Atlantic Leatherback Working Group, 2018).

Pritchard et al. (1982) hypothesized that leatherback reproductive philopatry may be weak relative to other sea turtle species, and that they may even select for a particular beach type rather than a specific beach (Pritchard, 1979). This may be due to their preference for nesting sites on beaches that are highly dynamic and experience seasonal erosion and high-energy waves (Eckert, 1987; Mrosovsky, 1983; Pritchard, 1971). Weak site fidelity is advantageous in these unstable environments, as it allows turtles to spread reproductive risks (such as predation and nest erosion) to multiple beaches which enables them to effectively respond to disturbances, reduce predator interactions, and colonize new beaches as old ones wash away (Buoro and Carlson, 2014; Den Boer, 1968; Stewart et al., 2014). Similarly, some migratory bird species (such as Arctic Terns) may choose different breeding sites in response to environmental and climatic conditions (Møller et al., 2006). As Sandy Point is expected to be one of the most climate-impacted leatherback nesting beaches due to climate change impacts such as increases in temperature and dryness (Santidrián Tomillo et al., 2015) and sea-level rise, having low fidelity to a particular beach may be a useful strategy for Sandy Point turtles adapting to a changing climate.

The results from this study raise questions about the characteristics and extent of beach switching that merit future study. First, we found that, after straying to another beach, turtles did not return to nest again at the initial beach. The turtles that strayed did so to multiple beaches in addition to the original beach. This raises the question of whether (and why) some individuals are simply more faithful to a particular beach than others. It also brings about the question of whether straying is reactionary, such as a response to predation, disturbance, or nesting habitat change, or if it is simply a life history strategy.

Reproductive Output

Reproductive output, defined as the total number of hatchlings produced by a female in one nesting season, is a critical parameter that determines an individual's contribution to the next generation. It is dependent on key metrics such as the number of nests, number of eggs per nest, and hatching success of each nest, which ultimately have profound implications for population growth and recovery (Santidrián Tomillo et al., 2009). Though leatherbacks typically have a clutch frequency (number of nests per turtle) of 5-6 (Boulon et al., 1996), turtles in this study each laid an average of 3.6 nests during the season. Other work has also documented declines in clutch frequency for leatherbacks nesting at Sandy Point relative to the historic record. Garner et al. (2017) reported a trend of declining clutch frequency at Sandy Point from 1992-2010 in an analysis of 30 years of nesting data. They also noted declines in hatch success, which, combined with declines in clutch frequency, means a lowered reproductive output for leatherbacks nesting at Sandy Point (Garner et al., 2017). The findings in our study align with the trends observed by Garner et al. (2017) and by ongoing nesting monitoring at Sandy Point (K. Stewart, personal communication, May 10, 2023). They also provide support for declining trends in overall nest abundances across Northwest Atlantic populations (Northwest Atlantic Leatherback Working Group, 2018). In this study, overall reduced clutch frequencies relative to historic values and instances of increased internesting interval lengths (indicative of skipped nesting events) contributed to a reduced number of nests and therefore reduced reproductive output for satellite-tagged leatherbacks nesting at Sandy Point.

Though the duration of most interesting intervals was around the expected range of 9-10 days (Eckert et al., 2012; Spotila and Tomillo, 2015), several turtles went 20+ days between visits to a beach. Because the 9–10-day interval represents the amount of time that it takes for eggs to develop in the oviduct, a 20-day interesting interval means that the turtle has effectively skipped a nesting event. Typically, when interesting intervals of a 20+ day duration are observed in nesting beach surveys, it is assumed that the turtle has been missed during a survey or has nested on another beach during that time. However, although that was often the correct explanation according to satellite tag data in this study, we also found that turtles did occasionally skip a nesting event. If population models extrapolate from generalized life history parameters (Turtle Expert Working Group, 2007), they may count each 20+ day gap as a nest, when they are only sometimes nests. This may cause them to over-estimate the number of nests/eggs produced by some individuals. To improve model accuracy, it is essential that models properly parameterize nesting characteristics; therefore, future studies should examine the prevalence of nest skipping in leatherbacks through satellite tagging and/or expanded nighttime patrols.

Energetic Cost of Reproduction

Reducing reproductive output may be a strategy to lower the energetic cost of reproduction under resource limitation. Little is known about prey distribution and availability in northwest Atlantic leatherback foraging grounds, and therefore it is difficult to assess whether they are resource limited. Leatherbacks gain most of their energy by consuming gelatinous zooplankton (jellyfish), primarily scyphozoan jellyfishes (*Cyanea capillata* and *Chrysaora quinquecirrha*) and ctenophores (*Beroe ovata*, *Mnemiopsis leidyi*, and *Pleurobrachia pileus*) in waters off eastern Canada and New England (Dodge et al., 2011; Nordstrom et al., 2020). Jellyfish populations are affected by environmental factors such as temperature, salinity, and chlorophyll-A (Sherrill-Mix et al., 2008). With climate change projected to impact the physical oceanography of the Northwest Atlantic (Alexander et al., 2020, 2018; Boyce et al., 2014), the timing, abundance, and spatial distribution of jellyfish will be altered (Nordstrom et al., 2020; Sherrill-Mix et al., 2008). While some studies have suggested that many jellyfish species will benefit from warming waters (Nordstrom et al., 2020; Purcell and Decker, 2005), others note that

climate change impacts may cause shifts in the timing of jellyfish blooms, geographic range, and abundance and distribution (Nordstrom et al., 2020; Purcell and Decker, 2005; Sherrill-Mix et al., 2008). These factors could have profound impacts on leatherback foraging opportunities; however, further work must be done in quantifying jellyfish abundance and distribution to draw concrete conclusions about the likelihood of resource limitation for leatherbacks. Under resource-limited conditions, leatherbacks may experience altered life history parameters, such as remigration interval, reproductive output, and body size at sexual maturity, to accommodate reduced energetic resources (Saba et al., 2008; Wallace et al., 2006).

Leatherbacks must allocate the finite energy reserves gained during foraging to activity, reproduction, or growth (Wallace et al., 2006). In a resource-limited environment, turtles may reduce energetic costs associated with reproduction; they could do this by (a) increasing remigration interval (the number of years between successive nesting seasons), (b) decreasing reproductive output during nesting (clutch frequency and clutch size), or in extreme scenarios (c) increasing remigration interval and decreasing reproductive output. There is evidence to support sea turtles increasing remigration intervals due to poor foraging conditions (Hays, 2000; Saba et al., 2008; Wallace et al., 2006). Additionally, life history comparisons between Eastern Pacific and Northwest Atlantic leatherbacks suggest that the relatively smaller body size, higher remigration interval, and lower reproductive output of Eastern Pacific leatherbacks are due to long-term resource limitations in Eastern Pacific foraging grounds (Saba et al., 2008; Wallace et al., 2006). Climate-induced changes in temperature and Chl-A regimes could have drastic impacts on prey availability in the Northwest Atlantic and ultimately cascading effects on leatherback energy allocation and reproductive strategies.

Many individuals in our study did not demonstrate increased remigration intervals relative to expected values, and there was no difference in clutch frequency for individuals with shorter (2-3 year) versus slightly longer (4-5 year) remigration intervals. Of the seven remigrant (non-neophyte) nesters, five had a two- or three- year remigration interval, which is typical for Northwest Atlantic leatherbacks (Boulon et al., 1996; van Buskirk and Crowder, 1994). These individuals laid 3, 3, 4, 6, and 7 nests. Two remigrants had a four-year remigration interval, and they laid 3 and 4 nests, respectively.

If leatherback foraging grounds become resource-limited and they do not increase remigration intervals, then perhaps they conserve energy by lowering their reproductive output. This strategy does not seem energetically efficient, as 80% of reproductive energy is consumed in round-trip migration (Wallace et al., 2006) and decreasing reproductive output effectively increases the cost of transport per clutch (Hays, 2000). However, in the face of a changing climate and increasingly unstable environment, it may be useful for leatherbacks to nest in as many years as possible, although not as many times per year. While this may increase their exposure to risks associated with migration, it spreads out the risk of nesting or hatching failure due to annual variables like hurricanes, erosion, resource availability, predator abundance, etc. Laying fewer nests in more years also minimizes the amount of time spent in the interesting interval (ex: 5 nests in one season means 4 interesting intervals, while 5 nests over 2 seasons means 3 interesting intervals), which could reduce predator encounters that are frequent during the interesting interval (Asada et al., 2021). On the contrary, it may also be advantageous to nest more frequently if there are increased risks to leatherbacks in foraging grounds which may not allow leatherbacks to live long enough to reproduce more.

Home Range and Behavior

This research revealed that leatherbacks nesting at Sandy Point use a large home range (> 100,000 km²) during the interesting interval spanning the waters surrounding St. Croix and numerous nearby islands. They move through this space with consistently high move persistence, exhibiting rapid and directed transit. We did not have distinct ocean variables that were indicative of change in move persistence, suggesting that these decisions are being made for other reason (predation risk, finer scale oceanography, etc.).

The individual and population home ranges for Sandy Point leatherbacks were significantly larger than those of Eastern Pacific leatherbacks nesting at Parque Nacional Marino Las Baulas (PNMB), Costa Rica (Shillinger et al., 2010). Sandy Point leatherback home range may be larger because, while PMNB habitat area is constrained by discrete and variable oceanographic features (Shillinger et al., 2010), the waters surrounding Sandy Point are relatively spatially and temporally consistent. These stable oceanographic conditions may allow

leatherbacks to move more freely through the area. Additionally, Sandy Point leatherbacks may use a larger habitat because of their high move persistence, evidence of consistent rapid transit, throughout the interesting interval. The relatively consistent ocean conditions, combined with high prevalence of transiting behaviors, enable leatherbacks to use a relatively large geographic area during the interesting interval.

We found that there was high variability in interesting home range size and location for individuals that nest at Sandy Point. That some individuals occupy a relatively small area during the interesting interval while others travel great distances and use broader habitat is critically important information for management and conservation. Individuals with a small home range spend considerably more time near the nesting beach, which highlights the importance of protecting in-water habitats near nesting beaches and understanding more about predation in this zone. However, the fact that many individuals in this study had relatively large home ranges also necessitates the consideration of larger spatial scales for protection. The high variability in home range size and location for these satellite-tagged individuals demonstrates the importance of continued satellite tagging efforts in this area, because only with a large sample size are we able to capture the individual variability that exists in the population.

Predator Interaction

The results of this study suggest that predator interactions may influence reproductive output, home range, and behavioral characteristics. Leatherbacks are vulnerable to tiger shark attack, and fresh wounds, missing flippers, and scars consistent with shark encounters are frequently observed on nesting females (DeLand, 2017). Shark interactions have been documented with direct observation, injury, satellite tag, and video data (Asada et al., 2021; DeLand, 2017), and Asada et al. (2021) reported that, upon entering and exiting the nesting beach, leatherbacks experienced these interactions at a rate of 4.5 shark encounters per day.

Turtles may reduce reproductive output or skip a nesting event in response to a negative experience, such as contact with a predator or difficulty on the nesting beach. As encounters are most common between dusk and dawn and in nearshore waters (Asada et al., 2021), the risk of predator interaction during nesting beach approach and departure is high. In this study, Ann

skipped a nesting event after a presumed shark attack injured her and removed the satellite tag while she was traveling to the nesting beach.

Additionally, consistent transiting behavior during the internesting interval may be driven by predator risk. Previous work at Sandy Point has demonstrated that leatherbacks rarely rest during the internesting interval, instead primarily moving using energetically-efficient dives (Asada et al., 2022). This rapid and consistent movement behavior may be an anti-predatory strategy; Asada et al. (2021) found that, although shark encounters occurred throughout leatherback internesting habitat, they were 53% higher within 6 km of St. Croix. Therefore, leatherbacks nesting at Sandy Point may move far offshore to reduce predator interactions, despite the energetic cost of transit.

Conclusions and Future Work

In conclusion, the ability of models to analyze population trends and assess population status is limited by our understanding of leatherback nesting characteristics. Life history parameters such as clutch frequency, clutch size, internesting interval, and remigration interval, have always been assumed to be constant. However, the results of this study suggest that leatherback life history parameters may be changing - satellite-tagged turtles had reduced reproductive output relative to historical estimates and several used multiple nesting beaches during a single season. It is essential to incorporate this variability into population models, perhaps through flexible life history tables that account for annual and decadal changes, as population status assessments and recovery plans rely on accurate and updated life history parameters. To monitor these nuances, long-term research on individual turtles and nesting beaches is critical, as well as continued satellite tagging and increased regional collaboration and data sharing.

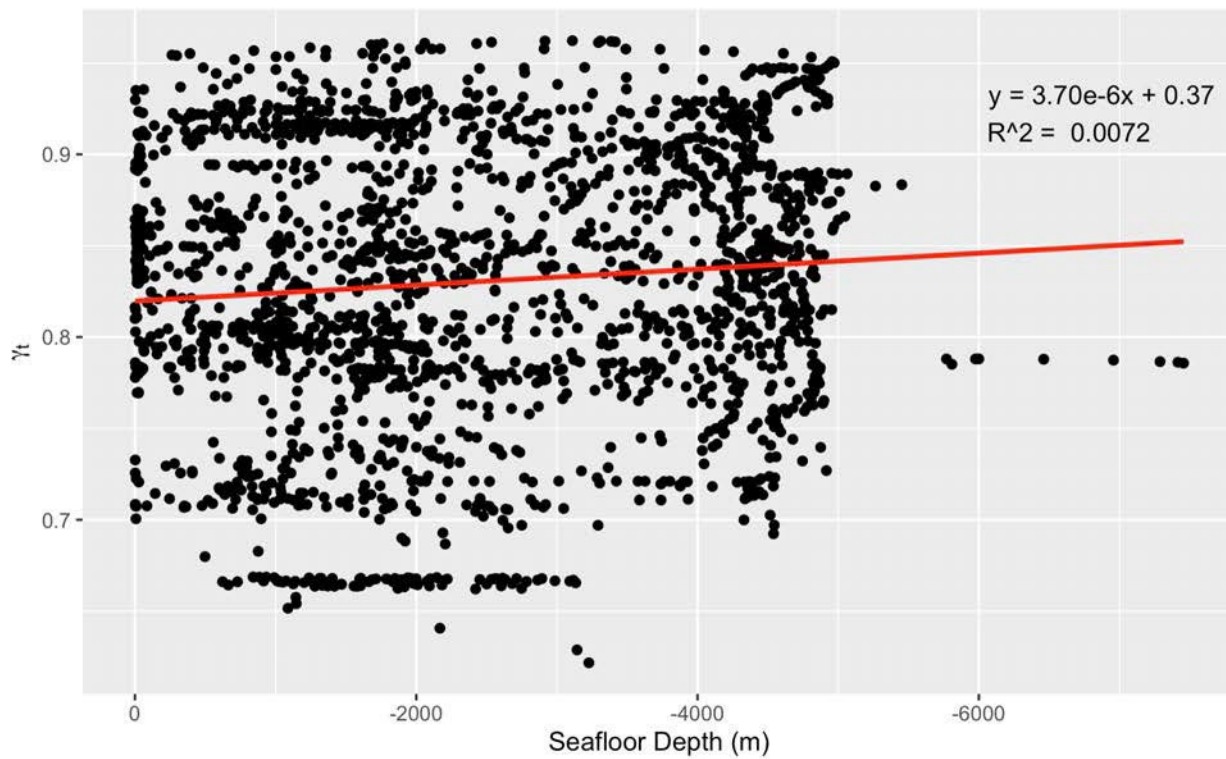
Additionally, because satellite-tagged leatherbacks occupy a relatively large home range area, which spans not only waters surrounding St. Croix and Puerto Rico but also the USVI, Antigua, and Barbuda, it is essential to consider broad spatial scales in conservation efforts. While the current in-water NOAA Critical Habitat for leatherbacks may be effective in protecting leatherbacks entering the nesting beach, the area should be expanded, as leatherbacks

spend extensive time during the internesting interval outside of the bounds of the existing Critical Habitat (Supplementary Figure 2). Additionally, the large home range for Sandy Point leatherbacks highlights the need for increased nesting beach monitoring, regional partnerships, and collaborative efforts with real-time data sharing, especially with regard to turtles that are switching beaches during the nesting season.

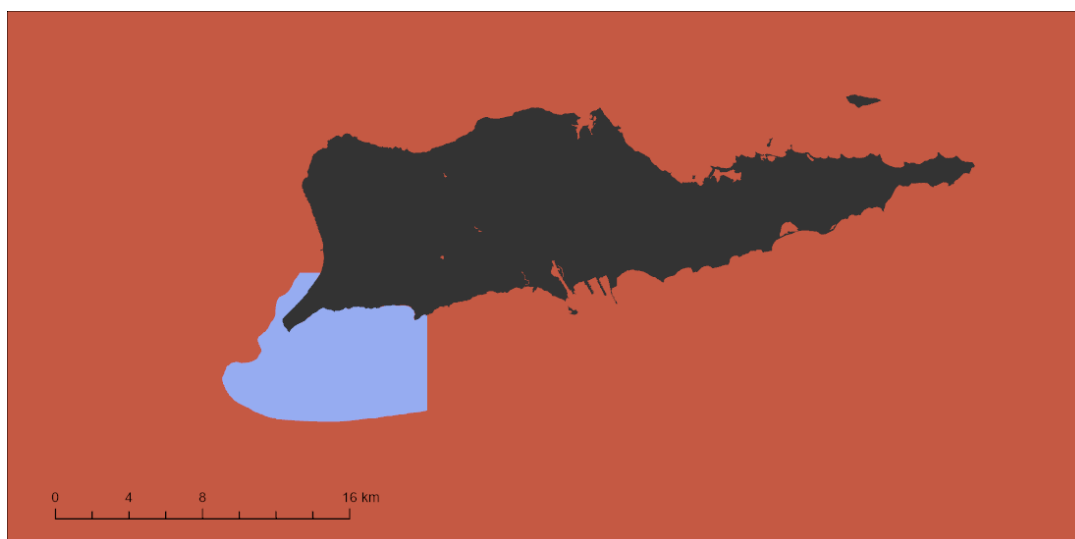
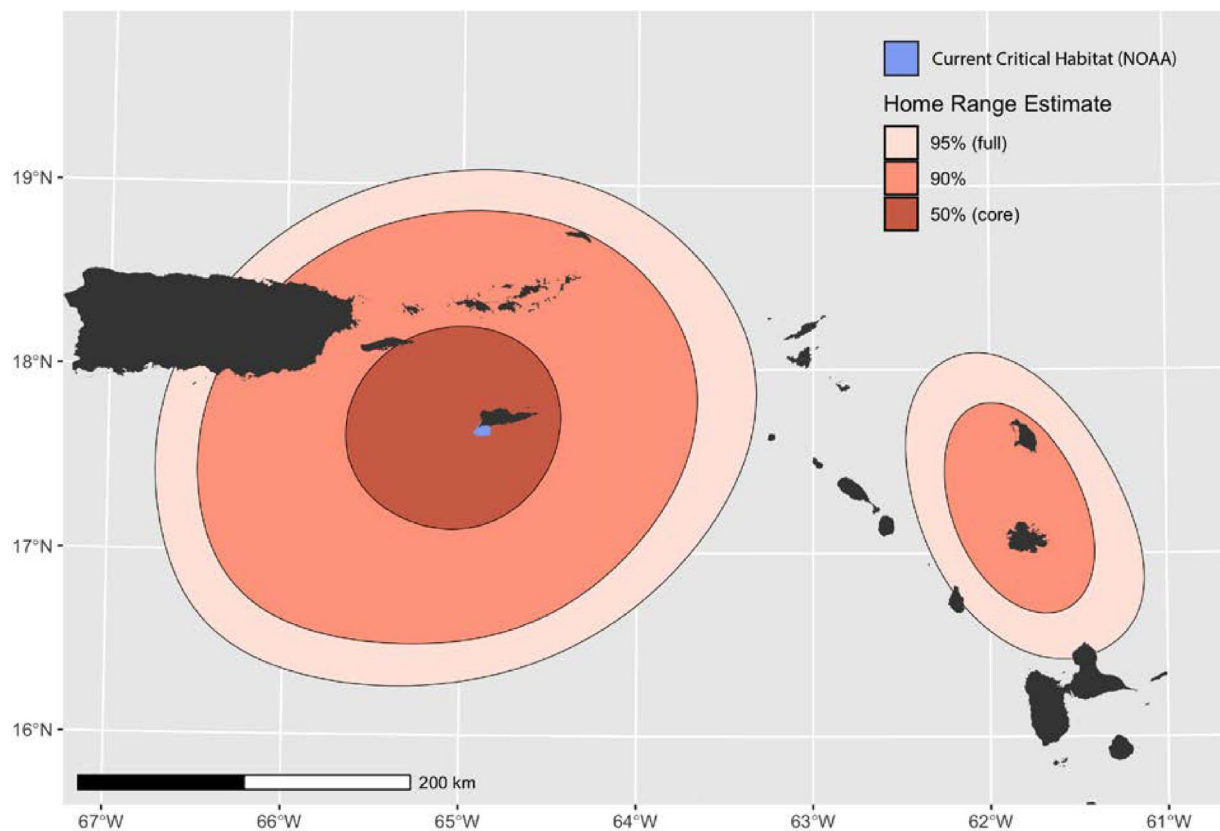
Finally, based on the amount of directed movement behavior, this study suggests that predator encounters may be influential in leatherback reproduction, movement, and habitat use. Predator interaction, or the risk of predator interaction, may drive leatherbacks to skip a nesting event, lay fewer clutches in a season, and move with rapid transit behavior across a broad habitat area. Future work should examine tiger shark abundance and distribution around St. Croix and their overlap with nesting leatherbacks.

The results of this study provide a more robust understanding of leatherback nesting and internesting behaviors. They suggest the importance of continued nesting beach monitoring and examination of internesting behaviors. The findings highlight the need for expanded protections for leatherback critical nesting habitat, increased regional collaboration, and expanded studies that examine leatherback-predator interactions during the nesting season.

APPENDIX A

Supplementary Figures

Supplementary Figure 1. Relationship between move persistence (γ_t) by seafloor depth (m) for leatherback locations during the interesting interval.



Supplementary Figure 2. Maps of (a) 50% (red), 90% (orange), and 95% (pink) PKDE home range estimates, with existing NOAA-designated Critical Habitat for leatherbacks denoted with a purple polygon and (b) St. Croix with NOAA Critical Habitat in purple.

*Supplementary Tables***Supplementary Table 1. Location class accuracy for Argos-derived positions.**

Argos Location Class	Estimated Accuracy
LC - 3	better than 250 m radius
LC - 2	better than 500 m radius
LC - 1	better than 1500 m radius
LC - 0	over 1500 m radius
LC - A	no accuracy estimation
LC - B	no accuracy estimation
LC - Z	no accuracy estimation

Supplementary Table 2. Parameters for best-fit autocorrelation model.

Flipper Tag Number	PTT ID	Name	Autocorrelation model	Position autocorrelation timescale / Home crossing time (days)	Velocity autocorrelation timescale (minutes)	Diffusion (km²/day)
SPP002	181165	Ann	OU error	2.6 (0.8 - 8.7)	-	539 (431.1 - 658.8)
SPP088	181170	Barb	OUF anisotropic error	27.2 (5 - 146.9)	8.5 (6.5 - 11.2)	151.3 (134.2 - 169.3)
SPP832	181172	Cindy	OUF error	8.3 (1 - 70.8)	29.9 (10.6 - 84.2)	520.6 (357.6 - 713.7)
SPP846	200614	Leona	OUF anisotropic error	14 (3.3 - 59.2)	8.1 (7.2 - 9.2)	428.6 (385.2 - 474.2)
SPP852	181169	Mona	OUF anisotropic error	4.9 (1 - 24.5)	19.6 (11.5 - 33.4)	701.7 (541.9 - 881.8)
SPP862	181168	Nellie	OUF anisotropic error	11.7 (1.2 - 112.2)	1.7 (0.3 - 9.6)	451.1 (362.9 - 548.8)
SPP319	181166	Spot_STX	OUF anisotropic error	32.7 (3.1 - 344.3)	33.5 (21.8 - 51.4)	998.5 (818.8 - 1,195.9)
		Spot_Antigua	OUF anisotropic error	-	-	1,582.1 (1,090.8 - 2,163.2)
SPP380	181167	Sunshine	OUF anisotropic error	9.5 (1.4 - 66.7)	18.7 (9.1 - 38.4)	1,871.4 (1,414.2 - 2,391.7)
SPP353	181171	Tito	OUF error	5.8 (2.2 - 15)	-	152.6 (95.2 - 244.5)
SPP421	200615	Winona	OUF anisotropic error	5.5 (1.1 - 27.8)	32.7 (26.8 - 39.9)	703.5 (542.9 - 884.6)

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