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In search of the "missing majority" of nesting loggerhead turtles: improved inter-seasonal recapture rates through subpopulation-scale genetic tagging

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Abstract

Capture–mark–recapture (CMR) studies on marine turtle nesting beaches provide data on reproductive periodicity that inform population trends and models. Annual survival is estimated from observations of remigration, the return of females in subsequent nesting seasons. However, a significant proportion of tagged females are never encountered remigrating in many studies, presumably due to weak nest site fidelity (NSF). We employed a genetic CMR approach based on subpopulation-scale clutch sampling to conduct a 5-year evaluation of inter-seasonal recapture rates and NSF for Northern Recovery Unit loggerhead turtles (*Caretta caretta*). Of 1770 females genetically tagged from Georgia through Maryland in 2010, 1156 (65%) remigrated between 2011 and 2015. Inter-seasonal NSF, measured as shifts in median latitude nesting locations between years, was highly variable among individuals but strong overall (mean: 15.08 ($\pm$44.61) km, median: 1.84 km). Among three focal beaches with nocturnal tagging projects, 69 of 173 females (40%) remigrated onsite whereas 115 (66%) were detected overall. Regional genetic sampling therefore yielded significantly higher inter-seasonal recapture rates, which may improve precision in future survival analyses. However, despite sampling ~ 1000 km with high annual detection probabilities ($p* \geq 0.94$), 35% of 2010-females were not detected remigrating. Several non-exclusive hypotheses to explain these remaining "missing" remigrants should be considered: longer remigration intervals, imperfect detection within the study area, emigration to Florida, anthropogenic mortality, and natural mortality or senescence. This genetic tagging approach can be applied over large spatial scales where nesting densities permit, better characterizing inter-seasonal dispersal.

Introduction

Marine turtles exhibit complex life cycles. Nesting females represent the most accessible life-history stage, and individual nesting histories generated by capture–mark–recapture (CMR) tagging projects on nesting beaches inform adult female abundance indices, trends, and survival estimates for

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population models. Important reproductive parameters that can be derived from CMR data include clutch frequency (the number of clutches a female lays during a reproductive year), and remigration interval (the number of years between successive reproductive seasons). Further, tracking females over multiple nesting seasons provides a basis for estimating annual survival. However, females encountered during a single nesting season can comprise a large proportion of tagged individuals, potentially confounding survival analyses.

Early CMR studies documented fidelity of females to specific nesting beaches within and between reproductive years (Baldwin and Lofton 1940; Hendrickson 1958; Carr 1960). However, as long-term data began to accumulate, it became clear that a significant proportion of females were never encountered again following their tagging year. Hughes (1974) lamented that the majority of loggerhead turtles (*Caretta caretta*) tagged in South Africa were never seen in subsequent years, prompting the hypothesis that

a large segment of the population may become reproductively senescent after just one breeding season. This pattern has persisted over four decades of tagging at this site, with 79% of females detected in only a single nesting season, and an additional 15% encountered in only two nesting seasons (Thorson et al. 2012). In discussing this pattern for green turtles (*Chelonia mydas*) nesting at Tortuguero, Costa Rica, Carr (1980) referred to these females that were never encountered remigrating as the "missing majority." He offered several potential hypotheses: weak site fidelity, anthropogenic mortality, mortality due to stress or predation following nesting, and reproductive senescence. Forty years later, evaluating these hypotheses remains challenging given logistical constraints.

Low inter-seasonal recapture rates are common in many loggerhead turtle CMR datasets globally, with remigrants (females observed nesting in previous years) typically representing < 25% of tagged females in most CMR studies (Table 1). In parts of the world where loggerhead turtles nest along continental coastlines, such as the southeastern United States, logistical constraints limit tagging to a small fraction of essentially continuous nesting habitat. Thus, weak nest site fidelity (NSF) and "offsite" nesting have been implicated to explain low observed remigration rates (Monk et al. 2011; Lamont et al. 2014; Phillips et al. 2014). Richardson (1982)

Table 1 Nesting female loggerhead turtles tagged and recaptured in subsequent nesting seasons (remigrants)

Beach	Interval	Total tagged	Remigrants	Rem Int	Survival	NSF	Sources
St. Joseph Peninsula, Florida, USA	1998–2011	433	31	4.4	0.86 (0.75–0.93)	Yes	Lamont et al. (2014)
Casey Key, Florida, USA	NA	NA	28	3.7 (± 2.1)	NA	NA	Tucker (2010)
Keewaydin Island, Florida, USA	1990–2009	841	161	3.2 (± 1.82)	0.73 (0.69–0.76)	No	Phillips et al. (2014)
Melbourne Beach, Florida, USA	1972–1978	2910	149	2.71 (± 0.90)	NA	NA	Bjorndal et al. (1983)
Melbourne Beach, Florida, USA	1982–2012	6341	837	NA	NA	NA	Ehrhart et al. (2014)
Little Cumberland Island, Georgia, USA	1964–1975	727	241 (453)[a]	2.54 (± 0.86)	NA	NA	Richardson et al. (1978)
Jekyll Island, Georgia, USA	1958–1961[b]	72	7	NA	NA	NA	Caldwell (1962)
Wassaw Island, Georgia, USA	1973–2011	1164	163	NA	0.87 (0.84–0.89)	Yes	Pfaller et al. (2013, 2018)
Kiawah Island, South Carolina, USA	1973–1976[c]	129	3 (21)[d]	NA	NA	NA	Talbert et al. (1980)
Bald Head Island, North Carolina, USA	1991–2006	415	67	2.84	0.85 (0.78–0.93)	Yes	Monk et al. (2011)
Northern Recovery Unit, USA	2010–2015[e]	1770	1156	2.67 (± 0.89)	NA	NA	Present study
Potamakia Beach, Cephalonia, Greece	1985–1989[f]	23	10	NA	NA	NA	Hays and Sutherland (1991)
Kwazulu-Natal, South Africa	1965–2009	12,774	2721	3.0 (± 2.2)	0.80 (0.72–0.86)	Yes	Thorson et al. (2012), Nel et al. (2013)
Senri Beach, Minabe, Japan	1991–2001[g]	443	108	2.7 (± 1.0)	NA	NA	Hatase et al. (2004)

Interval is the span of years during which tagging and resighting occurred. Many of these were truncated due to short tagging duration (where possible) to allow females sufficient time to remigrate. Rem Int is the mean remigration interval in years (reported or calculated based on raw data presented) or the estimated interval based on reported transition probabilities from open robust design models. Survival is the apparent annual survival estimate (and 95% confidence intervals) for nesting females generated from capture-mark-recapture analyses. NSF (nest site fidelity) indicates whether or not emigration was explicitly accounted for in the model structure for survival estimates

[a]Number within parentheses indicates total presumed remigrants due to inclusion of tag scarred individuals. Number without parentheses were individually identifiable

[b]Numbers reference individuals tagged in 1958 and resighted in 1960 and 1961

[c]Numbers reflect females tagged in 1973 and 1974 and resighted through 1976

[d]Number within parentheses indcates presumed remigrants due to inclusion of tag-scarred individuals. Number without parentheses were individually identifiable

[e]Numbers indicate females genetically tagged in 2010 and resighted through 2015

[f]Numbers indicate females tagged in 1985 and resighted through 1989

noted individual variation among female loggerhead turtles nesting on Little Cumberland Island, Georgia, USA. "Alpha" females were apparent neophytes (those arriving without tags or tag scars) that were never subsequently recaptured, whereas "beta" females were encountered laying more clutches and were more likely to be observed remigrating. These observations suggest that females with weaker intra-seasonal NSF may also exhibit weaker NSF across nesting seasons as well.

Data on the scale of and variation in NSF across remigrations are sparse for emigrant females due to low recapture rates. Historically, data sharing among several nighttime-tagging projects in the southeastern United States provided some insight. Of 1100 females tagged on Wassaw Island, Georgia from 1973 through 2000, only 114 returned to Wassaw Island in subsequent years (Williams and Frick 2001). Eighteen females were detected emigrating in subsequent reproductive seasons, dispersing as far south as Cumberland Island, Georgia (118 km) and as far north as Folly Beach, South Carolina (130 km) (Williams and Frick 2001). Conversely, 35 females initially tagged elsewhere (up to 125 km away) were recaptured nesting on Wassaw Island in later years (Williams and Frick 2001). Similarly, early tagging data from Melbourne Beach, Florida detected inter-seasonal dispersal up to 700 km, although this was considered an extremely rare case with most tag returns reflecting more local nesting dispersal along the Atlantic coast of central Florida (Bjorndal et al. 1983). These observations demonstrate that some proportion of the nesting population uses multiple beaches across reproductive years. However, contextualizing this dispersal remains challenging due to low tagging coverage relative to available nesting habitat, differences in nesting densities and tagging intensities among study sites, tag loss, and inconsistent resighting effort.

The southeastern United States loggerhead nesting aggregation comprises at least seven subpopulations based on mitochondrial DNA frequency variation (Shamblin et al. 2012). The northernmost of these has been designated the Northern Recovery Unit (NRU), and its females nest on barrier island beaches along the Atlantic coast from Georgia through Maryland (NMFS and US FWS 2008). There are four active nighttime-tagging projects in this region, operating on: Jekyll Island, Georgia; Wassaw Island, Georgia; Bald Head Island, North Carolina; and Bear Island, North Carolina. These beaches represent ~ 4% of the available NRU nesting habitat and host 5–6% of annual nest counts for the subpopulation (Online Resource Table S-1). As with other southeastern United States subpopulations, apparent neophytes comprise the majority of females encountered on these tagging beaches (Table 1).

We previously used a genetic tagging approach via clutch sampling to characterize clutch frequency and intra-seasonal NSF for this subpopulation (Shamblin 2017).

Among 4677 females that were detected laying at least two clutches within a season from 2010 to 2012, 58% laid all detected clutches within 5 km, and 78% laid all detected clutches within 20 km (Shamblin et al. 2017). Variation in NSF was apparent across the subpopulation nesting range, with a larger proportion of females exhibiting weak NSF in northern South Carolina through Virginia than among those nesting in southern South Carolina and Georgia (Shamblin et al. 2017).

Here, we extended this genetic tagging approach to provide a 5-year evaluation of inter-seasonal NSF and recapture rates for females nesting along ~ 1000 km of coastline from 2010 through 2015. We explored several questions about emigration germane to remigration detection and survival estimation that have previously been intractable due to logistical and methodological constraints. (1) To what extent does local emigration account for the "missing majority" of remigrant NRU females? (2) Do observed inter-seasonal recapture rates vary spatially across the subpopulation range? (3) Is the likelihood of subsequent inter-seasonal recapture influenced by intra-seasonal NSF and observed clutch frequency (OCF, at focal beach and subpopulation scales)? (4) At what spatial scales do females distribute their nesting effort across nesting seasons?

Materials and methods

Study site and sampling

The study site and sampling protocol were previously described in detail in intra-seasonal analyses covering the 2010–2012 nesting seasons (Shamblin et al. 2017). All projects conducting morning nest count surveys from the Florida-Georgia border through Maryland collected an egg from all detected loggerhead turtle clutches from 2010 through 2015 (Fig. 1). Surveys covered ~ 1000 km of beach, representing ~ 93% of barrier island nesting habitat in the region (Table S-1 in Online Resource 1). In most cases, participants collected a single egg from each clutch the morning following oviposition. Some beaches in South Carolina were surveyed less frequently due to logistical constraints. Depredation rates were high on these beaches, and depredated eggshells were collected where possible. For any identified "wild" nests (those not detected until hatchlings emerged), participants collected eggshells from undeveloped eggs and/or dead hatchling tissue during nest inventories.

Individual assignment

We previously assigned clutches to individual nesting females from 2010 and 2012 (Shamblin et al. 2017). Here, we extended this approach by assigning clutches to

Fig. 1 Study area map reflecting the recognized nesting habitat of Northern Recovery Unit loggerhead turtles. Black bars and numbers indicate latitudinal zones for characterizing recapture rates of females genetically tagged in 2010. Stars indicate the tagging beaches of Jekyll Island (JEK), Georgia; Wassaw Island (WAS), Georgia; and Bald Head Island (BHI), North Carolina. This map was created using the maptool function in www.seaturtle.org
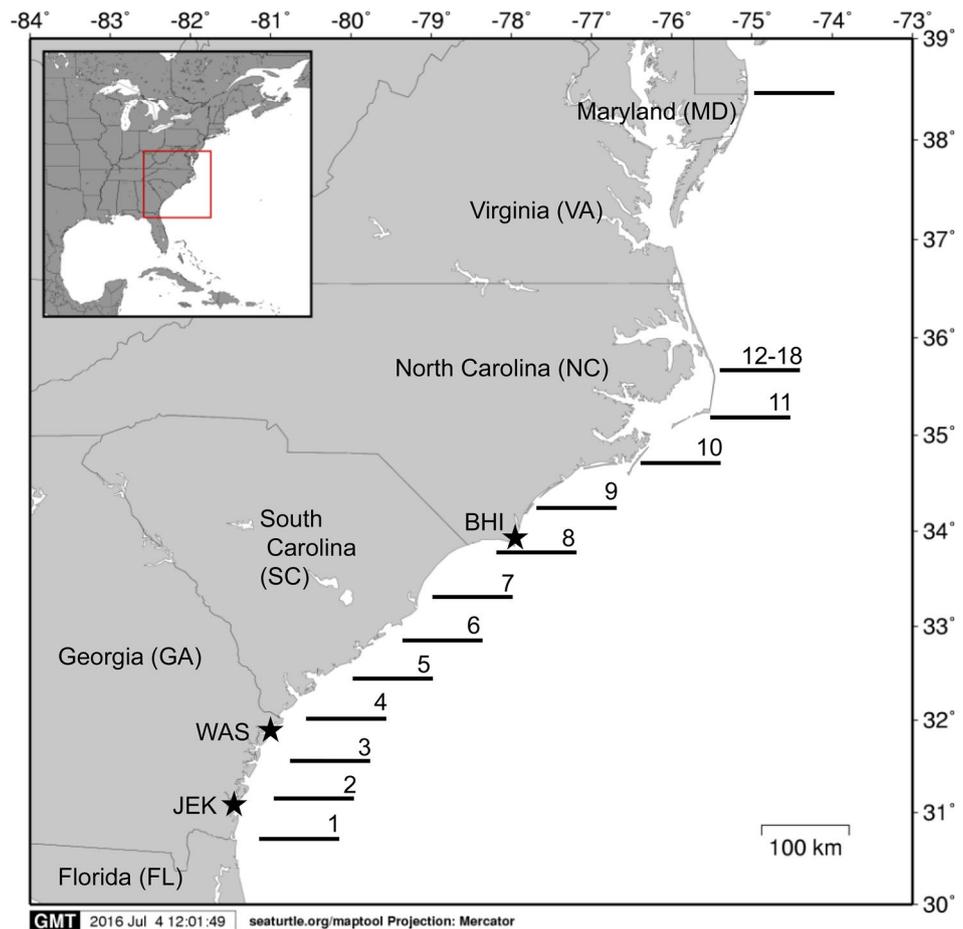
individual females from 2013 through 2015. We extracted maternal genomic DNA from eggshells using a modified Qiagen DNEasy tissue extraction protocol (Shamblin et al. 2011b) and genotyped samples at 18 microsatellite loci (Shamblin et al. 2007, 2009) (Table S-2 in Online Resource 1). Maternal genomic DNA was amplified in 10-µl reactions using PCR cycling conditions previously described (Shamblin et al. 2017). Beginning in 2015, clutches were genotyped at 16 of these loci in three multiplex PCR reactions (See Table S-3 in Online Resources 1 for primer concentrations and PCR dilutions). This was because despite several attempts at primer design, two loci (CcP2F11, CCP7E05) were ultimately dropped for being incompatible in multiplexes.

We assigned clutches to individual females through a matching protocol using the program CERVUS (Kalinowski et al. 2007) (Table S-4 in Online Resource 1). The pilot study identified two common sources of mismatches between eggshell-derived and skin-derived maternal DNA: allele dropout and the presence of non-maternal (presumably paternal) alleles (Shamblin et al. 2011b). We, therefore, chose a threshold of acceptable genotyping error that avoided the need for extensive reanalysis but still provided

strong individual resolution. Samples that perfectly matched across at least ten loci and had no more than two single allele mismatches at additional loci were considered to represent the same nesting female. The non-exclusion probability of sibling identity of the ten least informative loci was 1.0×10^{-5}. Samples that failed to match a consensus genotype or another sample by the end of each nesting season were subjected to a second round of DNA extraction and genotyping. If both extractions matched one another by the above criteria, they were considered to represent a new nesting female. This approach cannot differentiate among identical twins, but given the rarity of twinning in loggerhead turtles (Piovano et al. 2011) and presumably high mortality rates for neonate turtles, we considered the likelihood that twins would survive to reach sexual maturity negligible. Samples from depredated nests or post-emergence inventories were initially treated as maternal for direct comparisons. Any genotypes that failed to meet direct comparison thresholds were treated as embryonic and compared with maternal consensus genotypes via parentage analysis using CERVUS (Kalinowski et al. 2007). See Online Resource 2 for a more complete description of sample types and assignment approaches.

Inter-seasonal recapture rates and nest site fidelity

The 2010 nesting cohort provided a basis for characterizing an overall inter-seasonal recapture rate, observed remigration intervals, and a preliminary mean remigration interval over the 5-year recapture window. Based on observed remigration interval means and ranges reported globally (e.g., Schroeder et al. 2003), this 5-year interval should have been sufficient to allow the majority of females to remigrate at least once. All remigrations by these females over the period were included in the estimate. For each turtle-by-year observation, we generated a median nesting location (MNL) to represent a rough index of each female's nesting effort within a year in a spatially explicit context (Fig. 2). For any turtle-by-year observation with an odd number of encounters, this represented the female's median latitude nest site. For any turtle-by-year observation with an even number of encounters, the MNL was a new point representing the average between the two median latitude nest sites.

We initially calculated three intra-seasonal NSF indices for each female-by-year observation where at least two clutches were detected: (1) average (arithmetic mean) distance between clutches and the MNL (avg dMNL), (2) median distance between clutches and the MNL (med dMNL), and (3) nesting extent (NE)—the greatest distance between detected clutches. These were great-circle distances (the shortest distance between nesting locations that accounted for the curvature of the earth's surface). We characterized NSF for all females that nested in 2010 and remigrated at least once between 2011 and 2015, including multiple remigrations where available (Online Resource 1, Table S-5). Great circle distances between remigration MNLs relative to the most recently detected MNL (Rem Dist) provided an index of spatial shifts in nesting distribution between nesting seasons. We compared each of the three intra-seasonal indices for turtle-by-year observations with its associated inter-seasonal MNL displacement using Spearman's rank correlation. Given strong correlation among the three intra-seasonal indices and similar correlation values between all intra-seasonal and Rem Dist comparisons (Table S-6 in Online Resource 1), we focused on NE for simplicity and its precedence in previous studies (Tucker 2010; Shamblin et al. 2017). To minimize potential artifacts due to imperfect detection of clutches, we repeated these analyses for a

Fig. 2 Nest locations and illustration of intra-seasonal and inter-seasonal nest site fidelity indices for female CC000903. 2010 NE is the nesting extent—the maximum extent between clutches detected that year. MNLs are median nesting locations for each respective detection year. Rem Dist is the distance between these MNLs
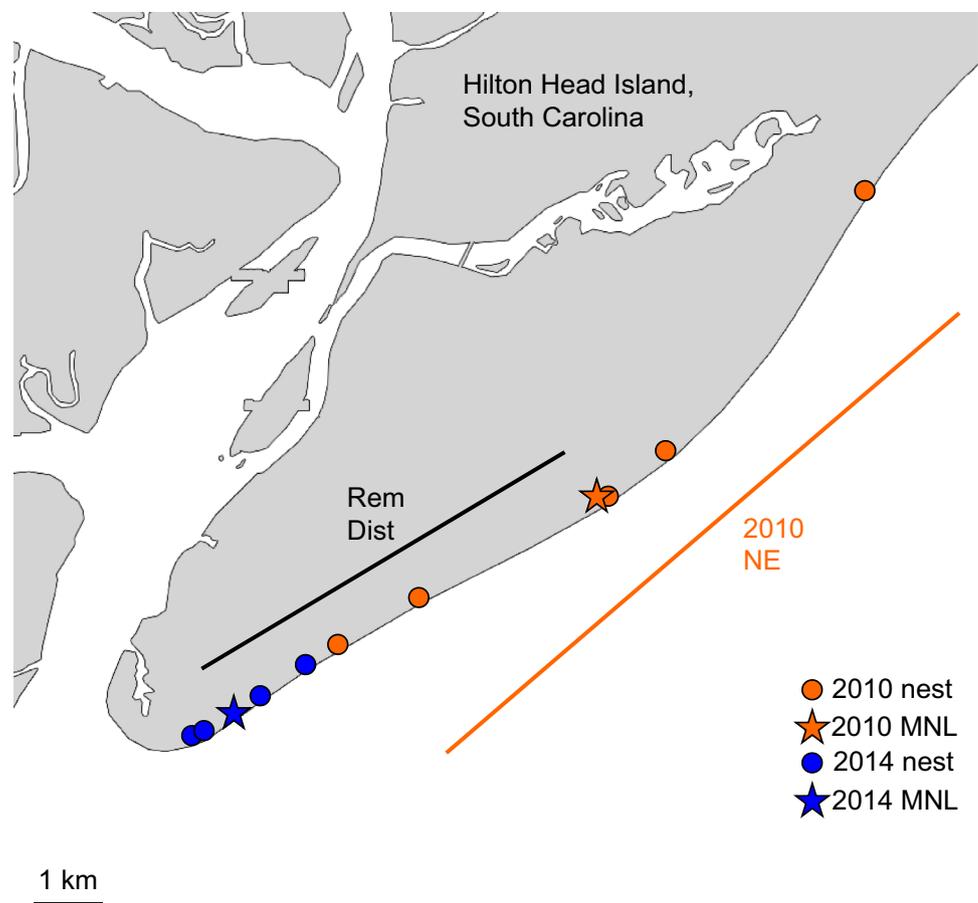
filtered dataset that included only females detected laying a minimum of four clutches during both nesting years.

To assess spatial variation in recapture rates across the subpopulation, we subdivided the study area into latitudinal zones (0.45 decimal degree spans, ~ 50 latitude km) and assigned each 2010-nesting female to a zone based on her MNL that year (Fig. 1), irrespective of where she was detected upon remigration. For each zone, we quantified: (1) the number of individual females, (2) the number of females detected laying only one clutch in 2010, and (3) the recapture rates for both (1) and (2). We tested for differences in recapture rates (proportion of remigrants) using a two-proportion z-test.

Finally, we explored whether OCF or NSF influenced subsequent remigration detection. Because females detected laying only a single clutch provide no data on intra-seasonal NSF, we considered OCF a potential proxy for NSF (i.e. that females detected laying only a single clutch may have also nested outside the study area). We compared OCF during 2010 for females that subsequently remigrated vs. those that were not detected in subsequent years. We also compared NSF (based on 2010 NE) for both groups of females. We tested for differences using Mann–Whitney U tests, hypothesizing that OCF would be larger and NE smaller for remigrants relative to females detected only in 2010.

Recaptures and nest site fidelity of 2010 focal beach females

Females nesting on the nighttime-tagging beaches ('focal beaches' hereafter) provided an opportunity to assess the effects of NSF (within and between years) on inter-seasonal recaptures from the perspective of each beach. We quantified recapture rates and calculated NSF indices and OCF for all females that nested on one of focal beaches in 2010 (Online Resource 1, Table S-7). We included females that nested on Jekyll Island, Georgia; Wassaw Island, Georgia; and Bald Head Island, North Carolina; but not Bear Island, North Carolina due to small sample size (12 females, 3 remigrants). One group comprised only those females that returned to nest at least once on the focal beach upon remigration (onsite remigrants). The second group subsequently nested elsewhere (offsite remigrants). For simplicity, only the immediately subsequent remigration following 2010 was

used for group assignments and calculations. However, any additional onsite and offsite remigrations were tallied.

Because our focus was on NSF (and not tagging methodology), all females that nested on these beaches (or were encountered and genetically sampled during non-nesting emergences) were included, regardless of whether they were identified by physical encounter or via genetic tagging. The number of females detected only during non-nesting emergences was small. Similarly, focal beach OCFs included any genetically assigned nests where the female was not encountered. We tested for differences in recapture rates between the focal beach and regional perspective using two-proportion z tests. We compared the 2010 NEs, 2010 OCFs, and Rem Dists for subsequent onsite remigrants and offsite remigrants for each focal beach using Mann–Whitney U tests. We hypothesized that onsite remigrants would have lower NEs, higher OCFs, and lower Rem Dists relative to females that remigrated elsewhere.

Results

Observed remigrations and inter-seasonal recapture rates

Beach survey projects recorded 41,957 loggerhead turtle clutches on the Atlantic coast of the United States north of Florida during 2010–2015. Of 41,576 nests for which genetic samples were available, we assigned 41,065 (98% of those recorded and 99% of those sampled) to 8074 individual females (Online Resource 1 Table S-4). The proportion of newly identified females declined annually and reached 32% by 2015 (Table 2). Of the 1770 females that nested in 2010, 1156 females (65%) remigrated at least once over the 5-year recapture period. Two-year and three-year remigrations were the most commonly observed intervals (Table 3), with a mean observed remigration interval of 2.67 (± 0.89 SD) years.

Observed remigration rates varied spatially across the study area (Table 4). Moreover, inter-seasonal recapture rates for single-clutch females were universally lower at the latitudinal zone scale than those for females that laid multiple clutches (Table 4). This difference was particularly apparent in the northern zones 9–18, where single-clutch females comprised a large proportion of individuals.

Table 2 Northern Recovery Unit loggerhead turtle clutch and individual female summary data

	2010	2011	2012	2013	2014	2015	Total
Clutches recorded	5770	6966	7946	8752	3834	8689	41,957
Clutches assigned	5587	6844	7790	8575	3753	8516	41,065
Females identified	1770	1972	2389	2475	1041	2380	8074
Proportion new females	1	0.987	0.824	0.484	0.416	0.321	

Table 3 Observed remigration intervals for 1156 female loggerhead turtles genetically tagged in the 2010-nesting cohort that returned for 1639 remigrations through the 2015 nesting season

	2011	2012	2013	2014	2015
1-year	26	6	35	6	4
2-year	–	385	12	128	162
3-year	–	–	540	0	130
4-year	–	–	–	114	0
5-year	–	–	–	–	91

Table 4 Observed remigration rates through 2015 for female loggerhead turtles genetically tagged in 2010

| Zone	N	SCF	Rem %	SCF Rem %
1	194	33	60.3	39.4
2	172	26	68.6	38.5
3	149	13	66.4	38.5
4	201	42	72.1	57.1
5	307	49	71.2	44.9
6	431	82	68.4	45.1
7	26	7	53.8	42.8
8	77	11	67.5	45.5
9	113	36	47.8	13.8
10	51	13	49.0	23.1
11	40	20	37.5	13.3
12–18	9	2	22.2	0.0

Individuals were grouped into latitudinal zones based on their geometric median nesting location in 2010, regardless of where they were encountered upon remigration. N was all females that nested in each zone in 2010. SCF were females detected laying a single clutch in 2010. Rem % is the proportion of 2010-identified females that remigrated from 2011 to 2015. SCF Rem % is the proportion of 2010 SCF females that remigrated from 2011 to 2015

Females nesting in these zones ($n = 213$) exhibited significantly lower inter-seasonal recapture rates than those that nested in zones 1–8 ($n = 1557$, $z = 6.50$, $p < 0.0001$).

Rem Dists were highly variable among individuals, ranging from 0.01 to 581.22 km (Online Resource 1 Table S-5). The mean Rem Dist was 15.08 (± 44.61 SD) km, $n = 1639$, with a median displacement of 1.84 km. The majority of remigration MNLs (70%) fell within 5 km of the previous observation year MNL, with 87% occurring within 20 km of the previous MNL (Fig. 3). NSF indices were available from 1492 female-by-year records in which the female nested at least twice within a season and later remigrated during the study period. NE was significantly correlated with MNL displacements (Spearman, $r_s = 0.503$, $p < 0.0001$), though there was considerable individual variation (Fig. 4). The filtered dataset consisting of female-by-year detections with four or more clutches yielded Rem Dists ranging from 0.01 to 225.73 km (mean = 6.01, SD = 19.26 km, median: 1.16 km, $n = 734$). Among these, 83% of Rem Dists fell within 5 km of the previous detection year MNL, and 94% fell within 20 km. NE and Rem Dist were significantly correlated (Spearman, $r_s = 0.557$, $p < 0.0001$).

Females that subsequently remigrated exhibited significantly stronger intra-seasonal NSF in 2010 (NE mean = 24.5, SD = 63.2 km, $n = 1026$) than those not detected remigrating (NE mean = 56.08, SD = 107.15 km, $n = 415$; $U = 264,210$, $p < 0.0001$). The 2010 OCF for subsequent remigrants (mean = 3.42, SD = 1.39 clutches per female, $n = 1156$) was significantly higher than for those not detected remigrating over the study period (mean = 2.64, SD = 1.49 clutches per female, $n = 614$; $U = 248,570$, $p < 0.0001$). Of the 334 females that were

Fig. 3 Distances between median nesting locations (Rem Dist) over 1639 consecutive remigrations by 1156 Northern Recovery Unit loggerhead turtles
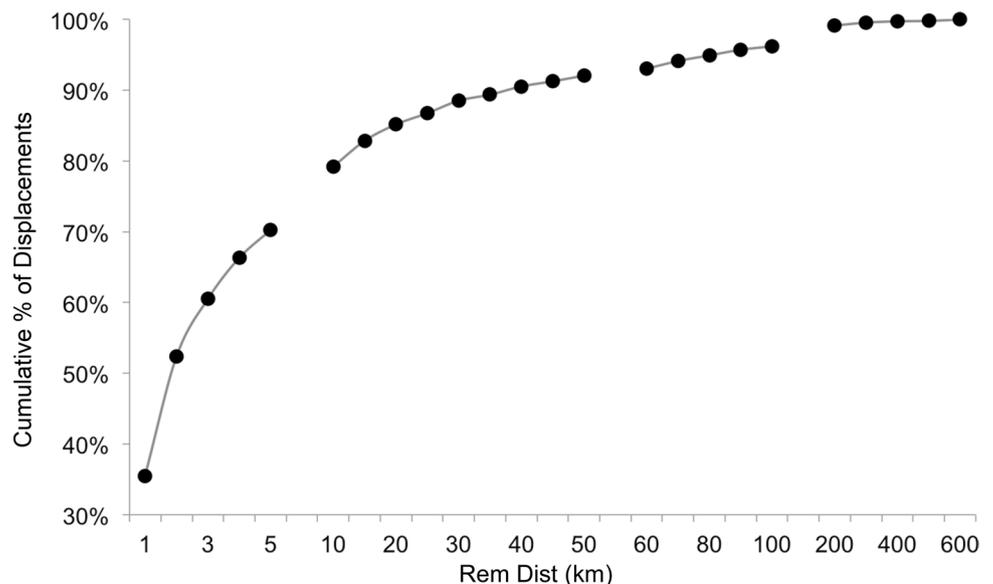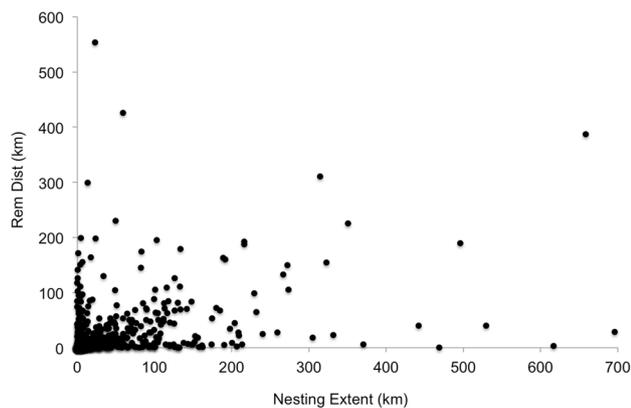
Fig. 4 Scatterplot of Rem Dist, the distance between median nesting locations between years, expressed as a function of nesting extent, the largest distance between clutches within a nesting season, for 1492 remigrations where two or more clutches were detected in the initial nesting year
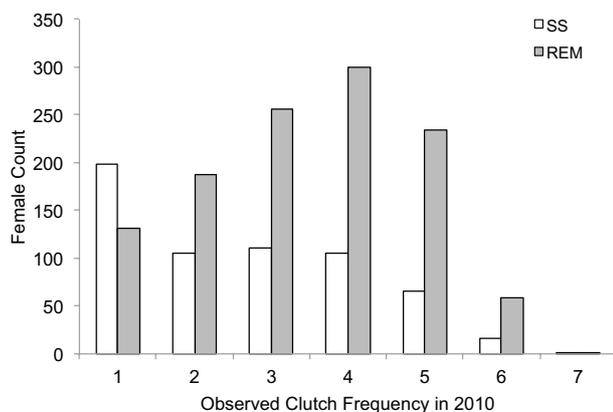

Fig. 5 Observed clutch frequency distribution for females genetically tagged in 2010. SS indicates females detected only during 2010 ($n = 614$). REM denotes females that were subsequently detected remigrating between 2011 and 2015 ($n = 1156$)

detected laying just a single clutch in 2010, only 40% were subsequently recorded as remigrants (Fig. 5).

Recaptures and nest site fidelity of focal beach females

Of 173 females that nested on the three focal beaches in 2010, 69 (40%) returned to their focal beaches and 115 (66%) were detected remigrating overall during the 5-year recapture window (Table 5). The relative proportion of detected remigrants that emigrated vs. returned onsite was variable among focal beaches (Jekyll: 31%, Wassaw: 42%, Bald Head: 50%). These offsite detections yielded significantly improved recapture rates relative to those from the focal beach perspective: Jekyll: 61% vs. 42% (z: 1.84,

$p = 0.0327$), Wassaw: 71% vs. 41% (z: 3.55, $p < 0.001$), Bald Head: 63% vs. 32% (z: 2.59, $p = 0.005$). Twenty-three females were detected during one additional remigration during the study period. Among these, 17 repeated their previous behavior. However, two females from each beach initially remigrated onsite but subsequently emigrated.

Subsequent onsite remigrants exhibited significantly stronger intra-seasonal NSF in 2010 (as expressed by NE) than did those that emigrated (Table 5, Jekyll: $U = 57$, $n1 = 24$, $n2 = 11$, $p = 0.021$; Wassaw: $U = 228$, $n1 = 31$, $n2 = 23$, $p = 0.013$; Bald Head: $U = 23$, $n1 = 12$, $n2 = 11$, $p = 0.004$). As expected, females that remigrated onsite also displayed significantly smaller Rem Dist than those that remigrated elsewhere (Table 5, Jekyll: $U = 51.5$, $n1 = 25$, $n2 = 11$, $p = 0.002$; Wassaw: $U = 244$, $n1 = 32$, $n2 = 23$, $p = 0.017$; Bald Head: $U = 32$, $n1 = 12$, $n2 = 12$, $p = 0.011$). In each case, females that laid only a single clutch on the focal beach were more likely to emigrate rather than return. OCF on each focal beach was significantly higher for females that subsequently remigrated onsite relative to those that emigrated (Table 5, Jekyll: $U = 36$, $n1 = 25$, $n2 = 11$, $p < 0.001$; Wassaw: $U = 174.5$, $n1 = 32$, $n2 = 23$, $p < 0.001$; Bald Head: $U = 30.5$, $n1 = 12$, $n2 = 12$, $p = 0.009$).

Discussion

Improved inter-seasonal recapture rates

With one exception, published long-term CMR datasets from the southeastern United States have yielded observed remigration rates < 25% (Table 1). The regional genetic tagging approach from our study detected 65% of 2010-nesting females remigrating from 2011 to 2015. Given the continuity of nesting habitats over much of this region, weak NSF has been considered a likely explanation for low recapture rates from the focal beach perspective (Monk et al. 2011). Regional genetic tagging confirmed that emigration explained 44% of these "missing" females. Emigration of this magnitude at the focal beach scale has important implications for survival analyses. Survival estimates can be negatively biased if site fidelity is not explicitly accounted for in the model structure (Pradel et al. 1997; Hines et al. 2003). This may explain, in part, the large difference in apparent survival estimates reported for two Florida loggerhead subpopulations that were otherwise analyzed using the same open robust design framework (St. Joseph Peninsula and Keewaydin, Table 1).

Creating artificial age structure within marine turtle survival models is a common approach to account for weak NSF behavior. Individuals are classified as "transients" (females detected only once) or "residents" (females that are detected at least twice) (Rivalan et al. 2005). This approach

Table 5 Spatial summary statistics and clutch detections for 173 loggerhead turtle females that nested (or attempted to nest) at least once on a focal tagging beach in 2010

Site	Remigration group	N	SC N	OCF (± SD)	Mean NE (± SD)	Mean Rem Dist (± SD)	Med Rem Dist
JEK	No remigraton	23	10	2.26 (± 1.32)	38.79 (± 52.58)	NA	NA
JEK	Offsite remigrant	11	9	1.27 (± 0.65)	26.56 (± 21.73)	47.91 (± 68.90)	11.19
JEK	Onsite remigrant	25	4	3.29 (± 1.43)	14.67 (± 21.19)	6.02 (± 8.80)	1.87
WAS	No remigraton	23	16	1.87 (± 1.42)	82.04 (± 92.98)	NA	NA
WAS	Offsite remigrant	23	18	1.48 (± 1.08)	55.61 (± 50.29)	25.69 (± 27.36)	17.36
WAS	Onsite remigrant	32	9	2.84 (± 1.59)	43.33 (± 71.11)	11.97 (± 16.71)	3.48
BHI	No remigraton	14	11	1.42 (± 0.93)	105.87 (± 120.40)	NA	NA
BHI	Offsite remigrant	12	10	1.25 (± 0.62)	157.31 (± 91.68)	60.40 (± 71.73)	26.62
BHI	Onsite remigrant	12	4	2.75 (± 1.48)	58.95 (± 97.38)	31.83 (± 60.55)	0.74

Two females nested on two focal beaches in 2010 and were included in analyses ("no remigration") for both focal beaches in both instances. Site codes are explained in Fig. 1. N is the number of females in each observed remigration group, with remigrants returning from 2011 to 2015. SC *N* indicates the number of females that were detected laying just a single clutch (or being detected only once during a non-nesting emergence) on each focal island in 2010. OCF is observed clutch frequency on the focal beach. Nesting extent (NE) is the distance between the most distant detected clutches for each female. Rem Dist represent the mean and median distances between 2010 median nesting locations and subsequent remigration median nesting locations for each group. All distances are in km. Offsite remigrants did not return to their original focal beach during their immediately subsequent remigration following 2010. Onsite remigrants nested at least once on the original focal beach upon remigration

provides more realistic survival estimates for the "resident" females, but often at the cost of dramatically reducing sample sizes, which may result in lower precision for these estimates. Additionally, even this "resident" survival rate may still be negatively biased because females that have permanently emigrated (remigrated offsite, for example) are confounded with those that have died (Monk et al. 2011). The combination of improved clutch detections via regional genetic tagging (Shamblin et al. 2017) and improved interseasonal recapture rates demonstrated in the present study has reduced the proportion of "transient" females while simultaneously reducing the proportion of permanent emigrants from the focal beach perspective.

The fate of remaining "missing" females

Despite confirmation of emigration as the cause of 44% of the "missing majority" of NRU females at the focal beach scale, 35% of the females from the 2010 cohort were not detected remigrating within 5 years. There are several non-exclusive explanations for the large proportion of "missing" remigrants. One possibility is that some females will require more than 5 years to remigrate. The mean observed remigration interval of 2.67 years from this study is broadly consistent with those reported for loggerhead turtles in the southeastern United States and globally (Table 1). However, remigration intervals of six or more years have been reported among Florida tagging projects (e.g., Lamont et al. 2014; Phillips et al. 2014). Simulations have suggested that these likely reflect lack of availability (offsite nesting) or imperfect tagging efficiency on the study beach (nested onsite but not encountered) (Ceriani et al. 2019; Casale and Ceriani

2020). Nonetheless, it is possible that some of these longer observed remigration intervals may reflect true reproductive periodicity, and that some of the "missing" remigrants from this study will require additional years to return.

A second possibility is that the "missing" females represent imperfect detection within the study area. Annual detection probabilities (p^*, the probability that a female was detected at least once during a nesting season) estimated using a robust design approach were high over the study period at the subpopulation scale ($p^* > 0.94$; Shamblin et al. 2017, unpublished data). Whereas generating robust clutch frequency estimates requires detecting a female multiple times over the course of the nesting season, observing remigration requires only a single encounter each nesting season (Schroeder et al. 2003). The proportion of females detected laying only a single clutch was highest in central North Carolina and northward (latitudinal zones 9–18), where inter-seasonal recapture rates were also the lowest (Shamblin et al. 2017, present study). This difference cannot be explained by survey effort, as all of these beaches were monitored under the same protocol as the remainder of the state. We, therefore, consider this an unlikely explanation for a majority of the "missing" remigrants.

A third explanation is that some "missing" remigrants may have emigrated to Florida and were, therefore, unavailable for sampling. Although the Florida/Georgia border was chosen to represent southern boundary of the NRU at the time it was designated (NMFS and US FWS 2008), subsequent mitochondrial DNA analyses suggested that the northernmost counties on Florida's Atlantic coast may represent the southern extent of the NRU or a transition zone (Shamblin et al. 2011a). Of ten females fitted with satellite

tags while nesting along the southern Georgia coast in 2004, one also deposited some clutches in northeastern Florida the same year (Scott 2006). Tag returns have also indicated some degree of connectivity between NRU nesting habitats and Florida as far south as Brevard County, with three females originally tagged in North Carolina recaptured in Florida (Stoneburner and Ehrhart 1981; Ehrhart et al. 2014). Although the number of recaptures is low, they should be considered in the context of the small number of North Carolina females tagged and low resighting effort in Florida. For example, the female recaptured at Canaveral National Seashore, Florida was one of only 15 females that had been tagged at Cape Lookout National Seashore, North Carolina that year (Stoneburner 1981; Stoneburner and Ehrhart 1981). Nesting beaches in Brevard County, Florida fall within the central eastern Florida management unit. These rookeries are significantly differentiated with respect to mitochondrial haplotype frequencies, but share a common lineage (CC-A1.1 frequency in the NRU and central eastern Florida is 100% and 63%, respectively; Shamblin et al. 2012). The central eastern Florida management unit hosts some of the highest nesting densities in the world (Ceriani et al. 2019), so unidirectional dispersal from the NRU to Florida would be impossible to detect with the mitochondrial DNA markers. Given the short time series and absence of sampling in Florida, it was not possible with this dataset to distinguish long-term NRU females that may have emigrated to Florida from vagrant females that regularly nest in Florida but may have deposited a clutch north of Florida.

Some of these "missing" females may represent anthropogenic mortality. Several threats to reproductive females persist in southeastern United States coastal waters where NRU females reside, including fisheries bycatch (Finkbeiner et al. 2011), accidental entrainment by dredges (Ramirez et al. 2017), and watercraft collisions (Foley et al. 2019). Beach strandings are likely poor indicators of mortality given that a large proportion of carcasses are never recovered (Epperly et al. 1996), making it challenging to place these threats in a broader population context. Further, juvenile loggerhead turtles in the southeastern United States exhibit regional natal homing (Bowen et al. 2005), suggesting that both NRU juveniles and adults would be subject to a similar distribution and intensity of threats that would affect reproductive longevity of adult females as well as recruitment. Increasing nest counts on NRU beaches during the study period (e.g. Bolten et al. 2019) suggest that anthropogenic mortality is not likely to account for most of the "missing" remigrants.

Finally, some portion of these females may represent natural mortality or senescence. Carr (1980) suggested that the energetic toll of migration and nesting might lead to increased risk of disease or predation, although he considered such a possibility an unlikely explanation. Should such mortality occur during migration back to their foraging grounds or shortly following arrival, when NRU females are further offshore than during their inter-nesting period (Scott et al. 2013; Griffin et al. 2013), it is plausible that they might be less likely to be encountered as strandings. However, dozens of satellite-tagged loggerheads have migrated along the Atlantic coast of the United States without any indication of such a scenario (Ceriani et al. 2012; Griffin et al. 2013). Alternatively, Hughes (1982) postulated that a segment of the population might nest during a single season but never reproduce again, living on but being reproductively senescent. Although irrefutable given current data, such a scenario would seem highly maladaptive given an estimated minimum age at first reproduction of 22.2–25 years (Avens et al. 2015). The estimated adult stage duration for southeastern United States loggerheads based on skeletochronology exhibited considerable individual variation (range 4–46 years, mean: 19 years). However, as these analyses were based on stranded turtles whose cause of death was typically not determined (Avens et al. 2015), many of these shorter apparent reproductive life spans may represent anthropogenic (rather than natural) sources of mortality.

Nest site fidelity across remigrations

The NRU mean inter-seasonal displacement of 21.1 km was considerably larger than the inter-seasonal nesting dispersal reported for loggerheads nesting at Cape Canaveral in central eastern Florida (3.5 km, Ehrhart 1980) and Kwa-Zulu-Natal, South Africa (5.5 km, Hughes 1974). However, these reported distances were between single clutches and therefore likely captured only a fraction of nesting effort. A small minority of NRU females with extremely large dispersal distances skewed the mean displacement estimate. If similar patterns occur among females nesting along the coasts of Florida and southeastern Africa, they would likely be underrepresented in data generated by tagging patrols that covered ~ 18 and 53 km, respectively (Ehrhart 1980; Thorson et al. 2012). The NRU median displacement of 1.84 km was similar to these previously reported means, suggesting that loggerhead turtle NSF over reproductive seasons may be broadly congruent where populations nest on contiguous habitat along continental coastlines.

Genetic tagging revealed relatively strong NSF for a majority of the females across reproductive years. Nonetheless, even this strong NSF included significant emigration at the scale of individual beaches, roughly congruent with the scale of intra-seasonal nesting dispersal displayed by a majority of these females. NE and Rem Dist were significantly correlated, albeit with considerable individual variation. Tag return data from Wassaw Island immigrants and emigrants previously demonstrated inter-seasonal nesting dispersal across the Georgia barrier islands (Williams and Frick 2001, 2008). Genetic tagging indicated that this

moderate-scale dispersal (20–100 km) was less common than finer scale displacements, but nonetheless occurred in ~10% of remigration detections. Larger-scale shifts were even less common (4% > 100 km), but these are likely underrepresented if Florida nesting accounts for a significant proportion of the remaining "missing" females. These NSF patterns highlight the importance of taking a broader regional perspective for demographic analyses.

At the focal beach scale, females that subsequently remigrated onsite had significantly higher OCF in 2010 than those that returned elsewhere. This pattern conforms to previous observations that female loggerheads detected laying more clutches on a particular beach within a season were also more likely to return there in subsequent nesting seasons (Richardson 1982; Hays and Sutherland 1991; Hatase et al. 2004). Focal beach NSF comparisons confirmed that emigration was the primary driver of this pattern, with onsite remigrants displaying significantly stronger NSF during 2010 as well as significantly shorter Rem Dist shifts across reproductive seasons. At the subpopulation scale, OCF was significantly higher and intra-seasonal NSF was significantly stronger in 2010 for females that remigrated relative to those not detected in subsequent years. These observations are consistent with the hypothesis that some of the "missing" remigrants may have distributed some of their nesting effort outside the study area in 2010 as well as in subsequent nesting seasons.

Future directions

Regional genetic tagging greatly increased the proportion of "resident" females, and accounted for 44% of the "missing" NRU remigrants from the focal beach perspective. The 6-year sampling interval precluded robust estimation of annual survival due to the presence of an unobservable foraging state (e.g., Kendall and Bjorkland 2001). However, with a few additional sampling years, survival analyses are the next step in assessing any potential gains in precision. The regional dataset will also provide an opportunity to determine the impact of subsampling at various spatial scales on annual survival estimates and their precision.

Despite demonstrating the importance of emigration at local scales, a large proportion of females were never detected remigrating. Determining the status of these remaining "missing" remigrants is critical for characterizing the dynamics of this subpopulation and will require additional investigation. Additional sampling years will permit testing of the hypothesis that some females display longer remigration intervals. While we consider imperfect detection within the study area an unlikely explanation, quantifying nest detection error rates via nighttime observational surveys could offer additional insight into this possibility. Although most females exhibited relatively strong NSF

across remigrations, availability constraints cannot be summarily dismissed without additional inquiry. Genetic tagging of Florida clutches as well as supplemental satellite telemetry of NRU nesting females could clarify the magnitude and scale of dispersal between nesting habitats north and south of the Georgia–Florida border.

The NSF indices generated from a 5-year resighting interval in this study represent a first step in characterizing complex NSF behavior. Quantifying shifts in MNL between years provided a first approximation of NSF across remigrations, but this approach obscured complex NSF patterns for some females. Future analyses would benefit from more sophisticated spatial analyses. Furthermore, the majority of females were represented by a single remigration, a small snapshot in time relative to a reproductive lifespan that can encompass more than three decades (Ondich and Andrews 2013; Barreto et al. 2019). Sampling of additional years will be required to determine the consistency of NSF across multiple remigrations. The degree to which the observed variation among individuals may be influenced by previous nesting experience is unclear because the 6-year sampling period precluded assignment of newly identified females as remigrants or neophytes. Additional sampling years should provide sufficient baseline data to facilitate more robust assignment of remigrants and apparent neophytes for comparisons of intra-seasonal and inter-seasonal NSF between groups.

Conservation and management implications

Low inter-seasonal recapture rates impede characterization of remigration intervals and complicate annual survival estimation. Satellite telemetry studies have demonstrated much higher clutch frequency than those detected by tagging patrols, with profound implications for abundance estimation (Tucker 2010; Weber et al. 2013; Esteban et al. 2017). Regrettably, technical limitations (battery life and transmitter and/or antennae fouling, damage, or detachment) typically limit data collection to a single reproductive season. Therefore, inter-seasonal recaptures to inform remigration intervals and survival estimates must still rely on CMR approaches. The genetic sampling demonstrated here provides an approach to collect these data without the need to directly intercept the nesting females, therefore permitting sample collection over larger geographical areas that would be logistically impossible to efficiently cover during tagging patrols. Where nesting densities and logistics permit, genetic tagging via clutch sampling (to supplement traditional CMR or standalone) may reduce the proportion of "missing" females in these studies, elucidating the magnitude and scale of connectivity among nesting habitats across reproductive seasons and potentially providing more robust vital rate estimates.

Compliance with ethical standards

Data availability Spatial and remigration data for individual females are provided in Online Resource 1.

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