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Nest site fidelity and clutch frequency of loggerhead turtles are better elucidated by satellite telemetry than by nocturnal tagging efforts: Implications for stock estimation

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ABSTRACT

Satellite telemetry and ground-based tagging studies are complementary methods to define the spatial and temporal patterns of nesting behavior by migratory sea turtles. Estimates of site fidelity and clutch frequencies are compared for satellite telemetry versus ground truth patrols over a 6 km stretch at a southwest Florida loggerhead (*Caretta caretta*) rookery. Site fidelity ranged from 1.9 km to 109.1 km for all nests deposited by a female within a season. The mean site fidelity was 28.1 km for all nests, but declined to 16.9 km if omitting the first nest. Nest frequency ranged from 2 to 8 nests per season, with a modal value of 5 nests. Satellite telemetry documented a mean nest frequency of 5.4 nests per female in comparison to 2.2 nests detected by monitoring patrols. The remigrant females had higher clutch frequency, were larger in size, and had higher site fidelity compared to newly tagged females. Satellite telemetry provided improved measurements of site fidelity and reveals a need for revised fecundity estimates. If measures of clutch frequency are representative of loggerhead assemblages nesting elsewhere within the South Florida grouping, the confidence bounds on Western Atlantic loggerhead stocks are approximately 32% lower than currently accounted for annual nesting individuals.

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1. Introduction

In deriving population density or abundance estimates for any species, non-biased estimates require adequate sampling regimes that account for behavioral heterogeneity. Sea turtle populations are understandably difficult to quantify at sea, and are usually surveyed at rookeries by counting turtle tracks left on beaches (Witherington et al., 2009) as an accessible index to biologists (Carr, 1980). A premise is that track counts present a reliable proxy for the stock of reproductive females nesting in a given year. Yet, challenges exist with estimating the size of nesting sea turtle populations when remigration intervals, annual female nest production, and the ratio of successful to unsuccessful emergences remain poorly known (Meylan et al., 1983). Other recognized difficulties in sampling sea turtle populations can include tag loss (Rivalan et al., 2005), incomplete capture–recapture records, variation in remigration schedules (Kendall and Bjorklund, 2001), variable female reproductive output (Hatase and Tsukamoto, 2008), and nesting events outside a study area.

Knowing the reproductive output of individual sea turtles is hugely important from both a conservation and life-history perspective. For sea turtles, estimates of a female's nest production within a season (hereafter referred to as clutch frequency) are based on internesting intervals following an initial tagging. However, clutch frequency tends to be underestimated when turtles are not always observed when they nest (summarized by Schroeder et al. (2003)). Incomplete beach coverage, broad geospatial spread of nests through a season, or late encounters in the nesting season will result in an underestimate of annual reproductive output per individual. Thus, observed clutch frequency (OCF) documented via encounters with tagged or identified females is acknowledged to be lower than the actual reproductive output, termed the estimated clutch frequency (ECF) (Frazer and Richardson, 1985; Rostal et al., 1991; Tucker and Frazer, 1991).

Satellite telemetry can circumvent the foregoing problems with a more exact determination of spatial use onshore for nesting and during an internesting period between subsequent nesting attempts (Godley et al., 2008). The approach requires that females be instrumented early in the nesting season and followed until a final nest is made and a post-reproductive migration begins (Zbinden et al., 2007). In principle, satellite telemetry and tracking should enable a broader and more complete spatial coverage of behavior than available to ground-based monitoring crews (Hays, 2008).

The present study evaluated a representative rookery within the south Florida nesting stock of loggerhead turtles *Caretta caretta* (Encalada et al., 1998). Free-ranging female loggerheads were intercepted at their first nesting event and satellite tags were attached. The telemetry data were used to infer when and where the turtles

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subsequently nested through the reproductive season. We tested the hypothesis that satellite telemetry would better define site fidelity than the constrained spatial coverage of a nocturnal monitoring program. The resulting track histories are predicted to rigorously evaluate the extent of site fidelity among nests within a season. A relative efficacy of nocturnal monitoring is determined by contrasting OCF and ECF determined by satellite telemetry. Because the Western Atlantic Loggerhead stock may soon be reviewed for change from Threatened to Endangered status under the United States Endangered Species Act (NMFS, 2009; Conant et al., 2009), the revised estimates of clutch frequency can enable refined estimates of population size in management and recovery plans.

2. Methods

2.1. Study area

Tagging studies were coordinated at Casey Key (28.7 N, 82.3 W), a barrier island on Florida's southwestern coast. The island hosts 35 to 70 loggerhead nests/km/year. The southern 6 km of Casey Key were patrolled hourly at night to encounter nesting female loggerheads. Standard patrol coverage was June–July for the period 1982–2005, and mid May through July during 2006–2009. The tagging study enabled many individual histories to be known but a prior known nesting history was not a requirement for inclusion in the telemetry study, nor was a history of site fidelity to a respective island. These guidelines minimized potential sources of bias in selecting animals for the study because females were chosen as they were randomly encountered.

2.2. Field methods

After oviposition was completed, turtles were inspected for flipper tags or PIT tags and were measured to the nearest 0.1 cm for standard morphometrics of the carapace; herein, measurements are reported only for midline curved carapace length (CCL). Turtles were held temporarily in a portable plywood corral to facilitate the transmitter attachment. The carapace was cleaned of epibiota and wiped with alternating washes of fresh water and alcohol to ensure dryness. ARGOS transmitters (Sirtrack Kiwisat 101 or Wildlife Computers SPOT5, approx. 200–400 g in air) were adhered to the carapace with two part epoxy (Powers or Sikaflex) that was smoothed into a hydrodynamic shape. The application process took 1–2 h to complete. The box was removed and the turtle resumed departure to the sea.

2.3. Telemetry analysis

From a larger 2005–2009 study of loggerhead migration, a subset of 52 females were selected (51 at Casey Key and one female on Manasota Key 8 km south that had nested at both beaches) that all met the study criteria. Females were included if instrumented on a first nesting encounter at the advent of the season and if there were no transmitter malfunctions during the tracking. Females were tracked for all remaining nests deposited that season, which was verified by a subsequent migration to a foraging ground (Girard et al., 2009).

Satellite data were organized, evaluated, and archived in Satellite Telemetry Analysis Tool (STAT) (Coyne and Godley, 2005). Turtle movements were reconstructed from latitude and longitude fixes of ARGOS Location Classes 3, 2, 1, 0, and A (and omitted Location Classes of B or Z) based on recommendations derived for marine turtles (Hays et al., 2001). We preprocessed location data in STAT to filter locations for water depth >0.5 m, speed >4 km/h, or for angles <15°. Distance between successive fixes was calculated using a great circle route equation. Images were plotted in MAPTOOL and all tracks were publicly available for educational outreach and archived at the website www.seaturtle.org/tracking. Seasonal residency was defined by the elapsed period in days between occasions of the first and last nests.

2.4. Criteria to determine an emergence from Argos data

Multiple criteria in combination were able to identify each presumed emergence. These criteria ranked from individually convincing to merely helpful inferences suggested by patterns in the Argos data were: (1) direct verification by nocturnal ground truthing, (2) genetic verification by parental assignment using DNA microsatellite markers (B. Shamblin, unpubl. data), (3) distance criterion from a nearest coastline of <1 km, (4) temporal criterion of emergences coinciding within the expected internesting intervals for loggerheads, (5) behavioral criterion for the turtle movements directed onshore for nesting followed by an immediate offshore departure, (6) depth criterion for bathymetry locations associated with depths of −0.5 to 0.5 m indicating time ashore, (7) location quality criterion for an improvement in multiple ARGOS Location Classes 2 or 3 within a short time span, and (8) signal frequency criterion for evidence of an increased surface interval in the PTT data. These criteria also distinguished false crawls from nests so within the scope of this study, we only evaluated emergences associated with nests.

2.5. Site fidelity

Ground truthing was necessary to verify a correct interpretation of ECF by satellite telemetry. A unique test case was established with a female, tagged in 2007, retagged in 2008, and retagged in 2009 with an uncommon one-year remigration cycle. The female had tight site fidelity in all years (from 2.3 to 3.0 km spread), nested in the middle of the study site, and was encountered regularly to verify OCF and ECF in all years. All telemetry records from this individual (as well as for other tracked females in the study) coincided with emergences (false crawls or nests) that were discerned from ARGOS location class data and restrictive criteria alone. The ground truthing thereby established that ECF estimates for unseen emergences (nests or false crawls) could be documented reliably from satellite telemetry outside the study area.

Each nesting turtle deposited too few nests to employ a kernel density analysis to quantify site fidelity (Blundell et al., 2001). Therefore site fidelity was defined operationally by the linear distance between two most distant nests. Nest coordinates by an individual were plotted and measured to the nearest 0.1 km in Google Earth Pro 4.3. Site fidelity was defined by the maximum straight-line distance among nests by an individual. A skewed distribution in the geospatial data was observed that was hypothesized to relate to navigational correction, so an exploratory analysis was conducted excluding the first nest position of the season to test whether nest site fidelity became more clumped during the season. The measured spatial dispersion among nests was defined separately for (1) site fidelity of all nests, and (2) site fidelity excluding first nest for all remaining nests by an individual.

2.6. Clutch frequency

Observed clutch frequency (OCF) and estimated clutch frequency (ECF) were determined for each instrumented turtle. OCF was established by encounters of tagged females by nocturnal patrol crews covering a 6 km segment of Casey Key. OCF is an acknowledged underestimate of true clutch frequency when subsequent nesting events are undocumented or occur beyond the patrol coverage. ECF is typically calculated by ascribing additional nests during longer than mean internesting intervals (Johnson and Ehrhart 1996; Tucker and Frazer, 1991). In contrast, this study derived ECF from location fixes determined by satellite telemetry, for all tracks consistent with the restrictive criteria (stated in Section 2.4). A pattern of offshore–onshore movements illustrated by satellite telemetry was able to verify nests that were otherwise inaccessible to nocturnal patrol staff. The OCF

encounters by nocturnal patrols verified that patterns of onshore–offshore movements were correctly interpreted to differentiate nests and false crawls. For example, a turtle that completed 6 nests and multiple false crawls was correctly described as having 6 nests. The ground truthing indicated that telemetry information was correctly interpreted for turtles whether nesting within (Fig. 1, top panel) or away from the study site after the first nest (Fig. 1, bottom panel). Thus, ground truthing in combination with telemetry locations, defined by multiple restrictive criteria, was able to rigorously define ECF.

2.7. Statistical analysis

The site fidelity and OCF estimates from ground truthing patrols were compared with site fidelity and ECF estimates from satellite telemetry. ECF counts were normally distributed but OCF counts were not; therefore a non-parametric test (Wilcoxon signed rank test) was used to test for differences between OCF and ECF for the study population. We also evaluated trends in reproductive output (ECF) against variables of female size (CCL), nest site fidelity (km measured between most northerly to southerly nests by a same female), and seasonal residency (days between the first and last nests) by non-parametric tests.

3. Results

An overlay representing the seasonal phenology for the Sarasota rookery and the dates of instrumentation are depicted by Fig. 2. Random encounters of 52 loggerheads in the early portion of four

nesting seasons yielded 34 females not previously tagged and 28 remigrant females. Remigration intervals ranged from 1 to 8 years and the mean remigration interval was 3.7 years (s.d. = 2.1 years). Two remigrant individuals were opportunistically re-instrumented to document individual consistency in site fidelity and clutch frequency by tracking in different years of the study (A-2007, 2008, 2009; B-2007, 2009). Although too sparse a sample for statistical analysis, these individuals showed similarity in reproductive output and nest distribution: Turtle A nested 6 + 6 + 5 times (2.4 km, 3.0 km, 2.3 km) and Turtle B nested 5 + 4 times (5.0 km, 5.6 km). Since random encounters of females are independent of year, and new Argos tags were applied each year, the data produced by the two females were acceptable to include for the analysis.

3.1. Site fidelity

The 52 females deposited 285 nests. Of these, 39.6% (113) were on the study site and documented by satellite location and confirmed by nocturnal monitoring, 14.4% (41) were documented on the study site by satellite locations but missed by nocturnal monitoring, and 46.0% (131) were away from the study site and known only by satellite determined locations.
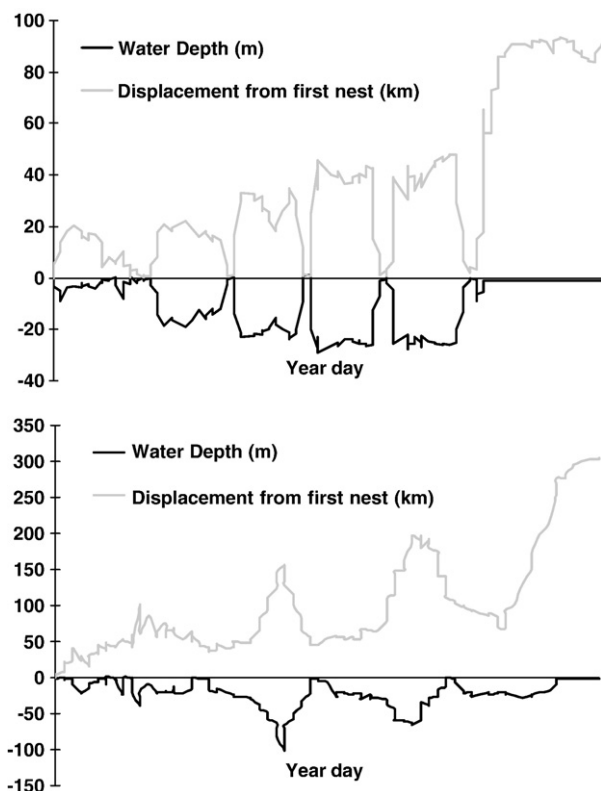

Fig. 1. Representative patterns of female nest site fidelity for high and low site fidelity depicted by displacement from original nest location (km) and water depth (m). (Top panel) On the Y axis, Displacement = 0 coincides with Depth = 0 to indicate a female returning on a beach near the same location as the first nest. The illustrated female deposited six nests with tight site fidelity (2.6 km) and all six nests were verified by nocturnal patrols to confirm that the satellite locations were associated with emergences. OCF = 6, ECF = 6. The same female produced OCF and ECF of 6 nests in both 2007 and 2008. (Bottom panel) On the Y axis, Displacement > 0 coincides with Depth = 0 to indicate a female returning to different locations than the first nest. The illustrated female made successive nests more distant after the first nest (site fidelity = 109 km), and only the first nest was observed by nocturnal patrols. OCF = 1, ECF = 4.
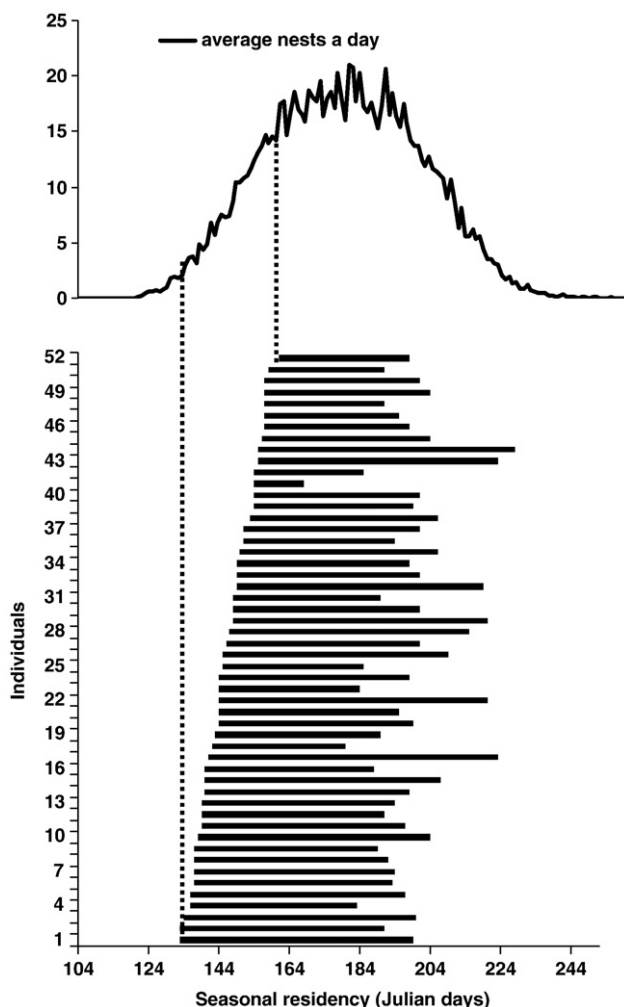

Fig. 2. In both graphs, the X axis gives the Julian date. The approximately normal distribution in the upper panel indicates the average number of loggerhead nests each day of the nesting season, derived from a 21 year average for Sarasota County. The horizontal bars in the lower panel indicate seasonal residency of the tracked females, beginning at the first nesting encounter and instrumentation and ending at the last nest date, prior to post-nesting migrations (that are not depicted). Dashed vertical lines indicate the first and last instrumented turtles on Julian days 133 and 161, respectively. Departure dates for the first and last nests were Julian days 168 to 228.

A difference in OCF and ECF of individual turtles was predicted if individual turtles made nests both within and outside the 6-km stretch of beach coverage. For all nests by an individual (Fig. 3a, x axis), the mean and standard deviation ($x + $ s.d.) for site fidelity was $25.8 + 23.1$ km, ranging 1.8 to 109.1 km (non-parametric comparisons are given in Table 1). Omitting the first nest of the season, the mean site and standard deviation for site fidelity was $16.4 + 14.6$ km, ranging from 1.8 to 69.0 km (Fig. 3a, y axis). Plasticity in nest spread remained obvious with 58.8% of all a female's nests found within 20 km, whereas 78.8% of all nests were found within 20 km after excluding the first nest (Fig. 3b).

3.2. Clutch frequency

Females deposited 2–8 nests per season, with a modal value of 5 nests (non-parametric comparisons are given in Table 1). Internesting intervals between nests ranged from 6 to 21 days, with a mean of 12.0 days (s.d. 2.2, $n = 221$). Mean OCF from beach monitoring was 1.9 nests per female (s.d. 1.3) compared to mean ECF from satellite telemetry which was 5.4 nests per female (s.d. 1.1) (Fig. 4). Coefficients of variation for OCF (0.662) were three times greater than ECF (0.207). OCF was significantly lower than ECF (Wilcoxon signed-ranks test: $Z = -6.3495$, $P = 0.0002$), indicating that OCF was a significant underestimate of the annual reproductive output. Consequently, there was no correlation of the seasonal residency

Table 1
Comparisons of newly tagged individuals and remigrants for selected reproductive characteristics, with outcomes of Wilcoxon signed rank sums test.

Trait	New	Remigrant	Z statistic	P value
Median OCF (nests)	1.0	2.0	−1.27	0.203
95% CL	1.3–2.0	1.7–3.0		
Median ECF (nests)	5.0	6.0	−1.27	0.203
95% CL	4.8–5.6	5.2–6.1		
Median fidelity (km)	23.7	13.8	3.35	0.0008
95% CL	24.1–42.9	9.7–20.6		
Median fidelity (km) excluding first nest	15.6	7.6	2.28	0.023
95% CL	13.7–25.1	6.8–18.0		
Median CCL (cm)	93.4	101.7	−4.1625	<0.0001
95% CL	91.5–95.8	98.8–103.6		

with OCF ($r^2 = 0.03$), but there was a significant correlation of seasonal residency with ECF ($r^2 = 0.79$) (Fig. 5).

3.3. Variance by nesting history

There was no significant difference in ECF estimates by year (ANOVA with year as covariate: $F_{3,49} = 0.83$, $P = 0.49$). Thus the four independent years of data were pooled to evaluate differences between remigrant females and newly tagged females in terms of female size and nest site fidelity as determinants of reproductive output (Table 1). The remigrant females were not significantly different in fecundity than newly tagged animals (i.e., marginally more nests were detected for OCF or ECF, but a difference was not statistically significant because of the variance), but larger in size (i.e., a larger CCL), and showed higher site fidelity (i.e., less distance spread among nests).

4. Discussion

The study illustrates a systematic effort to derive direct empirical measures of loggerhead site fidelity and clutch frequency solely by satellite telemetry. Satellite telemetry clearly outperformed beach patrols in quantifying seasonal movements and fecundity. The value of telemetry was suggested early on (Hays, 1992) and an impetus behind early studies (Hays et al., 1991). However, as the technology matured, investigators did not fully exploit the value of early season deployments because of an increasing focus on recording post-nesting movements (Dodd and Byles, 2003; Foley et al., 2008). Indeed, only in the second year of the 5 year study at Casey Key did attention shift away from documenting post-season migrations over to questions of site fidelity and fecundity that necessitated telemetry earlier in the season.
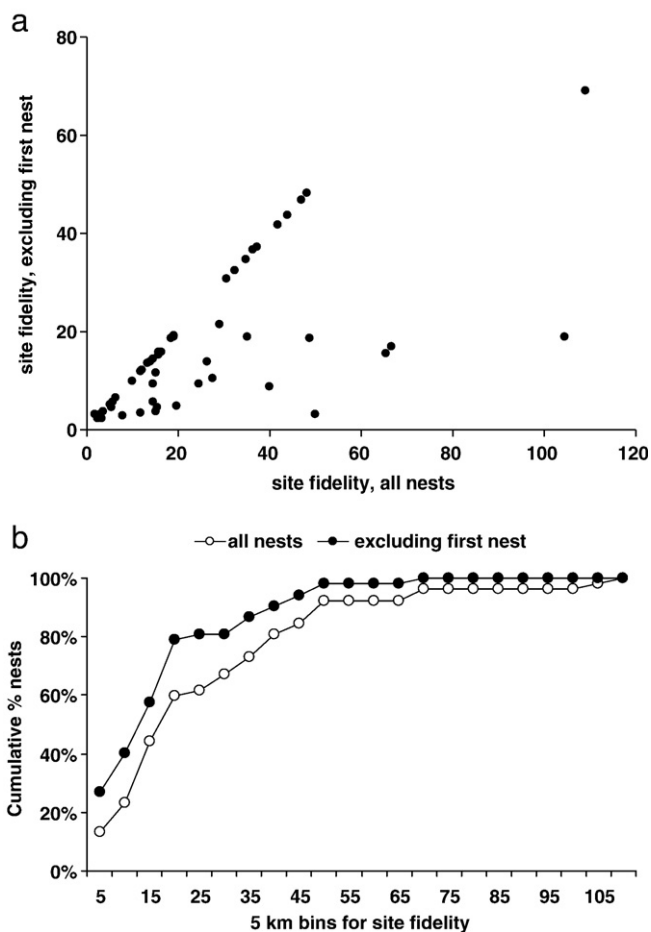

Fig. 3. Intraseason estimates of site fidelity (km) for all nests against latter nests by a female. (a) Site fidelity comparisons for all nests plotted against site fidelity excluding the first nests. With loggerhead turtles nesting at Casey Key there was a temporal tendency for the first nest of the season to be more distant than the remaining nests. (b) Skewness in nest spread remained obvious with 58.8% of all a female's nests found within 20 km, whereas 78.8% of all nests found within 20 km after excluding the first nest.
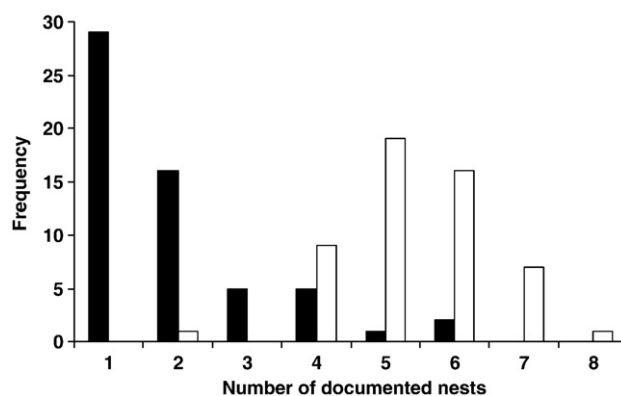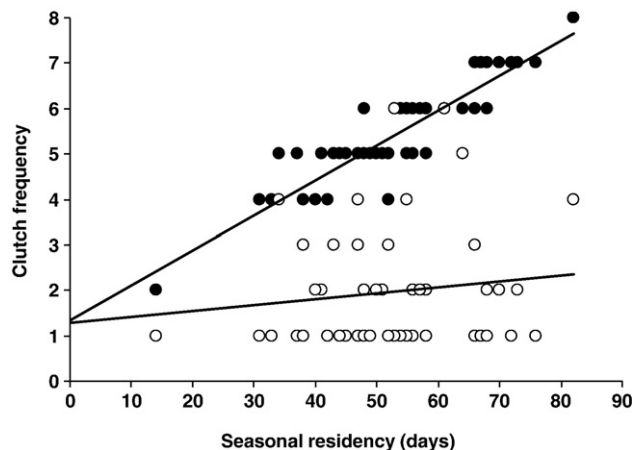

Fig. 4. Comparisons of loggerhead OCF (black bars) determined by nocturnal patrols and ECF (white bars) determined by satellite telemetry.

Fig. 5. A scattergram of the seasonal nesting residency and OCF (open circles) and ECF (closed circles) indicated that females with shorter residency deposited fewer nests (ECF) than females with longer residency. The occurrences documented by ECF were significantly different regardless of the seasonal residency because additional nests were deposited outside the scope of spatial or temporal coverage by nocturnal patrols. Linear regressions for OCF (lower trend line: $y = 0.013x + 1.2972$, $r^2 = 0.02$) and ECF (upper trend line: $y = 0.0777x = 1.3393$, $r^2 = 0.80$) are indicated.

In contrasting the newly tagged females and remigrants, the Casey Key study found variance in fecundity, but also that newly tagged females were less likely to be resighted, possibly related to a propensity to move farther from an initial nest for subsequent nests. Richardson (1982) first indicated that newly tagged females might have lower site fidelity than remigrants, and termed alpha or beta types to designate animals respectively with low or high site fidelity as one of several explanations. Studies of other turtles (Bjorndal, 1980; Mortimer and Carr, 1987; Tucker and Frazer, 1991) also document lower clutch frequencies by untagged animals than for the remigrants. The present study's documentation of divergent reproductive strategies may identify a shift in nest site fidelity by females after repeated seasons. These results suggest that younger turtles are spreading risk in space but not time, and conversely that remigrant turtles spread risk through time but have greater reproductive investment in spatially restricted zones, perhaps developed by spatial familiarity gained through experience. In a different perspective, life-history predictions suggest that younger individuals would potentially stray more often as colonizers than the experienced individuals with developed sense of site fidelity (Eckert et al., 1989).

4.1. Site fidelity

The present study documents that female site fidelity for a season can be substantial (2.4–109 km), encompassing scales readily intercepted by a monitoring patrol up to a broader geospatial scale that could only be tracked by satellite telemetry. The site fidelity of Casey Key nesters was 59.6% of all nests deposited within 20 km. Excluding the first nests, 78.8% of subsequent nests were within 20 km. For comparison, a satellite telemetry study conducted with loggerheads in Georgia (Scott, 2006) found that 73% of females had high site fidelity (mean 2.9 km, range 0.8 to 6.6 km, $n = 16$) and 27% had loose site fidelity (mean 41.6 km, range 17.6–64.6 km). Both studies illustrate that high site fidelity may be tractable to document at fine scale with ground truthing but that the full spatial scale of site fidelity is best documented through satellite telemetry. The Casey Key study also demonstrated that site fidelity and clutch frequency were underestimated by ground truth efforts, especially in cases of female variance in site fidelity from an initial nest to later nests of the season.

The documentation of seasonal readjustments in site fidelity suggests a new and unexplored research direction for future studies. How do females re-establish site fidelity after each migration to a rookery, as that may be a key determinant of spatial spread? A reproductive migration is guided by magnetic orientation (Lohman et al., 2008a,b) toward a rookery to presumably increase breeding success, provide a meeting place for mating, and reduce the costs of prospecting searching for a new site. A shift of site fidelity is akin to a repeated choice trial involving suitable beach prospects. For the 52 individuals in the study, migration distances may involve as little as 38 km paralleling the coast, or as much as 1384 km of open ocean navigation perpendicular to the coast (Girard et al., 2009). The components of navigation error involve a primary task of location finding after long distance migration guided by magnetic cues, followed by subsequent adjustments upon repeated exposure and possible orientation to local cues, possibly aided by olfactory or visual modes (Lohman et al., 2008a,b; Luschi et al., 2001). Loggerhead turtles in this study deposit up to eight nests a season (Tucker, 2009) and have documented reproductive histories spanning 21 years (Mote Marine Laboratory, unpubl. data). For a clearer understanding of how females spread their reproductive effort, new studies should evaluate the process during subsequent remigration intervals to document repeatability or shifts in nest site fidelity.

Consequently, a stricter definition is warranted for the term site fidelity in the lexicon of sea turtle biology. The present study proposes that site fidelity hereafter be defined as a distance measured between most distant nests deposited by an individual within a season, and that these distances preferentially be determined from telemetry studies rather than ground-based patrols. Adoption of a more restrictive definition for nest site selection will prevent confusion by descriptions of recapture events across years that may be unusual outlier events or discontinuous records of an individual in multiple years (e.g., LeBuff, 1974; Bjorndal et al., 1983; Stoneburner and Ehrhart, 1981; Hawkes et al., 2005), or incomplete intraseasonal histories, rather than the composite of sequential decisions that define site fidelity within a season.

Nest site choice (along an *X* axis) is addressed by previous studies as nest placement across the width of the beach and with respect to tidal exposure, dune proximity, and female experience (Kamel and Mrosovsky, 2004; Kamel and Mrosovsky, 2005; Tiwari et al., 2005; Pfaller et al., 2008). In contrast, studies of site fidelity (along a *Y* axis) have been viewed in a restricted sense as a tendency to repeatedly nest at or near the same location upon a single nesting beach (Nordmoe et al., 2004) or as a tendency to wander among multiple disjunct nesting beaches or from island to island (Eckert et al., 1989). The present study suggests that a more unified view is required to directly address questions about nest site fidelity as a spatial decision process. The revised definition of site fidelity proposed herein is suitable to contiguous nesting habitat (e.g., an extensive sandy coastline such as the Florida peninsula) or disjunct nesting habitat (such as island–island movements or among beaches separated by otherwise inhospitable coastlines).

4.2. Clutch frequency

Besides an improved understanding of site fidelity, the study concurrently yielded a higher ECF than previously reported for the species. The results by satellite telemetry could not be considered anomalous given the concordance across four seasons. This vital finding poses a related methodological question as to whether previous fecundity estimates based on ground-based monitoring efforts (Table 2) should be revisited, if not revised, by satellite telemetry efforts.

Individual fecundity of up to seven clutches per female was noted for loggerheads at intensely monitored beaches (Lenarz et al., 1981) but values reported for mean fecundity (summarized by Schroeder et al., 2003) encompassed a variety of loggerhead populations at varying levels of saturation or non-saturation ground patrol coverage (Frazer and Richardson, 1985; Webster and Cook, 2001). Species accounts (Bolten and Witherington, 2003) recognize that loggerheads from

Table 2
Current estimates of ECF by loggerheads for nests in a season (adapted from Schroeder et al. (2003), their Table 7.1).

ECF	Method	Location	Reference
5.4	Satellite telemetry	Casey Key, Florida	Present study
4.5	Satellite telemetry	Georgia coast	Scott (2006)
4.4	Satellite telemetry	Oman	Rees et al. (2008)
3.7–4.2	Beach patrol	Tongaland, Natal	Hughes (1974)
2.8–4.2	Beach patrol	Little Cumberland Island, Georgia	Frazer and Richardson (1985)
3.8–4.1	Beach patrol	Keewaydin Island, Florida	Addison (1996)
3.4	Beach patrol	Mon Repos, Queensland	Limpus (1985)
3.2	Beach patrol	S. Brevard County, Florida	Ehrhart, unpubl. data

different geographic regions are heterogeneous in their behavior and fecundity as one of the biological bases underlying the development of regional recovery plans (Godfrey and Godley, 2008). Consequently, a primary implication of this study is whether estimates of loggerhead abundance should be recalibrated with a range of ECF estimates as an envelope of uncertainty. Another OCF from the same region based on nocturnal patrols (Addison, 1996) suggested an average clutch frequency of 3.8–4.1 clutches per season, in comparison to the 5.4 nests for ECF determined by satellite telemetry in this study (Table 2). The National Research Council (1990) suggested that where limited data are available, an adult female population is estimated by the equation: $P_{nf} = (N_t/N_f) \div \rho_{nf}$ where P_{nf} = total population of adult females, N_t = total number of nests per year, N_f = average number of nests per reproductively active female, and ρ_{nf} = proportion of females that nest in a given year. Examining the N_f term, it is clear that variation in clutch frequency may have a profound effect on population estimates.

This study assumes that females that arrive asynchronously have similar ranges of clutch frequencies. However, individual variation in nesting phenology undoubtedly exists as influenced by factors such as water temperature (Weishampel et al., 2004; Mazaris et al., 2008), migration pathways (Girard et al., 2009), individual physiology (Hatase and Tsukamoto, 2008), nutritional state, or exposure to contaminants and harmful algal blooms (Arthur et al., 2008). Future studies may also require stable isotope analysis that better establish a nutritional basis linked to female fecundity, as outlined for leatherback turtles (Saba, 2007).

An experimental design criticism to address is whether a possible bias arises by tracking early nesters that might be avoided by a random selection of females throughout the season. For example, were females in May always more fecund for nests than the females who initiate nesting in June or later? This study's first encounters were distributed within the first quarter of the season, so in fact contains an asynchronous arrival of later nesters. The present study does fulfill much of the ideal, although hind-casting for nest frequency by an individual would be extremely imprecise later in the season if only from flipper tagging histories. Finally, taking females randomly and later in the season introduces the problem plainly illustrated by site fidelity results: later season encounters are always vulnerable to nests undetected by the ground truthing effort. Thus satellite telemetry was a viable approach when the logistic uncertainty of detecting first events was minimized by ground truthing and a decade-long study at a rookery with sufficient nesting density for reliable identification.

Future studies are strongly advised to quantify the extent of site fidelity before statements are made about presumed clutch frequency. It will prove difficult to identify whether a shift of clutch frequency from early to late season is real or an artifact of truncated sample opportunities later in the season, because of earlier nests deposited elsewhere or before the tagging encounter (Nishimura, 1994). The site fidelity results of the present study indicated that both were occurring. Future studies can target such potential biases by evaluating the clutch frequencies in early, mid, and late seasons. However, the results

offer a thorough evaluation of clutch frequencies at the onset of the season so that selective tagging later in a season may be useful to derive an adjustment factor in defining the fecundity envelope.

Technological advances in data relay should facilitate new studies that assess clutch frequency by satellite telemetry. Tags can directly record haul-out behavior and then store and relay the data via Argos (Georges et al., 2007) and it is now fairly commonplace to record movements with GPS tags (Schofield et al., 2009b). Another way forward is to capture females before the nesting season begins, either at courting or foraging grounds, or at the start of the breeding season when males and females congregate close to the nesting beaches. The capture and equipment of turtles as sea is logistically challenging, but achievable (Schofield et al., 2009a). Females can be screened via laparoscopy or ultrasound to determine vitellogenic status before transmitters are attached to track individuals for the season. This alternative has minimal uncertainty in accurately identifying females in vitellogenesis, but access is logistically limited to depths that are accessible to small boats or near shore trawlers. The pre-season tagging approach was infeasible in the present study because no nearby aggregations were known.

4.3. Conservation implications

Rigorous estimates of female fecundity provide a direct application of loggerhead biology to management concerns. For example, recent estimations of Mediterranean loggerhead stocks were strongly underpinned by clutch frequency estimates (Broderick et al., 2002). Similarly, first order estimates with an Indian Ocean loggerhead population stock were derived from studies of clutch frequency by a one-year study in Oman (Rees et al., 2008). Common methodologies are used in regional recovery plans, even though the Mediterranean and Oman population stock estimates are largely irrelevant to discussions concerning Western Atlantic loggerhead stocks.

Current estimates of the US loggerhead population are also based on nest counts rather than evaluations of females (NMFS, 2009). More accurate estimates of female annual fecundity can translate the information gleaned by standardized surveys (such as the Florida Index and State Nesting Beach Surveys discussed in Witherington et al. (2009)) toward a revised estimate of female population size. Studies involving satellite telemetry are an effective way to obtain these the necessary fecundity data when there are few ground truth efforts that can quantify the clutch frequency parameter as effectively.

The results of the present study outline a vital, if not novel, what-if question (Tucker, 1989): if female fecundity is being underestimated, by how much are populations potentially overestimated? ECF counts of 4.1 nests are given for loggerhead turtles in the US Recovery Plan (NMFS, 2007). By using guidelines of the National Research Council (1990) in estimations for an annual nesting population, a fecundity parameter N_f of 4.1 clutches a year (NMFS, 2009) and a nest tally of 10,000 nests yields an estimated 2439 females. However, with N_f at 5.4 nests per year (this study), the hypothetical population would be 1852 females. The degree of positive bias in this hypothetical example is approximately 32% as an overestimate (2439/1852). The same N_f terms can be applied to data from 1989 to 2008 compiled by the Florida State Nesting Beach Surveys (URL http://research.myfwc.com/features/category_sub.asp?id=2309). The annual extremes include a high of 88,988 nests in 1998 and a low of 45,084 nests in 2007. With fecundity parameters at 5.4 or 4.1 nests per season, the estimated annual female population would range from 15,816 to 21,217 females in 1998 and from 8197 to 10,996 females in 2007. It is widely recognized from the remigration intervals of sea turtles that a larger stock of adult females exists in a non-nesting status in any given year (Kendall and Bjorklund, 2001), but demographic extrapolations of this type are useful first approximations for annual nesters.

There are recent and substantial declines observed in the Florida loggerhead nest counts (Witherington et al., 2009) that represent 90% of the U.S. nesting and one of the two largest rookeries worldwide for

C. caretta (Ehrhart et al., 2003). These mounting concerns are an imperative to reevaluate site fidelity and clutch frequency estimates for other rookeries within the Western Atlantic loggerhead stock. Improved estimates of demographic parameters are among the measurable criteria that guide progress toward recovery and inaccurate population estimates are detrimental to the stated aims of the U.S. Loggerhead Recovery Team (NMFS, 2007).

It is also constructive to question whether the results from the Casey Key study can be considered valid for the context of regional management and stock assessment. For example, were the present study's estimates influenced by unique oceanographic factors operating regionally in the Gulf of Mexico that drive female reproductive through net primary productivity or trophic interactions (e.g. Saba, 2007; Hatase and Tsukamoto, 2008)? Probably not, as the Gulf of Mexico and Western Atlantic are mixed stock foraging grounds comprising females from multiple rookeries identified through genetic studies (Encalada et al., 1998; Shamblin, 2007), flipper tag returns (Meylan et al., 1983), and satellite telemetry (Dodd and Byles, 2003; Foley et al., 2008; Girard et al., 2009). The assemblage of animals studied at Casey Key is at lower nesting density than seen on the Atlantic Florida coast, but is part of the same Peninsular Florida Recovery Unit (Encalada et al., 1998). Until new studies can demonstrate otherwise, one must consider that the behaviors recorded by this study are likely representative of 90% of the US loggerhead population using Florida nesting beaches. These robust empirical estimates of site fidelity and clutch frequency suggest that population estimates of Western Atlantic loggerheads should be reviewed prior to future determinations on the loggerheads status (Conant et al., 2009).

Acknowledgements

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