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Genetic Differentiation of Hawksbill Turtle Rookeries on St. Croix, US Virgin Islands

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Abstract. – We collected tissue samples from 41 nesting hawksbill turtles (*Eretmochelys imbricata*) at Sandy Point National Wildlife Refuge, St. Croix, US Virgin Islands, to characterize the genetic structure of this rookery in terms of mitochondrial DNA; we compared haplotype frequencies from this rookery to those from Buck Island, another hawksbill nesting beach on St. Croix. Pairwise F_{ST} comparisons showed that Sandy Point was demographically distinct from Buck Island ($F_{ST} = 0.501$, $p < 0.001$), a finding reinforced by significantly different haplotype frequencies ($\chi^2 = 51.76$, $p < 0.001$) and a lack of interchange of nesting females between both sites based on mark–recapture data. Our results support the delineation of the nesting populations at Sandy Point and Buck Island into separate units for the purposes of management.

Female sea turtles return to their natal beaches to complete the reproductive cycle, a behavior known as natal homing. Individuals can migrate more than 2000 km to reach nesting grounds (Luschi et al. 1998) and typically make nesting migrations repeatedly over the course of their lives (e.g., Dutton et al. 2005; Beggs et al. 2007). As hatchlings, turtles are thought to imprint on the magnetic field of their natal beaches and use this information to navigate back to them as adults (Lohmann et al. 2008b). In the vicinity of the nesting area, they may also rely to various extents on auditory, chemical, and visual cues to locate the nesting beach (reviewed in Lohmann et al. 2008a).

This natal beach philopatry has important consequences for sea turtle population structure because it defines nesting populations (Bowen et al. 2005). Members of different nesting populations are reproductively isolated from one another at nesting grounds because of fidelity to their nesting locations. This has implications for management because the loss of nesting females from a nesting population would likely cause extirpation of the rookery. Females from other populations would be unlikely to repopulate it over ecologically relevant timescales because of their nesting beach fidelity (Bowen et al. 1993). Although sea turtles from other nesting populations could colonize the beach (e.g., Reis et al. 2010; Finn et al. 2016), their long maturation time would likely result in a drastic reduction in the number of nesting females at the site for several decades, rendering the rookery functionally obsolete. Distinguishing separate nesting populations is, therefore, necessary to ensure that conservation actions adequately address the threats facing each nesting population.

Matrilineally inherited mitochondrial DNA (mtDNA) from nesting turtles can be used to differentiate nesting populations and define management units (e.g., Dethmers et al. 2006). Management units are entities that are functionally independent because of low levels of gene flow between them (Moritz 1994). Nest site fidelity results in highly structured nesting populations in terms of mtDNA (Bowen and Karl 2007), and rookeries with significantly different mtDNA haplotype frequencies can be considered independent management units (Moritz 1994; Komoroske et al. 2017). Defining such management units is important for guiding conservation efforts for sea turtles and is considered a priority in the recovery plans for many species (e.g., National Marine Fisheries Service 1993; Hamann et al. 2010).

Molecular tools have been useful in clarifying the boundaries between nesting populations because the amount of nesting habitat used by a population varies widely. As a result, there can be considerable spatial variation in nesting population structure. This holds especially true for hawksbill turtles (*Eretmochelys imbricata*), which have a circumtropical nesting distribution. Hawksbill rookeries on the leeward and windward side of Barbados, for example, are genetically distinct, although they are separated by only 30 km (Browne et al. 2010). In the eastern Pacific, hawksbill rookeries separated by 115 km also have divergent mitochondrial haplotype frequencies (Gaos et al. 2016). However, there is sometimes no demographic distinction between more distant rookeries. There is no genetic differentiation between rookeries in the US Virgin Islands (USVI) and Barbados, despite being located 750 km apart (LeRoux et al. 2012). Rookeries in northern Queensland and the Northern Territory in Australia, separated by 800 km, are also not genetically differentiated (Vargas et al. 2015). Thus, hawksbill population structure is characterized by connectivity

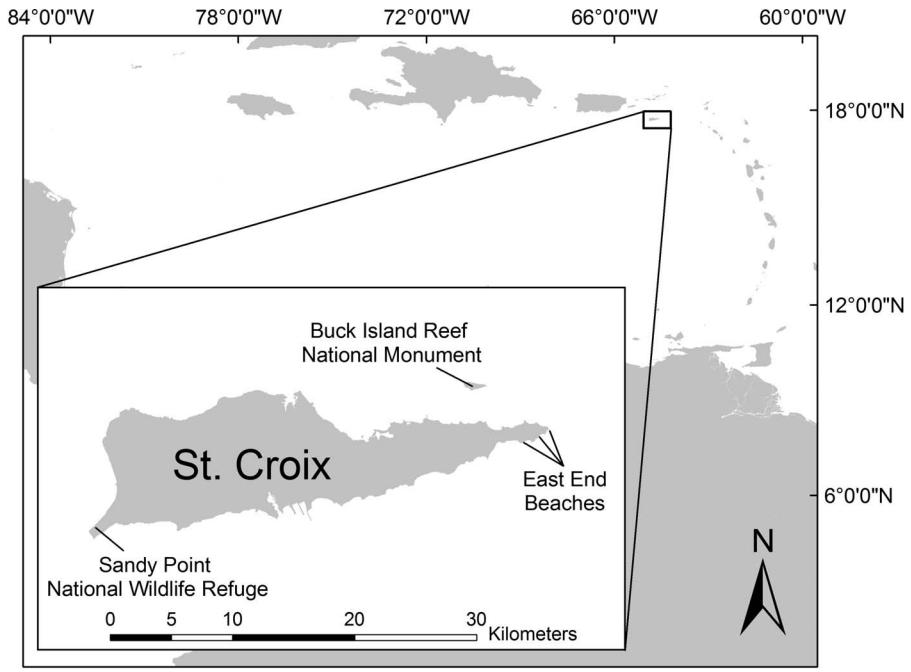

Figure 1. Map of St. Croix indicating locations of Sandy Point National Wildlife Refuge, Buck Island Reef National Monument, and East End Beaches.

between distant rookeries, whereas proximate rookeries are sometimes not genetically similar (LeRoux et al. 2012). As a result, examining genetic structure between nearby beaches to uncover potential fine-scale differentiation is often warranted.

At St. Croix, USVI, hawksbills have been recorded nesting on 31 beaches, but the density of nests is typically low with fewer than 10 nests laid annually at most sites (Mackay 2011). An exception is Buck Island Reef National Monument, located to the north of St. Croix (Fig. 1), which has between 500 and 1000 nesting activities (i.e., nests and nonnesting emergences combined) annually (Dow Piniak and Eckert 2011). Most hawksbill research efforts on St. Croix have been focused on Buck Island, and it has been the site of a saturation tagging project for hawksbills since 1988 (Hillis-Starr and Phillips 2002). Mitochondrial haplotypes have been determined from hawksbills nesting at Buck Island and have been used in several studies as representative of the genetic structure of hawksbill rookeries in the USVI (e.g., Bowen et al. 1996, 2007; Blumenthal et al. 2009; LeRoux et al. 2012; Cazabon-Mannette et al. 2016). However, recent studies at Sandy Point National Wildlife Refuge, on the southwest corner of St. Croix 40 km away from Buck Island (Fig. 1), have revealed a substantial amount of nesting at this location as well. The mean number of nesting activities at Sandy Point is around 300 annually, but in some years, it exceeds 500 (Hill 2014). Consequently, Sandy Point falls in the top 7% of hawksbill nesting beaches in the wider Caribbean based on numbers of annual nesting activities (Dow Piniak and Eckert 2011). In the Lesser Antilles, higher levels of nesting are only reported from rookeries at Buck Island and Barbados (Dow Piniak and Eckert 2011).

Despite the considerable level of hawksbill nesting that occurs at Sandy Point, the genetic structure of this nesting population has not been characterized. As a result, it remains unclear whether the nesting populations at Sandy Point and Buck Island are demographically distinct and whether these 2 beaches should be considered discrete units for the purposes of management. We analyzed the genetic structure of the hawksbill rookery at Sandy Point in terms of mtDNA and compared it with Buck Island. Our objective was to determine whether there is genetic differentiation among hawksbill rookeries on St. Croix and whether they should be considered independent management units.

Methods: Study Site. — Sandy Point National Wildlife Refuge (17°40′35N, 64°54′5W) is a 155-ha peninsula containing 3.2 km of continuous beachfront, located on the southwest corner of St. Croix, USVI. The shoreline of the refuge is one of the longest sandy beaches in the USVI and was established in 1984 to protect critical leatherback turtle (*Dermochelys coriacea*) nesting habitat (Meibohm 1979; Evans 2010). Although there has been a saturation tagging project of nesting leatherbacks at Sandy Point since 1981 (Dutton et al. 2005), research on hawksbill and green turtles (*Chelonia mydas*), which also nest at the site, has been primarily restricted to documentation of nesting activities. There has also been sporadic tagging of these two species when encountered during leatherback monitoring. In 2011, the US Fish and Wildlife Service began nighttime surveys to tag nesting green and hawksbill turtles and the data for this study were collected in conjunction with these efforts.

Table 1. Mitochondrial DNA haplotypes of hawksbill sea turtles nesting at Sandy Point National Wildlife Refuge and Buck Island Reef National Monument, St. Croix, US Virgin Islands.

Rookery	EiA01	EiA03	EiA09	EiA11	EiA20	EiA23	*n*
Sandy Point	33	1	0	7	0	0	41
Buck Island[a]	8	2	2	50	4	1	67

[a] From LeRoux et al. (2012).

Tagging and Tissue Collection. — We patrolled Sandy Point nightly during hawksbill nesting season (July through September) during 2012 and 2013 to encounter nesting turtles. During oviposition, we gave each turtle a unique identification by attaching an Inconel tag on the right front flipper and inserting a PIT tag in the left shoulder. We used a 6.0-mm Acuderm biopsy punch to collect tissue samples from the rear flipper (modified from Dutton 1996). Only turtles that could be identified through tagging were sampled to prevent collecting duplicates from the same individual. Samples were stored in 1.5-ml vials in 96% ethanol at –20°C. Research methods were carried out in accordance with Purdue Animal Care and Use Committee Protocol 1206000656.

Laboratory Analysis. — We extracted DNA from samples using a Qiagen DNEasy kit and then used the primers LCM-15382 and H950g to amplify an 832-base pair control region of the mitochondrial genome (Abreu-Grobois et al. 2006). Our 25-µl polymerase chain reactions (PCRs) consisted of water, 1× Thermopol buffer, 10 mM dNTPs, 10 µM of each primer, 0.25 units of *Taq* polymerase, and genomic DNA. The thermal cycling profile consisted of the following: an initial DNA denaturation for 2 min at 90°C, followed by 30 cycles of 1) DNA denaturing at 94°C for 50 sec, 2) primer annealing at 56°C for 50 sec, and 3) primer extension at 72°C for 1 min, followed by a final primer extension at 72°C for 5 min.

PCR products were confirmed using gel electrophoresis in a 2% agarose gel stained with ethidium bromide. Subsequently, PCR products were purified by combining 5 µl of PCR product with 2 µl of a combined Exonuclease I and Shrimp Alkaline Phosphate solution (ExoSAP-IT®) and incubating for 15 min at 37°C, followed by 15 min of incubation at 80°C. Both forward and reverse strands were sequenced using an ABI BigDye® Terminator v3.1 cycle sequencing kit and analyzed with Applied Biosystems Model 3730 automated genetic analyzer. The 12-µl cycle sequencing reactions consisted of 1 µM primer, 1:1 BigDye/buffer, and 3 µL PCR product. Cycle sequencing was performed under the following conditions: an initial DNA denaturation at 96°C for 1 min, followed by 30 cycles of 1) DNA denaturation at 96°C for 10 sec, 2) primer annealing at 50°C for 5 sec, and 3) primer extension at 60°C for 4 min. Sequences were aligned, edited, and cropped using the program SeqScape® v2.5 (Applied Biosystems). Haplotypes were designated by comparing sequences to those previously documented for hawksbills and publicly available via GenBank.

Statistical Analysis. — We used Arlequin v3.5 (Excoffier and Lischer 2010) to calculate haplotype and nucleotide diversity for these samples. Based on previously published haplotype data from Buck Island (LeRoux et al. 2012), we used Arlequin (Excoffier and Lischer 2010) to calculate pairwise F_{ST} comparisons (conventional haplotype frequency based) between Buck Island and Sandy Point. We also carried out exact tests of population differentiation using 10,000 steps in the Markov chain and 10,000 dememorization steps. Haplotype frequencies were also compared between rookeries using chi-square tests with Monte Carlo resampling with 1000 iterations using the program Chirxc (Zaykin and Pudovkin 1993).

Results. — We tagged and collected tissue samples from 41 individual hawksbills. Five of these turtles had been tagged previously at Sandy Point, whereas the remaining 36 turtles had no tags when first encountered. None of the hawksbills we tagged were recorded nesting on Buck Island after being encountered at Sandy Point (I. Lundgren, *pers. comm.*, January 2015).

Haplotype diversity of the Sandy Point rookery was 0.3305 ± 0.081 SD, and nucleotide diversity was 0.013 ± 0.007 SD. The haplotypes consisted of EiA01 (n = 33), EiA11 (n = 7), and EiA03 (n = 1) (Table 1). Sandy Point was highly differentiated from Buck Island (F_{ST} = 0.501, $p < 0.001$; exact test p-value < 0.0001), and haplotype frequencies were significantly different (χ^2 = 51.76, $p < 0.001$).

Discussion. — Our study demonstrated significant demographic differentiation between Buck Island and Sandy Point, the 2 main hawksbill rookeries on St. Croix. The existence of 2 separate nesting populations on the island is supported by genetic analysis based on fairly robust sample sizes for comparison and by the lack of interchange of nesting females between sites based on mark–recapture data. Because Buck Island has had a saturation tagging project of hawksbills for 30 yrs, untagged turtles presumably would have been tagged while nesting there. The high number of untagged turtles we encountered suggests that these turtles had not nested previously at Buck Island, and we also confirmed that the turtles did not nest on Buck Island after we tagged them.

These findings provide another example of differentiation between proximate hawksbill rookeries. This pattern may not be uncommon for hawksbills, because it has been documented throughout the geographic distribu-

tion of their nesting range, including sites in the Atlantic (Browne et al. 2010), Pacific (Gaos et al. 2016), and Indian oceans (Martínez et al. 2009; Vargas et al. 2015). Although differentiated from Sandy Point, located 40 km away, Buck Island is not differentiated from a rookery in Barbados that is 750 km away (LeRoux et al. 2012). This pattern of differentiation is consistent with the idea that there is no standard geographic distance between demographically distinct rookeries (Shamblin et al. 2012).

Similar patterns have been documented for other species as well. For example, loggerhead turtle (*Caretta caretta*) rookeries at 3 sites in Greece, each separated by 100 km or more, were not genetically differentiated (Carreras et al. 2007). However, haplotype frequencies at rookeries in eastern Turkey and northern Cyprus were significantly different, despite being also separated by 100 km (Carreras et al. 2007). At some locations in Florida, green turtles nesting at beaches 450 km apart are not demographically distinct, whereas differentiation occurs at other sites separated by less than 1 km (Shamblin et al. 2015). Our study reiterates the value of examining population structure of proximate rookeries because there can be differentiation even between rookeries separated by relatively small distances of less than 50 km.

Our results support the delineation of hawksbills nesting at Sandy Point and Buck Island into 2 separate management units. They should be evaluated independently to assess threats and population status, and recovery plans should target the unique threats facing each rookery. For example, mongoose predation on hawksbill nests is prevalent on St. Croix (Pollock and Hairston 2013), but eradication of mongoose at one of these sites will not incur a substantial benefit to nesting populations at the other site. Since individual females do not nest on both beaches, the extirpation of hawksbills on Sandy Point would have long-term effects because turtles from Buck Island would not be expected to colonize Sandy Point in the near future (Bowen et al. 1993). Conservation management plans for the region could be enhanced by incorporating information on population structure from this and future studies.

Genetic sampling of hawksbills nesting on the East End of St. Croix (Fig. 1), where approximately 200 nesting activities occur annually (Dow Piniak and Eckert 2011), could provide additional information on population structure. The East End beaches (composed of East End Bay, Isaac's Bay, and Jack's Bay) are 30 km away from Sandy Point and 10 km away from Buck Island. In contrast to Sandy Point, hawksbills nesting on East End beaches have also been documented nesting on Buck Island (Iverson et al. 2016). It is possible that East End beaches and Buck Island comprise a single nesting population distinct from that at Sandy Point. Further sampling would provide more precise information on the boundaries between nesting populations on St. Croix and could reveal differentiation between rookeries at a finer spatial scale than we documented.

Demographic distinction between hawksbill rookeries at Sandy Point and Buck Island also raises the possibility of similar patterns of differentiation among other sea turtle species nesting on St. Croix. More than 1000 green turtle nesting activities occur annually at Sandy Point (King et al. 2014), whereas there are 100–500 annual green turtle nesting activities at Buck Island (Dow Piniak and Eckert 2011). Along the east coast of Florida, green and loggerhead rookeries followed similar patterns of differentiation, with lack of differentiation between 2 sites for 1 species often occurring in the other species as well (Shamblin et al. 2015). The greatest shifts in haplotype frequencies also occurred at the same locations for both species (Shamblin et al. 2015). However, other studies have documented dissimilar patterns in population structure between species at the same locations. For example, loggerhead rookeries in eastern Australia and New Caledonia were not demographically distinct, whereas differentiation occurred between green turtle rookeries in the same locations (FitzSimmons and Limpus 2014). Determining nesting population structure of green turtles on St. Croix could better inform management of the species within the USVI and could lend further insight into interspecies patterns of nesting population structure.

Finally, a single hawksbill nesting beach from the USVI is not representative of all the genetic diversity in the territory. The additional population structure we discovered at St. Croix suggests a need to reexamine previous hawksbill foraging ground assessments. Studies of mixed stock analysis that were used to show the contribution of USVI hawksbill rookeries to foraging grounds have used data for Buck Island as the representative USVI rookery in baseline data sets (Bowen et al. 1996, 2007). These studies may have misrepresented potential contribution of the USVI because only one of multiple stocks of nesting hawksbills was included. Future region-wide analyses should include baseline rookery data from both Buck Island and Sandy Point to account for both management units.

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