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Movement of Hawksbill Turtles: What Scale is Relevant to Conservation, and What Scale is Resolvable with mtDNA Data?

BRIAN W. BOWEN^{1,2} AND ANNA L. BASS^{1,2}

¹Department of Fisheries and Aquatic Sciences, University of Florida, P.O. Box 110600, Gainesville, Florida 32611 USA; ²Archie Carr Center for Sea Turtle Research, 223 Bartram Hall, University of Florida, Gainesville, Florida 32611 USA [Fax: 904-392-9166]

Nesting aggregates of cheloniid sea turtles are distinguished from one another by unique genetic markers and differences in the frequency of mitochondrial (mt)DNA haplotypes. This strong population structure is attributed to a restriction of gene flow between nesting colonies due to natal homing behavior. In a few recent publications, rookery-specific genetic markers have been used to resolve the origin of turtles on coastal and oceanic foraging grounds, life history phases that are notoriously difficult to study (Broderick et al., 1994; Bowen et al., 1995; Bowen et al., 1996). These data have strong conservation implications: in many cases, wildlife managers may know the location of foraging grounds and nesting beaches but are unable to discern which nesting populations use which feeding grounds. Molecular markers can bridge this gap and indicate which foraging populations are impacted by human activities such as directed fisheries or incidental catch. In the next several years, genetic markers and maximum likelihood (ML) methodology are likely to be widely applied to resolve foraging ground composition in marine turtles. Hence this is an excellent time to explore the terrain between DNA sequence data and the implementation of wildlife management policy, and we are grateful to Mrosovsky (1997) for opening a dialogue. While we disagree on some points of interpretation, we share a mutual appreciation and respect for scientific truth as the foundation for conservation policy.

Sample Size on Nesting Beaches. — To address the basic criticism of Mrosovsky (1997) we must review the properties of mtDNA which make it such an appropriate tool for the analysis of questions concerning philopatry. In vertebrates, the mitochondrial genome is maternally inherited through egg cytoplasm; sons and daughters inherit only their mother's mtDNA, and only daughters transmit this lineage to the next generation. This mode of inheritance raises more considerations than are appropriate for discussion here, but the uniparental (haploid) inheritance of mtDNA makes 15 a reasonable sample of within-population diversity. This theoretical point is corroborated by empirical data on marine turtle popula-

tions. In resampling nesting colonies to determine interyear variation (green turtles, Chelonia mydas, at Aves Island, Venezuela, n = 8 in 1987, n = 22 in 1995 and Tortuguero, Costa Rica, n = 15 in 1988, n = 26 in 1996; loggerhead turtles, Caretta caretta, at Cumberland Island, Georgia, n = 10 in 1987, n = 33 in 1990; hawksbill turtles, Eretmochelys imbricata, at Buck Island Reef National Monument, U.S. Virgin Islands, n = 15 in 1993, n = 7 in 1994, n = 4 in 1995, n = 6 in 1996), no additional genetic variation was uncovered (Fig. 1). Larger sample sizes are always desirable, but the data shown indicate that even with smaller sample sizes we could still uncover a significant proportion of the genetic variation at a nesting location. The relationship between the number of haplotypes present in a population and the number of samples is not a simple one, and other factors play a role in the haplotypic diversity of populations: population turnover (both natural and anthropogenic), mutation rates, and population size to name a few. Larger sample sizes have been collected where possible, but many of the nesting colonies sampled in this study host only a few dozen females per year.

Geographic Scale of Nesting Colonies. — Mrosovsky (1997) invokes an important point about the limits of resolution for genetic assays. If populations are distinguishable with mtDNA data, then they can be considered as demographically isolated management units (see Avise, 1995). However, the converse may not be true: if two populations are indistinguishable with mtDNA data, they may still be separate demographic (and hence management) units. The boundaries of isolated demographic units are somewhat finer than can be distinguished with mtDNA sequence comparisons, because the time scale for resolving population separations with mtDNA is on the order of thousands or tens of thousands of years, whereas the time scale for management concerns is



Figure 1. Number of haplotypes found at three different Caribbean hawksbill nesting sites as a function of the number of samples analyzed. A cumulative count of the number of new haplotypes found among groups of five sequences was made until all the samples had been examined.

decades or centuries. Recognizing this limitation, we need to accept a coarse definition of populations when using mtDNA data. In some cases, nesting beaches that are suspected to be demographically isolated (as indicated by field studies) must be treated as a single source in the foraging ground assessments, simply because the two nesting areas are not resolvable with mtDNA data (see FitzSimmons et al., 1996). In general, sea turtle nesting sites separated by a few hundred km are distinguishable with mtDNA data, and nesting sites separated by less than about 100 km are not. Exceptions to this rule exist and are an expected byproduct of colonization events.

In the Caribbean, nesting populations of hawksbill turtles such as the ones on Mona Island (Puerto Rico), Buck Island (U.S. Virgin Islands), and Yucatan (distance between nesting locations = 350–2000 km) are distinct genetic entities by widely accepted scientific criteria (Bass et al., 1996). We disagree with Mrosovsky's interpretation that nearly two thirds of the foraging animals off Mona Island "come from the same nesting population," because nesting females at Mona Island and Buck Island are not part of a single extended nesting aggregate.

Sample Size on Foraging Grounds. — Mrosovsky (1997) invokes a legitimate concern about sample sizes on foraging grounds. We asserted in the original paper (Bowen et al., 1996), and reiterate here, that a sample of 41 feeding ground specimens is inadequate to precisely resolve feeding ground composition. Simulation studies indicate that sample sizes in excess of 100 would be desirable for this purpose (Chapman, 1996). We invite anyone with aspirations to such sample sizes to join one of the expeditions that collect these samples. It is true that larger sample sizes are possible from directed fisheries (such as the one in Cuba), but this source has not been available to us. Since we lack the resources to mount large-scale professional expeditions, our field studies are usually conducted by a team of 2-4 persons working from shore or small boats in a remote location. The 41 samples collected for this study required hundreds of hours of in-water work — an enormous effort by co-authors C. Diez and R. van Dam (Bowen et al., 1996). Catching these scarce animals by hand is the only way to collect samples without the cooperation of industrial (or artisanal/subsistence) fisheries.

The pertinent issue here is not whether the sample sizes on foraging grounds should be larger (this is obviously desirable), but rather how much information can we obtain from the sample sizes which are available with a realistic level of effort. To restate the original thesis: "We regard the results of the ML [maximum likelihood] analysis as general *qualitative* indicators of the contribution to Mona Island feeding habitat from regional nesting populations. Although the specific contribution of surveyed rookeries may not be precisely resolved, the ML analysis nonetheless provides clues as to the geographic scale of recruitment to the Mona Island foraging area" (Bowen et al., 1996). While not sufficient to satisfy rigorous statistical standards, such qualitative conclusions represent enormous advances over the information previously available.

Reinterpretation of Foraging Ground Composition. — Mrosovsky (1997) challenges our interpretation that hawksbill turtles recruit to the Mona Island foraging ground from throughout the Caribbean, and offers an interpretation that most of the foraging turtles come from nearby nesting colonies. He correctly points out that in our analysis about two thirds of the samples are attributed to nearby nesting areas in the eastern Caribbean (Bowen et al., 1996). In preparing the original manuscript, we gave much deliberation to this trend, but did not feel that a sample size of 41 was sufficient to justify such precision in our conclusions. We chose a less restrictive interpretation, "that turtles recruit to this feeding population on a scale > 100 km but less than the 7000 km that separate Mona Island from Bahia, Brazil" (Bowen et al., 1996). Future research may demonstrate that most recruitment to foraging grounds occurs on a scale smaller than the Caribbean basin. However, two points bear consideration in interpreting the current data set. First, we feel that Mrosovsky's reinterpretation is potentially correct, but speculative, based on a sample of only 41 individuals. Second, this reinterpretation does not substantially alter the conservation implications. Whether a harvest on eastern Caribbean foraging grounds impacts five nesting aggregates in the nearby eastern Caribbean, or ten nesting aggregates across the entire Caribbean, our conclusion is the same: an organized harvest of foraging subadults will impact multiple nesting colonies in several sovereign jurisdictions throughout the region. Under Mrosovsky's interpretation or our own, this conclusion remains completely intact.

Conclusions. — The present distribution of the hawksbill "is a ghostly outline of the primitive range" (A. Carr in Bustard, 1972). Costa Rican, Panamanian, and Cuban nesting beaches have been recognized as among the most important nesting beaches in the Caribbean; however, Meylan (1989) reported only 2 hawksbill tracks along a 29 km stretch of Chiriqui beach in Panama, and the nesting population at Tortuguero, Costa Rica, has suffered a continuous decline since monitoring began in 1956 (Bjorndal et al., 1993). While the evidence is incomplete, this species is clearly depleted in the Caribbean, and extreme caution must be exercised in the management of remaining populations.

In the original paper and related publications, we are attempting to apply the tools of population genetics to study the migratory behavior of marine vertebrates. It is a new endeavor at the junction of several scientific disciplines, so scrutiny and deliberation are appropriate. We appreciate Mrosovsky's inquiry regarding the boundaries of nesting populations and the limits of mtDNA data interpretation, in which he concludes with a famous philosophical query: is the glass half empty or half full?

We respond that until very recently that glass was empty. An Australian team made the first contributions to this glass (see Broderick et al., 1994, 1996), we have added a few drops, and we hope that our colleagues in many nations will continue to fill it with field and laboratory studies on marine turtle stock composition. Questions about the geographic scale of recruitment to feeding grounds will not be resolved by our scholarly discussions, but by studies that are underway in Mexico, Japan, Cuba, Australia, and our laboratory at the University of Florida. It will be especially informative to compare haplotype frequencies in foraging grounds from several widely distributed Caribbean locations. If foraging populations in eastern and western Caribbean areas are indistinguishable, this would indicate that turtles recruit at random from throughout the Caribbean. If foraging grounds in separate corners of the Caribbean are genetically distinct, this would favor a model of more localized recruitment. We live in an exciting time for sea turtle research, and we look forward to discussion of future results with Mrosovsky and our many colleagues among the readership of Chelonian Conservation and Biology.

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Resolutions of the Participants at the 17th Annual Symposium on Sea Turtle Biology and Conservation

Compiled by JEANETTE WYNEKEN¹ AND DEBORAH T. CROUSE²

¹President, 17th Annual Symposium on Sea Turtle Biology and Conservation, Department of Biological Sciences, Florida Atlantic University, 777 Glades Road, Boca Raton, Florida 33431-0991 USA [Fax: 561-367-2749; E-mail: jwyneken@acc.fau.edu]; ²Resolutions Committee Chair, 17th Annual Symposium on Sea Turtle Biology and Conservation, Center for Marine Conservation, 1725 DeSales Street, NW, Suite 600, Washington, D.C. 20036 USA

The following is a compilation of five of the six resolutions passed by the approximately 720 assembled participants attending the 17th Annual Symposium on Sea Turtle Biology and Conservation at Orlando, Florida, USA, on 6 March 1997.

Resolution on the Interamerican Convention for the Protection and Conservation of Sea Turtles

To: All governments of the Americas; FAO, UNEP, UNDP, OAS, OLDEPESCA, ALEP, IUCN, WWF, sea turtle specialists and managers, and all other concerned parties.

Whereas the assembled members of the 16th Annual Symposium on Sea Turtle Biology and Conservation (1996) passed a resolution supporting the adoption of the measures outlined in the *Interamerican Convention for the Protection and Conservation of Sea Turtles*;