Conservation implications of historic sea turtle nesting beach loss

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Populations of endangered Caribbean sea turtles are far more depleted than realized because current conservation assessments do not reflect historic nesting data. We used historical sources to analyze changes in the numbers of nesting populations and population sizes for green and hawksbill turtles on all known nesting beaches in the Caribbean over the past millennium. We present the first maps of historic nesting populations, which provide the basis for an objective measure of changes in distribution and abundance. Our results indicate that 20% of historic nesting sites have been lost entirely and 50% of the remaining nesting sites have been reduced to dangerously low populations. Recent conservation efforts have resulted in large population increases at several nesting sites, but loss of widespread nesting throughout the Caribbean and reductions in the Caribbean-wide population since human hunting began indicate that Caribbean turtles are far from recovered. Focusing attention on a small number of nesting populations is a risk-prone strategy; conservation programs should instead broaden their scope to protect both large and small nesting populations throughout the Caribbean.

By the beginning of the 20th century, green turtles (*Chelonia mydas*) and hawksbill turtles (*Eretmochelys imbricata*) had been decimated by human hunting, making both species globally endangered (Meylan and Donnelly 1999; Seminoff 2002). These species filled unique ecological roles in seagrass and coral reef ecosystems, and their removal diminished the complexity and stability of the food web, as well as the intensity of biological disturbance on seagrass beds and coral reefs (Jackson 1997; Bjorndal and Jackson 2003). Population declines and the ensuing ecological changes occurred over many centuries; without historic data, the magnitude of change has been underestimated, a phenomenon known as the shifting baselines syndrome (Pauly 1995). Historic reductions in sea turtle populations have been recognized (Jackson 1997; Bjorndal and Jackson 2003), but pan-regional changes in numbers and distribution of nesting populations have not been systematically reviewed. To that end, we compiled a comprehensive list of historic nesting beaches for green and hawksbill turtles in the Caribbean and used the number of nesting sites to refine previous estimates of historic population size and the ecological consequences of loss.

Historical and archeological data provide a wealth of information that can be used to estimate early geographic ranges and population sizes of easily visible species such as sea turtles that nest on land and whose high economic value stimulated exceptional records of their exploitation. For hundreds of years, green turtles provided nourishment for European colonists and African slaves on Caribbean sugar plantations. Hawksbill turtles were prized for their shells, which were fashioned into elaborate hair combs and other ornaments and distributed through carefully regulated trade networks (Roberts 1827; Dampier 1968). Both species of turtle were especially vulnerable to hunting during nesting (Roberts 1827; Dampier 1968; Rebel 1974; Jackson 1997). Early descriptions provide locations of nesting beaches, the magnitude of the population, sizes of adults found, and accounts of the hunt.

We compiled data on nesting beach location, density of turtles, and human exploitation summarized in trade records from 163 historic sources in four historic time periods for 20 regions of the Caribbean (WebTable 1). We mapped historic nesting beaches for green and hawksbill turtles, and used density descriptions and harvest data to categorize these sites as "major" and "minor" nesting sites (Figure 1; WebTable 2). Next, we calculated a range of Caribbean-wide population sizes for green and hawksbill turtles by estimating the number of adult turtles supported by one particularly well-documented major nesting site for each species and extrapolating across the region, using the total number of major and minor historic nesting beaches (WebTable 3). Two types of sources provided information about the size of populations: (1) observations from 20th century nesting beaches, and (2) historic harvest data. (Full materials and methods are available as Web-only material.) Finally, we refined calculations of historic turtle consumption in order to

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describe the ecological role of turtles in tropical marine ecosystems and the long-term effects of their removal.

■ Historic nesting beaches and population size

Historically, large nesting populations were found on beaches throughout the wider Caribbean. We found evidence for 59 historic green turtle nesting beaches, nine of which were considered to be major nesting populations based on density descriptions and harvest data (Figure 1a; WebTable 2). Green turtles in the Cayman Islands, for example, were found in "infinite numbers"; up to 50 nesting females could be taken in less than 3 hours (de Rochefort 1666). On the Moskito Coast of Nicaragua there were "inexhaustible supplies of the finest green turtle" (Roberts 1827) and settlers "turned so many that [they] were obliged to desist" (Williams 1969). For hawksbill turtles, we located 55 historic nesting beaches, seven of which supported major historic populations (Figure 1b; WebTable 2). Major nesting beaches included the island of Roncador, off the Nicaraguan coast, which was "famous for the number of its turtles…the shore seemed black with turtles" (Squier 1865), and Chiriqui, Panama, which was considered to be the "most important nesting aggregation in the Caribbean" (Carr 1956).

We used these geographic nesting data to calculate a range of population sizes, based on quantitative modern nesting data and historic export data. For green turtles, observations from 20th century nesting in Tortuguero, Costa Rica (Troëng and Rankin 2005) indicate that this nesting site supported an average of 130 500 adults (WebTable 3). We first assumed that each of the nine historic major nesting sites supported populations as large as this recent Tortuguero population and that the remaining 50 minor nesting aggregations were each 10% of that value. These calculations yield an estimated historic population of 1.8 million adult green turtles (WebTable 3). Large as this number may seem compared with modern abundances of less than 300 000 (Seminoff 2002), historic hunting data indicate that the 17th century Cayman Island green turtle population alone was approximately 6.5 million adults (Jackson 1997; WebTable 3). Assuming that each of the nine major nesting beach populations was as large as the historic Cayman Island population and the 50 minor nesting aggregations were only 10% of this size yields a historic population for the Caribbean of around 91 million adult green turtles (WebTable 3).

For hawksbill turtles, observations of 20th century nesting at Chiriqui Beach, Panama (Meylan and Donnelly 1999), indicate that this nesting site supported 135 000 adults in the 1950s (WebTable 3). Assuming that the seven major nesting sites each had abundances comparable to that of Chiriqui, and that each of the remaining 48 minor nesting sites had populations of only 10% of this number, the total Caribbean population was 1.6 million adult hawksbill turtles (WebTable 3), compared to fewer than 30 000 today (Bjorndal and Jackson
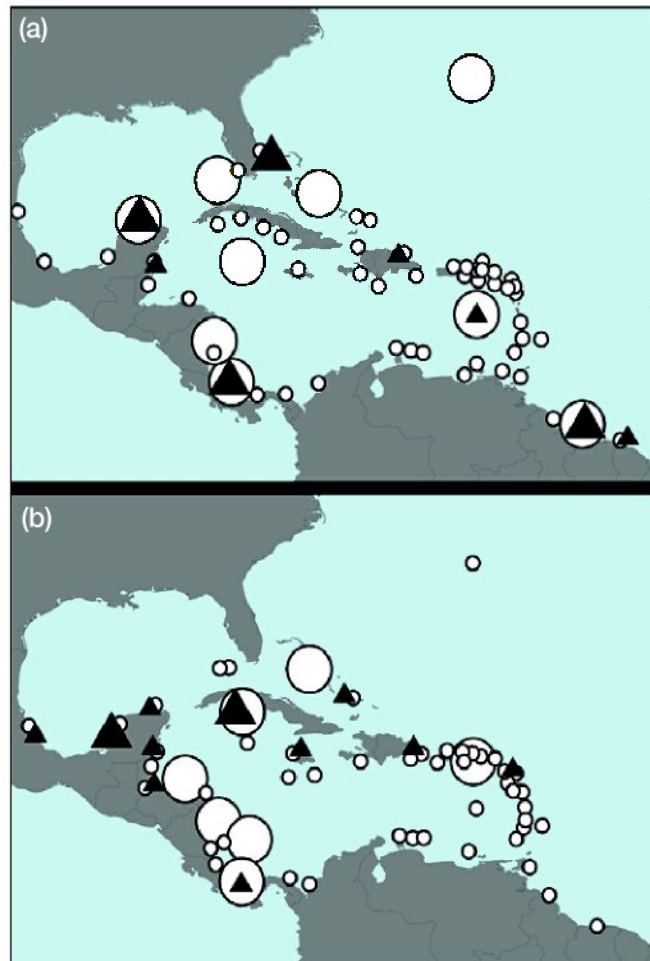

Figure 1. *Nesting beach loss in Caribbean sea turtles. (a) Green turtles and (b) hawksbill turtles have lost most of their historic nesting sites (circles) and all major nesting sites (large circles) have been reduced or eliminated. Modern nesting beaches with > 500 nesting females (large triangles) and 100–500 (small triangles) are mapped. All modern and historic nesting data are listed in WebTable 2.*

2003). However, historic export data from the 19th century Bahamian fishery (Northcroft 1900) provide an estimate of 936 600 adults from just this region (WebTable 3). Extrapolating across the seven major and 48 minor nesting beaches gives a historic population estimate of 11 million hawksbill turtles in the Caribbean region (WebTable 3).

Our green turtle population estimate based on historic nesting data is more than two times greater than the 33–39 million green turtles estimated by Jackson (1997), and our hawksbill turtle calculation is 20 times greater than the extremely conservative estimate of 540 000 adult hawksbill turtles by Bjorndal and Jackson (2003). Our estimates may be high, as they assume that all major nesting sites were as large as the Bahamian and Cayman Island populations. Furthermore, some non-nesting turtles may have been mistaken for nesting females, potentially increasing the estimated number of nesting beaches. Because they are based on conservative and offi-

cially recorded estimates of catch, however, our estimates could also be too low. For example, Cayman hunting data do not reflect exploitation by Spanish, French, Dutch, and other English settlers and pirates in the Caribbean, who did not report their catch (eg Jackson 1924). While extrapolations from anecdotal historic evidence will never be precise, using true historic data provides an accurate assessment of the order of magnitude of change that cannot be determined from traditional ecological data, particularly for severely hunted populations.

■ Population declines and nesting beach loss

Our calculations based on historic export data show that modern populations of green and hawksbill turtles are 0.33% and 0.27% of their historic numbers, respectively. These calculations assume modern populations of 300 000 green and 30 000 hawksbill turtles. Such staggering declines in abundance have been compounded by the elimination of entire nesting populations that are extremely unlikely to become re-established (Seminoff 2002). The loss of even a single nesting site makes a permanent, irreversible dent in the sea turtle population, but loss of nesting beaches has not been quantified, nor used as a measure of population change across the Caribbean region. Our data indicate that historic hunting completely eliminated at least 17 green turtle and seven hawksbill nesting sites, including three major nesting beaches: Bermuda; Moskito Coast, Nicaragua; and Dry Tortugas, US (WebTable 2). Hunting also severely thinned turtles at the remaining sites, so that half of modern nesting populations have an uncertain future. So-called "nesting aggregations" are pitifully small, often consisting of females that nest singly. Such small sites include the once great Cayman Island green turtle rookery. Today, 55% of green turtle and 44% of hawksbill nesting beaches host fewer than 10 nesting females, or are described as having only rare nesting (Figure 2; WebTable 2). Historic data clearly show that each of these nesting sites supported large populations in the past.

■ Ecosystem consequences

The severe reduction of turtle numbers is of concern not only because of the turtles themselves, but also with regard to their previously important roles as ecosystem engineers in Caribbean ecosystems (Bjorndal and Jackson 2003). Green turtles feed primarily on turtle grass (*Thalassia testudinum*; Thayer *et al.* 1982) and hawksbill turtles have a unique dietary preference for marine sponges (Leon and Bjorndal 2002). Both turtle grass and sponges are important habitat-structuring species throughout the region. We estimated total food intake of historic populations of green and hawksbill turtles (WebTables 3 and 4). Ninety-one million green turtles consumed between 11 and 22 million metric tons dry mass (DM) of turtle grass, which amounts to 86% of the total area and up to 45% of the

annual productivity of seagrass beds (WebTables 3 and 4). Eleven million hawksbill turtles consumed between 0.9 million and 2.0 million metric tons DM of sponges annually, or 83% of the biomass and annual growth of sponges (WebTables 3 and 4). The geographic scale at which historic populations of turtles disturbed coral reef and seagrass communities is inconsistent with modern observations of seagrass beds that grow virtually unchecked by grazing and of coral reefs where few large predators remain. Our calculations indicate that today's green and hawksbill turtle populations consume just 0.1% of the area of Caribbean seagrass and reef sponges, respectively.

In the 1830s, the great naturalist, John J Audubon described the seagrass beds of the Dry Tortugas as "cut near the roots" by vast numbers of grazing green turtles (Audubon 1926), an ecological state also described by William Dampier in the 1680s (Dampier 1968). Our calculations agree with these descriptions (WebTable 4). Ninety-one million grazing green turtles left behind large patches of actively growing seagrass clipped down to the blade–sheath junction (Thayer *et al.* 1982). The ecological extinction of green turtles transformed an ecosystem with diverse species of seagrasses dominated by large herbivores into a detritus-based ecosystem dominated by overgrown monocultures of *T testudinum*, with two important conservation implications.

First, the annual removal of 86% of mature seagrass blades would have greatly inhibited the spread of epiphytic organisms that characterize modern seagrass beds, and thus preempted the spread of seagrass wasting disease. The disease-causing parasitic protist, *Labyrinthula*, attaches preferentially to mature seagrass blades, from which it colonizes actively growing seagrass stems (Bowles and Bell 2004). Wasting disease is now widespread and is unlikely to disappear unless grazing is reintroduced on an appropriately large geographic scale, even if other factors such as excess nutrients also play a role in the spread of the disease (Pandolfi *et al.* 2005).

Second, in contrast to green turtles, grazing fishes and sea urchins lack the microbial symbionts that metabolize cellulose, which comprises most of the carbon in turtle grass blades. Their waste, as well as unconsumed turtle grass, is largely buried in sediments (Thayer *et al.* 1982), where it is no longer available to animals in the grazing food chain. The decline of green turtles has therefore resulted in a loss of productivity available to the animal food chain – including commercially exploited reef fishes – and therefore amounts to a reduction in protein-rich food available for Caribbean people.

Similarly, on reefs, historic consumption of sponges by hawksbill turtles was up to 800 times higher than that of modern populations (WebTable 4); this has implications for the sponge community composition and the relative abundances of sponges and reef corals (Bjorndal and Jackson 2003). Hawksbill turtles preferentially feed on non-toxic sponges when they are available, but can survive on a mix of toxic species (Leon and Bjorndal 2002).

Thus, as turtles declined in abundance, the relative quantities of toxic sponges that each hawksbill turtle consumed should also have decreased. Historical data support this hypothesis. Observations from the 17th through the 20th century indicate that toxicity of hawksbill turtle meat for human consumption has decreased over time (Table 1). This unanticipated result provides another independent measure of the extreme reduction in hawksbill turtle populations, as well as indirect evidence for changes in Caribbean benthic ecosystems.

The role of turtles as major agents of landscape-scale patterns of disturbance has been questioned, based on small-scale experimental studies that attempt to test the effects of turtle grazing in tiny plots (eg Bowles and Bell 2004). Such experiments cannot mimic the intensity of disturbance of tens of millions of turtles across the entire Caribbean any more than clipping a few small quadrats of prairie grass could possibly recreate the effects of 30 million American bison on the Great Plains (Isenberg 2000). Our historical data indicate that centuries ago, much of the mobile animal biomass in the Caribbean was concentrated in the bodies of large animals, an ecological possibility supported by modern surveys on isolated and protected reefs (Friedlander and DeMartini 2002). These data strongly suggest that the extirpation of large animals was the first step in dismantling Caribbean marine ecosystems, and circumstantial evidence – such as recent outbreaks of seagrass disease and coral overgrowth – supports the inference that breakdown in structural habitat magnified the loss of large animals. Clearly, successful conservation and management of turtles is an essential component in achieving ecosystem restoration.

■ **Good news for sea turtles?**

The protection of nesting beaches since the 1970s has resulted in extraordinary local population increases in short periods of time, particularly among green turtles (Hays 2004; Troëng and Rankin 2005). These encouraging results have led some to question whether green turtles are endangered within the Caribbean and greater Atlantic region (Broderick *et al.* 2006). Patterns in modern nesting data suggest that nesting beach conservation efforts have indeed been highly successful in reversing downward population
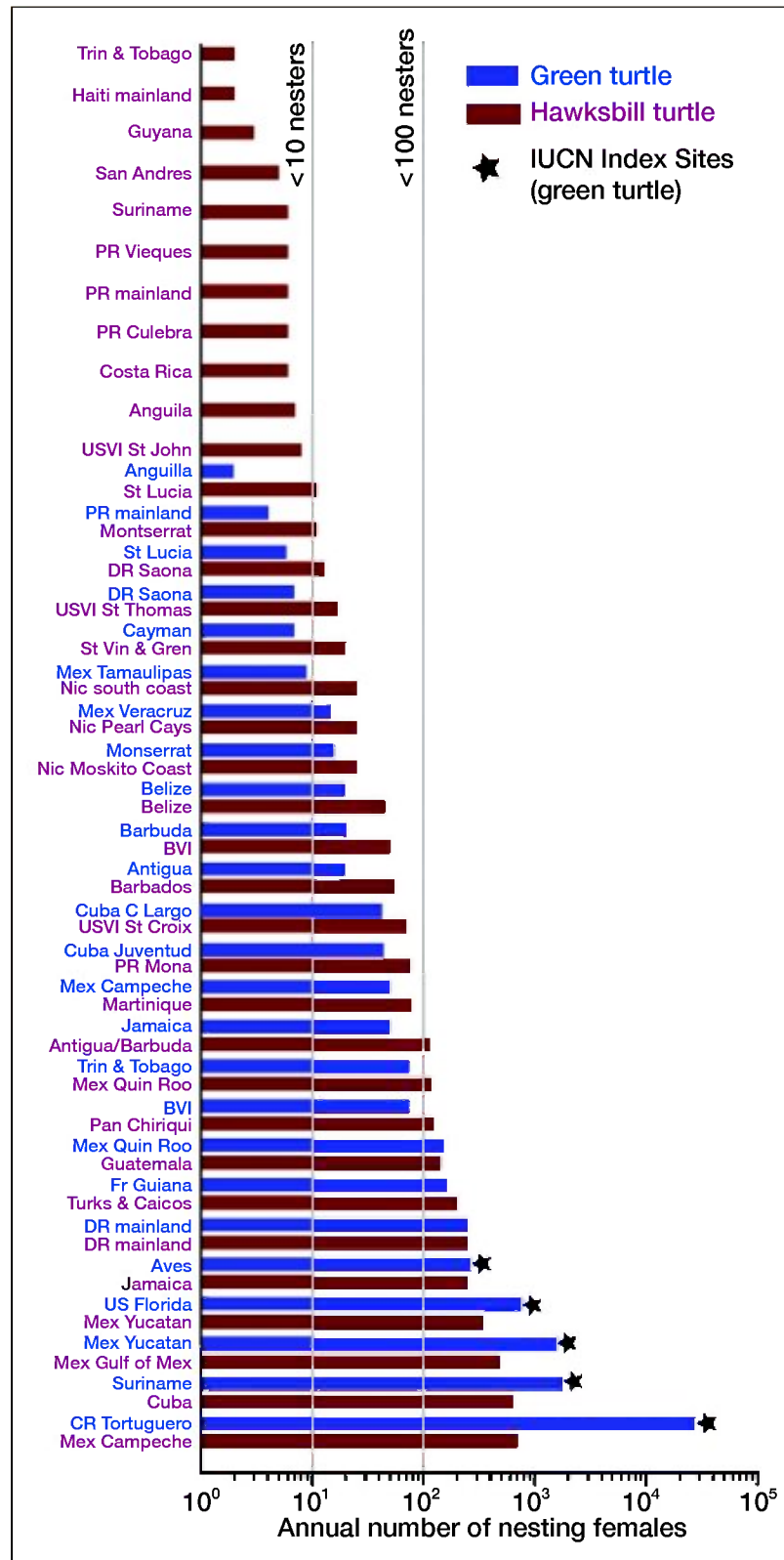

Figure 2. *The number of females nesting annually on modern sites is very small and unevenly distributed, with 10% of sites hosting 90–95% of nesters. Large sites are the focus of conservation assessments such as the IUCN Red List Global Status Assessment for green turtles. The figure does not include 29 nesting sites for which reliable quantitative data do not exist; 24 of these sites are described as having rare, scattered, or infrequent nesting. All modern nesting data are listed in WebTable 2.*

Table 1. Changes in hawksbill turtle toxicity

Date	Location	Observations of hawksbill turtle toxicity
1684	Panama	"Yet these Hawks-bills, in some places are unwholesome, causing them that eat them to purge and vomit excessively…" (Dampier 1968).
1760	French Caribbean	"…it is dangerous to eat of [the hawksbill's] flesh, which, though fat and delicious, is of so purgative a quality, that unless you take but a little, or are well assured that you have nothing to fear from its activity, you may expect to see yourself covered with pimples and blotches" (Jefferys 1760).
1770s	Nicaragua	"…this kind of Tortoise is not very agreeable to the taste, nor do we eate them" (Williams 1969).
1837	Florida	"The hawksbill … is not highly valued for food" (Williams 1837).
1884	Caribbean	"The flesh of the hawksbill turtle is comparatively valueless; indeed, in the West Indies it is said that it possesses cathartic qualities in a high degree… I have seen it in Washington several times recently, both in the markets and before several restaurants in the city" (True 1884).
1900	Bahamas	"All three kinds [green, hawksbill, loggerhead] are eaten. It is an unfortunate policy which takes them recklessly each season – though they are pleasant enough to eat and most nourishing – and thereby causes turtle to become scarcer each year" (Northcroft 1900).
1945	Jamaica	"Formerly the chief value of the Hawksbill was for the shell, which sold at high prices. Now…the market is for meat, which finds a ready market locally" (Thompson 1945).
1974	Barbados and Panama	"Fishing is mainly for hawksbill for meat and shell… The meat and eggs of the…hawksbill turtle are taken for local consumption" (Rebel 1974).

Hawksbill turtle meat was toxic until the mid to late 19th century when it began to be eaten without health consequences. These observations suggest that hawksbill turtles ate more desirable, less toxic sponge species as the turtles became less abundant and competition for food was reduced.

Instead, short-term data are extrapolated over longer time periods, a dangerous method considering that population trends are known to be quickly reversible (Hays 2004; Troëng and Rankin 2005; Broderick *et al.* 2006). Time series that span more than one turtle generation exhibit significant declines; data extending over more than 40 years are highly likely to show long-term declines when compared with recent data (Figure 3; difference in results, $P = 0.029$). Because of this systematic difference in results, short-term data should not be used to infer long-term change. Using modern data to speculate about historic change is certain to dangerously underestimate long-term population change.

Second, despite some success at a few sites, most nesting beaches across the region have suffered enormous, unmeasured losses and are much smaller than those used in conservation assessments. The Caribbean component of the IUCN Red List Global Assessment (Seminoff 2002) was based on data from five nesting sites, four of which have increased over the past three decades. These increases demonstrate the efficacy of nesting beach protection, but should not be mistaken for a sign of effective conservation across the region, because these sites are anomalously large and well protected. The five IUCN sites are the largest sites in the Caribbean. Annual aggregations of nesting females range from about 300 at Aves Island in Venezuela to a few tens of thousands at Tortuguero, Costa Rica (Seminoff 2002; Figure 2; WebTable 2). Therefore, generalizations based solely on these few large beaches inevitably gives a false picture of the overall status of Caribbean green turtle populations. A more accurate assessment of regional change would consider trends on all known nesting beaches, despite lack of precision in numbers of nesting females on some smaller sites.

trends on a few well-studied beaches. Our analysis of trends among IUCN-assessed nesting beaches (Seminoff 2002) suggests that the situation has improved in the past decade; nesting data collected since 1994 show a population increase when compared to data collected between 1980 and 1994 (Figure 3; $P = 0.011$).

Despite recent conservation achievements, declaring success would be a mistake for two reasons. First, there is very little long-term data, despite the IUCN mandate to determine nesting beach trends over three generations.

As Pauly (1995) emphasized in his landmark paper on "shifting baselines", most of the big changes to large marine vertebrate populations occurred many decades to centuries ago, prior to quantitative monitoring programs. Therefore, capturing the magnitude of these changes requires the use of historic data. Our imprecise but comprehensive historic nesting data describe changes over a

much broader geographic and temporal scale, providing a picture of regional depletion that has neither stabilized nor reversed. Of the 59 green turtle nesting beach sites documented in our study, 29% have been lost and 55% of the rest are so small that they will probably disappear if not protected. A strategy that focuses attention on a few exceptional nesting beaches runs the risk of allowing the destruction of smaller, historically important nesting beaches without realizing the losses that have occurred.

Determining conservation strategies for marine turtles over more than a few years inevitably involves a great deal of uncertainty. Important new tools, such as information gap theory, have been developed to explicitly include uncertainty when assessing possible management actions and determining the degree of risk that can be taken to achieve desired results (Ragen *et al.* 2005). The currently popular focus on nesting data from a few major nesting beaches (eg Broderick *et al.* 2006) ignores the uncertain future of nearly 90% of the remaining nesting beaches. This risk-prone strategy does not account for factors such as extreme storms, disease, or other catastrophic events.

Historically, green and hawksbill turtles were ubiquitous, abundant, and nested in high densities throughout the Caribbean. On an evolutionary timescale, widespread nesting was a risk-averse "evolutionary strategy" for the persistence of turtle species. Humans have reduced green and hawksbill turtles nesting beaches by one fifth and without proper protection, half of the remaining nesting beaches could soon be lost. Even very small nesting beaches do recover, however (Hays 2004), so that protection and scientific research funding should be extended across as many beaches as possible, especially those that were once important, but are now greatly reduced. Protecting more nesting beaches is not a politically or socially simple endeavor, but it is the only way to avoid the risk of putting all the remaining turtle eggs in a very few baskets.
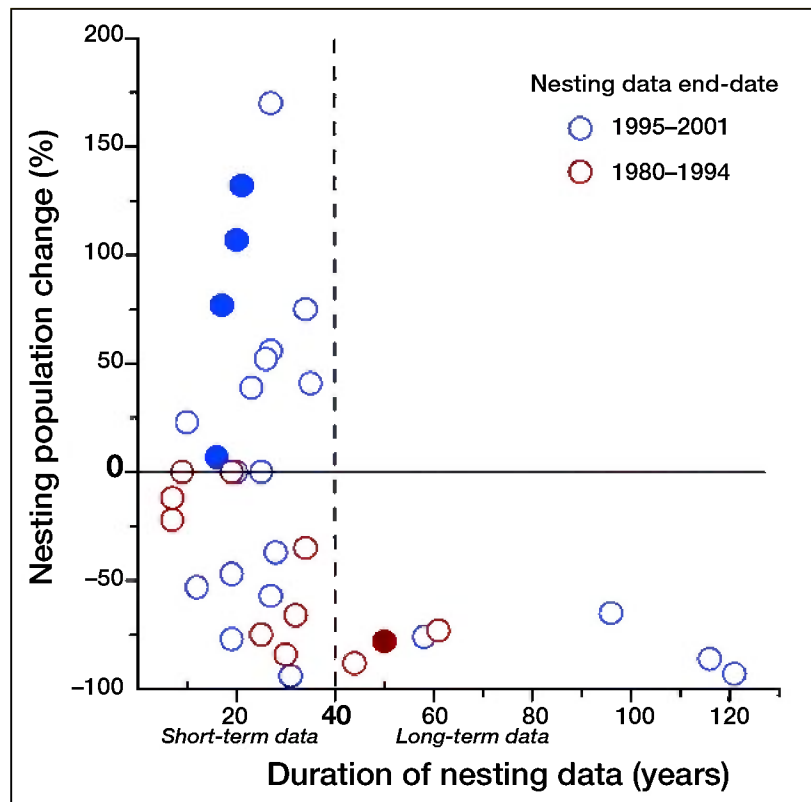

Figure 3. *Shifting baselines in green turtle nesting trends and recent conservation success. Data used in the IUCN Red List Global Status Assessment for green turtles (Seminoff 2002) show very large declines in numbers of nesting females over the past century, but increases on particular nesting beaches in the last decade. Each circle represents a single Index Nesting Site used in the IUCN Assessment. All time series > 40 years (right of vertical dotted line) record population declines of 65–93%. Long-term data are significantly more likely to record population declines than shorter time series (two-tailed Fisher's exact test, P = 0.029). However, short-term time series ending after 1994 (blue circles) show increases when compared to similar time series ending in 1994 or before (red circles; two-tailed Fisher's exact test, P = 0.011). We calculated percent change using past and present nesting data (Seminoff 2002) and used the midpoint when a range of years was given. Solid circles indicate Caribbean index sites.*

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