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Natural beaches confer fitness benefits to nesting marine turtles

David A. Pike*

School of Biological Sciences A08, University of Sydney,

Sydney NSW 2006, Australia

*david.pike@bio.usyd.edu.au

Coastal ecosystems provide vital linkages between aquatic and terrestrial habitats and thus support extremely high levels of biodiversity. However, coastlines also contain the highest densities of human development anywhere on the planet and are favoured destinations for tourists, creating a situation where the potential for negative effects on coastal species is extremely high. I gathered data on marine turtle reproductive output from the literature to determine whether coastal development negatively influences offspring production. Female loggerhead (*Caretta caretta*) and green turtles (*Chelonia mydas*) nesting on natural beaches (as opposed to beaches with permanent development) produce significantly more hatchling turtles per nest; all else being equal, females that successfully produce more offspring will have higher fitness than conspecifics producing fewer offspring. Thus, female marine turtles nesting on natural beaches probably have higher fitness than turtles nesting on developed beaches. Consequently, populations nesting on natural beaches may be able to recover more quickly from the historic population declines that have plagued marine turtles, and some species may recover more quickly than others.

Keywords: *Caretta caretta*; *Chelonia mydas*; coastal development; coastal habitat; hatching success; natural habitat

1. INTRODUCTION

Coastal ecosystems support high levels of biodiversity and represent critical linkages between the aquatic environment and terrestrial habitats for many species. However, coastal areas also support the highest densities of the human population (Small & Nicholls 2003) and are popular tourist destinations (Martínez *et al.* 2006); these two factors have been shown to negatively affect the environment (Miller & Auyong 1991; Garcia & Severa 2003) and many animal species at local scales (e.g. Amo *et al.* 2006; Arroyo & Razin 2006). Along these lines, research is rapidly focusing on the impacts of humans on wildlife. However, these studies are often restricted to single species living in local environments, and whether these studies can be generalized to other closely related species and across large geographical distributions is unknown.

To understand the consequences of human development on individuals and populations, we need to determine not just how individuals modify their

behaviours, but also how fitness changes when such altered environments are used. However, directly quantifying fitness is extremely difficult because it requires knowing the fate of all offspring produced by each female in the population. Since this is almost never known for wild populations, by necessity we must rely on other less accurate estimates of fitness. One strong indirect measure of fitness is the number of offspring a female successfully produces (Roff 2002); all else being equal, females that produce more offspring should have higher fitness than females producing fewer offspring. This generalization is often inferred in short-lived species, but recent population modelling of long-lived, iteroparous and highly fecund species has revealed that individual offspring are important contributions to the overall population, even when juvenile mortality levels are high (Mazaris *et al.* 2005, 2006). This finding is important because it reveals that we can use information on reproductive success, namely the number of offspring produced per reproductive bout, to understand and compare the relative fitness of populations that nest in different environments, such as those that differ in the degree of disturbance by humans.

Marine turtles are obligate terrestrial nesters that are ecologically important in both marine (Moran & Bjørndal 2005) and terrestrial (Bouchard & Bjørndal 2000; Hannan *et al.* 2007) systems, and are distributed in tropical, temperate and even sub-arctic waters worldwide. Nesting sites are generally limited to the area along the shoreline between the high-tide line and sand dunes, and these areas are also highly impacted by beach visitors and coastal development. To determine what (if any) effect these factors have on the reproductive success of marine turtles, I gathered data from the literature on the hatching success (percentage of eggs that hatch) of turtles nesting on developed (where nests are exposed to relatively high levels of direct human disturbance and other indirect effects) and natural (not developed) beaches. I used this dataset to ask whether nests laid on natural beaches produce more hatchlings than nests laid on developed beaches. Understanding the patterns of reproductive output on a large scale is an important step towards determining the susceptibility of the nesting cycle to anthropogenic impacts, and may reveal insights into how populations will recover from historical declines.

2. MATERIAL AND METHODS

I searched peer-reviewed journal articles published from 1900 to 2007 and compiled a database of marine turtle field studies reporting the following information: species, habitat (natural or developed nesting beach) and mean hatching success (the number of hatchlings successfully emerging from eggs as a function of the total number of eggs laid). Habitat type was split into two categories as follows: beaches that were devoid of permanent structures built by humans (natural beaches) and those that contained permanent structures such as houses and condominiums (developed beaches). When the authors did not directly state whether the beach was 'natural' or contained human development along the shoreline, I attempted to use the study site description to place the study into one of these two categories. When this was not possible, the study was excluded from further analysis. If the authors presented mean values for multiple nesting seasons, I used the grand mean in my analysis, and when a range of values were given (instead of the mean), I used the median for analysis.

Clutch size can vary geographically and among individuals (being generally greater in individuals with larger body sizes; Hirth 1980; Van Buskirk & Crowder 1994; Tiwari & Bjørndal 2000), and hatching

success can also increase with clutch size (e.g. Hewavisenthi & Parmenter 2002). I controlled for clutch size in all analyses by using the percentage of eggs that hatched from each nest. The percentages were arcsine-transformed prior to analysis to satisfy the assumptions of parametric statistical tests, but mean values using the raw data are presented in figure 1 for ease of interpretation.

3. RESULTS

Published data on hatching success from both natural and developed beaches were only available for two species of marine turtle (loggerhead, *Caretta caretta* and green, *Chelonia mydas*); data for the remaining five species were only available from natural nesting beaches.

Studies on hatching success of loggerhead and green turtles came from a wide geographical area, and this was largely representative of the overall geographical range of each species (table 1). Hatching success was significantly higher on natural beaches than on developed beaches for both loggerhead ($F_{1,41}=4.52$, $p=0.039$) and green turtles ($F_{1,16}=5.97$, $p=0.026$; figure 1). On average, loggerhead and green turtles nesting on natural beaches increased the hatching success of their nests by 12.7 and 16.0 per cent, respectively (figure 1a). In some cases, there were multiple studies from the same individual nesting beach, but when I restricted the analysis to only one unique site per species (using the most recent study), the above results remained qualitatively similar. A direct comparison between the two species revealed that green turtles had higher hatching success regardless of the type of nesting beach (two-way ANOVA with species and habitat type as factors; $F_{1,57}=10.11$, $p=0.002$), and confirmed the overall pattern of higher hatching success on natural beaches ($F_{1,57}=7.19$, $p=0.01$; no significant interaction term).

4. DISCUSSION

Hatching success of marine turtle nests varied greatly among beaches and by species, but one important trend remained consistent: more turtles hatched from nests laid on natural beaches than those laid on developed beaches, regardless of species identity (figure 1). Variation in hatching success can be caused by many different factors, including nest site location (e.g. microhabitat; Foley *et al.* 2006), temporal effects (within or among nesting seasons; Tucker & Frazer 1994; Pike & Stiner 2007), geographical variation (Tiwari & Bjorndal 2000) and species differences (Hirth 1980; Van Buskirk & Crowder 1994; figure 1). These factors represent random 'noise' in any attempt to discern predictable patterns of reproductive success over larger scales. Consequently, not accounting for such factors (as I have done here) should create sufficient variation in the data to lead to acceptance of a null hypothesis (that natural and developed beaches have similar rates of hatching success), rather than generating the distinct, statistically significant patterns that emerged (figure 1). Thus, it is likely that these patterns are real, and that nests laid on natural beaches consistently produce more hatchlings per nest than developed beaches. Although published data were not available to test this hypothesis for five of the seven marine turtle species, the reasons for this remain unclear (e.g. whether these species regularly

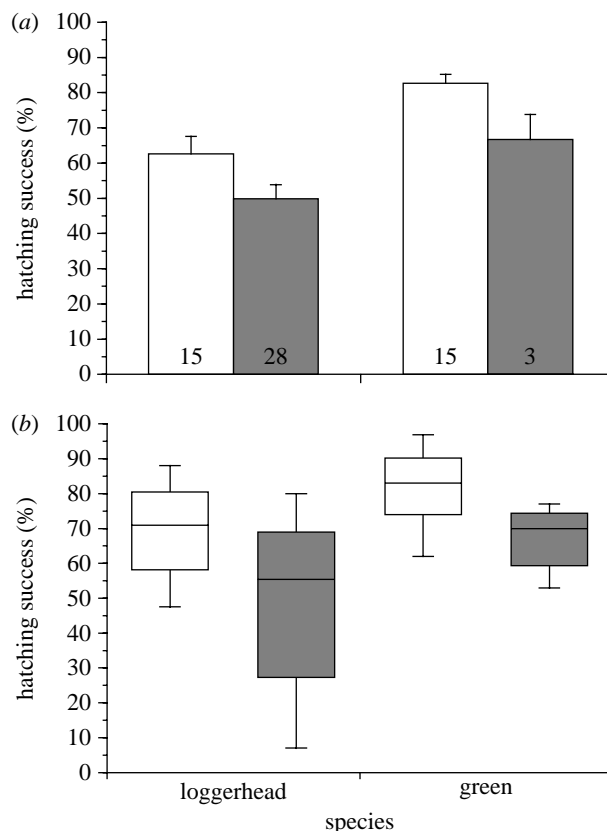


Figure 1. (a) Mean percentage (+s.e.) of loggerhead and green turtle eggs hatching from nests laid on natural (undeveloped; open bars) beaches compared with those laid on beaches with human development (grey bars). Numbers indicate sample sizes (number of individual studies) used in the analysis. (b) Box plots showing variation in hatching success (%) for the same two species and beach types. The lower bound of the box represents the first quartile, the middle is the median, the upper bound is the third quartile and the error bars represent minimum and maximum values.

Table 1. Number of studies included in the analysis of hatching success of loggerhead and green turtles, shown by region (the ocean or sea in which the study site occurs) and beach type (natural or with permanent human development).

region	loggerhead turtle		green turtle	
	natural beaches	developed beaches	natural beaches	developed beaches
Atlantic Ocean	8	11	4	
Caribbean Sea			2	
Mediterranean Sea	5	16		
Pacific Ocean	2	1	9	1
Red Sea				2

nest on developed beaches, studies from developed beaches are less likely to be published or researchers favour natural beaches as study sites).

The fitness consequences and conservation implications of this pattern are immediate and readily apparent; on average, female marine turtles nesting on natural beaches will successfully produce more offspring per clutch than conspecifics laying eggs on developed beaches (figure 1). This pattern should result in higher individual fitness for such females

(Roff 2002; Mazaris *et al.* 2005, 2006), and because offspring generally return to the region from which they hatched to mate and reproduce (Bowen *et al.* 1993; FitzSimmons *et al.* 1997), populations nesting at natural beaches may be able to recover faster from historical declines. The fact that green turtles have higher hatching success than loggerheads (regardless of habitat type; figure 1) also hints that in the absence of abiotic factors affecting one species more than the other (e.g. tropical storms; Pike & Stiner 2007), population growth rates may be higher in green turtles.

The mechanism that leads to lower hatching success on developed beaches is not known, but could well reflect a combination of direct (e.g. Jacobson & Lopez 1994; Steinitz *et al.* 1998; Foley *et al.* 2006; Pocock 2006) and indirect factors. Elucidating these causal links will be an important step towards guiding conservation and management decisions, including determining whether development of marine turtle nesting areas can progress while simultaneously minimizing negative impacts on the reproductive success of nesting turtles.

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