Invited reply

Natural beaches produce more hatchling marine turtles than developed beaches, despite regional differences in hatching success

Recently I used a meta-analysis to show that globally, both loggerhead (*Caretta caretta*) and green turtle (*Chelonia mydas*) nests laid on natural beaches have higher hatching success than nests laid on beaches with permanent human development (Pike 2008). My analysis pooled data from several geographical regions and was restricted to published studies reporting such data, owing to inherent problems with datasets that have not undergone peer review (e.g. Debachere 1995; Lacanilao 1997). Consequently, Fuentes & Hamann (2009) have three main concerns with my work: (i) the original analysis did not control for regional differences in hatching success, (ii) there may be fundamental differences in the quality of developed beaches, such that they have inherently low levels of hatching success, even prior to development occurring, and (iii) the conservation outcomes of this broad pattern may be difficult to apply at local levels. Here I re-analyse the original dataset and show that (i) the original pattern remains the same even after accounting for regional variation and genetic influences, and (ii) the developed and natural beaches used in the original analysis experience similar environmental conditions, thereby (iii) reinforcing the conservation implications of this pattern.

Regional variation in hatching success could have influenced my original results because I pooled data for natural and developed beaches, even when data from both beach types were not available for all geographical areas. However, even after controlling for regional differences, my original results remain significant for both loggerhead (ANOVA with region nested within beach type; $F_{2,37}=3.61$, $p=0.037$) and green turtles (one sample t -test; $t=5.08$, d.f. = 8, $p<0.001$; figure 1a). Furthermore, the same pattern appears in loggerhead turtles nesting in the south-eastern United States (the only species and country combination with sufficient sample sizes to analyse separately; $F_{1,12}=7.55$, $p=0.018$); and despite low sample sizes, the pattern also holds for each of two genetically distinct populations with sufficient data

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for analysis (US North Atlantic, one sample t -test: $t=-2.93$, $p=0.05$; US South Atlantic, ANOVA: $F_{1,6}=4.84$, $p=0.07$; figure 1b). The remarkable consistency in these analyses considerably strengthens my original conclusions, demonstrating that this result is robust, and suggesting that even at local scales, beach development lowers the number of offspring produced per nest (figure 1).

Fuentes & Hamann (2009) also point out that developed nesting beaches could be located on the periphery of nesting populations, and thus may have inherently low hatching success (e.g. owing to the hypothesized suboptimal temperatures at developed beaches). However, developed beaches were distributed within the geographical range of natural beaches in six of eight of the comparisons I made (both exceptions were in loggerhead turtles). Furthermore, I directly tested the possibility that temperatures differed between beach types by comparing the mean ambient temperatures (averaged for the period 1950–2000) during the warmest quarter of the year (when marine turtles generally nest; see electronic supplementary material 1 for full details). This comparison is biologically relevant because ambient temperatures correlate strongly with marine turtle nest temperatures (e.g. Hawkes *et al.* 2007). Temperatures differed significantly between

Figure 1. Mean percentage (+ s.e.) of loggerhead (*C. caretta*) and green turtle (*C. mydas*) eggs hatching from nests laid on natural (undeveloped; white bars) beaches compared to those laid on beaches with human development (grey bars). Sample sizes (number of individual studies) are indicated and error bars are precluded when $n=1$. Data are presented for (a) three regions and (b) one country and two distinct genetic populations with data for both beach types and a combined $n>4$ (see Pike (2008) for further details).

beach types in only two cases, and the greatest temperature difference was in green turtles at the global scale (1.7°C; electronic supplementary material 1). I therefore re-analysed the data on green turtle hatching success at the global scale using temperature as a covariate, which again showed that a significantly higher proportion of eggs hatch from nests incubating on natural beaches ($F_{1,15} = 4.51$, $p = 0.05$; with one statistical outlier excluded this result strengthens to $F_{1,14} = 10.38$, $p = 0.006$). This clearly demonstrates that the relationship between hatching success and beach development is not a by-product of thermal differences between the two types of beaches.

Overall, then, reanalysis shows a strong, consistent and significant pattern of lowered hatching success in both loggerhead and green turtle nests incubating on developed beaches, regardless of the way the data are analysed. This pattern holds at global (Pike 2008), regional and local scales (figure 1) and is not due to differences in ambient temperatures at nesting beaches (electronic supplementary material 1) or differences in when the studies occurred (electronic supplementary material 1). This finding is of distinct conservation value for marine turtle nesting areas where future development is planned or likely, especially because emerging global patterns of coastal development are predicted to occur in areas with little or no current development (Small & Nicholls 2003). Future studies could help determine the mechanism behind this pattern and whether certain types of development (e.g.

single houses versus high-rise condominiums) affect marine turtle hatching success in similar ways. However, simply being aware of the likely impacts is a solid beginning.

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