

A potential tool to mitigate the impacts of climate change to the caribbean leatherback sea turtle

JUAN PATINO-MARTINEZ*†, ADOLFO MARCO*, LILIANA QUIÑONES* and LUCY HAWKES‡

*Department of Biodiversity Conservation and Ethology, Estación biológica de Doñana, CSIC, Av Américo Vespucio, S/N 41092, Seville, Spain, †ARANZADI Zientzia Elkarte Society of Science, Zorroaga Gaina 11, 20014, Donostia-San Sebastián, Spain,

‡Brambell Laboratories, School of Biological Sciences, Bangor University, Deiniol Road, Bangor, Gwynedd LL57 2UW, UK

Abstract

It is now well understood that climate change has the potential to dramatically affect biodiversity, with effects on spatio-temporal distribution patterns, trophic relationships and survivorship. In the marine turtles, sex is determined by incubation temperature, such that warming temperatures could lead to a higher production of female hatchlings. By measuring nest temperature, and using a model to relate the incubation temperature to sex ratio, we estimate that Caribbean Colombian leatherback sea turtles currently produce approximately 92% female hatchlings. We modelled the relationship between incubation, sand and air temperature, and under all future climate change scenarios (0.4–6.0 °C warming over the next 100 years), complete feminization could occur, as soon as the next decade. However, male producing refugia exist in the periphery of smaller nests (0.7 °C cooler at the bottom than at the centre), within beaches (0.3 °C cooler in the vegetation line and inter-tidal zone) and between beaches (0.4 °C higher on dark beaches), and these natural refugia could be assigned preferential conservation status. However, there exists a need to develop strategies that may ameliorate deleterious effects of climate-induced temperature changes in the future. We experimentally shaded clutches using screening material, and found that it was effective in reducing nest temperature, producing a higher proportion of male hatchlings, without compromising the fitness or hatching success. Artificial shade in hatcheries is a very useful and simple tool in years or periods of high environmental temperatures. Nevertheless, this is only an emergency response to the severe impacts that will eventually have to be reversed if we are to guarantee the stability of the populations.

Keywords: Colombia, conservation, global change, hatchery, leatherback, Panama, reproduction, sea turtles, sex ratio, temperature

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Introduction

In 2007, the Intergovernmental Panel on Climate Change (IPCC) released their fourth report, in which dramatic changes to global climatic patterns were described for recent decades, and predicted for future ones (IPCC 2007). Accordingly, the threat of climate change to biodiversity has received considerable research attention recently (Hampe & Petit, 2005; Araujo & Rahbek, 2006; Heller & Zavaleta, 2009; Willis & Bhagwat, 2009), to try to predict the likely effects of climate change and to enable mitigation of any negative impacts. From a marine perspective, climate change may have several deleterious effects. Sea levels may rise by up to 3.4 mm per year (Rahmstorf *et al.*,

2007), although with substantial variation by location, encroaching on coastal shores and reducing total littoral habitat, if hard coastal structures (such as buildings and coastal fortifications) cannot be retreated (Fish *et al.*, 2008). Rising temperatures in coastal waters may cause ecosystem wide changes as the thermal tolerances of various species are exceeded: most notably those of corals, which expel symbiotic algae outside of a sensitive thermal range (Hoegh-Guldberg *et al.*, 2007; Hoegh-Guldberg, 2011). Such bleaching would dramatically affect the dynamics of coral reef systems, for example, causing a change in competitive interactions for space by algae and corals (Mumby *et al.*, 2007). Finally, mobile and migratory animals may alter their spatio-temporal abundance (Robinson *et al.*, 2009; Kaschner *et al.*, 2011), changing the dynamics of trophic food webs and other inter-specific interactions (Edwards & Richardson, 2004; Both *et al.*, 2009).

Correspondence: Juan Patino-Martinez,
tel. + 34 954 232 340; + 34 954 466 700 Ext. 178, fax + 34 954 621
125, e-mail: juanpatino@ebd.csic.es

Of the marine ectotherms, marine turtles have received considerable research attention, possibly because there are only seven species, and because some of the world's largest colonies occur in some of the world's most developed countries (Rees *et al.*, 2010; Hawkes *et al.*, 2011). In a recent review of marine turtle experts (Hamann *et al.*, 2010), the effects of climate change to marine turtles were named as a top global research priority for their successful future conservation. Specifically, information is yet incomplete to understand the direction of climate change impacts to marine turtles, how they may respond behaviourally, their capacity to adapt to such climatic changes and what conservation actions might be useful in the future (Poloczanska *et al.*, 2008; Hawkes *et al.*, 2009; Fuentes & Cinner, 2010). A growing body of literature is already addressing this shortfall (reviewed in Hawkes *et al.*, 2009): the effects of sea level rise (Fish *et al.*, 2005; Baker *et al.*, 2006; Fuentes *et al.*, 2010a,b), storms and hurricanes (Pike & Stiner, 2007; Fuentes & Abbs, 2010; Garcon *et al.*, 2010; Fuentes *et al.*, 2011a), coastal development (Rumbold *et al.*, 2001; Kamel & Mrosovsky, 2006; Fish *et al.*, 2008) and oceanographic changes (McMahon & Hays, 2006; Chaloupka *et al.*, 2008; Saba *et al.*, 2008; Witt *et al.*, 2010a) have already been described to a degree. The response of turtles through changes to phenology (Weishampel *et al.*, 2004; Pike *et al.*, 2006; Hawkes *et al.*, 2007; Tucker *et al.*, 2008b) and spatial distribution (McMahon & Hays, 2006; Witt *et al.*, 2010b) have accordingly been investigated. However, in the absence of rapid adaptation to climate change, some deleterious effects [e.g. alterations to sex ratios: (Glen & Mrosovsky, 2004; Hawkes *et al.*, 2007; Fuentes *et al.*, 2009a); and nest survivorship: (Hawkes *et al.*, 2007)] may be likely.

The sex of marine turtles is determined by incubation temperatures in the nest during the second third of the incubation period, the thermosensitive period, TP; (Mrosovsky & Yntema, 1980; Yntema & Mrosovsky, 1980; Dalrymple *et al.*, 1985) with females produced at higher temperatures, generally warmer than 29 °C (Mrosovsky, 1994; Chan & Liew, 1995; Davenport, 1997) and males at lower temperatures, with a mixture of sexes only within a narrow 'threshold range of temperatures' (TRT) (Mrosovsky & Yntema, 1980). Although successful incubation occurs between 25 and 33 °C (Miller, 1985), temperatures lower than, or exceeding, the upper thermal threshold could have reduced hatching rates due to increased mortality (Miller, 1985). In addition, incubation temperatures, and thus the sex ratio of hatchlings, vary over time and space (Hawkes *et al.*, 2007) in relation to the position and depth of nests, the colour (albedo) of the sand (Standora & Spotila, 1985; Spotila *et al.*, 1987; Hays

et al., 1995) and climatic conditions such as rainfall (Houghton *et al.*, 2007).

It is therefore evident that increases in ambient temperatures due to climate change have the potential to increase the proportion of female hatchling turtles produced. It is already known that sex ratios for marine turtles are heavily biased towards females (more than 90% female; reviewed in Hawkes *et al.*, 2009), and that recent increases in temperature have, or are expected to, reduce the proportion of males produced (Godley *et al.*, 2001; Glen & Mrosovsky, 2004; Hawkes *et al.*, 2007) and could eventually eliminate all male production. The survival of marine turtle populations thus depends on temperatures being appropriate for the production of both sexes (Chevalier *et al.*, 1999) and knowledge of the natural temperature regimes on marine turtle breeding beaches is essential for conservation to be effective (Hays *et al.*, 2003; Glen & Mrosovsky, 2004; Rahmstorf *et al.*, 2007).

Future global average surface temperatures are expected to warm by at least 0.1 °C per decade even if emissions patterns are kept constant at levels emitted in the year 2000. The Caribbean basin is expected to warm by 1–4 °C by the end of the century for scenario SRES B2; 2–6 °C for scenario SRES A2. In addition to increasing temperatures, anomalies in rainfall patterns (both positive and negative) are expected to increase, as well as the frequency and intensity of extreme storm events (hurricanes; Magrin *et al.*, 2007).

It therefore seems prudent to investigate management techniques with which to mitigate against the negative effects of climate change to marine turtles. Such management techniques may be controversial, set against a background of the gaps in our knowledge of the effects of climate change to marine turtles (Hawkes *et al.*, 2009; Hamann *et al.*, 2010). It is therefore imperative that such techniques are well tested and minimally invasive, and do not compromise aspects of marine turtle ecology. Management techniques must also be as easy and inexpensive as possible, to be deployed on nesting beaches in developing countries, where a majority of nesting probably occurs.

The leatherback sea turtle (*Dermochelys coriacea*) is thought to be at relictual population levels in the Pacific Ocean, potentially as a result of turtles being drowned in fishing nets (Ferraroli *et al.*, 2004; McMahon & Hays, 2006). Leatherbacks are thus listed as 'Critically Endangered' by the World Conservation Union (IUCN 2008, Seminoff & Shanker, 2008). Although mitigation strategies, such as by-catch reduction devices (Alfaro-Shigueto *et al.*, 2007; Read, 2007), and nesting beach protection (Dutton *et al.*, 2005) have been put in place, population recovery could be hampered by climate change (Spotila *et al.*, 1996; Angeles *et al.*, 2007; Semi-

noff & Shanker, 2008; Johnson & Purkey, 2009). Temperatures at leatherback turtle breeding sites worldwide have already experienced an increase in environmental temperatures in the last 100 years (Angeles *et al.*, 2007). Thus, it is essential that an understanding of the current sex ratios for leatherback turtles, and the effect of future changes in temperatures, is gained. The objectives of this study were (i) to investigate in detail the thermal biology of incubation in the leatherback turtle at a breeding site of international importance (Patino-Martinez *et al.*, 2008); (ii) to estimate the current and future sex ratio under possible climate change scenarios; and (iii) to evaluate the effectiveness and implications of using hatcheries to counteract/mitigate the impacts of predicted increase in temperatures to the Caribbean leatherback turtle.

Materials and methods

The study was conducted in the south-western Caribbean sea on the border between Colombia and Panama (8°43'N, 77°32'W, Fig. 1). Leatherback sea turtles (*D. coriacea*) nest on beaches here between February and June (Patino-Martinez *et al.*, 2008), comprising the third largest nesting rookery in the Caribbean and the fourth largest in the world (Patino-Martinez *et al.*, 2008). While Pacific leatherback turtles are thought to be at severe risk of future extinction (Spotila *et al.*, 1996; Spotila *et al.*, 2000), some nesting populations in the Atlantic Ocean are thought to be increasing (Dutton *et al.*, 2005; Girondot *et al.*, 2007; McGowan *et al.*, 2008), and thus somewhat less at risk of extinction. Throughout the breeding season in 2005, 2006 and 2007, temperature data loggers (Hobo StowAway Tidbit v2 www.onsetcomp.com, temperature accurate to within ± 0.2 °C, 3×1.7 cm cylindrical loggers) were buried at depths between 50 and 70 cm on the beach (mean leatherback turtle nest depth, J. Patino-Martinez, personal observation) and programmed to record temperature every 30 min. Data logger integrity was checked by deploying loggers simultaneously for at least 48 h before and after the data collection period. If loggers returned data that differed from the group

mean by more than 0.5 °C, their data were not carried forward to analysis.

Metabolic heat

In addition to insolation or sunshine, incubating clutches of marine turtle eggs experience additional warmth through metabolic heat from the developing eggs (MH), which may increase the temperature of the whole clutch by several degrees at various points during the incubation period (Godfrey *et al.*, 1997; Broderick *et al.*, 2001; Zbinden *et al.*, 2006; Sandoval *et al.*, 2011). We measured MH produced in leatherback turtle nests by deploying 20 loggers in 2006 and 2007 in nests across three beaches (Acandi, Armila and Playona, Fig. 1). The loggers were placed at approximately the centre of the clutch (after 35 eggs had been laid) and a control logger placed at the same depth one metre away from the nest (and equidistant from the tide line). MH was calculated as the difference between the nest and control loggers.

Intranest variation

To study variability in temperature inside incubating nests, data loggers were placed at three locations in five nests ($n = 15$ data loggers) on Playona beach between 28 March and 01 April 2005. The loggers were placed (i) at the bottom of the nest below the first egg laid; (ii) at the middle of the clutch after 35 first eggs had been laid; and (iii) on top of the eggs once oviposition was completed. The temperature differences between the middle of the nest and the top and bottom of the clutches were calculated daily.

Intrabeach variation

To investigate the variability in temperatures within each beach, data loggers were placed in three zones ($n = 27$ loggers) on Playona beach between 2 and 22 April 2005. The three zones were: (i) the inter-tidal zone (below the high water mark); (ii) the mid-zone (between the high tide line and where dune vegetation began); and (iii) the vegetated zone (above where the dune vegetation began and extending to the back of the beach). Three sites were chosen at random in each zone to deploy the loggers. Replicates for each site were placed at depths of 50, 60 and 70 cm. An additional six loggers were placed in the hatchery at two randomly chosen sites (with two replicates for depth).

On the same beach, temperatures from an area of high nesting density (>81 nests km^{-1}) and from another that was only sporadically used by females (<15 nests km^{-1}) were compared (Patino-Martinez, 2010). In this case, data loggers were placed at a depth of 55 cm in the mid-zone of each area.

Interbeach variation

To investigate the variability in temperatures between beaches, data loggers were placed on Playona beach (which has dark sand), Armila beach (which has white sand) and Capancito beach (which has yellow sand; $n = 27$ loggers) between 27

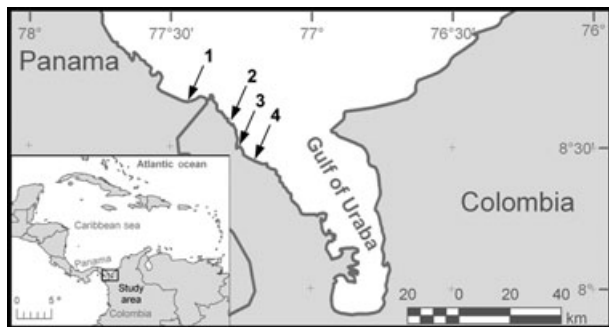


Fig. 1 Caribbean leatherback sea turtle nesting beaches included in this study: (i) Armila (Panama); (ii) Capitancito; (iii) Acandi; and (iv) Playona, Colombia.

April and 27 May 2006. Data loggers were deployed in the mid-zone (see above) at depths of 55 cm, but loggers were also deployed in 2007 at 50 and 70 cm depth (28 March–16 June, and 28 March–10 May respectively) on all three beaches. It was not possible to use the 50-cm data for Armila beach as the logger depth was compromised during deployment by unexpected beach erosion.

Logger deployments covered the entire incubation duration of at least 74% of the nests laid in this study (Table 1).

Sex ratios

We estimated sex ratio for each of the study seasons (2005, 2006 and 2007) for each nesting beach, over 2-week periods. The proportion of nests incubating in their middle third period (the 'thermosensitive period' Rimblot *et al.* 1985) during each 2-week period was determined, and the mean measured nest temperature during that period was calculated for each site and each year. Sex ratios were estimated using curves relating incubation temperature to sex ratio for French Guyana leatherback turtles (Chevalier *et al.*, 1999), the closest to the study sites. The estimated sex ratio for each 2-week period was thus the calculated sex ratio derived from mean nest temperature in that 2-week period multiplied by the proportion of nests incubating in that period. The overall sex ratio for each site and each year was the sum of the 2-weekly sex ratio periods for the duration of the nesting season.

Future sex ratios

Mean air temperature was recorded every year in Playona using Hobo StowAway Tidbit v2 data loggers, mounted three metres off the ground in a shaded weather station in an open area approximately 50 m behind the dune vegetation. Loggers recorded ambient temperature every 30 min (temperature accurate to within ± 0.2 °C). It was not possible to collect air temperature elsewhere. Air temperature (mean maximum temperature over 2 weeks) was significantly related to sand temperature (mean temperature over 2 weeks, recorded at 55-cm depth, where: sand T °C = $19.20 + 0.34 \times \text{Air } ^\circ\text{C}$; $R^2 = 0.61$; $P < 0.05$; $n = 8$), and thus could be used to predict sand temperature from forecasted future increases in air temperature for three future warming scenarios: (i) 0.9 °C (predicted increase for the next decade); (ii) 2.2 °C (predicted increase for 2050); and (iii) 3.5 °C (predicted increase for 2080) (Magrin *et al.*, 2007) see also (Janzen, 1994; Hays *et al.*, 1999; Hawkes

et al., 2007; Fuentes *et al.*, 2009b). The predicted climate change values in Magrin *et al.*, 2007 are mean values obtained from seven Global Climate Models and from four major emissions scenarios, with variation between wet and dry seasons and between Central America, Amazonia and southern South America. The modelled sand temperatures were then used to estimate sex ratios as above using the nesting season distribution in Patino-Martinez *et al.* (2008) for each site. The equation derived above relating air temperature to sand temperature was used as a predictor of the sand temperature for the different future warming scenarios. Then, sex ratios were estimated using published data for leatherback turtles relating incubation temperature to proportion of female hatchlings (Chevalier *et al.*, 1999), as above.

Hatchery shading

To investigate the potential for nest shading as a mitigation strategy for strongly biased sex ratios, we conducted two shading experiments within the beach hatchery (15×8 m on a 0° slope above the high tide line). For each experiment, a third of the hatchery (5×8 m) was marked out and two thicknesses of shading material (Agriplas Negro, <http://www.agriplas.com.ar/>, 40% and 60% radiation respectively) were stretched out 1.5 m above the sand surface. The remaining third of the hatchery was left unscreened. Two loggers were buried at each site at 50 and 70 cm depth respectively. Control loggers ($n = 2$) were buried outside the hatchery at the same depths and distance from the high tide line.

To describe the fitness of hatchlings from each treatment, 36 clutches originally laid outside the hatchery in 2007 were re-buried inside the hatchery in each of the three treatment areas (12 clutches in each; 0%, 40% and 60% radiation screening). Where possible, clutches were evenly distributed among treatments as they were relocated. Fitness metrics were collected for each nest as follows: hatching success (the proportion of eggs producing hatchlings emerging from the nest), incubation duration, straight carapace width and length of hatchlings (measured with Digital caliper Cen-Tech; Harbor Freight Tools, Pittsburgh, PA, USA; accuracy ± 0.01 mm) and mass (using a microbalance PK401DenverInstrument; accuracy ± 0.1 g). Fitness was derived as the ratio of hatchling mass to length (van de Merwe *et al.*, 2005).

Results

Metabolic heat

On average, metabolic heating contributed 0.7 °C of additional heating to nests (mean value = 0.68, SD = 0.16, range 0.52–0.92 °C, $n = 6$ clutches vs. control comparisons). In the first third of incubation, nest temperatures were not significantly different from control sites ($F_{1,250} = 0.005$, $P = 0.944$), but from the middle third onwards, nests were significantly warmer than their paired control sites (middle $F_{1,238} = 12.85$, $P = 0.0004$; final $F_{1,236} = 121.96$, $P < 0.0001$, Fig. 2). A

Table 1 Percentage of leatherback nests laid before, during and after temperature data loggers were deployed on Playona, Capitancito and Armila beaches

Year	Beach	% Before	% During	% After
2005	Playona	23.7	74.0	2.5
2006	Playona	5.0	87.0	8.0
2007	Playona, Capitancito, Armila	2.0	95.5	2.5

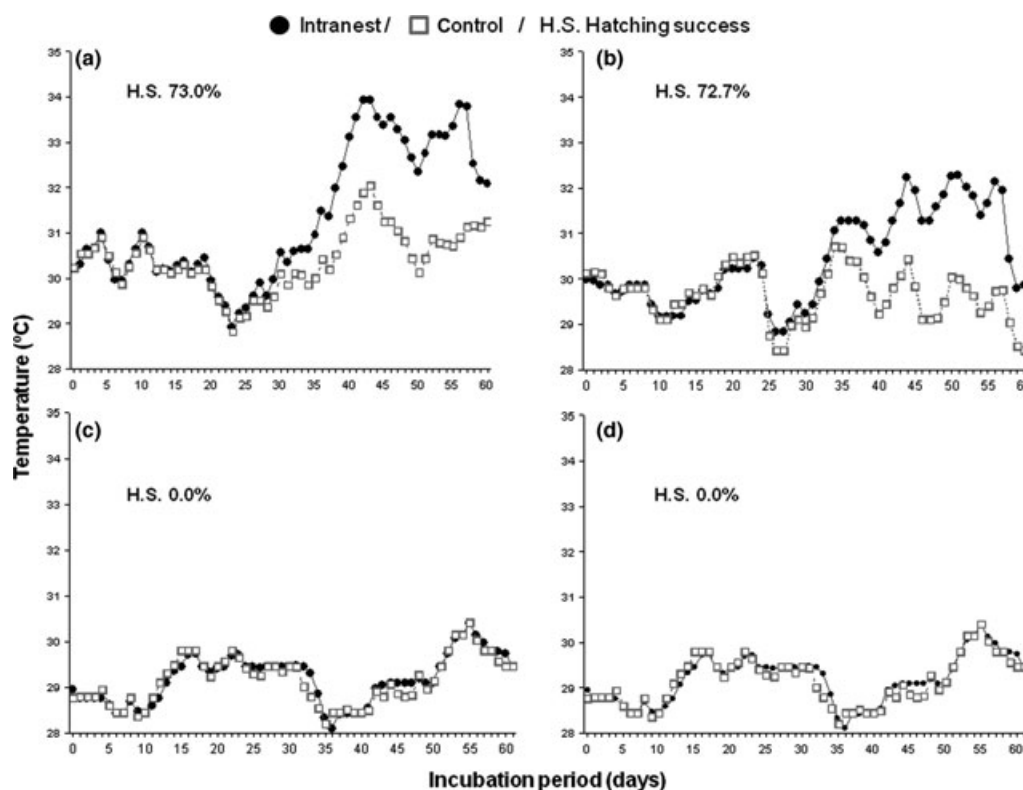


Fig. 2 Temperatures of nests with embryonic development (a and b) and of nests with early embryonic mortality (c and d). The line 'control' represents the temperature of the sand around the nest at same depth.

mean increase in temperature at the centre of the nests of 0.5 °C occurred around day 32 of incubation (mean value = day 31.9, range 25–38, SD = 3.64; range 25–38, $n = 8$) and the maximum MH values were reached in the final third period and fluctuated between 1.38 °C and 3.05 °C (mean = 2.47, SD = 0.59). During the middle third period, nests were (0.37 °C mean value, SD = 0.19, $n = 6$) warmer than their paired control sites with maximum values of MH values between 0.56 and 1.80 °C (mean = 1.07 °C, SD = 0.45). For the middle third and the entire incubation period, nest temperature was significantly correlated with hatching success ($R^2 = 0.42$, $df = 1.9$, $P = 0.03$ and $R^2 = 0.86$, $df = 1.9$, $P < 0.001$ respectively). Metabolic heating increased significantly with the number of successfully hatching eggs ($R^2 = 0.80$; $df = 1.9$; $P < 0.001$).

Intranest variation

The maximum observed variation in temperature within a single nest was 1.6 °C (mean 0.6 °C, minimum value 0.2 °C, Table 2). The temperature at the centre of the egg chamber was consistently higher than either the bottom (mean 0.7 °C in successful nests and 0.2 °C in nests that failed to produce viable hatchlings, Fig. 2b,c, Table 2) or the top of the clutch (mean 0.3 °C in success-

ful nests and 0.0 °C in nests that failed). The bottom of the nest was usually coolest throughout incubation (1.0 °C cooler on average; bottom = 3.5 °C, SD = 2.8 °C; centre = 4.5 °C, SD = 2.9; top = 4.5 °C, SD = 2.8; $n = 5$).

Intrabeach variation

Average beach temperatures were warmer in the mid-zone (29.90 °C, SD = 0.33, max = 30.69) than in either the inter-tidal zone (29.62 °C mean, SD = 0.36, max = 30.4) or vegetated zone (29.73 °C mean, SD = 0.30, max = 30.44; ANOVA: $F_{72,168} = 2.061$; $P < 0.001$). Sand temperatures in the hatchery were greater than in any other part of the beach (Hatchery = 30.17 °C mean, SD = 0.54, max = 31.72, Table 3). The temperatures of the areas with the greatest density of nests were not significantly different from the area in which egg-laying only occurred sporadically (High density = 30.03 °C mean, SD = 0.44; Low density = 30.06 °C mean, SD = 0.42; repeated measures ANOVA: $F_{24,57} = 0.852$, $p = 0.67$).

Interbeach variation

Playona beach (with dark-coloured sand: 29.60 °C mean temperature, SD = 0.92, range = 27.62–31.76 °C,

Table 2 Intranest temperature variation (in °C) between the top, middle and bottom of incubating leatherback turtle nests during the whole incubation period (IP), and during the thermo-sensitive period (TP)

IP					TP									
Nest	Date	Eggs	Hatching success	Difference	Mean	SD	Min.	Max.	N	Mean	SD	Min.	Max.	N
1	30 March–30 May	61	70.5	Middle-bottom	0.7	0.3	0.0	1.5	61	0.7	0.3	0.3	1.0	21
				Middle-top	0.3	0.5	−0.6	1.3	61	0.1	0.5	−0.6	0.8	21
				Top-bottom	0.4	0.5	−0.5	1.5	61	0.6	0.6	−0.5	1.5	21
2	29 March–3 June	108	0.0	Middle-bottom	0.1	0.1	0.0	0.3	65	0.1	0.1	0.0	0.3	22
				Middle-top	0.0	0.2	−0.4	0.2	65	−0.1	0.1	−0.3	0.1	22
				Top-bottom	0.1	0.2	−0.3	0.6	65	0.2	0.2	−0.1	0.4	22
3	1 April–6 June	100	0.0	Middle-bottom	0.2	0.2	−0.3	0.5	66	0.2	0.2	0.1	0.5	22
				Middle-top	0.0	0.2	−0.4	0.4	66	0.0	0.2	−0.4	0.2	22
				Top-bottom	0.2	0.3	−0.6	0.8	66	0.3	0.3	−0.1	0.8	22
4	28 March–25 May	87	50.6	Middle-bottom	0.7	0.2	0.3	1.3	59	0.7	0.2	0.3	1.0	20
				Middle-top	0.0	0.2	−0.5	0.6	59	0.0	0.3	−0.4	0.5	20
				Top-bottom	0.7	0.3	−0.2	1.3	59	0.7	0.4	0.1	1.3	20
5	29 March–29 May	65	36.9	Middle-bottom	0.6	0.4	−0.4	1.6	61	0.9	0.4	0.3	1.6	21
				Middle-top	0.5	0.4	−0.2	1.2	61	0.4	0.4	−0.2	1.0	21
				Top-bottom	0.1	0.6	−1.2	1.5	61	0.4	0.7	−0.7	1.5	21

Table 3 Temperatures recorded in different zones of the nesting beach

Zone	Temperature (°C)	SD	Range	Min.	Max.	N
Intertidal	29.62	0.36	1.37	29.09	30.46	1002
Mid	29.90	0.33	1.28	29.41	30.69	1008
Vegetated	29.73	0.30	1.38	29.06	30.44	1008
Hatchery	30.17	0.54	2.51	29.21	31.72	1008

$n = 1392$) was significantly warmer than either Armila (with white sand: 29.16 °C mean value, SD = 0.60, range = 27.77–30.52, $n = 1392$) or Capitancito beach (with yellow sand: 29.22 mean value, SD = 0.72, range = 28.37–30.78 °C, repeated measures ANOVA: $F_{90,80} = 1.480$, $P = 0.03$) during 2005 and 2006 (but not in 2007: $F_{48,111} = 0.893$, $P = 0.674$, $F_{92,156} = 1.161$, $P = 0.216$ at 50 and 70 cm depth respectively).

Sex ratios

Hatchling sex ratio for naturally incubating Colombian leatherback turtle nests, as estimated using the conversion equation from sand temperature to nest temperature, was 92% female (mean value for all three beaches across 2005–2007). However, significantly fewer females were produced overall in 2006 (83% females; $\chi^2 = 15.94$, df = 2, $P = 0.000$) than in either 2005 (97%) or 2007 (94%), but in all years, sex ratios are clearly female skewed. No males were produced from nests in the hatchery (100% female).

Future sex ratios

Using the regression equation relating sand temperature to nest temperature with future warming predictions (sand T °C = $19.20 + 0.34 \times \text{Air } ^\circ\text{C}$; $R^2 = 0.61$; $P < 0.05$; IPCC 2007), future productions of 100% female could be reached with only 0.9 °C daily temperature increases (Table 4). The predictions for sand temperatures in 2080 are close to the critical temperature for egg incubation (Table 4), suggesting that successful incubation may not be possible towards the end of the century.

Hatchery shading

Sex ratios from shaded nests (40% and 60% shading experiments) in the hatchery produced significantly fewer female hatchlings (25% and 4% respectively) than nests incubating without shade in the hatchery (100% females; $\chi^2 = 118.47$, df = 2, $P = 0.000$). In addition, hatching rates for shaded nests were significantly higher (66.4% and 65.2% respectively) than those of the nests incubating without shade (39.2%; ANOVA: $F_{2,28} = 3.922$; $P = 0.031$). Nests also incubated for significantly longer in shaded (67.2 and 68.0 days, 40% and 60% shading respectively) than un-shaded nests in the hatchery (63.6 days; ANOVA: $F_{2,28} = 6.435$; $P = 0.005$). Finally, hatchlings from the 60% shading experiment were significantly lighter (mean 0.74 g mm^{−1} carapace length, Table 5) than hatchlings from either the un-shaded experiment or the 40% shading experiment.

Table 4 Colombian leatherback hatchling sex ratios and future projections under three scenarios of climate change showing predicted air temperature (in °C; AT), nest temperature (in °C; NT), the proportion of nests incubating and the resultant percentage of female hatchlings (% F)

2011	2021 (+0.9 °C)				2041 (+2.2 °C)			>2081 (+3.5 °C)		
Date	AT	NT	% Nests	% F	AT	NT	% F	AT	NT	% F
8 March–23 March	31.4	30.4	8.9	100	32.3	30.7	100	33.6	31.1	100
24 March–7 April	30.4	29.8	12.5	94	31.3	30.3	100	32.6	30.8	100
8 April–22 April	31.5	30.4	17.2	100	32.4	30.7	100	33.7	31.2	100
23 April–7 May	30.5	29.9	18.1	94	31.4	30.4	100	32.7	30.8	100
8 May–22 May	30.3	29.7	19.7	85	31.2	30.3	100	32.5	30.7	100
23 May–6 June	31.8	30.6	16.3	100	32.7	30.8	100	34	31.3	100
7 June–19 June	32.4	30.9	7.4	100	33.3	31.0	100	34.6	31.5	100

Table 5 Variables in the quality of hatchlings incubated under three different types of shade conditions in the hatchery

Variable	Condition	Mean	SD	–95%	95%	N	F	g.l.	P
Weight (g)	Sun	44.7	0.4	43.9	45.5	69	9.308	2, 228	<0.001
	Shade – 40%	45.4	0.3	44.8	46.1	82			
	Shade – 60%	43.4	0.3	42.7	44.1	80			
Index of physical condition (g mm ^{–1})	Sun	0.76	0.01	0.75	0.78	49	7.673	2, 207	<0.001
	Shade – 40%	0.76	0.01	0.75	0.78	82			
	Shade – 60%	0.74	0.01	0.73	0.75	79			

Discussion

Highly skewed sex ratios

On the basis of assumption that patterns of thermal sensitivity for gender determination in the study population conform to the values derived from nearby populations (Binckley *et al.*, 1998) and in light of our detailed knowledge of current temperature ranges, we found that sex ratios in hatchlings were clearly female skewed by an average of 92% during the three nesting seasons of the study period. Our model predicts that the increase in temperatures induced by climate change could lead to a complete feminization of hatchlings within a decade. Previous studies (Janzen, 1994; Hays *et al.*, 1999; Hays *et al.*, 2003; Hawkes *et al.*, 2007; Hawkes *et al.*, 2009) have found similar results. Indeed, natural conditions may be causing a feminization of hatchlings at a number of different sites (Mrosovsky & Provancha, 1992; Binckley *et al.*, 1998; Godley *et al.*, 2001; Baskale & Kaska, 2005; Booth & Freeman, 2006; Fuentes *et al.*, 2009b), including a population at Rantau Abang in Malaysia where both beach and hatchery temperatures lead to the production of only female hatchlings (Chan & Liew, 1995). If climate change continues as predicted (IPCC 2007), it is thought that effects could be more dramatic towards the end of the century (Fuentes *et al.*, 2011b), when incubation temperatures could approach the limit of thermal tolerance and lead to a fall in hatching success.

Climate change and the future

It is clear that future climate change could probably have some negative impacts for biodiversity. The existence for millions of years of marine turtles (Hirayama, 1998) is, however, testimony to their capacity to adapt to past climatic change (Hawkes *et al.*, 2009). Nevertheless, modern climate change is occurring at unprecedented rates compared with the past (IPCC 2007, Rahmstorf *et al.*, 2007), and marine turtle populations are subject to many anthropogenic stressors that were not present in the past (Jribi *et al.*, 2008; Selkoe *et al.*, 2008; Mazaris *et al.*, 2009). Thus, their resilience to climate change may well be poorer than in the past, and it remains to be seen if they possess the capacity to continue to adapt (Fuentes *et al.*, 2009b).

Micro-evolution and adaptive capacity

The mechanisms through which marine turtles could adapt to climate change are a subject of great interest (Bell & Collins, 2008; Hamann *et al.*, 2010). In general, species could adapt to global change via either phenotypic plasticity or microevolution (Hulin *et al.*, 2009). The former includes changes in the distribution of breeding areas (Schofield *et al.*, 2010), the choice of egg-laying sites and the depths of nests (Hays *et al.*, 2001), as well as a tendency to breed during cooler periods of the year (Weishampel *et al.*, 2004; Pike *et al.*, 2006; Tucker *et al.*, 2008a). On the other hand, microevolutionary

changes depend on hereditary factors and genetic variability (Hulin *et al.*, 2009) that enable pivotal temperature to adjust to the new conditions found on breeding beaches (Davenport, 1989). Unfortunately, studies of semi-aquatic turtles indicate that changes in breeding phenology do not seem to suffice as a means of counteracting the negative effects of global warming on hatchling sex ratios (Schwanz & Janzen, 2008). Neither does it seem likely that changes in the selection of egg-laying sites as a response to global warming could be sufficient to “even out” the sex ratio in semi-aquatic turtles (Morjan, 2003a; Morjan, 2003b).

Production of male hatchlings

Importantly, however, our data suggest that male hatchling turtles could continue to be produced even under future warming scenarios – in nests lower on the shore, in those nests laid on lighter coloured beaches (where sand temperature at nest depth can be approximately 0.4 °C cooler), in deeper nests, in smaller nests, and in the periphery of nests, where the effects of metabolic heating would be less. Changes in patterns of rainfall, as well as over-wash of nests situated in the inter-tidal zone (Broderick *et al.*, 2001) may also produce locally cooler areas, where males could subsequently be produced. Such nests could be assigned enhanced conservation priority to ensure that male production occurs, provided that hatching success is not compromised. For Colombian leatherback nests, nest flooding makes up a majority of the nest mortality observed (Patino-Martinez *et al.*, 2008); however, for other rookeries where this is not the case, nests laid in the inter-tidal zone need not necessarily be moved, as tends to be common practice, if the threat of nest loss is not greater than the potential benefit of nest cooling. However, although intranest, intrabeach and interbeach thermal profiles are complex and variable, leatherback sea turtles appear for the majority to lay their eggs in the mid-zone of the beach (Binckley *et al.*, 1998); the warmest zone and in large clutches.

Conservation priorities

There are clearly, therefore, rookeries for which such opportunities for preferential conservation of male-producing nests are rare or even absent. In such instances (as confirmed by assessing the thermal variation of a nesting beach in question, as we have in this study), sex ratios of marine turtle populations may need to adaptively, and more directly, managed. Current management regimes for marine turtles on the beaches where they nest do not yet normally incorporate climate stressors. However, it may still be too early to predict the

direction or magnitude of climate change effects, lacking essential data from a wide range of rookeries to do so (Hawkes *et al.*, 2009).

Adaptive management

In this study, we have shown that shading of nests can not only enhance production of male hatchling turtles, but that it can do so without compromising hatching success and body condition (“fitness” although note the life-time fitness of these turtles cannot be estimated in this study) of the resultant turtles. Given future expected decreases in male hatchling production, this simple and cheap “tool” could potentially be used. However, temperatures in the hatchery (un-shaded nests) were consistently higher than on the other areas of the beach and thus could be artificially provoking a complete feminization of hatchlings, suggesting that un-shaded hatcheries may not be effective for conservation. The efficiency of decades of efforts to translocate nests is thus questionable if the result is the production of hatchlings of only one sex (Chan & Liew, 1995), or indeed of lowered survivorship. The challenge facing conservation programmes using hatcheries in light of global warming is to keep the temperature of translocated nests around the pivotal temperature (29.5 °C) for the species (Binckley *et al.*, 1998; van de Merwe *et al.*, 2005), but not much lower to ensure that selection for alteration of the pivotal temperature is not prevented (Doody *et al.*, 2006). The higher temperatures in hatcheries may be due to their location (distant from the sea), lower humidity levels and less natural shade. Moreover, high nest density and the metabolic heat generated during incubation may potentially increase average temperatures. Thus, the benefits of artificial shade in hatcheries in exceptionally hot years is evident, including a reduction in the percentage of female hatchlings, an increase in hatching success and the birth of heavier turtles in a “better” physical condition.

These results agree with those of previous studies that have shown the negative effects of high temperatures on hatching success rates (Bilinski *et al.*, 2001; Booth *et al.*, 2005) and hatchling vigour in marine turtles (Drake & Spotila, 2002; Glen *et al.*, 2005). It is possible that hatchlings that emerge in better physical condition will also be faster and more resistant swimmers from cooler nests (Reece *et al.*, 2002). This might increase the distance they can swim during the hatchling dispersal phase, enhancing survivorship (Pilcher & Enderby, 2001), in accordance with the ‘bigger is better’ theory (Congdon *et al.*, 1999).

However, we would caution extrapolation of our results to other species and rookeries – pilot data following the methods in this study should be collected

to ensure that reductions in survivorship and condition do not occur. Use of hatcheries for conservation purposes should only usually be considered as a last resort if *in situ* management of nests cannot take place, and we caution unnecessary use of hatcheries. It will additionally be necessary to invest considerable effort to collect additional sand temperature data with wider spatial and temporal scale to generate robust estimates of primary sex ratios from Caribbean nesting beaches, a global research priority for marine turtles (Hamann *et al.*, 2010).

Operational sex ratios

Finally, it is important to note that the hatchling sex ratio is not necessarily representative of the sex ratio of adult turtles attending the breeding area each reproductive season 'the Operational Sex Ratio' (Delgado *et al.*, 2010). It seems at present that a ratio of one male to two or three females is sufficient to ensure that demographically viable populations persist (Fuentes *et al.*, 2009a) and limited tracking of adult male turtles suggests that they may visit the breeding grounds annually, (but see Blanvillain *et al.*, 2008), whereas adult females nest only every 2–3 years (Reina *et al.*, 2002). The Operational Sex Ratios of only a few marine turtle populations worldwide have been studied to any degree and they remain a major knowledge gap for assessing the extent to which climate change may affect marine turtles (Hawkes *et al.*, 2009; Hamann *et al.*, 2010; Hays *et al.*, 2010). In addition, multiple paternity is known to occur in marine turtle nests (Zbinden *et al.*, 2007; Uller & Olsson, 2008; Theissinger *et al.*, 2009), suggesting that males are not yet limited at the breeding grounds (but note that with long durations to sexual maturity, the effects of climate skewed sex ratios may not yet have become apparent). Nevertheless, for some sites, we still lack the appropriate information if we are to establish what impact skewed sex ratios might have. For example, it is important to know to what extent mating between genetically distinct reproductive units occurs (a global research priority for marine turtles, Hamann *et al.*, 2010). Studies of the extent of multiple paternity are thus an essential additional information source to assess the effects of climate change to rookeries.

Concluding statement

In conclusion, the predicted rate of future climate change, the highly skewed sex ratios produced in the leatherback turtle and its long maturation time may all limit the adaptive capacity of this species. Conservation managers could establish priorities based on the impacts and threats present in each breeding area

to preferentially conserve male-producing beaches and nests. However, in extreme situations, manipulation of the incubation temperatures of some nests to ensure that they remain within the transition range (Naro-Maciel *et al.*, 1999; Hawkes *et al.*, 2007; Heller & Zavaleta, 2009) can be easily and cheaply achieved without compromising hatching success and hatchling vigour. Nevertheless, the tools outlined in this study would be an emergency response to the severe impacts of climate change that will eventually have to be reversed if we are to guarantee the stability of biodiversity beyond the confines of conservation programmes.

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