Global Change Biology (2004) **10,** 2036–2045, doi: 10.1111/j.1365-2486.2004.00865.x

Antigua revisited: the impact of climate change on sand and nest temperatures at a hawksbill turtle (*Eretmochelys imbricata*) nesting beach

F. GLEN and N. MROSOVSKY
Department of Zoology, University of Toronto, Toronto, ON, Canada M5S 3G5

Abstract

Whether a turtle embryo develops into a male or a female depends, as with many other reptiles, on the temperature during incubation of the eggs. With sea turtles, warm temperatures produce 100% females. Therefore, global warming has the potential to drastically alter their sex ratios. Air temperatures on Antigua have increased by 0.7 °C over the last 35 years. Measurements in both the sand and the clutches laid by hawksbill turtles (*Eretmochelys imbricata*) at Pasture Bay, Antigua, show that for important parts of the nesting season temperatures are already above the level producing 50% of each sex (pivotal level). Comparisons are made to sand temperature measurements taken on this beach in 1989 and 1990. It is estimated that fewer males were produced in 2003 than in the previous years. Recommendations are made for close monitoring of the fertility of eggs and for research on any turtles nesting at cooler times of year.

Keywords: air temperature, Antigua, caribbean, hawksbill, metabolic heating, sea turtles, sex ratio, temperature

Received 5 April 2004; revised version received and accepted 7 June 2004

Introduction

Phenotypic sex in sea turtles is determined by the temperature prevailing in approximately the middle third of incubation (Yntema & Mrosovsky, 1982; Desvages *et al.*, 1993; Hewavisenthi & Parmenter, 2001). This environmental influence on sexual differentiation provides mechanisms and opportunities, such as selection of time and place for nesting, for species to readily alter primary sex ratios from the relatively balanced ones commonly found in animals with chromosomal sex determination. To date, most of the studies of sex ratios of hatchling sea turtles have come up with estimates that are female biased, some extremely so (reviewed by Wibbels, 2003). A few cases of more or less balanced ratios have been proposed for some populations, but no instance of a strong male bias has been evident (Wibbels, 2003).

In this context, data on sand temperatures from a hawksbill nesting beach in Antigua were of some interest. It was found that in 1989 and 1990 the temperatures at 30 and 60 cm depth seldom exceeded the pivotal temperature. By definition, the pivotal temperature is that constant temperature producing 50% of each sex (Mrosovsky & Pieau, 1991). In this case the pivotal was determined for hawksbill eggs taken from the same beach in Antigua. With temperatures seldom above the pivotal value of 29.2 °C, it was inferred that this nesting beach was unlikely to produce 'strongly female biased sex ratios' (Mrosovsky *et al.*, 1992).

This cautious conclusion was based on a number of considerations. The 2 years in which temperature were measured may not have been thermally typical. The thermosensitive period within incubation has not been studied for hawksbill eggs; metabolic warming of a mass of eggs might elevate temperatures above pivotal levels (Mrosovsky *et al.*, 1992). Also, during the hottest part of the day, the sand at 30 cm might not become as warm as eggs in nests that were shallow (Mrosovsky, 1994).

Therefore, when an opportunity arose recently to revisit this beach, we concentrated on obtaining temperatures within actual nests to include metabolic warming, and on providing sand temperature for an additional year, in addition to assessing the features of that year by comparisons with retrospective meteorological data.

Correspondence: Fiona Glen, 16, Eshton Terrace, Clitheroe, Lancashire BB7 1BQ, UK, e-mail: fglen1@hotmail.com

Materials and methods

Study Site

Pasture Bay is a 0.5 km long, windward-facing beach located on Long Island, 2.5 km off the northern coast of mainland Antigua. Privately owned, Long Island is also host to a hotel and about 20 private residential estates, some of which have installed or modified beaches in front of their property. Although Pasture Bay is still the main nesting site for hawksbill turtles, over the last few years there has also been some nesting on the new artificial beaches.

Pasture Bay can be divided into three vegetation zones differing in nesting habitat quality (for a more detailed description, see Parrish & Goodman, 2002). The north-east section is covered with mixed shrubs and sparse maritime forest; this is probably the least managed area and is host to the majority of hawksbill turtle nests. The middle section has been managed, and most of the vegetation cleared. To encourage nesting and to improve the beach aesthetically, islands of vegetation have been cultivated here. The north-west-facing section consists of grassy lawn areas; the sand layer is thin and, until recently, this area saw few nests. However, with the addition of imported sand, nesting density has increased.

Sand temperatures

Hobo Water Temp Pro dataloggers (Onset Computer Corporation, Bourne, MA, USA) were set to record synchronously at hourly intervals. These dataloggers could be read to the nearest 0.1 °C. Accuracy was checked against a Sybron/Taylor mercury thermometer with 0.1 °C gradations (Sybron Corporation, Arden, NC, USA) that had certified calibration against platinum-resistant thermometers that had in turn been calibrated by the US National Bureau of standards. After the field work, the dataloggers were checked in a bath of melting ice against the mercury thermometer and were all within ± 0.2 °C of the mercury reading.

Pasture Bay. In 2003, temperature probes were placed at depths of 30 and 60 cm at 10 potential nesting sites on the beach. However, because of a programming error, temperature collected from 60 cm at site C had to be discarded, therefore only nine sites at a depth of 60 cm were available for analysis. Position and depth of the these control sites were generally similar to those in the previous study (Mrosovsky *et al.*, 1992, $n = 10–11$ sites), and, although the exact repositioning of the probes was impossible, sites chosen by this study were representative of the conditions recorded in 1989 and 1990. Temperature probes were buried on 15 June, removed and downloaded on 30 August and then replaced in their respective sites until 15 November. This period encompasses the majority of hawksbill nesting (Richardson *et al.*, 1999). Nightly patrols were carried out throughout this time.

Artificial beaches. Although the majority of turtles nest on Pasture Bay, there is some movement to two neighbouring artificial beaches; Hummingbird and Brooks Beach. Neither of these beaches are covered in vegetation; they are open expanses with little shade. In order to determine whether these two artificial beaches differed in sand temperature conditions from those present on Pasture Bay, we placed one temperature probe at 30 cm on each beach, recording sand temperature every hour from 24 June until 31 July.

Nest temperature

From 16 June until 17 August, temperature probes set to record synchronously every hour were placed in 15 nests laid on Pasture Bay. Once a turtle deposited her eggs, the clutch site was marked. The following day, 60 eggs were removed and a temperature datalogger was positioned within the clutch, approximately at 40 cm; the eggs were then replaced. Two days after the initial emergence of hatchlings had occurred, the nest was excavated, contents enumerated and the temperature probe removed and data offloaded.

Shading

Once all the probes had been placed in the nests, an estimate of the proportion of shade around the area of both nests and sand temperature sites was made. Shade was estimated as being nearest to either: 0%, 25%, 50%, 75% or 100% of the area within a 26 cm diameter circle centred around the site/nest. This was done every 4 h over one sunny day (17 August 2003) and values averaged to provide a single index of the amount of shade.

Meteorological data

Air and rainfall data were provided by Antigua and Barbuda meteorological services based at V.C. Bird International Airport, St Johns. For 2003, average daily temperature (°C) and total rainfall (mm) were collected. Average monthly temperatures and total monthly rainfalls were also provided from 1969 to 2003.

Results

Variation of sand temperature

Depth. Sand temperatures varied as a function of depth, with the sand at 60 cm generally cooler than at 30 cm (Table 1). Although the extent of the difference between depths was on average 0.2 ± 0.4 °C SD across each site ($n = 9$ sites, 3600 readings per site), the effect was consistent over the season, and highly significant in all cases, except at site F.

Time of day. At 30 cm, temperature changed with time of day in all Pasture Bay sites (Fig. 1), on average ranging over 0.4 ± 0.2 °C SD ($n = 10$ sites, each based on 150 days). The amount of diel variation was not correlated with the proportion of time during the day that the site was shaded ($n = 10$, $r = -0.3$, $P = 0.39$). At 60 cm depth, sand temperatures remained virtually constant over the course of the day (Fig. 1).

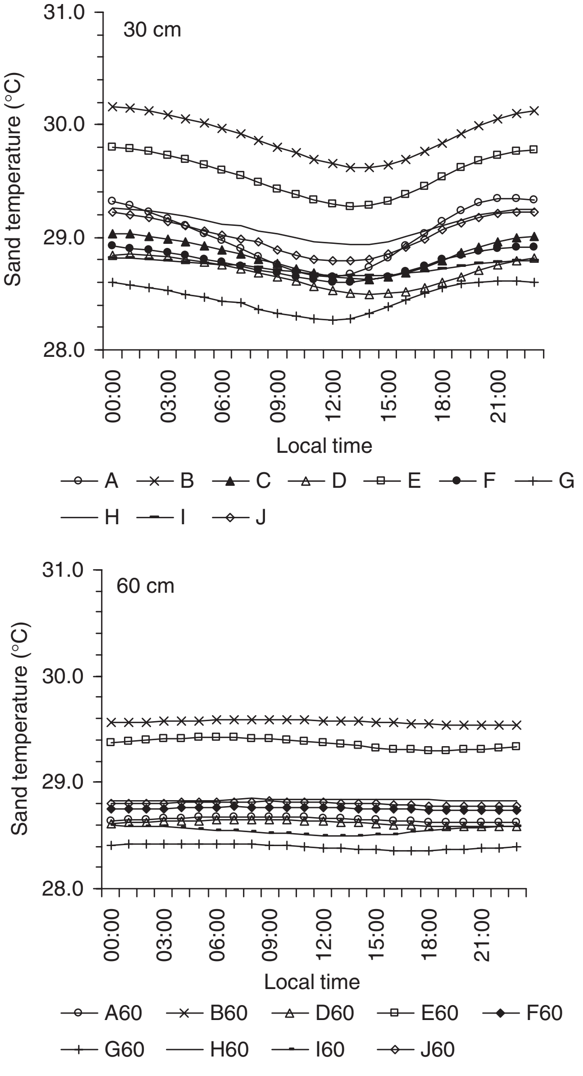

Fig. 1 Mean hourly sand temperatures recorded at 30 and 60 cm from 17 June to 15 November.

Season. Sand temperature increased from June until August, held level throughout September and then dropped in October and November (Fig. 2).

Sites. As is apparent from Table 1 and Fig. 1, different sites on the beach differed thermally. However, at 30 cm the difference between the warmest and coolest daily value recorded at any site within the same day, were only on average, 1.6 ± 0.5 °C SD, and at 60 cm,

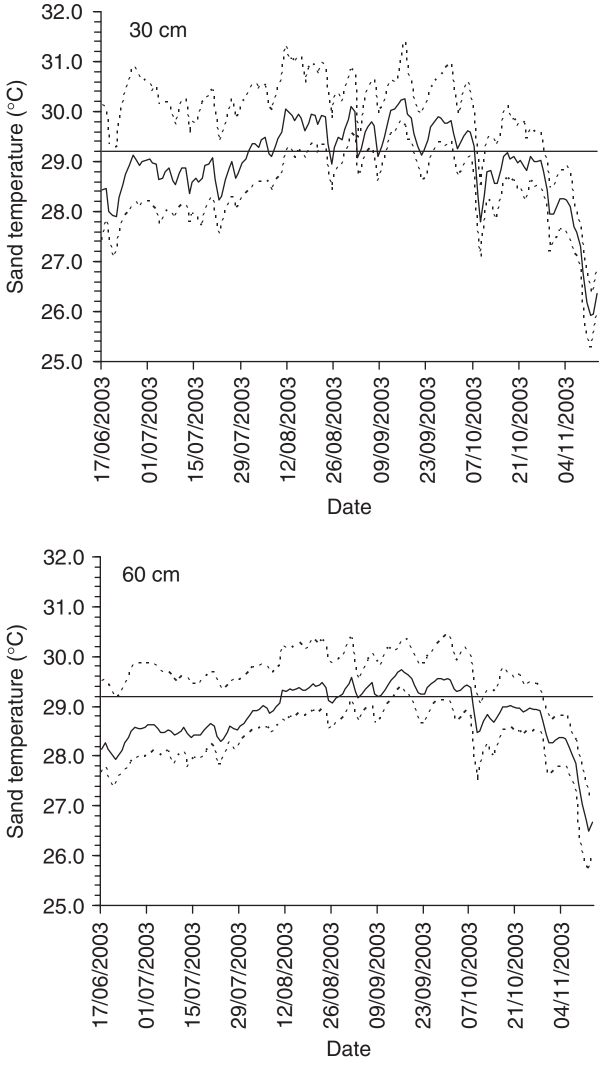

Fig. 2 The mean daily temperature of all sites on the beach at 30 cm ($n = 10$ sites, 150 days) and 60 cm ($n = 9$ sites, 150 days) at Pasture Bay from 17 June until 15 November. Dashed lines show values for those sites having the lowest and highest temperatures on each day. Pivotal temperature of 29.2 °C is shown by the horizontal line.

Table 1 Sand temperature recorded every hour from 17 June until 15 November at 30 and 60 cm depths at each site ($n = 3600$ readings per site)

Pasture Bay site	30 cm, mean ± SD (range)	60 cm, mean ± SD (range)	Shade index (% of area shaded)	Distance to high water mark (m)
A*	29.0 ± 1.0 (25.6–31.3)	28.6 ± 0.5 (26.6–29.4)	0.0	5.5
B*	29.9 ± 1.0 (26.0–32.3)	29.6 ± 0.6 (26.9–30.4)	25.0	5.5
C	28.8 ± 0.7 (25.6–30.2)		31.3	7.2
D*	28.7 ± 0.8 (25.4–30.3)	28.6 ± 0.6 (26.0–29.6)	18.8	13.0
E*	29.6 ± 1.0 (25.6–31.3)	29.4 ± 0.8 (26.0–30.5)	37.5	15.4
F	28.8 ± 0.9 (25.7–30.9)	28.8 ± 0.6 (26.8–29.8)	50.0	26.9
G*	28.5 ± 0.9 (24.9–30.2)	28.4 ± 0.7 (25.5–29.5)	68.8	9.9
H*	29.1 ± 0.8 (26.2–30.7)	28.8 ± 0.7 (26.9-29.7)	31.3	5.8
I*	28.7 ± 0.8 (25.8–30.3)	28.6 ± 0.6 (26.5–29.5)	12.5	4.5
J*	29.0 ± 0.8 (25.9–32.9)	28.8 ± 0.7 (26.5–29.8)	18.7	4.5
Mean (range)	**29.0 ± 1.0 (28.5–29.9)**	**28.8 ± 0.6 (28.4–29.6)**	**29.4 ± 19.6 (0.0–68.8)**	**9.8 ± 7.1 (4.5–26.9)**

*Sand temperatures at 30 cm were significantly warmer than at 60 cm (paired *t*-test, $P < 0.005$, $n = 9$ sites). Data unavailable for temperature at 60 cm for site C. Shade and the distance to the high water mark are also provided for each site

1.3 ± 0.3 °C SD ($n = 150$ daily averages). We were unable to detect any characteristic of the beach that correlated with the mean site sand temperature (see Table 1). There was no significant correlation between the overall mean site temperature and the amount of shading, either at 30 or 60 cm depth (30 cm: $n = 10$, $r = -0.2$, $P = 0.59$; 60 cm: $n = 9$, $r = -0.1$, $P = 0.84$). Horizontal distance of the site to the high water mark was unrelated to mean site temperature (30 cm: $n = 10$, $r = -0.1$, $P = 0.75$; 60 cm: $n = 9$, $r = 0.0$, $P = 0.98$). Moreover, although sections along the beach differed in the amount of vegetation, our sites for sand temperatures were not different among the three sections (Kruskal–Wallis, 30 cm: $n = 10$, $P = 0.64$; 60 cm: $n = 9$, $P = 0.29$).

Artificial beaches. Sand temperature at 30 cm on the two artificial beaches fell within the range of sand temperatures observed on Pasture Bay over the corresponding period (Fig. 3).

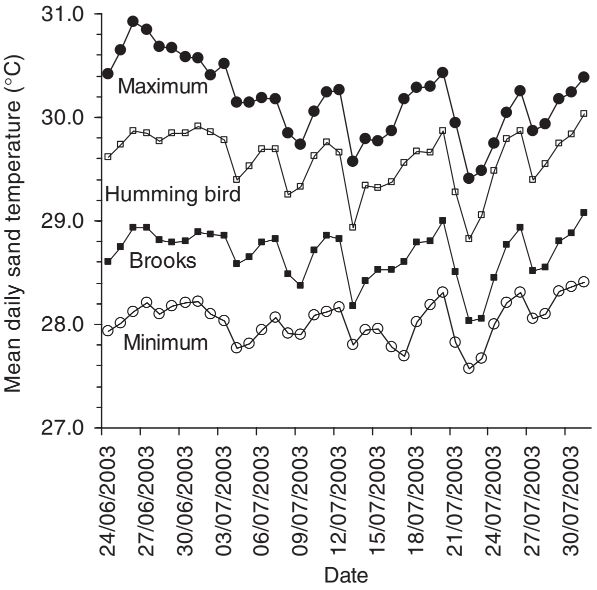

Fig. 3 Sand temperatures recorded at 30 cm from the two artificial beaches, Hummingbird and Brooks Beach, and over the corresponding recording period at Pasture Bay. Mean daily sand temperature values for those probes having the lowest and highest temperatures on each day at 30 cm over the 10 sites at Pasture Bay (38 days from 24 June until 31 July).

Comparison of sand temperatures 1989, 1990 and 2003

Sand temperatures for Pasture Bay for 1989 and 1990 are reported in Mrosovsky *et al.* (1992). The sand temperatures in these years were generally cooler during the main turtle nesting season than those for 2003 (Fig. 4).

Meteorological data

Air temperature and rainfall. Because sand temperatures are only available for 3 years (1989, 1990 and 2003), we turned to data on air temperature to assess whether these 3 years were thermally typical. Although air temperatures fluctuate more than sand temperatures, air temperature can be used as an index for comparing thermal conditions among sand temperatures recorded from different years. To substantiate this point we correlated the mean daily air temperature recorded by the meteorological office with the calculated mean of all sites on the beach for both 30 and 60 cm depths, during the period of 15 June until 15 November. The beach

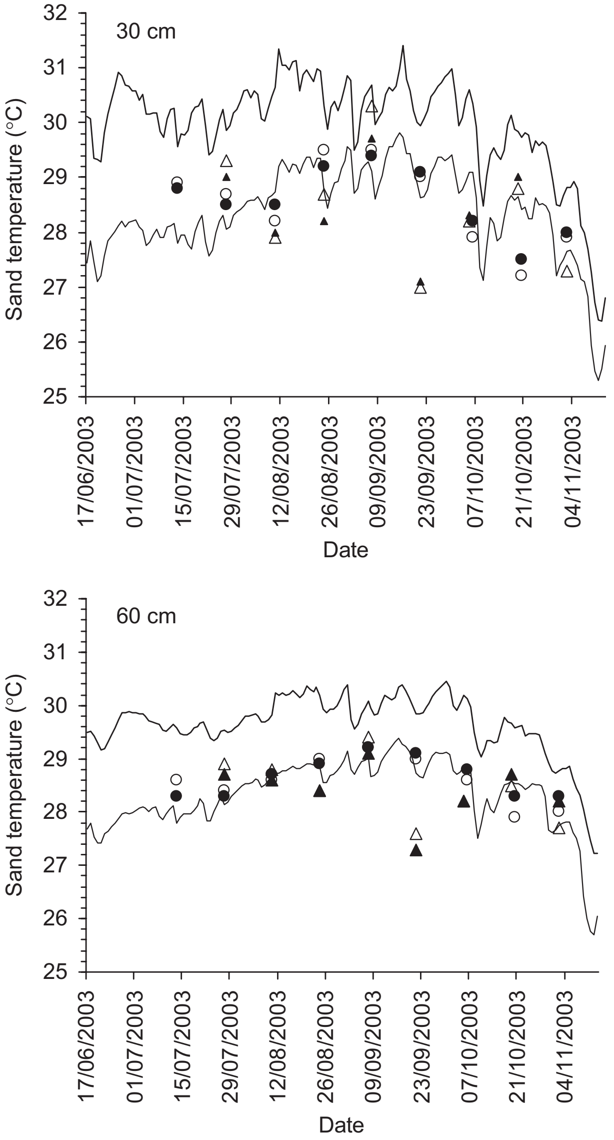

Fig. 4 Comparison of sand temperatures at 30 and 60 cm in 2003 with sand temperature data digitized from Figures 1 and 2 of Mrosovsky *et al*. (1992) for 1989 and 1990. Data for 2003 are mean daily sand temperature values for those probes having the lowest and highest temperatures on each day throughout the nesting season. For 1989 and 1990, temperatures are daily means. 1989 shaded and open sites are indicated by closed and open triangles, respectively; for 1990, shaded and open sites are shown using closed and open circles, respectively.

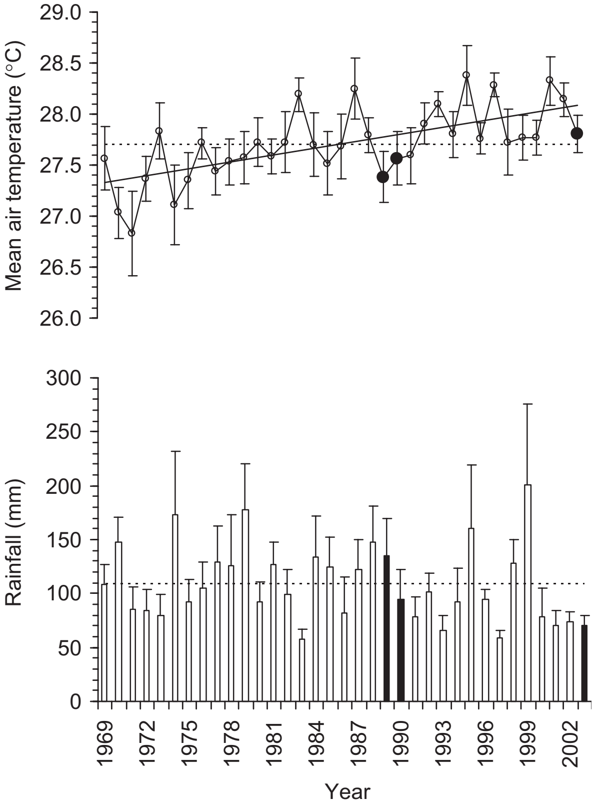

Fig. 5 Mean air temperature and the average rainfall (± SE) measured by the Antigua and Barbuda Meteorological Office from 1969 until 2003. Data provided are yearly values calculated only for the months June–November for each year. Closed bars/ circles indicate the years when sand temperatures were recorded. Dashed lines on each graph indicate the overall mean recorded for these 6 months from 1969 to 2003. A gradual increase in the average temperature for the months of June–November was recorded over the 35 years (linear regression $r^2 = 0.40$, $P < 0.005$, $F_{1,34} = 23.98$; mean air temperature (°C) = −16.9 + 0.0225 years).

mean was calculated by summing each mean daily sand temperature recorded from the 10 sites at 30 cm, or the nine sites at 60 cm, and averaging to give one overall mean daily sand temperature at each depth of Pasture Bay for each day of the study. Positive correlations existed between air and beach mean sand temperatures, at both 30 and 60 cm depth, although a stronger relationship was observed at shallower depths (30 cm: $r^2 = 0.61$, $P < 0.005$, mean daily sand temperature at 30 cm = 0.79 mean daily air temperature + 7.1; 60 cm: $r^2 = 0.46$, $P < 0.005$, mean daily sand temperature at 60 cm = 0.50 mean daily air temperature + 14.8).

When air temperatures for the months of June–November (the main hawksbill nesting season), are plotted from 1969 to 2003 (Fig. 5), it can be seen that the years in which sand temperatures were recorded were reasonably representative of the normal prevailing weather conditions in Antigua. Nevertheless, the nesting season in 2003 was warmer than in 1989 and 1990 (1989: mean ± SE: 27.4 ± 0.3 °C; 1990: 27.6 ± 1.3 °C; 2003: 27.8 ± 0.2 °C; $n = 6$ months) with less rainfall during this period (1989, mean ± SE:

135.1 ± 34.0 mm; 1990: 95.0 ± 72.1 mm; 2003: 70.3 ± 9.5 mm; $n = 6$ months).

Nest temperatures

An increase in temperature, attributable to metabolic heat produced by the developing eggs, was evident in all 15 study nests (Table 2). Levels of metabolic heating varied systematically during incubation. A similar temporal pattern of metabolic heating was observed in all nests, with relatively low levels in the first half of incubation with a steady increase from around the start of the middle third, peaking in intensity during the final third of incubation. An average increase ($n = 15$ nests) of 1.1 °C was observed during the middle third of incubation and an increase in temperature of on average 3.4 °C during the final third of incubation (values provided are those recorded at 30 cm sand depth).

Of the 15 nests monitored, only one, the first in which temperature was recorded, was found to have a mean middle third incubation temperature below 29.2 °C. The remaining nests had mean middle third temperature values above the pivotal temperature (Table 2).

Sex ratio

Although the 15 nests monitored throughout their incubation typified the conditions present at the start of the season, they were not necessarily representative of the conditions experienced by nests laid during the remainder of the nesting period. As can be seen in Fig. 6, the middle third of these 15 nests were found to lie during a period of high-density nesting, and when the beach mean temperature was increasing towards or above 29.2 °C.

During the period of August until the middle of October, the mean temperature calculated from all sites on Pasture Bay at 30 cm was generally higher than 29.2 °C (Fig. 6). Figure 6 also details the lowest and highest temperatures recorded by any site at 30 cm during the same period. From the start of the nesting season until mid-November, the highest temperatures predominantly exceeded 29.2 °C, while the lowest temperatures only fluctuated above the pivotal temperature throughout August and September.

A total of 179 nests were laid from 15 June to 15 November 2003. The weekly distribution is provided in Fig. 6. Although we cannot provide an exact figure, it is likely that any nest whose middle third of incubation fell into the months of August until the middle of October would incubate under female producing conditions (Fig. 6). We therefore tentatively suggest that during the 2003 nesting season on Pasture Bay an appreciable number of females were produced.

Discussion

The present study was not designed to provide a numerical estimate of sex ratio, which would have required more extensive sampling. For one thing, although the large majority of turtle nesting on Pasture Bay occurs during the months of June–November, occasional but unquantified nesting occurs throughout the rest of the year (Richardson *et al.*, 1999). Some of these months are generally cool and nests laid then could be producing males. Even if only the main nesting season is considered, some validation by histology of gonads would be needed for estimates made from the sand temperature records. At the hatchling stage, sea turtles cannot be sexed by external morphology.

Nevertheless, our study does suggest that Pasture Bay is not predominantly male producing. There are several points in support of this. In 2003, sand temperatures were higher than those recorded in 1989 and 1990 during the main nesting season. In the two earlier years, these temperatures were closest to the coolest rather than to the average sand temperature of the 2003 sites (Fig. 4); this is consistent with the air temperatures in 1989 and 1990 having been cooler than in 2003 (Fig. 5). Because the 2003 values were higher than those for 1989 and 1990, they were also higher relative to the pivotal level, and were above that level more often, than in the previous years. In particular, temperatures in the 2003 nesting season were above the pivotal level during portions of the season when a considerable number of nests would have been in their thermosensitive period (Fig. 6). Moreover, the 2003 temperatures were not atypically high for recent years. In fact, of the 10 last years (1994–2003), 5 have been warmer during the nesting season than 2003 (Fig. 5).

A second reason for discounting Pasture Bay as of particular importance for the production of males is that the records for 1989 and 1990, from which this idea originated, were of sand temperatures at the depth of nests, but not temperatures of actual nests. The present work shows that appreciable metabolic warming occurred within at least some parts of the nest. When sand temperatures are close to the pivotal level, a 1 °C change during the thermosensitive period (Table 2) is enough to have considerable effects on sex ratio. This implies that in the previous years when only sand temperatures were measured, egg temperatures may have been above pivotal level, and so resulted in the production of females more often than the measurements of sand temperature then would indicate.

However, although the present work implicates metabolic warming as a feminizing influence on this beach, the effect cannot be translated into numerical

Table 2 Mean ± SD (and range) of daily temperatures (°C) recorded from each of the 15 nests, and the beach (sand) means of all sand sites for Pasture Bay over the corresponding period of days

					First third of incubation			Middle third of incubation			Final third of incubation		
		All incubation			Difference from			Difference from			Difference from		
	Date laid and ID	Nest	Sand at 30 cm	Sand at 60 cm	Nest	Sand at 30 cm	Sand at 60 cm	Nest	Sand at 30 cm	Sand at 60 cm	Nest	Sand at 30 cm	Sand at 60 cm
1	16/06/03	30.20 ± 2.3	28.91 ± 0.5	28.59 ± 0.3	28.24 ± 0.4	−0.44 ± 0.4	−0.14 ± 0.2	29.12 ± 0.7	0.42 ± 0.6	0.64 ± 0.6	33.29 ± 1.1	3.92 ± 0.8	4.36 ± 0.9
	60	(27.4–34.8)	(27.6–30.5)	(27.9–29.4)	(27.4–28.8)	(−1.3 to 0.0)	(−0.7 to 0.3)	(28.3-31.0)	(−0.5 to 2.0)	(−0.1 to 2.4)	(30.8-34.8)	(2.1–4.9)	(2.3–5.4)
2	17/06/03	32.05 ± 1.9	28.83 ± 0.4	28.53 ± 0.2	30.27 ± 0.6	1.50 ± 0.3	1.80 ± 0.4	31.38 ± 0.8	2.68 ± 0.8	2.90 ± 0.7	34.59 ± 0.7	5.53 ± 0.5	5.88 ± 0.6
	53	(28.8–35.5)	(27.6–29.8)	(27.9–29.0)	(28.8–30.9)	(0.6–2.2)	(0.8–2.3)	(30.3-32.9)	(1.5–4.4)	(1.9–4.3)	(32.5-35.5)	(4.1–6.2)	(4.2–6.6)
3	18/06/03	32.00 ± 1.9	29.01 ± 0.5	28.66 ± 0.3	28.38 ± 0.3	−0.38 ± 0.2	−0.05 ± 0.2	29.32 ± 0.7	0.57 ± 0.6	0.82 ± 0.7	32.60 ± 0.7	3.03 ± 0.5	3.50 ± 0.6
	62	(27.3–34.6)	(27.6–30.5)	(27.9–29.4)	(27.3–29.0)	(−0.7 to 0.0)	(−0.6 to 0.4)	(28.2-31.3)	(−0.4 to 2.0)	(−0.2 to 2.7)	(31.0-34.6)	(2.0–4.5)	(2.3–5.2)
4	04/07/03	30.57 ± 2.1	29.23 ± 0.5	28.89 ± 0.4	28.44 ± 0.2	−0.24 ± 0.3	−0.03 ± 0.2	30.18 ± 1.1	0.88 ± 0.8	1.31 ± 0.9	33.12 ± 0.7	3.41 ± 0.7	3.80 ± 0.6
	60*	(28.0–34.0)	(28.0–30.5)	(28.3–29.5)	(28.0–28.9)	(−1.0 to 0.5)	(−0.5 to 0.3)	(28.7-32.9)	(−0.4 to 2.9)	(0.3–3.6)	(31.7-34.0)	(1.6–4.2)	(2.4–4.5)
5	06/07/03	31.22 ± 1.2	29.21 ± 0.5	28.87 ± 0.4	29.95 ± 0.4	1.28 ± 0.4	1.48 ± 0.4	31.06 ± 0.7	1.81 ± 0.5	2.20 ± 0.5	32.74 ± 0.2	3.02 ± 0.2	3.42 ± 0.2
	55	(28.9–33.1)	(28.0–30.5)	(28.3–29.5)	(28.9–30.5)	(−0.1 to 2.1)	(0.3–2.1)	(29.9–32.5)	(0.8–2.7)	(1.4–3.2)	(31.9–33.1)	(2.5–3.4)	(2.9–3.7)
6	06/07/03	30.57 ± 2.0	29.23 ± 0.5	28.89 ± 0.4	28.67 ± 0.2	−0.02 ± 0.2	−0.20 ± 0.1	30.22 ± 1.1	0.85 ± 0.8	1.29 ± 0.9	33.12 ± 0.7	3.46 ± 0.5	3.81 ± 0.6
	57	(28.3–34.2)	(28.0–30.5)	(28.3–29.5)	(28.3–29.1)	(−0.5 to 0.3)	(−0.1 to 0.6)	(28.7–32.6)	(−0.1 to 2.6)	(0.2–3.3)	(32.0–34.2)	(2.5–4.2)	(2.9–4.8)
7	07/07/03	30.97 ± 2.4	29.27 ± 0.5	28.93 ± 0.4	28.50 ± 0.2	−0.19 ± 0.2	−0.02 ± 0.2	30.56 ± 1.3	1.08 ± 1.0	1.55 ± 1.1	34.04 ± 0.7	4.41 ± 0.5	4.71 ± 0.6
	61	(28.0–35.1)	(28.0–30.5)	(28.3–29.6)	(28.0–29.0)	(−0.6 to 0.2)	(−0.3 to 0.4)	(28.6–33.3)	(−0.3 to 3.6)	(0.1–3.9)	(32.1–35.1)	(2.4–5.2)	(2.9–5.6)
8	17/07/03	31.66 ± 1.9	29.41 ± 0.5	29.06 ± 0.3	29.59 ± 0.4	0.62 ± 0.2	0.94 ± 0.2	31.73 ± 1.2	2.01 ± 1.1	2.47 ± 1.0	33.77 ± 0.7	4.26 ± 0.5	4.49 ± 0.6
	58	(28.9–35.0)	(28.0–30.5)	(28.3–29.6)	(28.9–30.3)	(0.0–1.1)	(0.6–1.3)	(30.0–33.9)	(0.3–4.5)	(1.1–4.4)	(32.2–35.0)	(2.3–5.1)	(3.0–5.4)
9	21/07/03	30.77 ± 1.7	29.49 ± 0.5	29.12 ± 0.3	28.86 ± 0.4	−0.23 ± 0.2	0.13 ± 0.2	30.73 ± 0.7	1.01 ± 0.9	1.42 ± 0.7	32.96 ± 0.4	3.31 ± 0.3	3.62 ± 0.3
	58	(28.0–33.8)	(28.0–30.5)	(28.3–29.6)	(28.0–29.5)	(−0.8 to 0.2)	(−0.4 to 0.1)	(29.5–32.2)	(0.6–2.9)	(0.4–2.9)	(32.1–33.8)	(2.5–3.8)	(2.9–4.3)
10	27/07/03	30.72 ± 1.2	29.61 ± 0.4	29.26 ± 0.3	29.38 ± 0.4	−0.08 ± 0.2	0.39 ± 0.2	30.48 ± 0.5	0.81 ± 0.6	1.15 ± 0.4	32.17 ± 0.4	2.48 ± 0.3	2.74 ± 0.2
	60*	(28.5–32.7)	(28.7–30.5)	(28.6–29.8)	(28.5–30.1)	(−0.8 to 0.5)	(0.0–0.7)	(29.9–31.7)	(−0.1 to 2.4)	(0.6–2.1)	(31.2–32.7)	(1.7–3.0)	(2.1–3.1)
11	08/08/03	31.58 ± 0.5	29.71 ± 0.3	29.39 ± 0.2	31.80 ± 0.6	2.02 ± 0.5	2.47 ± 0.6	31.25 ± 0.3	1.65 ± 0.3	1.95 ± 0.2	31.70 ± 0.3	1.93 ± 0.2	2.19 ± 0.1
	60*	(30.1–32.9)	(28.7–30.5)	(29.0–29.8)	(30.1–32.9)	(0.4–2.8)	(1.1–3.5)	(30.5–31.7)	(1.0–2.3)	(1.4–2.4)	(31.1–32.2)	(1.3–2.3)	(1.9–2.4)
12	11/08/03	30.54 ± 1.6	29.68 ± 0.3	29.39 ± 0.1	29.17 ± 0.2	−0.54 ± 0.2	−0.15 ± 0.1	30.03 ± 1.2	0.27 ± 1.1	0.59 ± 1.1	32.57 ± 0.4	3.01 ± 0.2	3.16 ± 0.3
	60	(28.7–33.2)	(28.7–30.5)	(29.0–29.8)	(28.7–29.5)	(−1.0 to 0.0)	(−0.4 to 0.1)	(28.7–30.3)	(−0.8 to 2.8)	(−0.5 to 2.8)	(31.8–33.2)	(2.2–3.4)	(2.5–3.6)
13	11/08/03	31.56 ± 1.5	29.70 ± 0.4	29.39 ± 0.2	30.19 ± 0.3	0.49 ± 0.2	0.87 ± 0.2	31.04 ± 0.9	1.32 ± 0.7	1.67 ± 0.7	33.58 ± 0.4	3.90 ± 0.4	4.10 ± 0.4
	54	(29.5–34.4)	(28.7–30.5)	(29.0–29.8)	(29.5–30.6)	(−0.2 to 0.8)	(0.4–1.2)	(29.9–33.1)	(0.4–2.8)	(0.6–3.4)	(32.8–34.4)	(2.7–4.6)	(3.3–4.8)
14	17/08/03	30.97 ± 0.9	29.56 ± 0.5	29.34 ± 0.2	29.99 ± 0.2	0.36 ± 0.2	0.67 ± 0.2	30.90 ± 0.6	1.21 ± 0.7	1.47 ± 0.6	32.09 ± 0.3	2.76 ± 0.5	2.83 ± 0.3
	58	(29.5–32.6)	(27.6–30.5)	(28.4–29.8)	(29.5–30.5)	(−0.2 to 0.9)	(0.2–1.1)	(30.0–32.0)	(0.1–2.5)	(0.7–2.6)	(31.5–32.6)	(1.9–4.1)	(2.2–3.4)
15	17/08/03	30.12 ± 1.4	29.54 ± 0.5	29.33 ± 0.3	28.90 ± 0.4	−0.72 ± 0.2	−0.42 ± 0.3	29.68 ± 0.9	−0.02 ± 0.8	0.24 ± 0.8	31.90 ± 0.8	2.62 ± 0.5	2.67 ± 0.5
	59	(28.1–33.4)	(27.6–30.5)	(28.4–29.8)	(28.1–29.6)	(−1.3 to −0.1)	(−1.2 to 0.3)	(28.2–31.3)	(−1.2 to 1.5)	(−1.1 to 1.9)	(30.1–33.4)	(1.5–3.7)	(1.5–4.0)
Mean	**58.3 ± 2.6**	**31.03 ± 0.6**	**29.35 ± 0.5**	**29.04 ± 0.3**	**29.36 ± 1.0**	**0.23 ± 0.8**	**0.52 ± 0.8**	**30.51 ± 0.8**	**1.10 ± 0.7**	**1.44 ± 0.7**	**32.95 ± 0.8**	**3.40 ± 0.9**	**3.69 ± 0.9**
***n* = 15 (range)**	**(53–62)**	**(30.1–32.1)**	**(28.8–29.7)**	**(28.5–29.4)**	**(28.2–31.8)**	**(−0.72 to −2.0)**	**(−0.4 to 2.5)**	**(29.1–31.7)**	**(0.0–2.7)**	**(0.2–2.9)**	**(31.7–34.6)**	**(1.9–5.5)**	**(2.2–5.9)**

Nest temperature during each third of nest incubation duration (ID) is also provided.

*Hatching was missed, therefore average incubation duration (Parrish & Goodman, 2002) was used.

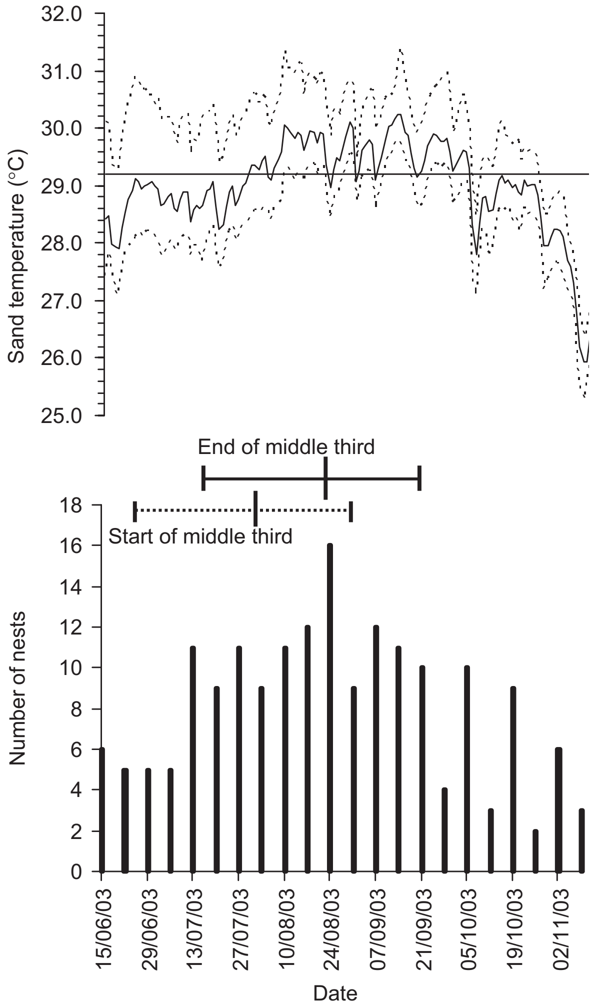

Fig. 6 The mean daily temperature of all sites on Pasture Bay at 30 cm ($n = 10$ sites, 150 days). Dashed lines show values for those probes having the lowest and highest temperatures on each day. Pivotal temperature of 29.2 °C is shown by the horizontal line. The frequency histogram details the weekly distribution of nests laid during June–November 2003. Bars indicate the minimum, median and maximum dates of the start (dashed line) and end (solid line) of the middle third of incubation for the 15 nests.

values of sex ratio in any simple way. As in most such investigations, our dataloggers were placed within the egg mass. Previous studies have shown that regional variations in the quantity of metabolic warming does occur within the nest. For example, eggs at the edge of a clutch can be cooler than those in the centre (Godfrey *et al.*, 1997; Booth & Astill, 2001); or variations can exist between the top and bottom of the clutch (e.g. Kaska *et al.*, 1998; Houghton & Hays, 2001). Also, the magnitude of metabolic heating is influenced by clutch size (Booth & Astill, 2001; Broderick *et al.*, 2001). Therefore, exactly what correction should be made for converting sand temperatures to egg temperatures to allow for metabolic warming will differ for different parts of the egg mass. Also, it is not known exactly how great the overlap of metabolic warming and thermosensitivity is. In broad terms, as a rule of thumb, the middle third of incubation may be used to approximate the period when sexual differentiation is influenced by temperature, but there are only a few detailed studies defining the limits of this period (Yntema & Mrosovsky, 1982; Desvages *et al.*, 1993), and none with hawksbills. Moreover, when one uses the average temperature during the middle third of incubation to predict sex ratio, by comparing that average to the pivotal level, the assumption is made that there is a simple additive effect of temperature over the thermosensitive period. But it is just as likely that temperatures during the start and during the end of the thermosensitive period may be weighted differently. Also, large but short excursions away from pivotal level may not be equivalent to smaller but longer excursions. Thus, the use of average temperature during the middle third of incubation provides some guide about sex ratio bias, but is not an adequately validated or elaborated procedure.

Another caution concerns the limited data currently available on the pivotal temperatures in sea turtles and the possibility of the pivotal varying among turtles or within a season with the same turtle. Bowden *et al.* (2000), working with freshwater turtles, *Chrysemys picta*, have reported that within clutches, there is a tendency for the proportion of females produced to increase as the season progresses; this may be interpreted as a lowering of pivotal temperature. Only about 10% of the variance in sex ratio could be accounted for by the date in the season. Nevertheless, the possibility of plasticity in pivotal temperatures should be kept in mind, and further research is needed. That said, at present there is no particular evidence of pivotals changing in sea turtles. The pivotal temperature appears to be a relatively conservative characteristic with values in hawksbill and loggerhead turtles (*Caretta caretta*) estimated to be quite close to 29 °C (Mrosovsky, 1994; Wibbels, 2003).

The possibility of the pivotal temperature differing from the value previously found with Antiguan hawksbills does not alter our principal conclusion: the main point we stress here is that temperatures in the present investigation were higher than those taken 14 years earlier, and that air temperatures for Antigua have increased significantly over the last 35 years. Based on the sand and nest temperatures relative to the pivotal level and relative to the previous years, this beach is estimated in 2003 to produce an appreciable number of females. Therefore, Pasture Bay beach in Antigua cannot be considered as a potential buffer for Caribbean hawksbills against the femininizing effects of warming trends there. Altogether, the credentials for the beach providing a cool environment favourable to the consistent common production of many males is weakened by what we know currently compared with the information available in Mrosovsky *et al.* (1992).

What may be expected to happen to this population of turtles in the future? Given that temperatures are already above the pivotal during some time of the main nesting season, even without allowing for metabolic heating of at least some of the eggs, if the warming trend continues, a shortage of males could detract from demographic health. We do not think this point has been reached yet because there is no evidence of high infertility of eggs laid at Pasture Bay. Indeed, nest success on Pasture Bay is relatively high, with an average hatching success of 72% in 2002 (i.e. 72% of eggs within the nest produced hatchlings, which were successful in emerging at the sand surface, Parrish & Goodman, 2002).

Nevertheless, it might be worthwhile making a graph of hatch rates over the years and monitoring for infertility more systematically. We suggest also that it would be worthwhile for those managing this beach to devote more research to nesting outside the main season. If there is a shortage of males, these few turtles could become disproportionally important. Indeed, frequency-dependent pressures for producing males could result in the long term in more turtles nesting at these times (cf. Mrosovsky & Provancha, 1989).

Finally, more thought should be given to artificial incubation and artificial beaches with cooler thermal characteristics. The present artificial beaches were designed with needs of people rather than of turtles in mind. On the basis of our data, there is no indication that the two artificial beaches are thermally adverse. Nevertheless, it has been indicated (A. Parrish & K. Goodman, personal communication) that nests laid on these artificial beaches do have a low hatching success. Sand for these beaches is generally imported, usually at a high price, and sometimes is used to conceal cheaper material underneath. We were only able to record sand temperature at 30 cm, but further investigation found that at depths greater than 50 cm, the sand was damp, which may be attributable to a somewhat high water table in both beaches. Therefore, these factors should be kept in mind if further manipulation or addition of beaches is to occur on Long Island.

From the present study, we conclude that Long Island in Antigua is unlikely to be a strongly male producing area for hawksbill turtles. In 2003, sand temperatures were often higher than the pivotal temperature, putting the cool temperatures of 1989 and 1990 in a different perspective. Over the past 100 years, the global average temperature has increased by approximately 0.6 °C and is projected to continue to rise at a rapid rate (Root *et al.*, 2003). The slow maturation time of sea turtles makes it harder to adapt to rapid climate changes. For a population of turtles such as that found on Pasture Bay, with the majority of nests incubating around or above the pivotal temperature, year-to-year variations in temperatures have profound consequences on the resultant sex ratio. More generally, the question of female biased sex ratios in sea turtles (Wibbels, 2003) remains a challenge, both theoretically and for conserving species in a world that is likely to be warmer and to favour even greater proportions of female sea turtles.

Acknowledgements

This project would not have been possible without the help provided by Allison Parrish, Keri Goodman and Ian McIntosh. We are grateful for the support and advice from Jim Richardson, the Jumby Bay Island Company Limited, John and Sarah Fuller, Keighley Meade of the Antigua and Barbuda Meteorological Office, David Rayney and the Stubbs family. This work was supported from a grant from the Natural Sciences and Engineering Council of Canada.

References

Booth DT, Astill K (2001) Temperature variation within and between nests of the green sea turtle, *Chelonia mydas* (Chelonia: Cheloniidae) on Heron Island, Great Barrier Reef. *Australian Journal of Zoology*, **49**, 71–84.

Bowden RM, Ewert MA, Nelson CE (2000) Environmental sex determination in a reptile varies seasonally and with yolk hormones. *Proceedings of the Royal Society of London, Series B*, **267**, 1745–1749.

Broderick AC, Godley BJ, Hays GC (2001) Metabolic heating and the prediction of sex ratios for green turtles (*Chelonia mydas*). *Physiological and Biochemical Zoology*, **74**, 161–170.

Desvages G, Girondot M, Pieau C (1993) Sensitive stages for the effects of temperature on gonadal aromatase activity in embryos of the marine turtle *Dermochelys coriacea*. *General and Comparative Endocrinology*, **92**, 54–61.

Godfrey MH, Barreto R, Mrosovsky N (1997) Metabolically generated heat in sea turtles nests and its potential effect on the sex ratio of hatchlings. *Journal of Herpetology*, **31**, 616–619.

Hewavisenthi S, Parmenter CJ (2001) Influence of incubation environment on the development of the flatback turtle (*Natator depressus*). *Copeia*, **2001**, 668–682.

Houghton JDR, Hays GC (2001) Asynchronous emergence by loggerhead turtle (*Caretta caretta*) hatchlings. *Naturwissenschaften*, **88**, 133–136.

Kaska Y, Downie R, Tippett R *et al.* (1998) Natural temperature regimes for loggerhead and green turtle nests in the eastern Mediterranean. *Canadian Journal of Zoology*, **76**, 723–729.

Mrosovsky N (1994) Sex ratios of sea turtles. *Journal of Experimental Zoology*, **270**, 16–27.

Mrosovsky N, Bass A, Corliss LA *et al*. (1992) Pivotal and beach temperatures for hawksbill turtles nesting in Antigua. *Canadian Journal of Zoology*, **70**, 1920–1925.

Mrosovsky N, Pieau C (1991) Transitional range of temperature, pivotal temperatures and thermosensitive stages for sex determination in reptiles. *Amphibia-Reptilia*, **12**, 169–179.

Mrosovsky N, Provancha J (1989) Sex ratio of loggerhead sea turtles hatching on a Florida beach. *Canadian Journal of Zoology*, **67**, 2533–2539.

Parrish A., Goodman K. (2002) *Tagging and nesting research on hawksbill turtles (Eretmochelys imbricata) at Jumby Bay, Long Island, Antigua, West Indies*. Annual Report, 23pp.

Richardson JI, Bell R, Richardson TH (1999) Population ecology and demographic implications drawn from an 11-year study of nesting hawksbill turtles, *Eretmochelys imbricata*, at Jumby Bay, Long Island, Antigua, West Indies. *Chelonian Conservation Biology*, **3**, 244–250.

Root TL, Price JT, Hall KR *et al*. (2003) Fingerprints of global warming on wild animals and plants. *Nature*, **421**, 57–60.

Wibbels T (2003) Critical approaches to sex determination in sea turtles. In: *The Biology of Sea Turtles* (eds Lutz PL, Musick JA, Wyneken J), pp. 103–134. CRC Press, Boca Raton, FL.

Yntema CL, Mrosovsky N (1982) Critical periods and pivotal temperatures for sexual differentiation in loggerhead turtles. *Canadian Journal of Zoology*, **60**, 1012–1016.