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Journal of Experimental Marine Biology and Ecology xx (2007) xxx – xxx

Journal of EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY

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Protracted rainfall decreases temperature within leatherback turtle (*Dermochelys coriacea*) clutches in Grenada, West Indies: Ecological implications for a species displaying temperature dependent sex determination

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Received 19 October 2006; received in revised form 1 February 2007; accepted 2 February 2007

Abstract

Protracted or intense rainfall may affect the reproductive success of reptilian species on a number of levels ranging from the availability of prey, the integrity of the nesting site and the subsequent survivability of offspring. For sea turtles (a species displaying temperature sex determination) nesting throughout the tropics and subtropics, rainfall has previously been shown to influence the development environment of clutches; in its extreme resulting in high levels of egg or hatchling mortality. Yet when compared to other abiotic variables affecting clutch success, rainfall has received relatively little attention. We therefore examined how fluctuations in local rainfall at a tropical nesting site for leatherback turtles (*Dermochelys coriacea*) affected the nest environment. Temperature data loggers placed within clutches ($n = 8$) revealed that protracted rainfall had a marked cooling effect on nests, so that seasonally improbable male-producing temperatures (<29.75 °C) were produced. We use these data to explore how rainfall may ultimately influence the sex ratios of sea turtle hatchlings both within and between nesting seasons, and discuss the importance of robust estimates of rainfall for future demographic models.

Keywords: Caribbean; Precipitation; Reptile; Sand temperature; Sex ratio

1. Introduction

The sex ratio of offspring in many reptilian species is determined by temperatures experienced within the egg clutch during the middle third of embryonic development. In simplest terms, a 50:50 sex ratio will be produced within clutches at a 'pivotal temperature' above and below which the ratio will be skewed towards either females or male, depending on the species (e.g. Janzen and Paukstis, 1991; Mrosovsky and Pieau, 1991). One group displaying temperature sex determination (TSD) which has received considerable attention in recent years is the sea turtles which nest widely on sandy beaches throughout the tropics and subtropics. In sea turtles males are produced below the pivotal temperature and vice versa. Although

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doi:10.1016/j.jembe.2007.02.001

Please cite this article as: Houghton, J.D.R. et al. Protracted rainfall decreases temperature within leatherback turtle (Dermochelys coriacea) clutches in Grenada, West Indies: Ecological implications for a species.... J. Exp. Mar. Biol. Ecol. (2007), doi:10.1016/j.jembe.2007.02.001

female turtles partially buffer the effects of local climatic variations through the construction of deep egg chambers, and the time of year at which they lay, the production of numerous clutches within a single season means that each in turn will be subject to subtle differences in incubation conditions (Miller et al., 2003). For many reptilian species such seasonal shifts in temperature significantly modify both the hatchling sex ratio and the developmental trajectories of developing embryos (Shine, 2004), thus having important demographic implications. For sea turtles, this effect is most pronounced in populations nesting away from the tropics, such as the Mediterranean Sea, where the marked seasonality results in clutches laid at the start of the season developing under starkly different conditions to those laid towards the end (e.g. Miller et al., 2003). Within the tropics, the climatic shift between seasons is less pronounced allowing a longer breeding season as conditions remain thermally conducive to the production of successful clutches for a greater part of the year.

However, any consideration of reptilian TSD cannot be merely limited to a discussion of seasonal shifts in ambient air temperature. Indeed, beneath the surface of the sand, there are a host of variables that play a role ranging from the depth of the clutch (e.g. Hanson et al., 1998; Houghton and Hays, 2001), the number of eggs deposited, thermal conductivity and particle of the substrate, the position of the water table (e.g. Ragotzkie, 1959; Prange and Ackerman, 1974; Ackerman, 1980; Kraemer and Bell, 1980), shading from vegetation or shoreline human developments (Mrosovsky et al., 1995). These variables are further compounded by the intensity and duration of rainfall at a particular site which affects clutch development in a number of ways. Primarily, heavy rainfall serves to decrease gas diffusion throughout the sand column (Miller et al., 2003), which in its extreme can induce clutch mortality in the same way as prolonged tidal inundation (e.g. Ragotzkie, 1959; Kraemer and Bell, 1980). Additionally, it may also influence the thermal environment of the clutch itself as shown by Matsuzawa et al. (2002) working at nesting sites in Japan, whereby sand temperature increased steeply as the rainy season ended.

Nonetheless, despite a general acceptance that rainfall may play an important role in sea turtle clutch development (e.g. Ragotzkie, 1959; Godfrey et al., 1996; Matsuzawa et al., 2002) this variable has received comparatively little attention. There is corresponding requirement, therefore, to better understand the effects of this variable under field conditions if projections of sea turtle demographics are to be truly robust and representative at a population level. This notion has been previously alluded to before by Godfrey et al.

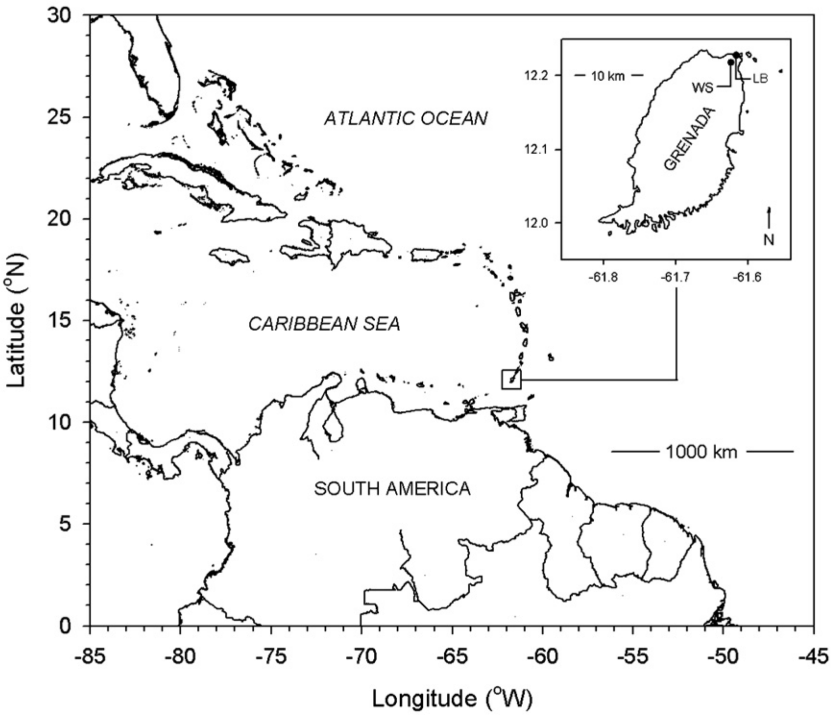

Fig. 1. Map of the wider Caribbean basin showing location of Grenada. Inset shows Grenada in detail with reference to Levera Beach (LB) and proximate weather station (WS).

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(1996) in their study of leatherback (*Dermochelys coriacea*) and green turtles (*Chelonia mydas*) nesting in Suriname. In this study, changes in rainfall produced subsequent changes in sand temperature, which in turn influenced the sexual differentiation of incubating sea turtle embryos. The influence was such that the authors were able to derive significant negative relationships between monthly rainfall and monthly sex ratios for both species concerned (Godfrey et al., 1996). Here we re-visit this discussion by considering the effects of rainfall for leatherback clutch development on an intra-seasonal scale at an alternative site within the Caribbean region. Specifically, we examined the temperature of clutches deposited at different times of year in conjunction with measurements of local rainfall on the Caribbean island of Grenada during 2003. The potential influence of rainfall on clutch development is considered together with a broader discussion of how pronounced rainfall may play an important role in the demographics of sea turtle populations in general.

2. Methods

2.1. Study site

Grenada (12.2°N, 61.6°W) is the island furthest south in the group comprising the Lesser Antilles and Windward islands, about 100 km south of St. Vincent and 130 km north of Venezuela (Fig. 1). Data were collected from Levera Beach, a known leatherback nesting site on the north shore of the island and the meteorological station at Levera Hill < 1 km from the study beach (Fig. 1).

2.2. Precipitation data

Precipitation data were gathered over two timescales: (1) real time data were collected form 16-July to 28-August during the 2003 nesting season by dividing each 24 h period into 4 quarters (6 h each) and noting how many quarters were characterised by rainfall in any particular day (denoted 1–4). (2) Long-term historical data (mean monthly rainfall as mm/day) were obtained from Levera Hill weather station for the years 1987–2003 (Fig. 2).

2.3. Clutch temperature data

Clutch temperatures were measured using Tinytalk II temperature data loggers (TDLs) (Gemini data loggers, Chichester, UK). Although factory calibrated, all TDLs were re-calibrated prior to deployment, against a thermometer of known accuracy (NAMAS) over the range of temperatures expected in the field (16–36 °C). Following this, recorded temperatures were, on average, identical to NAMAS with a standard deviation of ±0.1 °C.

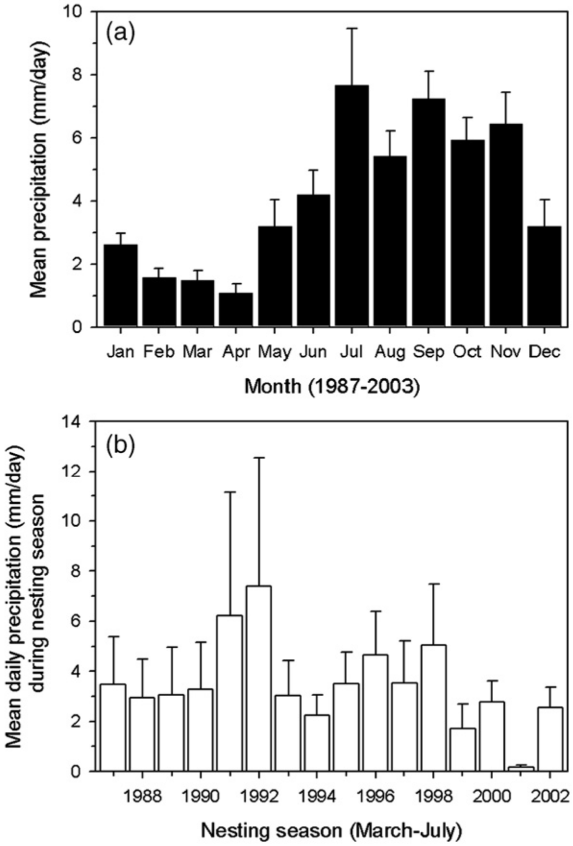

Fig. 2. (a) Mean monthly rainfall (+/− 1 SD) collected from Levera Hill weather station (<1 km from study site) from 1987–2003. (b) Mean monthly precipitation (Levera Hill) during the breeding season (March–July) expressed as mm/day (+/− 1 SE).

Five control TDLs were deployed on Levera Beach prior to the start of the nesting season (03-March). A further 15 loggers were placed in the centre of egg clutches (one per clutch) from 10-March through to 16-June 2003 (Table 1). TDLs were retrieved from clutches following a period of 7 days since the last emergence of hatchlings from nests. Nest contents were subsequently examined and levels of hatching success determined.

3. Results

3.1. Precipitation data

Mean values for rainfall in each month (cm) are given in (Fig. 2a). This revealed a seasonal pattern of rainfall with driest months occurring at the start of the nesting

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Table 1
Descriptive information and statistics for temperature data loggers deployed on Levera Beach, Grenada during 2003

Nest no.	Date	Notes	Mean temperature (°C) (SD)	Max/min temperature (°C)	No. of readings (1/h)	Hatching success (%)
Control 1	03-Mar	Washed out to sea	–	–	–	–
Control 2	03-Mar	Washed out to sea	–	–	–	–
Control 3	03-Mar	Washed out to sea	–	–	–	–
Control 4	03-Mar	Washed out to sea	–	–	–	–
Control 5	03-Mar	Failed	–	–	–	–
1	10-Mar	Recovered	31.65 (1.76)	36.00–29.00	1379	59.0
3	12-Mar	Recovered	32.00 (1.68)	34.50–28.80	1516	30.4
5	19-Mar	Recovered	31.98 (0.70)	33.00–29.90	1777	–
13	29-Mar	Recovered	31.78 (0.93)	34.10–29.90	1354	–
18	30-Mar	Poached	–	–	–	–
39	09-Apr	Recovered	32.48 (1.04)	34.90–29.20	1445	12.4
45	11-Apr	Recovered	30.28 (1.35)	31.80–26.30	1770	–
80	19-Apr	Recovered	31.23 (0.83)	32.60–29.90	1799	–
99	23-Apr	Washed out to sea	–	–	–	–
208	10-May	Recovered	30.47 (0.58)	31.40–29.00	1797	–
220	12-May	Poached	–	–	–	–
265	19-May	Not relocated	–	–	–	–
366	02-Jun	Washed out to sea	–	–	–	–
373	03-Jun	Not relocated	–	–	–	–
468	16-Jun	Not relocated	–	–	–	–

Note: ‘Date’ is the date of oviposition. ‘Washed out to sea’ refers to nests and data loggers which were entirely swept out to sea during storm activity. ‘Not relocated’ means that the nest was excavated but data logger was not retrieved/present.

season (March–April), growing increasingly wetter from May to July, before decreasing again during December. To assess inter-annual variability we plotted mean precipitation (mm/day) for each nesting season (March–July) from 1987–2002 (Fig. 2b). Patterns of rainfall during this period again followed a normal distribution (Anderson–Darling; $p > 0.05$) with significant variation in rainfall between nesting seasons. This ranged from the highest mean of 7.40 mm/day (SE±5.15) during 1992 through to an incredibly dry season in 2001 where a mean of only 0.16 mm/day (SE±0.09) was recorded (Fig. 2b).

3.2. Clutch temperature data

Four of the five control TDLs were washed out to sea during adverse weather conditions. Of the 15 TDLs deployed in nests, four were not recovered, one was found close to the surface after the nest had been poached by egg collectors and a further three failed when down-loading was attempted (as did the one recovered control TDL). Of the datasets recovered, only three were from nests that produced hatchlings. Descriptive statistics for each clutch in turn are given in Table 1. Temperature profiles for all clutches, successful and unsuccessful are shown in Fig. 3. Regarding clutch failure, evidence of tidal inundation can be seen for clutch 45, on 8th May when temperatures within the clutch fell from 30.03 °C–26.3 °C in ~4 h (Fig. 3f). This event cannot be attributed to rainfall as none was recorded during this, or any of the preceding days. Moreover, it appears that the factor(s) driving this event was/were localised as no corresponding decrease in temperature was recorded for any other clutch at that time (Fig. 3).

‘Troughs’ in the temperature profiles of clutches deposited later in the season (nests 45, 80 and 208 respectively) appeared to correspond to increases and decreases in daily rainfall (Fig. 3f–h). For example, when precipitation levels were high (i.e. rainfall recorded in 3–4 diel quarters) and lasted for several consecutive days, there was a marked drop in clutch temperature (Fig. 4). For clutches 45, 80 and 205 respectively, this could be most clearly seen during the period from 8th June through to the 24th July. Changes in clutch temperature during this period are shown in detail for clutch 208 in Fig. 4a. The temperature time-series was divided into 4 key stages when temperatures were decreasing (A1 and B1) or increasing (A2 and B2). One tailed t-tests revealed that rainfall was higher when temperatures were falling (A1, B1) than they were during periods of temperature increase (A2, B2) (A1 vs. A2: $T_{12} = 6.98$, $p < 0.05$. B1 vs. B2: $T_{12} = 3.44$, $p < 0.05$) (Fig 4b). This test was repeated for nests 45 and 80 again suggesting that periods of heavy or light rain resulted in corresponding decreases of increases in temperature within the respective nests (t-test: $p < 0.05$).

Regarding potential sex ratios, it is notable that during the middle third of incubation (the period critical for TSD) all three fecund nests (nos. 1, 3 and 39) were

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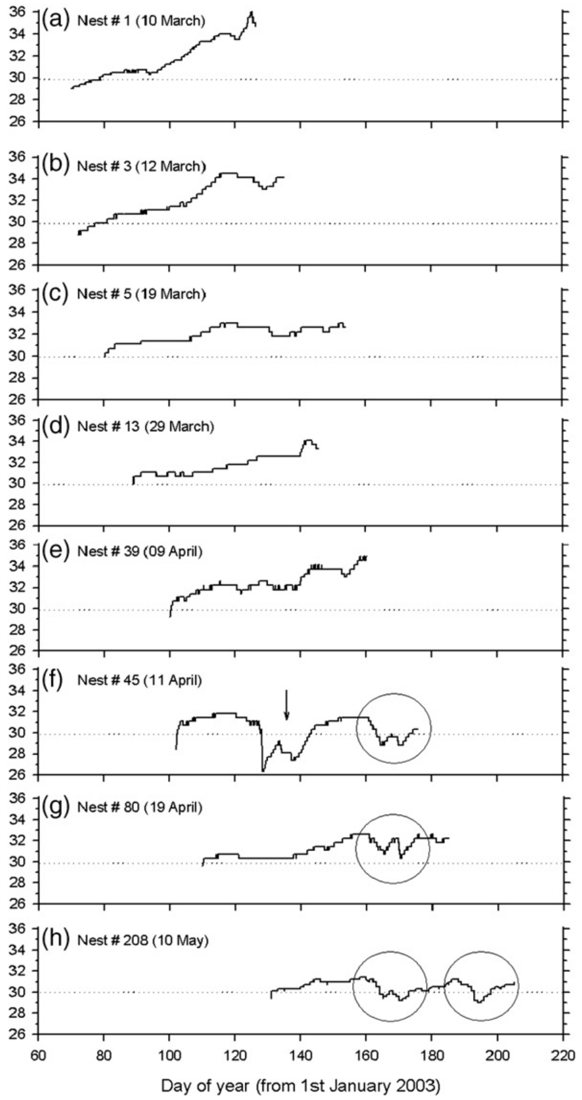

Fig. 3. Temperature profiles from TDLs within the 8 experimental clutches laid between 10th March and 10th May 2003. Dotted lines represent the temperature (29.75 °C), above which entirely female clutches are produced in French Guiana (Chevalier et al. 1999). Circled areas show ‘troughs’ in temperature profiles that coincided with periods of protracted rainfall (see Fig. 4). Tidal inundation event for Nest 45 (f) is marked with an (↓).

consistently warmer than the pivotal temperature of 29.4 °C determined for leatherback turtles in French Guiana (Chevalier et al., 1999). The mean temperatures of these 3 clutches (Nest 1 = 31.65 °C (SD ± 1.76); Nest 3 = 32.0 °C (SD ± 1.68); Nest 39 = 32.48 °C (SD ± 1.04)) also exceeded the transitional range of temperatures (above which males are no longer produced) for French Guiana where 100% females were produced at 29.75 °C (Chevalier et al., 1999). In its broadest sense, these data suggest that sand temperatures on Grenada during 2003 were more conducive to the production of female hatchlings for the greater part of the season. Although no offspring were produced from the latter experimental clutches (Table 1) the thermal conditions within the egg chambers did provide a useful insight to the potential effects of rainfall for developing sea turtle clutches. For example, with the exception of the tidal inundation for Nest 45 on 8th May (day 128; Fig. 3) the only occasions when temperatures were seen to fall below 29.75 °C were following periods of protracted rainfall (Fig. 4). Additionally, given that failed clutches would also be devoid of metabolic heating, the temperature profiles from failed nests must be taken as conservative estimates with the implication that more fecund

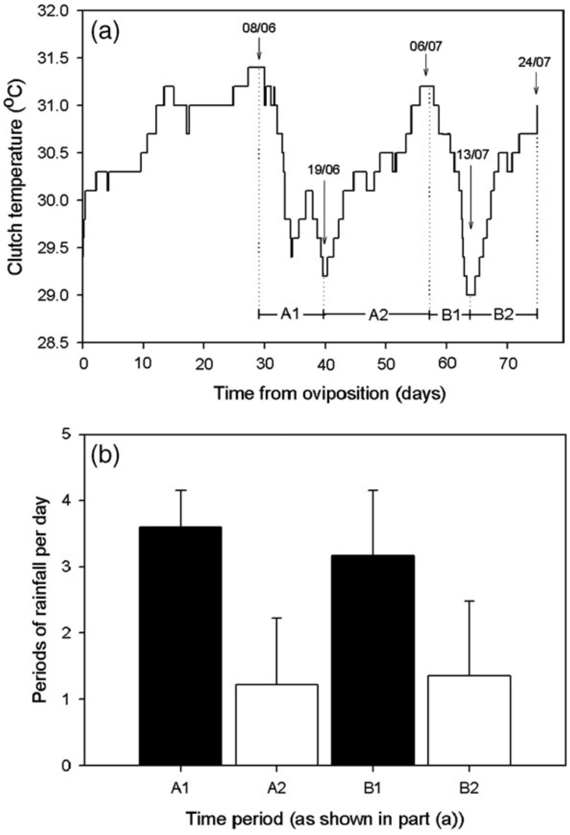

Fig. 4. (a) Temperature profile for nest no. 208 deposited on 11th May 2003. Highlighted on the figure are two distinct troughs (marked A1/A2 and B1/B2) when temperature dropped substantially following periods of prolonged rainfall, and increased once precipitation had decreased. (b) Shows the number mean number of quarters when rain fell in each of the four periods highlighted in (a) (A1: $n = 7$/A2: $n = 18$/B1: $n = 6$/B2: $n = 11$). *t*-tests revealed that significantly more rain fell during A1 and B1 than during A2 and B2 ($p < 0.05$), suggesting that marked decreases in temperature followed protracted periods of heavy rainfall (3–4 quarters per day).

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nests would be even warmer and more prone to female production.

4. Discussion

The influence of fluctuating weather conditions for the reproductive success of reptilian taxa has been explored for a wide range of species (e.g. Janzen, 1994; Godfrey et al., 1996; Dickman et al., 1999; Shine, 2002, 2004). Through such efforts it is becoming increasingly apparent that the immediate response of egg clutches to short-term weather fluctuations might in fact be a common trait amongst reptilian species (e.g. Shine and Elphick, 2001). It is now accepted that rainfall (and its variability) may affect species in a number of ways ranging from prey availability, physiological stress, reproductive success and survivability of offspring. For example, in arid areas of Australia, Dickman et al. (1999) suggested that rainfall might not only enhance the survival and growth of agamid (dragon) lizards (*Ctenophorus nuchalis* and *C. caudicinctus*), but also clutch size and hatching success. Therefore, to provide further empirical data for leatherback turtles nesting in the Caribbean, we attempted to tackle a specific ecological question: namely, how might rainfall affect the reproductive success of females and sex ratio of offspring both within and between nesting seasons.

The key point to emerge from our data was the suggestion that 'male-producing' conditions within clutches laid on Grenada (a proxy for the wider Caribbean region) might not simply result from sand temperatures responding to seasonal shifts in ambient air temperature, but also to the levels of precipitation experienced. However, the extent to which any given sea turtle clutch is affected by rainfall must, however, vary between species, populations and individuals given inherent differences in nesting locality and the construction of the egg chamber itself. For example, Matsuzawa et al. (2002) showed that pronounced rainfall at a loggerhead nesting site in Japan had implications beyond the manipulation of sex ratios, as it decreased sand temperatures at nest depth (50 cm) below the optimal thermal range for clutch development (27–32 °C; Bustard, 1972). In the present study the influence of rainfall appeared more demographic as it led to clutches being exposed to less lethal, yet potentially 'male-producing' conditions below 29.75 °C (Chevalier et al., 1999) (Figs. 3 and 4). However, we make no assertions as to the exact influence of decreased clutch temperature on sex ratios, as this factor is determined by the proportion of development at a given temperature, not daily fluctuations in exposure (Georges et al., 1994). Furthermore, any inferred influence should only be taken as representative for 2003 as rainfall can vary tremendously between different seasons as shown by the extremes of 1992 and 2001 (see Fig. 2b). Taking this into account, however, our data still provide some empirical evidence that 'wetter' seasons (or periods within a season) may be more prone to male hatchling production than 'dry' seasons. This would comply with Godfrey et al. (1996) who also suggested that the sex ratio for leatherback hatchlings in Suriname were largely driven by patterns of rainfall across the years.

As well as the impact of rainfall on nest temperature, we also recorded very low hatchling success from clutches. This low success seems to be a general feature of leatherback turtle rookeries (Ackerman, 1996) although our hatchling success values are lower than those reported elsewhere. Tidal inundation will certainly contribute to low hatchling success in leatherback nests, but additionally other features of the nest environment (e.g. water levels or oxygen levels) may presumably play a role (Ackerman, 1980). How populations, such as that on Grenada, remain viable despite high levels of mortality within nests remains enigmatic. Yet their persistence alone raises an intriguing demographic question given that sites conducive to male production (at least for part of the season) may also be prone to high levels of environmentally induced mortality. When one considers the possible predominance of female-producing sites in the Caribbean, it is arguable that the risk is worth it with high levels of clutch failure buffered by the production of demographically important male hatchlings. A full discussion of this point is well beyond the scope of this present study, yet the need to raise the issue remains valid.

Over a broader time scale, the relationship between localised weather conditions and clutch development raises further questions regarding the potential of TSD to produce demographically viable sex ratios (Fisher, 1930) in the light of predicted climate change (e.g. Janzen and Paukstis, 1991; Janzen, 1994). Not surprisingly this remains a contentious issue as the complexity of climate modelling poses a serious challenge to anyone seeking to interpret subsequent effects for any particular species (e.g. Portner, 2002; Guisann and Hofer, 2003; Hays et al., 2003). Regarding rainfall, the challenge of interpreting the long-term effects on reptilian populations is increasingly pertinent given that: (1) precipitation in the subtropics (from 10°N to 30°N) continues to decrease by 0.3% per decade (IPCC Summary for Policy Makers, 2001), and (2) future models for the wider Caribbean region predict marked fluctuations in rainfall throughout the next century (Fig. 2b; Angeles and Gonzales, 2006). In light of these predictions, there is a pressing requirement to better understand the influence

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of rainfall for sea turtle populations under field conditions. Without this information, any predictions of future sex ratios may underestimate the potential of particular sites to produce male offspring, with implications for ecologists and conservationists alike.

Acknowledgements

This work was supported by grants to G.C.H. from the Natural Environment Research Council of the U.K. (NERC). We thank the Grenadian Ministry of Agriculture, Forestry, Land and Fisheries for permission to conduct this work. **[SS]**

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