

Thermal control of hatchling emergence patterns in marine turtles

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Abstract

The emergence patterns of green turtle (*Chelonia mydas*) hatchlings on two beaches on Ascension Island, South Atlantic were monitored and related to thermal patterns in the sand at 10, 20, 30 and 40 cm depth. A total of 6001 hatchlings were recorded emerging on Long Beach, and 3171 emerged on North East Bay during the study period. No significant difference was observed in the temporal pattern of hatchling emergence among nights, or between the two beaches. Hatchling emergence predominantly occurred at night with over 93% of hatchlings emerging during the hours of darkness. Almost all hatchlings emerging in daylight suffer predation by the Ascension frigatebird (*Fregata aquila*). Counts of frigatebirds both above the study beaches and offshore were highest just after sunrise, with a smaller peak prior to sunset, when frigatebirds were found to predate hatchlings emerging, crawling down the beach or detected in inshore waters. The likely thermal cues controlling hatchling emergence were investigated (temperature at different depths, thermal gradients in the sand and temperature change). The most plausible thermal factor appears to be the change of temperature at superficial sand depths, with hatchling emergence inhibited when subsurface sand temperatures were increasing. This simple mechanism is likely to ensure predominantly nocturnal hatchling emergence regardless of sand albedo, seasonality or latitude as long as night is relatively cooler than day.

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1. Introduction

Once sexually mature, a female sea turtle will make regular pilgrimages to her natal beach to lay eggs. After completing mating, fertilisation and laying of individual clutches, the female returns to the sea investing no more care in the ensuing offspring. Roughly 50–80 days later, the eggs will hatch and the offspring begin the arduous journey from the egg, through the sand column and eventually to the sea (Miller, 1996). In order to complete

this successful journey, sea turtle hatchlings must emerge from the sand above their nest at night, when the sand surface is cool enough to prevent overheating and desiccation, and it is dark, meaning the probability of detection by visually hunting predators is low (Bustard, 1967; Mrosovsky, 1968; Witherington et al., 1990; Gyuris, 1993). Consequently, the timing of emergence from the sand is critical in terms of hatchling survivorship and, although diurnal emergence does occur, in general this accounts for the emergence of a small number of hatchlings (Bustard, 1967; Balazs, 1974; Drake and Spotila, 2002; Glen et al., 2005). At night, hatchlings typically emerge en masse, and it has been suggested that this aids survivorship via social

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facilitation during their ascent through the sand column (Carr and Hirth, 1961) as well as creating a dilution effect when detected by predators (Dehn, 1990). However, the time spent waiting for the optimal conditions for emergence to occur is certainly not trivial, both in overall energy expenditure (Hays et al., 1992) and the chances of predation (Godley and Kelly, 1996) or infestation (McGowan et al., 2001) which can increase dramatically the longer the hatchling remains in the nest.

The factors governing turtle hatchling emergence have been the matter of some discussion. Most studies have suggested temperature as the predominant controlling factor (Hendrickson, 1958; Bustard, 1967; Mrosovsky, 1968; Witherington et al., 1990; Hays et al., 1992; Moran et al., 1999). Three alternative mechanisms have been proposed: Hypothesis 1: A temperature threshold exists above which hatchlings will not emerge (Hendrickson, 1958; Mrosovsky, 1968; Bustard, 1967; Moran et al., 1999; Drake and Spotila, 2002); Hypothesis 2: A negative temperature gradient through the sand column promotes hatchling emergence. As the hatchlings ascend through the sand column, this will act as a trigger for emergence (Gyuris, 1993); Hypothesis 3: Hatchling emergence will be triggered by cooling of the sand (Witherington et al., 1990; Hays et al., 1992). Although convincing evidence for the suggested mechanisms have been presented, data from different sites appear to conflict suggesting that a more experimental approach might provide greater elucidation.

Ascension Island hosts one of the largest nesting colonies in the Atlantic for the green turtle (*Chelonia mydas*) (Mortimer and Carr, 1987) and is unusual in that no beaches are exposed to shading from vegetation. Nesting begins at the start of December and carries on until August, with the peak of nesting occurring in March (Godley et al., 2001, 2002a). Emergence of hatchlings from their nests peaks in May. The main diurnal predator of green turtle hatchlings on Ascension Island is the endemic Ascension frigatebird (*Fregata aquila*) with additional nocturnal predation by feral cats and yellow and purple land crabs (*Gecarcinus lagostoma*) (Pers. Obs.). Undoubtedly hatchling predation is carried out by numerous inshore marine fish and it is likely that this will occur by day and night (Stancyk, 1995).

We set out to examine the patterns of emergence of green turtle hatchlings on two different beaches on Ascension Island, to compare emergence patterns and elucidate the thermal cues that may control emergence. We chose two beaches of widely differing sand albedos, leading to markedly different sand temperature regimes

which have been shown to influence thermal conditions throughout the sand column to nest depth (Hays et al., 2001; Godley et al., 2002b). Our fundamental questions were: (1) what is the pattern of hatchling emergence at these two beaches with radically differing thermal conditions? (2) what are the consequences of getting the time of emergence wrong? and; (3) what is the thermal cue if any, used to stimulate or inhibit hatchling emergence?

2. Methods

2.1. Study site

Hatchling emergence was monitored on two nesting beaches, Long Beach and North East Bay on Ascension Island (7°57'S, 14°22'W) in the South Atlantic Ocean during April 1999. The two study beaches differed in sand colour with North East Bay being darker and consequently warmer than Long Beach (Hays et al., 1999; Broderick et al., 2001).

2.2. Data collection

Each beach was monitored for seven consecutive nights between 18:00 and 08:00 GMT. This fully encompassed the hours of darkness during the period (19:30–06:00). The overall estimated nest density for the season on Long Beach and North East Bay were 5200 and 4037 nests km⁻¹, respectively (Godley et al., 2001), therefore, it was not logistically possible to monitor hatchling emergence from individual nests. Consequently the part of the beach that was subject to high density nesting was selected and connectable plastic piping of 11cm diameter in 6m lengths was placed above the high water mark on the beach. The pipes were connected in order to funnel hatchlings emerging from nests to the landward side of the pipe into buckets buried in the sand at 12m intervals to act as pit-fall traps, the hatchlings taking only a few minutes to reach the piping. In total, the pipe stretched along 150m of the beach. The pipe was small enough to cause no obstruction to adult turtles moving up the beach to find suitable nesting sites; females simply crawled over the top. The barrier and buckets were checked every 30 min from 18:00 until 08:00. Any hatchlings observed in the buckets were counted and then released to make their way to the sea. The barrier was removed each morning so that any hatchlings which emerged during the daytime could make their way to the sea unhindered. To ensure that any diurnally emergent hatchlings were recorded, the sand in the study area was raked at 08:00

each morning. The area was checked at 18:00 for any hatchling tracks.

2.3. Temperature collection

Sand temperature at 10, 20, 30 and 40 cm depths was recorded throughout the study period at each beach using temperature dataloggers (Tinytalk, Orion Components Ltd., Chichester, UK). Position of the temperature logger was measured in relation to the sand surface using a semi-rigid tape measure. The loggers were set to record synchronously every 5 min, with a precision of 0.3 °C. Previously the dataloggers had been calibrated with a mercury thermometer of known accuracy (NAMAS certified to read ± 0.1 °C of absolute temperature: Hays et al., 1999). We used only one temperature recording station per beach as previous studies have shown within beach albedo and related thermal variation on Ascension Island to be negligible (Broderick et al., 2001; Hays et al., 2001).

2.4. Manipulation of temperature data

Temperature readings were averaged to give values for each half-hour. Using the values obtained, we calculated the temperature gradient through the sand column between 10–20, 20–30 and 30–40 cm for each half-hour. Values were obtained by subtracting the temperature at the greater depth e.g. 20 cm from the temperature recorded at a shallower level for the corresponding half-hour e.g. 10 cm. We also calculated the rate of temperature change ($^{\circ}\text{C h}^{-1}$) between successive half hour periods.

To allow us to clearly visualise the importance of different thermal cues on hatchling emergence, we calculated the relative proportion of hatchling emergence occurring at each temperature increment of the thermal mechanism under investigation. We defined ‘increment’ in hypothesis one as 1.0 °C, in hypothesis two as 0.5 °C and in hypothesis three as 0.4 °C h^{-1} . For example, 20.8% of hatchlings on Long Beach emerged when the temperature at 10 cm was between 28.0 and 28.9 °C and these temperatures were present for 9.3% of the time. The index of relative emergence for this increment of sand temperature was 2.3 (20.8/9.3). Thus values greater than 1.0 indicate a relative over-representation.

2.5. Additional temperature collection

High density green turtle nesting beaches are highly cratered as a result of the nesting activities of adult

female turtles. Following the main body of the study, in April 2004 we set out to investigate if the heterogeneous surface would have an impact on the thermal conditions experienced by hatchlings. At three sites for each beach we buried loggers at 10, 20, 30 and 40 cm below the sand surface in the bottom of a pit. We buried another set of temperature loggers at a control sites at the same depth approximately 2 m away from the pit in an area of relatively flat un-pitted beach. Loggers were allowed to equilibrate for 24 h and then data were gathered for 2 days.

2.6. Frigatebird observations

Between dawn and dusk (06:00 until 19:30) from the 9th April until 14th May, we undertook point counts of the number of frigate birds onshore and offshore to a distance of 300 m at both Long Beach and North East Bay. For each hour we calculated a mean value for each category for each site (range and mean of the number counts carried per hour: Long Beach: 1–5, mean=2.9; North East Bay: 1–4, mean=2.6).

3. Results

3.1. Hatchling emergence patterns

During the study we recorded 6001 hatchling emergences on Long Beach and 3171 on North East Bay. Assuming similar clutch size and emergence success, this represents the complete emergence of the order of 60 and 30 clutches, respectively. The temporal pattern of hatchling emergence was both spatially and temporarily invariant. No significant difference was observed in hatchling emergence patterns among the seven nights for each site (Kruskal–Wallis test: Long Beach $H_{1,6}=2.46$ $p>0.1$, North East Bay $H_{1,6}=2.13$ $p>0.1$). No significant difference was observed between the overall hatchling emergence distributions on Long Beach (Fig. 1a) and North East Bay (Fig. 1b) (Kolmogorov–Smirnov two sample test: $D=0.09 < D_{0.01}=0.192$).

During the study 93% and 95% of emergences occurred at night on Long Beach and North East Bay, respectively (Fig. 1). Only 6% and 2% of hatchlings emerged after 06:00 on Long Beach and North East Bay, respectively. In the evening prior to sunset, 1% and 3% of hatchlings emerged between 18:00 and 19:30 on Long Beach and North East Bay, respectively. All hatchlings emerging during these daylight periods were subject to predation unless they were collected by observers for later release. We feel the number of

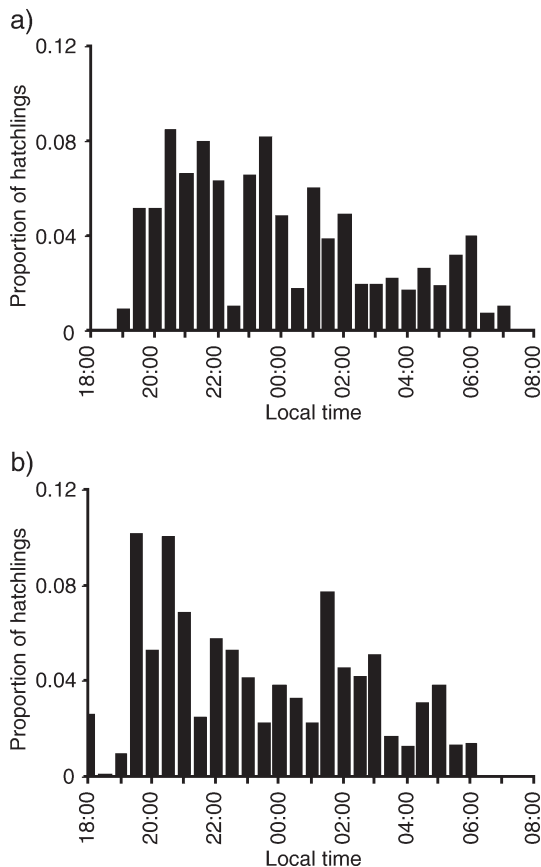


Fig. 1. Proportion of hatchlings that emerged during each half-hour period throughout seven days of monitoring on a) Long Beach and b) North East Bay.

hatchlings emerging between 08:00 and 18:00 was negligible as no hatchling tracks to the sea were discovered at the start of data recording each evening. It is possible however, that any hatchlings emerging during the day may have been taken by frigatebirds whilst on the beach, perhaps so soon as to not leave a detectable track. However, despite continual presence of frigatebirds at both beaches, during the course of frigatebird observations, very few ($n=3$) predation events were recorded during the day other than at dawn and dusk. In addition, groups of hatchlings were often observed immobile near the surface with small parts of their heads exposed.

3.2. Patterns in sand temperature

The temperature on Long Beach was significantly cooler than that recorded on North East Bay at all depths (ANOVA, $p < 0.001$) (Fig. 2). Although there were slight day-to-day variations in temperature regimes these were minimal on both beaches. Despite the

absolute levels being starkly different, diel patterns were quite similar, with the amplitude of the diel signal being dampened with increasing depth (Fig. 2).

In general the mean temperature experienced at sand depths below the base of a turtle nesting pit was slightly higher on North East Bay (Pit mean $\pm$ SD: 10 cm: 32.78 ± 0.4 ; 20 cm: 32.67 ± 0.1 ; 30 cm: 32.58 ± 0.1 ; 40 cm: 32.26 ± 0.0 ; Non-pit mean $\pm$ SD: 10 cm: 31.32 ± 0.4 ; 20 cm: 31.52 ± 0.2 ; 30 cm: 31.30 ± 0.1 ; 40 cm: 31.18 ± 0.0). Differences were less clear on Long Beach (Pit mean $\pm$ SD: 10 cm: 28.30 ± 2.0 ; 20 cm: 28.49 ± 0.6 ; 30 cm: 28.43 ± 0.2 ; 40 cm: 28.57 ± 0.0 ; Non-pit mean $\pm$ SD: 10 cm: 28.07 ± 1.9 ; 20 cm: 28.19 ± 0.6 ; 30 cm: 28.34 ± 0.3 ; 40 cm: 28.37 ± 0.1).

When the rate of temperature changes and thermal gradients were compared, there were no significant differences on either beach between pits or non-pits that might represent fundamental differences in cues presented (Kolmogorov–Smirnov two sample test for each depth comparison in temperature change and within sand temperature gradient, $p > 0.05$).

3.3. Thermal cues controlling hatchling emergence

Within the context of the pattern of emergence being the same at both beaches despite dissimilar thermal conditions, we can compare and evaluate the three hypotheses as to the cues controlling hatchling emergence.

Hypothesis 1. Temperature

Data regarding the range of temperature present at each depth and the proportion of this range which accounted for hatchling emergences are given in Table 1. All hatchlings emerged onto Long Beach and North East Bay when the sand temperature at 10 cm ranged between 25.5 and 32.6 °C (63% of the available range) and 28.8 and 35.7 °C (85% of the total range), respectively. Emergence of hatchlings occurred when the sand at 20 cm was between 28.1 and 32.2 °C (85% of the thermal range) on Long Beach and 30.3 and 35.7 °C (89% of the thermal range) on North East Bay. Emergence of hatchlings occurred across much of the available temperature range at 30 and 40 cm (Table 1). As these encompassed 81%–100% (Table 1) of the thermal ranges at these depths and there was no overlap in the range of temperatures experienced at these depths between beaches, we suggest that hatchlings were not using temperature at these depths as the primary cue controlling hatchling emergence.

As there was no significant difference between the emergence patterns observed on the two study beaches, we might expect that a similar emergence response

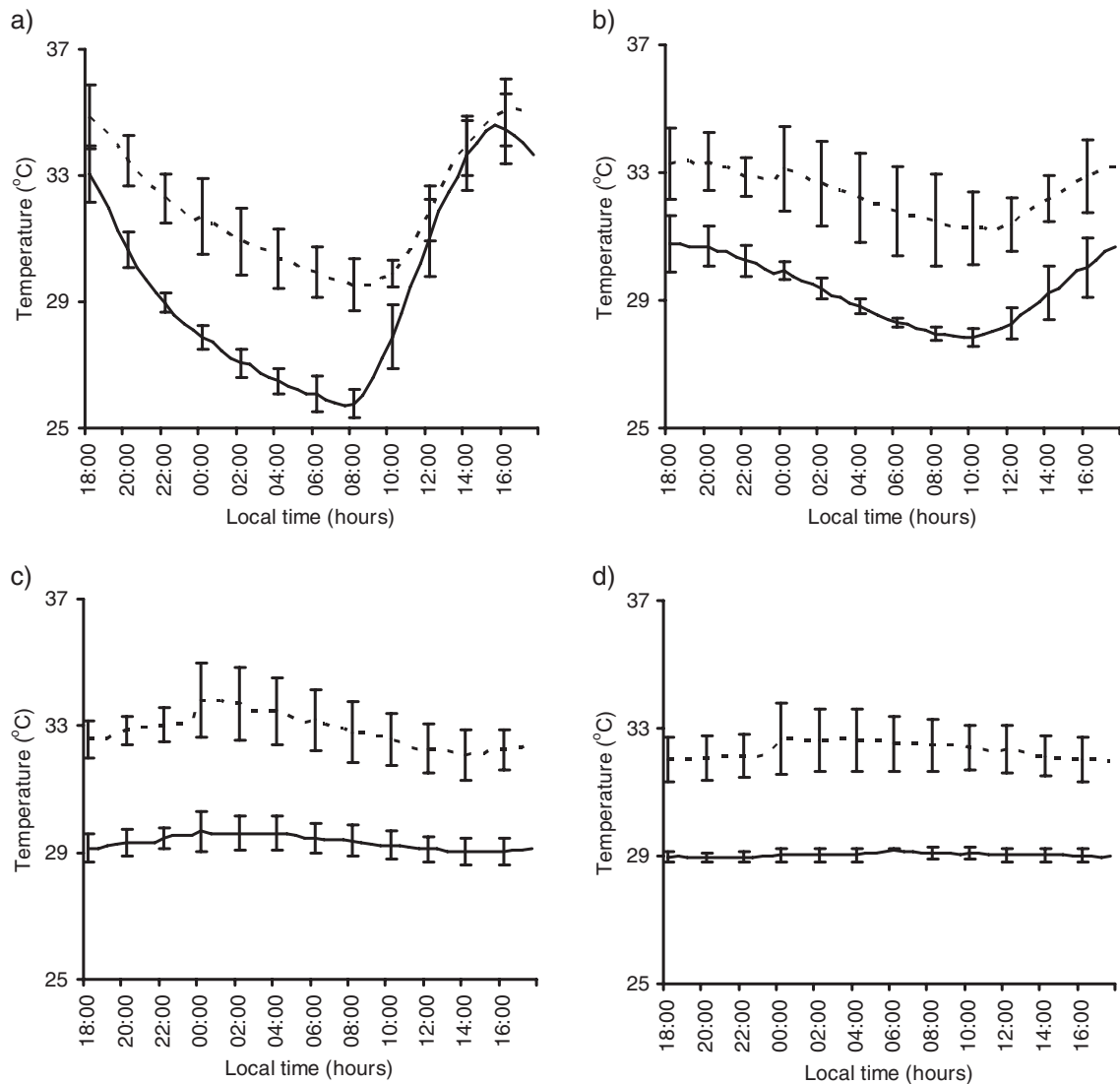


Fig. 2. Average temperatures recorded in each half-hour period during the seven days of monitoring for Long Beach (solid line) and North East Bay (broken line) at sand depths of a) 10 cm, b) 20 cm, c) 30 cm, d) 40 cm. Error bars are ± 1 SD and are shown for every fourth value.

would occur when the same putative cue was available on each beach. However, when the relative emergence at the different increments of coincidental temperature is visualised (Fig. 3) it can be seen that this is not the case. Although there is a sharp drop off in the number of hatchlings emerging when the temperature at 10 cm is greater than 30.5 °C on Long Beach (Fig. 3a), on North East Bay a significant amount of hatchlings emerged when the temperature was higher (Fig. 3b; (72% at >31, 48% at >32, 34% at >33, 10% >34), with hatchlings emerging when the sand at 10 cm measured as high as 36.5 °C. Given our evidence we reject the hypothesis that an upper thermal maximum is controlling the timing of hatchling

emergence on North East Bay but we consider it may possibly play a role on Long Beach. However, given the marked differences between the two sites in apparent response to higher temperatures, this seems unlikely.

Hypothesis 2. Within sand temperature gradients

Data regarding the range of temperature gradients present at each depth and the proportion of this range which was experienced during hatchling emergences are given in Table 1. Hatchlings emerged at times coincidental with a wide range of temperature gradients between 20 and 10 cm (Long Beach –3.3 °C to +2.3 °C; 62% of the thermal range; North East Bay: –3.1 °C

Table 1

The range of the proposed thermal mechanisms experienced at the different sand depths on the two study beaches

Possible cue	Overall range		Range during emergence	
	Long Beach	North East Bay	Long Beach	North East Bay
Absolute temperature (°C)				
10 cm	25.2–36.5	28.4–36.5	25.5–32.6 (62.8%)	28.8–35.7 (85.2%)
20 cm	27.4–32.2	29.6–35.7	28.1–32.2 (85.4%)	30.3–35.7 (88.5%)
30 cm	28.4–30.7	31.4–35.7	28.8–30.7 (82.6%)	32.2–35.7 (81.4%)
40 cm	28.8–29.2	31.4–34.9	28.8–29.2 (100%)	31.4–34.9 (100%)
Thermal gradient (°C)				
10–20 cm	–3.3–5.7	–3.1–3.1	–3.3–2.3 (62.2%)	–3.1–2.7 (93.5%)
20–30 cm	–2.1–2.6	–3.1–2.3	–1.7–2.6 (91.5%)	–3.1–1.9 (92.6%)
30–40 cm	–0.4–1.5	–0.8–3.5	–0.4–1.5 (100%)	–0.4–3.5 (100%)
Rate of temperature change (°C h ^{–1})				
10 cm	–1.6–2.4	–1.6–2.2	–1.6–0.0 (40.0%)	–1.6–0.0 (42.1%)
20 cm	–0.8–0.8	–0.8–0.8	–0.8–0.8 (100%)	–0.8–0.8 (100%)
30 cm	–0.8–0.8	–0.8–0.8	–0.8–0.8 (100%)	–0.8–0.8 (100%)
40 cm	–0.8–0.8	–0.8–0.8	–0.4–0.8 (75.0%)	–0.8–0.8 (100%)

The range of values experienced during hatchling emergence on the two study beaches are given with values in parentheses representing the proportion of the range (%) which these values represent.

to +2.7 °C, 94% of the thermal range). However, the proportion of hatchlings which emerged at times when the gradient between 20 and 10 cm was negative was 89% on Long Beach and 77% on North East Bay.

Hatchling emergence occurred irrespective of whether the thermal gradient was positive or negative (Fig. 4). Indeed, on Long Beach 15% of hatchlings emerged

during the presence of a positive gradient at 20–30 cm and 45% at 30–40 cm. On North East Bay 35% and 44% of emergence occurred when 20–30 and 30–40 cm gradients, respectively were positive. Given our evidence, for North East Bay we reject the hypothesis that as their primary cue, hatchlings continue to emerge as long as the negative temperature gradient is present in

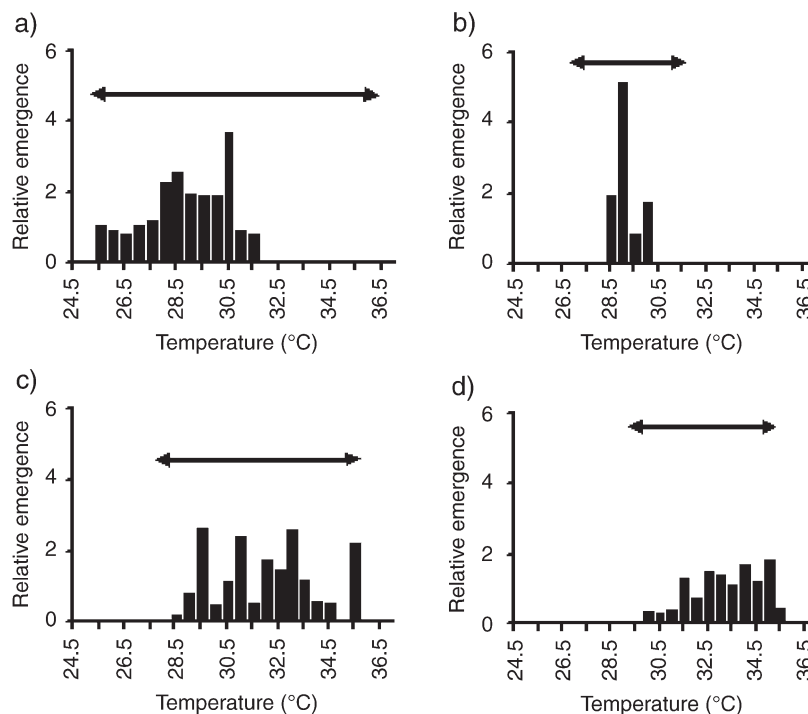


Fig. 3. Relative proportion of hatchling emergences according to the coincidental sand temperature recorded at sand depths of a) 10 cm and b) 20 cm on Long Beach and at c) 10 cm and d) 20 cm on North East Bay. The arrows indicate the full range of temperature experienced at these depths.

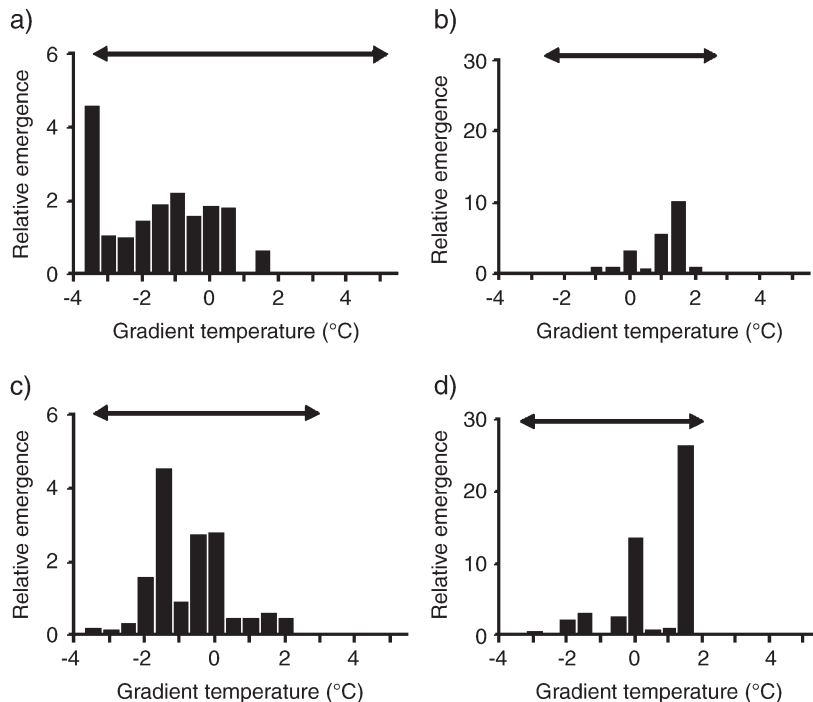


Fig. 4. Relative proportion of hatchling emergences according to the coincidental within-sand temperature gradients between a) 10–20 cm b) 20–30 cm on Long Beach and between c) 10–20 cm d) 20–30 cm on North East Bay. The arrows indicate the entire range of thermal gradients experienced at these depths.

the superficial sand layers but, given the data collected at Long Beach, this cue may play a role at this site. However, as with an upper critical threshold, the marked between-site differences render the likelihood of thermal gradient as the primary cue unlikely.

Hypothesis 3. Temperature change

Data regarding the range of temperature changes present at each depth and the proportion of this range which was experienced during hatchling emergences are given in Table 1. All hatchlings emerged onto Long Beach and North East Bay when the sand temperature at 10 cm on both beaches was stable or decreasing (Long Beach: 0 to $-1.6^{\circ}\text{C h}^{-1}$ and North East Bay: 0 to $-1.6^{\circ}\text{C h}^{-1}$). Remarkably these conditions constituted only 40–42.1% of the thermal range on both beaches. At depths greater than 10 cm, emergence of hatchlings predominantly occurred when the change in temperature was negative (Fig. 5). Indeed, at 20 cm on North East Bay all hatchlings emerged when there was a stable or negative change in temperature (Fig. 5c). Over 80% of hatchlings emerged when the change in temperature at greater depths was either stable or decreasing suggesting that there may be some influence of temperature at these depths on the timing of emergence.

No significant difference was observed in the rate of change of temperature at 10 cm between the two beaches (Mann–Whitney $W_{1,47}=2291.5$ $p>0.05$). Thus given the available evidence we cannot reject the hypothesis that change in temperature at shallow depths controls hatchling emergence. Indeed, our evidence is highly suggestive that an increase in sand temperature at superficial levels (in our case as measured at 10 and 20 cm) on both beaches inhibits hatchling emergence with the close concord of the data between sites increasing the plausibility of this being the primary mechanism controlling the emergence of green turtle hatchlings.

3.4. Frigatebird predation

The greatest number of frigatebirds counted offshore on both beaches occurred at 07:00 (Fig. 6). Numbers of birds offshore peaked at the same time, or soon after the onshore counts with birds moving offshore once hatchling emergence had ceased on the beach. During the middle of the day, numbers were low and variable. On North East Bay birds were seen to soar over the beach and were occasionally observed picking up hatchlings ($n=3$). A pronounced peak in offshore

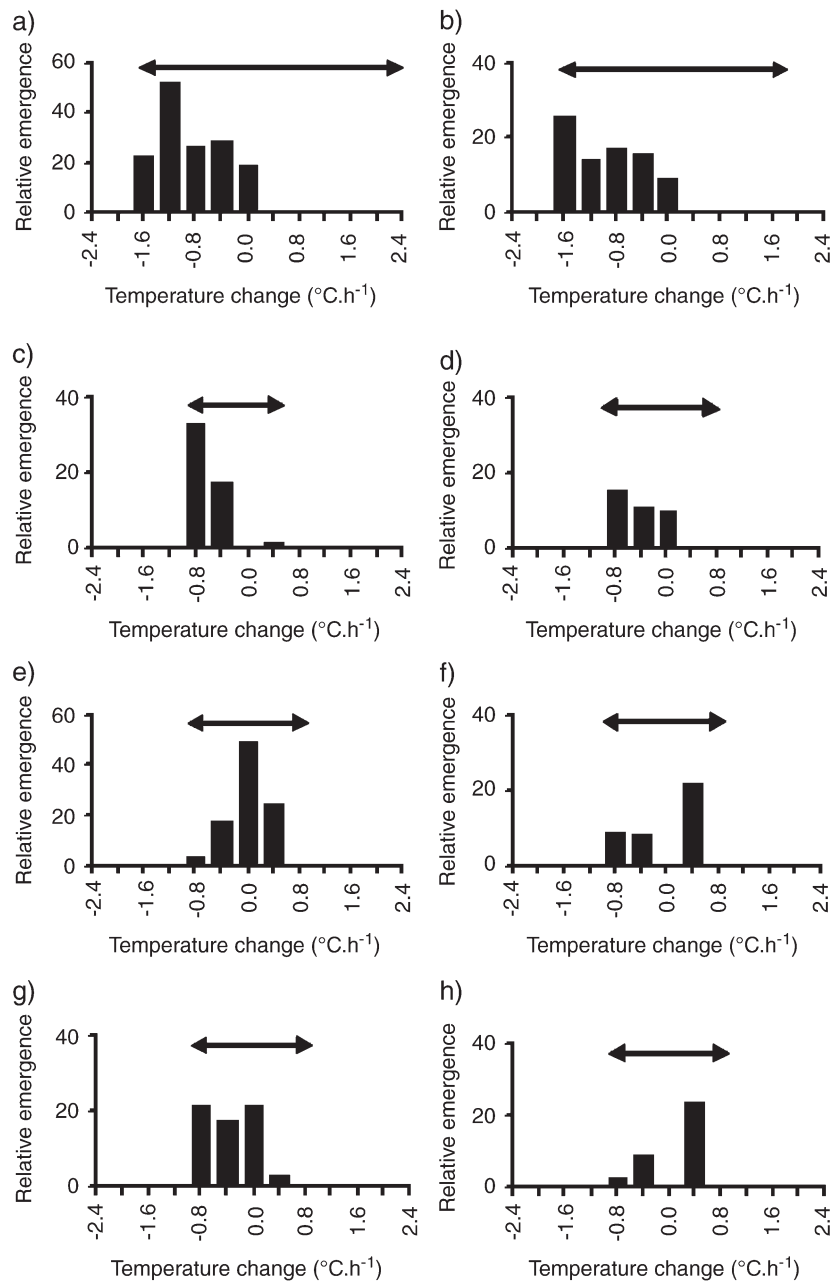


Fig. 5. Relative proportion of hatchling emergences according to the coincidental temperature change at a) 10 cm, c) 20 cm, e) 30 cm and g) 40 cm on Long Beach and at b) 10 cm, d) 20 cm, f) 30 cm and h) 40 cm on North East Bay. The arrows indicate the entire range of temperature change recorded at these depths.

frigatebird activity was observed at North East Bay in the mid-afternoon, which we attribute to this site being one where birds gain height from thermals en route to the roosting site on nearby Boatswain Bird Island. However, leading up to dusk, when small numbers of hatchlings start to emerge, there was a small peak of onshore activity on both beaches followed by one offshore, with birds moving offshore to pick up any

hatchlings which reached the surf. In summary, of those hatchlings emerging during the day, the vast majority if not all, are subject to predation.

4. Discussion

Since thermal variations within beaches are minimal at Ascension, temperature loggers were not placed in

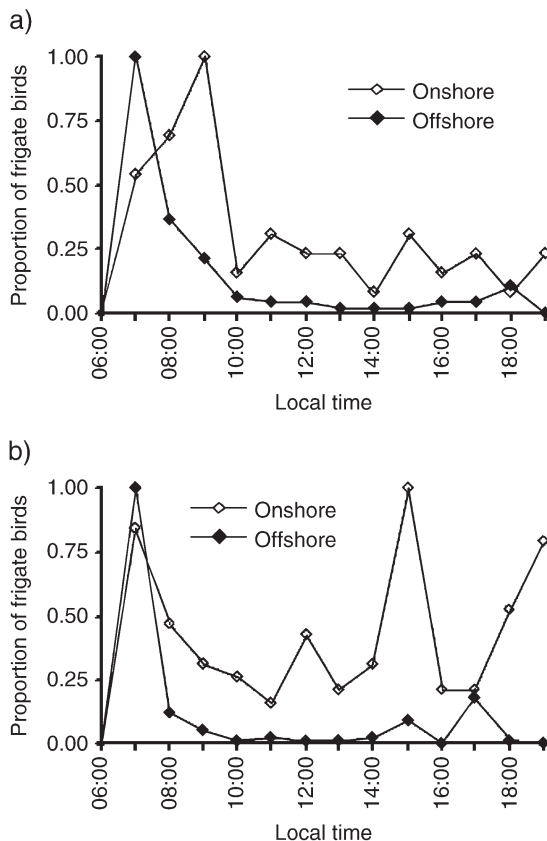


Fig. 6. The distribution of frigatebirds onshore (open circle) and offshore (closed circle) for a) Long Beach and b) North East Bay from the 9th April to 14th May 1999. Numbers shown are mean values for point counts in each hour which are scaled to the maximum number of frigatebirds recorded for each category at each site (Long Beach onshore: 13, offshore: 47; North East Bay onshore: 19, offshore: 74).

association within individual nests. Furthermore, the traps caught hatchlings from many nests, with this design implemented to increase the sample size of hatchlings and effectively provide an integration of the overall emergence patterns for a beach, i.e. our results (both thermal properties and emergence patterns) focussed on the level of the beach rather than the level of individual nests. The strength of our study lay in the fact that we compared emergence patterns of the same population from two beaches of markedly differing thermal regimes, with North East Bay being significantly warmer. Despite differences in temperature between the two beaches, it appears that the system of cues which has evolved does well to allow hatchlings maximum chance of survivorship by largely ensuring emergence occurs at night on both beaches.

Frigatebirds over Long Beach and North East Bay were present throughout daylight hours but peaked just after sunrise and prior to sunset, when the chances of

detecting hatchlings were increased. As soon as hatchlings emerged, they were predated by any opportunistic frigatebirds over the beach. Although we may have slightly underestimated the number of daytime hatchling emergences, the fact that few predation events were recorded during frigatebird counts suggest that the number of daytime emerging hatchlings is very small. This is not surprising given the consequences of emerging at the wrong time are likely to be fatal. We suggest that there will have been profound adaptive value in the evolution of mechanisms to ensure nocturnal hatchling emergence.

Emergence of hatchlings on North East Bay were observed to occur above all previously proposed thermal limits for the green turtle i.e. above 28.5 °C (Mrosovsky, 1968), 31 °C (Bustard, 1967) and 33 °C (Hendrickson, 1958). Uncoordinated movements of the black turtle (*Chelonia mydas agassizi*) have been observed above a thermal limit of 33.4 °C (Drake and Spotila, 2002), although experiments in this study were limited to hatchlings from one nest. Black turtle hatchlings were found to emerge when the sand temperature was decreasing, but as this coincided with a drop in sand temperature below 33.4 °C, Drake and Spotila (2002) erred away from considering only rate of temperature change as that being the primary cue controlling emergence. On Long Beach however, emergence did not occur above 32.6 °C at 10cm, a value similar to that observed by Moran et al. (1999) when comparing the emergence patterns of loggerhead turtles (*Caretta caretta*). Moran et al. (1999) dismissed the rate of temperature change as a mechanism controlling the first emergence from a nest, rejecting this hypothesis on the grounds of cooling being a positive cue, not from the perspective of increasing temperature acting as an inhibitory factor. Direct comparisons of our study with this work should be made tentatively due to species and data collection differences.

It has been established that incubation temperatures at North East Bay are higher than at Long Beach (Broderick et al., 2001; Godley et al., 2002b), whether this may lead to the ability of hatchlings to tolerate higher temperatures during emergence at North East Bay is unknown. Nevertheless, geographical variation in thermal tolerance within some lizards has been shown (Ulmasov et al., 1992), where a positive correlation exists between the range of stress temperature and the average temperature of a niche inhabited. Apparent differences in the upper thermal maxima of green turtle hatchling emergence between the two beaches monitored within this study, could be indicative of variation in the temperature at which heat shock proteins are

expressed within marine turtles. Therefore, although it appears unlikely that hatchlings are responding to absolute temperature alone as the primary cue controlling emergence, we cannot refute some role of a thermal inhibitory effect working in synergy with other cues. However, if as a result of a combination of sand albedo, seasonal or latitudinal variation, a putative upper thermal limit was not reached during daylight hours, emergence would not be confined to night time alone. Therefore, this would not appear a sufficiently robust mechanism upon which to base a behavioural repertoire with such profound fitness consequences.

Our results gave little support to the hypothesis that a negative thermal gradient is the primary cue controlling emergence as per Gyuris (1993). Although high proportions of hatchlings emerged during the presence of a negative thermal gradient at 10–20 cm on both beaches, significant numbers of hatchlings were found to emerge when the within-sand temperature gradient was positive. However, the temporal distribution of emergence observed by Gyuris (1993) of green hatchlings in Australia shows a similar pattern to those observed in this study, with the peak of emergence occurring between 20:00 and 21:00, tailing off during later hours. Gyuris (1993) did not however, discuss the possibility of temperature change controlling emergence patterns, but did refute the presence of an upper thermal limit controlling hatchling emergence at her study site. Moran et al. (1999) stated that most hatchlings emerged when negative gradients were present in the sand column but suggested that a positive reaction to negative gradients may act in conjunction with the primary threshold mechanism.

Witherington et al. (1990) suggested that loggerhead turtle hatchlings appeared to emerge when the sand was cooling. This was further investigated and supported by Hays et al. (1992). On both North East Bay and Long Beach hatchling emergence was restricted to times when the sand at 10 cm was either stable or cooling. It is most relevant that no significant difference in the temporal pattern of temperature change was observed between the two beaches, which given the fact that the pattern of hatchling emergence is the same on both beaches suggests change in temperature at shallower sand depths is the most likely mechanism controlling the pattern of emergence. Our data are most strongly supportive of increasing temperature in the near surface sand inhibiting hatchling emergence behaviour.

Given that hatchlings are not likely to have a perception of depth, we propose that they are likely to continue to dig through the sand column until they are inhibited by some negative cue. At clutch depths there is

no diel thermal signal (Broderick et al., 2001), we would therefore not expect any diel bias in the timing of the start of emergence behaviour, which is thought to have a duration of the order of four days (Christens, 1990; Godfrey and Mrosovsky, 1997). Thus, in the absence of inhibitory cues we would expect on average that 2.1% of hatchlings would emerge in each half-hour period. Our data and those of others (Witherington et al., 1990; Gyuris, 1993) clearly show that this is not the case. If increasing temperature inhibits hatchling emergence between the hours of 08:00–16:00 on Long Beach and 09:00–17:00 on North East Bay, some 33.6% ($16 \times 2.1\%$) of hatchlings would be in the superficial layers of the sand column awaiting emergence each evening. If all of these hatchlings were to emerge immediately as the sand temperature stopped increasing we would expect a pronounced peak of emergence accounting for >35% of hatchlings at this time. Although a pronounced peak in emergence occurs in the early part of the evening and this largely accounts for this proportion of hatchlings, the peak is much more temporally spread than would be expected. The dampening of this peak may be the result of hatchlings emerging from a variety of waiting depths, and/or between individual and between group variation in delay in the alleviation of the inhibition and the translation into active emergence behaviour. At depths greater than 10 cm, temperature increase may also exert an inhibitory effect on emergence. We cannot be sure of the rate in perception of temperature change of hatchlings, nor their rate of movement through the sand column so we cannot estimate the temporal lag in order to fully appraise the role of temperature change at increased depth.

We do not discount the role of other secondary mechanisms as contributing to the observed pattern of hatchling emergence. In the periods immediately before dusk and after dawn the sand temperatures at 10 cm on both beaches were cooling, and because no inhibitory thermal factor was present, some hatchlings emerged. However, we feel that in some cases, light may also have an inhibitory effect. On reaching the sand surface during daylight hours some hatchlings stop moving, accounting for the observations in this study and those of Bustard (1967) and Glen et al. (2005), of hatchlings waiting at the sand surface, their head slightly protruding. However, if siblings not exposed to the light are moving up through the sand column, those hatchlings waiting at the sand surface may be pushed out, suffering a high risk of mortality from diurnal predators and high sand surface temperatures. This may account for both the apparent inadequacy of this cue and for some of the previous observations of daytime emergence (Bustard, 1967;

Table 2

The presence or absence of certain factors during each temperature hypothesis

Factor	Hypothesis 1	Hypothesis 2	Hypothesis 3
	Absolute temperature	Thermal gradient	Rate of temperature change
Hatchling ability to detect without moving	Yes	No	Yes
Correspondence to night time	Yes	No	Yes
Across beach mechanism	No	Yes	Yes

Balazs, 1974; Drake and Spotila, 2002; Glen et al., 2005).

Theoretical considerations add weight to our findings that temperature change will control the temporal pattern of hatchling emergence. Heating of the sand will always occur during the day, a factor not likely to be affected by seasonal change or inter-annual variation in temperatures. In addition, although nesting green females do show a certain degree of nest site fidelity, an individual female may vary the beach on which she lays different clutches (Mortimer, 1988; Miller, 1996). Consequently, the thermal environment of the sand above different nests of the same female may change according to variation in sand albedo and thus temperature (Hays et al., 2001). By using the change in sand temperature rather than an absolute temperature cue, hatchlings would still be able to emerge during optimum conditions i.e. at night regardless of the date of hatching or nest location.

In conclusion, ideally hatchlings need to detect a cue while stationary, especially those waiting at the sand surface. Any potential cue should work across different nesting beaches, and the cue should indicate night time. As can be seen in Table 2, only rate of temperature change satisfies all these criteria.

By using a quasi-experimental approach we have collected data that strongly suggest that the heating of subsurface sand is likely to be the primary signal inhibiting hatchling emergence at Ascension Island. This is the cue which is likely to yield similar results i.e. nocturnal emergence, regardless of sand albedo, seasonality or latitude as long as nights are relatively cooler than day. Future controlled laboratory studies of the effect of thermal variation on hatchling activity would be illuminating. Considering future field studies, potential improvements might expand the range of depths at which temperature is measured, including depths shallower than 10 cm where our results suggest that

diel patterns will be most pronounced. In addition, future studies would benefit from being able to record the speed and depth of hatchlings, although this will require new methodologies to be developed.

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