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Temperature variation within and between nests of the green sea turtle, *Chelonia mydas* (Chelonia:Cheloniidae) on Heron Island, Great Barrier Reef

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Abstract

Four temperature data-loggers were placed in each of five green sea turtle nests on Heron Island in the 1998–99 nesting season. Temperatures in all nests increased as incubation progressed due to general sand heating and increased metabolic heat production of the developing embryos. Even at the top of nests no daily diurnal fluctuation in temperature was evident. The temperature of eggs in the middle of the nest increased above those in the nest periphery during the last third of incubation. However, this metabolic nest heating would have little effect on hatchling sex ratio because it occurred after the sex-determining period. Small differences in temperature between regions of a nest persisted throughout incubation and may be important in ensuring the production of at least some individuals of the opposite sex in nests that have temperatures close to either the all-male or all-female determining temperatures. Location and degree of shading of nests had little effect on mean nest temperature, but deeper nests were generally cooler and therefore were predicted to produce a higher proportion of males than were shallower nests. Nest temperature profile data indicated that the 1998–99 nesting season on Heron Island would have produced a strongly female-biased sex ratio amongst hatchlings.

Introduction

Green sea turtles (*Chelonia mydas*), like all other sea turtles, have their sex determined by nest temperature during embryonic development (Miller and Limpus 1981; Spotila *et al.* 1987). Hence, females have the potential to manipulate the sex ratio of hatchlings emerging from their nests by choosing the thermal environment of their nest. Factors influencing nest temperatures include geographic location, beach orientation, nesting time within the nesting season, sand type and colour, and the degree of shade the nest experiences during incubation (Limpus *et al.* 1983; Spotila *et al.* 1987). Whether or not female sea turtles actively select a particular thermal environment is still the subject of speculation (Stoneburner and Richardson 1981), but some nesting females are known to swap nesting islands within a single night (Limpus *et al.* 1984) so this indicates at least the possibility of choosing thermally different beaches. From a species management point of view, knowing the thermal environment of nests is important. Managers must ensure that sufficient numbers of nests that produce hatchlings of both sexes are maintained in order to ensure recruitment of both sexes into the adult breeding population.

A few studies have documented nest temperatures of green sea turtles (Bustard 1972; Limpus *et al.* 1983; Spotila *et al.* 1987) but no studies have investigated the possible role of regional temperature differences within a nest on hatchling sex ratios. Green sea turtles construct quite deep nests (20–90 cm) on Heron Island and the bottom of the nests are about 30 cm deeper than the top (Limpus *et al.* 1984). This difference in depth of nests may cause differences in temperature between the top and bottom of nests. Also, because of the relatively large size of eggs (35–55 g: Limpus *et al.* 1984) and large clutch size (42–195: Limpus *et al.* 1984), the metabolic heat generated by embryos late in incubation is likely to increase egg temperature above that of the surrounding sand (Bustard 1972; Spotila *et al.*

1987; Mrosovsky 1994). If a thermal gradient is set up between the nest of eggs and the surrounding sand, then eggs in the middle of the nest will be significantly warmer than eggs at the nest's periphery. In this study we monitored the temperature at four locations within individual nests throughout incubation to determine whether significant thermal differences exist within a nest, and to see if egg location within the nest was likely to be a significant factor in determining its hatchling's sex.

Materials and Methods

This study was conducted on Heron Island (23°26′S, 151°55′E) within the Capricorn group of islands, southern Great Barrier Reef (GBR). The Capricorn group of islands is the largest *C. mydas* rookery in the southern GBR (Limpus *et al.* 1984; Limpus 1996). Although Heron Island is not the largest rookery within this group (Limpus *et al.* 1984; Limpus 1996), it is the most easily accessed, and consequently the nesting population at Heron Island has been intensively studied (Limpus *et al.* 1983, 1984; Limpus 1996). The island is roughly rectangular in shape with the long sides facing north and south (Fig. 1). Turtles emerge from the sea and nest on the north-, south- and east-facing beaches, but the west-facing beach consists of a harbour and helipad and turtles cannot nest there. Five nests were monitored, three from the east side, one from the north side and one from the south side of the island (Fig. 1). Nests 1 and 2 were monitored from 01:00 hours on 22 November 1998, Nests 3 and 4 from 01:00 hours on 23 November 1998 and Nest 5 from 01:00 hours on 24 November 1998. All nests were constructed during the peak laying period for *C. mydas* on Heron Island (Limpus *et al.* 1984). Four temperature data-loggers (Tinytag miniature temperature data-oggers; 45 mm diameter × 65 mm length) set to log temperature every 30 min throughout incubation were placed in each nest during the egg-laying process. The first data-logger was placed at the bottom (bottom) of the nest after 5 eggs had been laid. The second was placed in the middle (middle) of the nest when 40 eggs had been laid. The third was placed in the nest at the same time as the second, but at the periphery of the nest (side). The fourth was placed amongst the top eggs (top) when oviposition had finished and the female had begun to back-fill the chamber with sand. During oviposition of each clutch, a sample of 10 eggs was taken and the diameter of each was measured with callipers to obtain an estimate of egg size. Once measured, these eggs were returned to the nest before the female back-filled the nest. Monitored nests contained 69–118 eggs. As each female back-filled the nest her curved carapace length was measured as an indication of her size. The position of each nest was recorded so that data-loggers could be recovered after the eggs had hatched in late January 1999. When the nests were excavated the depth from the sand surface to the bottom of the nest was measured.
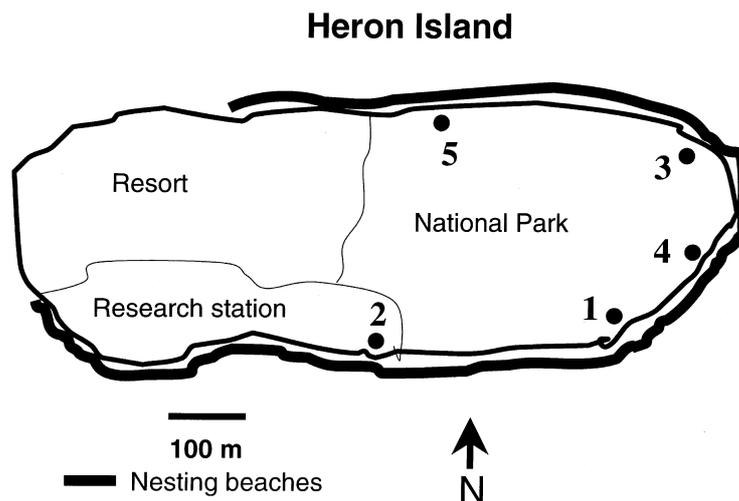
Heron Island

Fig. 1.   Map of the Heron Island study site indicating location of nesting beaches and monitored nest sites.

The nest sites were visited over a 6-day period (25–30 November 1999) to estimate the amount of shade falling on the sand surface above nests. Nests were visited at 09:00–10:00, 12:00–13:00 and 15:00–16:00 hours to note whether the nests were shaded or exposed to the sun.

Maximum daily air temperature and rainfall data were collected from a weather station located at the Heron Island Research Station.

In turtle species that have temperature-dependent sex determination, sex is determined by egg temperature during the middle third of incubation (Yntema 1979; Bull and Vogt 1981; Pieau and Dorizzi 1981; Yntema and Mrosovsky 1982; Standora and Spotila 1985; Spotila *et al.* 1987; Gutzke and Chymiy 1988). For this reason, nest temperature analysis was divided into three periods: first third, second third (sex-determining period) and final third of incubation. Friedman repeated-measures analysis of variance on ranks followed by a Dunnett's multiple-comparison procedure were used to compare within-nest temperatures to each other for each of these periods. Time of hatchling emergence from the nest was estimated by a relatively rapid fall in nest temperature (4–5°C over two days) in late January. Hatching was deemed to have occurred 3 days before nest emergence as hatchlings remain in the nest for approximately 3–5 days before emerging from the nest (Balazs and Ross 1974). Estimates of the sex ratios of hatchlings emerging from nests were calculated from temperatures during the sex-determining period. We assumed that all hatchlings were male at temperatures less than or equal to 26°C, all hatchlings were female at temperatures greater than or equal to 29°C and that the proportion of females increased linearly between 26°C and 29°C (Miller and Limpus 1981). We also assumed that one quarter of each clutch experienced the temperatures associated with each of the four regions of the nest in which temperature was monitored.

Pearson product-moment correlation and least-squares regression were used to explore possible relationships between different variables. Statistical significance was assumed if $P < 0.05$. The statistical programs 'Sigma Stat' and 'Statistica' were used for statistical calculations.

Results

The sand on Heron Island consists of course white calcareous grains derived from coral rubble. The tops of the nests were deep enough to preclude any distinctive daily diurnal pattern of temperature fluctuation (Fig. 2). For this reason an arithmetic mean daily
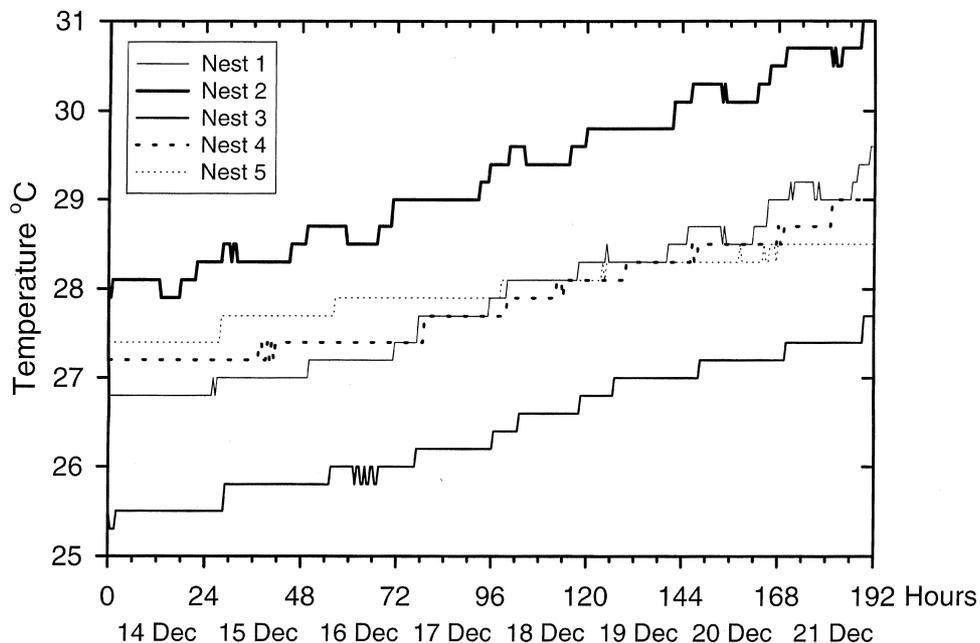

Fig. 2. A week's sample of the top nest temperatures of all 5 monitored nest during mid-December 1998. Note the absence of distinct diurnal cyclic fluctuations in temperature.
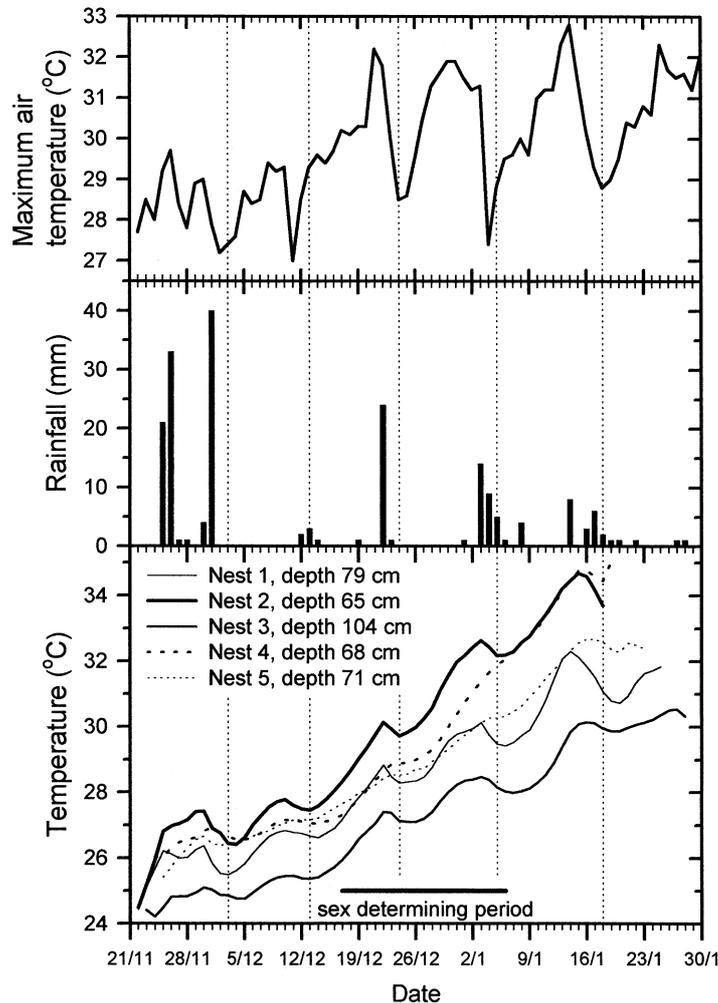
Fig. 3. Mean nest temperatures, maximum daily air temperature and rainfall during the monitored period. Vertical dotted lines indicate synchronous falls in nest temperature of Nests 1–3.

temperature was calculated for each position in the nest by averaging the 30-min readings over each 24-h period (00:00–23:30 hours). A mean daily temperature was also calculated for each nest by averaging the values from the four positions in the nest. There was a trend for mean nest temperature of all nests to increase from 24–25°C to 30–34°C as incubation proceeded (Fig. 3, Table 1). Nests 2 and 4 experienced the warmest temperatures while Nest 3 was the coolest (Fig. 3, Table 1). Nests 1–3 experienced simultaneous falls in mean nest temperature 1–2 days after steep drops in maximum daily ambient air temperature were recorded (Fig. 3). The sharp drops in maximum ambient temperature were usually associated with rainfall (Fig. 3). Examples of within-nest regional differences in temperature are illustrated in Fig. 4. In all nests, there were small but significant differences in temperature between regions within the nest over the last third of incubation, and the same was true for most regional comparisons for the first two-thirds of incubation (Table

Table 1.   Mean temperatures (°C ± s.e.) within different regions of 5 natural *C. mydas* nests and over different stages of incubation and predicted sex ratio of hatchlings at Heron Island during the 1998–99 nesting season

An asterisk denotes regional temperatures within a nest that were not significantly different

Region	Nest 1	Nest 2	Nest 3	Nest 4	Nest 5
First third of incubation					
Entire nest	26.1	26.8	25.0	26.7	26.6
Bottom	25.9* ± 0.1	26.5 ± 0.2	24.9* ± 0.1	26.4 ± 0.1	26.5 ± 0.1
Middle	26.1 ± 0.1	26.7* ± 0.2	25.0 ± 0.1	26.7 ± 0.1	26.6* ± 0.1
Side	26.0* ± 0.1	26.8* ± 0.2	24.9* ± 0.1	26.4 ± 0.1	26.6* ± 0.1
Top	26.3 ± 0.2	27.2 ± 0.2	25.0* ± 0.1	26.9 ± 0.1	26.6* ± 0.1
Sex-determining period					
Entire nest	28.5	29.1	27.2	28.4	28.4
Bottom	28.0 ± 0.2	28.5 ± 0.2	27.0 ± 0.2	28.0 ± 0.2	28.1 ± 0.2
Middle	28.6 ± 0.3	29.1* ± 0.3	27.3 ± 0.2	28.5* ± 0.2	28.6* ± 0.2
Side	28.4 ± 0.2	29.1* ± 0.3	27.1 ± 0.2	28.5* ± 0.2	28.4 ± 0.2
Top	28.8 ± 0.3	29.7 ± 0.3	27.3 ± 0.2	28.7 ± 0.2	28.6* ± 0.1
Last third of incubation					
Entire nest	31.0	33.0	29.4	32.9	31.4
Bottom	30.5 ± 0.2	32.4 ± 0.2	29.7 ± 0.2	32.3 ± 0.3	31.6 ± 0.3
Middle	31.4 ± 0.2	33.5 ± 0.2	29.9 ± 0.2	33.3 ± 0.4	32.4 ± 0.3
Side	30.7* ± 0.2	32.9 ± 0.2	29.1 ± 0.2	33.1 ± 0.3	31.4* ± 0.2
Top	31.2 ± 0.3	33.3 ± 0.2	28.8 ± 0.2	32.9 ± 0.3	30.3 ± 0.1
Entire incubation					
Entire nest	28.4	29.7	27.2	29.2	28.8
Bottom	28.1 ± 0.3	29.1 ± 0.4	27.2 ± 0.3	28.8 ± 0.4	28.7 ± 0.3
Middle	28.6 ± 0.3	29.8 ± 0.4	27.4 ± 0.3	29.4 ± 0.4	29.2 ± 0.3
Side	28.3 ± 0.3	29.6 ± 0.4	27.1 ± 0.2	29.3 ± 0.4	28.8 ± 0.3
Top	28.7 ± 0.3	30.1 ± 0.4	27.1 ± 0.2	29.4 ± 0.4	28.5 ± 0.2
Predicted % female	82	96	39	81	81

1). With the exception of Nests 3 and 5, bottom temperature was coolest and the top temperature warmest throughout incubation (Table 1). In Nests 3 and 5 the middle temperature was warmest during the last third of incubation (Table 1). For the first half of incubation there was no apparent difference between the middle and side temperatures, but from midway onwards the middle temperature gradually became warmer than the side temperature, the difference being greatest just before hatchlings emerged from the nest (Fig. 5). After hatchling emergence the difference again fell to zero (Fig. 5).

Nest characteristics are given in Table 2. Nest 3 was the only nest that was not shaded for some time during the day (Table 3). All nests were exposed to the sun during the middle of the day, when solar radiation was the most intense (Table 3). A 'sun index' was constructed in which 'exposed' was given a value of 1 and 'shaded' a value of 0. Thus, a nest exposed to sun all day would score 3 while a nest in shade all day would score 0. There was a significant negative relationship between the sun index and the mean nest temperature throughout the entire incubation (Fig. 6). Nest depth was negatively correlated with mean nest temperature (Fig. 7) and time to emergence negatively correlated with nest temperature (Fig. 8). The difference between middle and side nest temperatures over the last week of incubation was positively correlated with estimated clutch mass (Fig. 9). Stepwise multiple regression analysis with mean nest temperature throughout incubation as the dependent variable and nest depth, clutch size and sun index as independent variables
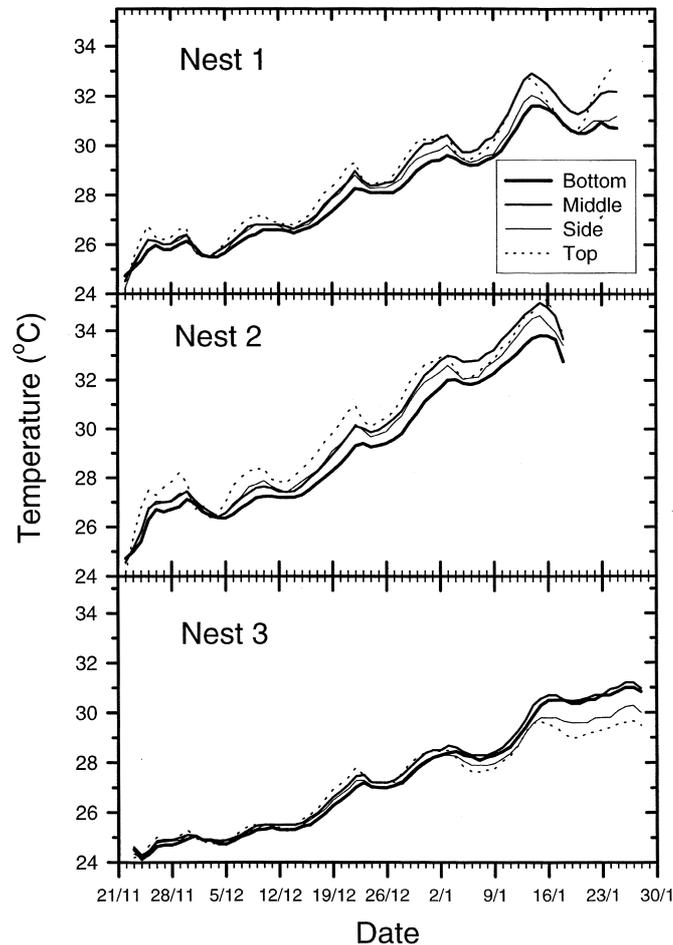
Fig. 4. Bottom, middle, side and top nest temperatures of Nests 1–3 throughout incubation.

indicated that nest depth was a significant factor ($P = 0.016$), but clutch mass ($P = 0.99$) and sun index ($P = 0.802$) were insignificant factors in the regression. There was no correlation between female size and nest depth ($R^2 = 0.36$, $P = 0.109$).

Discussion

Nest temperature

C. mydas nests are deep enough to avoid the daily cyclic fluctuations of nest temperature typical of shallower turtle nests (Booth 1998). However, incubating *C. mydas* eggs on Heron Island do experience changes in temperature as incubation proceeds. The increase in nest temperature during incubation in the current study was due to two phenomena: (1) a general increase in sand temperature due to seasonal heating by the sun, and (2) an increase in heat production by the embryos as they grew in size during incubation.

Temperature in Nests 2, 4 and 5 fell to 30°C five days after hatchling emergence, indicating that general sand temperature at nest depth had risen by approximately 6°C (24–

Table 2.   Parameters for the five sampled green sea turtle nests from Hero Island

Initial egg mass was estimated from egg diameter using a conversion factor of 1.0649 gram per millimetre diameter based on green sea turtle egg diameter and mass data in Limpus *et al.* (1984). Estimated clutch mass was calculated by multiplying estimated egg mass by clutch size. See text for explanation of sun index. 'Temperature difference' is defined as (middle nest temperature) – (side nest temperature)

Parameter	Nest 1	Nest 2	Nest 3	Nest 4	Nest 5
Curved carapace length of female (cm)	103	106	101	121	122
Nest depth (cm)	79	65	104	68	71
Clutch size	84	71	97	69	118
Egg diameter (mm)	46.1	44.9	46.8	45.5	46.9
Estimated egg mass (g)	49.1	47.8	49.8	48.6	49.9
Estimated clutch mass (g)	4124	3394	4540	3140	5534
Time to nest emergence (days)	64	57	66	57	60
Temperature difference over last week of incubation (°C)	0.9	0.6	1.0	0.3	1.4
Sun index	2	1	3	2	2

Table 3.   The occurrence of shade falling on the five natural nests studied on Heron Island during the period 25–30 November 1999

Nest	9:00–10:00 hours	12:00–13:00 hours	15:00–16:00 hours
1	exposed	exposed	shaded
2	shaded	exposed	shaded
3	exposed	exposed	exposed
4	shaded	exposed	shaded
5	shaded	exposed	shaded

30°C) during the course of incubation. Because the generally warm weather persisted until the end of February, it is likely that general sand temperatures would have continued to increase well into February. The fact that the bottom of the nest was generally the coolest during the monitored period supports the hypothesis that general sand heating was due to heat derived from solar-heated surface sand. The drop in general nest temperatures in Nests 1–3 associated with rain and decreased maximum daily temperatures also indicates that general sand heating was due to solar heating. Sharp drops in sand temperature associated with inclement weather have previously been reported (Limpus *et al.* 1983; Spotila *et al.* 1987). Sand temperature at 50 cm depth also increased during the latter stages of the 1980–81 nesting season on Heron Island from 25°C to 29–30°C (Limpus *et al.* 1983). However, in the 1980–81 study, the increase in sand temperature did not start until mid-January and did not reach a maximum until mid-to-late February and sand temperatures on the south side of the island were consistently 1–2°C cooler than on the north side of the island. In the current study nests on north-facing beaches (3 and 5) were no warmer than nests on the south-facing beaches (1 and 2); indeed the coolest nest (3) had a north-facing aspect. Clearly, yearly differences in weather patterns during the nesting season can have marked effects on general sand temperatures at nest depth, and this has important consequences for the sex ratio of hatchlings for any particular year (see below). In contrast, sand temperatures in the green sea turtle rookery at Tortuguero, Costa Rica remained relatively constant throughout the nesting season in 1980 (Spotila *et al.* 1987).
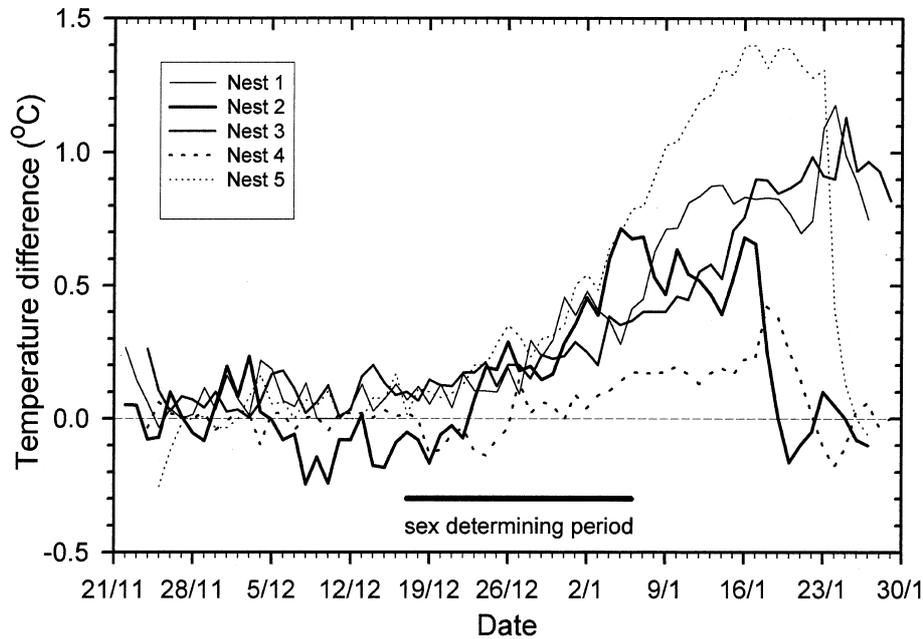
Fig. 5. Plots of difference between middle nest temperature and side nest temperature of the 5 monitored nests throughout the incubation period.

Unexpectedly, there was a negative relationship between the amount of sun exposure and mean nest temperature (Fig. 6). Logically, one expects nests that experience greater exposure to sun to be warmer (Limpus *et al.* 1984; Spotila *et al.* 1987; Booth 1998). Confounding effects such as the fact that all nests were exposed to the sun in the middle of the day when the heating effect is greatest, and differences in the intensity of shading produced by vegetation, clutch size and nest depth probably resulted in this unexpected result. Indeed, the stepwise multiple regression analysis indicated that nest depth was the only significant factor influencing nest temperature.

Mean nest temperature was strongly correlated with nest depth, deeper nests being cooler than shallow nests (Fig. 7). This phenomenon is a result of the general sand warming that occurred during the monitored period. The nesting season begins in October and ends in March with a peak in mid-November–December (Limpus *et al.* 1983, 1984). Before the nesting season begins the sand is quite cool (<24°C) at the nest depths (Limpus *et al.* 1983). However, as nesting begins the surface sand is warmed by increasing intensity of solar irradiation and increasing air temperatures. This heat is then conducted down through the sand. Thus, a temperature gradient is set up, with warm sand at the surface and the sand becoming progressively cooler at greater depths. At the end of summer, when ambient temperatures become cooler, this gradient is reversed, i.e. the deeper sand is warmer than the surface sand. If nesting persists into this time, then deeper nests will experience warmer temperatures than shallow nests. The finding that nest temperature varies significantly with nest depth is very important, particularly from a management point of view. Past studies that have monitored beach sand temperatures throughout sea turtle nesting seasons have monitored temperatures from only a single depth (usually 50 cm, e.g. Limpus *et al.* 1983; Spotila *et al.* 1987) and made predictions of hatchling sex ratios entirely from temperatures at this level.
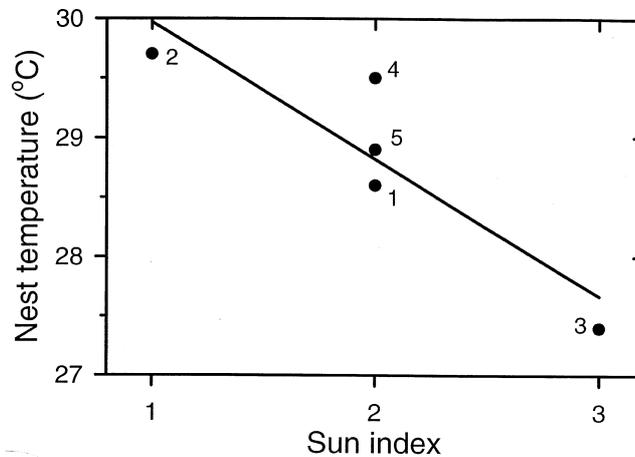
Fig. 6. Plot of mean nest temperature throughout incubation against the sun index. Least-squares linear regression: $y = 31.12 - 1.15x$; $R^2 = 0.80$, $P < 0.001$.

The heating of nests above surrounding sand temperatures due to the metabolic heat production of embryos becomes noticeable about two-thirds of the way through incubation as embryos begin the rapid growth phase of embryonic development (Fig. 5). Metabolic heating raised nest temperature some 3–5°C above surrounding sand temperature by the end of incubation, but had little influence on the sex-determining process because the sex-determining period had all but finished by the time metabolic heating of the nest became significant. The temperature difference between the middle and periphery of a clutch of eggs should be a function of the clutches's heat production. The total amount of metabolic heat produced by a clutch will depend on the biomass of embryos within the clutch and this is a function of the egg size and number of eggs in the clutch. Hence the strong correlation between clutch mass and middle-to-side temperature difference (Fig. 9) is expected.

Within a nest there were consistent regional differences in temperature. During the first two-thirds of incubation the bottom temperature was the coolest and the top temperature the warmest in all nests and this can be explained by the thermal gradient in the sand due to surface sand heating. During the last third of incubation the top temperature continued to be warmest in Nests 1, 2 and 4 (although middle nest temperatures were very close to top nest temperatures), while in Nests 3 and 5 (which had the largest clutch masses) mid-nest temperature was the warmest. Greater metabolic heating due to larger clutch mass may explain the higher mid-nest temperatures in these two cases. The mean maximum difference between regions within a nest was 0.4°C for the first third, 0.5°C for the second third, and 1.0°C for the last third of incubation. Metabolic heat production is probably responsible for the increase in the difference between regional nest temperatures during the last third of incubation. Overall, regional differences throughout incubation varied from 0.3°C in Nest 3 to 1.0°C in Nest 2. Differences in temperature have the potential to influence incubation time, with embryos experiencing cooler temperatures taking longer to hatch (Miller and Limpus 1981; Ackerman 1997) and thus asynchronous hatching may occur within a nest, which is undesirable. Synchronous emergence of hatchlings from a nest has two potential advantages: the work of digging out of the nest can be shared amongst all hatchlings and thus be an energy-saving device (Carr and Hirth 1961), and secondary
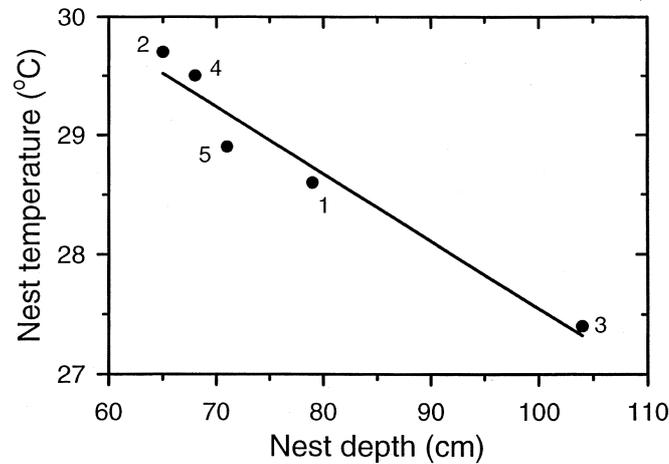
Fig. 7. Plot of mean nest temperature throughout incubation against nest depth. Least-squares linear regression: $y = 33.18 - 0.056x$; $R^2 = 0.95$, $P < 0.001$.

'predator swapping' may reduce the chance of being eaten by a predator while making the trip from the nest to the water. However, despite these differences in temperature within a nest, sea turtle hatchlings are well known to emerge from the nest synchronously (Carr and Hirth 1961; Balazs and Ross 1974). Two possible mechanisms may ensure that synchronous nest emergence occurs despite regional differences in nest temperature. Firstly, the movement within the nest of the first hatched hatchlings may trigger the premature hatching of the slower-developing embryos. Secondly, hatching typically spend 3–5 days in the nest before breaking the nest surface (Balazs and Ross 1974) and this allows some 'catch-up time' for slower-developing embryos.

Incubation period was negatively related to nest temperature (Fig. 8), as has been previuosly noted (Miller and Limpus 1981; Ackerman 1997). An increase in temperature speeds up physiological processes, including growth (Schmidt-Nielsen 1997), so a decrease in incubation period with an increase in nest temperature is expected.

Hatchling sex ratio

The relatively small differences in regional temperature within a nest during the sex-determining period resulted in up to a 30% difference in the predicted hatchling sex ratio from different regions of the nest. Such differences may play an important role in producing at least some hatchlings of a different sex in nests that are close to the all-male- or all-female-determining temperatures. For example, in the warmest nest monitored (Nest 2), only a few eggs from the bottom region of the nest were predicted to produce males; the other three regions of the nest had temperatures above 29°C and were therefore predicted to produce only female hatchlings.

The predicted hatchling sex ratio from the five monitored nests is strongly female-biased, with four nests producing more than 80% females and only one nest producing a majority of males (Table 1). The current study was conducted at the beginning of the peak nesting season on Heron Island (mid-November–December: Limpus *et al.* 1983). Because of the general rise in sand temperature occurring at this time, clutches laid after November during the 1998–99 nesting season are likely to be even more female biased. Indeed, the
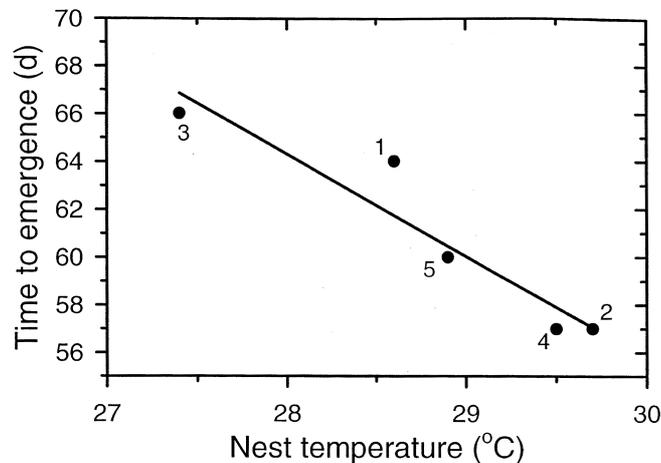
Fig. 8. Plot of time to emergence against mean nest temperature throughout incubation. Least-squares linear regression: $y = 183.5 - 4.256x$; $R^2 = 0.90$, $P = 0.005$.

only clutches that were likely to produce a significant number of male hatchlings were the relatively few clutches laid early in the season and the very deep nests constructed in the middle of the season. However, 1998–99 was a warmer-than-average year on Heron Island (Hoegh-Guldburg 1999) and the sex ratio may not be as strongly female biased in more normal years. Indeed, the sand temperature profiles from the 1980–81 nesting season suggest only a slight female hatchling bias (Limpus et al. 1983, 1984). There was a strong bias for females (63–88% female) from northern beaches and strong male bias (26–30% female) on southern beaches at this time and also in February of the 1979–80 nesting season (Limpus et al. 1984). However, more nests are constructed on the north-facing beaches so the overall sex bias would favour females. Hence, differences in weather patterns can result in large differences in the proportions of males and female hatchlings from year to year at Heron Island.

An intriguing finding was that during the time of peak nesting, only the deepest nest examined was predicted to produce a majority of male hatchlings. In general terms, bigger turtles dig deeper nests because their hind legs are longer (Ewert 1979). This could imply that only the oldest, largest females produce a high proportion of male hatchlings during the peak nesting time. However there was no correlation between nest depth and female size in the current study. This lack of correlation may be due to the fact that nesting green sea turtles dig a body pit before they begin construction of the egg chamber, and thus nest depth is a function of both body pit depth and egg chamber depth. Egg chamber depth is probably directly dependent on hind flipper length, but body pit depth can be highly variable and is not necessary dependent on body size. Thus, a deep nest could be the result from a small female digging a deep body pit before she starts excavating her nest chamber.

The pivotal temperature (the temperature that produces a sex ratio of 1:1) of sea turtles is dependent on the nesting location, with populations that nest in warmer climates having a higher pivotal temperature (Limpus et al. 1985; Miller 1997). Despite adjustments in the pivotal temperature to local nesting circumstances, green sea turtle rookeries worldwide produce more females than males (Limpus et al. 1983, 1984; Standora and Spotila 1985; Spotila et al. 1987; Morosovsky 1994; Godfrey et al. 1996; this study). The threat of global
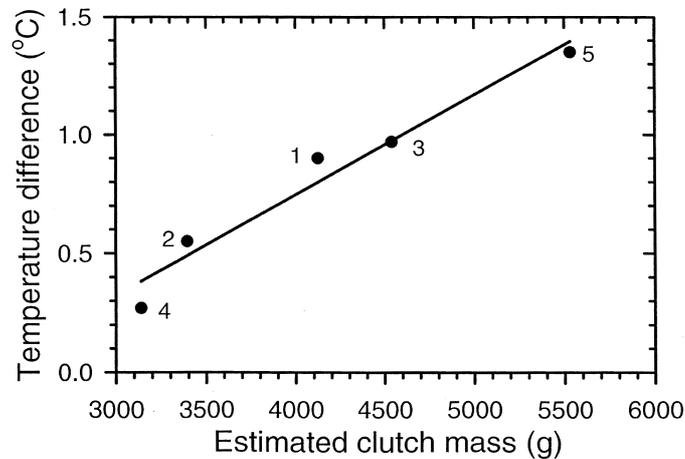
Fig. 9. Plot of mean difference between middle nest temperature and side nest temperature during the last week of incubation against estimated clutch mass. Least-squares linear regression: $y = 0.0004233x - 0.947$; $R^2 = 0.96$, $P < 0.022$.

warming has the potential to increase the female hatchling bias even further (Davenport 1989; Limpus 1993; Formia 1996; Miller 1997) so that the identification and maintenance of male-producing nests is vital for long-term population viability.

Besides being of conservation interest, a female-biased breeding population is at odds with Fisher's population genetics theory (Fisher 1930) that predicts a 1:1 sex ratio in sexually reproducing organisms. Females that construct nests that produce males probably have greater fitness compared with females that produce female hatchlings because male progeny are more likely than female progeny to transmit their genes to the next generation due to the relative shortage of adult males. So the perplexing question is, why do female-biased rookeries persist? One possibility is that female mortality is greater over the juvenile period so that the adult sex ratio is 1:1. Assessing the sex ratio of adult sea turtles is fraught with difficulties (Limpus *et al.* 1983, 1994), but it appears that the female sex bias persists into the adult population at feeding grounds (Limpus *et al.* 1994).

Acknowledgments

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