A micro-environmental study of the effect of temperature on the sex ratios of the loggerhead turtle, *Caretta caretta*, from Tongaland, Natal

J.A. Maxwell, M.A. Motara* and G.H. Frank

Department of Zoology, University of Durban-Westville, Private Bag X54001, Durban, 4000 Republic of South Africa

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Sex determination in *C. caretta* is, under natural conditions, dependent on incubation temperature. In general, below 27°C all hatchlings are male while above 29,3°C 80% or more are females. The sex ratios of the nests were also dependent on the time of season which is directly related to temperature. Metabolic heating of the nest was evident only towards the end of the critical period i.e. post-sexual differentiation. There was no correlation between sex ratios and the physical characteristics of the beach. The implications of temperature sex determination on the limitation of geographical populations are also discussed.

Geslagsbepaling in *C. caretta* is onder natuurlike toestande afhanklik van die temperatuur tydens uitbroeiing. In die algemeen word daar by temperature onder 27°C slegs manlikes uitgebroei, terwyl bokant 29,3°C is 80% of meer vroulik. Die geslagsverhouding van die broeisel was ook afhanklik van die tyd van die seisoen wat direk in verband staan met temperatuur. Metaboliese verhitting van die nes was slegs teen die einde van die kritieke tydperk, d.w.s. na geslagsbepaling, waarneembaar. Daar was geen korrelasie tussen die geslagsverhouding en die fisiese eienskappe van die strand. Die implikasies van geslagsbepaling deur temperatuur op die geografiese beperking van bevolkings word ook bespreek.

*To whom correspondence should be addressed

In South Africa the loggerhead turtle, *Caretta caretta*, is found between Pomene (23°S) and St Lucia estuary mouth (28°S) (Hughes 1974). However, there are reports describing the loggerheads nesting as far as 34°S and 22°E (Hewitt 1937).

Most species of marine turtles are in danger of extinction. This has resulted in a series of studies on turtle biology in order to coordinate conservation strategies. Research direction which includes the sex ratios of adults and hatchlings is important in implementing conservation programmes.

Recent research has been aimed at both modification of conservation programmes and elucidation of the temperature sex determination (TSD) mechanism. One speculative selective advantage of TSD has been based on the assumption that skewed sex ratios result from a lack of genetic control, but latest estimates have suggested that a 1 : 1 sex ratio is evident in some marine turtles when the season is considered in it's entirety (Mrosovsky, Hopkins-Murphy & Richardson 1984a; Mrosovsky, Dutton & Whitmore 1984b). Bull (1980) and Mrosovsky (1980) have suggested that TSD may have no particular advantage but occurs in these species because 'they have been unable to evolve anything better'. However, it has been suggested that TSD allows the mother to control the sex of her offspring by choosing nest sites in relation to temperature. This applies particularly to those species whose pivotal temperature is constant throughout their range as in map turtles (Bull, Vogt & McCoy 1981; Vogt & Bull 1984) or where sex ratios are influenced by spatial factors as in Tortuguero (Spotila, Standora, Morreale, Ruiz & Puccia 1987). It was here that investigators established that the sex ratio varied according to the beach zone; primarily females are produced in the low- and mid-beach zones with significantly fewer females in the high beach zone. Recently a methodology was suggested for nest temperature monitoring of the natal (or nesting) beach according to demarcated thermal zones (Spotila, Standora, Morreale, Ruiz & Puccia 1983) but Mrosovsky *et al.* (1984b) found only marginal differences in temperature between zones and sex ratios in Suriname.

The present study on the Tongaland population of *C. caretta* was therefore undertaken to answer three specific questions. In the first instance the influence of environmental temperature on the natural sex ratios was investigated. The second phase of this study, undertaken in the laboratory, analysed the effects of temperature on the sex ratios of the loggerhead turtles. The final phase involved a histological study of gonadogenesis in *C. caretta.* This paper describes the micro-environmental effect of temperature on the sex ratios of the loggerhead turtle. In two subsequent papers the findings of phases two and three will be presented.

Materials and Methods

Study area

A 4-km section of beach north of Boteler Point was selected as the study area. This area is a narrow strip of land between Lake nHlange and the sea. Seepage from the lake to the sea occurs at various points along the beach (Figure 1). The predominant vegetation in this area comprised *Mimusops caffra* and *Casuarina equisetifolia.*

The study area was patrolled every night for turtles on the crawl. During the process of egg laying a probe of about 55 cm deep was placed in the centre of the egg mass. A probe about 1 m from the nest acted as the control.

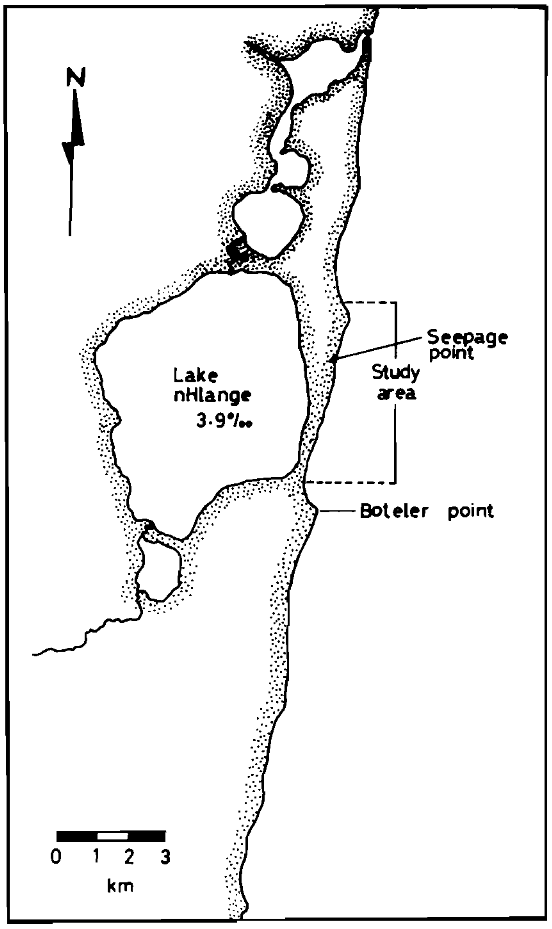

Figure 1 The study area showing Boteler Point and the seepage point from Lake nHlange into the sea. (After Hughes 1974).

Nest site measurements

Nest temperature measurements were undertaken using thermistors of the negative co-efficient type. Ninety probes were used for the field study. In two selected nests, top, bottom, centre and side probes were placed within the nest to measure temperature variation and establish the metabolic heating throughout the developmental period. A control probe was also sited in the usual manner.

Each nest site was also measured for a variety of physical characteristics such as: distance of the nest from the High Water Springs (HWS) mark; height above the HWS mark which was measured by using a spirit level and a vertical pole; beach slope at the nest site was measured with a clinometer; direction of the dune face on which the nest was located was recorded using a compass and was expressed as degrees deviation from the magnetic north; depth constancy of the nest; moisture content of the nest was recorded at least once a week with a 'Speedy moisture tester'; sand grain size was determined using sieves placed in the following mesh order from the bottom to the top: 0,106 mm; 0,212 mm; 0,424 mm and 1,18 mm; and rainfall was recorded daily using a rain gauge.

Source of eggs

The nest was sampled between day 56 and 60. The egg chamber was excavated and all the eggs counted. Non-viable eggs were discarded and a random sample of 20 to 25 were selected for the sex ratio study. All the remaining eggs were replaced in the chamber and covered. The nest was inspected on a daily basis for hatchling emergence.

Histology and sexing

The embryos were removed from the eggs and killed. They were weighed, the gonads and associated structures removed and fixed in Allens fluid (Gray 1954) for 48 h. They were transferred for a further 48 h to 70% ethanol containing a few drops of lithium carbonate before bulk staining in Carazzis haematoxylin for 24 h. After the usual dehydration and embedding in paraffin wax the sections were counterstained with eosin for sex diagnosis. The criterium for sexing was based on the amount of cortex in relation to the medulla (Yntema 1979; Yntema & Mrosovsky 1980).

Results

Sex of the Tongaland population of *C. caretta* hatchlings is, under natural conditions, dependent on incubation temperature. With an increase in incubation temperature a complete reversal of the sex ratio took place from all males to all females. The reversal was correlated with various environmental factors.

Sex ratios

The nests were placed in rank order of mean incubation temperature and compared with the percentage of females in the nest. Figure 2 correlates the sex ratio with the mean incubation temperature. In general, below 27°C all the hatchlings were male whereas above 29,3°C 80% or more were females. However, there were two exceptions; nests 9 and 17. The former had a mean incubation temperature of less than 28,5°C but produced 35% females whereas the latter with a mean temperature greater than 29°C produced no female offspring.

Sex ratios, where correlated with the mean critical temperature period, revealed that below 28,5°C all the hatchlings were male. However, temperature means of 29,6°C and above produced 100% females. Nest number 23 was the only one with less than 100% females at 29,7°C (Figure 3). Gonadal differentiation is sensitive to temperature during the middle third of the incubation period. As with all reptiles, incubation duration is correlated with temperature, and therefore the critical period is not a fixed number of days. Hence, it is safe to assume that the critical period occurs in the middle third of any given incubation period provided that the temperatures are stable throughout.

Sex ratios can also be correlated with the season. Males are produced in the early part of the season while females predominate from mid-season onwards (Figure 4).

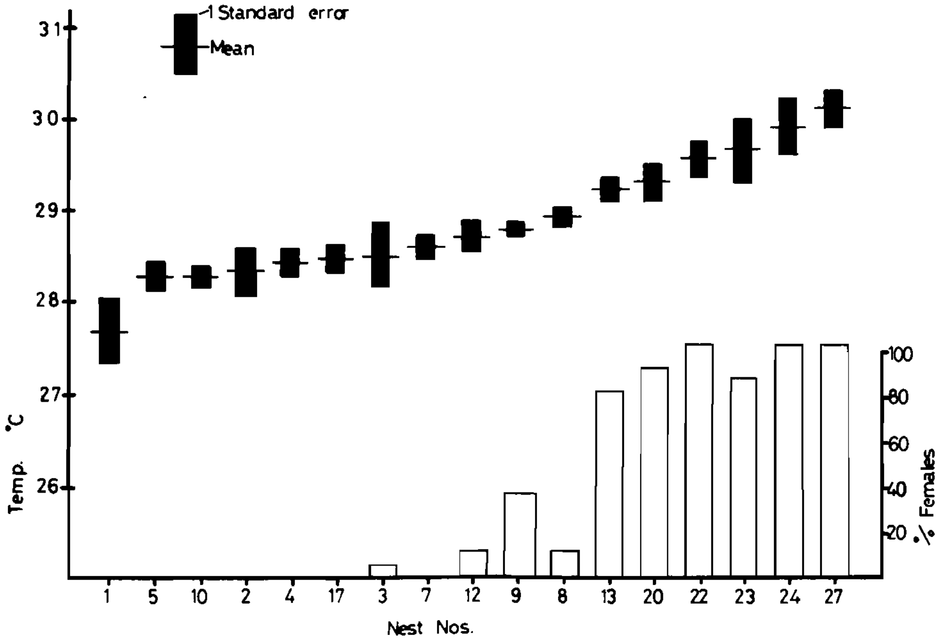

Figure 2 Mean incubation temperature of nests, placed in rank order, to compare with the percentage of females per nest.

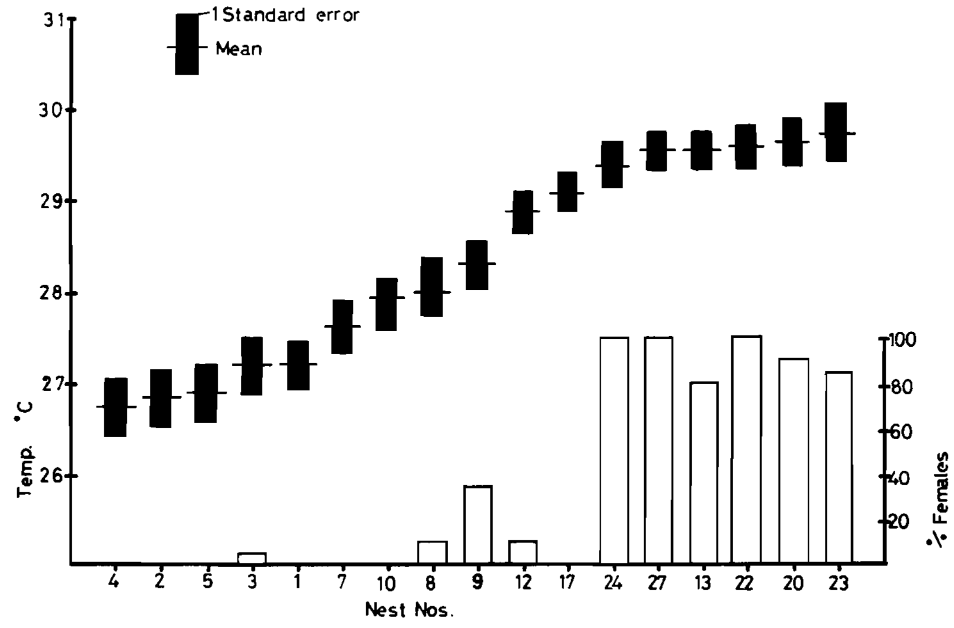

Figure 3 Mean critical period temperature of nests, placed in rank order, to compare with the percentage of females per nest.

There was no correlation of sex ratios with the physical character of the natal beach. The data in Table 1 list the 27 nests studied and provide information on the parameters of the physical characteristics. Seven of the nests produced 75% or more females, while another seven produced no females at all.

Nest temperatures

The difference in mean temperature variation recorded within the nest by the top and bottom probe was 0,7°C; the top and middle probe was 0,1°C; the middle and bottom probe 0,7°C. The top probe measured the greatest variation over a 24-h period which was in the region of 2°C under extreme weather conditions. The top and the middle probes also measured the lowest and highest temperatures respectively (Figure 5).

The onset of metabolic heat has been defined as occurring when the egg mass becomes more than 1°C warmer than the control site. From day 34 metabolic heating was evident in the middle of the nest. At the top and bottom of the nest metabolic heating was evident from days 39 and 37 respectively. After day 45 metabolic heating accounted for a 3°C increase in the middle of the nest. That metabolic heating affected the entire nest is confirmed by the control probes which had the lowest mean temperatures.

During the period that temperatures were monitored

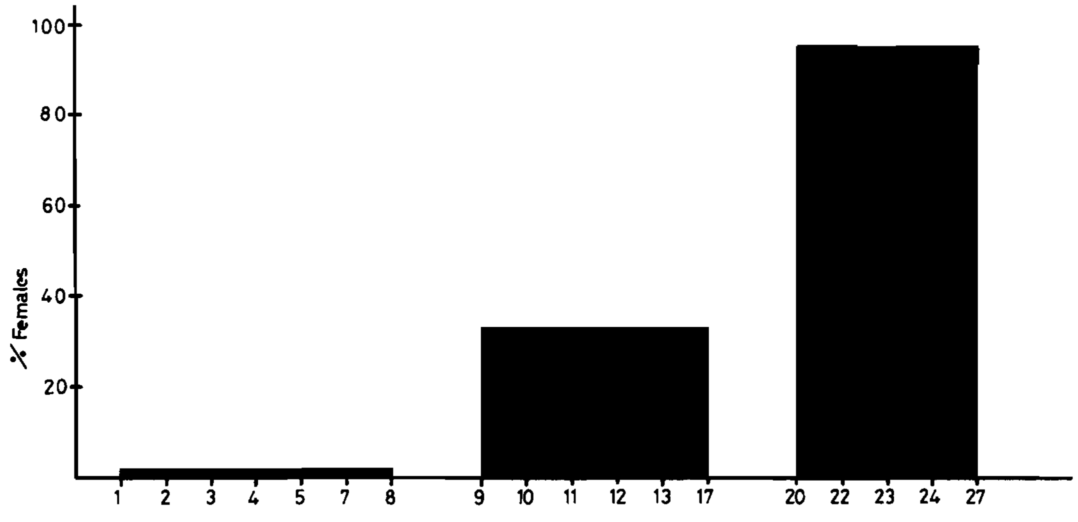

Figure 4 Seasonal sex ratios showing an increase in the number of females as the season progresses. Dates refer to the date of laying.

Table 1 Date of nesting and physical characteristics of each nest with the resultant percentage of females

Nesting date	Nest no.	Dist m	Slo	Ht mm	Dir	Moist cont	%Fem
27/10	1	6,00	14	1050	135	3,60	0
29/10	2	7,25	17	1620	130	3,73	0
01/11	3	6,25	17	1200	125	3,49	5
01/11	4	6,50	12	1200	120	3,10	0
08/11	5	9,00	7	1215	100	3,73	0
11/11	7	4,25	2	290	125	3,55	0
15/11	8	3,50	11	350	90	2,89	10
16/11	9	3,50	15	550	115	4,36	35
22/11	10	21,00	15	5300	80	3,40	0
22/11	*11	8,50	0	1500	20	3,02	75**
22/11	12	9,50	7	2230	115	4,34	10
01/12	13	14,00	–1	560	130	3,96	80
01/12	14	34,00	15	5890	120	3,65	–
05/12	15	16,00	7	3750	130	1,64	–
06/12	16	8,00	0	1370	130	3,53	–
07/12	17	23,00	19	2240	130	3,00	0
09/12	18	20,00	3	0	30	3,09	–
09/12	19	13,00	3	0	45	2,60	–
17/12	20	28,00	14	2230	130	2,91	90
18/12	21	8,00	11	560	105	3,44	–
18/12	22	19,00	4	940	105	3,84	100
19/12	23	37,00	12	3000	130	3,91	85
19/12	24	19,00	12	2200	105	4,25	100
01/01	25	25,00	15	1200	105	3,91	–
01/01	26	23,00	13	1500	115	2,33	–
01/01	27	30,00	10	800	115	3,82	100

* – relocated nests
** – intersexes present
Dist – distance in metres from the HWS
Ht – height in mm above the HWS
Slo – slope in degrees from the horizontal
Dir – direction in degrees from north
%Fem – percentage females
Moist cont – moisture content
– – nest destroyed

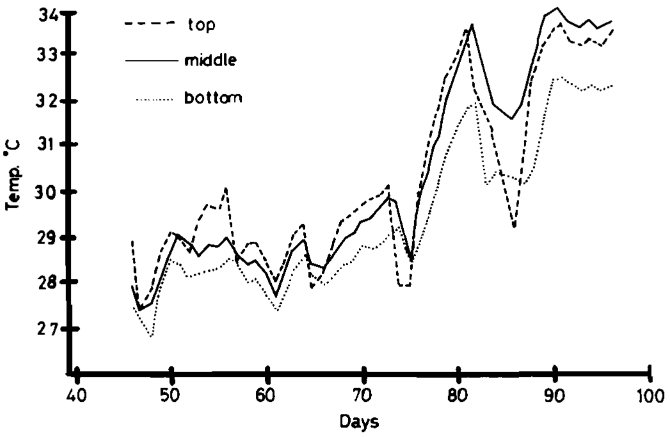

Figure 5 The temperature recorded by the top, middle and bottom probes of nest 19 from the time of nesting on 09.12.1984 to 30.01.1985. The approximate depths of probes were as follows: top = 30–35 cm; middle = 40–45 cm; bottom = 50–55 cm.

on a two-hourly basis for periods up to 48 h at a time, the diurnal variation in the middle of the nest did not exceed 1,3°C whereas the ambient temperature was 6°C (Figure 6). Plotting the ambient temperature and the nest temperature against time shows that the coldest temperature experienced by the nest in a 24-h period was between 11h00 and 14h00 and the warmest between 05h00 and 07h00 (Figure 6).

The nesting beaches appeared to be dominated by the prevailing north-easterly and south-westerly winds at various strengths. Therefore the effects on nest site temperature were compared after a wind calm day, a moderate north-easterly day and a south-westerly day. For the assessment of nest site temperature, only data from the control probes were used so that the influence of metabolic heating could be excluded. This is referred to as the 'nest site temperature' as opposed to actual nest temperature. Overall the nests were coolest under the

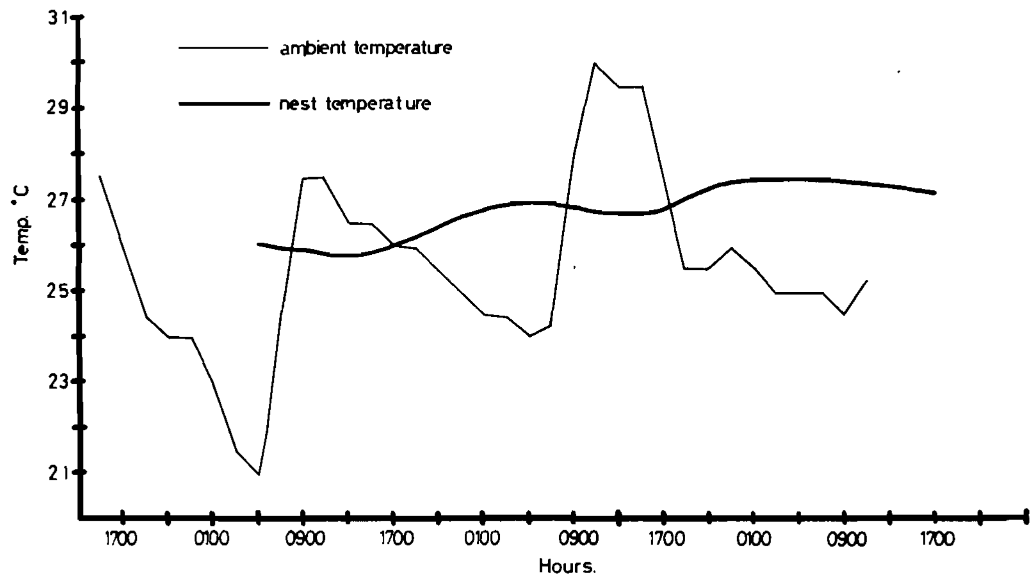

Figure 6 Diurnal temperature variation within a nest compared to the ambient temperature. For a 24-h period during 01.12.1984 to 05.12.1984 the probe was approximately 50 cm deep.

Table 2 Nest site temperatures on days following various weather conditions as listed below

Nest No.	Sunny & calm	Over-cast	L.S.W.	M.N.E	HWS tides
1.	29,2	27,8	29,0	----	28,8
2.	29,2	27,6	27,9	----	27,9
3.	28,9	27,8	28,2	28,4	28,0
4.	29,0	27,6	28,3	28,1	27,9
5.	28,9	27,7	28,6	28,4	28,2
7.	29,0	28,0	28,8	28,4	27,0
8.	29,8	28,1	29,8	30,1	28,4
9.	29,4	27,5	29,0	28,3	27,8
12.	28,5	27,2	28,1	28,2	27,4
13.	29,4	28,3	29,0	28,9	28,5
15.	29,1	27,7	28,2	27,9	28,1
17.	28,8	27,3	28,1	27,7	27,4
18.	27,7	26,7	27,3	26,9	26,5
19.	29,0	27,8	28,7	28,5	27,9
20.	29,2	----	28,6	28,4	----
22.	28,6	----	28,2	28,0	----

---- no information
Sunny & calm – wind-calm
L.S.W. – light south-westerly wind
M.N.E. – moderate north-easterly wind
HWS tides – high water spring tides

influence of the north-easterly wind. This wind also caused some nests to become shallower. The south-westerly wind was responsible for the nests becoming deeper with the deposition of sand. This resulted in nests 25 and 26 becoming up to 2 m deep at the time of sampling.

Only two nests were washed over by high water springs (HWS). Comparing their temperatures with other incubating nests present indicated that in such instances the distances from the HWS could influence nest temperature. For example nest site No. 8 which always recorded the highest temperatures under the three wind types was in fact cooler than two other nest sites examined the day after high tide and a light south-westerly wind (Table 2). Also nest site No. 9, the third warmest after a sunny day ranks 10th on a day following the HWS.

There was no correlation with nest site temperature in any of the physical characteristics such as distance of the nest from the HWS mark, height above the HWS mark, slope of the nest site, moisture content of the nest, compass bearing and coarseness of the sand studied.

As the season progressed all the nests became warmer (Figure 7). This correlates well with the increasing ambient temperature from the beginning of the season to the end of the study period. The sea temperature also showed an increase although no direct comparison could be made to assess the effect of sea temperature on the nests as the sea temperature was recorded by the Department of Transport at 10-day intervals only.

Moisture content

With the exception of one dry nest on the forest fringe, the moisture content of the nests varied on a weekly basis from 1,8–3,8% in the drier periods to 7,8% after rainfall of 30 mm or more over a 4-h period. The mean moisture content of each nest varied over a narrow range: 2,6–4,4 with an average moisture content of 3,4% (the figures refer to the mean moisture content of each nest during the incubation period and not to the mean moisture content of all the nests per week). Although the mean moisture content of all the nests during the drier periods never dropped below 2,8% it correlated very nicely with the total weekly rainfall picture (Figure 8).

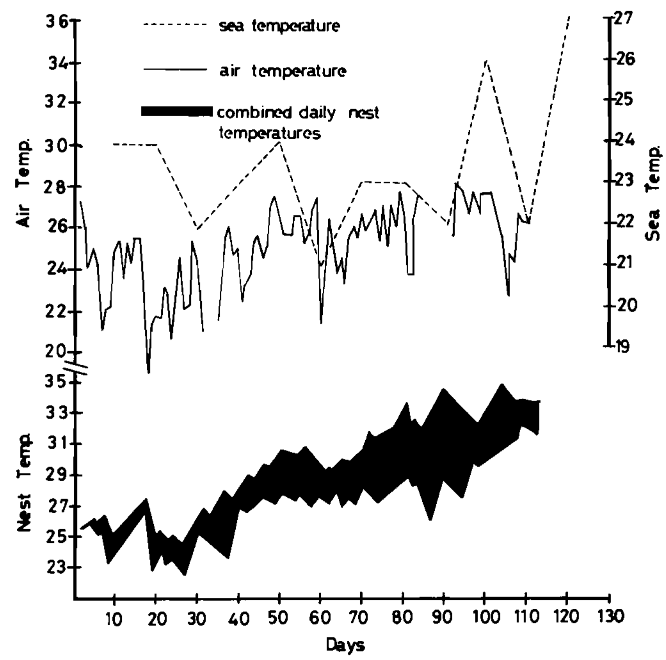

Figure 7 Increase in ambient temperature and sea temperature compared to increase in nest temperature over the season. Temperature recordings commenced on 28.10.1984 and ended on 07.02.1985.

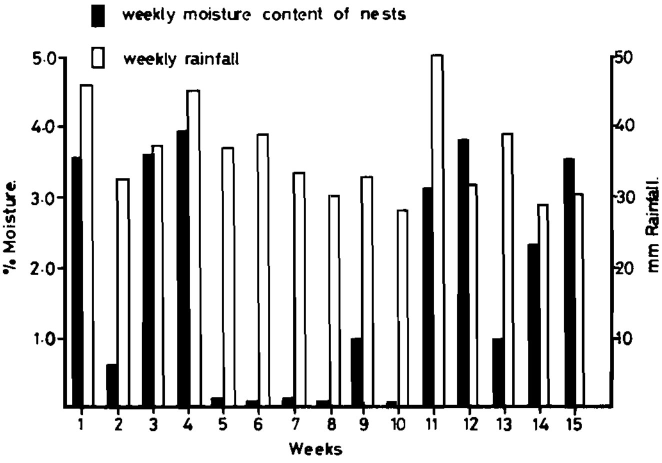

Figure 8 Rainfall and moisture content of nests recorded on a weekly basis. The recordings commenced on 28.10.1984 and ended on 07.02.1985.

Coarseness of sand

This varied considerably from one nest to the next with nest No. 17 being the finest and nest No. 13 the coarsest. As expected the sand coarseness correlated with the height above the HWS so that the finer nests were located higher up dunes while the coarser nests were found lower down the beach (Table 3).

Potential hatch rate and nest success

Of the 27 nests monitored for temperature and moisture content only 18 were sampled. The other nine were destroyed (seven by ants of the *Dorylus* spp. and two by feral dogs) prior to sampling. Of the 18 sampled nests seven more were destroyed (Table 4). The potential hatch success per clutch was calculated on the assumption that the nest had not been disturbed for sampling.

Table 3 Sand coarseness for the nests as marked given as the percentage of the sample of sand recovered in each sieve (mesh size of sieves in millimetres)

	Mesh size (mm)			
Nest no.	1,18	0,425	0,212	0,106
1.	0	59,2	37,4	0,7
2.	0	47,0	50,2	1,0
3.	0	6,0	90,2	3,2
4.	0	26,2	71,0	1,1
5.	0	54,3	42,3	1,0
7.	0,4	68,6	24,9	0,5
8.	0,2	36,0	59,8	2,9
9.	0,9	36,0	56,5	5,0
10.	0	37,3	56,7	3,8
11.	0,14	49,6	46,7	1,42
12.	0	3,9	82,8	12,2
13.	9,5	69,6	18,6	0,6
14.	0	1,8	88,9	8,1
15.	0	2,7	87,4	9,2
16.	0	5,9	76,6	16,3
17.	0	0,4	87,8	11,4
18.	0,2	49,4	46,7	1,4
19.	0,14	48,3	47,4	1,3
20.	0,2	35,8	59,9	2,5
21.	2,3	50,3	43,6	2,3
22.	0	3,5	81,7	13,4
25.	0	8,8	76,1	12,8
26.	0	17,6	73,6	7,1
27.	0	9,7	68,3	21,0

Discussion

The skewed sex ratios in favour of males at the beginning of the season with a reversal by the end of the season confirm that epigenetic factors such as temperature overrides genetic sex determination in specifying sexual phenotype. With genetic sex determination the sex ratio would have been 1 : 1 throughout the season.

This study of natural beaches confirms that of Mrosovsky *et al.* (1984a) who showed a seasonal variation of sex ratios for the eastern United States population of *C. caretta*. When the nesting season is considered as a whole the sex ratio is close to 1 : 1. The sex ratios of *C. caretta* of Mon Repos and Heron Island (Limpus, Reed & Miller 1983) and Tortuguero (Spotila *et al.* 1987), do not appear to be affected by a seasonal (or temporal) variation. Indeed only a spatial variability has been demonstrated with the percentage of females consistently lower on Heron Island and greater on Mon Repos (Limpus *et al.* 1983). Spatial factors also appear to influence the sex ratios of some freshwater turtles (Bull *et al.* 1981).

Table 4 Potential hatch success calculated assuming nest had not been disturbed for sampling (Clutch size − sterile and dead eggs × 100 = %)

Nest no.	Clutch size	Sample size	Potential hatch success (%)	Day of emergence
1	127	20	82,7	74
2	124	24	84,7	74
3	110	23	92,9	69
4	115	23	95,7	##
5	134	22	92,5	60
7	129	23	96,1	60
8	114	9	0,0	#
9	114	21	95,6	72
10	98	22	61,2	70
11	121	23	92,6	59
12	139	22	98,6	#
13	139	22	87,9	60
17	104	21	96,2	#
20	100	21	97,0	#
22	60	9	0,0	#
23	132	21	97,0	#
24	58	23	84,5	*
27	120	24	93,4	*

– destroyed by feral dog
– destroyed by ants
* – missed emergence

Findings from the present study suggest that nest site selection by the female marine turtle is of minimal importance in influencing the sex ratio of hatching turtles. The dynamic prevailing wind beach environment appears to overshadow the importance of the physical features of the natal beach.

In the present study the percentage of females in the natural nests did correlate with the mean incubation temperature. All the nests became progressively warmer during the course of the season and the female ratio increased. Furthermore, the apparent discrepancies were overcome when the mean temperature of incubation was replaced with the mean temperature of the critical period. The critical period was estimated according to the mean incubation temperature and expected incubation duration. This confirms the existence of a critical period during incubation when the developing gonads are sensitive to temperature. The high critical period mean temperature of nest 23 with less than 100% females could have resulted from the greater fluctuation of temperature in that nest. Considering that the time of temperature recording every morning was during the hottest period of the nest and the warm pulses lasted for about 2 h every day, this may not have a direct effect. If means from the recorded temperatures were calculated every few hours they could have been even lower. This could indicate that pulses of temperature are adequate in specifying sex (Bull & Vogt 1981).

The time of season chosen for nesting is also important. Similar sex ratios of two species of marine turtles with different pivotal temperatures using the same nesting beaches have also recently been attributed to nesting at different times of the season (Mrosovsky *et al.* (1984a).

This study clearly indicates a lack of relationship between the spatial or physical characteristics of a nesting beach and the hatchling sex ratio. Indeed the sex ratios were closely correlated to temperature as reflected by season, which is in keeping with Mrosovsky *et al.* (1984a & b). Contrary to the findings of Morreale, Ruiz, Spotila & Standora (1982) and Spotila *et al.* (1987) we could not establish clearly defined zones related to sex ratios. In Suriname, Mrosovsky *et al.* (1984b) also reported no sex ratio differences between the different zones on the beach and only minor differences in sand temperatures. However, zones are of importance in a stable inland environment where spatial factors play a role in the sex ratios of a population. According to Bull *et al.* (1981) the choosing of a nest site in such an environment would be selected for.

Parameters such as distance, height, slope, compass bearing, coarseness of the sand and moisture content were determined for each nest. These, together with daily nest temperature monitoring, were useful in assessing the effect of the physical characteristics on the thermal performance of the nest. On a wind-calm day no single characteristic appeared to have an influence on the temperature. Neither were the combined interactions of the various factors significant. Yet the influence of the prevailing wind types could change the rank order of a nest site temperature. Furthermore, the highest nest had the greatest temperatue variation when compared to a wind-calm day. In fact, variation of nest temperature owing to prevailing winds could explain the difficulty of establishing reliable temperature zones on the beach.

Any attempt to establish the effect of the physical characteristics of a beach on the thermal behaviour of nest sites would require details in addition to those studied, such as adjacent dune height and height and fluctuation of the water table including the tides. Also, climatic factors need more attention such as wind duration and strength, cloud cover and the sunlight hours of each nest on a daily basis. Distance and height above the HWS mark was significant only during high spring tides accompanied by a south-westerly wind. This resulted in certain nests being washed over by high seas and becoming temporarily cooler than other nests during this period. Further the highest nest was also the driest.

Controversy exists regarding the influence of moisture content on sex determination of turtles. Gutzke & Paukstis (1983), in contrast to Packard, Packard & Boardman (1984) reported that hatchling sex ratios, owing to hydric conditions, vary significantly over the range of 26,5 and 28,5°C. However, other investigators (Mrosovsky *et al.* 1984b; Webb, Choquenot & Whitehead 1986) have assigned such a possibility to departures from sex ratios based on incubation temperatures. Surprisingly, there was no relationship between moisture content and nest site temperature since a wetter nest with more conductance is expected to be cooler than a drier nest. Perhaps the moisture contents of the nests were too similar and hence a significant thermal influence could not be demonstrated.

Temperature regime within the nest is largely influenced by the outside environment. A time lag appears to be in the region of 20 h and could possibly depend on the extent of ambient variation. This is similar to the findings of Dutton, Whitmore & Mrosovsky (1985) with the maximum around 15h00 and a minimum around 03h00. However, Dutton *et al.* (1985) took readings three hourly which could account for the difference. Variation of ambient temperature was four-fold that of nest temperature under 'average' weather conditions. Knowing the lag response it would be better to monitor temperature of nests on a continuous basis. This could lead to an understanding of the TSD mechanism since sex determination does not appear to rely on constant temperature but on pulses of temperature (Bull & Vogt 1981).

Significant metabolic heat is produced by the eggs towards the end of the second third of the incubation period. This heat is only indirectly dependent on the environment outside the nests. In agreeing with Mrosovsky & Yntema (1980), we also find that metabolic heating has little influence on sex determination especially in the cooler nests where a 1°C increase in temperature is only evident after the lapse of the critical period. Therefore, in contrast to Morreale *et al.* (1982) metabolic heating does not become consequential mid-way through the incubation period in most cases.

The hatch rate or success was greatly influenced by predation and wind. Predation by *Dorylus* spp. was the predominant reason for nest failure. Not only did these ants attack and destroy hatchlings on the way to the surface but also destroyed embryos still within the eggs. Nests were attacked regardless of their location. This is contrary to previous findings that only the nests on the fringe of the dune forest were affected (Hughes 1974). Wind accounted for much of the nest failure, especially those high up on the dunes. During the north-easterly wind some nests were blown open despite daily vigilance, and their exposed eggs eaten by feral dogs or destroyed by the heat of the sun. Because of destruction by ants, wind and feral dogs the overall hatch success of the study nests was low (53,6% before sampling). This is possibly a direct effect of cyclone Demoina earlier that year. The driftwood on the beach permitted ant access to an otherwise inaccessable zone. Barring natural disasters the reported emergence success for the Tongaland population is 68,7% (Hughes 1974).

The persistence of TSD over GSD in some reptiles is perplexing and a selective evolutionary advantage has not been demonstrated for chelonians. However, Charnov & Bull (1977) suggest that TSD could offer advantages by allowing the sex of the embryos to respond to its immediate environment. This is the reason why the TSD mechanism is maintained where individuals are strongly influenced by the environment. Thus, if certain conditions associated with nest temperatures enhance male fitness, then TSD will be selected for instead of GSD. On the other hand the persistence of TSD need not imply that it is advantageous but only that mutations to cause GSD to evolve are lacking. They further proposed that the TSD mechanism has been maintained and not replaced by GSD because it has been favoured by natural selection. As yet, there is no reason to suppose that incubation temperature differentially affects the fitness of adult male or female turtles. Since hatchlings require many years to mature and increase in weight several hundred fold, this eliminates any residual effects extending from hatching to maturity (Bull 1981). However, more recently Ferguson & Joanen (1983) have, in fact, been able to demonstrate just such a selective advantage for TSD in the alligator, *Alligator mississipiensis*. In these reptiles the cooler temperature produces females which are heavier than the males from the same clutch.

The occurrence of TSD has other wide-ranging implications such as the geographical limitation of populations. A small decrease in temperature can lead to a bias in sex ratio and consequently, unstable populations (Pieau 1982). Also, of interest is the possibility of the TSD mechanism being the reason for the extinction of the dinosaurs (Pieau 1982; Ferguson & Joanen 1983; Mrosovsky *et al.* 1984b). A sudden continuous change of the Cretaceous climate could have resulted in a progressive skewing of dinosaur sex ratios until only one sex remained, after which the animals became extinct.

An Environmental Protection Agency (U.S.A.) has predicted a 2°C increase in temperature by the year 2040 (Mrosovsky *et al.* 1984b). This could lead to a massively biased sex ratio in favour of females in all the populations of chelonia. However, the cue for the start of the nesting season on the Tongaland beaches is reported to be the sea temperature (Hughes 1974). Thus, with an increase in temperature it would be reasonable to expect that the Tongaland population would start nesting earlier in the year. Selection pressure would, therefore, favour turtles that vary their nesting time to suit their pivotal temperature.

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