Aust. J. Zool., 1992, **40**, 511-21

Thermal Characteristics and Sex Determination in Field Nests of the Pig-nosed Turtle, *Carettochelys insculpta* (Chelonia : Carettochelydidae), from Northern Australia

Arthur Georges

Applied Ecology Research Group, University of Canberra,
P.O. Box 1, Belconnen, A.C.T. 2616, Australia.

Abstract

Carettochelys insculpta lays its eggs in shallow nests constructed in clean fine sand adjacent to water. Six nests had the following thermal characteristics: (1) core temperatures ranging from 26·1 to 33·7°C early in September, from 30·0 to 38·7°C early in October and from 28·4 to 36·8°C early in November; (2) a pronounced daily cycle in core temperatures of up to 6·4°C in amplitude, with the minimum occurring after sunrise in mid-morning and the maximum occurring in the evening; (3) a difference in the temperatures experienced by the top and bottom eggs in a single nest of up to 3·5°C at any one time. Nest heating and the maximum temperatures achieved were principally driven by solar irradiation, not ambient air temperatures. Hot nests produced females exclusively, nests intermediate in temperature produced a mixture of sexes, and the sole cool nest produced males exclusively. In nests that produced both sexes, males emerged from the deepest coolest eggs whereas females emerged from the shallowest eggs. Hence, field nests may yield both sexes either because egg temperatures are on the sex-determining threshold or because thermal gradients in nests span both male- and female-producing temperatures.

Introduction

The influence of temperature on the outcome of sexual differentiation in many reptiles has generated considerable interest since first reported for the lizard *Agama agama* (Charnier 1966). Temperature-dependent sex determination (TSD) has now been demonstrated for species from eight families of turtle, for crocodilians and for some species of lizard (reviewed by Bull 1980, 1983; Ewert and Nelson 1991). For most species of turtle, females are produced at high temperatures and males at low temperatures. A very narrow range of temperatures, referred to as the threshold temperature, produces both males and females and divides the male-producing temperatures from the female-producing temperatures (Bull 1983). A few species have upper and lower thresholds, with females produced at both extremes (Yntema 1976; Gutzke and Paukstis 1984). The critical period for sex determination, during which embryonic sex can be irreversibly influenced by temperature, is generally considered to lie in the middle third of development (Yntema 1979; Bull and Vogt 1981).

Most studies of sex determination of reptiles have been conducted in the laboratory at constant temperatures. The influence of temperature on sex in natural nests is less well understood, yet this understanding is necessary if we are to appreciate the ecological significance of TSD. In the field, hot exposed turtle nests produce female hatchlings whereas cool shaded nests produce males, in broad agreement with laboratory studies conducted at constant temperatures (Bull and Vogt 1979; Vogt and Bull 1984). However, the thermal regime in field nests can be expected to be more complex than in the laboratory. The present study was designed to document the thermal characteristics of natural nests of *Carettochelys insculpta* and to determine their influence on sex ratios of hatchlings.

0004-959X/92/050511$05.00

Carettochelys insculpta is a large freshwater turtle, with temperature-dependent sex determination (Webb *et al.* 1986), that inhabits permanent water, both lentic and lotic, in northern Australia and southern New Guinea (Groombridge 1982; Cogger 1986). It is relatively abundant in the upland billabongs of the Alligator Rivers region and in the continuously flowing waters of the Daly R., both of the Northern Territory, where it feeds on a variety of plant and animal material (Georges and Kennett 1989). *C. insculpta* nests in clean fine sand adjacent to water where it deposits between 8 and 20 eggs in shallow nests (Webb *et al.* 1986; Georges and Kennett 1989). As the sole surviving member of a once widespread group (Meylan 1988), the species has generated considerable scientific interest (reviewed by Georges 1988), but its remote distribution in New Guinea and its relatively recent discovery in Australia (Cogger 1970) have meant that few studies of the species have been undertaken.

Study Area

The study site was a 16-km stretch of the Daly R. well above the tidal reaches between the inflow of Jinduckin Ck (14°07'S.,131°17'E.) and the inflow of Cattle Ck (14°03'S.,131°13'E.). The river bed was composed of sand, gravel and silt (*sensu* McIntyre and Loveday 1974) interspersed with occasional rock outcrops. Water flows continuously throughout the year, with levels rising in March to an average peak of 13·6 m (range 5·8–21·7 m; Dorisvale Stage, 1961–88) above dry season levels. The banks were of sand or sandy loam sloping steeply to a height of 20 m and covered in dense vegetation. Exposed beds of clean fine sand suitable for nesting by *C. insculpta* (Webb *et al.* 1986) generally accumulated on bends in the river, at the junction of small drainage gullies and the main channel, or behind fallen trees or debris.

The climate is typical of the wet–dry tropics of northern Australia (Taylor and Tulloch 1985), with a mean monthly rainfall of less than 7 mm from May to September, rising to 284 mm in February (Stn 014139/014941, Oolloo, 1962–85). Mean relative humidity (at 1500 hours, Stn 014908, Daly R., Woolianna, 1966–80) ranges from a low of 32% in August to a high of 73% in February. Mean monthly maximum air temperature ranges from 30·9°C in June to 36·8°C in October.

Materials and Methods

Exposed beds of sand at the study site were checked for the distinctive tracks and the nests of *C. insculpta* between 6 August and 15 December 1986. Nests were located by probing the sand with a fine spring-steel rod (1 mm in diameter; after Blake 1974). With practice, likely locations of nests could be seen as a barely perceptible depression where the disturbed sand had settled with time. A total of 38 nests were located.

Distance to water, height above water, slope, depth to the uppermost egg, depth of the nest chamber and core temperatures were recorded for each nest. Core temperatures were measured (to ±0·1°C) with a Diehl Thermatron electronic thermometer calibrated against a certified mercury thermometer. Point core temperatures were also later remeasured as the opportunity arose.

Eggs were removed from each nest and numbered in order of their removal. Care was taken to maintain the original orientation of eggs at all times, always with the white patch (Thompson 1985) uppermost. They were classed as infertile if a white patch had not developed within 24 h of the estimated date of laying. One viable egg from each nest was opened and the embryo was removed and stored in 10% formalin. Maximum head width (including the otic capsules) was measured with a graduated eyepiece under a stereo microscope and expressed as a proportion of the maximum diameter of the egg to yield a head:width ratio (HWR). Approximate date of egglaying was estimated by comparing HWR for each embryo to a relationship between HWR and duration of incubation at 30°C established for *C. insculpta* by Webb *et al.* (1986).

Six clutches of viable eggs, laid early in the season between 20 August and 9 September 1986, were returned to their nests immediately after measurement, together with temperature probes for monitoring the 24-h cycle and seasonal trend in nest temperatures. The probes each comprised an AD590 transducer and appropriate circuitry to rescale the signal to yield a precise (to ±0·1°C) temperature reading. The probes were calibrated against a certified mercury thermometer before and after the experiment. One probe was placed immediately below the lowest egg of each nest, a second was placed in the centre of the nest, and a third was placed immediately above the top egg.

Surface temperatures were measured with the calibrated Diehl thermometer. Temperatures were recorded at approximately 2-h intervals for two 24-h periods, one in September (12–13th) and one in October (10–11th). Point temperatures were recorded for these nests on several other occasions as the opportunity arose.

Thermal scores, defined as the mid-point between daily maximum and minimum core temperatures, were calculated for each of the six nests for days 15, 20, 25, 30 and 35 of incubation, where the required estimates of daily minimum and maximum were obtained by linear interpolation. Days 15–35 were chosen because they lay within the middle half of incubation (roughly estimated at 60 days) when sex is likely to be determined (Yntema 1979; Bull and Vogt 1981; Webb *et al.* 1986).

The eggs were removed from the nests after yolk internalisation (Webb *et al.* 1986) and returned to the laboratory. Many hatched spontaneously on removal or during transit and the remainder were stimulated to hatch by immersion in water (see Webb *et al.* 1986). The hatchlings were killed by intracranial injection of absolute alcohol and dissected. A preliminary assessment of the sex of each hatchling was based on the condition of the gonad and paramesonephric duct. The right kidney, gonad and associated ducts were removed, embedded in wax, sectioned, and dyed with haemotoxylin and eosin. The sex of each gonad was determined by examination under a light microscope. In one case, histological examination of gonads did not yield a clear indication of sex, and sex was assigned on the basis of the condition of the paramesonephric duct.

Results

Nest Characteristics

Nests were constructed at an average distance of 4·0±0·3 m (range 0·7–7·4 m, $n=38$) from the waters edge and 1·6±0·1 m (range 0·3–3·0 m) above the water level. They were shallow, with an average chamber depth of 21·7±0·4 cm (range 15–24 cm, $n=36$) and an average depth to the first egg of 14·1±0·5 cm (range 6·5–21·0 cm, $n=36$). Clutch size ranged from 7 to 15 eggs (mean 10·5±0·4 eggs, $n=38$), although one aberrant clutch contained only 4 eggs. Characteristics of the six nests selected for detailed examination are shown in Table 1.

Table 1. Characteristics of six nests of *Carettochelys insculpta* selected for detailed study of temperatures and hatchling sex ratios

Mean egg measurements are given with standard errors and ranges

Nest	Date laid	Distance from water (m)	Height above water (m)	Depth to first egg (cm)	Chamber depth (cm)	Clutch size	Mean maximum egg diameter (mm)	Mean egg weight (g)
4	20.viii.86	5·4	2·3	18·0	25·0	9	36·4±0·2 (35·6–37·5)	28·2±0·6 (26·6–31·2)
2	23.viii.86	4·8	2·1	12·0	25·0	9	41·0±0·1 (40·6–41·4)	39·3±0·3 (38·1–40·0)
7	25.viii.86	2·7	1·1	12·0	17·0	7	38·5±0·2 (38·0–39·4)	33·4±0·4 (32·3–34·9)
8	25.viii.86	2·7	1·1	12·0	18·0	10	39·6±0·3 (38·3–41·2)	36·3±0·6 (32·8–39·4)
5	22.viii.86	6·2	3·0	13·0	21·5	13	37·5±0·2 (36·3–38·5)	31·0±0·4 (27·5–32·9)
15	9.ix.86	3·6	1·5	14·0	20·5	13	39·6±0·3 (37·2–41·0)	36·8±0·6 (31·6–39·0)

Thermal Characteristics of Nests

Point measurements of nest core temperatures ranged from 26·1 to 33·7°C early in September ($n = 86$), from 30·0 to 38·7°C early in October ($n = 113$) and from 28·4 to 36·8°C early in November ($n = 19$). There was a general increase in nest temperatures in September and October as air temperature, solar radiation and day length increased (Fig. 1). Although the data for November were fewer, it was clearly evident that nest temperatures were cooler than in October, probably a result of the increased cloud cover of the impending wet season, and occasional showers.

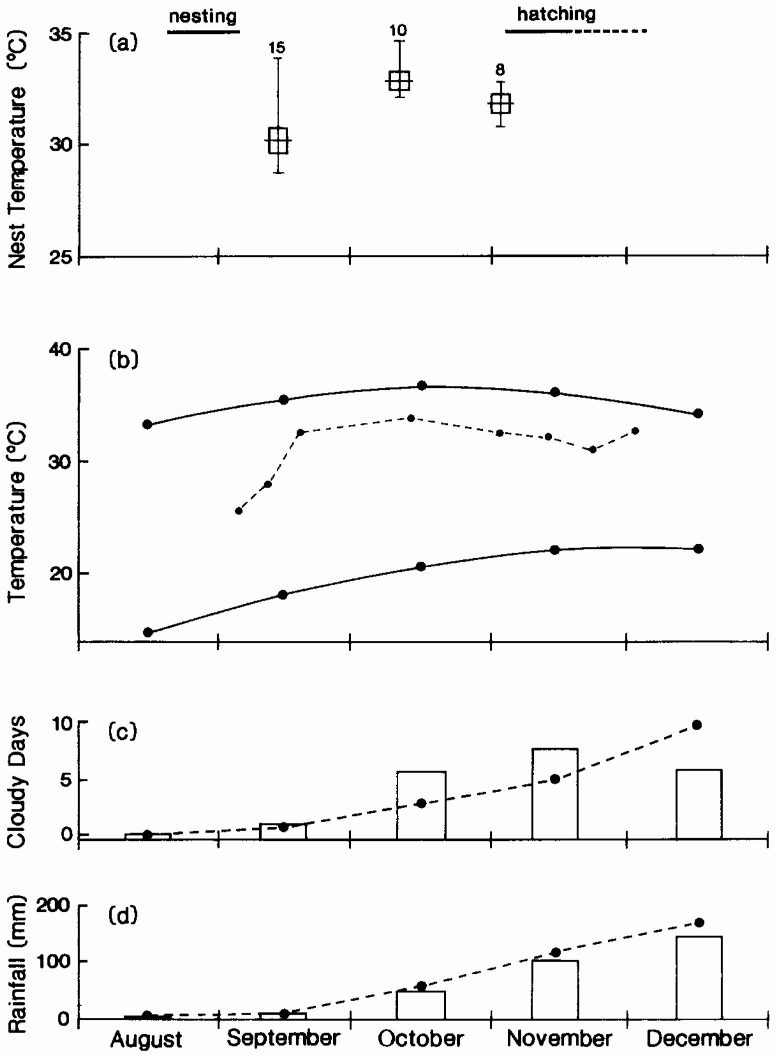

Fig. 1. Seasonal trends in (*a*) nest core temperatures, showing the mean (horizontal line), standard error (box), range (vertical bar) and sample sizes; (*b*) average monthly minimum and maximum air temperatures (solid lines) and water temperature (dashed line); (*c*) number of cloudy days per month (average, dashed line; 1986, bars) and (*d*) monthly rainfall. Water temperatures were collected on site. Other meteorological data were obtained from Woolianna Meteorological Station.

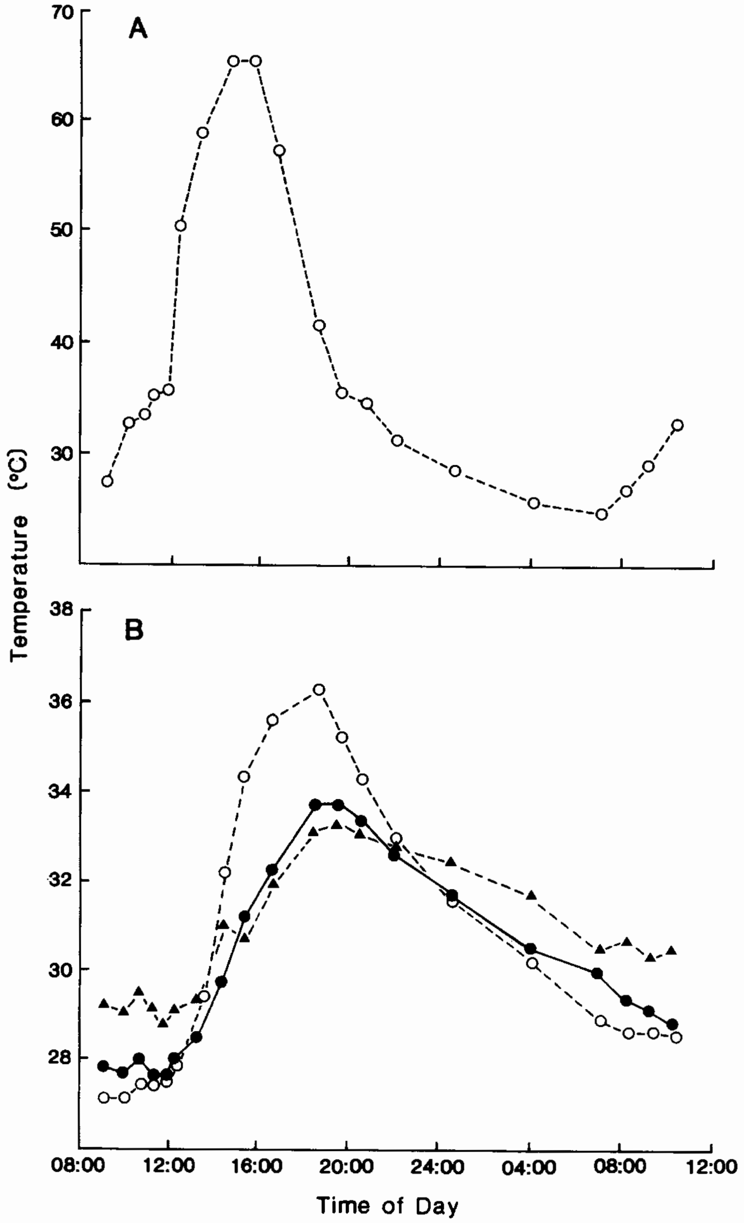

Fig. 2. The daily cycle of temperatures (*A*) at the sand surface immediately above the eggs and (*B*) amongst the eggs, for a typical nest of the pig-nosed turtle, *Carettochelys insculpta*, at the Daly R. site of northern Australia. The data are for Nest 5 of Table 1 in early September. Symbols in (*B*) represent core temperatures (●), temperatures immediately adjacent to the uppermost egg (○) and temperatures immediately adjacent to the deepest egg (▲).

Nest temperatures varied considerably over a 24-h period, the pattern for Nest 5 (Fig. 2) being typical of that shown by each of the six nests. Data from these nests combined with point temperatures from other nests revealed that the minimum daily core temperature consistently occurred after sunrise in mid-morning and that the maximum was reached in the evening (Table 2). This provided the nocturnally nesting *C. insculpta* with the opportunity to gauge the maximum temperature to be experienced by the eggs. At least one turtle, the marine *Caretta caretta*, appears to respond to sand temperatures when selecting nesting sites (Stoneburner and Richardson 1981) but there are no data to establish whether *C. insculpta* makes use of this opportunity when selecting nest sites.

Table 2. Diel and seasonal range of temperatures experienced by the nests of *Carettochelys insculpta* in 1986

Ranges are based on 218 point measurements. Mean point temperatures were calculated for 2-h intervals and the minimum and maximum 2-h mean determined. These are presented with their standard errors, ranges (in parentheses) and sample sizes. Time of sunrise and sunset are given in parentheses for comparison with the time that the minimum and maximum, respectively, was achieved

	Minimum	Maximum
8–13 September		
Mean temperature	27·8 ± 0·2°C (26·1–29·5) $n = 23$	31·7 ± 0·5°C (30·7–33·7) $n = 7$
Time achieved	0900–1100 hours (0642)	1900–2100 hours (1841)
10–12 October		
Mean temperature	31·2 ± 0·2°C (30·0–32·7) $n = 16$	34·8 ± 0·7°C (33·2–38·0) $n = 8$
Time achieved	0700–0900 hours (0621)	1800–2000 hours (1842)
1–2 November		
Mean temperature	30·2 ± 0·4°C (28·4–33·1) $n = 13$	35·7 ± 0·5°C (34·0–36·8) $n = 5$
Time achieved	0800–1000 hours (0610)	1800–2000 hours (1847)

Sand-surface temperatures varied the most, under the influence of direct sunlight, and ranged each day from about 25°C to about 60°C for all nests irrespective of month. Core temperatures fluctuated by 2·3–6·4°C (mean 4·3 ± 0·4, $n = 12$) each day. The hottest eggs at the top of the nest experienced the greatest daily range in temperature (mean 5·9 ± 0·7, range 2·9–9·2, $n = 10$) whereas the coolest eggs at the bottom experienced least variation (mean 3·0 ± 0·4, range 1·6–5·2, $n = 10$).

In September, temperatures of all eggs in a single nest often spanned temperatures which, if held constant in the laboratory, would produce entirely males or entirely females (Webb *et al.* 1986). Temperatures experienced by the top and bottom eggs in a single nest differed by as much as 3·5°C at any one time (mean maximum differential 2·4 ± 0·3, $n = 10$), with the maximum differential occurring close to when maximum nest temperatures were achieved (Fig. 2). Both the marked diel variation in nest temperatures and the marked temperature differential that develops within nests can be expected to have important consequences for sex determination.

Sex Ratios

Results of the field experiment on sex determination concurred broadly with what would have been expected from the laboratory experiments of Webb *et al.* (1986). Hot nests produced females exclusively, nests intermediate in temperature produced a mixture of sexes and the sole cool nest produced males exclusively (Table 3). A thermal score of 31·3°C (Day 35) best separated male-producing and female-producing nests.

Table 3. Hatchling sex ratios from field nests of *Carettochelys insculpta*

Temperatures were monitored for two 24-h cycles, one in September (12–13th), one in October (10–11th). Diurnal ranges are given separately for Top (immediately above uppermost egg), Core and Bottom (immediately below deepest egg) temperatures. Thermal scores were calculated from regressions of temperature against date, as the midpoint between the predicted minimum and maximum daily core temperatures on days 15, 20, 25, 30 and 35 of incubation. Thermal scores shown in bold type, if held at constant temperatures of equal magnitude, would produce either 100% males or 100% females. Those shown in normal type lie within the range known to contain the threshold for *C. insculpta* (Webb *et al.* 1986). Best agreement between the thermal scores and hatchling sex ratios occurs at day 30 to 35 of incubation

Nest	Probe	September	October	Thermal scores					% males		% females
				15	20	25	30	35			
4	Top	26·9–31·6	30·8–35·3								
	Core	27·3–30·8	31·4–34·8	**27·8**	**28·6**	**29·3**	**30·0**	30·8	100·0		0·0
	Bottom	27·7–30·2	—							(*n* = 7)	
2	Top	25·8–33·1	31·0–35·5								
	Core	26·3–31·7	31·3–34·9	**28·2**	**29·0**	**29·7**	30·5	31·2	57·2		42·8
	Bottom	27·0–31·2	31·8–34·6							(*n* = 7)	
7	Top	—	30·5–35·7								
	Core	—	31·1–35·3	**28·6**	**29·4**	30·1	30·8	31·6	25·0		75·0
	Bottom	—	31·3–34·5							(*n* = 4)	
8	Top	—	31·0–36·1								
	Core	—	31·1–35·3	**28·6**	**29·4**	30·1	30·8	31·6	0·0		100·0
	Bottom	—	31·3–34·5							(*n* = 7)	
5	Top	27·1–36·3	31·3–39·6								
	Core	27·7–33·7	31·6–37·9	**29·8**	30·5	31·3	**32·0**	**32·7**	0·0		100·0
	Bottom	28·8–33·3	32·3–37·3							(*n* = 8)	
15	Top	26·4–33·2	31·7–35·8								
	Core	26·9–32·2	31·8–35·1	31·2	31·9	**32·6**	**33·4**	**34·1**	0·0		100·0
	Bottom	27·8–31·1	32·2–34·5							(*n* = 11)	

A profile of Nest 2, which produced hatchlings of both sexes, shows that males emerged from the deepest and therefore coolest eggs whereas females emerged from the shallowest eggs (Fig. 3). The situation in the slightly warmer Nest 7, which also produced mixed sexes, is less clear because only four eggs survived to an age at which they could be sexed. Of the four, two females were from the upper layer of eggs and one male and one female were from the lower layer.

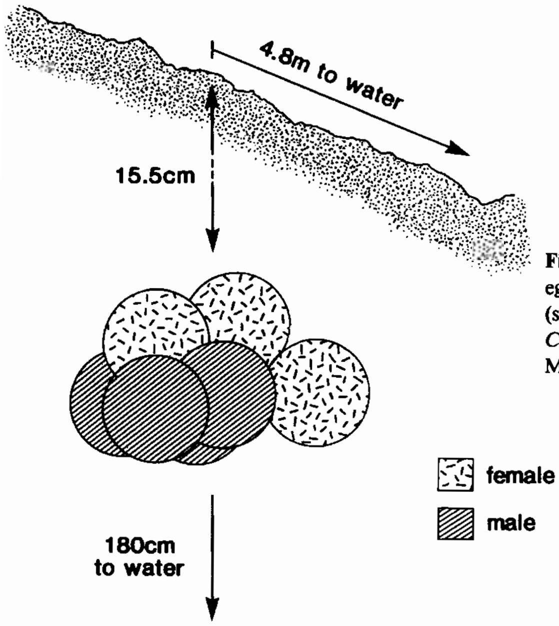

Fig. 3. Lateral view of the distribution of eggs producing males (hatched) and females (stippled) in a nest of the pig-nosed turtle, *Carettochelys insculpta* (Nest 2 of Table 2). Males emerged from the deepest eggs.

Discussion

The shallow nests of *Carettochelys insculpta* and proximity of the eggs to the soil surface have several implications for the thermal biology of the eggs and their embryos. The nests were relatively hot, especially when compared with temperatures traditionally used in laboratory experiments, with core temperatures recorded as high at 38·7°C in viable nests. Core temperatures varied considerably each day (up to 6·4°C) under the influence of daily fluctuations in solar irradiation and air temperature, and substantial thermal gradients developed within single nests, both a direct result of their proximity to the sand surface. If seasonal trends in nest temperatures are also considered, the thermal regime in natural nests of *C. insculpta* is complex indeed.

A complex thermal environment within nests is not unique to *C. insculpta* (see Thompson 1988), nor are its implications for sex determination. In some nests of *C. insculpta*, the thermal gradients spanned both male- and female-producing temperatures, with females produced from the upper, hotter eggs and males from the lower, cooler eggs. Similar vertical thermal gradients resulted in female hatchlings from the warmer upper strata of eggs and males from the cooler lower strata in nests of the freshwater turtle *Chelydra serpentina* (Wilhoft *et al.* 1983). Slight but biologically significant vertical and horizontal thermal gradients in nests of the marine turtle *Chelonia mydas* resulted in female hatchlings from eggs near the centre of nests and males from the periphery (Standora *et al.* 1982). Thermal gradients that developed in nests of the crocodilian *Crocodylus johnstoni* were not necessarily in the vertical plane and eggs producing one sex or the other tended to be clumped in their distribution within nests (Webb and Smith 1984). In natural nests, both mean nest temperature and variance in temperature are required to explain hatchling sex ratios (Bull 1985) and to convert fluctuating nest temperatures to constant temperature equivalents (Georges 1989, 1992). Pronounced seasonal trends in sex ratio have been demonstrated for both marine and freshwater turtle species (Mrosovsky *et al.* 1984; Vogt and Bull 1984) and crocodilians (Webb *et al.* 1986; Smith 1987) with measurable consequences for sex ratios. These studies, together with the present study, demonstrate clearly that seasonal variation in nest temperatures during the developmental period critical for sexual differentiation (Yntema 1979; Bull and Vogt 1981), wide daily fluctuations in nest temperatures, and thermal gradients within single nests may all complicate the influence of environment on the outcome of sexual differentiation.

The temperature range that produces both sexes is very narrow for most species studied in the laboratory, and it has been argued that, as a result, the effective heritability of threshold temperature is low in natural populations (Bull *et al.* 1982). If egg temperatures fall outside the narrow range that produces mixed sexes, genotypic variation in the threshold temperature will have little influence on sex determination. However, the present study demonstrates that field nests may yield hatchlings of both sexes either because egg temperatures are equal to the threshold or because the thermal gradients in nests span both male- and female-producing temperatures. Furthermore, sex ratios are influenced by both mean temperatures and the variance in temperature (Bull 1985; Georges 1989), and the greater variance for the uppermost eggs (maximum 9·2°C) than for the deepest eggs (maximum 5·2°C) will act to inflate the effective thermal gradient within nests. While field studies involving large numbers of clutches have shown that most nests produce one sex or the other, thermal gradients within nests may in part explain the high proportions of nests that produce mixed sexes in some studies (20% of nests in *Graptemys ouachitensis*, 30% for *G. pseudogeographica*: Vogt and Bull 1984); these proportions are greater than would be expected on consideration of the range of temperatures that produce mixed sexes in the laboratory. This may in turn provide greater scope for variation in threshold temperature among populations to evolve under natural selection.

On the Daly R., sand-surface temperature varied each day by 35°C (25–60°C), whereas nest core temperatures varied by up to 6·4°C, indicating that the eggs were buffered from the more extreme temperature variations at the sand surface. The degree of buffering depended on the depth of the eggs, because eggs at the top of a nest varied in temperature by up to 9·2°C each day compared with only 5·2°C at the bottom. Air temperatures ranged from 23·4 to 32·4°C, considerably less in both range and magnitude than sand-surface temperatures. Thus, temperatures at the sand surface were principally driven by solar irradiation. As the temperatures in a nest depend proximally on the temperatures experienced at the sand surface, this indicates that nest heating and the maximum temperatures achieved in nests were principally driven by solar radiation, not by ambient air temperature. This observation may explain in part the failure to demonstrate clear latitudinal trends in the threshold temperature for populations of a single species: Bull *et al.* (1982) could not demonstrate any clear latitudinal trend in the value of the threshold temperature for emydid turtles of Wisconsin and Tennessee in North America. While daily mean air temperatures were between 2°C and 4°C higher at the southern Tennessee locality than at the northern Wisconsin locality, the mean solar radiation was similar at the two localities.

Relating the temperature that best separates 'male' and 'female' nests in the field to the temperature that best separates male and female eggs incubated under constant conditions in the laboratory is difficult. Nests 2 and 7 yielded hatchlings of both sexes, suggesting that characteristics within those nests most closely approximated, in their effect on sex ratios, the threshold temperature for this species. A constant 30°C yields 100% males and 32°C yields 100% females (Webb *et al.* 1986), so the threshold must lie somewhere between the two. Thermal scores that most closely approximate this threshold correspond to days 30–35 of incubation. This conflicts with the findings of Webb *et al.* (1986), who reported that sex had already been determined in nests brought in from the field when 18–20 days old. It is this lack of agreement that initiated the development of a model of sex determination that takes into account both the mean and daily variation in nest temperatures (Georges 1989). When nest temperatures vary each day, the 'average' nest temperature that can be considered equivalent to a constant temperature regime is somewhat higher than the mean. A correction of 2–3°C, quite within the realms of possibility given the observed magnitude of daily ranges in temperature (Georges 1992), would be sufficient to bring the two disparate sets of observations into agreement. Unfortunately, at this stage there are insufficient data to enable calibration of the model for *C. insculpta*.

For most species of turtle, females are produced at high temperatures and males at low temperatures (Bull 1983) whereas the reverse is generally true of crocodilians and lizards (Charnier 1966; Ferguson and Joanen 1983). Some species have upper and lower thresholds, with females being produced at both extremes (Yntema 1976; Gutzke and Paukstis 1984). Webb and Smith (1984) have suggested that the potential for a two-threshold pattern may exist in all reptiles having temperature-dependent sex determination, and that poor survival at the extremes of temperature may tend to eliminate the low-temperature threshold in most turtles and the high-temperature threshold in crocodilians and lizards. The relationship between survivorship and temperature has traditionally been studied at constant temperatures. The present study suggests that, for the shallow nests of *C. insculpta* at least, temperatures may fluctuate considerably, reaching extremes for short periods each day that probably could not be tolerated if maintained under constant conditions. In such nests, the effect of low survivorship in masking a second threshold may be quite different from that expected from studies at constant temperature. For example, a low-temperature threshold may operate in the field under fluctuating temperature regimes while in the laboratory its presence is obscured by poor survivorship at constant low temperatures of equal magnitude. This possibility warrants further investigation.

Acknowledgments

I thank Glenda Georges, Harvey Cooper-Preston, Lee Moyes, Rod Kennett, David Choquenot and Sarah Kerin for assistance in the field. John Cann and John Berryman provided advice on nesting dates and methods of locating nests. Preparation of histological sections was kindly undertaken by Margaret Gabel of the Northern Territory Department of Primary Production. Peter Whitehead, Stephen Sarre and Mike Thompson provided critical comments on early drafts of the manuscript. Ros Stoutjesdijk drew the figures. The study was funded by the Canberra C.A.E. Research Fund and the Conservation Commission of the Northern Territory.

References

Blake, D. K. (1974). The rearing of crocodiles for commercial and conservation purposes in Rhodesia. *Rhodesian Science News* **8**, 315–24.

Bull, J. J. (1980). Sex determination in reptiles. *Quarterly Review of Biology* **55**, 3–21.

Bull, J. J. (1983). 'Evolution of Sex Determining Mechanisms.' (Benjamin Cummings: London.)

Bull, J. J. (1985). Sex ratio and nest temperature in turtles: comparing field and laboratory data. *Ecology* **66**, 1115–22.

Bull, J. J., and Vogt, R. C. (1979). Temperature-dependent sex determination in turtles. *Science* **206**, 1186–8.

Bull, J. J., and Vogt, R. C. (1981). Temperature-sensitive periods of sex determination in emydid turtles. *Journal of Experimental Zoology* **218**, 435–40.

Bull, J. J., Vogt, R. C., and McCoy, C. J. (1982). Sex determining temperatures in turtles: a geographic comparison. *Evolution* **36**, 326–32.

Charnier, M. (1966). Action de la temperature sur la sex-ratio chez l'embryon d'*Agama agama* (Agamidae, Lacertilien). *Societe de Biologie de L'Ouest African* **160**, 620–2.

Cogger, H. G. (1970). First record of the pitted-shelled turtle, *Carettochelys insculpta*, from northern Australia. *Search* **1**, 41.

Cogger, H. G. (1986). 'Reptiles and Amphibians of Australia.' (Reed: Sydney.)

Ewert, M. A., and Nelson, C. E. (1991). Sex determination in turtles: diverse patterns and some possible adaptive values. *Copeia* **1991**, 50–69.

Ferguson, M. J. W., and Joanen, T. (1983). Temperature-dependent sex determination in *Alligator mississippiensis*. *Journal of Zoology, London* **200**, 143–77.

Georges, A. (1988). The warradjan *Carettochelys insculpta* Ramsay (Testudinata: Carettochelydidae): a literature review and annotated bibliography. Report to the Australian National Parks and Wildlife Service, Canberra. February 1988.

Georges, A. (1989). Female turtles from hot nests: is it duration of incubation or proportion of development at high temperatures that matters? *Oecologia* **81**, 323–8.

Georges, A. (1992). The influence of fluctuating temperatures on hatchling sex ratios—a model and proposed test using *Caretta caretta*. Proceedings of the Marine Turtle Conservation Workshop, Sea World Nara Resort, Gold Coast, 14–17 November 1990. (Australian National Parks and Wildlife Service: Canberra.) In press.

Georges, A., and Kennett, R. (1989). Dry-season distribution and ecology of *Carettochelys insculpta* (Chelonia: Carettochelydidae) in Kakadu National Park, northern Australia. *Australian Wildlife Research* **16**, 323–35.

Groombridge, B. (1982). 'I.U.C.N. Amphibia–Reptilia Red Data Book. Part 1. Testudines, Crocodylia, Rhynchocephalia.' (IUCN Publications: Gland.)

Gutzke, W. H. N., and Paukstis, G. L. (1984). A low threshold for sexual differentiation in the painted turtle, *Chrysemys picta*. *Copeia* **1984**, 546–7.

McIntyre, D. S., and Loveday, J. (1974). Particle size analysis. In 'Methods for Analysis of Irrigated Soils'. (Ed. J. Loveday.) pp. 88–99. *Commonwealth Bureau of Soils (Canberra), Technical Communications* **54**, 1–208.

Meylan, P. A. (1988). *Peltochelys* Dollo and the relationships among the genera of Carettochelyidae (Testudines: Reptilia). *Herpetologica* **44**, 440–50.

Mrosovsky, N., Hopkins-Murphy, S. R., and Richardson, J. I. (1984). Sex ratio of sea turtles: seasonal changes. *Science* **225**, 739–41.

Smith, A. M. A. (1987). The sex and survivorship of embryos and hatchlings of the Australian freshwater crocodile, *Crocodylus johnstoni*. Ph.D. Thesis, Australian National University, Canberra.

Standora, E. A., Morreale, S. J., Ruiz, G. J., and Spotila, J. R. (1982). Sex determination in green turtle (*Chelonia mydas*) hatchlings can be influenced by egg position within the nest. [Abstract.] *Bulletin of the Ecological Society of America* **63**, 83–4.

Stoneburner, D. L., and Richardson, J. I. (1981). Observations on the role of temperature in loggerhead turtle nest site selection. *Copeia* **1981**, 238–41.

Taylor, J. A., and Tulloch, D. (1985). Rainfall in the wet-dry tropics: extreme events at Darwin and similarities between years during the period 1870–1983 inclusive. *Australian Journal of Ecology* **10**, 281–95.

Thompson, M. B. (1985). Functional significance of the opaque white patch in eggs of *Emydura macquarii*. In 'Biology of Australasian Frogs and Reptiles'. (Eds G. Grigg, R. Shine and H. Ehmann.) pp. 387–95. (Royal Society of New South Wales: Sydney.)

Thompson, M. B. (1988). Nest temperatures in the pleurodiran turtle *Emydura macquarii*. *Copeia* **1988**, 996–1000.

Vogt, R. C., and Bull, J. J. (1984). Ecology of hatchling sex ratio in map turtles. *Ecology* **65**, 582–7.

Webb, G. J. W., and Smith, A. M. A. (1984). Sex ratio and survivorship in the Australian freshwater crocodile *Crocodylus johnstoni*. *Symposia of the Zoological Society of London* **52**, 319–55.

Webb, G. J. W., Choquenot, D., and Whitehead, P. J. (1986). Nests, eggs and embryonic development of *Carettochelys insculpta* (Chelonia: Carettochelidae) from northern Australia. *Journal of Zoology, London* **1B**, 521–50.

Wilhoft, D. C., Hotaling, E., and Franks, P. (1983). Effects of temperature on sex determination in embryos of the snapping turtle, *Chelydra serpentina*. *Journal of Herpetology* **17**, 38–42.

Yntema, C. L. (1976). Effects of incubation temperatures on sexual differentiation in the turtle, *Chelydra serpentina*. *Journal of Morphology* **150**, 453–62.

Yntema, C. L. (1979). Temperature levels and periods of sex determination during incubation of eggs of *Chelydra serpentina*. *Journal of Morphology* **159**, 17–28.

Manuscript received 11 February 1991; revised and accepted 28 August 1992